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More than a Mentor: Leonard Darwin's Contribution to the Assimilation of Mendelism into Eugenics and Darwinism*

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Abstract. This article discusses the contribution to evolutionary theory of Leonard Darwin (1850–1943), the eighth child of Charles Darwin. By analysing the correspondence Leonard Darwin maintained with Ronald Aylmer Fisher in conjunction with an assessment of his books and other written works between the 1910s and 1930s, this article argues for a more prominent role played by him than the previously recognised in the literature as an informal mentor of Fisher. The paper discusses Leonard's efforts to amalgamate Mendelism with both Eugenics and Darwinism in order for the first to base their policies on new scientific developments and to help the second in finding a target for natural selection. Without a formal qualification in biological sciences and as such mistrusted by some ''formal'' scientists, Leonard Darwin engaged with key themes of Darwinism such as mimicry, the role of mutations on speciation and the process of genetic variability, arriving at important conclusions concerning the usefulness of Mendelian genetics for his father's theory.

Keywords: Evolutionary theory, Eugenics, Genetics, Biometrics, Mendelism, Mutationism, Hugo De-Vries, Karl Pearson, Ronald Aylmer Fisher, Leonard Darwin

Introduction

From its proposal by Charles Darwin (1809–1882) and Alfred Russell Wallace (1823–1913) in 1859 up to the late 1930s the theory of evolution by natural selection (Darwin, 1859) was, as one scholar put it, at a ''critical juncture'' (Richmond, 2006, p. 447). At the centre of this

* The paper assesses the contribution for evolutionary theory of Leonard Darwin, (Charles Darwin's son) during the first 30 years of the twentieth century.

"critical juncture" was the questioning of the role of natural selection as a mechanism to explain the process of organic evolution, alongside wider processes such as a move in science towards experimentalism and the concomitant emergence of new disciplines.[1] Despite this being an intense transformative period for Darwinism, many perceived it as an "eclipsed" theory, and the study of evolution, because of its lack of experimental support, as Bateson succinctly put it, as an "exercising-ground of essayists" (Bateson, 1913, p. 3).[2]

More critically, especially during the 1910s–1920s the theory was confronted with an alternative way of explaining the origin of species, which was known as "mutationism," a theory formulated between 1901 and 1903 by Hugo de-Vries (1848–1935).[3] Mutationism, because of the sudden changes that it proposed for the process of speciation resonated better with the observed discontinuity of the fossil record than the blending style of heredity and the gradualism proposed by Darwinism (Allen, 1969; Bowler, 1978, 2003, p. 269). Contributing to Darwinism's "critical juncture" were also changes that began to occur in the culture of science, changes driven partly by genetics. The so called "rediscovery" of the Mendel laws by a group of experimental scientists among whom was Hugo de-Vries, set in motion an experimental programme in biological sciences that expanded from the 1900s onwards. Genetics, alongside other lines of biological inquiry, such as physiology and biochemistry, belonged to a growing scientific culture hailing experimentation as a hallmark of what counted as scientific. Laboratory-based genetics work was taken by a new generation of scientists as an exemplar of an increasingly highly valued experimental culture in biology (Bowler, 2003, p. 266).

This new institutional context did not benefit a science as Darwinism that because of its reliance on anatomical and embryological observa-

[1] Norton (1973, pp. 286–287). For an idea of the authors of books on evolution during the 1920s and 1930s that opposed Darwinism see Mayr (1982, p. 549).

[2] Huxley (1942) referred to this period as "the eclipse of Darwinism," a term subsequently adopted by many scientists and historians of evolution alike to mark a period characterised by a refusal of Darwinism and by the stagnation, if not full halt, of research on evolution. This outlook has recently been challenged by Largent who argues that "the eclipse of Darwinism" vision constitutes a "historiographical blunder," for evolutionary research never stopped in that period (Largent, 2009, p. 4). Largent proposes instead the use of "interphase" to refer to that period, as one in which "a great deal of vital activity is taken place" (*Ibid*., p. 17). This idea of an active period rather than a stagnant one also emerges when reading other sources such as Richmond's paper (2006) on the state of Darwinism in 1909, the year of the celebration of the hundredth anniversary of Charles Darwin's birth and the fiftieth anniversary of the publication of the Origins of Species.

[3] Original version in German, De Vries (1901–1903). English version 1909.

tions, and its lack of substantiation by experiment was perceived by most of the new breed of experimental scientists as outmoded (Richmond, 2006, p. 474). This was the situation to which Huxley referred when he declared that "[the] death of Darwinism has been proclaimed, not only from the pulpit but from the biological laboratory" (Huxley, 1942, p. 22). It was from the 1920s and through the 1930s and 1940s that, in a very convoluted process, (dubbed by its promoters as evolutionary synthesis[4]) that the results from different experimental lines of genetics, finally convinced scientists of the relevance of a particulate inheritance for the smooth evolutionary change predicted by Darwin.

Darwinism alone wasn't the only intellectual movement immersed in a process of transformation during the first twenty years of the twentieth century. Eugenics, with many scientists among its devotees and members, also began to view the rigour and accuracy offered by the experimental science of Mendelism[5] as a fix for its lack of a sound and renewed scientific base to back up their proposed policies on population control of the unfit, which in turn would warrant people's support (MacKenzie, 1976; Mazumdar, 1992; Kevles, 1995; Stepan, 1982, 1991; Comfort, 2012).

Key for the process of transformation both Darwinism and Eugenics were immersed in during the first thirty years of the twentieth century was the so called "rediscovery" of the Mendel's laws of inheritance, during the 1900s by Hugo de Vries (1848–1935) Carl Correns (1864–1933) and Erich von Tschemak (1871–1972).[6]

Leonard Darwin, a fervent eugenicist and evolutionist was one key figure envisaging a functional role for these "re-discovered" inheritance

[4] For the traditional account of "the synthesis" see Mayr and Provine (1980), Mayr (1982), and Bowler (2003). For a critical standpoint, see Largent (2009), who argues that the eclipse of Darwinism vision, is a "propagandistic" "historiographical blunder," constructed by the protagonists of the synthesis and subsequently supported by some historians that had served to justify the "synthesis" as a successful and discontinuous event led by a new generation of scientists very different from their predecessors that fixed an arguably stagnation in evolutionary research and all the ills Darwinism suffered. (p. 8). In Largent's view "evolutionary synthesis" is a construction aimed to differentiate Darwinian evolutionism from "eugenics, social Darwinism and the connection many Americans made between evolution, imperialism and militarism" (p. 4.). See also Smocovities (1996).

[5] Mendelism refers to the work on the hereditability of traits by Gregor Mendel (1822–1884) as viewed in the 1900s.

[6] The idea of rediscovery of Mendel's ratios independently by De Vries, Correns and Tschemark is controversial on many fronts. A key question on this controversy is the following: Had these scientists used Mendel's paper of 1865 to interpret their own previous experimental results, or did they begin experimenting after reading Mendel's paper? (Monagham and Corcos, 1985).

laws for both sets of ideas. The relevance of Leonard's work for evolution began to emerge in 1983, when John Henry Bennett an academic from Adelaide University compiled and published the correspondence that Leonard and Ronald Aylmer Fisher (1890–1962) maintained from 1915—1942. (Bennett, 1983) From the ideas discussed in those letters (also made explicit at times by Bennett), it is clear firstly how Leonard stimulated, and constantly encouraged Fisher to write his book *The Genetical Theory of Natural Selection* (GTNS), published in 1930, a book hailed by historians of biology as an essential pointer for the synthesis between Mendelism and Darwinism. It is also clear how Leonard creatively engaged with debates on the putative role of Mendelism for both Eugenics and Darwinian theory.[7]

By reviewing some of the correspondence that he maintained from 1915 with Fisher and by analysing Leonard Darwin's books *Organic Evolution* (1921), *The Need for Eugenic reform* (1926) and some other relevant articles he published in *The Eugenics Review* and other journals from the 1910s to the 1940s, I argue for a far more prominent role in the evolutionary debate for him than the one underlined by Bennett.

Many of Leonard Darwin's ideas, acted as relevant nodal points in the development of the evolutionary ideas. Leonard offered key arguments on the role of genetics for evolution, such as the conceptualisation of mutations as key agents for gradual change and species adaptation, and the role of mimicry for adaptations, all arguments that were expanded and refined by Fisher in his book, and that represented a clear, strong and well-timed opposition to De Vries'' mutationism.

In this paper I argue that Leonard Darwin, without a formal qualification in biological sciences, was a theorist of genetics and evolution in his own right. He intensely and creatively mused with Mendelism, attempting to engage it with his father's theory and simultaneously to tune it with Eugenics all along the lines of the improved arguments opened by laboratory based experimentalism to which Mendelism belonged.

Leonard Darwin the Eugenicist

Leonard Darwin (1850–1942), the fourth son of Charles Darwin and Emma Wedgwood (1808–1896) was born in 1850 when his father was classifying the barnacles he collected in Chile in 1835 during his voyage on the Beagle around the world (Desmond and Moore, 1992, p. 371). When Leonard died on March 26th 1943, Arthur Keith's obituary in *Nature*

[7] As Bennett put it: ''In some respects, Darwin seems to have filled a role not unlike that of a research supervisor'' (Bennett, 1983, p. 19).

underlined that he not only "bore a closer resemblance to his father than any of his brothers" but also had "his father's honesty of expression, openness of mind […] and happy sense of humour" (Keith, 1943, p. 42).

Leonard entered the Royal Engineers in 1871 where he pursued an engineering education and graduated as major in 1889. His father encouraged Leonard as a child to learn photography as a hobby. Leonard took a deep interest in it and while studying at the Royal Engineering School he maintained a warm correspondence with his father on his attempts to find proper combinations of chemicals to improve the quality of his photographic prints.[8] Leonard would not only become a sort of family photographer but he would teach photography alongside chemistry at the School of Military Engineering at Chatham between 1877 and 1882 (Berra, 2013, p. 139). Leonard went on not only to produce one of the best well-known photographs of his father (reproduced in Berra, 2013, p. 40), but he would extensively use photography during his period in the army (1885–1890).

Leonard belonged to the staff of the Intelligence Department at the War Office where he served several scientific expeditions, one in 1874 to New Zealand and another in 1882 to Queensland to observe the transit of the planet Venus (Keith, 1943, p. 442), alongside another one to Grenada to photograph a total eclipse of the sun (Berra, p. 141). The results and conclusions of this last expedition were published in the Journal of the Royal Society in 1889. (Darwin, L, 1889).

Leonard actively participated in politics, being a Liberal Unionist MP for Lichfield (1892–1895) and candidate for that constituency in 1895 and 1896 and had an active interest in economics. In 1897, he published a book (Darwin, 1897) on the importance of keeping a balance of gold and silver (to keep a fixed exchange rate between them) for the smooth running of a nation's economy, work that was praised by the well-known economist John Maynard Keynes (Berra, 2013, p. 145).

Leonard was the president of the Royal Geographical Society from 1908 to 1911 (Keith, 1943, p. 442; Searle, 1976, p. 116) and although he was awarded an honorary doctorate of science from Cambridge University (*The Eugenics Review*, 1943), he never formally studied science or graduated as a scientist. What is best known about Leonard Darwin's life is that he was a committed and passionate eugenicist.[9] In

[8] The Archives of Cambridge University (UK) holds the letters Leonard exchanged with his father. Archives consulted by the author in February 2013.

[9] Berra (2013). http://en.wikipedia.org/wiki/Leonard_Darwin. http://www.oxforddnb.com/view/article/54078. http://www.kingscollections.org/exhibitions/specialcollections/mind-matters/from-alienism-to-psychiatry/leonard-darwin.

effect, after Galton's death in 1911 Leonard immediately succeeded him as the president of the Eugenics Education Society (EES)[10] serving until 1929. The EES reached the pinnacle of public confidence and popularity in 1912 when the British government introduced the mental-deficiency bill, a bill that gave the Home Office compulsory powers to detain and segregate the ''feeble-minded'' (Kevles, 1995, p. 99; Searle, 1976, pp. 10–11, 110–111). In addition when the society organised, with Leonard as one of its key planners and co-ordinators, The First international Congress of Eugenics in 1912, Ronald Fisher was, as a Cambridge undergraduate, one of its stewards (Fisher Box, 1978, p. 27). The congress was widely reported by journals such as *Science* (Pearl, 1912), *Nature* (1912) and the *British Medical Journal* (1912) and hailed by *The Times* (1912) and *The Eugenics Review* (1912–1913) as one that attracted many eminent scientists from all over the world, for eugenics issues were discussed ''scientifically'' for the first time in a grand forum. The three main themes dealt with in the congress were natural selection, Mendelian Genetics and pedigree analysis- a chart of genealogical relationships used to represent and demonstrate how some human characteristics, as diverse as height, genius, feeblemindedness, idiocy, pauperism and alcoholism, run in families.[11] Pedigree analysis did not relied on a complicated theoretical framework, for they showed, as Mazumdar put it, ''hereditability per se and not a theory of transmis-

[10] The EES was amongst the eugenics societies that started to flourish at the outset of the twentieth century in different European countries and in the United States against the background of fears of biological and social degeneration as the dark side of evolutionary ideas (Chamberlain and Gilman, 1985; Bowler, 1989b; Mazumdar, 1992; Kevles, 1995). A central aim of the EES was the lobbying of governments to apply policies directed at improving the ''quality of the human race,'' and educating the general public on the social imperative and importance of supporting those policies. Despite their common goals, eugenics societies worldwide had different priorities. In Britain the main ethos guiding the action of the EES was class (MacKenzie, 1976; Mazumdar, 1992; Kevles, 1995), being particularly concerned with the welfare of a professional elite. On this regard Searle shows that the membership the Eugenic Education Society attracted was largely formed by scientists, medical men, university lecturers and men of letters (Searle 1976, pp. 59–60). In Britain, the EES was founded in 1907; Francis Galton was its honorary president from 1908 until his death in 1911 (MacKenzie, 1976).

[11] Galton originally introduced pedigrees together with other statistical tools, such as the normal distribution and the correlation coefficient in the 1860s. He took statistics into new areas by transforming it into a more comprehensive theoretical analysis with the inclusion and re-deployment of new techniques such as Gaussian distribution and the coefficient of correlation (Kevles, 1995, p. 13). Leonard Darwin proposed at a council meeting of the Eugenics society in 1911 a standardisation of pedigrees (see Mazumdar, 1992, p. 77).

sion'' (Mazumdar, 1992, p. 71). Natural selection and Mendelian analysis were subjects that the scientific members of the EES alongside Leonard were very keen in engaging with. A central ambition for Leonard and other society members, in order to sustain the public support for their policies on social intervention so far achieved, was to base their policies on new scientific findings based on a growing experimentalism rather than on oversimplification, anecdotal evidence and unfounded claims (Allen, 2011). By the 1920, pedigree analysis, although still serving the society's aims to educate and persuade audiences, began to be perceived by the eugenicists of a genetic leaning, and in a context of an emergent experimental science, as an old methodology and hence soon began to fall into discredit (Mazumdar, 1992, pp. 58–75, 142–143). The limitations of pedigree studies and to some extent of Galton's statistics would start to be exposed chiefly by the relentless appearance of studies showing the role of the environment on the hereditability of human traits,[12] as well as by the rise of Mendelism.

Leonard's role as president and organiser of the first international congress of Eugenics was part of his constant efforts since he stood as president of the EES, to make it a learned and a scientific based society. Leonard wanted the EES to be a society able to accommodate the most up-to-date scientific advances to sustain its agenda, as manifested regularly in the pages of its journal, *The Eugenics Review*. Leonard, much in line with his conviction that ''the advocacy of eugenic reform, if founded on a false scientific basis, might have disastrous results'' (Darwin, L, 1929–1930, p. 11), got the society involved on many occasions with new scientific advances by for instance, financing small

[12] The role of the environment on the hereditability of genetic traits in humans and other populations was becoming more and more of a pressing issue for the EES, due in part to the appearance of more and more studies on the subject. The growing influence of nutritional research that started to gather momentum from 1918, from which the MRC study of 1919 on the effect of a daily pint of milk on children's growth is a clear example, started to set up limits to those who thought that the inheritability of human traits was exclusively governed by genetic factors (Mazumdar, 1992, pp. 186–188). Leonard Darwin himself actively engaged with the role of the environment on evolution and eugenics and published several articles on it (see for instance: *Environment as a factor in evolution*, 1918). Although agreeing that the environment played a key role in the hereditability of human traits, he considered that its actions, due to the Lamarckian style of transmission, was very slow and consequently of much less importance than ''breeding'' to promote ''progress in the inborn qualities of the race'' (Darwin, L, 1918). He would, however, change his views 6 years later and admit that ''observable differences between individuals were due to both heredity and environment and even considered a truism the idea that human beings can be benefited by improvements in their ''surroundings'' (Darwin, L, 1924).

research projects (Bennett, 1983, pp. 12–15). As part of this initiative Leonard was also instrumental in enlisting key scientists to the EES, for instance Professor Ernest MacBride (1866–1940), a Darwinian evolutionist and renowned professor of Zoology at Imperial College (1913–1934). This was openly recognised by MacBride, who in a paper published in 1929 in *The Eugenics Review* affirmed that Leonard had "laboured with great perseverance to induce scientific men to join the Society, so as to obtain for it the prestige of a solid phalanx of scientific opinion" (MacBride, 1929–1930). On that occasion MacBride also admitted that the 1913 EES presidential address given by Leonard was instrumental in him recognising that eugenics "was based-as indeed all science ought to be-on common sense" (MacBride, 1929–1930). Leonard engaged MacBride to give a series of introductory lectures for the society that ended in the form of a three part article for *The Eugenics Review* in 1916 on the inner details and novelties of the science of heredity (MacBride, 1916–1917), a work that later became a pamphlet.

Leonard's Darwin as a Theorist of Evolution

Delivering the inaugural speech at The First International Congress of Eugenics in 1912, Leonard remarked that "it is increasingly evident that the inborn qualities of the child are derived from his ancestors in accordance with laws [Mendel laws] which though now but imperfectly known, are gradually but surely being brought to life,"[13] a statement that showed his awareness of the profile of Mendelism in those days. Twelve years later, consistent with that first positive appraisal of Mendelism in a lecture Leonard gave at the London School of Economics (Darwin, L, 1924), he alerted the audience to the importance of understanding the transmission of "natural qualities" for eugenics and how inheritance studies had been stimulated by the controversies on evolution" (*Ibid*., p. 99). Leonard also argued that ignorance on how the evolutionary process works should not deter the eugenicist from striving for racial progress by using a method of selection (*Ibid*., p. 102). In that lecture he openly recognised that, in line with the concerns of the time, evolution is a process that may entail deterioration (*Ibid*., p. 101), and that racial selection should be a priority for the British Empire if Britons wished to avoid the kind of decline that the Roman Empire experienced (*Ibid*., p. 105). As the previous paragraphs show, Leonard's initial interest in Mendelism was intimately related to his interests in eugenics. In fact, he was very keen in knowing if "Galton's law of ancestral

[13] The Times London, 1912. My remarks in brackets.

heredity could be given a Mendelian interpretation'' (Bennett, 1983, p. 13) an understandable interest for a eugenic movement that was in search of new methodologies to advance its agenda.

Despite the fact that Galtonian statistics and biometrics[14] were questioned by the adherents of Mendelism, Leonard never put them out of his mind and thought instead that they might still be of use to evolutionary studies. Nevertheless, although sympathetic on the utility and theoretical reach of Galton's ideas, he clearly began to view Mendelism as an alternative to it. This was manifested when he published *The Need for Eugenic reform* (TNER) in 1926, a book originally written to spread the eugenic ethos, but that contained a chapter on Mendelian theory (Darwin, L, 1926, pp. 11–25). In this chapter, although Leonard argued that the differences between the Galtonian and the Mendelian schools were about methods rather than conclusions (*Ibid.*, p. 12), he maintained that the particulate inheritance put forward by Mendelism was an alternative to the failures and limitations of the Galtonian law of ancestral heredity (*Ibid.*, p. 14). In line with this argument and based on Fisher's paper of 1918 ''Correlation between relatives'' (Fisher, 1918), Leonard also claimed that the knowledge on the balance between dominant and recessive characters brought about by Mendelism helped to explain Galton's famous conundrum, of regression to the mean (Darwin, L, 1926, pp. 18–25).

Another issue that deeply concerned Leonard was ''mutationism.'' He was well aware of its popularity among the new generation of scientists and of the negative impact it was having in damaging the reputation of Darwinism as a functional theory. In effect, the work of Hugo De Vries. based on his experimental crosses with the evening primrose (*Oenothera Lamarckiana*), proposed the existence of large mutations able to produce the sudden appearances of variant individuals that were able to pass those drastic changes on to their descendants and thus to

[14] The biometricians were a group of academic scientists many with eugenic linings and with some belonging to the EES, that believed in the appliance of mathematics and statistics to solve the riddles of evolution and heredity and as such were reluctant to Mendelism. See: Bowler (1983, 1989a), Kevles (1995, p 35). Bowler (2003, pp. 256–260). See also Mayr (1982) and Olby (1988). Their leader was Karl Pearson (1857-1936), Galton's protégé and professor of Eugenics at University College London since 1907. Despite not belonging to the emergent experimentalism Pearson himself criticized the lack of sound science at the EES, a fact that risked ruining his own aims of turning eugenics into an academic scientific discipline (Kevles, 1995, p. 104).

create new species (Bowler, 1978, 1983; Mayr, 1982; Norton, 1973).[15] This alternative understanding of the process of organic evolution as a discontinuous one damaged the already dented reputation of Darwinism not only because it reduced the role of natural selection to a minimal role (by selecting the mutant form to die or to survive into a new species), but also because it questioned the Darwinian concepts of adaptation and natural selection.[16] The ''crude visibility'' of De Vries'' ''progressive mutants'' from his crossing experiments, together with the sudden appearance of mutants of the fruit fly *Drosophila melanogaster*, obtained in the first experiments performed by the Thomas Morgan (1866–1945) group at Columbia University by 1908 seemed to explain quite straightforwardly for many, the process of formation of new species, and hence the whole process of organic evolution (Allen, 1979).

The ''crude visibility'' of these mutants, even though short lived, silenced at least for a while any critical assessment of his proposals, so that, arguably, De Vries's mutationism, was not only the most popular theory of evolution in the early decades of the 20th century, but also the most popular form of inheritance (Bowler, 1983, pp. 197–226; Bowler, 2003, p. 268; Mayr 1982, pp. 546–547, 728–744). In 1904 the influential biologist and foremost American eugenicist Charles B. Davenport (1866–1944) for instance, described mutationism ''as the most important work on evolution since Darwin's ''Origin of Species'' a work destined to be the foundation stone of the rising science of experiential evolution'' (cited in Richmond, 2006, p 477, ref 74).

[15] Despite signs of a growing discredit from the early 1920s well up to the early-1930s, mutationism was supported by many renowned scientists such as Charles B Davenport, Daniel T McDougal, Reginal R Gates and Thomas H Morgan among others. For an idea of the many scientists that supported mutationism and viewed Darwinism with suspicion see Allen (1969, p. 57) and Magnus (2000, p. 97). For discussions on its lifespan as an accepted theory see Olby (1992, p. 61). For ideas of the calibre of the debate in the 1900s see Castle (1905) and Ortmann (1907). The scientific support for mutationism began to fade as a result of Morgan's group experiments in *Drosophila melanogaster*, finding a correlation between chromosomal dynamics in cells and the Mendelian factors together with the results of the experiments in *Oenothera* based on cytological on its reproductive stages, showing that the phenotypical difference among plants were due to chromosomal duplications that produced different conditions of polyploidy rather than mutations (Mayr, 1982, p. 744. Allen, 1979, p. 124, ref 63). Muller's work on Drosophila was also aimed to debunk De Vries mutation theory (Carlson, 1981, pp. 94–96). See also Allen (1979, p. 124, ref 63).

[16] This even if De Vries himself presented his theory not as a strict alternative to Darwin's (Bowler, 2003, p. 269). For a discussion on this issue in the early 1900s see Richmond (2006, pp. 469–471).

There were also other reasons why mutationism effectively contested Darwinism as a credible theory of evolution, during the first two decades of the twentieth century. On the one hand, mutationism exposed and deepened most of the objections that Darwinism had been previously subjected, chiefly among: (a) its inability to explain the discontinuity of the fossil records, (b) its inability to explain the existence of non-adaptive structures, c) the problem of blending heredity and d) the popularity of Lamarkism and Orthogenesis (Allen, 1969, pp. 69–80; Bowler, 1983, pp. 23–26; Bowler, 2003, pp. 224–256; Mayr, 1982, pp. 526–531). On the other hand, contrary to biometrics and Darwinism, mutationism openly belonged to a ''more manipulative'' and experimental form of science, one that was increasingly practiced by many scientific disciplines and that was supported not only by many prominent figures in the field of genetics such as William Bateson (1861–1926), (Allen, 1979), and De Vries himself,[17] but that was backed up by an ascendant positivism inside biosciences (Allen, 1969). This experimentally based science in biology was also promoted by the creation of new research groups inside scientific institutions, such as that set up by Thomas Morgan at Columbia University,[18] as well as supported by a

[17] De Vries himself was originally a botanist belonging to that new tradition that actively promoted the ''new'' experimental science as opposed to the observational one that was deployed by the anatomical and phylogenetic tradition in zoology and botany respectively (the two main traditions that originally supported Darwinism). De Vries in fact viewed this last school of thought as speculative and bitterly criticised them as creating ''poetical fantasies'' (Cited in Theunissen, 1994). Theunissen (1994) argues that although De Vries incorporated Mendelism into his ideas on heredity and evolution and he supported its experimental base, he saw it as a laboratory phenomena with no relation to ''normal'' heredity. For a deeper analysis of the issues discussed here see Bowler (1983, pp. 182–226); Bowler (1989a, pp. 113–127); Bowler (2003, pp. 264–273) and Mayr (1982, pp. 540–550).

[18] Morgan displayed a research agenda and experimental approach originally aimed to prove correct the results of De Vries mutationism in animals (*Drosophila Melanogaster*). For more detail on Morgan's life and work see Allen (1979). Results in Morgan's lab however soon began to show in experiment after experiment that mutations were lethal and that the ''white eye'' and other mutants obtained proved not to be a new species as the mutationists initially proposed (Allen, 1979, pp. 116–125).

growing agricultural lobby interested in the potential application of genetics.[19]

One scientist that distrusted Hugo De Vries mutationism, and in particular his typological concept of species was Ronald Aylmer Fisher, a young prominent statistician and respectable member of the EES.[20] Fisher's major work GTNS (1930), portrayed by a scholar as ''arguably the deepest and most influential book on evolution since Darwin'' (Crow, 1990, p. 208) represented the first comprehensive synthesis of concepts of population genetics, biometrics, the environment and the action of natural selection.[21] Fisher's statistical-populational approach not only got the EES to rely more firmly on an experimentalist Mendelism rather than on the growingly discredited Galtonian methods and biometry (Mazumdar, 1992, pp. 96–145), but also began to attract the support of key-funding bodies such as the Medical Research Council who saw Fischer's work at Rothamsted as in line with its policy of awarding grants for genetics projects based on experimental laboratory practices aiming to ''show how theoretical concepts were mobilised to meet the needs of particular applications'' (Fisher Box, 1978, p. 100).

[19] Agricultural interests were also a basis for Gregor Mendel's work. For a discussion on Mendel's work as an attempt to find empirical laws for the formation of hybrids (a clear agricultural interest) rather than the laws of inheritance, see Monagham and Corcos (1990).

[20] See Bennett (1983, pp. 15–16). During his time at the EES he wrote about 200 reviews for *The Eugenics Review*. Fisher's genetic approach was based on taking further the work on statistics by the German school of mathematical Mendelism that, through the work of Weinberg in 1908, managed to mathematically express the Mendelian binomial in relation to the frequency of genes in a given population (Crow, 1988; Mazumdar, 1992, p. 164).

[21] Fischer's approach in GTNS alongside the work of S. Wright (1869–1988) on the fate of genes in populations, the experimental work performed by Theodosius Dobzhansky (1900–1975) on *Drosophila* populations (in particular his meticulous gathering of all the data produced by other scientists that had accumulated between 1920 and 1940 (Dobzhansky, 1937), and the work of other scientists such as Haldane, Huxley, Mayr, Simpson, Stebbins, Rensch and Chetverikov (Mayr, 1992, pp. 556, 568) constituted the final blow for large mutations as agents of evolutionary change and the final vindication of Darwinism as a rigorous theory. As a result, by the late 1950s, Darwinism, unquestionably became, as Smocovities (1996) put it, an ''unifying doctrine'' in biology, that is a body of thought able to cement together all the different and diverse biological disciplines under the same philosophical roof. This unifying role was bluntly expressed by Dobzhansky's well-known maxim: ''Nothing in biology makes sense except in the light of evolution'' (Dobzhansky, 1973).

Fisher was the honorary secretary of the EES from 1914 to 1942 and during this time he upheld a robust personal and professional bond with Leonard Darwin (Bennett, 1983, p. 88). Their relationship was cemented as much by their eugenics ideals as for the shared belief that Mendel's laws could have an important and positive effect on both Darwinism and eugenics. As Bennett suggested, an analysis of the letters that they sent to each other, especially the early ones, from 1915 to 1930, spanning part of the period when GTNS was written, clearly shows not only Leonard's decisive role in influencing, advising, stimulating and encouraging Fisher to undertake original research and to improve his book, but also allows us to get an insight into Leonard's mastering of the new Mendelian science of heredity.[22]

An analysis of the Fisher–Leonard correspondence and Leonard's own writings shows that he was interested in three main subjects concerning evolution, all of particular relevance for safeguarding the scientific status of his father's theory, namely: adaptation, animal fecundity and mimicry.[23] All critical themes for Darwinians to argue for the existence of the action of natural selection in adaptation (Bowler, 1983, p. 29; Mayr, 2001, pp. 134–137).

In a letter dated January the 22nd 1928, Leonard subtly invited Fisher to speculate on issues of animal reproduction, in particular the parasitic practices exhibited by cuckoos when nesting (Bennett, 1983, pp. 82–84), initiating a rich and original discussion, entailing an exquisite deployment of ideas on natural selection, Mendelian genetics and Charles Darwin's views on the phenomenon of sexual selection in

[22] To appreciate the importance of Leonard's own contribution to Fisher's book, it is important to bear in mind that, as highlighted by Bennett (1983, p. 13), before 1930 Fischer discussed issues of natural selection and heredity with none other than Leonard Darwin. Leonard corrected most of the chapters of Fischer's GTNS and in a letter dated July the 18th 1929, close to its publication, he praised Fischer's book with these words to him: "My feeling on reading these chapters is that you have written a very important book, and one which will slowly-though slowly- influence public opinion" (Bennett, 1983, p 105). Fischer in turn dedicated his book to Leonard. He wrote: "In gratitude for the encouragement given to the author, during the last fifteen years, by discussing many of the problems dealt with in this book" (Fisher, 1930). The Darwin/Fisher scientific exchange continued even after Fisher's book was published. In a letter Leonard wrote to Fisher dated June the 24th 1930, he restated his conviction about the relevance GTNS would have for Darwinism in the future by saying: "I feel the value of your work in showing how Mendelism is capable of putting the lid on to the theory of natural selection" (Bennett, 1983, p. 123).

[23] Mimicry refers to the mimicking of a given species for instance by edible butterflies of the coloration of poisonous ones resulting in the avoidance of getting eaten by birds.

monogamous birds.[24] The issue of animal fecundity was a subject of intense questioning in those years especially concerning the evolutionary advantage that could signify for a given species to care for their descendants as it was for some eugenicists concerned with the high rate of reproduction of the pauper class (Mazumdar, 1992). Fisher himself attributed the solution of the problem to Leonard who himself discussed the issue and attempted an answer in a paper that he published in *The Eugenics Review* in 1922.[25]

In relation to mimicry, the subject particularly interested Fisher and Leonard for two reasons, firstly, because mimicry served to back up mutationism and secondly, because it was one of the many critical nodes in the controversy between biometricians and Mendelians. As Bowler pointed out, early geneticists were convinced that new characters arising from mutations in an individual were able to perpetuate themselves regardless of any adaptive value; assuming thus that mimicry was the

[24] Charles Darwin's sons were hailed and consequently treated by many as special persons. Leonard Darwin, together with his brother Francis (1847–1925), epitomized for evolutionists, eugenicists, geneticists and the like, a rich and unequalled source from which to recover any hint of his father's ideas on evolution that would serve to enhance their arguments. Both brothers had been involved to some extent with their father's theorising; whilst Francis helped his father in organising his collections (Desmond and Moore, 1992, pp. 617, 63) and completed in 1887 Charles *Life and Letters*, Leonard participated in the corrections of Charles' book *The expression of the Emotions in Man and Animals* (Darwin, C, 1872), by actively discussing with him (Desmond and Moore, 1992, p. 594). Leonard's uniqueness in projecting his father's concepts and reasoning to explore new areas is manifested in Fisher's attitude of constantly urging Leonard to recall his father's "spoken words" (Bennett), 1983, p. 14). See letter from Fisher to Leonard dated 13 November 1928 in Bennett (1983, pp. 89–90). For this last theme, as we anticipated above, the role Leonard played in refreshing Fisher's ideas on Charles Darwin's work would become paramount for his scientific pursuits.

[25] See Darwin, L, (1922–1923). Concerning the issue Fisher stated in GTNS, "In this connection Major Leonard Darwin has pointed out that the principal importance should be given to the factor of parental care, including in that term all expenditure in the form of nutriment, effort or exposure to dang, incurred in the production and nurture of the young. In organisms in which that degree of parental expenditure, which yields the highest proportionate probability of survival, is large compared to the resources available, the optimal fertility will be relatively low. Any circumstance which materially lightens the burden on the parent will necessarily have an immediate effect in favouring survival [...]. Major Darwin illustrates this principle by the example of the parasitic cuckoos, which have found a way to relieve themselves of a great part of the parental burden borne by other birds, and have in fact, acquired a considerable greater fecundity than their non-parasitic allies" (Fisher, 1930, pp. 185–186). It has been argued that the theme was first discussed by Leonard's father Charles in the first edition of his *Descent of Man* (1871) but has fallen into oblivion because of its omission in the second edition (1889) (Burbridge, 1992).

product of coincidental variation in different species rather than the result of the selection of minute variations concurrent with environmental changes (Bowler, 1983, pp. 188–190). Viewing variation as discontinuous, mutationists like Bateson proposed a solution to the problem of how selection could produce adaptive characters when those characters were too small to confer any advantage (Bowler, 1983, p. 191).[26] Moreover, Reginald Punnett (1875–1967) in his influential book *Mimicry in butterflies* (1915), despite giving some credit to selection as a "factor for change in a population," reinforced Bateson's views, by proposing a mutationist explanation for the evolution of mimicry (Bennett, 1983, pp. 8–9), thus reinforcing the status of mutationism to explain organic evolution.[27]

Both Leonard Darwin and Fisher were conscious that the evolution of mimicry was the greatest post-Darwinian application of natural selection and would consequently engage in discussions over issues of mimicry intensively (Bennett, 1983, pp. 99–100).

Leonard kept providing Fisher with key knowledge on butterfly morphology and habitats (Bennett, 1983, p. 106) as well as contributing with important conclusions, for instance on the importance of the coordinated action of natural selection upon the different parts of organisms (*Ibid.*, p. 91), all issues that proved crucial for certain evolutionary conclusions that Fisher would later include in his conclusions on mimicry in GTNS (Fisher, 1930, pp. 146–169).

Finally, it is important to mention that Leonard had given some input to Fisher concerning his more challenging theories. This is manifested in two letters they sent to each other between the 5th and 7th of July 1928, where they discuss the evolution of a hypothetical species by displaying the use of Mendelian binomials to deal with the problem of evolution of dominance proposed by Fisher (For a full appreciation of this discussion see Bennett, 1983, pp. 86–89).

Although from the Fisher/Darwin correspondence it is possible to get a picture of Leonard's efforts to amalgamate Mendelism with his father theory and his ability to theorise on evolutionary issues, it is from his own book "*Organic Evolution: Outstanding difficulties and possible*

[26] As we will see later Leonard proposed an alternative explanation to it by assuming the existence of small frequent mutations in his book *Organic Evolution* (1921).

[27] Punnett on the whole argued that, "if protective resemblances had been built gradually, its incipient stages would have been of not real value and could not have been aided by selection." Cited in Bowler (1983, p. 214). Punnet viewed mimicry as coming into being as a "sudden sport or mutation," with natural selection "responsible merely for its survival," rather than as the result "of very numerous variations in the right direction through the operation of natural selection" (Punnett, 1915, pp. 61–62).

explanations,'' (OE) published in 1921, that this can be better appreciated. In OE Leonard reached essential conclusions concerning the way Mendelism worked and how this might explain the mechanism of evolution by natural selection. According to one reviewer of OE, its reading would be beneficial for experts, for the book thesis not only was substantiated by the most recent experimental work, but because OE was a well-crafted, clear and concise book (A.M.C.S. 1921–1922, pp. 540–543).

In the preface of OE Leonard bluntly expresses his allegiance to his father's theory by stating: ''In the course of my studies, of course, I learnt that my father theories had been subjected to severe criticism […]; but as regards the probability to mark his full work fall into pieces, these criticisms, so I judge, might be compared to the removal of a dozen bricks from a well built house'' (Darwin, L, 1921, p. 1).

To this he later expressed his confidence in the positive influence Mendelism would have for Darwinism:

> No doubt the bright light of Mendelism has modified or destroyed certain arguments relied on by Darwin, in whose time light was not shinning. But if we are bound to rely on small and frequent mutations to a considerable extent in explaining organic evolution, and if there is no bar to our so doing dependent on facts, then the edifice erected by the author of *Origin of Species* still remains intact in all its essential features (Darwin, L, 1921, p. 47).

This solid allegiance to Darwinism was not only applied to the concept of evolution but extended to the second and most controversial part of his father's doctrine that was under intense scrutiny in those years, which is natural selection. Concerning this, he bluntly added, ''rule out natural selection and the process of evolution becomes inexplicable'' (Darwin, L, 1921, p. 9). Having taken such a strong commitment to natural selection he then straightforwardly denied the existence of ''large and infrequent mutations,'' which were sustained at the time by the adherents of mutationism as the key factor in the formation of new species. In clear defiance to a prevailing mutationism, Leonard claimed that natural selection does not make any sense in a scenario where only ''large and infrequent'' mutations take place. This because these sudden large changes cannot explain adaptation, in particular in those cases were several large mutations have to occur simultaneously to change the different parts of an organism involved in that process (*Ibid.*). Instead, he, ahead of or at least timely with its use on the scientific literature of the 1920s,[28] argued that small and frequent mutations, because of their silent nature, would not be easily cleared out by selection (Darwin, L, 1921, p. 11). Leonard's proposals on the accumulation in individuals of inheritable frequent small mutations had quite deep implications for Darwinism at the time, for they allowed: a) natural selection to be back on the scene by having a more creative role in adaptive divergence, b) evolutionary divergence not being specified by "mutation pressure" and c) the possibility of statistically estimating the rate of mutation for genes under specific conditions (Olby, 1992, p. 63). Leonard Darwin's theorising also displays signs of populational thinking, entailing a flux of genes among its members and the elimination of "harmful" (deleterious) mutations by natural selection (Darwin, L, 1921, p. 10).

A significant feature emerging from *OE* as a whole is Leonard's recognition of the combined role for organic evolution of both mutations as a source of variability and of natural selection, this last, acting not only as a negative force as proposed by the adherents to mutationism, but as one that, because of its action upon that source of variability, would have a more creative role. Small and frequent mutations, however, were elusive to find experimentally at the time, as the work of Wilhelm Johannsen (1857–1927) of 1915 with pure lines, suggested (Allen 1979, pp. 121). Aware of the hurdle Johannsen's work represented for his hypothesis Leonard argued, that this was not enough to deny their existence (Darwin, L, 1921, p. 14) and that "to hold […] that a theory must be altogether rejected until proved to be true by experiment is illogical" (*Ibid*., pp. 16–17). Nine years later (1930), in an article in *Nature*, he further elaborated on this epistemological point claiming that:

> Negative evidence, or rather the absence of positive evidence, can do but little towards condemning any evolutionary theory; whilst is to positive evidence where we must look in order to decide whether in our existing state of knowledge natural selection is to be accepted as the most probable hypothesis (Darwin, L, 1930, p. 127).

Another interesting feature of OE is that Leonard criticised the core of the assumptions and methodology followed in the experiments with pure lines. He reasoned that even accepting that an intense cross fertilisation procedure in plants would produce identical gametes it was not necessarily a proof that mutations were not taking place (Darwin, L,

[28] Olby found that expressions on "small and recurrent mutations" appeared in the scientific literature from 1923 onwards (Olby, 1992, p. 63). If this is correct it would then be quite possible that Leonard was one of the first personalities using this term.

1921, p. 16). He argued that by assuming that the gametes are absolutely identical the experiments ‘‘either might have to be carried on for a great number of generations, in order to secure visible results, or might fail altogether’’ (Darwin, L, 1921, p. 39). He claimed that individual differences existing between gametes (referring to the existence of different alleles for a given character presumably arising by the accumulation of small frequent mutations) have not been detected because those experiments have not been carried out for long enough (*Ibid.*). This discussion, although superseded by present standards, was of key relevance at the time to counterbalance the strength of the concept of pure lines which encouraged and extended the opposition to natural selection from supporters of mutationism and biometrics, who argued that selection cannot produce a deviation from the mean; a view that was sustained even by Morgan well into the 1930s when he argued in his ‘‘*The Scientific Basis of Evolution*’’ (1932) that by selecting the more extreme individuals of a population, the next generation would not necessarily move in the (selected) direction (Mayr, 1982, p. 585). It is worth remembering that Leonard's opposition to these groups on this point was to a great extent motivated by his eugenic leanings. The discussion on how long or how many generations it would take for a selective character to become established in a population, or how long it would take to reduce the impact of mental defects in a population, was cherished knowledge for the eugenicist to justify the extent and rapidity of his/her social intervention (Darwin, L, 1931–1932).

It is worth mentioning, that in OE, Leonard also raises a couple of interesting questions related to the putative genetic advantage of sexed species over non-sexed ones (Darwin, 1921, p. 40). This was a theme that Leonard began discussing with Fisher in 1915 (Bennett, 1983, p. 65) and that would feature later in chapter VI of Fisher's GTNS, where he argues in favour of the evolutionary advantage of sexual over asexual reproduction on the grounds that, in the first, evolution would occur more rapidly than in the second, because beneficial mutations for different gene loci have a greater probability of survival in single individuals (Bennett, 1983, p. 31). In this relation, Leonard wondered if ‘‘there are any plants, which, without doubt, being always self-fertilised, have for long existed as pure lines?’’ (Darwin, L, 1921, p. 40). These were certainly questions that, if answered, could have given clues to the importance of sexual recombination in generating variability, a hypothesis that Leonard valued as an additional explanation for the process of creation of variability by small frequent mutations.

Interestingly, Leonard proposed that the origin of the small and frequent mutations, hence of genetic variability, was linked to sex (*Ibid.*, p. 45). Although wrong about the moment at which small frequent mutations occurred (he thought they arose during the process of gamete fusion, instead of the current view that it occurs during the meiotic division of the reproductive cells), he anticipated its occurrence as an extra source of genetic variability.[29]

There is an extra point from OE that deserves our attention, for it would help us to better visualise Leonard Darwin's role as a theorist of evolution in his own right, and that is his pertinent use of analogical models. He used them to explain the dynamics of evolution based on the existence of two kinds of mutations each with opposite effects for the adaptation of organisms, and aimed to explain the existence of a mechanism for the transmission of characters due to their use and/or disuse. Concerning the first point, in chapter III Leonard presents a model of evolution by natural selection consisting of a balance between two different types of mutations – "centripetal," those that make descendants close to their progenitors, and "centrifugal," those that make for difference between progenitors and their descendants, to account for the generation of genetic variation upon which natural selection could act alongside the environment to produce different states of equilibrium and thus result in the formation of new species (Darwin, L, 1921, pp. 25–29). With this, Leonard was giving a far more active role to natural selection than that proposed by mutationism. With reference to the second point, fully aware of the fatal blow Weismann's work with mice signified for an effective transmission of acquired characters, he nevertheless attempted a Neo-Lamarckian model of muscle inheritance (*Ibid.*, p. 4). To avoid the conundrum of an ever-increasing mass of muscle over generations due to persistent use, he speculated about the existence of a substance that if produced beyond a threshold when the muscle develops because of exercise, it would only then in some way influence the germ-plasma and thus prevent that organ from developing in future generations (*Ibid.*, p. 7). He also believed that the production of this substance before that threshold could also explain the disappearance of organs or structures in further generations. Remarkably, the existence of this feedback mechanism is similar to what is currently understood – without its association to inherited transmission, as a mechanism to be commanded by proteins produced by regulatory genes.

[29] As the reviewer of OE remarked, the occurrence of small frequent mutations "is an entirely permissible deduction from the evidence" (A.M.C.S. 1921–1922, p. 541.).

Even though no major scientific journal such as "*Nature*" or "*Science*" reviewed OE and hence the impact on the scientific community might have been scarce, Leonard's book seemed to have passed through some specialists" scrutiny. This is manifested in a letter that Fisher sent to Leonard where he expressed his anxiety about having the book reviewed and ask Leonard if he was happy to suggest a reviewer.[30] Having surveyed the main arguments of Leonard's Darwin OE, a pertinent question arises and that is, what was, if any, the significance of this book? I would like to argue that by the 1920s, when the De Vries mutationism was still a viable alternative theory to Darwinism to explain organic evolution, Leonard's proposal of the existence of "small frequent mutations" accumulating in inbreeding populations embodied a gradual process of accumulation of variability, that although later proved partially wrong, conceptually confronted De Vries" drastic mutationist thesis that was being backed up by the work with pure lines. In this regard, it has to be remembered that prominent geneticists retained a confidence in a saltationist model of evolution in the 1920s. As Bowler pointed out, R. Goldsmith (1879–1958), a renowned geneticist that would play a pivotal role for the Mendelisation of Darwinism, for instance, remained convinced that "the selection of minute genetic differences could only create subspecies (microevolution), but could not achieve the production of genuine new species (macroevolution)" (Bowler, 1983, pp. 209).

Lastly on this, it is important to mention that by that time Fisher did not fully support the idea of small frequent mutations and started to mature what later became a different thesis to explain the problem of genetic dominance. Instead of small frequent mutations Fisher stressed the existence of "innumerable and minute" genes involved in the expression of a character (evolution of dominance) as more important.[31]

Leonard's arguments on Mendelian genetics and evolution would become more sophisticated in his next book, "The Need for Eugenic Reform," (TNER), (1926), a book that, as anticipated, was chiefly dedicated to the spread of the eugenic ethos for both eugenicists and a

[30] Letter dated 13th October 1921, in Letters and Notes by R.A. Fisher, The Wellcome Trust archive, U.K. (Consulted April 2006).

[31] Bennett (1983, p. 26). Although not fully explicit it is clear that Leonard understood small mutations as being accumulated in a pool from which they could be potentially used. This idea, as discussed later, became explicit in paper he published in the Eugenics Review in which he opposed a proposed version of Orthogenesis by Berg (Darwin, L, 1926–1927).

wider audience.[32] In TNER, Leonard skilfully refined his arguments concerning Mendelism and indeed comfortably displayed his capabilities as a theorist and educator.

In Chapter VIII on Natural Selection, Leonard confronts the mutationist thesis head on by arguing that:

> Small changes in the genes, here always termed mutations, are ever taking place from time to time; but that their immediate results are masked by the much larger differences always found in every family because of the differences in the collections of genes by chance allotted to its different members'' […]. (To what he adds concerning the role of natural selection that), ''The range of variations due to Mendelian rearrangements indicates the range of innate differences available for selection and the width of this range is determined by a balance being struck between the opposite forces of mutation and selection […] If we are to believe that any difference between two individuals is hereditary, we are in fact affirming our belief that that difference depends upon the existence of some difference between the genes from which the two originated'' (adding that) ''wherever differences between the genes exist, there natural selection may be able to operate (Darwin, L, 1926, pp. 120–121. My remarks in brackets).

Most importantly, without mentioning it as such, he implicitly postulates the population as the level on which natural selection acts upon. He does this by equating the role of selection to that of ''picking out and discard darker grains of sand from a heap consisting of various shades of grey,'' a phenomenon that ''makes selection continually increase the number of grains of lighter hue inside the heap'' (Darwin, L, 1926, p. 124). What is remarkable about all this is that, without a formal scientific education, he used a language comparable to that used twenty years later by the so-called mentors of ''the new synthesis.''

In chapter II of *TNER*, titled ''The Laws of natural inheritance,'' Leonard deploys his pedagogical skills by using an analogical model to explain the functioning of Mendel's laws of inheritance, in particular the segregation of alleles. In this model, individuals are analogous to a house, one in which the walls are its genetic material, which in turn are composed of two different sets of bricks (alleles) (*Ibid.*, pp. 12–18). With this model he attempts to explain the process of meiosis that takes place during gametogenesis when the homologous alleles split. His analogy

[32] As discussed later in this paper, Leonard's book contained many controversial discussions on positive and negative eugenic measures to be adopted on the undesired; measures that as Berra remarks (2013, p. 148), were shocking by today's standards.

also puts in more accessible terms ideas such as, why despite differences brothers and sisters resembling each other and the idea of genetic dominance ‘‘the power one kind of brick has of hiding (or partially hiding) another kind of brick’’ (*Ibid.*). Furthermore, although he identifies genes as the connecting links between two generations, he argues that their action in building the body of organisms is mediated (presumably by proteins). He argues that genes have pleiotropic effects and that the many parts of an organism are dependant on the action of many genes (*Ibid.*, pp. 14–16).

As with many of his contemporary professional scientists[33] and members of the EES Leonard Darwin never disposed of his eugenic leanings when speculating on issues of evolution; he was in actual fact convinced that they were, alongside human heredity, part of the same account. In the introduction, for instance, he claims ‘‘[it] is folly not to utilise those laws of nature which are derived from a study of the physical world in order to ascertain what steps we should take to secure for ourselves and for our descendants the best attainable surroundings’’ (*Ibid.*, p. 4). Although Leonard foresaw a clear role for natural selection to play in the physical constitution of the human race (*Ibid.*, p. 9), he was convinced that natural selection played a ‘‘little role in the mental and moral roles of mankind’’ (*Ibid.*, p. 130). He argued in fact that human evolution needed our intervention to avoid leaving natural selection to operate on its own in view of the disastrous outcomes it could produce (*Ibid.*, p. 130).

Leonard clearly gave primacy to the eugenic ideal over the status of scientific research. He stated for instance that ‘‘our eugenic policy in no way depends on the success or failure of one or the other of these rival theories,’’ referring to the theories that argued for or against a role for natural selection on the process of evolution. To this he added, ‘‘nothing is to be learnt from biology as to the ultimate aims of our existence, and little as to the exact ways in which the evolutionary methods should be utilized in eugenic reform’’ (*Ibid.*, pp. 120, 124–125). Concerning the specific policies to achieve the eugenic ideal, Leonard calls for a) a stop to the state benefits for those groups whose fertility should not be encouraged (the feebleminded and paupers), b) the sterilisation or segregation of the common criminal, c) the deployment of methods to restrain the size of the family and hence to diminish the size of the population. Interestingly, in chapter XI, ‘‘methods of elimination,’’ he discusses and dismisses the lethal chamber on the grounds that it would

[33] For an idea on the extent of scientific support for eugenics between 1910 and 1945 in the UK and the US see Allen (2011).

signify "to associate the idea of murder with that of social progress" and that as such it would undermine the "eugenist demands (of) self-sacrifice in order to lessen the sufferings of further generations" (*Ibid*., pp. 168–185). Overall, his argument for eugenic reform was quite upfront, by claiming that eugenics is to the human race what natural selection is to natural forms, Leonard was not only trying to make the "human race" responsible for the future course of its own evolution but to highlight the central role that the EES should play in that process.

A further issue from TNER worth mentioning are Leonard Darwin's diffident views on a still influential Lamarckism especially in its relationship to eugenics. Although with a hesitant style, Leonard quite frequently opposed the Lamarckian concept of inheritance of acquired characters in his writings. So, for instance, on Weismann postulates he would affirm that "no one […] believes for a moment that, for example, a wounded soldier's child would suffer as the direct result of the father's wounds" (*Ibid*., p. 100). Nevertheless, his refusal of Lamarckism was never complete, for he would simultaneously affirm that alcoholism and syphilis may damage the germ plasm of the affected person and as such damage her/his descendants (*Ibid*., p. 99). This last statement entailed for him and for the eugenic movement the hard and unexpected conclusion; that eugenics policies should not rely on the inheritance of acquired differences (*Ibid*., p. 111), because, "the effects of use and disuse will take many generations before materially affecting the inborn qualities of the nation" (*Ibid*., p. 107). He thus reluctantly concluded that the movement "must look elsewhere when framing practical proposals for eugenic reform" (*Ibid*., p. 111). It is interesting to speculate that perhaps Leonard never fully closed the doors to Lamarckian inheritance despite being too slow to act, because he was himself a neo-Lamarckian.

Although Lamarckism ranked highly in Leonard's interests as a eugenicist, natural selection was also one of his uppermost priorities. One of the more nuanced of Leonard Darwin's arguments was his defence of the role of natural selection on evolution featured in an article he wrote for *The Eugenics Review* in 1927 (Darwin, L, 1926–1927) and in the corrections to that article he sent to the Review the following year (Darwin, L, 1928). Leonard's aim in this article was to riposte Leo S. Berg's theory of Nomogenesis, an Orthogenesis-like theory (evolution determined by law) that questioned Darwinian natural selection's capabilities to determine the direction of evolutionary change (Berg, 1926). In order to appreciate Leonard's role as a theorist of evolution this article deserves a full reading. However, a glimpse at some of its arguments will suffice to realise Leonard's mastery of key concepts on evolutionary theory. In open opposition to Berg's thesis on the impossibility of multiple genic variations (small frequent mutations) occurring to explain the emergence of complex organs, like the eye, Leonard argued that, small frequent mutations because they a) originate in longer intervals, b) they occur independently from each other, c) they have less chance of being harmful and d) they can be selected simultaneously; they are better suited to be the basis of the many simultaneous hereditable modifications required for the adaptation of particular organs such as the eye and in general for the adaptation of the organism to the environment (Darwin, L, 1926–1927, p. 286). By arguing that small mutations for each character have independent probabilities of occurrence Leonard was confronting a central critique against the existence of the accumulation and concerted action of small mutations for adaptation (*Ibid*., pp. 288–289). This allowed him to visualise an adaptive process based on different speeds according to the number of parts in need of change. Finally, in developing his arguments for a more creative role for natural selection to that assigned to it by mutationism, Leonard used a model of a box filled with different colours as representing genes in a population, inviting the reader to think about a role for natural selection as not producing uniform types, but rather as he put it, to "maintain in perpetuity a certain degree of differentiation amongst the organisms composing any freely interbreeding group" (*Ibid*., pp. 289–290).

Concluding Remarks

Contemporary historical accounts have dissected and highlighted the convoluted and creative relationship that unfolded at the outset of the twentieth century among evolution, eugenics and Mendelism. These accounts, however accurate, have left improperly addressed, the contribution to evolutionary theory of those not belonging to the "scientific community." One particular case is that of Leonard Darwin, whose scientific contributions to these debates have been under appreciated despite being relevant, not only in its own times the 1900s, but also from the 1940s onwards partly because we have mistakenly accepted the synthesis generation characterisation of the preceding generation's work.[34] Understanding Leonard Darwin and his colleagues" work on

[34] Even a recent work on the life of Charles Darwins descendants, where many aspects of Leonard's life are discussed, his role as a theorist of evolution and genetics is not mentioned (Berra, 2013, pp. 131–152). Berra's book on the life of Charles Darwin's children portrays Leonard as a military man, a politician, an economist and a eugenicist. Berra also recognises Leonard's role in mentoring Fischer.

its own terms help us to realise how intermingled these areas were during the first 30 years of the twentieth century and how the synthesis generation account succeeded in their attempts to artificially demarcate evolutionary from eugenic thinking.

By analysing Leonard's Darwin own work, I have argued that he himself was a theorist of genetics and evolution contributing to the debate with fresh and original ideas. Leonard Darwin in his writings (books, articles and letters) resolutely attempted to answer all of the problems that Darwinism and Eugenics faced, by amalgamating them with Mendelism. Leonard's ideas and concepts were seriously taken on board by Fisher and some of them would permeate and be further developed in his book GTNS, which was published in 1930.[35]

Leonard Darwin's first book, *Organic evolution*, represented one of the first attempts, coming from a non-trained professional biologist, to conceptualise Darwinism within a Mendelian perspective. It was largely an achievement that wasn't recognised by the scientific community, as suggested by the fact that the book wasn't reviewed by scientific journals, such as *Nature* and *Science,* nor was it cited by specialists books of the times. However Leonard's theorising, for instance his proposal of the existence of "small frequent mutations," which was a central concept in his book, acted as a pivotal device to challenge De Vries"mutationism, a challenge that helped the conceptual approximation of Mendelism, a discontinuous process, with Darwinism, a continuous one. Another of Leonard's critical contributions to the evolutionary debate was his defence of natural selection as a more active force than the one assumed by mutationism throughout his writing. In a paper he

[35] On Leonard's ideas subsequently being expanded and refined by Fisher, compare the letter Leonard wrote to Fisher dated 17 December (Bennett, 1983, pp. 91–92), with Fisher's chapter II of GTNS. The following is an extract of Leonard's letter, where he expressed to Fisher: "What I had mainly in mind about Chap. II was probably the point I tried to make on my article on N.S in the *Review*, and the letter subsequently correcting it. It was that the necessity of co-ordinating the different parts of the same organism is the same check on the pace of N.S., and consequently that, with complex organisms, the pace is very slow when coordinated changes have to be effected […]. It seems to me therefore probable that is generally true that the simpler the organism *and the simpler the surroundings* the quicker will adaptation take place. […] On the other hand a highly complex organism in a highly complex environment will move so slowly, and will have such vast possibilities before it, that it would take practically unlimited time to reach the stage when no further improvement will take place." In the summary of chapter II of GTNS, Fisher wrote: "The intensity of adaptation is inversely proportional to a standard magnitude of change for which this probability is constant. Thus the larger the change, or the more intense the adaptation, the smaller will be the chance of improvement" (Fisher, 1930, p. 46).

published in 1926 (including a subsequent one with corrections in 1927) he accomplished the most nuanced and scientifically up to date version of this defence. In it Leonard argued for a process of adaptation in which natural selection plays a central role by promoting in each successive generation the survival of individuals carrying small mutations, mutations that in turn, by producing changes in different organs, were all involved on the adaptation of the organism to a given environment.

Leonard Darwin's extensive use of models in his writings also highlights his role as a theorist of evolution. In *OE* Leonard used analogical models to explain, firstly, the existence of a balanced mechanism of centripetal and centrifugal mutations describing the adaptation of organisms to their environments and, secondly, a biochemical model describing the transmission of acquired characters. In his second book, *The Need for Eugenic Reform* (1926), having refined his knowledge on Mendelian genetics and in a clear attempt to keep the eugenic audience informed of the latest scientific developments, he used an analogical model relating the Mendelian laws of heredity with a more day-to-day experience phenomenon, such as house building.[36]

Although many of Leonard's concepts and ideas did not currently survive as such, it is fair to affirm that his basic conclusions on mutations,[37] for instance, were close to those that went on to survive in the synthesis. George. G. Simpson (1902–1984), in his book ''The Meaning of Evolution'' (1950), echoing Leonard's view, reasoned that small mutations, by being ''slight but cumulative,'' may not be lethal and become noticeable in later stages of the development of an organism and thus spread in populations. Similarly, Huxley, in the second edition of his renowned book ''Evolution, The Modern Synthesis'' (1963) admitted that, although there's no complete proof for the utilisation of mutations in evolution under natural conditions, because of their small effects and the experimental difficulties to detect them; they have been ''proved in every organism subjected to genetic analysis'' (Huxley, 1963,

[36] Darwin, L, (1926, p. 12). In one of what is perhaps the first models of what went to be known as ''bean bag genetics,'' Leonard also used analogies, such as that of boxes filled with balls of different colours selected out by chance to explain the way genes grouped together to form individuals (Darwin, L, 1926–1927). For more on the concept of beanbag genetics, see Dronamraju (2011).

[37] A concept that has been constantly changing its meaning: Mutation meant changes occurring in the paleontological record (1900s), soon later as the changes (discontinuous variation) occurring at the individual level in populations as viewed by De Vries and his followers (1910s–1920s) and ending in mutations as molecular changes occurring at the gene/molecular level (1940s–to date). See Olby (1992, pp. 60–64) and Carlson (1981, 2011).

p. 116). Although Huxley characterises small mutations as normally deleterious, he concedes that under different environmental circumstances they may became advantageous, a process that he dubbed "pre-adaptations" (Huxley, 1963, p. 119).

Finally, a genuine question arises here of why Leonard Darwin's contribution to the scientific debate has been largely neglected? One possible answer to this question could be that because of his eugenic convictions scientists at the time had never taken his biological thinking as serious scientific thinking. This last, as anticipated above, is a situation that had been historically reinforced by the synthesis generation attitude of cleansing evolutionary thinking from any trace of eugenics. Another possible, but not exclusive, answer could be that "experimental scientists" did not take on board Leonard Darwin's viewpoints on evolution and genetics because of his lack of "official scientific credentials."[38] Conceivably, in a scenario of disciplinary institutionalisation, they considered that it was not a credible practice to include an outsider's views on scientific debates, especially when biology was going through important changes and a new wave of institutionalisation, one in which the different internal cultures (systematicists, biochemists, evolutionists, physiologists, etc.) were struggling for supremacy.

Two different cases would serve to argue for the case of scientists distrusting and disqualifying comments on scientific issues by personalities who were not scientists. Firstly, soon after TNER was published, a review in *Nature* (1926), presumably written by a male scientist, criticized the chapter on Mendelian theory in it as:

> by far the weakest section of the book, for Major Darwin labours under the disadvantage of not being a biologist," a disadvantage that is magnified "by the fact that [...] he has relied for assistance and advise mainly on Mr R. A. Fisher and Mr C. B. S. Hodson. Of this the first is a mathematician and the second name is obviously a slip for Mrs Hodson, the respected assistant secretary of the Eugenics Education Society, who undoubtedly has had some training on biology, but is scarcely fitted to give serious criticism on this subject (E.W.M. 1926).

[38] This situation has an antecedent in the nineteenth century. When Robert Chambers anonymously published *Vestiges of the Natural History of Creation* in 1844, despite having massive public support, it was heavily criticised by scientists because in their view it was a compendium of speculative ideas without research to back them up, and above all because the book was written by someone who was not a scientist. See Secord (2000).

The second case is exemplified by Karl Pearson's angrily reaction against Leonard in 1914 in a paper the first published the same year in *Biometrika* (Bennett, 1983, pp. 73, 118). In it Pearson bitterly disqualified Leonard's arguments for the proposal of two different correlation coefficients one for the environment and another for heredity (Darwin, 1913) as stemming from someone who has not properly studied the subject. He stated:

> […] Why should we follow such advise as that given by the president of the EES to avoid as far as possible ''such phrases as the relative influence of heredity and environment'' when on his own showing he does not in the least appreciate the methods by which this relative influence is measured?[39]

Far from being a one off, this clash was the first from a series that would mark the turbulent relationship existing between Leonard and Fisher on one side and Pearson on the other.[40] A key catalyst for these clashes was the biometrician's perceptions of Fisher as a tactless and arrogant young man who belonged to another school of statistics and who was constantly trying to undermine Pearson's statistical reputation by intruding on his professional territory (Porter, 2004, p. 51; Fisher Box, 1978, pp. 82–83; Yu, 2004). In addition, Pearson never really accepted Leonard as an adequate intellectual figure behind Fisher because of his lack of official scientific credentials. A couple of Leonard's attitudes that particularly offended Pearson were firstly, Leonard's refusal to reveal to him the identity of the statistician that helped Leonard to publish his 1913 paper in *The Eugenics Review*,[41] and secondly Leonard's efforts to get Fisher's first paper published in a rival journal (the *Proceedings of the Royal Society of Edinburgh*, Fisher, 1918) soon after been rejected for publication in the *Notes and Records of The Royal Society of London* by him and Punnett (Bennett, 1983, pp. 116–117, ref 12).

[39] Pearson (1914). Cited in Bennett (1983, pp. 65, 116). For more details on the confrontation between Leonard and Pearson see also Fisher Box (1978, p. 51). Leonard sent a letter to Pearson in 1916 apologising for his mistake. UCL archives Pearson Letters. Ref: Pearson/11/1/4/17 (consulted February 2015).

[40] Leonard wrote a letter to Pearson dated January 14th 1914 in which he regretted their differences. In it he stated: ''I continue to live in hope that someday we may cooperate on the field of Eugenics, though I agree it is useless to attempt to do so with divergent aims.'' (UCL archives Pearson Letters. Ref: Pearson/11/1/4/17. Consulted February 2015).

[41] Letter dated 11th of September 1916. (UCL Pearson's archives. Ref: Pearson/11/1/4/17. Consulted February 2015).

The difficult relationship between Leonard and Pearson was also marked by their differences on issues such as the relationship between science and eugenics and the role of scientists in British society. Whilst Pearson prioritised science over eugenics by envisaging for instance the creation of different scientifically literate elites to rule Britain (Porter, 2004, pp. 286, 292–293), Leonard, despite his keenness in the EES informed by science, he disregarded the professional status of the adherents to the society and wanted the involvement of prominent scientists only as a means to the end of increasing the prestige and popularity of the society. Pearson's refusal to be a member of the EES and constant refusal of Leonard's many invitations to become, for instance, the vice president of the First International Congress of Eugenics, or to give talks at eugenics forums organised by the EES under Leonard's presidency, could not only explain Pearson's misgivings about eugenics and dissatisfaction with a society run by a non-scientist, but also Leonard's critical and strong view on scientists in general and on Pearson in particular.[42] Concerning scientists, in 1929 Leonard alerted Fisher that, "My experience is that scientific men are, outside their own narrow sphere of work, just as narrow conservative and touchy as any other class" (Bennett, 1983, p. 103). Moreover, in the 1930s he openly criticised the numbers given by Punnett on the generational reduction of mental defectives as a result of curtailing their reproduction and challenged the position taken by scientists critical of eugenics, for he sought their position as "a definite impediment both to racial progress and to the prevention of racial decay" (Darwin, 1931–1932).

Leonard's personal opinion on Pearson emerges from a letter he wrote to Fisher in 1920, soon after Pearson refused another of Fisher's papers for publication in Biometrika. In this letter Leonard stated:

> As someone said, one must no treat Pearson like anybody else. I think he means to be civil. But it is an astounding attitude to take up. To allow nothing to be published which does not back him up, or which he personally does not have time to read? & pitch into-it is going far.[43]

[42] In a letter dated 17th of May 1911 Leonard invited Pearson to become vice president of the congress. In a letter dated 25th of February 1911 Leonard invited Pearson to become a member of the EES council (UCL Pearson's archives. Ref: Pearson/11/1/4/17. Consulted February 2015).

[43] Letter from Darwin to Fisher dated 17th November 1928, cited in Bennett, 1983, p. 73. See also p. 118.

Regarding Leonard's eugenics leanings as a cause for the disregard and rejection by scientists of Leonard's scientific ideas, it has to be remembered that while many saw Mendelism as the necessary step to make eugenics scientific, other influential scientists such as Bateson, Haldane and others, openly refused to associate the knowledge that emanated from Mendelism with Eugenics. To this it did certainly not help that Leonard's writings gave primacy to the eugenic ideal over the status of scientific research (he questioned it on several occasions in his work)[44] and that was an act to be condemned by an influential group of biologists who were more seriously considering the role of the environment on human genetics and started to move, as Mazumdar defined it, away from class prejudice and towards the left (Mazumdar, 1992).

In addition to all the issues mentioned it is possible that Leonard Darwin was not recognised as a theorist of evolution because of his age and modesty. Concerning the first issue, it is important to recall that Leonard was 71 years old when he published *Organic Evolution* in 1921, and hence may have been considered too old to give scientific opinions, especially for the new generations of emerging experimentalists.

Regarding the second point, Leonard expressed his modesty on many occasions, modesty that was also noticed and highlighted many times by many people. Fisher-Box for instance commented in her autobiography on his father that Fisher highly appreciated Leonard's scientific perception as much as his lack of self-seeking (Fisher Box, 1978, p. 52). Furthermore, in Leonard's obituary, in *The Eugenics Review*, the president of the Eugenics society Lord Horder wrote:

> Through he used to say that he had never had any scientific education. I should say he had all the outlook of a scientist, and that he would have accomplished even more that he in fact did, if he had not been obsessed by a modesty as to his own abilities which often made him fear to tread where others were quite willing to rush out (Horder, 1943, p. 111).

To sum up, Leonard Darwin a non-formally trained scientist strove with scientific "allure" to tune the new hereditary science of Mendelism with both eugenics and the evolutionary theory that his father, alongside Wallace, put forward in 1859. His work proved essential in raising

[44] Despite this Leonard would have clear views about what it meant to practice science. In a letter to Fisher dated 22 August 1919 he stated, "You must not take your facts only when they fit your theories and neglect theoretical conclusions when facts are not available" (Bennett, 1983, p. 71).

the level of debate on scientific issues, chiefly among a eugenics audience, but also among scientists and the public in general, all at times when a part of his father's ideas were under intense scrutiny.

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