

## The Neo-Modern Synthesis: The Confluence of New Data and Explanatory Concepts

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## The Neo-Modern Synthesis: The Confluence of New Data and Explanatory Concepts

**Evolution—the Extended Synthesis.** Massimo Pigliucci and Gerd B. Müller, eds. MIT Press, 2010. 504 pp., illus. \$35.00 (ISBN 9780262513678 paper).

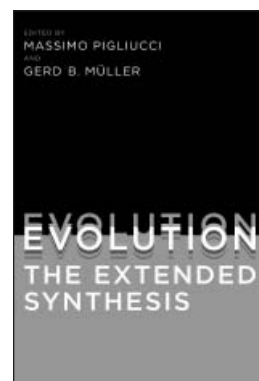
The relentless advance of biotechnology has provided evolutionary biologists with a growing stream of genetic, epigenetic, and paleochemical data. Plasmids, transposable elements, and microRNAs are subjects of study, and new concepts are challenging the established theory—which, in many ways, has absorbed the majority of the newer findings reasonably well. New fields have grown around the new data, among them genomics, proteomics, and metabolomics, whereas older fields, such as statistical genetics, have found new life in the realm of bioinformatics, microarray expression analysis, and association studies. In *Evolution—the Extended Synthesis*, the product of a 2008 conference in Altenberg, Austria, contributors describe and discuss these and other topics with the overall aim of “extending beyond the boundaries of the classical framework.” This edited volume is an impressive and provocative overview; it should become the focus of semester-long graduate student reading groups across the country, as it has at my home institution.

One of the most important fruits of the advances in biotechnology is a better understanding of the complex relationship between genotype and phenotype. Taken together, the chapters by Wray and Purugganan, in conjunction with concepts discussed in those of Müller, and Wagner and Draghi, provide a fairly thorough and synthetic overview. Importantly, each chapter raises current unsolved questions, an approach that will serve beginning graduate students excep-

tionally well. I would encourage these students to pursue the empirical implications of Wray’s remark: “Evidence is accumulating that the traditional focus on coding sequences misses out on a large fraction of mutations of adaptive significance within a genome” (p. 105). Much of the current focus of molecular evolutionary biology is on variations among structural genes among closely related species, even as evidence builds that these may remain invariant while changes in the regulatory process continue apace. Where classic statistical genetics gave us variance components and whole-genome average effects, modern association studies give insight into the contributions of single genes or gene combinations to standing variation. Sewall Wright’s viewpoint (expressed during the modern synthesis) was that the classic one-gene model with constant fitness effect is “wholly inadequate” as a description of phenotypic evolution. This view has been abundantly supported by the subsequent flood of genomic data. Microarray studies have revealed that Wright’s idea—pleiotropy of single-gene effects pertaining to a handful of morphological traits (that he studied in guinea pigs)—is nothing compared with the extensive levels of pleiotropy observed among gene expression phenotypes, which can involve the simultaneous up- and down-regulation of hundreds, if not thousands, of different genes.

My biggest concern with this volume *in toto* is the tendency of some of the chapter authors to award to “new discoveries” the function of a “better and faster” adaptive process. In a changing environment, adaptive variants may fare better than less flexible ones. Imagine a scenario in which the environment points, the generative processes click, and novel adaptive variants appear. What could possibly be the problem with a capac-

ity for instantaneous adaptive plasticity, whereby an organism lets go of one phenotype in order to express another, more fit phenotype, exactly when and where it is environmentally required? If possible, why not do so by extra-Mendelian methods, since the classical adaptive process (the substitution of one gene for another) is so gradual and tediously incremental? If adaptation by natural selection is good, isn’t faster adaptation by other methods better?



The concepts of capacitance, facilitated variation, and evolvability tend to be coupled with known or inferred modes of epigenetic inheritance as a means to rapidly achieve adaptive plasticity, which in turn may facilitate the invasion of new niches, speciation, and even entire adaptive radiations. Such terms grate on the nerves of some of my theoretical colleagues. Will such ideas elbow their way to the front of academic discourse and investigation, as did the discovery of genes at the beginning of the 20th century? Maybe, but it will not happen without researchers addressing a number of sticky problems and supporting their hypotheses with concrete, well-worked empirical examples. For example, if the cellular machinery underlying such processes is influenced by genes, then there are important limitations to this

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argument and serious constraints on its usefulness.

The book discusses amazing examples in the literature of plastic and adaptive phenotypes, including the famous defensive morphologies of *Daphnia* induced by the presence of predators; the winged and wingless morphs of bean beetles induced by resource depletion; and the quorum-sensing genes of bacteria, which control suites of genes, induced by high density. The latter are particularly important to human health because of their role in virulence and the formation of biofilms.

In contrast, when a gene is expressed only in response to a specific environmental stressor, spatially or temporally restricted in its extent—such as extreme temperatures, density, or disease—that gene does not experience very strong natural selection. Copies of the gene are not expressed in those individuals who do not encounter the environment. As a result, these genes are not screened by natural selection but rather become targets for mutation. Total selection on the genes underlying the capacity for plastic phenotypic responses is the average of the selection experienced by the proportion of copies expressed and the proportion not expressed. Total selection is weakened because of this averaging, and the mutational load of these genes is increased in proportion to the rarity of the environment. Indeed, adaptation to very rare environments is hardly possible: If not expressed frequently enough, mutation, accumulation, and mutational meltdown eliminate the genetic basis for the capacity for such flexibility. If all is not lost, then the expected level of polymorphism for persisting genes will be higher, as will the divergence of these genes among closely related taxa. Although evolutionary biologists prefer to interpret genetic differences among taxa as being the result of strong positive natural selection, these “plasticity genes” diversify among taxa for the opposite reason—a relaxation of selection. The pattern across taxa is the same—immense diversification—but the explanations are polar

opposites: strong diversifying selection versus relaxed constraint. This type of alternative explanation, founded in classical theory, is not often discussed and is overlooked in the enthusiasm to embrace newer, but untested, concepts.

One field likely to be enhanced by this volume is evolutionary developmental (evo-devo) biology. Anticipation of the merging of these two disciplines has been ongoing for 100 years; in fact, Wright, who joined the faculty of the University of Chicago in 1925, was hired by the great embryologist and then chair of the Department of Zoology Frank R. Lillie, with the expectation that Wright’s research would help integrate the fields of evolution and development. Almost every chapter in this work is relevant to evo-devo students. Although some current topics also construed as extensions of the modern evolutionary synthesis (e.g., new discoveries in human evolution, biochemical taphonomy, geoinaging technologies) do not appear in this book, I strongly recommend the reading and critical discussion of *Evolution—the Extended Synthesis* to all.

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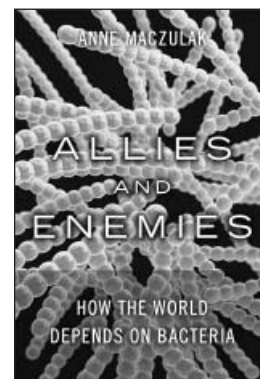
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### WHERE IS THE BEAUTY AND EXCITEMENT OF THE BACTERIAL WORLD?

**Allies and Enemies: How the World Depends on Bacteria.** Anne Maczulak. FT Press, 2010. 224 pp., illus. \$24.99 (ISBN 9780137015467 cloth).

As the primary title of Anne Maczulak’s book promises, most of the content of *Allies and Enemies: How the World Depends on Bacteria* concerns the dichotomy of bacterial pathogens

versus bacteria as useful facilitators of various industries and technologies. The book’s subtitle, however, may require more of a departure from a human-centered point of view. Although Maczulak hints at it throughout, I don’t think she quite captures with examples the overwhelming and pervasive existence of microbes that is completely separate from (and oblivious to) the narrow interests of humans. Maczulak may interpret the “world” to mean the human world, but the fact is that we humans dwell *within* a bacterial world, which Maczulak fails to firmly establish.



It is a challenge with any popular book on bacteria to know the background and expectations of its target audience. Maczulak attempts to include general information on cells throughout the book, but with a volume of just 170 pages, it may have been more efficient to start with basic microbiology, make several main points understood in the first chapter, and then move on to the illustrative examples. Instead, her efforts at introduction were confusing. For example, archaea are briefly introduced as being synonymous with extremophiles, which they are not; there may be many more mesophilic archaea. Meanwhile, Maczulak confounds her assertion by introducing various interesting extremophiles, among them both bacteria and archaea, but she fails to distinguish between the two. Ten pages later comes the canonical Woeseian family tree that typically introduces archaea.

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