

Polemics and Synthesis: Ernst Mayr and Evolutionary Biology

Renee M Borges

A hundred years is but an instant in evolutionary time; however during his life that spanned a century, Ernst Mayr (1904-2005) made outstanding contributions to our understanding of the pattern and process of evolution. An ornithologist and systematist by training, Mayr embraced Darwinism and championed the cause of evolutionary biology throughout his long and highly productive career. Though best remembered for his proposal of the biological species concept, Mayr was also one of the architects involved in the evolutionary synthesis of the twentieth century that unified Darwin's ideas of evolution and Mendel's laws of heredity and brought together population geneticists and naturalists-systematists. This article is a tour through the shifting contours of the intellectual landscape of evolutionary thought during Mayr's lifetime. It will, however, be a selective tour because it will only highlight concepts and controversies that Mayr was either involved in, or those that are necessary to understand Mayr's contributions to the study of evolution and his interactions with other biologists.

The Conflict between Biometry, Darwinism and Mendelism

We begin the tour in the period 1900–1918. Although Mendel outlined his laws of heredity in the 1860s when he proposed that each hereditary trait is transmitted in the form of a discrete unit that he called “factor” (what we now call the gene), his ideas remained unknown until their re-discovery by Hugo de Vries, Carl Correns and Erich von Tschermak in 1900. This led to the rise of the Mendelians who recorded variation in discontinuous biological traits in populations, such as the colour of flowers or the shape of seeds, what in statistics would be known as categorical variables. At around that time also, the field of biometry was being developed in



Renee M Borges is an evolutionary biologist and behavioural ecologist with a strong interest in interactions between species. She studies mutualism and parasitism between plants and animals and the phenomenon of mimicry.

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the UK, mainly by Darwin's cousin Francis Galton and by Karl Pearson. As the name suggests, biometry is the measurement of biological traits in populations, and thus the examination of the distribution of the population variation in these traits. The biometricians naturally, were only able to measure traits that exhibited continuous variation in populations, viz. height, and were thus on a collision course with the Mendelians who recorded discontinuous traits. The biometricians did not believe that Mendel's laws of inheritance could be applied to continuous traits and thus they doubted the generality of Mendel's findings. Furthermore, Galton and Pearson appeared to be more concerned with developing descriptions of continuous variation using statistical tools such as regression, and the populations that they were examining were mostly human populations, although Galton had formed a Royal Society committee specifically for the measurements of plants and animals.

While the controversy between the Mendelians and the biometricians was on-going, there was concomitantly a rejection of Darwinism by important founders of Mendelism such as William Bateson, Hugo de Vries and Wilhelm Johannsen. This was because Darwinism at that time meant gradual evolution, as enunciated by Darwin: "nature does not make leaps". The Mendelians who were observing discontinuous traits seemed to think that nature did indeed make leaps, and this formed the basis of the rejection of evolution by gradual steps. It thus appeared as if Darwinism and Mendelism were incompatible. According to historian and philosopher of science Sahotra Sarkar, this conflict was resolved, though not entirely satisfactorily, by Sir Ronald Fisher, in an important paper in 1918. This paper dealt with similarities between related individuals. Fisher assumed that continuous traits were determined by a large number of Mendelian factors, which mostly acted independently of each other, expanding the scope of Mendel's original proposal. By doing so, Fisher reduced biometry to Mendelism and thus broke the impasse between Mendelism and Darwinism. Fisher's crucial assumption was empirically supported by

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work on *Drosophila* by researchers of the Morgan school who were also finding out at about that time that small variations could be caused by Mendelian factors. This meant that all biological traits could come under the purview of population genetics, which was a very important development.

The Synthesis Begins

Beginning in the 1920s, the classical genetics of Morgan was being integrated with disciplines such as cytology that deals with the study of cells and biochemistry. Morgan's *The Theory of the Gene* (1926) also played an important inter-disciplinary role in this process. More importantly, evolutionary biology was also being put on a strong theoretical foundation with the work of what has been called the "triumvirate" – a set of three individuals whose contributions were quite different yet extremely significant. Sir Ronald Fisher (1890-1962) believed that significant evolutionary change took place only in large populations, almost exclusively by natural selection on near-independent loci. He discussed this in his classic book *The Genetical Theory of Natural Selection* (1930). Sewall Wright (1889-1988) was more interested in the behaviour of genes in small populations, and stressed the importance of random genetic drift in such small populations, which could result in non-adapted genotypes. He also formulated his famous Shifting Balance Theory of evolution which essentially provided a powerful heuristic tool to conceptualise the movement of populations over a fitness landscape, from non-adapted valleys to more adapted peaks, a movement that could be brought about by a combination of mutation, migration and selection within and between populations. The third member of this select club was JBS Haldane (1892-1964) who, among many other issues, was concerned specifically with examining the time available for evolution by natural selection to occur given known mutation rates. In 1932 Haldane wrote *The Causes of Evolution* – one of the most important books on evolution for the intelligent layperson. *The Causes of Evolution* is an extremely valuable book, not only because it explains very lucidly the processes contributing to evolution, but in an Ap-

Related *Resonance* Special Issues

1. R.A. Fisher, Vol. 2, No.9, 1997.
2. J.B.S. Haldane, Vol. 3, No.12, 1998.
3. S. Wright, Vol. 4, No.12, 1999.
4. T. Dobzhansky, Vol.5, No.10, 2000.
5. T.H. Morgan, Vol. 8, No.11, 2003.



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pendix at the end of the book, it gathered together all the then known mathematical models of population genetics, providing a useful and scholarly source of reference. It was clear that Haldane's vision and concerns went much beyond the framework of population genetics and included all of evolution.

It is often believed that the work of the Haldane-Fisher-Wright troika was what was largely responsible for initiating the Modern Evolutionary Synthesis; however, the contributions of non-Anglo-US researchers should not be forgotten. Ernst Mayr and Theodosius Dobzhansky were particularly careful later on to highlight the efforts of Russian naturalist-geneticists who, for example, studied variation in natural populations of *Drosophila*. Thus, they believed that the triumvirate should be extended to a quadrumvirate by the inclusion of Sergei Chetverikov (1880-1959) who proposed that mutations are not necessarily deleterious and that natural populations are a storehouse of mutations on which natural selection can act. Chetverikov's student Timofeeff-Ressovksy went on to found a vibrant school of genetics in Germany.

The Modern Evolutionary Synthesis

In spite of the substantial progress made by the population geneticists in bringing together Darwinian ideas and Mendelian genetics, important issues of evolution such as speciation remained unaddressed. Beginning in the 1930s, the Jesup lecture series at Columbia University was influential in focusing the efforts of key scientists who played an important role in professionalising evolutionary biology. These scientists and the books which resulted from their lectures in the series in America were Theodosius Dobzhansky: *Genetics and the Origin of Species* (1937); Ernst Mayr: *Systematics and the Origin of Species from the viewpoint of a zoologist* (1942); George Gaylord Simpson: *Tempo and Mode in Evolution* (1944) and G Ledyard Stebbins: *Variation and Evolution in Plants* (1950). Julian Huxley (the grandson of T H Huxley) in England also played an extremely important role in this process in three ways. Firstly, in 1930 he co-authored a



book entitled *The Science of Life* along with H G Wells and his son G P Wells. This book was a sequel to H G Well's earlier book *The Outline of History*, the same book which had earlier caused much controversy because of its materialistic perspective. Secondly, in 1940, Huxley edited an important book entitled *The New Systematics* in which he emphasized the importance of plant and animal classification. Thirdly, in 1942, he wrote *Evolution: The Modern Synthesis*, which was where, for the first time, he used the term "Modern Synthesis" for the process that was occurring among the evolutionary biologists wherein conflicts between geneticists and naturalist-systematists were being resolved.

It is beyond the scope of this article to summarise the content of all these books. Since our focus is on Ernst Mayr, I will summarise the central idea of his 1942 book and thus of Mayr's intellectual contribution at that time. Although the title seems quite innocuous, Mayr's 1942 book is a powerful statement, as was Huxley's, in the cause of protecting the intellectual status of systematics as well as of systematists. It makes the point that, although Darwin's 1859 opus was called *On the Origin of Species*, Darwin himself did not have a species concept and neither adequately defined a species nor the process of species formation. For example, in 1859 Darwin said: *In determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgment and wide experience seems the only guide to follow.* And: *[T]he only distinction between species and well-marked varieties is that the latter are known or believed to be connected at the present day by intermediate forms, whereas species were formerly thus connected.* In his book, Mayr set out both to define a species as well as to bring together known mechanisms of speciation. The species concept that appealed most to Mayr was that of the biological species wherein species are defined as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups". The process of speciation that Mayr thought was most plausible was that of allopatric speciation wherein a once continuous

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What Mayr achieved in his remarkable *Systematics and the Origin of Species from the viewpoint of a zoologist* was a synthesis of thought on species concepts and therefore not much original work itself. He brought his vast experience on bird systematics to bear on the field of systematics and was able to successfully couple it with the various species concepts available at that time.

population of a species may become split into two or more geographically isolated populations; these isolated populations may achieve reproductive isolation in allopatry such that when they later meet in sympatry, they are already separate species incapable of interbreeding. It is important to remember, however, that these ideas of sympatric and allopatric species, of the biological species concept, as well as of reproductive isolating mechanisms had already been articulated by the lepidopterist E B Poulton in papers that date back to 1904. What Mayr achieved in his remarkable *Systematics and the Origin of Species from the viewpoint of a zoologist* was a synthesis of thought on species concepts and therefore not much original work itself. He brought his vast experience on bird systematics to bear on the field of systematics and was able to successfully couple it with the various species concepts available at that time. Perhaps one original contribution of Mayr in this regard was a 1954 paper in which he proposed peripatric speciation. Mayr claims that in this paper he was the first to develop a detailed model of the connection between speciation, evolutionary rates and macro-evolution. The 1954 paper was also apparently his favourite paper. In this paper, he proposed that founders from peripheral parts of the population of a species could, if isolated for a sufficiently long time, form separate species. However, the rate of evolution and probability of speciation in such peripheral isolates would also be determined by the size of the founding population.

With the inception of these ideas, the main features of the evolutionary synthesis thus came to be established. These were firstly that gradual evolution (Darwinian evolution) could be explained by mutations and recombination; secondly that natural selection was an important force that could influence the pattern of genetic variation, and thirdly that macro-evolutionary processes, i.e. speciation, could be explained by known genetic mechanisms. Ernst Mayr was certainly an important contributor to the synthesis, and one of its principal architects, and in an edited volume in 1980 entitled *The Evolutionary*



Synthesis: Perspectives on the Unification of Biology, he had this to say about the intellectual process that was taking place during this period: *When I read what was written by both sides [experimental geneticists and population-naturalists] during the 1920s, I am appalled at the misunderstandings, the hostility, and the intolerance of the opponents.....Just as in the case of warring nations, intermediaries were needed..... These bridge builders were the real architects of the synthesis. What qualifications did an evolutionist require to be able to serve as a bridge builder?.....None of the bridge builders was a narrow specialist. They all had, so to speak, a foot in several camps.*

Ernst Mayr and the Controversy over Beanbag Genetics

Another major controversy that Mayr was involved in was on the importance of “classical” population genetics. Beginning in the 1950s, there appeared to be a disenchantment with the contributions of the population genetics troika of Fisher–Wright–Haldane, and their relevance to “real” evolution, viz. evolution as observed in nature. This disenchantment was largely the result of a conflict between experimental biologists, naturalists-systematists and theoreticians. In the 1955 Cold Spring Harbor Symposium Session on Integration of Genotypes, Mayr said: *The study of the integration of genotypes has shown that population genetics can no longer operate with the simplified concepts it started out with.* In this Symposium, Mayr spoke strongly of the limitations of theoretical population genetics and praised the contributions of field naturalists who were doing the “real” biology. In 1959, Mayr gave a plenary talk at the Cold Spring Harbor Symposium organized on the occasion of the celebration of 100 years after the publication of Darwin’s *Origin of Species*. In his address entitled “*Where are we?*”, Mayr seemed to be saying that theoretical population genetics, especially of the “classical” kind could go only so far and no more. He portrayed the work of Haldane, Fisher and Wright as *..one of gross simplification. Evolutionary change was essentially presented as an input or output of genes as in the adding certain beans to a beanbag and the withdrawing of*

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others. In the proceedings of the meeting he wrote: *Fisher, Haldane and Wright have worked out an impressive mathematical theory of genetical variation and evolutionary change. But, what precisely, has been the contribution of this mathematical school to evolutionary theory, if I may be permitted to ask such a provocative question?*” Later, in his 1963 classic *Animal Species and Evolution*, he brought back the “beanbag” argument once again: *“The Mendelian was apt to compare the genetic contents of a population to a bag full of colored beans. Mutation was the exchange of one kind of bean for another. By terming it “beanbag genetics”, he appeared to be disparaging it and attempting to elevate the genetics practiced by individuals such as Dobzhansky to a higher, more relevant status compared to that of the classicists.*

In Defense of Beanbag Genetics

It was inconceivable that Mayr’s remarks about beanbag genetics would remain unanswered. Wright reviewed the Symposium volume that resulted from this Darwin Centennial at Cold Spring Harbor for the *American Journal of Human Genetics*, and spent almost the entire review criticizing Mayr’s comments on beanbag geneticists. In this review, Wright, however, praised Dobzhansky as one who seemed to have truly understood the value of interaction between empiricism and theory. By this time, Haldane was in India and missed the 1959 Cold Spring Harbor Symposium as he was denied a visa to the US owing to his Communist beliefs (a relic of the McCarthy era that saw the persecution of those who were seen as anti-nationals). He had read Mayr’s remarks about beanbag genetics in the 1963 book which he was reviewing for the *Journal of Genetics*. In 1964 Haldane wrote his celebrated paper entitled *A Defense of Beanbag Genetics* that appeared in *Perspectives in Biology and Medicine*. This classic paper is essential reading for students of evolution because in it Haldane proceeds to demolish the opposition, with characteristic wit and satire. I reproduce a few extracts from this paper to provide a flavour of Haldane’s counter-attack: *Of course, Mayr is correct in stating that beanbag genetics do not explain*

the physiological interaction of genes and the interaction of genotype and environment. If they did so they would not be a branch of biology. They would be biology.....

In my opinion, beanbag genetics, so far from being obsolete, has hardly begun its triumphant career.....I have retired to a one-storied "ivory tower" provided for me by the Government of Orissa in this earthly paradise of Bhubaneswar and hope to devote my remaining years largely to beanbag genetics. Haldane passed away in 1964, the year his defense of beanbag genetics was published.

What might one make of all of this polemic? Did Mayr truly believe that population genetics was not terribly useful in the progress of evolutionary thought? Perhaps this quote from Mayr's book *The Growth of Biological Thought* may provide some insight: *My tactic is to make sweeping categorical statements. Whether or not this is a fault, in the free world of the interchange of scientific ideas, is debatable. My own feeling is that it leads more quickly to the ultimate solution of scientific problems than a cautious sitting on the fence.....histories should even be polemical. Such histories will arouse contradiction and they will challenge the reader to come up with a refutation. By a dialectical process this will speed up a synthesis of perspective.* In a sense, he was being deliberately provocative to initiate debate on such central issues of evolutionary biology.

Ernst Mayr and the Defense of Organismal Biology

Mayr played another important role in evolutionary biology and that was in the defense of organismal biology. After the discovery of the structure of DNA in 1953, the 1950s and 1960s saw the rise of molecular biology. With the arrival of James Watson as a member of the Harvard faculty in 1956, the organismal or the non-molecular biologists were, in the words of E O Wilson "forced by the threat [of molecular biology] to rethink our intellectual legitimacy". Statements such as "all biology is molecular" made by the Nobel laureate and biochemist George Wald, seemed to reinforce the view that organismal biology was being perceived as not keeping up with the Watsons. Mayr, Dobzhansky and Simpson began a counterattack on molecular

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biology. They attempted to do so by speaking out for organismal biology at various forums and also by writing in important journals such as *Science*. Mayr wrote an impassioned piece in *Science* in 1961 entitled *Cause and effect in biology. Kinds of causes, predictability, and teleology are viewed by a practicing biologist*, in which he defined the difference between proximate and ultimate causation in biology. Molecular biology may provide, for example, a proximate cause for biological phenomena, however the ultimate and most important causation was provided by natural selection. In a similar vein, Dobzhansky wrote about Cartesian versus Darwinian science, with Cartesian science being the mechanistic aspect of a science like biology while the Darwinian approach to science provided the *vera causa*. Simpson also followed with a paper in a similar vein. The central goal of Mayr, Dobzhansky and Simpson was to establish that organismal biology was unique and autonomous since it was neither deducible from nor reducible to molecular biology. Dobzhansky well known saying: *Nothing makes sense in biology except in the light of evolution*, appeared in his paper entitled *Biology, Molecular and Organismic* in the *American Zoologist* in 1964. According to the philosopher and historian of science Michael Ruse (in an online eulogy of Ernst Mayr, 5 Feb 2005): *When Dobzhansky said that nothing in biology makes sense except in the light of evolution, he was not just making an epistemological claim; he was making a political statement – a war cry to rally the troops.*

Mayr attempted to do even more. In 1963, he wrote an editorial in the journal *Science*, entitled *The New versus the Classical in Science*. I provide some quotes from this paper to illustrate the tone and the type of points he was making; furthermore, although he was attacking molecular biology, the word molecular biology itself did not appear; yet all who read the paper knew the target of Mayr's attack. *There long has been a bandwagon tendency in American science, but today it seems particularly rampant.... In addition, there is an inclination to equate "classical" with "old-fashioned" and passé"..... the new should supplement the classical and not totally displace it.*



Dobzhansky and Mayr were also having difficulty reconciling new findings which seemed to indicate that the rate of change of molecules was much higher than the rate of change of morphology. Furthermore, the rate of evolution at the molecular level seemed to be constant, e.g. the work of Linus Pauling and Emile Zuckerkandl on haemoglobin and sickle cell anaemia was revealing that the rate of amino acid change in primates was constant. This disjunction between molecules and morphology was hard to explain.

Ernst Mayr and Neutral Evolution

The paradox between molecular and morphological evolution was resolved by the brilliant insight of Motoo Kimura as well as by King and Jukes who declared that “non-Darwinian” evolution took place at the molecular level. By this was meant that, neutral substitutions or neutral mutations could occur at the molecular level. These had no impact on the functionality, for example, of the protein in whose gene the mutations occurred. This could happen, for instance, by mutations occurring in non-coding sites of the gene or in non-functional parts of the protein. Kimura formalized these ideas in the Neutral Theory of Evolution in 1968 and this theory has been hailed as one of the most important insights on evolution at the molecular level that the 20th century had seen. According to Zuckerkandl, Mayr, Dobzhansky, and Simpson were more “irritated” by molecular biologists than by molecular evolution. They were trying to forge a secure relationship between organismal biology and molecular biology such that the two could be successfully integrated. Central to this position was the issue of natural selection: on what did natural selection act – the gene or the organism? According to these three advocates, natural selection acted only on the organismal level. The issue of levels of selection and of reductionism in biology is still an important topic of debate in biology. It is therefore interesting that even today, many decades after Mayr’s initial advocacy, biologists still feel compelled to write papers entitled “The return of the whole organism”.

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On the matter of neutral evolution Mayr was still extremely ambivalent and in his 1971 book *Populations, Species, and Evolution*, he had this to say: *A random replacement of amino acids unquestionably occurs occasionally in evolution, but it appears at present that it does not anywhere near approach selection in importance as an evolutionary factor.* In his opinion, chance causes disorder, while selection causes order. The evolutionary biologist Mark Ridley has remarked that in an essay Mayr wrote in 2004 in *Science* on the occasion of his 100th birthday, he summarized the importance of the neutral theory of evolution by failing to mention it. In this essay entitled *80 years of watching the evolutionary scenery*, Mayr goes on to say: *It would seem justified to assert that, so far, no revision of the Darwinian paradigm has become necessary as a consequence of the spectacular discoveries of molecular biology*

Summary

Mayr has justifiably earned for himself the title “Darwin of the 20th century”. He declared himself Darwin’s champion, and was particularly wont to point out that a most important consequence of the Darwinian revolution was the destruction of typological thinking. Mayr also repeatedly stressed that there were important differences between Darwinism and contemporary theories of evolution. Evolution as conceived by Darwin was not goal-directed, while contemporary theories were orthogenetic or aristogenetic in the sense that they believed in a pre-determined progression of lower to higher forms. Furthermore, by focusing on individuals, Darwin destroyed the tyranny of typological thinking, which was a left over from the essentialism of Plato, who believed that groups of organisms were constructed according to certain homogeneities. By attacking the concept of essentialism, Darwin provided a mechanism by which individuals became both a focus and an essential ingredient in the evolutionary process. This was a paradigm shift and according to Mayr, a conceptual leap that constituted a true scientific revolution. Mayr’s zeal in defending Darwin and in protecting



organismal biology and evolution from the “non-believers” has formed the subject of this entire article, but it can also be seen in the titles of some of his recent books, e.g. *One Long Argument. Charles Darwin and the Genesis of Modern Evolutionary Thought* (1991), *This is Biology – the Science of the Living World* (1997), and *What Evolution Is* (2002).

On the occasion of Mayr’s 90th birthday, Douglas Futuyma wrote in the journal *Evolution* in a special section to honour Mayr: *He may be given to categorical assertions that provoke or irritate; he may fight battles we suppose were long since won, but which we can hardly appreciate (because he helped to win them for us); his interpretations of genetic theory and evidence are sometimes questionable; and no one will agree with all his positions, analyses, and opinions. But that his style demands counterargument is itself one of the reasons to read him.... Anyone who has failed to read Mayr can hardly claim to be educated in evolutionary biology.*

Suggested Reading

- [1] J B S Haldane, *The Causes of Evolution*, Longmans, Green & Co. Ltd., London, 1932.
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Address for Correspondence

Renee M Borges
Centre for Ecological
Sciences
Indian Institute of Science
Bangalore 560 012, India.
Email: renee@ces.iisc.ernet.in

