
INTRODUCTION
ERNST MAYR AND
THE THEORY OF EVOLUTION

FRANCISCO J. AYALA

THE MODERN SYNTHESIS

Ernst Mayr is an eminent evolutionist who surely counts as one of the most important authors contributing to the formulation of the Synthetic Theory of Evolution. The Synthetic Theory, also known as the Modern Synthesis of Evolutionary Theory, embodies a complex array of biological knowledge centered around Darwin's theory of evolution by natural selection couched in genetic terms. The epithet "synthetic" alludes to the artful combination of Darwin's natural selection with relevant knowledge from biological disciplines. Four books are considered emblematic of the synthesis: Theodosius Dobzhansky's *Genetics and the Origin of Species* (1937); Ernst Mayr's *Systematics and the Origin of Species* (1942); G.G. Simpson's *Tempo and Mode in Evolution* (1944), and G. Ledyard Stebbins' *Variation and Evolution in Plants* (1950).

The current Synthetic Theory has grown around that original synthesis. It is not just one single hypothesis (or theory) with its corroborating evidence, but a multidisciplinary body of knowledge bearing on biological evolution, an amalgam of well established theories and working hypotheses, together with the observations and experiments that support accepted hypotheses (and falsify rejected ones), which jointly seek to explain the evolutionary process and its outcomes. These hypotheses, observations, and experiments originate in disciplines such as genetics, embryology, zoology, botany, paleontology, and molecular biology. Currently, the "synthetic" epithet is often omitted and the compilation of relevant knowledge is simply known as the Theory of Evolution. This is still expanding, just like one of those "holding" business corporations that have grown around an original enterprise, but continue incorporating new profitable enterprises and discarding unprofitable ones.

Darwin summarized the theory of evolution by natural selection in the *Origin of Species* as follows:

Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 29697, USA. / fjayala@uci.edu

As many more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life... Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations, useful in some way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations? If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind? On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favorable variations and the rejection of injurious variations, I call Natural Selection (Darwin, 1859).

Darwin's argument is that natural selection emerges as a necessary conclusion from two premises: (i) the assumption that heredity variations useful to organisms occur, and (ii) the observation that more individuals are produced than can possibly survive. The most serious difficulty facing Darwin's evolutionary theory was the lack of an adequate theory of inheritance that would account for the preservation through the generations of the variations on which natural selection was supposed to act. Theories then current of "blending inheritance" proposed that offspring merely struck an average between the characteristics of their parents. As Darwin became aware, blending inheritance could not account for the conservation of variations, because differences among variant offspring would be halved each generation, rapidly reducing the original variation to the average of the preexisting characteristics.

The missing link in Darwin's argument was provided by Mendelian genetics. About the time *The Origin of Species* was published, the Augustinian monk Gregor Mendel was performing a long series of experiments with peas in the garden of his monastery in Brnn, Austria-Hungary (now Brno, Czech Republic). Mendel's paper, published in 1866, formulated the fundamental principles of a theory of heredity that accounts for biological inheritance through particulate factors (now called "genes") inherited one from each parent, which do not mix or blend but segregate in the formation of the sex cells, or gametes (Mendel 1866).

Mendel's discoveries, however, remained unknown to Darwin and, indeed, did not become generally known until 1900, when they were simultaneously rediscovered by several scientists. In the meantime, Darwinism in the latter part of the nineteenth century faced an alternative evolutionary theory known as neo-Lamarckism. This hypothesis shared with Lamarck's original theory the importance of use and disuse in the development and obliteration of organs, and it added the notion that the environment acts directly on organic structures, which explained their

adaptation to the ways of life and environments of each organism. Adherents of this theory rejected natural selection as an explanation for adaptation to the environment.

The rediscovery in 1900 of Mendel's theory of heredity led to an emphasis on the role of heredity in evolution. In the Netherlands, Hugo de Vries (1900) proposed a new theory of evolution known as mutationism, which sought to do away with natural selection as a major evolutionary process. According to de Vries (joined by other geneticists such as William Bateson in England), there are two kinds of variation in organisms. One is the "ordinary" variation observed among individuals of a species, which is of no lasting consequence in evolution because, according to de Vries, it could not "lead to a transgression of the species border even under conditions of the most stringent and continued selection." The other consists of the changes brought about by mutations, spontaneous alterations of genes that yield large modifications of the organism and give rise to new species. According to de Vries, a new species originates suddenly, produced by the existing one without any noticeable transition.

Mutationism was opposed by many naturalists, and in particular by the so-called biometricians, led by Karl Pearson and W.F.R. Weldon, who defended Darwinian natural selection as the major cause of evolution through the cumulative effect of small, continuous, individual variations (which the biometricians assumed passed from one generation to the next without being subject to Mendel's laws of inheritance).

The controversy between mutationists (at the time also known as Mendelians) and biometricians approached a resolution in the 1920s and 1930s through the theoretical work of several geneticists, who used mathematical arguments to show, first, that continuous variation (in such characteristics as size, number of progeny, longevity, and the like) could be explained by Mendel's laws; and second, that natural selection acting cumulatively on small variations could yield major evolutionary changes in form and function (Provine 1971). Distinguished members of this group of theoretical geneticists were R.A. Fisher and J.B.S. Haldane in Britain and Sewall Wright in the United States (Fisher 1930; Haldane 1932; Wright 1931). Their work contributed to the downfall of mutationism and, most importantly, provided a theoretical framework for the integration of genetics into Darwin's theory of natural selection. Yet their work had a limited impact on contemporary biologists because it was formulated in a mathematical language that most biologists could not understand; because it was almost exclusively theoretical, with little empirical corroboration; and because it was limited in scope, largely omitting many issues, like speciation, that were of great importance to evolutionists.

Dobzhansky's *Genetics and the Origin of Species* (1937) advanced a reasonably comprehensive account of the evolutionary process in genetic

terms, laced with experimental evidence supporting the arguments developed by the theoreticians. This book had an enormous impact on naturalists and experimental biologists, who rapidly embraced the new understanding of the evolutionary process as genetic change in populations. Interest in evolutionary studies was greatly stimulated, and contributions to the theory soon began to follow, extending the synthesis of genetics and natural selection to a variety of biological fields.

One key development of the Synthetic Theory was the replacement of "population thinking" for "typological thinking." Darwin had postulated that hereditary variations occur in organisms that are useful to the organisms themselves. Natural selection could only occur if such variations were pervasive. In genetics, populational thinking gave rise to a new branch of genetics that, as Dobzhansky noted, "has as its province the processes taking place in groups of individuals—in populations—and therefore is called the genetics of populations... The rules governing the genetic structure of a population are distinct from those governing the genetics of individuals" (Dobzhansky 1937, p. 11).

MAYR: THE MODERN SYNTHESIS AND BEYOND

Mayr's *Systematics and the Origin of Species* (1942) is a self-conscious effort to explicate the significance of population variation in the understanding of evolutionary processes and the origin of new species.

It is true that the change from the static species concept of Linnaeus to the dynamic species concept of the modern systematist has not entirely escaped the attention of progressive students of genetics and evolution. However, the whole significance of the polytypic species, of the phenomena of geographic variation, of the differences between geographic and other forms of isolation are by no means as widely appreciated... as they deserve (Mayr 1942, Preface).

Mayr would later write:

Systematics, contrary to widespread misconceptions... was not at all in a backward and static condition during the first third of the twentieth century... Population thinking was widely adopted and, as a consequence, variation within and between populations was actively studied, which led to the development of the biological species concept, to the widespread adoption of polytypic species taxa, and to the study of species in space and time as adapted systems... [T]he experimental geneticists, with few exceptions, were quite unaware that a populational species concept had been widely adopted by naturalists (Mayr 1980, p. 33).

The biological species concept emphasizes the species as a community of populations, reproductive isolation... and the ecological interactions of sympatric populations that do not belong to the same species (Mayr 1980, p. 34).

Mayr's scholarly publications span more than eighty years, starting with his first two scientific papers, published in 1923, and reaching to 2004¹. Walter J. Bock (1994), who has written the most comprehensive overview of Mayr's career, divides his contributions into three major periods.

The first period (1923 until 1953, when he left the American Museum of Natural History) was devoted mainly to avian systematics and the theory of systematics. This work formed the foundation for the second period (beginning in 1942, but becoming more dominant in the latter part of the 1940s and lasting until his formal retirement from Harvard University in 1974) which was devoted largely to evolutionary theory. His systematic and evolutionary contributions, in turn, provided the basis for the last period (beginning in the early 1970s) devoted chiefly to the history and philosophy of biology (p. 267).

I do not intend here to provide an, even schematic, summary of the scientific and philosophical subjects to which Mayr has importantly contributed. Those unfamiliar with Mayr's work may get an inkling of how extensive his reach has been by the following listing of the headings used in Bock's article:

- Naturalist
- Ornithology
- Historical Events
- A Unified Approach to Biodiversity
- Systematics
- Biogeography
- Nomenclature
- Evolutionary Biology
 - General Analysis of Evolution and Darwinism
 - Terms in Systematics and Evolution
 - Species Concepts
 - Sibling Species
 - Ontological Status of Species
 - Geographic Variation and the Subspecies
 - Intrinsic Isolating Barriers versus External Barriers
 - Speciation *versus* Phyletic Evolution
 - Process of Speciation
 - Beanbag Genetics
 - Cause and Effect
 - Accident *versus* Design.

The bibliography listed by Bock includes 176 publications, all but a baker's dozen single-authored by Mayr.

Ludus Vitalis dedicates this special issue to Professor Ernst Mayr, one of the giants of evolutionary theory—its science, its history, and its philoso-

phy—in awe and admiration of the capaciousness and eminence of his achievements, on the occasion of his one hundredth birthday, 5 July 2004. The project was proposed by Francisco J. Ayala and enthusiastically accepted by the editor, Raúl Gutiérrez Lombardo, and the editorial board. All the papers herein included were solicited specifically for the present purposes.

Very especially, *Ludus Vitalis* and I are grateful to Professor Mayr for his decision to add to this collection his own paper, “The autonomy of biology.” It would be trite for me to comment on this contribution or extol its significance. It bears witness to a magnificent mind, which continues to be grand at one hundred years of age. We are as well obliged to the other authors for enthusiastically accepting our invitation, for their promptness and, most of all, for their excellent contributions.

ERNST MAYR'S EVOLUTION

Jared Diamond provides a bird's-eye view of Ernst Mayr's career and significance for evolutionary theory. The phrase “bird's-eye-view” is here particularly apposite, since Mayr started his scientific career as an ornithologist of the South Pacific Islands, and so did Diamond, if only forty years later. These two authors would later report thirty years of collaborative research in a joint compendium, *The Birds of Northern Melanesia. Speciation, Ecology and Biogeography*, published in 2001. Also in 2001, Mayr published *What Evolution Is*, which distills for the educated public, Diamond tells us, Mayr's unparalleled experience and knowledge.

David Hull's “Ernst Mayr y la filosofía de la biología” is one philosopher's introduction to some of Mayr's distinctive philosophical constructions, such as the epistemological and metaphysical implications of “population thinking,” the disparate significance of the notion of “natural laws” in the physical sciences *versus* the evolutionary sciences, and the explanation of adaptation as the outcome of a teleonomic process.

ADAPTATION AND DESIGN

The subject of adaptation is, again, taken up by Richard Dawkins. Natural selection, writes Dawkins, may not be the only driver and guide of evolution, but it is the only force capable of producing adaptation. The “illusion of design” pervades the living world, in the body shapes and behavior patterns of organisms, as well as in the arrangement of species into communities and ecosystems. At all levels, however, “the process is mirrored at the level of every species' ‘own’ genes.” The unit in the hierarchy of life at which natural selection acts is, for Dawkins, the gene, while for Mayr it is the organism, as Dawkins notes.

William Paley developed an argument-from-design based on his own biological knowledge, as extensive and accurate as it was available around

the year 1800. Paley's claim is that there "cannot be design without a designer." Darwin would show otherwise. The most significant of Darwin's achievements, writes Francisco Ayala, is not that he provided convincing evidence for evolution, but that he discovered natural selection, the process that accounts for the "design" of organisms. Paley sought to explain away the imperfections and deficiencies of organisms by assigning them "little or no weight" compared to the copiousness of organisms and the functionality of their parts. Indeed, claims Michael Behe, a contemporary exponent of the argument-from-design, why should one expect excellence of design? Ayala points out that it is not only that organisms and their parts are less than perfect, but also that deficiencies, dysfunctions, and "cruelties" are pervasive and incompatible with any kind of design expected from an intelligent designer.

EXTENSIONS OF EVOLUTIONARY THEORY

Richard Lenski reviews emerging opportunities for research in two areas of evolutionary biology. Exploring the evolutionary connections between molecular genetics, organismal development, and ecological phenotypes is one area. One theme within this area emerges from recent investigations of the mechanistic processes yielding adaptation, as evolving, for example, in laboratory bacterial populations over thousands of generations. A second theme concerns molecular processes, such as mutational mechanisms that influence a population's capacity for future evolution. Lenski's second area is artificial life: human-created systems that self-replicate, mutate, and evolve by natural selection. Artificial life offers powerful opportunities for investigating evolutionary dynamics and mechanisms. Moreover, Lenski claims, genetics and evolutionary knowledge applied to technologies, such as software and robotics, may alter the evolution of our own species.

Human groups are adaptive units and not only collections of self-interested individuals, writes David Wilson. Social scientists shared this view from the start, but this construction became diminished, if not altogether obliterated by evolutionists. Multilevel selection theory has returned and is here to stay, claims Wilson: "thinking about groups as potentially adaptive units, in the same way that everyone is accustomed to thinking about individuals."

PHILOSOPHY AND EPISTEMOLOGY

Mayr (2002) has written that in evolutionary literature, the word "species" occurs in three combinations, "species concept, species taxon, and species category." Michael Ghiselin's paper is a critical gloss of the two-page publication by Mayr from which that phrase has been extracted. Ghiselin concludes that the word "species" should be identically used in taxonomy

as in the study of evolutionary mechanisms. "Having a system of classification in which the units of systematics are identical to those of population genetics is essential for clear thinking about biology."

Elliott Sober writes about two philosophical topics that have engaged Mayr's sustained attention for decades: population thinking and essentialism. Darwin's theory of evolution by natural selection is, for Mayr, a new kind of theory, says Sober, which is anti-essentialist and replaced essentialist modes of thought with "population thinking." Sober seeks to explicate how "are we to understand the difference between essentialism and population thinking in terms of what each holds to be 'real' about biological reality."

Mayr has argued for the autonomy of biology as a science, writes Franz Wuketits, because biology has distinctive methods, explanations, and theories. Wuketits reviews Mayr's arguments and, in the second half of the paper, summarizes them as elucidated in *This is Biology* (1997): biology is a historical science, which classifies and systematizes an enormous variety of objects; has laws and principles that are different from physical ones; and requires teleological explanations, which are answers to the question "what for."

Teleology in biology is the subject investigated by Ana Barahona and Erica Torrens. Aristotle saw that a full account of an object or process requires that four questions be answered: what is it made of? what is its distinctive configuration? how it was produced? what is its function or purpose? These questions identify the *aitia*, or "grounds of explanation," that we need to know in order fully to understand the object or entity: material, formal, efficient, and final. The word *aition* was translated into Latin and modern languages as "causa" or "cause", with no end of misunderstandings because cause in modern usage refers only to Aristotle's efficient *aition*. Teleological explanations were suitably excluded from the physical sciences but, according to Barahona and Torres, are indispensable in evolutionary biology, because organisms have functions and have evolved to meet environmental challenges. It does not make sense to ask what is the natural function of a mountain or a galaxy, but it is appropriate to investigate the function of the kidneys and the process by which they evolved in order to meet certain organisms' needs.

There is an "internalist" view of evolution, where genetic mutation and genomic recombination (including symbiosis) appear as the fundamental processes and natural selection plays a secondary role, acting as a sieve or filter. Recent genetic developmental approaches to the study of evolution, so much in vogue and so successful, are representative, according to Andrés Moya and Amparo Latorre, of internalist evolution. Population genetics represents the "externalist" approach to evolutionary theory. Natural selection is the predominant process that yields adaptation and

highly-organized entities (*i.e.*, organisms), while mutation and genome dynamics provide, so to speak, the raw materials. Moya and Latorre explore the controversies emanating from claims of molecular neutrality and quantum equilibria, and conclude arguing for the need of a fourth “dimension” in evolutionary explanations, namely self-organization. The other three dimensions are mutation, chance, and natural selection.

Gerhard Vollmer’s “New arguments in evolutionary epistemology” starts from the consideration that our brain construes the world, as three-dimensional and time-oriented, from signals flowing from our sense organs, but based on principles that are not fully emanating from external stimuli. The question of how these principles “come into our head” is the central question of evolutionary epistemology. Vollmer characterizes evolutionary epistemology as a naturalistic position, resting upon organic evolution, and responds to familiar objections: Does the concept of truth make sense? Is cognitive justification circular? How can cognitive structures become adapted to environments that presuppose adaptation? Vollmer justifies evolutionary epistemology with clever arguments based on creole languages and on language learning by children and deaf-mutes.

HISTORICAL CONTEXT

Garland Allen seeks to ascertain Mendel’s “real” motivation for his experiments. Allen convincingly defends Mendel’s true discovery of the fundamental laws of biological heredity, against the claim made by Robert Olby and others that this “discovery” was a twentieth century construction perpetrated by Bateson and other early Mendelians. After considering the recent advances of genomics and the fertile convergence of developmental and evolutionary genetics, Allen concludes that we are “standing at a continental divide between an old and a new genetics: a mosaic and mechanical view of the organism and a holistic and integrated perspective that promises to yield exciting results.”

“Mayr introduced me to historical figures I had not met before,” writes Jane Maienschein, while pointing out Ernst Mayr’s original views of biological history in his monumental *The Growth of Biological Thought* (1982). Mayr “presented familiar figures like Oscar and Richard Hertwig or August Weisman in different ways casting light on the historical figures and ideas while also illuminating his own.” Maienschein’s paper is a fruitful interpretative amalgam of Darwin’s embryological ideas and Mayr’s interpretation of Darwin’s ideas. She notes Mayr’s sympathies for the late nineteenth century use of descriptive and then comparative embryology for understanding evolution, because this approach, although problematic, seemed far preferable “to falling back on von Baer’s essentialist and linear thinking.” Mayr at times belittled embryology’s relevance to evolution, because the “translation of the genetic program into molecular chains

of events during ontogeny [refer] to proximate causations." But, Maienschein argues, "proximate causes matter the most because they turn what would be an inert evolutionary past and genetic program into actual living organisms."

NOTE

¹ I want to note that Mayr published two important books at age 97 (Mayr 2001 and Mayr and Diamond 2001), and that as I write this in May 2004, Mayr has one additional book in press. On 18 February 2004, he wrote to me: "My next book is in the hands of Cambridge U. Press, but it won't come out until August or September [2004]."

REFERENCES

- Bock, W. J. (1994), "Ernst Mayr, naturalist: His contributions to systematics and evolution," *Biology and Philosophy* 9: 267-327.
- Darwin, C. (1859), *On the Origin of Species by Means of Natural Selection*. London: Murray.
- de Vries, H. (1900), *Revue générale de botanique* 12: 257-271.
- Dobzhansky, T. (1937), *Genetics and the Origin of Species*. New York: Columbia University Press.
- Fisher, R. A. (1930), *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.
- Haldane, J. B. S. (1932), *The Causes of Evolution*. New York: Harper.
- Mayr, E. (1942), *Systematics and the Origin of Species*. New York: Columbia University Press.
- Mayr, E. (1980), "Prologue: Some thoughts on the history of the Evolutionary Synthesis," in Mayr, E. and W. Provine (eds.), *The Evolutionary Synthesis*. Cambridge, MA: Harvard University Press, pp. 1048.
- Mayr, E. (1982), *The Growth of Biological Thought. Diversity, Evolution, and Inheritance*. Cambridge, MA: Harvard University Press.
- Mayr, E. (1997), *This is Biology: The Science of the Living World*. Cambridge, MA: Harvard University Press.
- Mayr, E. (2001), *What Evolution Is*. New York: Basic Books.
- Mayr, E. (2002), "Comments by Ernst Mayr," *Theory in Biosciences* 121: 99-100.
- Mayr, E. and Diamond, J. (2001), *The Birds of Northern Melanesia. Speciation, Ecology, and Biogeography*. Oxford, New York: Oxford University Press.
- Mendel, G. (1866), *Verhandlungen des Naturforschenden Vereines, Abhandlungen, Brünn* 4: 3-47.
- Provine, W. G. (1971), *The Origins of Theoretical Population Genetics*. Chicago and London: University of Chicago Press.
- Simpson, G. G. (1944), *Tempo and Mode in Evolution*. New York: Columbia University Press.
- Stebbins, G. L. (1950), *Variation and Evolution in Plants*. New York: Columbia University Press.
- Wright, S. (1931), "Evolution in mendelian populations," *Genetics* 16: 97-159.