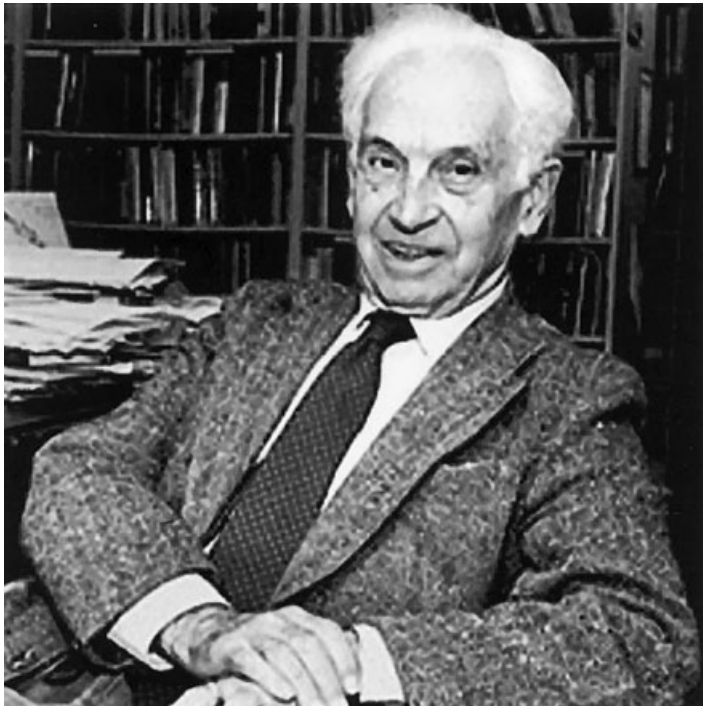


Ernst Mayr, 1904–2005



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Ernst Mayr, the pre-eminent evolutionary biologist of the twentieth century, died on February 3, 2005 at the age of 100 (Fig. 1). Although trained principally as an ornithologist, Mayr's work and ideas came to affect, if not dominate, nearly all aspects of evolutionary studies, including evolutionary anthropology.

Mayr emigrated to the United States from Germany in 1931, and took up a post at the American Museum of Natural History the following year. He left that museum in 1953 to

become Alexander Agassiz Professor at the Museum of Comparative Zoology at Harvard, from which he retired in 1975. He remained active, indeed highly prolific, through his retirement, having produced close to 700 publications at the time of his death.

As one of the main architects of "the synthetic theory of evolution,"¹ Mayr could have enjoyed a solid reputation for his contributions just to avian biology and evolutionary theory. Nevertheless, he must also be credited with almost singlehandedly starting the study of the philosophy of biology, and for developing the study of the history of biology. He was very much a radical in these fields: The philosophy and history of science existed in the early twentieth century, but was dominated by the study of physics. As

seen through the eyes of physics, biology, and especially evolutionary biology, was an inferior kind of science, if a science at all. Mayr argued that with different phenomenologies and different epistemologies, biology was not inferior to physics; it was different from, not comparable to, physics.²

Some of Mayr's philosophical explorations remain the best words on the subject, such as his discussions of causality and teleology. Many of these explorations were collected in his 1988 book *Toward a New Philosophy of Biology*, and generally focus on the differing uses of terms and concepts in different sciences, in particular biology and physics, often highlighting the particular difficulties of finding physics-like laws when dealing with living systems.³

Mayr's early radically relativistic position would permit the growth of a scholarly discipline concerned with position of biology in science and the complex nature of science itself. Although commonly grouped with the synthetic theorists Sewall Wright, Ronald Fisher, J. B. S. Haldane, and Theodosius Dobzhansky, Mayr in fact found the reductive approach of population genetics repugnant, and argued strenuously against reductionism in biology. While the anti-reductive position in biology is widely associated with the later Marxist critique, Mayr was its first and strongest champion, and is most responsible for the blossoming of "organismal biology" as an academic field to contrast with the genetic or molecular biology that came to dominate biology departments.

Although Mayr wrote a few papers about anthropological topics, he relied mostly on derivative information and consequently showed little originality or insight into particularly anthropological matters. His influential 1951 Cold Spring Harbor paper,

which took a “lumper” view of hominid systematics,⁴ actually articulated a position that had already been laid out by others. (Weidenreich had lumped *Pithecanthropus* into *Homo* and Simpson,⁵ in 1945, had articulated the case for lumping all fossil hominids into *Homo*.) Mayr’s 1962 review of Carleton Coon’s *The Origin of Races* in *Science* praised the book for the brilliant synthesis that it is,⁶ although he utterly failed to connect it to the segregationists. They were invoking the book as a scientific manifesto for their side with the author’s silent blessing, an issue that Dobzhansky and the anthropologists saw very clearly.

Mayr’s lasting contribution to evolutionary anthropology will certainly be of a more general form, clearing the intellectual landscape for the construction of an evolutionary theory to explain the emergence of human beings. His persuasive and insightful contributions to various aspects of that theory are consequently worth recapitulating.

SPECIES

Although the interbreeding criterion was used by Buffon in the eighteenth century, Mayr formalized the most widely accepted definition of species as “groups of actually or potentially interbreeding populations, reproductively isolated from other such groups,” which he called the “biological species concept,” familiar even as its acronym, BSC.⁷ By the end of his life he had jettisoned the “actually or potentially” part, but it is not clear that he fully grasped its major problem. The BSC only tells us what a species is *not*, by zooming in on its boundary, but fails to address what a species *is*—namely, organisms that recognize one another as either potential mates or competitors for mates. The BSC focuses on what species cannot do (that is, reproduce outside the limits of the gene pool); but Patterson’s “recognition concept” shifts the emphasis to the self-perception of organisms as being parts of the same reproductive community.⁸ This also shifts the study of speciation from the development of “isolating mechanisms” (keeping animals apart) to the development of “specific mate recog-

nition systems” (keeping animals together). Moreover, as Ledyard Stebbins was quick to point out, Mayr’s BSC is highly “zoöcentric,” for plants are quite profligate outside the limits of recognized species.

When Michael Ghiselin and David Hull suggested a “radical solution to the species problem,” that species should be philosophically considered as individuals (temporally and spatially bounded, and capable of reproduction and interaction) rather than as classes or sets (organisms possessing a common property),^{9,10} Mayr appreciated the compatibility of this view with his own and accepted the role of godfather of the idea.¹¹ As a set or class, a species cannot evolve, it can only be redefined; as an individual, a natural unit, a species assumes emergent properties irreducible to the properties shared by its constituent organisms.

SPECIATION

In 1942, Mayr promoted the role of geography in cladogenesis, putting evolutionary theory in three dimensions—one or two more than the population geneticists of the 1930s had been playing with. (His long-time paleontologist colleague, George Gaylord Simpson, receives credit for adding the fourth dimension, deep time.) Mayr, inspired by Dobzhansky’s (1937) *Genetics and the Origin of Species*, entitled his book, in homage to both Darwin and Dobzhansky, *Systematics and the Origin of Species*. The problem was his classification of speciation modes into allopatric and sympatric; after establishing that nearly all speciation occurs allopatrically, what good is a classification that differentiates speciation modes by geography? A more informative classification would use a more varying criterion, such as genetic mechanisms.¹² Mayr also appropriated Sewall Wright’s idea of genetic drift as a potent microevolutionary force and transformed it into a macroevolutionary force, in contrast to Wright’s own view of it.

SYSTEMATICS

In 1969, Mayr fended off the challenge of numerical taxonomy,¹³ argu-

ing that it denied the biological reality of species, explored difference at the expense of phylogeny, and placed too much faith in naïve inductivism as a source of knowledge.¹⁴ No sooner had numerical taxonomy been beaten down than Mayr was faced with the challenge of “cladistics” (his own coinage). Proponents of this school still didn’t play with species; their phylogenetic species concept, which focused on the emergence of derived features, failed to differentiate between species and other taxonomic levels. Moreover, they now placed too much emphasis on phylogenetic branching sequence, to the extent of deliberately ignoring divergence.¹⁵ Mayr felt that phylogeny, as biological history, had two equally important aspects, branching sequence and adaptive change. Mayr certainly underappreciated the role that quantitative techniques would come to play in systematics, especially molecular systematics, and the merit that the rigorous methodology of cladistics offered. However, his argument that phylogeny has a dual nature, descent and divergence, and that a systematic philosophy focusing exclusively on one of them is unnecessarily restrictive, remains powerful.

TEMPO AND MODE

Although Eldredge claimed from the outset that the notion of punctuated equilibria was an outgrowth of Mayr’s own ideas on speciation, Mayr felt very threatened by the interest generated by Eldredge and Gould’s work in the 1980s. While they credited the theory of punctuated equilibria to Mayr’s ecological and Simpson’s (especially 1944) paleontological research into the role of speciation in evolution, it was clear that they were conceptualizing “the big picture” rather differently.¹⁶ In the hands of Eldredge and Gould, species were fundamentally stable units through deep time; speciation was not adaptive *per se*, but represented a morphological shift in a random direction in a paleontological instant. Gould confused the issue by resurrecting the work of Richard Goldschmidt, a geneticist who had promoted a saltational (single-generation) model of speciation in the 1930s. This was not an outgrowth

of Mayr's work on speciation or evolution at all. By the 1950s the major "synthetic theorists" had worked hard to bury saltational ideas of evolution and marginalize their advocates. Tying punctuated equilibria to saltational genetic models was unnecessary in the 1980s, given the difference in scope of paleontological time versus genetic time. Mayr was, self-consciously like Darwin, committed to the proposition that "nature does not make leaps."

HISTORIOGRAPHY

Mayr especially did not like the history of evolutionary theory in the twentieth century as Gould and Eldredge were writing it, emphasizing the failings of evolutionary theory before they arrived.¹⁷ Mayr preferred to write the history of evolutionary theory himself, emphasizing the failings of evolutionary theory before *he* arrived. His magisterial survey, *The Growth of Biological Thought* (1982), was structured in just that way, so that when his old friend George Gaylord Simpson was asked to review it for *Evolution*, Simpson couldn't help but observe that Mayr was using the grand scope of the history of biology as essentially a backdrop for what was really the story of his own career. Simpson titled the review "auto-biology."

ANTI-REDUCTIONISM

Mayr coined the term "beanbag genetics" in 1959 to characterize the

reductive approach of population genetics to evolutionary biology,¹⁸ engendering a fierce rebuttal from J. B. S. Haldane.¹⁹ Nevertheless he still employed a reductive minimal definition of evolution as "a change in gene frequencies" in *Animal Species and Evolution* (1963), and would only distance himself from it years later. Mayr also never bought into the "gene's-eye-view" of evolution promoted by first-wave sociobiologists like Hamilton, Dawkins, and Williams. To Mayr, the only important unit of selection was the individual organism.²⁰ In his last book, *What Makes Biology Unique?*, Mayr supported group selection but was still curiously reluctant to accept species selection, the principal exponent of which was, of course, the late Stephen Jay Gould.

In Mayr we lost a figure who influenced so much of evolutionary biology that it is hard to imagine anyone else ever having such an impact. Perhaps the greatest tribute to his influence is that his passing was actually noted on Saturday Night Live, with Tina Fey wryly speculating that the greatest evolutionary biologist of the twentieth century had ultimately succumbed "to a bigger, stronger evolutionary biologist."

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