The New Biology

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DEVELOPMENTAL BIOLOGY, NATURAL SELECTION, AND THE CONCEPTUAL BOUNDARIES OF THE MODERN EVOLUTIONARY SYNTHESIS

by David J. Depew and Bruce H. Weber

Abstract. Using the evolution of the stickleback family of subarctic fish as a touchstone, we explore the effect of new discoveries about regulatory genetics, developmental plasticity, and epigenetic inheritance on the conceptual foundations of the Modern Evolutionary Synthesis. Identifying the creativity of natural selection as the hallmark of the Modern Synthesis, we show that since its inception its adherents have pursued a variety of research projects that at first seemed to conflict with its principles, but were accommodated. We situate challenges coming from developmental biology in a dialectic between innovation and tradition, suggesting on the basis of past episodes that even if developmental plasticity and epigenetic inheritance are aligned with its principles the Modern Synthesis (and its image in the public reception of evolution) will be significantly affected.

Keywords: adaptation; epigenetic inheritance; Modern Evolutionary Synthesis; natural selection; phenotypic plasticity; population genetics; sticklebacks

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[*Zygon*, vol. 52, no. 2 (June 2017)]

DARWIN, DARWINISM, AND THE CREATIVITY OF NATURAL SELECTION

Charles Darwin distinguishes in various places between the phenomenon, the power, and the theory of natural selection. The first refers to the nonrandom survival of individuals of the same species in single lifetimes. Responding to critics who pointed out that he was not the first to observe a struggle for existence within species as well as between them or to appreciate in the light of Thomas Malthus's "principle of population" how pervasive that struggle is, Darwin predicated his originality on what he called "the paramount power" of natural selection (Darwin 1868; Gayon 1997). He meant its capacity over many generations to evolve adaptations and species out of small but heritable variations that initially appear in individuals independently of the utility they sometimes subsequently acquire. It is in the second sense that Darwin construed natural selection as a process creative enough to displace the argument from design that played such a large role in the eighteenth-century British theological-political ideology. He accepted intelligent design's *explananda*, but not its explanations.

Early critics who were unable or unwilling to accept the "paramount power" Darwin attributed to natural selection mistakenly construed it as survival by pure chance (John Herschel's "law of higgledy-piggledy") or as covertly guided by God (Asa Gray's directed variation) or by deflating the wonder-inspiring process that Darwin saw unfolding over many generations to the bloody scene of death and destruction that takes place on the ground in each. Any of these lines of argument, if they could be made to stick, would undermine Darwin's *theory* of natural selection: the claim he defended in the second half of the *Origin of Species* that natural selection in the transgenerational sense solves biology's puzzles. With characteristic candor, Darwin admitted that his *theory* would be falsified if its gradualist axiom were ever proven unsound (Darwin [1859]1964, 189, 194, 471).

Historians of biology tend to agree that Darwin's view of adaptive natural selection as evolution's leading edge might not have prevailed if, unlike its rivals, it had not been reframed in terms of statistics and probability (Hodge 1987). It is not a coincidence that Herbert Spencer's inappropriately named Darwinism was both devoid of statistical thinking and assigned a merely eliminative role to natural selection in Darwin's first sense. It was called on to weed out the antecedently unfit, not to gradually evolve the fit. Although Darwin himself had only a toehold on the probability revolution, his half-cousin Francis Galton, Karl Pearson, and their "biometrical" followers made considerable progress in making evolutionary biology more closely resemble statistical physics. Walter Frank Raphael Weldon, the first biologist empirically to prove the existence of gradual natural selection in the wild, wrote in 1894, "The questions raised by the Darwinian hypothesis are purely statistical, and the statistical method is the only one at present obvious by which that hypothesis can be experimentally checked" (Weldon 1894).

In 1908 the notion that evolution is a multigenerational, population-level, statistically trackable process was given a boost by Godfrey Harold Hardy's and Wilhelm Weinberg's independent but simultaneous mathematical demonstration that in freely interbreeding populations heritable variations will recur with the same frequency generation after generation unless and until evolutionary agencies, factors, or forces set afoot dynamical changes. The Hardy-Weinberg equilibrium formula made evolutionary advance theoretically easier because it eliminated Galton's assumption that over time hereditary factors will naturally regress to an undistinguished mean. In 1918, the statistical genius R. A. Fisher used this insight to show that over multiple generations natural selection can evolve adaptations out of genetic mutations each of whose effect is quite small (Fisher 1918, 1930). Fisher's American counterpart and rival Sewall Wright combined mutation rate and natural selection with another statistically accessible evolutionary agency, genetic drift, to sketch a population-genetic model of speciation. Theodosius Dobzhansky harked back to Darwin's title in his 1937 *Genetics and the Origin of Species* in order to intimate that the general theory of biological evolution that Darwin hoped to erect was now at hand. Natural selection, he said, is the innovative or "creative factor" in evolution, not mutation, as Thomas Hunt Morgan, under whom Dobzhansky did a 10-year stint as a glorified post doc, believed (Morgan 1932; Beatty, 2016). "Selection," Dobzhansky wrote, "is ... much more than a sieve retaining lucky and losing the unlucky mutations" (Dobzhansky 1962, 430–31). Recommending this principle as capable of integrating biology's diverse fields in his 1942 *Evolution: The Modern Synthesis*, Julian Huxley remarked, "The statement that selection is a destructive agency is not true if it is meant as merely destructive ... It has a share in evolutionary creation. Neither mutation nor selection alone is creative of anything important in evolution; but the two in conjunction are creative" (Huxley 1942, 28; see also Gould 1977, 44; Mayr 1980, 2, 18).

The creativity of natural selection is the defining mark of the Modern Synthesis and the source of its claim to have validated, and thereby rescued, Darwin's insight into selection's paramount power (Beatty, 2016; Mayr 1993). The history of the Synthesis since its articulation in the 1940s and 1950s is best represented as a process in which biological fields not brought under its sway in its formative period have been recast in its terms, not without controversy but usually with a gain in explanatory perspicuity. Of particular importance since the 1970s have been efforts to integrate molecular biology, ecology, and ethology.

Developmental biology is the focus of attention and controversy these days, and in this article. Its omission from the formation of the Synthesis did not go unnoticed. The developmental geneticist C. H. Waddington is said to have remarked that "people would have to come back to embryology in the end if they wanted to really understand the properties of higher living systems" (Needham 1984, vii–viii). With the maturation of regulatory genetics, Waddington's prediction seems to have come true. Disputes are currently raging about whether the sensitivity to environmental influences of regulatory sectors of the genome and of modestly heritable epigenetic modifications of DNA can generate and spread evolutionarily significant novelties in ways that violate the premises of the Modern Synthesis, and even of Darwinism generally. In particular, they can appear to violate the "chance" relation Darwinism postulates between the origin of heritable variation and its transgenerational retention, as well as its "gradualist" assumption that the etiology of adaptations requires differential retention of heritable variation in more than one, and presumptively many, generations.

From the start the ghost of old disputes has haunted efforts to integrate developmental biology with the Modern Synthesis. The fact that organisms are developmental entities with life cycles was at the heart of what the embryologist Scott Gilbert has identified as the "unmodern synthesis" that dominated evolutionary thinking in the last two decades of the nineteenth century, according to which successional ecology and phylogenetic diversification are merely ontogeny or development writ large (Gilbert 1998, 170). It has been hard to liberate embryology from this "non-Darwinian revolution," as Peter Bowler has called it (Bowler 1988). It has also been hard to liberate the regulatory genetics that are a key to development's relation to evolution from the stress on random allelic mutations in genes coding for structural gene products that dominated the unification of molecular genetics with the population genetics of the Modern Synthesis in the 1950s and 1960s. More than historical headwinds, however, obstruct the integration of development with the Modern Synthesis. The only moment of the life cycle of an organism that figures in population genetics is mating, which is understood in such isolation from other phases of the life cycle that it can hardly be called a moment at all. An exception that proves the rule is the application of the principles of the Modern Synthesis to the evolution of life cycles themselves. In this admittedly interesting body of work life cycles are framed as phenomena to be explained, but not as offering resources for explaining either the production of selectable variation or the means by which it spreads through populations. Life cycles are (taken to be) naturally selected strategies for survival.

In what follows we will present some facts about the evolution of stickleback fish as a way of more sharply posing questions about whether the new developmental biology can be brought under the aegis of the existing or of an "extended" Modern Synthesis, as Massimo Pigliucci and other have been urging (Pigliucci and Müller 2010; Laland et al. 2014), or whether a "new synthesis" is called for. Framing this question in a way that will facilitate its eventual resolution depends, we argue, on the fact that in the course of solving a range of problems and integrating various fields, the Modern Synthesis has come to contain within its conceptual boundaries a number of research programs and rival theoretical formulations. Some of these may be able to incorporate developmental insights into the origin and retention of variation, but others are less welcoming. To the extent that they identify the Modern Synthesis with the latter, partisans of the intimate relationship between development and evolution ("evo-devo") can easily be tempted to call for a new post–Modern Synthesis. If they see the supposed flaws of the Modern Synthesis as flaws in Darwinism as such, they may even call for a post-Darwinian theory of evolution. Empirical facts must in the end decide these issues. But getting to that point requires clarifying conceptual frameworks and mapping the fault lines of controversies. We offer this article in this spirit.

STICKLEBACK SPECIATION AND THE MODERN SYNTHESIS

Sticklebacks, a family of sixteen or so species of small, scaleless, spiny subarctic fish phylogenetically related to pipefish and seahorses, have served as a model system for students of speciation for several decades. The three-spined stickleback (*Gastoleus aculeatus*) has been especially prominent in debates about the future of evolutionary theory. This is not because its ways straightforwardly defy the explanatory resources of the Modern Synthesis, but because discoveries about sticklebacks hover at or sometimes seem to stray beyond its conceptual boundaries.

Some of the relevant facts are as follows. Ocean-going sticklebacks are ancestral to species that dwell in streams or lakes, into the bottom or at the surface of which they began to diversify when the glaciers retreated, leaving surviving populations trapped in isolated bodies of fresh water. Speciation is rapid in sticklebacks. It can occur in as few as ten generations, as researchers found when they introduced saltwater sticklebacks into a lake that had lost its freshwater stickleback population (McKinnon and Rundle 2002).[1] It is also fragile. Reproductive isolation of surface and bottom dwelling lake species can degenerate into a "hybrid swarm" in only a few generations (Taylor et al. 2006). In some stickleback species males tend offspring and are differentially favored by females for this task. Accordingly, sexual selection helps disruptive natural selection secure reproductive isolation, making speciation in three-spined and other stickleback species at least partially sympatric (Bakker 1993; Blouw 1996; Reimchen, Nosil, and Wainwright 2004; Bolnick 2011). Genetic drift and gene flow complicate these factors in many lineages, but even when they play a role in stickleback speciation they are less important than natural selection (Gelmond, von Hippel, and Christy 2009); and, as we will see, they often play no role at all.

The migration of sticklebacks from salt to fresh water is associated with more or less simultaneous shifts in phenotypes and genotypes early in the life cycle (Jones et al. 2012). The most salient phenotypic change is reduction or full elimination of the protruding dorsal spines that give these fish their name. Genotypically, specific base pairs in the homeobox regulatory gene *Pitx1* are deleted; alleles coding for the protein ectodysplasin that are found in ocean-going sticklebacks in much lower gene frequencies are greatly amplified; and a raft of recombination-blocking chromosomal inversions are put in place (McKinnon and Rundle 2002; Colosimo et al. 2004; Colosimo et al. 2005; Chan et al. 2010; Jones et al. 2012).

Although the Modern Synthesis, especially in its earliest versions, does not require that speciation be an adaptive process, it has been supposed that dorsal spines help maintain the reproductive fitness of ocean-going sticklebacks by deterring predatory fish, which would lacerate themselves if and when they bit into them. Since no such predators exist in fresh water, the thought goes, spines are either not expressed or their size is diminished. The suspicion that rationales like this might be what Stephen Jay Gould and Richard Lewontin famously called "just so stories" is intensified, however, by experiments showing that when the diet of saltwater sticklebacks is changed dorsal spine expression is almost immediately reduced (Wund et al. 2008; Pfennig et al. 2010; on "just-so stories" Gould and Lewontin 1979). Adaptationist rationales that conform to the Modern Synthesis presuppose a multigenerational and so far forth a gradual shift in gene frequencies in populations, but what looks like an adaptive response to dietary changes in saltwater sticklebacks seems to take place in each generation under the immediate influence of environmental contingencies. The Modern Synthesis is able to regard this phenomenon as an expression of the plasticity of genes already fixed in a population, but not *stricto sensu* as an adaptation, a term it reserves for transgenerational change in gene frequencies driven by natural selection.

In spite of these puzzles, sticklebacks may not pose as dire a threat to the explanatory prowess of the Modern Synthesis as the facts we have recited might suggest. In the course of integrating new fields and phenomena, the Synthesis has often opened itself to evolutionary models, mechanisms, and scenarios that at first seemed anomalous (Depew and Weber 2013). The revelation that in protein evolution DNA sequences often go to fixation by chance was initially announced as "non-Darwinian evolution" (King and Jukes 1969). Relaxation of the presumption that what goes for the level of structural gene sequences that code for proteins also goes for evolution at higher levels of organization made way for a major restatement of the Modern Synthesis that allowed evolutionary factors to work differently at different levels of biological organization (Gould 1980; Eldredge 1985). What in retrospect was obstructing an "hierarchically expanded Synthesis" turned out to be little more than a philosophical prejudice in favor of reductionism on the part of molecular evolutionists in decade after Crick and Watson's discovery.

Similarly, Ernst Mayr may have believed that all speciation must be allopatric, but sympatric speciation is now widely accepted. Nor is rapid speciation as telling as it used to seem. After the controversy about punctuated equilibrium in the 1970s and 1980s calmed down, the rapidity of the speciation process and the clustering of adaptive change around speciation events seemed at odds with only the most dogmatically gradualist versions of the Synthesis. To be sure, more than one generation is required for the fixation of an adaptation. But how many more is now regarded as an open and non-threatening question.

What makes stickleback evolution anomalous for the Synthesis is less its rapidity than the fact that failure to express dorsal spines can occur in freshwater species without benefit of gene flow or adaptive radiation between geographically isolated lakes and streams. There is no evidence of any connection between the bodies of water in which freshwater sticklebacks speciate. There need be no "founder effect," in which outliers spread their genetic peculiarities to larger populations, including the one they came from, and even where there is speciation proceeds pretty much as it does in isolated bodies of fresh water. Populations that evolve separately can mate successfully and enjoy rapid gains in fitness (Schluter and Nagel 1995; Colosimo et al. 2004).

These phenomena have been accommodated to the Synthesis by appealing to a concept already found in the tool kit of evolutionary biologists: parallel evolution. In contrast to convergent evolution, in which populations with different ancestors hit on the same solution to similar environmental problems, parallel evolution occurs when populations sharing the same ancestors repeatedly but independently evolve the same adaptations in similar environments or, in parallel speciation, share enough genotypes to interbreed (Pfennig et al. 2010). Nonetheless, parallel adaptation and speciation are generally thought to be exceptional rather than ubiquitous and transgenerationally gradual rather than immediate. In the next section we will concede that this phenomenon poses a challenge for the Modern Synthesis, but we will also suggest that lines of thought about phenotypic plasticity that are deeply embedded in its history but have been less prominent until recently make it possible to see more continuity than might have been imagined (Pfennig et al. 2010; Fierst 2011). Discussions of this issue can be muddied, however, by neglecting the fact that the Modern Synthesis contains within its conceptual borders a variety of research projects and programs, some of the most prestigious of which are more congenial to a solution along these lines than others.

DIVERSITY AND ITS LIMITS IN THE MODERN SYNTHESIS

How seriously an empirical discovery casts doubt on the continuity of the Modern Synthesis depends to some extent on which of its ongoing research projects is assumed to best incarnate its basic ideas. By our count there have been three major projects in the Modern Synthesis since its formation in the early 1940s, each generating numerous research programs that make use of an ever-growing array of methods, models, and materials.

The first project was dedicated to reforming systematics by explaining speciation and evolution above the species level in terms of natural selection working at the level of organisms in conjunction with mutation, interpopulational gene flow, and genetic drift. Dobzhansky, Mayr, and George Gaylord Simpson figure as founders of this project and, with Julian Huxley, as advocates for integrated biology departments that unify a previously disparate array of disciplines around the evolutionary principles we have summarized. This is what Dobzhansky was alluding to when late in his life he famously said, “Nothing in biology makes sense except in the light of evolution” (Dobzhansky 1973).

In this project natural selection appears mostly in its normalizing, stabilizing, balancing, and diversifying or disruptive modes. A certain holism is inherent in it. The target of natural selection is the entire organism. “Talking about traits as though they were independent entities,” Dobzhansky wrote in 1970, “is responsible for much confusion in biology and especially in evolutionary thought” (Dobzhansky 1970, 65). If maintaining a balance between preserving and using variation is to be an effective way of keeping populations of organisms adapted to environments that are in constant flux, not least because of the activities of organisms themselves, the entire genome must be presumed to be the least unit of selection (Lewontin 1974). When Mayr famously attacked “beanbag genetics” he was swearing fealty to this presupposition (Mayr 1963, 263). The hierarchical expansion of the Modern Synthesis in the 1980s grew out of his and his collaborators’ profession of faith on this point.

A second project was coeval with the first. The “population ecology” of the Oxford School contributed to the “new systematics” by proving that traits previously assumed to be nonadaptive are actually adaptations to very specific environments that have evolved under the influence of directional natural selection. The old assumption that species markers are adaptively neutral having been defeated (the arguments are laid out in Huxley 1942) the point now was to find evolutionary rationales for most, if not all, traits, the dorsal spines of sticklebacks presumably among them.

The Oxford School has its roots in a rather pious movement founded by Edward Poulton, Frederick Dixey, and Aubrey Moore, “who defended natural selection through the long ‘eclipse of Darwinism’ in the decades around 1900. [They] recognized that Darwin had described the universal, natural laws that produced the phenomenon of universal adaptation observed in living nature” by clerical predecessors such as William Paley (England 2001, 271). On the authority of Fisher’s Fundamental Law of Natural Selection, it is axiomatic in this project that natural selection in its directional mode can optimize the design of traits taken one by one as long as mutation rates are high or enough genetic variation remains in the recessives of heterozygotes to serve as fuel for evolving adaptations. Results such as those of David Lack on Darwin's finches and Bernard Kettlewell on peppermoths gave prestige to this project in the 1950s (Lack 1947; Kettlewell 1955, 1956). Associated more often now with the atheistic naturalism of Richard Dawkins than the theism of Canon Moore, a High Church Anglican cleric, this project sees Darwinism as design without a designer, a framing that has more often stimulated creationists to look for an intelligent designer than to accept evolutionary naturalism. Both parties have a stake in regarding the adaptationist program as the acme of the Darwinian tradition in evolutionary natural history.

A third project is the attempt since the 1960s to prove that the Modern Synthesis can unify (more of) biology by bringing ecology and animal behavior, especially cooperative behavior, into the range of disciplines it synthesizes. This effort has resulted in a still-unfolding conflict about whether successfully prosecuting this project sorts better with the holistic presuppositions about organisms and genomes of the "speciationist" New York School, as we might call it, or with the trait-centered adaptationism of the Oxford School. Since the 1970s the general tendency has been to identify the Modern Synthesis with adaptationism and, once it had been extended to the traits of humans, sometimes to proclaim the triumph of a materialistic "Darwinian worldview" (Ghiselin 1969; Dawkins 1986; Dennett 1995).

This triumphalism rests on impressive deployment of new analytical tools. William Hamilton's use of George Price's equations to model inclusive fitness and kin selection and John Maynard Smith's pioneering use of game theoretical calculations to model optimal interactions between two or more interacting species were soon being applied to a problem that had dampened the prospects of Darwinism from the outset: cooperation within species (Hamilton 1964; Maynard Smith and Price 1973; Wilson 1975). At this point, a still smoldering war broke out between the adaptationist and speciationist wings of the Synthesis. By extending inclusive fitness and kin selection from the behavior of social insects to the behavior of modern humans, Edward O. Wilson's *Sociobiology: The New Synthesis* provoked the geneticist Lewontin, whom Wilson had brought to Harvard from the University of Chicago to help him and Robert McArthur integrate community ecology into the Synthesis, to bite the hand that fed him (Segerstråle 2000; Erickson 2015). In spite of ungenerous criticisms of his mentor, Lewontin remained true to Dobzhansky's assumptions that organisms (and for Lewontin sometimes groups [Lewontin 1970]) are the level at which selection acts and that pervasive linkage disequilibrium makes the whole genome the presumptive least unit of selection (Lewontin 1974). Lewontin and Gould saw sociobiology as undermining these presuppositions when it opted for traits rather than organisms as objects and sites of selection and postulated "genes for" these traits (Gould and Lewontin 1979).

Evidence that genotypes sweep through populations because they obey game-theoretical laws in searching in gradual transgenerational time for optimal solutions to problems posed by particular environments is often no stronger than the belief that the prevalence of adaptation is already secure enough to license this assumption (Huneman 2014, in which this is called "formal Darwinism;" Erickson 2015). Lewontin, Gould, Steven Rose, and others objected that this approach inevitably underestimates the dynamic interaction between organisms, genes, and constantly changing environments (Lewontin 1982, 2000; Rose, Kamin, and Lewontin 1985; Levins and Lewontin 1985; all anticipated by Lancelot Hogben [Hogben 1933; see Tabery 2014).

No less troubling is the assumption that reference to the same entities persists with reduction of the classical gene of Morgan and Mendel to the molecular gene of Crick and Watson. Although the effects of both are highly context-dependent, the former are found by inferring their location on chromosomes from observed effects, while the latter are identified by changes in base pairs of DNA whose effects and hence evolved functions are initially unknown. It is increasingly likely that the notion of "gene for" is so dependent on the concepts and methods of classical genetics that all the reductionist impulses in the world cannot make the different ways in which chunks of DNA combine and recombine confirm and explain stable phenotypic differences (Keller 2000, 2010; Moss 2001; Burian and Kampourakis 2013).

Lewontin was also faithful, albeit in his own way, to a view Dobzhansky acquired from his close collaboration with American anthropologists: the distinctively human capacity for culture brings into existence a new way of exerting agency that gets in the way of treating particular behavioral traits and psychological propensities as independently selected biological adaptations (Dobzhansky and Montagu 1947; Dobzhansky 1962; Fracchia and Lewontin 1999; Jackson and Depew, forthcoming). "Fitness at a single locus ripped from its interactive context," Lewontin wrote, "is about as relevant to the real problems of evolutionary genetics as the study of the psychology of individuals isolated from their social context is to understanding man's sociopolitical evolution" (Lewontin 1974, 318). The ecological holism about social insects that Wilson inherited from Benjamin Wheeler may have played a role in his subsequent abandonment of kin selection as an explanation of cooperation in social insects in favor a more game-theoretically informed idea of group selection first proposed by David Sloan Wilson (on Edward O. Wilson's holism, see Ruse 2017; on his belated repudiation of kin selection, Nowak, Tarnita, and Wilson 2010; on trait-group selection, Sober and D. S. Wilson 1998). This does not mean, however, that we should expect a deathbed *rapprochement* between Edward O. Wilson and Lewontin. Wilson's subscription to theory reductionism, in which phenomena at a higher level are fully explained by descriptions and regularities at the next level down, simply freezes what Lewontin regards as Wilson's biological and social scientific mistakes into a philosophical dogma (Wilson 1998).

True, Wilson's sociobiology has largely been replaced by a successor research program, evolutionary psychology, which conforms better to the adaptationist project by turning discoveries about the modularity of the brain into the idea that stereotyped responses to problems that confront individuals in any and all cultures are genetically encoded, species-specific adaptations (Barkow, Cosmides, and Tooby 1992). But this idea offends even more egregiously than sociobiology against the reduction of cultural ways of life to psychological proclivities. When Lewontin compared the "the fitness of a gene ripped from its interactive context" to the belief that "man's sociopolitical evolution can be reduced to the behavior of individuals isolated from their social context," he was implying that the latter is so absurd that it can be justified only by projecting it onto nature in order to give it ideological sway and normative force (Levins and Lewontin 1985; Lewontin 1993).

Like Dobzhansky before him, Lewontin holds that the complex interaction of organisms, genes, and changing environments, including cultural environments, requires that what natural selection evolves are not traits as such, but genotypes with a range of phenotypic expressions under different conditions: genotypes with more or less wide "norms of reaction" (Lewontin 1974, 2000; Levins and Lewontin 1985). As early as the first edition of *Genetics and the Origin of Species,* Dobzhansky was arguing that the environment–organism interface is so dynamic that at an (unattainable) extreme the fittest genotype will be able to express itself differently in every environment (Dobzhansky 1937, 170). If natural selection had not favored phenotypically plastic genes with wide norms of reaction, he reasoned, the history of life on earth would have come to a halt a long time ago. Evolutionary biologists never repudiated this idea, but it became less prominent in the last quarter of the twentieth century for a number of entwined reasons that historians have yet fully to examine. Among these were the perceived irrelevance of phenotypic plasticity to problems such as why Darwin's finches have slightly differently shaped beaks; Dobzhansky's inability to prove that heterozygotes have inherently wider norms of reaction than homozygotes and that natural selection favors them for this reason, which left the idea of phenotypic plasticity hostage to this conjecture (Beatty 1987); the growing focus after the molecular revolution on point mutation in structural gene products rather than chromosome-level rearrangement as the paradigmatic sources of the variation on which selection works; and a growing insistence, born of the allergy to anything smacking of Lamarckism that was shared by all enemies of Soviet-sponsored Lysenkoism during the Cold War, that the Central Dogma of Molecular Biology requires genetic causes to be not just chancy, but random in relation to their phenotypic effects, and stipulates that in order to meet this criterion genes must cause and so must precede their effects (Gilbert and Epel 2009, 456).

Under these presumptions, the prospects of phenotypic plasticity as a major cause and effect of evolution were not very good. In recent decades, however, growing appreciation of the sensitivity of promoter and enhancer sectors of the genome to environmental inputs has led to recasting phenotypic plasticity as developmental plasticity (Schlichting and Pigliucci 1993, 1998; Pigliucci 2001; West-Eberhard 2003). In treating genes as lagging, not leading indicators of evolutionary change, Mary Jane West-Eberhard has pointed out that development takes place in environments stabilized by the activities of organisms themselves and that niche construction of this sort is so robust across generations that it provides a phenotypic platform for recruiting genetic factors to support it. She recalls that this notion was widely accepted as a major factor in evolutionary change at the end of the nineteenth century, but that as "the century of the gene," as Evelyn Fox Keller has called it, unfolded, "the Baldwin effect" (so dubbed by Simpson in 1953 after one of its early proponents, James Mark Baldwin) was increasingly pooh-poohed, presumably for reasons some of which we surveyed in the previous paragraph (West-Eberhard 2003; on niche construction, Odling-Smee, Laland, and Feldman 2003; on "century of the gene," Keller 2000; on the Baldwin effect, Baldwin 1896; Simpson 1953 Weber and Depew 2003).

Students of stickleback speciation are among those who have made their way back to phenotypic plasticity in its development-oriented rearticulation and to the notion that the transgenerational niche-constructing activities of organisms can clear space for changes in gene frequencies, or even induce them through what is called "genetic assimilation":

> Because of its unique ability to generate an immediate phenotypic response to the environment, phenotypic plasticity plays a key role in fostering divergent phenotypes within populations and subsequently driving diversification [in freshwater sticklebacks]. . . . Although these ideas are fundamentally consistent with the Modern Synthesis (in that they ultimately rely on genetic changes to mediate evolution) they enhance our understanding of evolution by emphasizing the importance of environmentally initiated change (Pfennig et al. 2010, 459, 466).

Support for this interpretation has focused on correlating phenotypic plasticity with a prior history of it in lineages, including those of sticklebacks (Wund et al. 2008; Fierst 2011). Turning the genocentrism of the adaptationist project on its head (or, its defenders will doubtless insist, right side up), this approach prompts a new look at even paradigmatic cases of adaptation such as the spread of melanic forms of peppermoths in the sooty environments of industrial Britain. The shift from light to dark forms may well express cryptic variation, some of it phenotypically plastic, already latent in gene pools (Schlichting 2008).

Responses to proposals of this sort fall along the lines of conceptual divergence we have already identified. Advocates of the universality of locus-by-locus, mutation-by-mutation, trait-by-trait, little-by-little conceptions of adaptation are likely to see in it a recrudescence of Lamarckism, especially if they think of the Darwinian tradition as having come into its own by radically separating development from evolution. It might seem that just such worries drive the resistance of a long list of distinguished evolutionary biologists to the proposition that "evolutionary theory needs a rethink" (Wray et al. 2014). What these defenders of the Modern Synthesis are defending, however, is not aprioristic universal adaptationism, but the "pluralist" Modern Synthesis that grew out of the speciationist project by incorporating a wide variety of evolutionary phenomena, causal and contributing factors, levels of organization, and mechanisms—if and when (but only if and when) they pay their way empirically. "We already study . . . phenotypic plasticity, niche construction, inclusive inheritance, and developmental bias," say the defenders. If "having rolled up our sleeves and got to work," we find merit in new insights along these lines, we will incorporate them as "add-ons" (Wray et al. 2014, 164).

The pressing, if also still open, question, then, is whether the Modern Synthesis in its pluralistic form can be extended to accommodate claims "that variation is not random, that there is more to inheritance than genes, and that there are multiple routes to the fit between organisms and environments" (Laland et al. 2014). Those who are sympathetic to this possibility might find some encouragement by recalling that in its first, mid-twentieth century version the Synthesis explicitly predicated the dynamic interaction of gene, environment, and organism not only on the importance of phenotypic plasticity and wide norms of reaction, but also on the fact that organisms are developmental systems with life cycles. Under the influence of his fellow Russians I. I. Schmalhausen and I. M. Lerner, for example, Dobzhansky modeled natural selection's various modes—stabilizing, normalizing, diversifying, balancing, and directional—on processes so closely tied to phases and aspects of ontogeny that, *pace* Daniel Dennett, it makes no sense to treat natural selection as a substrate-neutral mechanism for optimizing design that can run as well on silicon-based computer programs as on hydrocarbon-based genetic programs (Schmalhausen 1949; Lerner 1954; Dobzhansky 1951, 1970; Dennett 1995; Depew 2011).

Nonetheless, this allusion to the fact that adaptive natural selection occurs only in organisms considered as environmentally sensitive developmental systems affects only how variation is retained or eliminated. It does not touch on how selectable variation is generated or on whether organisms that construct their own niches can over time recruit or bias the retention of genes that enhance the heritability of the variations on which their adaptedness depends. The new idea is that epigenetic processes—processes that occur in development after meiosis—are the proximate source of selectable variation and that variation arising from this nongenetic source has adaptive capabilities or tendencies from the outset. Can this idea be accommodated to the Modern Synthesis without transgressing its conceptual boundaries, which in any and all of its versions requires as a matter of definition that natural selection is adaptive only if it works on heritable genetic variation that arises independently of utility?

The quantitative geneticist Massimo Pigliucci, whose 2001 book *Phenotypic Plasticity* led to his subsequent call for an "extended synthesis," is optimistic about this possibility (Schlichting and Pigliucci 1993, 1998; Pigliucci and Kaplan 2000; Pigliucci 2001; Pigliucci and Müller 2010). By contrast, in his discussion of parallel evolution in sticklebacks the developmental biologist Scott Gilbert is skeptical:

> Parallel evolution can result from the independent recruitment of similar developmental pathways by different organisms. Instead of the view that extrinsic selection pressures play the dominant role in such phenomena, the current view is that intrinsic developmental factors are critical in producing these parallel variations. Such parallel evolution was once the justification for the "creativity" of natural selection. Now we can see that development is what is creative (Gilbert and Epel 2009, 341, citing Gilbert 2006).

As an accomplished historian of evolutionary biology, Gilbert knows just how loaded the terms *creative* and *creative factor* are. In denying that natural selection is the creative factor in the parallel evolution of sticklebacks, he is bringing the concept of adaptation forward in ontogenetic time to name responses of individual organisms to environmental contingencies. The deletion of base pairs of *Pitx*1 when sticklebacks encounter freshwater should be considered incipiently adaptive *ab initio*. As adaptive, these deletions are not fortuitous. Nor are they functions of a merely impinging environment, as Spencer had it. Agency is accorded to the developing embryo in and through its constitutive relationship with its ecological setting. If anything flirts with environmental determinism, Gilbert intimates, it is the Modern Synthesis, with its "extrinsic selection pressures." Whatever genetic factors make this possible, including genes that have been selected for phenotypic plasticity, they are not the crucial difference makers and hence not *the* cause. Accordingly, neither adaptedness nor its biological causes are at root population-level properties.

To be sure, Gilbert acknowledges that "loss of *Pitx1* expression in the pelvis can be readily selected" (Gilbert and Epel 2009, 341, citing Colosimo et al. 2004). It can be readily selected, however, not because it results in adaptedness, but because each developing organism's response to its environment is already adaptive. This is what Gilbert has in mind when he says that the accent now falls on the "arrival," not the survival, of the fittest (Gilbert and Epel 2009, 324). In spite of the misleading Spencerian language of this *bon mot*, Gilbert admits that the Modern Synthesis was a great improvement over Spencer's stress on the elimination of the unfit, which gave Darwinism a bad name that dogs it to this day in some circles. The Synthesis, Gilbert says, showed how natural selection can facilitate the spread of innovations through populations. But gradual natural selection working across generations on heritable genetic variations, each of whose effect is too small to explain organic form, is not the author of adaptedness, the Synthesis notwithstanding, at or above the species level. What Gilbert calls the "aging Mayr-Dobzhansky Synthesis" can no longer keep up with empirical discoveries in developmental genetics, embryogenesis, ecology, and the origin of evolution's major body plans (*Baupläne*). Accordingly, Gilbert concludes that the "Mayr-Dobzhansky Synthesis," and *a fortiori* its trait-adaptationist first cousin, needs "major revision" (Gilbert and Epel 2009, 398). Revision, however, does not seem to us quite the right word. Once it is correctly understood and enforced to the letter, the creative role of natural selection in the Modern Synthesis entails that what Gilbert is calling for is a new synthesis.

The philosophers of biology Denis Walsh, André Ariew, and Mohan Matthen have been making a related claim about the relation between the developing organism and adaptation (Ariew and Matthen 2002; Walsh 2006; Walsh, 2015). Their point is that the statistical-probabilistic shift to population genetics that undergirds the Modern Synthesis cannot be as causal or, in its ability to evolve functional traits, as telic as its makers took it to be. Statistical representations and methods should be retained as mathematical tools for tracking what is happening in a large number of organisms, which are to be construed as Aristotle construed them: as goal-oriented developmental systems. Statistical tracking is explanatory in a weak, explicative sense, but attributing causal or goal-oriented force to population-level processes simultaneously mystifies populations and deprives organisms of their self-formative, adaptive, goal-oriented properties.

Other philosophers of biology have contested this "formalist" interpretation of the statistical dimension of the Modern Synthesis. In response to the argument that transgenerational natural selection is no more causal than random genetic drift, they argue that in point of fact genetic drift is physically real, differing from natural selection as fortuitous or nondiscriminating differential retention of genetic variation differs from nonfortuitous and discriminating differential retention (Millstein, Skipper, and Dietrich 2009). If transgenerational, population-level natural selection is noncausal, moreover, so must be natural selection in Darwin's single-generational sense. For the former is simply the latter writ large enough to see a great many causes and effects that are invisible in single generations. To deprive population-level phenomena of causal import is tantamount to limiting natural selection to a reiterated within-generation process that has almost none of the explanatory power that turns transgenerational natural selection into a general theory of evolution (Hodge 2016).

For us the lesson imparted by this debate is that we seem to have arrived at another pivotal moment in the history of Darwinism. At an extreme, whatever is attributed to organisms as members of statistical ensembles appears to subtract from them as complex adaptive developmental systems whose life cycles are entrained with their environments to the point of codefinition. Conversely, whatever is attributed to organisms considered as developmental systems seems to strip away from population-genetic representations of evolutionary trajectories Darwin's "paramount power" of natural selection, thereby undermining his and his successors' *theory* of natural selection, endangering the epistemic security of a vast amount of knowledge about evolutionary processes that has been accumulated and stored under its aegis, and potentially reviving the less-than-creative view of natural selection that in an earlier day nearly drove the Darwinian research tradition to extinction.

It is possible, although far from a sure thing, that newly salient facts about developmental processes will eventually be better aligned with the Modern Synthesis than they are at present. If this happens it is unlikely, however, that they will be "incorporated" as "add-ons." In this matter history should be our guide. The integration into the Synthesis of neutral mutation in protein evolution, punctuated equilibrium in paleontology, cooperative behavior in animals, and other phenomena and biological fields has been achieved in and through hard-fought controversies in which empirical evidence and conceptual analysis on both sides of a question were put forward in a discursive context in which the failure of the Synthesis was a palpable possibility and in which successful integration involved reframing it in significant ways and keeping the peace by multiplying its versions. The incorporation of developmental phenomena that have hitherto been insufficiently attended to, or like genetic assimilation call for revisiting issues once regarded as settled, is highly unlikely to go any more smoothly.

One flash point is whether epigenetic inheritance in the form of the short-range heritability of chemical side chains that attach themselves to DNA (methylation) can be a source of variation with evolutionary significance (Jablonka and Lamb 1995, 2005; see Gadjev 2017 for a detailed treatment). In the course of defending the cumulative track record and continued explanatory power of the pluralist Synthesis, Jerry Coyne, Lewontin's former student and an authority on mechanisms of speciation, doubts it. The heritability of methylated DNA segments, he argues, is too evanescent to have any lasting effects (Coyne 2009). Coyne accepts the framing of the question, however, that arose when the human genome and other gene mapping and sequencing projects failed to find what they had been expected to find: enough genetic variation to drive evolutionary diversification. Genes, it seems, are too well conserved across too many *taxa* to be trait-specific heritable difference makers. When organisms are regarded as self-formative developmental systems, however, epigenetic variation appears as significant as any other of the many interacting "developmental resources" in complex, environmentally entrained living systems (Oyama, Griffith, and Gray 2001).

A related scene of contention is Stuart Newman's and Gerd Müller's claim that the genetic machinery necessary for the evolution of many highly conserved morphological features, such as limb buds, is so old, so primitive, and so invariant that it stretches the concept of genotypic norms of reaction and phenotypic plasticity beyond recognition (Newman and Müller 2005). Instead, the causal and creative accent falls on developmental sensitivity to environmental contingencies even more than for Gilbert.

Newman's and Müller's aim is not exactly to falsify the Modern Synthesis, but to limit its explanatory scope. It roughly applies, they say, to metazoa, with their need for command and control of complex, highly modularized, hierarchically organized, genetically sequestered subsystems. Genetic Darwinians, including the musketeers of the Modern Synthesis, falsely generalized this range of applicability by relying on model organisms that were supposed to prove it, but were tacitly chosen because they illustrated it (Newman and Müller 2005). This criticism is not, however, as modest as it appears. It implies that what Gould once called "a new and general theory of evolution" will put not only the Modern Synthesis in its place, but Darwinism more generally (Gould 1980). This line of argument is even more prominent in Eva Jablonka's decision to take the Lamarckian tradition in evolutionary biology as "more general" in Gould's sense. It can be seen in "directed mutation" in bacteria, lateral gene transfer in *archaea* and plants, and even in metazoa the effect of epigenetic inheritance that the Modern Synthesis has screened from view (Jablonka and Lamb, 1995, 2005).

In advancing Big Ideas of this sort it does not help when advocates of a "new and more general evolutionary theory" characterize the Modern Synthesis as adaptationism run amuck or denigrate natural selection as nothing but a nasty process of elimination. As we have seen, any Darwinism worthy of the name rests on transgenerational selection's "paramount power" to evolve adaptedness. By the same token, however, neither does it help partisans of the Modern Synthesis to protect the knowledge they have acquired by waving the bloody shirt of creationism at dissenters. This sort of "*après moi le deluge*" rhetoric is not only a red herring, but can all too easily draw self-proclaimed pluralists about evolutionary factors closer to universal adaptationism and talk about "the gene for" than their professed openness to new phenomena and concepts allows. If the Modern Synthesis manages to recover phenotypic plasticity as developmental plasticity, to recast the Baldwin effect as transgenerational niche construction that biases selectable variation of all sorts in an adaptive direction, and to situate epigenetic inheritance in the light of Dobzhansky's nod toward cytoplasmic inheritance (Dobzhansky 1951, 228–30), it is unlikely that the adaptationist project will continue to play as prominent a role in the professional articulation and the public projection of the Modern Synthesis as it has since the 1960s. If anything, the binary between nature and nurture, rather than being deconstructed, will switch from genetic to environmental determinism, as Maurizio Meloni predicts (Meloni 2016).

To be sure, it will remain possible to frame non-question-begging hypotheses that attribute this or that evolutionary change to adaptive natural selection and to answer these questions by finding correlated changes in the distribution of variation and other factors. Gould's, Lewontin's, and Rose's objections to adaptation*ism* arise from its alleged universality, not from its situation-specific applicability. Discoveries about sticklebacks are a case in point. Still, in the absence of suitably generalized, or generalizable, evidence it would be as unedifying for Darwinian scientists to insist on a materialist Darwinian worldview that eats like acid through human illusions as it was for Vatican astronomers to refuse to look through Galileo's telescope. By the same token, advocates of a new post-Darwinian synthesis cannot appeal to the metaphysics of the organism to make their case in a way that outruns or sidesteps scientific evidence. There can be little doubt that change is coming to the Modern Synthesis from the direction of developmental biology. The extent of that change and its implications for our understanding of the human condition are still matters of speculation. The task at hand is to make sure that this speculation is both biologically and historically well informed.

ACKNOWLEDGMENTS

The authors would like to thank Templeton World Charity Foundation for funding this article through the International Society of Science and Religion's grant "The New Biology: Implications for Philosophy, Theology, and Education."

NOTE

1. These findings are not unique to sticklebacks. "Scientists have observed at least one more example of rapid speciation—a new breed of sockeye salmon in Lake Washington that took thirteen generations to emerge—as well as numerous smaller instances of evolution at breakneck speed, most recently the blue moon butterfly of the South Pacific, which abruptly developed a new gene for repelling a parasite." http://www.skepticalinvestigations.org/Examskeptics/Dace_Shermer.html.

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