

EVOLUTION—THE EXTENDED SYNTHESIS

edited by Massimo Pigliucci and Gerd B. Müller

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1 Elements of an Extended Evolutionary Synthesis

Massimo Pigliucci and Gerd B. Müller

More than half a century has passed since the integration of several strands of evolutionary thought into what came to be called the Modern Synthesis (MS), the conceptual framework that has defined evolutionary theory since the 1940s. Despite significant advances since then in all methodological and disciplinary domains of biology, including molecular genetics, developmental biology, and the “-omics” fields, the Modern Synthesis framework has remained surprisingly unchanged. Although it is still regarded as the standard theoretical paradigm of evolutionary biology, for several years now dissenters from diverse fields of biology have been questioning aspects of the Modern Synthesis, and pivotal novel concepts have been elaborated that extend beyond its original scope (e.g., Maynard Smith and Szathmáry 1995; Jablonka and Lamb 1995; Schlichting and Pigliucci 1998; Gould 2002; Müller and Newman 2003; Odling-Smee et al. 2003; West-Eberhard 2003; Kirschner and Gerhart 2005). As a result, calls for an expansion of the Modern Synthesis framework have intensified (R. L. Carroll 2000; Love 2003a; Kutschera and Niklas 2004; Müller 2007; Pigliucci 2007; Rose and Oakley 2007; S. B. Carroll 2008), prompting further scientific debate (Pennisi 2008; Whitfield 2008).

Under the heading “Extended Synthesis” this volume represents a broad survey of key ideas in this multifaceted research program, and a first look at an expanded theory of evolution as a work-in-progress. We have gathered some of the most prominent authors who have been writing about new directions in evolutionary biology and asked them to explain where they think the field is headed, and how the new concepts square with the Modern Synthesis’s view of what evolution is. Some of these authors are skeptical that any fundamental changes are discernible in the current positions, while others lean toward major revisions of the MS. Most contributors fall somewhere in between, accepting many of

the central tenets of the current framework, while wanting to relax some of its assumptions and to introduce what they see as significant conceptual augmentations of the basic MS structure— just as the architects of the Modern Synthesis themselves had done with previous versions of Darwinism and the ideas that had been debated by biologists around the turn of the twentieth century.

Whenever we talk to colleagues who are inclined toward a conservative position about the status of evolutionary theory, we are confronted with the question “So, what exactly is so new that we may speak of an Extended Synthesis?” This volume is the beginning of a response to that question, and we shall provide the reader with an overview below. The commonest reaction to our explanations is something along the lines of “But that is already understood as part of the Modern Synthesis anyway.” We beg to differ. Many of the empirical findings and ideas discussed in this volume are simply too recent and distinct from the framework of the MS to be reasonably attributed to it without falling into blatant anachronism. Concepts such as evolvability (Wagner and Altenberg 1996; R. L. Carroll 2002; Love 2003b; Wagner 2005; Hansen 2006; Hendrikse et al. 2007; Colegrave and Collins 2008; Pigliucci 2008), for instance, did not exist in the literature before the early 1990s; phenotypic plasticity (West-Eberhard 1989; Scheiner 1993; Pigliucci 2001; Schlichting and Smith 2002; West-Eberhard 2003; Borenstein et al. 2006) was known, but consistently rejected as a source of nuisance, not of significant micro- and macro-evolutionary change. Or consider *EvoDevo*, an entirely new field of evolutionary research that has emerged in full only since the late 1980s, precisely because of the perceived explanatory deficits of the MS in the realm of phenotypic evolution (Laubichler and Maienschein 2007; Müller 2007, 2008; Sansom and Brandon 2008). Yet another common retort to our arguments is that the new ideas are “not inconsistent” with the framework of the Modern Synthesis; this may very well be true—and most of us would gladly agree—but being consistent with the MS is not at all the same thing as being a part of the MS!

Much of the confusion and resistance to new ideas may derive from the fact that evolutionary biologists of course have gradually updated their thinking beyond the Modern Synthesis, without necessarily paying too much attention to the fact that in so doing, they have stepped well outside of its original boundaries. Also part of the problem is that most practicing biologists do not have the time to read the papers, and especially the books, that shaped and solidified the MS during the 1930s and 1940s, and therefore may not be too familiar with its actual claims.

Therefore, before plunging into this book's examination of how the Synthesis is already extended in the current usage of evolutionary biologists, it may be useful to briefly summarize the conceptual history of evolutionary thought as well as the basic tenets of the Modern Synthesis. This will put us in a better position to judge how the ideas advanced in this volume relate to the central corpus of the discipline, and how much of an extension is really warranted or provided.

Modern evolutionary thought, of course, began with Charles Darwin and Alfred Russel Wallace's paper to the Linnean Society (1858), although the idea of biological change over time had been around since ancient Greek philosophy. The original Darwinism, as it was soon to be known, was based on two fundamental ideas: the common descent of all living organisms, and the claim that natural selection is the major agent of evolutionary change, as well as the only one that can bring about adaptation. The first idea was quickly accepted (indeed, it had been advanced by others before Darwin, though nobody had done the hard work of systematically collecting evidence in its favor). Natural selection, on the other hand, was more controversial, and Darwinism underwent a period of "eclipse" (Bowler 1983) in the scientific community toward the end of the nineteenth century. According to Julian Huxley, who actually coined the term "eclipse" for that period, several alternative evolutionary mechanisms were proposed at the time, including a revival of Lamarckian-type inheritance (which Darwin himself had flirted with), so-called orthogenesis (macroevolutionary trends directed by internal forces), and saltationism, the idea that evolutionary change is not gradual, as assumed by Darwin, but proceeds in major leaps.

During the same period, by contrast, Wallace and August Weismann pushed a view of evolution that again situated natural selection at the forefront, but eliminated any vestiges of Lamarckism. The physiologist George Romanes famously coined the term neo-Darwinism (not to be confused, as it so often is, with the Modern Synthesis) to mock Wallace and Weismann's pan-selectionist theories. Things did not look any better for the Darwinian view of evolution at the onset of the twentieth century, when the rediscovery of Mendel's work and the beginnings of genetics appeared to deal a blow to the theory. The problem was that Mendel's laws, as well as the newly discovered phenomenon of mutations, implied that there could not be any "blending of inheritance" (the second idea about inheritance, after Lamarckism, to which Darwin had turned in a halfhearted attempt to complete his theory). Mendelian traits seemed to be inherited as discrete units, which would imply the impossibility of

gradual evolutionary change: Lamarck may have been definitely abandoned by then, but saltationism was alive and well.

It is this perceived contrast between Mendelism and neo-Darwinism that set up the conditions for what was to become the Modern Synthesis. A group of mathematically oriented biologists, including Ronald Fisher, J. B. S. Haldane, and Sewall Wright, began work that eventually showed that there was no contradiction between Mendelian genetics, the observation of mutations, and the more continuous variation in so-called quantitative characters that was the focus of neo-Darwinism. Fisher's 1918 paper, "The Correlation between Relatives on the Supposition of Mendelian Inheritance," which in particular was the milestone that demonstrated that Mendelian traits affected by several genes would produce the phenotypic distribution typical of quantitative characters (a bell curve), the smoothing of the distribution being ensured by the combination of the additive effects of several loci and the blurring effect of environmental variation. Fisher's 1930 book, as well as seminal papers by Haldane (1932) and Wright (1932), established the field of population genetics, today still considered the theoretical-mathematical backbone of evolutionary biology.

That work by itself, however, did not constitute the Modern Synthesis. The process took another several decades to complete (essentially ranging from 1918, when Fisher's paper appeared, to 1950, the year of publication of Stebbins's seminal book on plant evolution). What was needed was the understanding and acceptance of population genetics by the majority of practicing evolutionary biologists, as well as an articulation of the new ideas in direct reference to the classic disciplines of natural history, systematics, paleontology, zoology, and botany. This happened thanks to the now classic books by Dobzhansky (1937), Mayr (1942), Simpson (1944), Stebbins (1950), and Rensch (1959), although it was the 1942 volume by Julian Huxley that introduced the term Modern Synthesis into evolutionary jargon.

The major contributions of these authors are now well known, but need to be briefly revisited in order to build our case that the MS did not, in fact, include most of the concepts examined in this volume. Dobzhansky was one of the first geneticists to work with natural populations, and contributed mounting evidence (especially with his famous "GNP" series; Provine 1981) that there is much more variation for quantitative traits than previously suspected; since this variation is the fuel for natural selection, and hence essential to the neo-Darwinian process, Dobzhansky helped to establish population genetics as the empirical

field that provided the long-missing piece to the original Darwinian puzzle.

Up to this point one could consider the MS as, in fact, a synthesis: from Fisher to Dobzhansky, it was a fusion of neo-Darwinism and Mendelism achieved through the theory and practice of the new population-statistical genetics. The other major contributions, however, went beyond synthesis to actually adding new concepts to the neo-Darwinian edifice, and in some cases to even contradicting some of Darwin's own positions. Take, for instance, Mayr's related ideas of the so-called biological species concept and of allopatric speciation. Despite the fact that they are both still controversial today (Mishler and Donoghue 1982; Templeton 1989; Grant 1994; Sterelny 1994; Barraclough and Nee 2001; Hey 2001; Schluter 2001; Pigliucci 2003; Coyne and Orr 2004; Gavrilets 2004; de Queiroz 2005), they were a direct rebuttal of Darwin's conception of species as arbitrary demarcation lines imposed by the human mind on an otherwise continuous process of diversification (which is why *The Origin of Species* does not really deal with, well, the origin of species). Mayr made species into the fundamental unit of the biological hierarchy, a move that implied that the study of the process of speciation is part and parcel of what an evolutionary biologist ought to do. This was definitely going beyond, not just synthesizing, neo-Darwinism and Mendelism.

The contributions of Simpson (paleontology) and Stebbins (botany), while historically important, are much less clear from a conceptual perspective. Simpson's *Tempo and Mode in Evolution* (1944) reflects the author's own ambiguity about what is often referred to as "the hardening" of the synthesis in the late 1940s and beyond, when more heterodox ideas were purged or marginalized to yield the core that still characterizes evolutionary theory today. Here the "synthesis" was achieved as much through exclusion as it was through integration. For instance, Simpson initially defended—on the basis of paleontological evidence—the idea that macroevolutionary change may occur very rapidly, on a geological scale. While his concept of tachytelic (fast) evolution may not have been intrinsically incompatible with the MS emphasis on gradualism, it was eventually dropped in favor of a more prosaic view in which microevolutionary processes directly extrapolate to macroevolutionary time scales, rendering paleontology little more than an appendage to the population genetic view of things. We had to wait until Eldredge and Gould's (1972) challenge of punctuated equilibria for that debate to be reignited.

The situation is similar for Stebbins: it is hard to see why, exactly, botany needed to be “brought in” with the Modern Synthesis, unless the plant world offered a perspective significantly different from the typically animal-centric (mostly, in the case of population genetics, *Drosophila*-centric) view. The work of Stebbins and others did have the potential to challenge central concepts of the MS, beginning with Mayr’s insistence on the “biological” species concept and allopatric speciation. Plants are known to exhibit a variety of isolating mechanisms that make it difficult to fit one simple criterion to the reality of plant species, and instantaneous, sympatric speciation is common in plants through hybridization and both allo- and auto-polyploidization. But none of this came to be considered anything other than a set of curious “exceptions” by the central architects of the Modern Synthesis, particularly Mayr, or by their modern intellectual heirs (Coyne and Orr 2004).

As is well known, other branches of biology were left entirely out of the Modern Synthesis, which is a major reason why so many authors in recent years have clamored for its expansion. Most famously, embryology and developmental biology were not incorporated, despite a long tradition of research that had yielded tantalizing insights into the evolution of organismal form (Gould 1977). This may very well have been at least in part a result, as Mayr often claimed, of the lack of interest on the part of developmental biologists, or perhaps it happened because there was at the time no figure in that field comparable to the likes of Simpson or Stebbins. In any case, the need for the growing field of *EvoDevo* to be explicitly and organically incorporated into evolutionary theory is obvious and largely undisputed (Robert 2004; Müller and Newman 2005; Müller 2007; Love 2006; S.B. Carroll 2008).

Curiously largely unnoticed is the fact that ecology also missed out on the Modern Synthesis. The closest the MS came to ecology was the establishment of the field of evolutionary ecology, almost single-handedly started by Ford (1964). But Ford and his intellectual descendants worked very much within the standard Fisherian model of almost exclusive emphasis on natural selection and population genetics, and ecology as a field kept developing with little to add to, or import from, evolutionary biology (a situation that persists today, despite the widespread existence of departments of “ecology and evolutionary biology” throughout the world). This lacuna began to be addressed only much later by unorthodox researchers such as Van Valen (1973) with his “Red Queen Hypothesis” and Odling-Smee (2003) with his work on the concept of “niche construction.” Much still needs to be done in this area.

Be that as it may, the Modern Synthesis became the established framework in evolutionary biology, which has been summarized by Douglas Futuyma (1986: 12) in the following fashion:

The major tenets of the evolutionary synthesis, then, were that populations contain genetic variation that arises by random (i.e., not adaptively directed) mutation and recombination; that populations evolve by changes in gene frequency brought about by random genetic drift, gene flow, and especially natural selection; that most adaptive genetic variants have individually slight phenotypic effects so that phenotypic changes are gradual (although some alleles with discrete effects may be advantageous, as in certain color polymorphisms); that diversification comes about by speciation, which normally entails the gradual evolution of reproductive isolation among populations; and that these processes, continued for sufficiently long, give rise to changes of such great magnitude as to warrant the designation of higher taxonomic levels (genera, families, and so forth).

As we will see in the rest of this volume, several of these tenets are being challenged as either inaccurate or incomplete. It is important, however, to understand the kind of challenge being posed here, in order to avoid wasting time on unproductive discussions that miss the point of an extended evolutionary synthesis. Perhaps a parallel with another branch of biology will be helpful. After Watson and Crick discovered the double-helix structure of DNA, and the molecular revolution got started in earnest, one of the first principles to emerge from the new discipline was the unfortunately named “central dogma” of molecular biology. The dogma (a word that arguably should never be used in science) stated that the flow of information in biological systems is always one way, from DNA to RNA to proteins. Later on, however, it was discovered that the DNA > RNA flow can be reversed by the appropriately named process of reverse transcription, which takes place in a variety of organisms, including some viruses and eukaryotes (through retrotransposons). Moreover, we now know that some viruses replicate their RNA directly by means of RNA-dependent RNA polymerases, enzymes also found in eukaryotes, where they mediate RNA silencing. Prions have shown us how some proteins can catalyze conformational changes in similar proteins, a phenomenon that is not a case of replication, but certainly qualifies as information transfer. Finally, we also have examples of direct DNA translation to protein in cell-free experimental systems in the presence of ribosomes but not of mRNA. All of these molecular processes clearly demolish the alleged central dogma, and yet do not call for the rejection of any of the empirical discoveries or conceptual

advances made in molecular biology since the 1950s. Similarly, we argue, individual tenets of the Modern Synthesis can be modified, or even rejected, without generating a fundamental crisis in the structure of evolutionary theory—just as the Modern Synthesis itself improved upon but did not cause the rejection of either Darwinism or neo-Darwinism.

Specifically, this book presents six sections aimed at outlining the directions that contribute to an Extended Synthesis, with the goal of stimulating further conceptual discussion and empirical work to move the field forward. Part II concerns significant advances in our understanding of the tightly linked ideas (in the MS) of natural selection and adaptation. John Beatty explores the relative roles of contingency and chance variation in evolutionary theory, important because the balance between these and determining processes such as natural selection seems to be perennially shifting in the minds of biologists. Sergey Gavrilets writes about what happens when one takes seriously the idea that adaptive landscapes—introduced as a powerful metaphor by Sewall Wright in the 1930s—are mathematical constructs of very high dimensionality and surprising properties. David Sloan Wilson revisits the debate on group selection, a concept that has experienced vertiginous ups and downs since the 1960s, and brings it up to modern standards within the broader context of multilevel selection theory.

Part III deals with the new information from molecular genetics and genomics that brings significant new issues to evolutionary theory. It begins with Gregory Wray's characterization of the consequences of a shift of focus from individual genes to gene networks. Michael Purugganan continues with his analysis of the revolutionary impact of genomic science on the study of evolution.

Part IV tackles the kinds of hereditary and replicatory mechanisms that are not considered within the framework of the Modern Synthesis, and that pose theoretical and empirical hurdles for it: Eva Jablonka and Marion J. Lamb present the case of transgenerational epigenetic inheritance, John Odling-Smee treats niche inheritance, and Chrisantha Fernando and Eörs Szathmáry discuss replication in systems chemistry and extend the replicator principle to neuronal evolution, brains, and language.

Part V is dedicated to the ongoing revisions of the MS that come from the new field of evolutionary developmental biology (EvoDevo), and contains chapters by Marc Kirschner and John Gerhart on the contribution of developmental systems to evolutionary variation, by Stuart Newman on the developmental-genetic mobilization of physical forces

in the origin of animal body plans, and by Gerd Müller on the roles of development in the generation of phenotypic innovation. Part VI considers principles of macroevolution and evolvability that are outside the scope of the traditional Modern Synthesis. David Jablonski writes about the large-scale evolutionary processes underlying patterns of innovation, and Massimo Pigliucci considers the potential role of phenotypic plasticity in macroevolution. Günter P. Wagner and Jeremy Draghi present an essay on the evolution of evolvability.

We conclude with part VII, which consists of two essays, by the philosophers of science Alan Love and Werner Callebaut, which explicitly discuss the conceptual structure and theoretical implications of both the Modern Synthesis and the ongoing expansions, presented in this volume and elsewhere, that we collectively term the Extended Synthesis (figure 1.1).

Though part VII provides detailed considerations of the theoretical and philosophical implications of an extended evolutionary framework, we will briefly reflect here on whether the extended approach differs in any principal aspects from the traditional account. Couldn't it be argued, for instance, that the new views introduced through molecular genetics

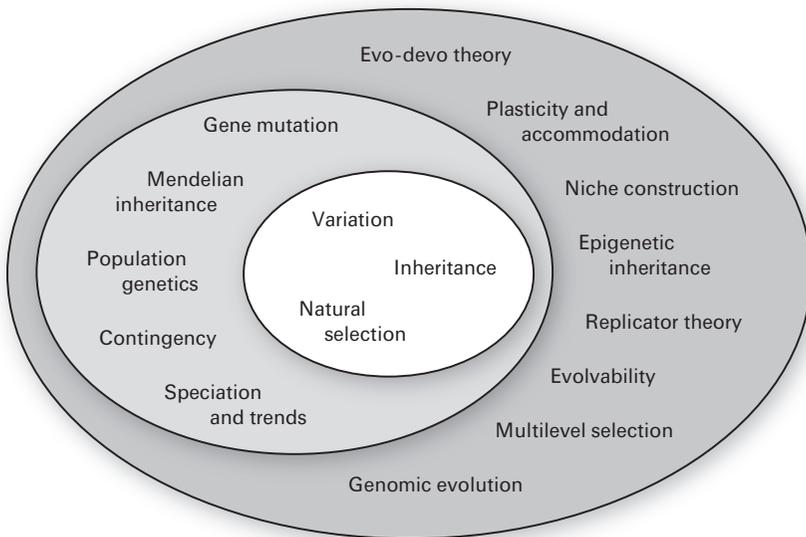


Figure 1.1

Schematic representation of key concepts of Darwinism (center field), the Modern Synthesis (intermediate field), and the Extended Synthesis (outer field). The scheme is meant to depict the broad steps in the continuous expansion of evolutionary theory, not to enumerate all concepts belonging to each of these steps.

and genomics merely add more detail to the classical concepts of variation and selection? Or that non-DNA based mechanisms of inheritance are still part of the inheritance component implicit in the theory anyway? Isn't the environment given merely a little more weight as one effective factor of change, with EvoDevo only adding new mechanistic detail explaining how development itself evolves? That is, besides the obvious disciplinary expansions, one may ask whether any of the general principles of the population-dynamical core of the classical theory are compromised by these new views. Well, no. The concepts we bring together in this volume for the most part do not concern population dynamics, our understanding of which is improved but not fundamentally altered by the new results. Rather, the majority of the new work concerns problems of evolution that had been sidelined in the MS and are now coming to the fore ever more strongly, such as the specific mechanisms responsible for major changes of organismal form, the role of plasticity and environmental factors, or the importance of epigenetic modes of inheritance. This shift of emphasis from statistical correlation to mechanistic causation arguably represents the most critical change in evolutionary theory today.

Underlying the shift toward a causal-mechanistic approach in evolutionary theory is a hugely expanded knowledge base consisting of large data sets in genetics, development, plasticity, inheritance, and other empirical domains. While the MS, in the absence of such data, had to contend with black-boxing all mechanistic aspects, and thus was unable to explain how organismal change is realized at the phenotypic level, the organism as an explanandum has returned through the extended accounts. The traditional theory treated phenotypic traits as abstract quantitative measures, but, as shown in this volume, it is now possible to establish naturalized models of evolutionary variation and innovation based, for instance, on gene regulatory and cell behavioral parameters. Similar functional and dynamical models of evolving processes are used in genetics, development, ecology, behavior, systems biology, and other fields of biology (Laubichler and Müller 2007). The predictions that follow from such qualitative models can be experimentally tested, and the outcomes can be compared with natural patterns of organismal change, a new feature entirely beyond the scope of the MS.

The ongoing shift from a population-dynamic account to a causal-mechanistic theory of phenotypic evolution brings with it a significantly expanded explanatory capacity of evolutionary theory. It has become possible to address phenomena of evolution that were untreatable by

the MS, and to cast them as “how” questions, such as How did body plans originate? How did homoplasies arise? How did novelties evolve? How do organisms change phenotypes in response to different environments? Whereas in the classical theory the traits used for quantitative studies were taken as given, the extended accounts can address the conditions of trait generation, fixation, and variation. That is, evolutionary theory is no longer confined to the explanation of the increase in frequency and maintenance of favorable variants, but also becomes a theory of the mechanistic conditions for the origin and innovation of traits.

The extended framework overcomes several basic restrictions and methodological commitments that had been necessary for the correlational approach of the MS to work. One is gradualism. Because the population-dynamic formalism operated on the assumption of continuous and incremental genetic variation, all nongradualist forms of evolutionary change were excluded. Several approaches discussed in this volume show that nongradual change is a property of complex dynamical systems, including biological organisms, and that various kinds of mechanisms for discontinuous change are now known from the domains of genome evolution, phenotypic plasticity, epigenetic development, and nongenetic inheritance. The dynamics of biological systems illuminates the capacity of continuous selectional regimes to produce the nongradual phenotypic change frequently observed in the paleontological record. Accounting for these forms of discontinuous change amounts to a significant extension of the evolutionary synthesis.

A second restriction overcome by the new approach is externalism. The nearly exclusive concentration of the Modern Synthesis on natural selection gave priority to all external factors that realize adaptation through differential reproduction, a fundamental feature of Darwinism not rooted solely in scientific considerations (Hull 2005). Organismal shape and structure were interpreted as products uniquely of external selection regimes. All directionality of the evolutionary process was assumed to result from natural selection alone. The inclusion of EvoDevo in particular, as shown in section five of this volume, represents a major change of this paradigm by taking the contributions of the generative processes into account, as entrenched properties of the organism promote particular forms of change rather than others. On this view, natural selection becomes a constantly operating background condition, but the specificity of its phenotypic outcome is provided by the developmental systems it operates on. Hence the organisms themselves represent the determinants of selectable variation and innovation. At the theoretical

level, this shifts a significant portion of the explanatory weight from the external conditions of selection to the internal generative properties of evolving phenotypes.

A third restriction of the Modern Synthesis is its gene centrism. The focus on the gene as the sole agent of variation and unit of inheritance, and the dogmatic insistence on this stance by the popularizers of the Synthesis, quelled all calls for more comprehensive attitudes. Although gene centrism has been a major point of contention, including strong criticism from philosophy of science (Keller 2000; Moss 2003; Neumann-Held 2006), this aspect could not be changed from within the paradigm of the MS, which rested on it both explicitly and implicitly. But gene centrism necessarily disappears in an extended account that provides for multicausal evolutionary factors acting on organismal systems' properties, including the non-programmed components of environment, development, and inheritance. Far from denying the importance of genes in organismal evolution, the extended theory gives less overall weight to genetic variation as a generative force. Rather, the opinions expressed in several contributions to this volume converge on the view of "genes as followers" in the evolutionary process, ensuring the routinization of developmental interactions, the faithfulness of their inheritance, and the progressive fixation of phenotypic traits that were initially mobilized through plastic responses of adaptive developmental systems to changing environmental conditions. In this way, evolution progresses through the capture of emergent interactions into genetic-epigenetic circuits, which are passed to and elaborated on in subsequent generations.

The overcoming of gradualism, externalism, and gene centrism are general hallmarks of the Extended Synthesis, whether in the forms presented here or in various other accounts to a similar effect published since the late 1990s. The editors and authors of this volume offer this extended view of evolutionary theory to the scientific community as, we hope, much food for thought and a stimulus for constructive discussions. It took almost four decades for the Modern Synthesis to take shape, and we certainly do not expect to achieve an equivalent result with a single edited volume. Others, including many not represented here, have advanced along similar intellectual lines, and more will undoubtedly do so in the near future. No matter what the final outcome, 150 years after the publication of the *Origin of Species*, evolutionary theory is still making enormous progress in its capacity to explain the world we live in.

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