# The Extended (Evolutionary) Synthesis Debate: Where Science Meets Philosophy

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*Recent debates between proponents of the modern evolutionary synthesis (the standard model in evolutionary biology) and those of a possible extended synthesis are a good example of the fascinating tangle among empirical, theoretical, and conceptual or philosophical matters that is the practice of evolutionary biology. In this essay, we briefly discuss two case studies from this debate, highlighting the relevance of philosophical thinking to evolutionary biologists in the hope of spurring further constructive cross-pollination between the two fields.*

For a number of years now, there have been debates in the biological literature about the status (i.e., whether it is necessary) of the so-called *extended (evolutionary) synthesis* (ES). The idea has been put forth and elaborated by a number of authors (e.g., Pigliucci and Müller 2010 and the references therein) that the time has come for a broad reevaluation of the current standard model in evolutionary biology, known as the *modern synthesis* (MS), which was crystallized by the classical writings of Dobzhansky, Huxley, Mayr, Simpson, and others during the 1940s and early 1950s (Mayr and Provine 1980).

At one extreme of a broad and complex spectrum of positions are perhaps authors such as Michael Lynch, who rejects any talk of ES and—paraphrasing a famous quip by Dobzhansky—boldly claims that "nothing in evolution makes sense except in the light of population genetics" (Lynch 2007, p. 8597). Lynch and other population geneticists (most prominently, Jerry Coyne, who is interviewed in almost every example of press coverage of the controversy; e.g., Whitfield 2008) think that the MS provides all the theoretical framework that evolutionary biologists need, despite mounting empirical discoveries of new phenomena (e.g., epigenetic inheritance) and the elaboration of entirely new concepts (e.g., evolvability; Pigliucci 2008) during the past several decades. Indeed, Lynch (2007) went so far as charging his scientific opponents of engaging in little more than uninformed musings comparable to those of intelligent-design creationists.

At the opposite extreme are some prominent proponents of the ES, such as Eva Jablonka (Jablonka and Raz 2009), who—on the basis of the very same empirical discoveries and conceptual advancements just mentioned—claim that the new biology has dealt an essentially fatal blow to the orthodox Darwinian, genecentric worldview of the MS (see also Newman and Linde-Medina 2013). The ES would therefore constitute something akin to what philosopher and historian of science Thomas Kuhn (1962) called a "paradigm shift."

Finally, somewhere in a (broad) middle ground, one can find most of the authors of a recent collection on the ES (Pigliucci and Müller 2010), who maintain that, ever since Darwin, evolutionary theory has actually never seen a paradigm shift (and it is not about to experience one now), but that it has nevertheless been characterized by continuous conceptual expansions, each of which has both added something significantly new and worthwhile and eliminated or greatly modified previous elements of its theoretical architecture. This sequence of expansions, roughly speaking, started out with the original Darwinism, as exemplified in the six editions of *On the Origin of Species*; expanded to neo-Darwinism, which was chiefly characterized by a more forceful rejection of Lamarckism than had been the case for Darwin, as well as by the introduction of Weismann's germ plasm theory; then expanded to the MS of Mendelism and Darwinism, largely made possible by the new science of population genetics. More recently, the theory has expanded again, it is argued, to the ES, which builds on earlier work previously considered peripheral to the MS (e.g., Simpson 1944, Eldredge and Gould 1972, Gould and Lewontin 1979, parts of Fisher 1999). This expansion includes new or

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highly revised concepts such as multilevel selection theory, transgenerational epigenetic inheritance, niche inheritance, facilitated variation, evolvability, and a distinction between microevolutionary and macroevolutionary processes, among others.

The sort of vigorous debate briefly sketched above is, we suggest, both typical of many areas of biology (including discussions on species concepts and on a number of ecological theories) and an excellent example of a dialogue at the interface of empirical biology, theoretical biology, and philosophy of biology. These are issues that can be settled decisively neither on empirical grounds (it is hard to imagine what sort of evidence, on its own, could possibly do that) nor even on a theoretical (as opposed to a broader conceptual) level—say, framed in the kind of mathematical terms that are the bread and butter of population genetic theory. The reason for this is that some of the crucial issues are conceptual (i.e., philosophical) in nature and hinge on not just matters of definition (what, exactly, counts as a *paradigm*?) but also on the entire framework that biologists use to understand what it is that they are doing (e.g., what is the relationship between systems of inheritance and natural selection, or, in multilevel selection theory, what counts as a *level* and why?). Kuhn (1962) famously referred to this as the "disciplinary matrix" characterizing a given field of inquiry.

In the rest of this essay, we explore two examples of discussions pertinent to the distinction, if there is one, between the MS and the ES and argue that such discussions hinge on an empirical–theoretical–conceptual triumvirate, thus constituting issues at the interface of biology and philosophy. We then conclude with some broader observations about why and within what limits continued discussions between biologists and philosophers of science may be fruitful. The two case studies in question have been chosen for exegetical purposes only, on the basis of their prominence in the literature discussing MS versus ES and because they are relatively straightforward to treat within the constrained space available here. However, we could have just as easily explored a number of other cases, including but not limited to the status of evo-devo (evolutionary development) research (Love 2009), the concept of niche construction (Laland and Sterelny 2006), issues surrounding evolvability (Pigliucci 2008), or any of the topics mentioned above.

## Case Study 1: Inheritance systems and the eternal specter of neo-Lamarckism

A major goal of evolutionary theory is to explain adaptation. Naturalists have explained the apparent end-directedness of biological traits using two theories: Darwinism and Lamarckism. Historically, these two options have been viewed as mutually exclusive and jointly exhaustive: Those who reject one are ipso facto committed to the other (Bowler 1989, Gould 2002).

Lamarckism is defined by claims about the mechanism and ontology of evolution. In Lamarckian evolution, individual organisms adapt themselves to their environments

and bequeath these adaptations to their offspring (Gould 2002). The claim about this mechanism is therefore that evolution follows from the transmission of acquired characteristics (i.e., traits acquired after the completion of ontogeny) from one generation to the next. The claim about ontology is that individual organisms evolve through their responses to environmental stimuli. As an explanation of adaptation, then, Lamarckism has two implications: first, that evolution is teleologically directed by the organism's responses to environmental input and, second, that individuals are the units of evolution—that is, the entities that change because of evolutionary processes (Grene 1990).

Darwinism, by contrast, is nonteleological and recognizes populations as the units of evolution. The theory of natural selection holds that when individuals in a population vary in some trait, transmit that trait to the next generation, and differentially reproduce as a result of the trait's instantiation, the population will evolve (Lewontin 1970). It is for this reason that Lamarckism is defined by the aforementioned claims about its mechanism and ontology and that Darwinism has been formulated (at least in part) in opposition to Lamarckism (Gould 1979, Bowler 1989).

The rediscovery of Mendelian genetics at the turn of the twentieth century seemed to settle the debate in favor of Darwinism, but research within the framework of the ES has spurred a reevaluation of this view. According to conventional wisdom, Mendelian genes exert the majority of the causal influences on phenotypes, and environmental influences on these genes are either limited or irrelevant to natural selection (Jablonka and Lamb 2010). The view of the early neo-Darwinists was that these genes are passed through germ-line cells, which are segregated from somatic cell lines in early development and are supposedly unaffected by the organism's conditions of life (Fisher 1999). Recent research into epigenetic inheritance, however, has shown that neither of these claims is universally true: The expression of some phenotypes is not attributable only to genes, and the germ line may be affected by environmental factors (Jablonka and Lamb 2005, 2010, Jablonka and Raz 2009, Lamm 2012, Planer 2014). Consequently, some have claimed—and others have been dismayed to imagine—that the ES constitutes a resurrection of Lamarckism.

Given that Lamarckian and Darwinian explanations of evolution are assumed to be mutually exclusive and given that the ES accommodates Lamarckian mechanisms of inheritance, it should follow that the ES constitutes a paradigm shift away from Darwinism (see Gissis and Jablonka 2011 for a collection of arguments to this effect). Nevertheless, as we have seen, most proponents of the ES maintain that the synthesis is meant to complement—rather than replace—Darwinian theory (Pigliucci and Müller 2010).

This is a debate that can profit from conceptual (and even historical) analysis: What are Lamarckian explanations, what are Darwinian explanations, and which of those are explanations that invoke the inheritance of acquired traits? Practical consequences follow from the answers to

these questions: Acceptance of Lamarckism would require evolutionary models that are quite different from those now in use because of attendant changes in their mechanism and ontology.

Two issues are, surprisingly, conflated in this debate and should be disentangled here: inheritance and evolution. Lamarckian mechanisms of inheritance are often taken to be both necessary and sufficient for Lamarckian evolution (e.g., Huxley 2010, Jablonka and Lamb 2010, Lamm 2012). This is because Lamarckian evolution requires the inheritance of acquired characteristics: If the locus of evolution is the individual and if evolutionary change is to be perpetuated, any evolutionary change in the individual must be transmissible to that individual's offspring. By contrast, Darwinian explanations of evolution are agnostic with respect to the mechanisms of inheritance (indeed, Darwin, himself, notoriously vacillated on this issue). Mendelian inheritance is the standard model in the MS, but, of course, populations may evolve by natural selection, in principle, even if variations are transmitted by non-Mendelian mechanisms.

Examples of epigenetic inheritance provide an excellent case in point. Jablonka and Lamb (2005, 2010) focused on four kinds of cellular epigenetic transmission: (1) *self-sustaining metabolic feedback loops*, wherein a metabolic gene in a parent cell produces its own activator, creating a positive feedback loop perpetuated down the cell lineage; (2) *structural inheritance*, wherein protein conformation is transmitted from parent to daughter cells; (3) *chromatin marking*, wherein DNA transcription is modified by the bonding of nucleotides to chemical groups that are transmitted down the cell line; and (4) *RNA-mediated inheritance*, wherein the transcription in a cell lineage is altered by the inheritance of small interfering RNA molecules from a parent cell. At least some of these changes are heritable, not only along somatic lines but also between somatic and germ lines, which means that acquired characteristics may be passed from ancestral to descendant organisms. These are Lamarckian mechanisms of inheritance; however, they are not sufficient for Lamarckian explanations of evolution.

The inheritance of epigenetic effects is not teleological. As Lamm (2012) noted, the epigenetic mechanisms listed above bias the transmission of phenotypes; however, bias is not the same as end-directedness. By definition, the mechanisms listed above transmit different phenotypes without changes in the genome, which implies that these sorts of inheritance are expressions of genotypic plasticity. Indeed, Jablonka and Lamb (2010) acknowledged that phenotypes changed by these epigenetic mechanisms may revert, given the proper environmental conditions. The persistence or reversion of an epigenetic change may depend on the change's selective advantage (Jablonka and Raz 2009). Therefore, the ostensibly acquired characteristics are, in fact, variations on genetic mechanisms preserved by natural selection (Haig 2007). Natural selection is not teleological, and, if the inheritance of epigenetic effects is the result of selection, epigenetic inheritance cannot be teleological either.

This raises another point that undermines the resurgence of the specter of Lamarckian evolution: The unit of evolution due to epigenetic effects remains the population, not the individual. Epigenetic effects provide a source of variation on which selection may act. Jablonka and Raz (2009) suggested that the prevalence of epigenetic effects implies a reformulation of natural selection's ontology: Natural selection would follow from the differential propagation of phenotypes, rather than from differential reproduction of individuals. One might expect that this revision would make individuals the units of evolution, but Jablonka and Raz (2009) made no such suggestion. They argued that epigenetic effects are useful for evolution in that they aid reproductive isolation, which would matter only if it is populations that evolve. Indeed, the suggested ontology may not even be revisionist: Eldredge (1989) argued that the MS explains evolution through the selection of phenotypes. Because true Lamarckism would require a revision of evolutionary theory's ontology and because epigenetic inheritance requires no such revision, it follows that the ES does not entail a Lamarckian theory just because it accommodates epigenetic inheritance.

Acceptance of epigenetic inheritance in the ES therefore does not constitute a paradigm shift, and this, in turn, does not require any radical revision of the models developed in the MS. Explanations of evolution are still given in terms of natural selection; what changes is the recognition of additional possible sources of variation. Understanding evolution still requires an acceptance of the sort of population-level thought that is antithetical to the Lamarckian model.

## Case study 2: The levels of selection and major evolutionary transitions

The dichotomy between units of selection and units of evolution that was relevant to the previous case study is also complicated by the fact that new kinds of candidate unit have emerged through evolutionary history. Nucleotide sequences came to be arranged in chromosomes, which became packaged in cells, which organized into multicellular organisms. The emergence of at least some of these levels of complexity marked a so-called *major evolutionary transition* (MET)—for instance, the one between pro- and eukaryotic cells or that between uni- and multicellular organisms. The ES has provided key insights into METs (e.g., Okasha's 2006 analysis of at least some METs in terms of shifts between levels of selection), which have come not from new data per se, but from introducing conceptual tools different from those of the MS. To clarify, what follows is a treatment of METs that zooms in on transitions of individuality, because these constitute an important subspecies of METs that are particularly relevant to the debate about the ES, given that the MS simply assumes levels of individuality as preexistent, without accounting for how they arose.

To begin with, recall Lewontin's (1970) formula for natural selection: When individuals vary in some heritable trait and

when those individuals vary in fitness because of the phenotypic variations those traits instantiate, populations of those individuals will evolve as more beneficial variations increase in proportional representation. That there have been METs would seem to imply that *individual* in this sense is a heterogeneous class, but this is controversial in the context of the MS.

Williams (1966, 1985) argued that evolution always ought to be explained by the lowest efficacious level of selection and that the data on the basis of which we reconstruct evolutionary patterns do not demand explanation by any process other than nucleotide-level selection. Following Williams (1966, 1985), Dawkins (1982) famously defended gene selection as sufficient to explain all evolution: Although he admitted that explanations of evolutionary patterns that invoke selection at higher levels of organization have heuristic value, preference for one explanation over another, according to him, is merely "linguistic." Not for nothing does the MS characterize evolution as a change in gene frequencies over time, as is clearly stated in popular evolutionary biology (Futuyma 1998) and population genetic (Hurtl and Clark 2006) textbooks (and despite the well-known protestations of some prominent exponents of the MS itself, such as Mayr 1963).

There has been some disagreement among proponents of the MS about the appropriate unit of selection. Mayr (1963) argued that a single selection process, wherein organisms (rather than genes) are the locus of selection, explains all evolutionary patterns (also see Futuyma 1988, but cf. Eldredge 1989). According to this view, gene selection is a mere statistical artifact of organismal selection; regardless, this remains an account with a single level of selection (Gould 2002).

This monistic view is problematic if one accepts the idea of METs. If the emergence of a new unit of selection in each MET is merely heuristic, one would expect that the fitness of those individuals would always be "synergistic with or at least orthogonal to" the fitness of the genes within them, as Gould (2002, p. 692) noted. This is demonstrably not the case. The fitness of entities at lower levels of complexity sometimes conflicts with the fitness of the entities in which they are enclosed: Think of the initial stages of the symbiotic events that led to the evolution of eukaryotic cells and some of their subcellular organelles. More obviously, cancer is the consequence of a cell lineage increasing its own fitness at the organism's expense (Crespi and Summers 2005). These cross-level conflicts are one reason that ES endorses a hierarchy of selection processes.

Certainly, in many—and perhaps even most—cases, the fitness of a higher-order individual does not conflict with the fitness of lower-order individuals. These are cases in which Dawkins may be correct: Higher-order evolutionary patterns may be explained equally well in terms of—say—genes or cells or organisms, and so discrimination of those explanations amounts to a linguistic choice. Sometimes, however, the structure of a population of lower-order individuals is

such that the population's fitness will be decoupled from the fitness values of the individuals within it. There are several properties that characterize this sort of population structure: the division of labor, cooperation between different kinds of individuals, and policing activity among them (Buss 1987). Once a population is structured in this way, it then emerges as a new, higher-order individual that participates in a new, higher-order selection process (Okasha 2006).

Proponents of the MS hold that there is a single level of selection that accounts for all evolutionary patterns. Proponents of the ES are more inclined toward pluralism, allowing for evolutionary processes at multiple levels to account for the observable patterns. It would be a mistake, however, to qualify the MS and the ES as wholly opposed on this point. Here, as in the case of epigenetic inheritance, we have an example of theoretical modification (based in part on philosophical insight) rather than theoretical replacement.

There are two reasons to consider the process pluralism of the ES as an extension of the process monism in the MS. The first is methodological; the second is ontological.

Beginning with the methodological reason, consider that Darwin's original argument for natural selection is an argument from analogy: Domestic breeding and speciation share important similarities, and so a single process can equally well explain both. In this way, the normally unobservable process of evolution could be rendered in terms of observable phenomena. A similar concern motivates proponents of the MS to extrapolate all evolutionary patterns from one evolutionary process. Evolutionary biology can be an empirical science only if its theoretical processes can be observed. Gene selection can be—and has been—observed; therefore, gene selection ought to explain all processes studied by evolutionary biologists (Gould 2002, Jablonski 2010).

The validity of this *extrapolationism* depends on a priori assumptions. Since gene selection predicts slow and steady evolutionary change, all evolutionary patterns ought to be gradual and uniformitarian; any failure of this prediction must be explained by mitigating factors. Most famously, Darwin and the proponents of the MS explain away the appearance of what became known as *punctuated equilibria* in the fossil record as artifacts of preservation biases. If punctuated equilibria are taken as real data rather than mere illusions, however, process monism is then insufficient to explain the rapid origin and diversification of taxa (Jablonski 2008, 2010). This argument is often given in favor of species-level selection (see also Eldredge 1989, Gould 2002, Ezard et al. 2012); although the emergence of species as new individuals in a MET remains controversial, the example does suffice to show that extrapolationism in the MS is a methodological choice that may not be justified by the interpretation of data within the context of the ES (again, see Okasha 2006—particularly, chapter 8).

Furthermore—and this is the ontological point—the process pluralism of the ES may not actually differ in kind from the process monism of the MS. Lewontin's (1970) formula

for natural selection describes a process *schema* that works for multiple ontologies. For his own part, Lewontin remains agnostic about which sort of biological entity is rightly called an *individual* and so a unit of selection. He acknowledges ostensible examples of nucleotide- (i.e., gene), cell-, and organism-level selection. Williams (1966) similarly allowed for the possibility of selection above the genic level, although he would later qualify that possibility as merely theoretical (Williams 1985). This implies that the differences between—say—gene, cell, and organism selection are ontological rather than formal; the structure of evolutionary models would remain the same, but applications would differ across the levels of selection.

Finally, the determination of ontology is only partly empirical. Williams and Dawkins deny that higher-order selection processes emerge in METs, because they deny that cells and organisms emerge as individuals in METs. This depends in large part on the definition of *individuality*. Traditionally, *individuals* are defined as functionally integrated and spatiotemporally delimited wholes (Ghiselin 1974, Hull 1978, 1980). This is not the same sense of *individual* used in the explanation of METs given in the ES (Buss 1987, Okasha 2006). To say that a population has a certain structure does not imply that it is functionally integrated or spatiotemporally connected in the same way as individuals described in the traditional sense obviously are (Finkelman 2013; see Brigandt and Love 2012 for a similar discussion about senses of the term *novelty*). Deciding between these two senses of the term *individual* requires a priori considerations about how data should be interpreted, and so the determination of ontology on which the current debate rests is partly conceptual. Indeed, the recent philosophical literature on the ontology of individuals is particularly rich and worth the time for interested biologists to explore (e.g., Bouchard and Huneman 2013).

## When is a philosophical perspective useful in biological research?

In soliciting the attention of practicing scientists, philosophers of science often quote Daniel Dennett (1995): "There is no such thing as philosophy-free science; there is only science whose philosophical baggage is taken on board without examination" (p. 210–211). It is clear that biologists can—and often do—conduct their research without examining any philosophical baggage. The case studies discussed above have been chosen to illustrate ways in which a baggage check may be of value in biology, at least from time to time.

Debate over epigenetic inheritance and its role in evolution demonstrates the importance of theoretical structure in accommodating data. To date, efforts to assimilate epigenetic inheritance into the broader framework of the MS have either recast putative examples of epigenetic effects as "extended" gene effects (e.g., Hull 1980, Dawkins 1982) or have relegated epigenetic inheritance to a subsidiary role (relative to that of genetic inheritance) in evolution (e.g., Godfrey-Smith 2000). If epigenetic inheritance were

inconsistent with Darwinian theory, these efforts would be necessary to reconcile recalcitrant evidence of the heritability of nongenetic variations with the apparent health of the MS paradigm (Futuyma 1988). Alternatively, Jablonka and Lamb (2005) argued that the viability of epigenetic inheritance demonstrates the complete insufficiency of the MS. As we have seen, however, we may find a path between the horns of this apparent dilemma by way of a more careful conceptual analysis of the Darwinian theory and its differences from the Lamarckian alternative.

It is a philosophical task rather than an empirical one to determine a theory's commitments and implications. A biologist may empirically determine whether variations are inherited through nongenetic mechanisms, but there is no a posteriori test of whether any such mechanism can be properly called "Darwinian." Gould (2002) and Dennett (1995), for example, offer conceptions of Darwinism that are, respectively, more and less accommodating of epigenetic inheritance. We believe that there is a stronger case to be made for the more accommodating view, which would allow proponents of the ES to persist in the belief that "we all are… Darwinians" (Kottler 1985, p. 1). There may be arguments to the contrary, but this constitutes an arrangement of the pertinent biological facts into background philosophical baggage.

Whereas the first case study demonstrates how theoretical content may determine the interpretation of data between the MS and the ES, the second case study demonstrates how the interpretation of data may influence theoretical content. In the MS, the explanatory value of extrapolationism commits adherents to a single level of selection. This may yield a very different explanation of the METs from that provided by the ES, which accommodates a view of data that permits multiple levels of selection. The differences between these accounts ultimately provide different ontologies: In the MS, there is a single sort of evolutionary individual; in the ES, there may be many that have emerged in the course of evolutionary history. All of this follows from the resolution of the prior question of whether macroevolutionary patterns that prove intransigent in the MS are factual or mere artifacts.

Although we have focused on the debate about the limits of the MS and its expansion into an ES in this article, exactly the same philosophical approach can be used to analyze and criticize the conceptual structure of the ES itself, as Craig (2010) and Weber (2011) did, for instance. But we also have to remember that the scope of philosophy in everyday scientific practice is limited. It is not the place of a philosopher of biology to say that biologists cannot find evidence of nongenetic inheritance or that different kinds of functional organization have appeared in evolutionary history, because these are empirical questions. Let us not forget the cautionary tale of Immanuel Kant (1951) and his prediction that there would never be a Newton for the blade of grass: Attempts to establish a priori limits on empirical evidence often end in embarrassment.

The role of philosophy in biology—and, indeed, in any science—is nevertheless vitally important. Philosophers may not be able to anticipate future data points, but it is philosophers—or scientists engaging in philosophy—who contextualize those data points in the broadest sense. Let us, likewise, remember another important lesson imparted by Kant: that perception without conception is blind.

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