

Commentary

In memoriam: Ernst Mayr (1904–2005)

Ernst Mayr's death at the age of 100 earlier this year (3 January 2005) has left a void that will not easily be filled. Not only was Mayr one of the great evolutionary biologists and naturalists of the last century, his breadth and erudition in the history of biology had few equals among his peers. By founding the journal *Evolution*, he was instrumental in establishing evolution as a professional sub-discipline within biology in the United States. His efforts were critical in preventing evolutionary biology from being entirely cast aside by the new molecular biology of the late 1950s and 1960s. His paper, "Cause and Effect in Biology" (Mayr 1961), often regarded as the source of the distinction between proximate and ultimate causes in biology (especially by those unaware of the ancient Greek tradition connected to Aristotle), was intended as an attempt to establish a domain for organismic, especially evolutionary, biology on which molecular biology, in principle, could not encroach. Molecular biology studied only proximate causes; if we want ultimate causes, Mayr argued, we must turn to evolution by natural selection. The rhetoric was impeccable: surely, the best science is about ultimate causes, not merely proximate ones? The causes of evolution must therefore be more important than the proximate mechanisms of molecular biology. It was an astute move in a political struggle for prestige and research funds.

Interestingly, Mayr's paper was also one of the two papers published in 1961 that independently introduced the idea of a genetic program for development. The other contained Jacob and Monod's (1961) proposal of the operon. Mayr was thus the first prominent evolutionary biologist to endorse the informational interpretation of genetics which molecular biologists had been formulating during the previous five years [Williams' (1966) influential advocacy came five years later]. Mayr remained true to this interpretation until his death. It served him well, allowing him to embrace molecular genetics while denying that physics was having any success in explaining biology. Information, for Mayr, was accumulated through natural selection – informational laws were thus laws of evolutionary biology, not physics. Natural selection was the programmer; the molecules merely executed the program.

I almost always disagreed with Mayr's positions, both within biology and in the history and philosophy of the field. Given that, it is telling that it is so easy for me to write an appreciation such as this. Mayr was vehemently opposed to mathematical evolutionary theory [see, e.g. Mayr (1963)]; my view has been that it is central to understanding evolution (Sarkar 2004). Mayr equally strongly opposed molecular reductionism, clinging on to a nineteenth-century claim of the autonomy of biology from the physical sciences (Mayr 1982); I have always defended molecular reductionism (Sarkar 1998). Mayr (1983) endorsed adaptationism; I was convinced that it is useless (Sarkar 2005). The ease with which I compose this appreciation is a mark of how unfailingly courteous and helpful Mayr was to younger scholars, especially in his later years. Moreover, he was one of the few biologists of his generation who appreciated the philosophy of biology. At a time when most philosophers of biology were skeptical of the viability of a new journal, Mayr encouraged Michael Ruse to establish *Biology and Philosophy*. Today it is hard to imagine the field without that journal. Mayr (1988) also dabbled in the philosophy of biology himself but his contributions there were of little value and are unlikely to contribute anything significant to his legacy – the positions he advocated, for instance, anti-reductionism and a distinction between functional and mechanistic explanation, had long been analysed by philosophers with far greater depth and precision.

In the early 1990s, when I lived in Boston, some of my most memorable afternoons were spent with Mayr when he took me to lunch to talk about where evolutionary biology was going. He also spoke of the birds, books, and places he had loved. But evolution was always his greatest interest. Sometimes, it was difficult to remember that he had started his career as one of the most promising field

ornithologists of his generation, going on collecting expeditions to New Guinea and the Solomon Islands. At the very first such lunch, at the Harvard Club – made even more pleasurable by seeing Mayr tell the anti-naturalist analytic philosopher, Hilary Putnam, that a good Philosophy Department was impossible without a philosopher of biology – I found out that he and I had one point of agreement: we both felt that the organization of the genome was the next great challenge for evolutionary explanation. Why, Mayr asked, do horses have more chromosomes than humans? We still do not know. But every time a serious disagreement emerged in conversation I found a way to talk about genome evolution. The disagreement always receded to the background; this ploy made for a pleasant relationship. When I gave a talk on frequency-dependent selection in Lewontin's laboratory at Harvard in 1993, my prestige was considerably enhanced by Mayr's coming to listen to it. He must have been disappointed. It was an excruciatingly mathematical talk with no earthshaking implication (Lachmann-Tarkhanov and Sarkar 1994). But Mayr remained courteous; at least he did not say anything.

Mayr was invariably forthright about his views. Natural history was the central part of evolutionary biology. John Maynard Smith was the best evolutionary biologist in Britain. But, other than that, British evolutionary biology was just not very good. Like Maynard Smith, Mayr endorsed adaptationism though he saw little of value in the numerical calculations of evolutionary game theory. David Hull was the first philosopher of biology, and remained the best. Bill Wimsatt had been the great hope but he had switched to development. No one else had come close. Young philosophers of biology should begin by studying Darwin and Mayr. No, he did not think much of Bob Richards's *The Meaning of Evolution* (Richards 1992) which was then competing for attention with his own *One Long Argument* (Mayr 1991).

Mayr had few good things to say about the Indian ornithologist, Salim Ali, whom he had first encountered in Stresemann's laboratory during his graduate student days and had later met in New York. Mayr had not been impressed. Many of a younger generation of Indians – including me – who were inspired by natural history had subsequently entered the field of biodiversity conservation partly because of Ali's influence. But I had to concede to Mayr that, beyond classification, there was scanty science in Ali's corpus. We should note that Salim Ali was equally unimpressed by Mayr. In his autobiography, Ali (1985, p. 60) recalled their interactions: "Ernst Mayr is currently . . . undisputably [*sic*] among the topmost biologists of the world. . . . Unfortunately – in marked contrast to his mentor Stresemann's unassuming modesty – Mayr makes you feel he is not unaware of the fact". Ali is not the only one to note Mayr's immodesty. It was legendary. Some passages of *The Growth of Biological Thought* read as if the theory of evolution came to be empirically proven purely because of Mayr's work.

Mayr and I also agreed on another point on which perhaps no other biologist, historian, or philosopher of biology agreed with us. We both felt that, of the holy trinity of evolutionary genetics, Fisher, Haldane, and Wright, Haldane was the most important. For me, this was because of an interpretation of Haldane's *Causes of Evolution* as the first truly synthetic work in 20th-century evolutionary biology (Sarkar 2004). Mayr liked the book but doubted its influence – according to him, it was unavailable in most libraries in the United States in the 1930s and 1940s (Mayr 1992). For Mayr, Haldane was simply the only good biologist among the three. (Fisher and Wright, supposedly, did not understand biology.) Mayr's fondness for Haldane was somewhat puzzling given that his greatest bias – and failing – was to appreciate the significance for evolutionary biology of the theoretical population genetics of the 1920s and early 1930s. But the fondness was genuine. He visited Haldane in Kolkata in 1959 and they went birdwatching in Orissa. Haldane's wife, Helen Spurway, was apparently infatuated with Mayr, much to Haldane's (and Mayr's wife's) amusement. Haldane actively encouraged the infatuation. Some forty years later, the episode still embarrassed Mayr. (Because I was working on a scientific biography of Haldane at the time, Mayr produced for me a four-page typescript of his encounters with Haldane – it remains one of my more cherished possessions.)

Future historians will have to grapple with the reasons for Mayr's myopia about mathematical population genetics. He once told me that the only contribution that the mathematical theory had made was to show that evolution by natural selection could take place in the time available for it during the history of life on Earth. Interestingly, this was also the question that motivated Haldane to enter evolutionary biology (Sarkar 2004); and it may also account for Mayr's preference for Haldane

over Fisher and Wright. But, according to Mayr, that task had already been achieved in H T J Norton's table published in 1915 in Punnett's *Mimicry in Butterflies* (Punnett 1915). The subsequent work of Haldane, Fisher, and Wright was, therefore, irrelevant. He kept returning to this point. For him, it sufficed as a response to any defense of mathematical evolutionary theory.

Within evolutionary biology, Mayr will probably be remembered most for the dogmatism with which he argued for the role he ascribed to allopatry in speciation and the so-called biological species concept (Mayr 1942). His ultimate reputation will rest on whether allopatry is the only mode of speciation, as he argued; recent developments have not been in his favour (Coyne and Orr 2004). But even in the context of allopatry, Mayr did not adequately acknowledge the earlier contributions of Wright and others who had also recognized that geographic isolation may be critical for speciation and macroevolution. In general, Mayr's treatment of Wright was less than charitable. In the 1970s he organized two major conferences on the history of the evolutionary synthesis. Fisher and Haldane were dead, but Wright, still alive, was invited to neither. The proceedings were eventually published as *The Evolutionary Synthesis*, edited by Mayr and Provine (1980). There is no contribution from Wright.

Mayr's often-expressed skepticism about mathematical population genetics produced one good effect. It provoked Haldane to deliver his justly celebrated lecture, "A Defense of Beanbag Genetics" [subsequently published as Haldane (1964)], in which he accused Mayr of not following the mathematical arguments of Wright, Fisher, and himself. For those who have no metaphysical bias against reductionism, Haldane's paper remains a methodological classic. Many years later, when Warren Ewens (1993), also a theoretical population geneticist, questioned some of Haldane's arguments (during a celebration of the latter's centenary), Mayr was ecstatic. He happily presented me with a reprint of Ewens's paper and was delighted that Ewens had already sent me several copies, to be shared with my students. For Mayr, the theoretical population geneticists were finally coming around to his perspective, although this was hardly what Ewens had intended.

Mayr's views on evolution – the science, as well as its history – will lurk in the background of much of our work for decades to come. We will probably emerge from it only when we have a theory of evolution that is fully developmental and molecular. But that is exactly what Mayr wanted. Such a full biology will allow the exploration of evolution in phenotypic space while incorporating the molecular processes of heredity. According to Mayr, it will both show exactly how reductionism falls short, and how natural selection molds both form and behaviour of organisms. If we ever get such an account, I predict that Mayr will be shown to be wrong. Unfortunately, he is no longer around to respond.

References

- Ali S 1985 *The fall of a sparrow* (New Delhi: Oxford University Press)
 Coyne J A and Orr H A 2004 *Speciation* (Sunderland, MA: Sinauer Associates)
 Ewens W J 1993 Beanbag genetics and after; in *Human population genetics* (ed.) P P Majumder (New York: Plenum) pp 7–29
 Haldane J B S 1964 A Defense of Beanbag Genetics; *Persp. Biol. Med.* **7** 343–359
 Jacob F and Monod J 1961 Genetic Regulatory Mechanisms in the Synthesis of Proteins; *J. Mol. Biol.* **3** 318–356
 Lachmann-Tarkhanov M and Sarkar S 1994 The Alternative Fitness Sets Which Preserve Allele Trajectories: A General Treatment; *Genetics* **138** 1323–1330
 Mayr E 1942 *Systematics and the origin of species* (New York: Columbia University Press)
 Mayr E 1961 Cause and effect in biology; *Science* **134** 1501–1506
 Mayr E 1963 *Animal species and evolution* (Cambridge, MA: Harvard University Press)
 Mayr E 1982 *The growth of biological thought* (Cambridge, MA: Harvard University Press)
 Mayr E 1983 How to Carry Out the Adaptationist Program; *Am. Nat.* **121** 324–334
 Mayr E 1988 *Towards a new philosophy of biology* (Cambridge, MA: Harvard University Press)
 Mayr E 1991 *One long argument* (Cambridge, MA: Harvard University Press)
 Mayr E 1992 Haldane's *Causes of Evolution* 60 Years Later; *Q. Rev. Biol.* **67** 175–186
 Mayr E and Provine W B (eds) 1980 *The evolutionary synthesis* (Cambridge, MA: Harvard University Press)
 Punnett R C 1915 *Mimicry in butterflies* (Cambridge: Cambridge University Press)
 Richards R J 1992 *The meaning of evolution* (Chicago: University of Chicago Press)
 Sarkar S 2004 Evolutionary Theory in the 1920s: The Nature of the Synthesis; *Philos. Sci.* **71** 1215–1226

Sarkar S 1998 *Genetics and reductionism* (New York: Cambridge University)
Sarkar S 2005 Maynard Smith, Optimization, and Adaptation; *Philos. Sci.* **72** (in press)
Williams G C 1966 *Adaptation and natural selection* (Princeton: Princeton University Press)

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