

Perspectives

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Ernst Mayr: Genetics and Speciation

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AFTER a flurry of publishing in the past few years (MAYR 1997, 2001; MAYR and DIAMOND 2001), Ernst Mayr turned 100 on July 5, 2004. His deep influence in systematics, systematic nomenclature, evolutionary biology, history of biology, and philosophy of biology over the past 7 decades is unmatched by anyone in his generation, or probably after. I am probably best qualified to write about his contributions to the history of biology, but suspect that geneticists might rather learn more about Mayr's love/hate relationship with genetics as he developed his controversial theory of genetic revolutions to explain speciation. His views on genetics have not changed much since he published his *Animal Species and Evolution* in 1963. When, over the course of a 2-day interview (MAYR and PROVINE 1986), I asked Mayr to tell me his most important contribution to evolutionary biology during his life, he replied without hesitation, "genetic revolutions." For a fuller account, see PROVINE (1989).

MAYR, GENETICS, AND SPECIATION BEFORE 1950

Although a champion of the biological species concept, Mayr never claimed credit for inventing the idea. Seven years before Mayr published his influential *Systematics and the Origin of Species* in 1942, Theodosius Dobzhansky published an article arguing for the biological species concept (DOBZHANSKY 1935). He argued there and in his book, *Genetics and the Origin of Species* (DOBZHANSKY 1937), that the biological species concept was far more useful than the older museum views based on morphological differences and contended that the isolating mechanisms that prevented crossing between good biological species were the key to understanding speciation. Dobzhansky, however, included geographi-

cal separation as one of the isolating factors. In a 1940 article, "Speciation phenomena in birds," Mayr offered a different definition of the biological species concept:

A species consists of a group of populations which replace each other geographically or ecologically and of which the neighboring ones intergrade or hybridize wherever they are in contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers (MAYR 1940, p. 256).

In short, Mayr disallowed geographical separation as a valid isolating mechanism. He quoted the same definition of species in *Systematics and the Origin of Species* (1942) and added a shorter version: "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (MAYR 1942, p. 120). Although Mayr removed geographical separation as an isolating mechanism itself, he and Dobzhansky both thought that geographical separation was required for speciation to happen.

By using the biological species concept, both Dobzhansky and Mayr were now tied to the concept of isolating mechanisms as the key to understanding speciation. Since most isolating mechanisms were genetically determined, Mayr was, from this point forward, inevitably tied to genetics. No concept of speciation could be complete without a genetic interpretation of the rise of isolating mechanisms.

Mayr understood this point perfectly in *Systematics and the Origin of Species*, but faced a major problem. He did not know much recent genetics. His primary source for the genetics of speciation in his 1942 book came from *Genetics and the Origin of Species*, in which Dobzhansky had relied heavily upon Sewall Wright's insights into genetics and evolution (PROVINE 1986, Chaps. 10–11). Mayr assumed that most speciation took place after geographical isolation was firmly in place, even if only temporarily:

Naturalists have known for a long time that island populations tend to have aberrant characteristics. WRIGHT (1931, 1932, and elsewhere) found the theoretical basis

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FIGURE 1.—A recent photograph of Ernst Mayr.

for this by showing that in small populations the accidental elimination of genes may be a more successful process than selection. Furthermore, recessive mutations have a much better chance to become homozygous than in a large panmictic population. It is therefore very important to learn something about the actual size of distributional islands and of their populations (MAYR 1942, p. 234).

Mayr then offered examples of small isolated populations of cave animals, lizards, fish, birds, and mice, all of which exhibited aberrant characteristics. His analysis of these examples again drew upon the work of Wright:

An exact determination of the size of an isolated population is of importance, in view of Sewall Wright's work on gene loss in small populations. Owing to "accidents of sampling," small populations have a trend toward genetic homogeneity or at least toward a much-reduced variability. This is quite apparent in taxonomic work, although only a few systematists have taken the trouble to make careful measurements and to work out the coefficients of variation (MAYR 1942, p. 235).

Why, exactly, did population size have consequences for the speciation process?

The calculations of SEWALL WRIGHT (1931, 1932, and elsewhere) indicate that effective populations have to be rather small, in the order of several hundred individuals or less, before they can be expected to approach genetic homogeneity due to accidental gene loss. If the population size is larger (thousands to tens of thousands of individuals), there still may be rapid evolution owing to mutation pressure (in the absence of appreciable selection), but the population will remain much more variable. If the size of the effective breeding population is still greater, approaching panmixia in varying degrees, evolution will be slowed down considerably. The consequence of this consideration is that evolution should proceed more rapidly in small populations than in large ones, and this is exactly what we find (MAYR 1942, p. 236).

Mayr did not actually read Wright's articles at this time, but relied upon Dobzhansky's writing for Wright's

views. Thus he saw Wright basically as a random drifter, whereas Wright's "shifting balance" theory clearly emphasized strong gene interaction and subdivided larger populations, not just small isolated ones (PROVINE 1986, Chap. 9). Mayr relied upon Dobzhansky's distilled version of Wright's theoretical formulations for analyzing reduced variability and increased rate of evolution in relatively small, geographically isolated populations. According to Mayr, however, random genetic drift was not the only way to produce reduced variability in isolated populations:

The reduced variability of small populations is not always due to accidental gene loss, but sometimes to the fact that the entire population was started by a single pair or by a single fertilized female. These "founders" of the population carried with them only a very small proportion of the variability of the parent population. This "founder" principle sometimes explains even the uniformity of rather large populations, particularly if they are well isolated and near the borders of the range of the species (MAYR 1942, p. 237).

This was the first statement of the founder principle.

Mayr also relied upon Wright's calculations of effective population size, usually much smaller than a mere count of individuals in a natural population. In these passages, Mayr was attempting to explain the mechanisms of geographical speciation. He and other naturalists had observed that island populations exhibited characters different from those of mainland organisms, and he concluded that the speciation process was accelerated by the isolation of relatively small populations. Mayr argued that evolution was faster in small populations than in large ones because inbreeding led to random genetic drift, accidental gene loss, and consequent increase of homozygosity and decrease of genotypic and phenotypic variability in the small populations. These mechanisms caused rapid, divergent evolution in the small populations. "The potentiality for rapid divergent evolution in small populations explains also why we have on islands so many dwarf or giant races, or races with peculiar color characters (albinism, melanism), or with peculiar structures (long bills in birds), or other peculiar characters (loss of special male plumage in birds)" (MAYR 1942, p. 236).

Why or how random genetic drift led to "rapid divergent evolution" and potential speciation Mayr did not say, but he clearly was relying upon Wright's analysis of evolution in small populations, although not invoking Wright's shifting balance theory. When I interviewed Mayr in the summer of 1986, he clearly indicated that, in hindsight, he lacked a genetic understanding in his 1942 book of why small populations might become new species. He described himself as a "beanbagger" in 1942.

Thus, to Mayr in 1942, speciation required geographical isolation and was much accelerated by small population size, as in small island populations. Citing Wright, Mayr argued that even a very large population, if it under-

went periodic crashes, would have a small effective population size that increased the probability of rapid evolution.

The “founder” principle, as introduced by Mayr in 1942, was an auxiliary mechanism (less important than random drift) for producing reduced variability in an isolated population started by a few individuals or even by a single fertilized female. Mayr saw a distinction between the “founder” effect and random drift. The founders were not a random sampling of the main population, but, once isolated as a small population, would undergo random drift. There was no hint in the 1942 book that the founder principle was a frequent factor in speciation. This founder principle, according to Mayr, could even explain the relative uniformity of “rather large” isolated populations. Although he did not say so directly, the implication was that the founder principle, like gene loss from random genetic drift, promoted rapid evolution and led to possible speciation. Again, as in the case of random drift, Mayr gave no indication of precisely how or why the founder principle led to speciation, that is, to the rise of new genetic isolating mechanisms. Mayr published many articles between his 1942 book and 1950, but never advanced his genetical theory of the origin of isolating factors beyond that presented in the book.

WHERE ARE WE?

Nine years later, in the centenary year of Darwin's *On the Origin of Species*, the Cold Spring Harbor Symposium was devoted to the topic, “Genetics and Twentieth Century Darwinism.” Mayr gave the keynote speech, entitled, “Where Are We?” Genetics in relation to evolution had two roots, Mayr argued. One was the contribution of theoretical population genetics:

The emphasis in early population genetics was on the frequency of genes and on the control of this frequency by mutation, selection, and random events. Each gene was essentially treated as an independent unit favored or discriminated against by various causal factors. In order to permit mathematical treatment, numerous simplifying assumptions had to be made, such as that of an absolute selective value to a given gene. The great contribution of this period was that it restored the prestige of natural selection, which had been rather low among the geneticists active in the early decades of the century, and that it prepared the ground for treatment of quantitative characters. Yet this period was one of gross simplification. Evolutionary change was essentially presented as an input or output of genes, as in the adding of certain beans to a beanbag and the withdrawing of others (MAYR 1959a, p. 2).

Mayr continued the argument further:

There is no doubt that the classical period of population genetics was dominated by the mathematical analyses and models of FISHER (1930), WRIGHT (1931) and HALDANE (1932).

These authors, although sometimes disagreeing with each other in detail or emphasis, 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 the evolutionary theory, if I may be permitted to ask such a provocative question? . . . However, I should perhaps leave it to Fisher, Wright, and Haldane to point out themselves what they consider their major contributions (MAYR 1959a, p. 2).

Essentially, Mayr had just dismissed the primary authority, Sewall Wright, upon whom he had relied for his theory of speciation 17 years earlier. And he revealed in our interview that, at this time, he still had not made any careful study of the articles or books of Wright, Haldane, or Fisher. He was being controversial to promote, in his words, “better science.”

In 1959, according to Mayr, the shortcomings of this period of “beanbag genetics” had “become obvious as a result of the work of the experimental population geneticists, and the animal and plant breeders, and the population systematists, which ushered in a third area of evolutionary genetics” (MAYR 1959a, p. 2). Regarding specific genetical theories not in the “beanbag genetics” category, Mayr named Dobzhansky's “balance theory,” I. M. Lerner's “genetic homeostasis,” and Kenneth Mather's work on quantitative inheritance (“genetic inertia”).

Obviously, by 1959 Mayr had another theory of speciation based, not upon the work of Wright, but upon the work of geneticists whose work, to him, had superseded that of theoretical population geneticists. Mayr has never to this day changed his attitude toward “beanbag genetics.” Fisher died before answering Mayr, Haldane wrote a famous “defense of beanbag genetics” (HALDANE 1964), Wright answered Mayr's accusations in many articles, and James F. Crow more recently also has defended “beanbag genetics” (CROW 2001).

MAYR, GENETICS, AND SPECIATION: 1950–1963

In the spring of 1950, Mayr had just finished a major exhibition at the American Museum of Natural History. The intense flurry of activity gave him heart irregularities, and his doctor recommended relaxation. Mayr decided to rest and at the same time learn more about genetics. He faced the continual problem of a genetic interpretation of the rise of isolating mechanisms that were the key to speciation. Dobzhansky was too busy to relax and talk genetics with Mayr, but Bruce Wallace, a former student of Dobzhansky and new employee at Cold Spring Harbor Laboratory, was the perfect teacher. Wallace had hired James C. King to work with him, and during the summer of 1950 the two of them would sit with Mayr either in the lab or on the lawn, depending on the weather, and talk for hours. Both Mayr and Wallace recall these conversations with great pleasure.

From these sessions, Mayr learned of a new genetics that seemed so different from the models of Wright, Haldane, or Fisher. In 1950, Dobzhansky invented the term “gene pool” and also redefined the Mendelian population: “A Mendelian population is a reproductive

community of sexual and cross-fertilizing individuals which share in a common gene pool" (DOBZHANSKY 1950, pp. 404–405). The new genetics concerned gene pools, in which the selective value of a gene depended on the genetic environment rather than on having a constant value. The gene pool had a cohesion, or exhibited homeostasis, a term invented by I. Michael Lerner (1950) in his book, *Population Genetics and Animal Improvement*, and quickly picked up by Dobzhansky and Wallace. Mayr was delighted by this new genetics and discovered that many geneticists who studied natural populations, or domestic populations, had given up "beanbag genetics." Instead, they practiced genetics in ways that Mayr thought he could apply to understanding the genetics of speciation. But he did not see exactly how to do this during the summer of 1950 and continued to read more and more genetics.

The next year Mayr traveled to Pavia, Italy, for a conference, and on the way back had a lot of time to think about genetics and speciation. On this return trip, he invented the idea that would fulfill his hope of understanding speciation: the genetic revolution. He had an invitation to contribute to a volume honoring Julian Huxley and used his new idea to explain how a new founder population, geographically isolated, could occasionally undergo a genetic revolution that could produce isolating mechanisms in a short time. Mere random drift, with consequent homozygosity, by itself, no longer could produce speciation as Mayr imagined in the years 1942–1950. Mayr wrote this paper in 1951, handing only one copy to Wallace, and revised it early in 1952 before submitting it to the editors, who did not get their book in print for almost 2 years (MAYR 1954).

Mayr's article, "Change of genetic environment and evolution," begins where he left off in *Systematics and the Origin of Species*. Mayr was particularly impressed by Wallace's emphasis upon the high degree of integration and coadaptation of the genome. In the 1954 article, Mayr again emphasized "the conspicuous difference of most peripherally isolated populations of species." But whereas in 1942 he left only a vague connection between the aberrant characteristics of these isolated populations and random genetic drift, he now argued that

... for such a striking dissimilarity of peripherally isolated populations two reasons are usually cited: difference of physical and biotic environment or genetic drift. It seems to me that neither of these factors nor a combination of the two can provide a full explanation, even though both may be involved (MAYR 1954, p. 158).

The answer to such aberrant characteristics, Mayr suggested, lay in understanding that the selective value of a single allele depended greatly upon the overall genetic environment.

The genome of an individual was a highly interactive, coadapted gene complex, Mayr argued. More importantly, the individuals in an entire species shared significant portions of that coadapted gene complex, which

resisted changes: "Such a well-integrated, coadapted gene-complex constitutes an evolutionary unit in spite of its intrinsic variability. Any disharmonious gene or gene-combination which attempts to become incorporated in such a gene-complex will be discriminated against by selection" (MAYR 1954, p. 165).

Therefore, the major problem was to discover how it was possible to overcome the inertia of such a coadapted gene complex. One way was to send the gene-complex through a founder population (italics are Mayr's):

One of the obvious effects of the sudden reduction of population size in the founder population will be a strong increase in the frequency of homozygotes. As a consequence, homozygotes will be much more exposed to selection and those genes will be favored which are specially viable in the homozygous condition. Thus, the "soloist" is now the favorite rather than the "good mixer."

We come thus to the important conclusion that *the mere change of the genetic environment may change the selective value of a gene very considerably*. Isolating a few individuals (the "founders") from a variable population which is situated in the midst of the stream of genes which flows ceaselessly through every widespread species will produce a sudden change of the genetic environment of most loci. This change, in fact, is the most drastic genetic change (except for polyploidy and hybridization) which may occur in a natural population, since it may affect all loci at once. Indeed, it may have the character of a veritable "genetic revolution." Furthermore, this "genetic revolution," released by the isolation of the founder population, may well have the character of a chain reaction. Changes in any locus will in turn affect the selective values at many other loci, until finally the system has reached a new state of equilibrium (MAYR 1954, pp. 169–170).

Mayr emphasized that a genetic revolution was not to be expected in every founder population: "A 'genetic revolution' in the founder population is only a potentiality but does not need to happen every time a population is isolated, if the genetic constitution of the founders does not favour it" (p. 171). He also emphasized that "during a genetic revolution the population will pass from one well integrated and rather conservative condition through a highly unstable period to another new period of balanced integration. The new balance will be reached after a great loss of genetic variability" (p. 172). Many such populations, after undergoing a genetic revolution, would be severely depleted of genetic variability and subject to extinction should the environment change. Some populations, however, might find a new ecological niche after the genetic revolution and gradually accumulate genetic variability. Mayr illustrated this possibility with his famous diagram (Figure 2), with the point C representing the genetic revolution. Mayr really worried about the reaction of geneticists to his theory of genetic revolutions. Only Wallace had seen the paper before publication, and Mayr sent reprints of the article to many people, including Arthur Cain, Sewall Wright, and Hampton Carson. But he recalls hearing nothing back regarding his theory of "genetic revolutions." Indeed, despite his detailed explanation of "genetic revolutions"

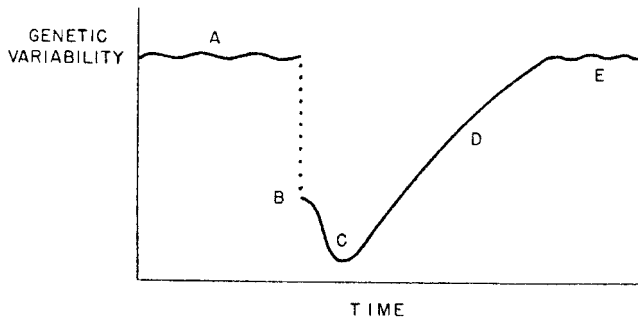


FIGURE 2.—Mayr's diagram of a "genetic revolution." A population (A) goes through a bottleneck, by which the variability is greatly reduced (B). Then through further increases of homozygosity a genetic revolution occurs (C), after which the population again regains variability with a new genetic structure (D and E).

in his *Animal Species and Evolution* (1963), with little change from the basic explanation in his 1954 article, Mayr recalls seeing little response until the early 1970s.

In *Animal Species and Evolution*, Mayr presented large sections on gene pools, homeostasis of gene pools, ubiquitous gene interaction, balanced polymorphism, and all the genetics that Wallace had introduced to him. Mayr, for example, had taken the trouble to read carefully many of the books and articles of Kenneth Mather, Dobzhansky, Lerner (especially LERNER 1954), and even, finally, the works of Wright. He discovered that Wright had believed all along in gene interaction, the biological species concept, and had his own theory of speciation tied to his shifting balance theory.

MAYR (1959b, p. 228), beginning a few years earlier, and again in *Animal Species and Evolution* (MAYR 1963), had called attention to the genetic interpretation of isolating mechanisms. His argument was the same as that of Charles Darwin: isolating mechanisms are not produced directly by natural selection. Never is it an advantage for a single, sexually breeding organism to be cut off from breeding with another of its species. Thus, isolating mechanisms must be "an incidental by-product of the genetic divergence of isolated gene pools and acquired during this isolation" (MAYR 1959b, p. 228). This view echoes the earlier ideas of Muller and Dobzhansky that isolating mechanisms arise incidentally in geographically separated populations (ORR 1996). Investigation of these "incidental by-products" was not likely ever to reveal a coherent theory of the rise of isolating mechanisms, and thus of speciation. In any particular case, however, the issue boiled down to the genetics of natural populations.

Incidentally, Mayr later, in our 1986 interview, regretted classifying Wright as a beanbagger, except in his one-locus-two-allele models. His physiological genetics, emphasis upon gene interaction, and shifting balance theory all were more congenial to Mayr's views. After

winning the Balzan Prize in 1984, Mayr nominated Wright for the same prize the following year. When Wright's win of the Balzan Prize was announced in September of 1984, Mayr wrote me a handwritten letter telling me how glad he was that Wright had received the prize.

CONCLUSION

Mayr's theory of genetic revolutions in relation to speciation presented a challenge to geneticists and required understanding of the origin of genetic isolating mechanisms. Mayr's own theory of "genetic revolutions" was vague and devoid of much genetic content. He wanted to stimulate geneticists to throw their efforts into the fray and sort out how these genetic isolating mechanisms occurred between geographically separated populations, or even between sympatric populations, or even if one rejects the biological species concept in sexually breeding taxa. I think Mayr's challenge gave a major impetus to this investigation, but it took a while to begin. After 1970 a series of articles evaluated Mayr's genetic revolutions and presented new proposals: CARSON (1971); LANDE (1980, 1982); TEMPLETON (1980); BARTON and CHARLESWORTH (1984); CARSON and TEMPLETON (1984); and many later articles and books on speciation and isolating mechanisms. Even those who reject the idea of a "genetic revolution" still face the problem that Mayr threw to geneticists: How do these genetic isolating mechanisms arise during speciation, and not under the direct effect of natural selection?

LITERATURE CITED

- BARTON, N. H., and B. CHARLESWORTH, 1984 Genetic revolutions, founder effects, and speciation. *Annu. Rev. Ecol. Syst.* **15**: 133–164.
- CARSON, H. L., 1971 Speciation and the founder principle. *Stadler Symp.* **3**: 51–70.
- CARSON, H. L., and A. R. TEMPLETON, 1984 Genetic revolutions in relation to speciation phenomena: the founding of new populations. *Annu. Rev. Ecol. Syst.* **15**: 97–131.
- CROW, J. F., 2001 The beanbag lives on. *Nature* **409**: 771.
- DOBZHANSKY, T., 1935 A critique of the species concept in biology. *Philos. Sci.* **2**: 344–355.
- DOBZHANSKY, T., 1937 *Genetics and the Origin of Species*. Columbia University Press, New York.
- DOBZHANSKY, T., 1950 Mendelian populations and their evolution. *Am. Nat.* **74**: 401–418.
- FISHER, R. A., 1930 *The Genetical Theory of Natural Selection*. Oxford University Press, Oxford.
- HALDANE, J. B. S., 1932 *The Causes of Evolution*. Longmans Green, London.
- HALDANE, J. B. S., 1964 A defense of beanbag genetics. *Perspect. Biol. Med.* **7**: 343–359.
- LANDE, R., 1980 Genetic variation and phenotypic evolution during allopatric speciation. *Am. Nat.* **116**: 463–479.
- LANDE, R., 1982 Rapid origin of sexual isolation and character divergence in a cline. *Evolution* **36**: 213–223.
- LERNER, I. M., 1950 *Population Genetics and Animal Improvement: As Illustrated by the Inheritance of Egg Production*. Cambridge University Press, Cambridge, UK.
- LERNER, I. M., 1954 *Genetic Homeostasis*. Oliver & Boyd, London.
- MAYR, E., 1940 Speciation phenomena in birds. *Am. Nat.* **74**: 249–278.

- MAYR, E., 1942 *Systematics and the Origin of Species*. Columbia University Press, New York.
- MAYR, E., 1954 Change of genetic environment and evolution, pp. 157–180 in *Evolution as a Process*, edited by J. HUXLEY, A. C. HARDY and E. B. FORD. Allen & Unwin, London.
- MAYR, E., 1959a Where are we? Cold Spring Harbor Symp. Quant. Biol. **24**: 1–14.
- MAYR, E., 1959b Isolation as an evolutionary factor. Proc. Am. Philos. Soc. **103**: 221–230.
- MAYR, E., 1963 *Animal Species and Evolution*. Harvard University Press, Cambridge, MA.
- MAYR, E., 1997 *This Is Biology: The Science of the Living World*. Harvard University Press, Cambridge, MA.
- MAYR, E., 2001 *What Evolution Is*. Basic Books, New York.
- MAYR, E., and J. DIAMOND, 2001 *The Birds of Northern Melanesia: Speciation, Ecology, and Biogeography*. Oxford University Press, London/New York.
- MAYR, E., and W. B. PROVINE, 1986 Oral interview, 7 hours. Library of the American Philosophical Society, Philadelphia.
- ORR, H. A., 1996 Dobzhansky, Bateson, and the genetics of speciation. *Genetics* **144**: 1331–1335.
- PROVINE, W. B., 1986 *Sewall Wright and Evolutionary Biology*. University of Chicago Press, Chicago.
- PROVINE, W. B., 1989 Founder effects and genetic revolutions in microevolution and speciation: an historical perspective, pp. 43–76 in *Genetics, Speciation, and the Founder Principle*, edited by L. V. GIDDINGS, K. KANESHIRO and W. W. ANDERSON. Oxford University Press, New York/Oxford.
- TEMPLETON, A. R., 1980 The theory of speciation via the founder principle. *Genetics* **94**: 1011–1038.
- WRIGHT, S., 1931 Evolution in Mendelian populations. *Genetics* **16**: 97–159.
- WRIGHT, S., 1932 The roles of mutation, inbreeding, crossbreeding, and selection in evolution. Proc. Sixth Int. Congr. Genet. **1**: 356–366.