Editorial TRENDS in Ecology and Evolution Vol.20 No.8 August 2005

Ernst Mayr, a retrospective

William B. Provine

Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, NY 14853-2701, USA

During the late summer of 1979, Ernst Mayr and I (Figure 1) had finished editing *The Evolutionary Synthesis: Perspectives on the Unification of Biology* [1]. He knew that I was working on a long essay about Theodosius Dobzhansky and also planning a book about Sewall Wright. From his farm in Wilton, New Hampshire, Ernst handwrote me a letter (Figure 2) from which this excerpt is taken:

'In your work, both on Dobzhansky and on Wright, please always remember that a scientist's achievement may lie in many different areas: As an *innovator* (new discoveries, new theories, new concepts), as a *synthesiser* (bringing together scattered information, sharing relationships and interactions, particularly between different disciplines, like genetics and taxonomy), as a *disseminator* (presenting specialized information and theory in such a way that it becomes accessible to non-specialists [popularizer is a misleading term]), as a *compiler* or *cataloguer*, as an *analyst* (dissecting complex issues, clarifying matters by suggesting new terminologies, etc.), and in other ways.'

Perhaps Mayr was really thinking of his own, many-faceted scientific career, rather than the careers of Dobzhansky and Wright. Here, I evaluate Mayr's scientific career according to his own categories.

All of Mayr's work on the systematics of birds fits into his category of compiler or cataloguer. He began this work as a graduate student and continued until he was 97 years old. From the beginning of his work in New Guinea and the South Sea Islands, Mayr tried to catalog and organize the birds in these regions from an evolutionary perspective. Most of his day-to-day scientific work from the beginning of his participation in the Whitney South Sea Expedition (1927–1930) until he left the American Museum in New York for the Museum of Comparative Zoology in Harvard in 1953 was spent on these birds, and every one of his publications from graduate school to 1942 concerned them [2–5]. From 1960 to 1986, he was the senior editor of many volumes of the *Check-List of the Birds of the World*, which was a huge endeavor. Even after reaching the Museum of Comparative Zoology and the blossoming of his work in evolutionary biology, Mayr authored or coauthored a steady stream of papers about his favorite birds.

Figure 1. Mayr, with the author, at home in Cambridge, MA, in 1997.

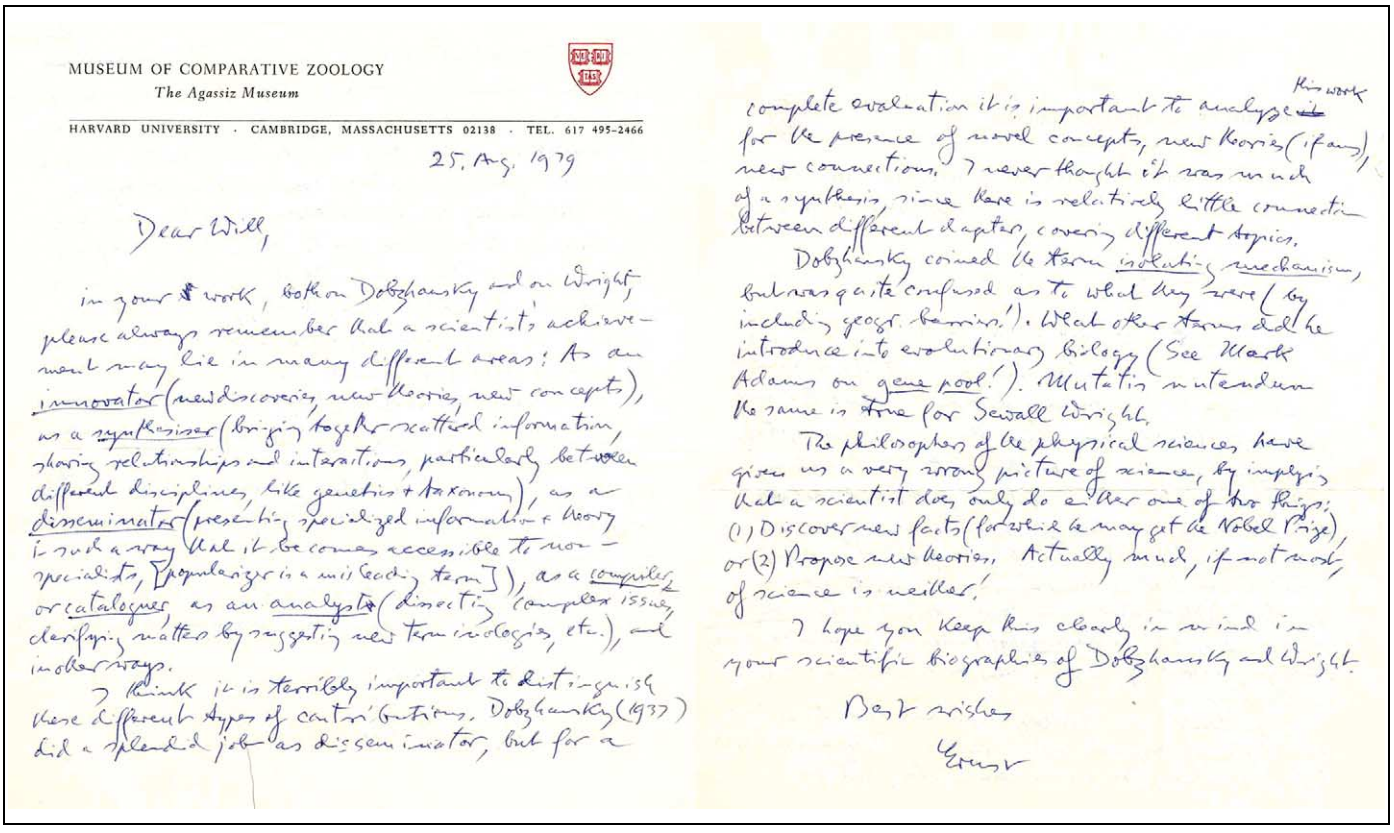
Perhaps Mayr's greatest influence upon evolutionary biology and systematics came from his role as an analyst, particularly in relation to suggesting new terminologies for new or older concepts. He published a brief article in 1978 under the title 'Origin and History of Some Terms in Systematic and Evolutionary Biology' [6], the contents of which are stunning. Mayr invented, and vigorously defended, the following terms: allopatric, cladogram, coefficient of difference, dendrogram, founder principle or founder effect (although this concept was probably around earlier, Mayr named it), genetic revolution, non-dimensional species, phenetics, phenogram, philopatric, phylogram, polytopic, population thinking, semispecies, sibling species, superspecies, sympatric speciation and teleonomic. When Alan Templeton invented a new term, 'genetic transilience,' for a 'genetic revolution' caused by changes in a few major genes (unlike the many genes in Mayr's genetic revolutions), Mayr wrote him a long letter of persuasion, hoping to suppress this new term, thus preserving his own terminology [7]; his attempt, however, was futile [8]. For many terms that Mayr did not invent, he was their disseminator, including the biological species concept, gene pool, genetic homeostasis (especially as applied to gene pools), and isolating factors in speciation.

As a disseminator of systematics and evolutionary biology, Mayr had no equal. His major books about systematics and evolution were clearly written and widely read ([9–14], the last two for general audiences), and he was the founding editor of *Evolution*, the primary journal of the field. Mayr adored evolution and systematics, and his enthusiasm was catching. He also disseminated his views through a massive personal correspondence throughout his lifetime. He promptly answered most letters that reached him, and initiated much correspondence. His influence through his correspondence has yet to be evaluated, although only after careful study.

Mayr's abilities as a synthesizer were not visible in his published work before 1942. Judging from these publications, one would expect from Mayr during the 1940s the three bird books referred to above [2–4]. One would not expect, however, *Systematics and the Origin of Species* [9], his synthetic work tying together systematics, evolutionary biology, natural history and the genetics of natural populations, mostly drawn from Dobzhansky's *Genetics*

Corresponding author: Provine, W.B. (wbp2@cornell.edu).
Available online 2 June 2005

 0169-5347/$ - see front matter doi:10.1016/j.tree.2005.05.009



MUSEUM OF COMPARATIVE ZOOLOGY
The Agassiz Museum

HARVARD UNIVERSITY · CAMBRIDGE, MASSACHUSETTS 02138 · TEL. 617 495-2466

25. Aug. 1979

Dear Will,

in your work, both on Dobzhansky and on Wright, please always remember that a scientist's achievement may lie in many different areas: As an innovator (new discovery, new theories, new concepts), as a synthesizer (bringing together scattered information, showing relationships and interactions, particularly between different disciplines, like genetics + taxonomy), as a disseminator (presenting specialized information + theory in such a way that it becomes accessible to non-specialists, [popularizer is a misleading term]), as a compiler or cataloguer, as an analyst (dissecting complex issues, clarifying matters by suggesting new terminologies, etc.), and in other ways.

I think it is terribly important to distinguish these different types of contributions. Dobzhansky (1937) did a splendid job as disseminator, but for a complete evaluation it is important to analyse his work for the presence of novel concepts, new theories (if any), new connections. I never thought it was much of a synthesis, since there is relatively little connection between different chapters, covering different topics.

Dobzhansky coined the term isolating mechanisms, but was quite confused as to what they were (by including geogr. barriers!). What other terms did he introduce into evolutionary biology (See Mark Adams on gene pool!). Mutation unterdrum the same is true for Sewall Wright.

The philosophers of the physical sciences have given us a very wrong picture of science, by implying that a scientist does only do either one of two things: (1) Discover new facts (for which he may get the Nobel Prize), or (2) Propose new theories. Actually most, if not most, of science is neither!

I hope you keep this clearly in mind in your scientific biographies of Dobzhansky and Wright.

Best wishes

Ernst

Figure 2. Letter from Mayr to Provine, dated 25th August, 1979.

and the Origin of Species [15]. Mayr evaluated his own book as being more synthetic than that of Dobzhansky: 'I never thought it was much of a synthesis, since there is relatively little connection between different chapters, covering different topics' (Figure 2). Mayr's 1963 book, *Animal Species and Evolution* [10], was his *tour de force* of synthesis in evolutionary biology.

The consistent failing of Mayr in his synthetic endeavors, however, was his understanding of genetics. After coming to the American Museum in 1932, Mayr quickly rejected his early belief in the inheritance of acquired characters and adopted 'genetics' as his view of heredity. He was influenced significantly by Dobzhansky's *Genetics and Origin of Species* [15] and by Sewall Wright, whose ideas Dobzhansky had incorporated into his book [15]. The genetics in Mayr's 1942 book was clearly derivative. During the early 1950s, Mayr learned a lot of new genetics from discussions with Bruce Wallace and James C. King [16]. He left behind what he later termed 'beanbag genetics,' and opted for gene interactions that prevent the modeling of individual genes and homeostatic gene pools that resist change. In truth, however, his new genetics also had little content. Gene pools exist only in the minds of people, not in natural populations or species, and talking of the homeostasis of the gene pools is biological nonsense. Mayr's 1954 concept of a 'genetic revolution' [17] was devoid of genetic content, and his long discussions of gene pools and homeostasis of gene pools in his most influential book, *Animal Species and Evolution* [10], seem vacuous from the perspective of modern genetics. Thus, the limitation of Mayr's genetic views hampered his synthesis of genetics with the rest of evolutionary biology.

Mayr was not a strong innovator of new discoveries, new theories, or new concepts. I interviewed him at his Wilton farm in 1986 and asked him for his greatest original contribution to evolutionary biology; he replied, 'the concept of genetic revolutions.' This idea was indeed invented by Mayr in 1954 [16], but, when first published, was devoid of genetic content, which was only added later by others. Mayr was intensely aware that he was less of an innovator and more of a synthesizer, disseminator and

Box 1. Mayr on species and speciation

Many of the obituaries following his death credit Mayr with the solving the problems of species and speciation. Mayr was a great champion of the biological species concept, but he knew that it did not apply to the first 3 billion years of evolution on Earth, was less applicable to plants than it was to birds, and that the concept entailed focusing upon isolating factors in speciation. He had no idea how isolating factors evolved and thought of them as *ad hoc* factors that did not evolve through the causes of natural selection, and were not correlated with morphological differences. Closely related species with marked phenotypic differences can often interbreed easily and Mayr cited many examples of species that looked so similar that only experts could tell them apart, yet they could not interbreed.

Mayr focused upon species and speciation and influenced many others to focus upon the same issues, all to the good of modern evolutionary biology. He often argued that his views on species and speciation were superior to those of Darwin. My suspicion is that Mayr's views did not advance as far from those of Darwin on species and speciation as he thought. Darwin's provisional hypothesis of pangenesis in 1868 is about as vague and biologically useless as Mayr's 1963 homeostatic gene pools.

analyst. Although he received many prestigious awards (as he said, every one he cared about), the only one that Mayr never had a chance of receiving was the Nobel Prize, because it was not given in evolutionary biology. Nobel Prizes, however, are generally given for new innovations, rather than for other reasons (although we should remember that Thomas Hunt Morgan won the Nobel Prize based upon the concepts of his students and his wife). Based on this criterion, Mayr would not have won a Nobel Prize even if it were awarded in either systematics or evolutionary biology (Box 1).

Mayr's letter to me (Figure 2) asserted that scientists can influence science deeply in many ways other than the invention of new ideas. His own career demonstrates this thesis.

References

1 Mayr, E. and Provine, W.B. (1980) *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, Harvard University Press
2 Mayr, E. (1941) *List of New Guinea Birds: A Systematic and Faunal List of the Birds of New Guinea and Adjacent Islands*, The American Museum of Natural History
3 Mayr, E. (1945) *Birds of the Southwest Pacific: A Field Guide to the Birds of the Area between Samoa, New Caledonia, and Micronesia*, Macmillan
4 Mayr, E. and Delacour, J. (1946) *Birds of the Philippines*, Macmillan
5 Mayr, E. and Diamond, J. (2001) *The Birds of Northern Melanesia: Speciation, Ecology, and Biogeography*, Oxford University Press
6 Mayr, E. (1978) Origin and history of some terms in systematic and evolutionary biology. *Syst. Zool.* 27, 83–88
7 Provine, W.B. (1989) Founder effects and genetic revolutions in microevolution and speciation: an historical perspective. In *Genetics, Speciation and the Founder Principle* (Giddings, L.V. *et al*., eds), pp. 43–76, Oxford University Press
8 Carson, H.L. and Templeton, A.R. (1984) Genetic revolutions in relation to speciation phenomena: the founding of new populations. *Annu. Rev. Ecol. Syst.* 15, 97–131
9 Mayr, E. (1942) *Systematics and the Origin of Species*, Columbia University Press
10 Mayr, E. (1963) *Animal Species and Evolution*, Harvard University Press
11 Mayr, E. (1969) *Principles of Systematic Zoology*, McGraw-Hill
12 Mayr, E. (1976) *Evolution and the Diversity of Life*, Harvard University Press
13 Mayr, E. (1997) *This is Biology: The Science of the Living World*, Harvard University Press
14 Mayr, E. (2001) *What Evolution Is*, Basic Books
15 Dobzhansky, T. (1937) *Genetics and the Origin of Species* (2nd edn), Columbia University Press
16 Provine, W.B. (2004) Ernst Mayr: genetics and speciation. *Genetics* 167, 1041–1046
17 Mayr, E. (1954) Change of genetic environment and evolution. In *Evolution as a Process* (Huxley, J. *et al*., eds), pp. 157–180, Allen and Unwin