Adaptation as Process: The Future of Darwinism and the Legacy of Theodosius Dobzhansky

David J Depew, University of Iowa

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Conceptions of adaptation have varied in the history of genetic Darwinism depending on whether what is taken to be focal is the process of adaptation, adapted states of populations, or discrete adaptations in individual organisms. I argue that Theodosius Dobzhansky's view of adaptation as a dynamical process contrasts with so-called “adaptationist” views of natural selection figured as “design-without-a-designer” of relatively discrete, enumerable adaptations. Correlated with these respectively process and product oriented approaches to adaptive natural selection are divergent pictures of organisms themselves as developmental wholes or as “bundles” of adaptations. While even process versions of genetical Darwinism are insufficiently sensitive to the fact much of the variation on which adaptive selection works consists of changes in the timing, rate, or location of ontogenetic events, I argue that articulations of the Modern Synthesis influenced by Dobzhansky are more easily reconciled with the recent shift to evolutionary developmentalism than are versions that make discrete adaptations central.

1.1. Introduction

My topic is the current and prospective status of the concept of adaptation as it appears in various versions of the Modern Evolutionary Synthesis. My point of departure is the late Stephen Jay Gould’s claim that the Modern Synthesis ‘hardened’ in the 1950s in a way that led directly, if also in Gould’s view wrong-headedly, to contemporary adaptationism (Gould, 1983). Although he is far from my main target, I think Gould was wrong on two points. First, he dismissed too quickly the claim that “the Synthesis was ‘hard’ [adaptationist] in Britain from the first” (Gould, 1983, p. 86). Second, he failed to recognize that, although the most seminal figure in the American Modern Synthesis, Theodosius Dobzhansky, did in some sense become more adaptationist over time, both early and late his view of adaptation differed in kind from the adaptationism that was Gould’s target.

Adaptationism, as Gould defines it, depends on seeing organisms as aggregates of relatively discrete, though mostly mutually supportive, adaptations (Gould, 1983; see also Gould & Lewontin, 1979). Dobzhansky never saw organisms that way. In concentrating on states of relative adaptedness in populations responding to dynamically changing environments, he treated organisms as sufficiently integrated to respond holistically to environmental challenges.¹ He explicitly denied that organisms are “bundles of adaptations.” “Talking about traits as though they were independent entities,” he wrote in 1970, “is responsible for much confusion in biological and especially in evolutionary thought” (Dobzhansky, 1970, p. 65). On this point he differed from Julian Huxley. Although in the 1942 tract that gave the Modern Synthesis its name he made extensive use of Dobzhansky’s 1937 Genetics and the Origin of Species, Huxley took his place in a dominantly British tradition that both before and after him treated discrete adaptations as the primary products of evolution and organisms as their aggregates, bearers, or vehicles. The hardening of the Modern Synthesis to which Gould refers was for this reason more British in style than American, at least until a brand of adaptationism inspired by W.H. Hamilton’s theory of
inclusive fitness began to crop up in the 1970s style Sociobiology
that was Gould’s target.

In making my argument, I will use as clues distinctions between closely related locutions such as ‘adaptation,’ ‘adaptive,’ ‘adaptedness,’ ‘adaptability,’ and ‘an adaptation’ as they appear in the writings of Dobzhansky, Huxley, and others. I do not read these vocabulary preferences as either ontologically innocent or as scientifically neutral. They imply conceptual frameworks, and not all conceptual frameworks highlight the same evolutionary phenomena or favor the same ways of explaining them. Eight decades (and counting) of controversy have ensued about how best to formulate and apply the genetic Darwinism that by 1930 had put an end to the thirty years war between mutationism and natural selection (Fisher, 1930; Provine, 1971). The result has been versions of the Modern Synthesis that conceptually diverge in large part because in each rival version one inflection or another of the verb ‘to adapt’ plays the starring role: the process of adaptation in some, in others traits or genotypes said to be adaptively adaptive in virtue of the relative adaptedness of populations across which variation is distributed, and in still others individuated, nominalized adaptations.

One might, indeed one should, treat different articulations of the Synthesis as implying differences about how statistically distributed genotypes and phenotypes are related to each other and to the organisms that bear them. At the root of these differences will be found, I think, differences about how deeply the probabilistic revolution that led to the rebirth of Darwinism in the 20th century is inscribed into the very nature of the entities—organisms—over which statistical Darwinism ranges. These issues will surface now and again in what follows. In this essay, however, my accent falls instead on a less analytical, more polemical, and more topical question.

Both contemporary intelligent design (ID) creationists and many proponents of evolutionary developmentality (“Evo-devo”) take the self-proclaimed adaptationist Darwinians whom they oppose, such as Richard Dawkins, Daniel Dennett, Leda Cosmides, John Tooby, and Steven Pinker, at their word. They agree, that is, that adaptationism, which more often than not casts adaptive natural selection as design without a designer of adapted functional modules, as the best current representative of the Darwinian tradition. This makes it all the easier for advocates of both ID and Evo-devo to dismiss Darwinism altogether.2 ID proponents are happy with accounts that have natural selection producing quasi-designed analogues of artifacts because this trope grants them, at least in their own mind, standing to argue with Darwinians about who or what the designer might be. For their part, new developmentalists see changes in ontology as the locus of the variation on which evolutionary innovation depends and see the active adapting of developing organisms as inseparable from the process of adaptation. Tensions between these perceptions and the genetic theory of natural selection tend to make advocates of Evo-devo happy enough with the assumption that genocentric adaptationism represents Darwinism in its most advanced form. Its most advanced form is also its most vulnerable. Acutely aware that the Modern Synthesis’s foundational moment consisted in marginalizing developmental biology, the current prominence of genocentric adaptationism and its aggressive colonization of the human sciences inclines the heirs of those who were pushed aside by the makers of the Modern Synthesis to treat Darwinism as a whole as a crypto-creationist fantasy that enjoys public salience today mostly because in framing organisms as assemblies of replaceable parts rather than as differentiating and integrating developmental processes it misjudges the ecological matrix of life and serves, wittingly or not, as an ideological prop for eschatological hopes improperly invested in genetic technoscience. My own inclination is to question the shared premise on which both of these lines of argument rely. I do not think that genocentric adaptationism is in fact the best articulation of contemporary Darwinism. I favor versions that derive from Dobzhansky, Mayr, and Simpson, especially the first of these makers of the Modern Synthesis. These have been analyzed and affirmed by many astute philosophers of biology (Brandon, 1978, 1990; Buller, 2007; Burian, 1983; Lloyd, 1988; Richardson, 2007, among others). Moreover, if the fate of Darwinism actually does rest on the validity and soundness of contemporary genocentric adaptationism the entire Darwinian research tradition is in real danger. This approach cannot explain the origins of organic form, the origins of species and other clades, or the complex ways in which organisms, genes, and environments actually interact (Gilbert & Epel, 2009; Newman & Miller, 2000; West-Eberhard, 2003). Luckily, however, the contrast between the new developmentalism and the approach to Darwinism that Dobzhansky initiated is not quite as intractable—or so I will argue. Admittedly, some of Dobzhansky’s most famous bon mots seem at odds with this claim. He declared [biological] evolution simply to be change in gene frequencies in populations (Dobzhansky, 1937, p. 11). He wrote, albeit “reluctantly” and ex hypothesi, that we must treat macroevolution as reducible to microevolution (Dobzhansky, 1937, p. 12). I will try to say of why he made such claims. But my main purpose is to show that Dobzhansky’s conception of the adaptive process does more justice than we might have thought, even if still not enough, to organisms considered as developmental processes. Since Gould’s story of a monolithic Modern Synthesis that on both sides of the Atlantic permanently shifted in the 1950s and 60s away from the presumption that most traits are not adaptations to the presumption that they are blocks the view, I labor to undo his argument.3

I begin with a summary of Dobzhansky’s theory of adaptive natural selection (2.1) and its philosophical leanings (2.2). I then contrast it with Huxley’s account in Evolution: The Modern Synthesis and even more with the adaptationism of the Oxford School that followed (3.1). I find the flaw in Gould’s argument in his assumption that this line of argument permanently pulled the entire Modern Synthesis, including the approach of Dobzhansky and his followers, into the adaptationist orbit that now dominates Darwinian thinking (3.2). I go on to respond to a possible objection. My account, it might be said, puts too much emphasis on mere choice of words to sustain its view that Dobzhansky’s articulation of genetical Darwinism was not only different in kind from genocentric adaptationism, but remains vital. My reply is that language matters. It encodes interpretive frameworks that sometimes make it difficult, if not impossible, for inquirers even to see the same phenomena through different conceptual lenses, let alone to explain them (4.1). I end by disstinating developmentalists in Dobzhansky’s theory and by speculating about how his brand of genetic Darwinism can, if stretched, affirm facts about genes, organisms, and environments brought to light by the new developmentalists (4.2).

2.1. Dobzhansky’s dynamical Darwinism

Dobzhansky’s basic idea about what organisms must be like if natural selection is to be their primary cause—and what natural selection must be like if it is to range over organisms—is as follows.

2 This is just the inference drawn by Jerry Fodor and Massimo Piattelli-Palmarini (Fodor & Piattelli-Palmarini, 2010). Although my essay was not written with their contentious book in mind, its argument can be taken as a claim that a third position is possible: Darwinian and developmental, anti-adaptationist but pro-adaptation.

3 This claim is sometimes called “empirical adaptationism” on the ground that it asserts that most traits, or most important traits (whatever that means), are in fact adaptations. See Sterelny & Griffiths (1999, p. 226).
“A precarious balance between a living being and its environment,” he wrote in the 1st edition of his seminal *Genetics and the Origin of Species*, “must be preserved by some mechanism or mechanisms if life is to endure” (Dobzhansky, 1937, p. 150). The reason for this enduring sense of the contingent, slippery, and evanescent nature of adaptedness is that the environment of organisms is constantly changing. The balance is precarious because, as Leigh Van Valen recognized in what he later dubbed the “Red Queen Hypothesis,” organisms must constantly work to reconstruct the very niches that their life activities are busy degrading (Van Valen, 1973). Over the long run, there is selection pressure for niche-constructing agency, and for a conception of organisms not as passively molded by environments but as co-creators of environments that their own activities partially define (Lewontin, 1983; Odling Snee, Laland, & Feldman, 2003).

Dobzhansky’s characteristic themes—selection as favoring polyphenism, phenotypic plasticity, norms of reaction as the primary products of the adaptive process, adaptability, and evolvability—flow from this ecological-energetic beginning point. The relationship between genotypes and phenotypes must be, and in lineages that have had an evolutionary future must have been, increasingly competent to elicit phenotypes adapted to widely differing and constantly changing environments. “An ideal genotype,” Dobzhansky wrote in the 1st edition of *Genetics and the Evolution of Species*, would be capable of producing an optimal response to any environment. It appears, however, that no organism has evolved such a paradigm of adaptability. A second method of becoming adapted has been resorted to, namely genotypic specialization. A change in the genotype alters the reaction norm, and some of the alterations may enable the new genotype to produce a harmonious response where the ancestral has been a failure... Selection deals not with the genotype as such, but with its dynamic properties, its reaction norm, which is the sole criterion of fitness in the struggle for existence (Dobzhansky, 1937, p. 170).

In this passage, Dobzhansky explicitly claims that his is a dynamical theory in the technical sense. As in its physics analogues, environment, genotype, and phenotype are instantaneously interacting variables to the point of inter-definability. The concepts have no meaning or applicability-conditions outside of this framework. The amount of variance explained by environment and inheritance, for example, depends on fixing environments that are, in any real world case, changing at every moment in an ongoing process. There is also, it should be noted, an animus against R.A. Fisher in these sentences. Since Dobzhansky’s *explanandum* is genetic adaptability in dynamically changing environments, his first conclusion is that although Fisher, too, is in possession of an authentically statistical-dynamic conceptual framework his theory is restricted to only two variables, mutation and selection, and so cannot account for the fact that lineages have enjoyed an evolutionary future because they have evolved genetic adaptability. Under the realistic assumption of constantly changing environments that is Dobzhansky’s beginning point, Fisher’s theory would quickly have led to more extinction than we see. Accordingly, Dobzhansky follows Sewall Wright by adding isolating mechanisms, population size, genetic drift, and migration to “scatter,” and hence preserve, the genetic variability on which natural selection must work if it is to keep up. He notes that chromosomal rearrangements widen the sources of variation beyond point mutation and in doing so afford mechanisms for preserving it. Point mutation is only a remote cause of variation. Chromosome-level innovations are its proximate cause.

What happens to all this variation under selection? It evolves into generatively-entrenched phenomena whose adaptive value, and indeed whose very existence, is invisible when viewed through non-evolutionary lenses. Diploidy, polymorphism, dominance, seasonal inversion, heterosis, and other phenomena with which Dobzhansky’s laboratory experience acquainted him are reliably inherited across very large clades because they preserve sources of variation in populations that foster adaptability in changing environments.

Dobzhansky brought this vision of genotypical adaptability or flexibility—what is sometimes called evolvability and evolutionary capacitance—to America from his early acquaintance with the work of the Russian geneticist Sergei Chetverikoff (Adams, 1980). Increasingly discounting worries about the effects of genetic load that dog the 1st and 2nd editions of *Genetics and the Origin of Species*, by the time he wrote *Genetics of the Evolutionary Process* Dobzhansky was claiming that “the level of adaptedness of every existing species is fairly close to the maximum achievable in its present environment” (Dobzhansky, 1970, p. 89). He arrived at this conviction by verifying the perserviveness of variation in natural populations and, to that extent, validating his theory of “balancing selection,” in which natural selection finds a “balance” between using and preserving genetic variation.

Heterozygote superiority or heterosis, the ground of the well-known phenomenon of hybrid vigor, was especially important to Dobzhansky. Long under the spell of Chetverikov’s notion that heterozygotes soak up variation and save it for a rainy day, Dobzhansky came to think of heterosis—enhanced fitness of heterozygotes—as illustrative as well as probative of the process of adaptation. He believed he had hit on an adequate general theory of biological evolution by work done after World War II on allelic variation in hemoglobin molecules. The higher fitness in malarial environments of heterozygotes that pair a dominant with a sickled, oxygen-starving allele can be traced to the fact that the heterozygous form confers some immunity to malaria on its possessors. In *Genetics of the Evolutionary Process*, which updates his earlier text in the light of the new molecular biology, the genetics of this case are presented as paradigmatic of Dobzhansky’s general theory of adaptation (Dobzhansky, 1970, pp. 48–49, 157–199).

### 2.2. Dobzhansky’s Philosophy of Biology

In every edition of *Genetics and the Origin of Species*, as well as its post-Watson and -Crick successor, *Genetics of the Evolutionary Process*, Dobzhansky encoded his theory in a technical vocabulary that makes relative adaptedness its central concept. This concept is properly predicated of gene pools and of individuals only insofar as they are members of gene pools or elements in genetic arrays. A given frequency of genes may be adaptive in one environment, but not in another. In malarial environments, for example, heterozygotes carrying only one S allele of the hemoglobin molecule are adaptive. In non-malarial environments they lower fitness. Nonetheless, the S allele is retained in the gene pool not just because it is difficult to get rid of, but also because in a continually changing

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4 Lewontin, Dobzhansky’s former student, theoretical heir, defender, and friendly critic, asserts that Dobzhansky’s conception of organisms as anticipatory problem solvers is not active enough because it makes the environment set the problems to which organisms must respond (Lewontin & Lewontin, 1985). This may or may not be fair to Dobzhansky. Still, it is noted that what was important to both teacher and student is a dynamical theory of natural selection and a shared perception that static, crypto-Paleyean adaptationism is not remotely up to the job.
world it contributes to the adaptability of that gene pool to future environments.

A number of remarks about the philosophical implications of this conceptual framework may be ventured: 5

1. As I have mentioned, the phenomena that Dobzhansky's theory are intended to explain cannot be seen at all by non-evolutionists. They are evolutionary phenomena. This fact seems to me to put a very strong spin—a spin that admittedly goes beyond its original context—on Dobzhansky's famous remark that "Nothing in biology makes sense except in the light of evolution" (Dobzhansky, 1973). It is not (only) that non-evolutionists have poor explanations of biological phenomena. They don't, and can't, even see the most important phenomena to be explained.

2. Phenomena such as variation-preserving traits are no more visible to evolutionists who have not adopted what Mayr calls "population thinking" than they are to creationists. These are not only evolutionary phenomena, but population-level phenomena. If your theory of evolution is as non-populational as late 19th century ontology-phylogeny recapitulationism you won't see them. It was because developmental biology remained captured by this picture that the makers of the Modern Synthesis cast it aside.

3. Although many genetic Darwinians do rise to the population level it is far from clear that seeing evolution by natural selection through the trope of "design-without-a-designer," as some do, is a perspicuous conceptual framework for identifying and a fortiori explaining Dobzhansky's focal explanation. Tilted as that trope is to the design of artifacts and the assembly of their discrete parts, design-without-a-designer framing (and the engineering conception of fitness that attends it) tends toward seeing the products of evolution as modular adaptations that are predicated of individual organisms independently of population-level considerations. Indeed, the paradigms of design are phenomena that the natural theologian William Paley identified with no help from population thinking at all.

There is, of course, no inherent reason why the variation-preserving traits on which Dobzhansky concentrated cannot be called adaptations. Many admirers of Dobzhansky do just that. Still, the plain fact is that Dobzhansky himself never did so, referring to them instead as adjectivally "adaptive" or, especially in the third edition of his book, as having "adaptive value." 6 Is this because the nominalized locution 'an adaptation' seemed to him contaminated by its association with creationist design talk, a strong tilt toward artifacts rather than developmental processes, and optimization assumptions that attend engineering measures of fitness I believe so. At the very outset of Genetics of the Evolutionary Process Dobzhansky makes much of just this distinction, going as far as to call the view he rejects "Cartesian" (Dobzhansky, 1970, pp. 4-5).

(4) Dobzhansky's failure to use the locution 'an adaptation' explains, at least to my satisfaction, why in his later years he was willing, indeed eager, to cast himself as a biological teleologist. Adaptedness, he says, is teleological (Dobzhansky, 1970, p. 4). It is not only that the differential survival and subsequent generative enhancement of diplody, for example, are results of their variation-enhancing effects. They have been favored by natural selection precisely because they have these effects. They are there for a purpose.

Many of Dobzhansky's successors and philosophical explicators have taken this point to heart (Ayala, 1970; Brandon, 1981; Depew, 2008; Lennox, 1994; see Wright, 1967). There is a natural form of teleology (inferred from what is variously called consequence etiology, the historical theory of adaptation, or the selected effects account of functions) that makes no reference at all to the future, and a fortiori no mysterious causal reference to it, but depends entirely on ex post facto, if often unpredictable, events. This idea has, however, consistently fallen on deaf ears among those who frame adaptive natural selection through the design-without-a-designer trope. Since they identify teleology with intentional design, the subtraction of intentionality from adaptive natural selection definitionally means for them the death of teleology, even sometimes the death of God (Ghiselin, 1984; Dennett, 1995; Ruse, 2003). The fact that Dobzhansky had no truck with the design paradigm, with or without a designer, was thus a necessary condition of his embrace of a natural form of biological teleology.

(5) Dobzhansky was led by his canonical vocabulary itself to define biological evolution as change in gene frequencies. Definition is appropriate only when one is laying down a theoretical framework, as he well knew. The concepts of adaptedness and adaptability that lie at the heart of Dobzhansky's theory are formally predicated of populations of gene pools. Even if there are important phenomena that spread through populations by chance rather than by natural selection, as in what Wright called genetic drift, the process is no less genetic and no less populational. What is excessive is Dobzhansky's belief that all of biological evolution, including evolution above the species level, can be explained by his theory. This belief was animated by Dobzhansky's clear understanding of the inadequacies of rival theories. But the exclusion of rivals does not logically entail the adherence to a clearly superior one, although it may do so in the light of a rival's ex post facto, if not a fortiori, inadequacy.

(6) Dobzhansky's peculiar rhetorical trick was to map the genetic distributions that are the proper objects of his theory onto real populations of real organisms. He systematically implies that fitness landscapes are actual landscapes. He persistently ascribes properties that in his canonical language belong to populations, such as adaptability to changing environments, to the individual organisms that are members of those populations. He views organisms as problem-solvers. As the rhetorical scholar Leah Ceccarelli has

5 By "philosophical implications" I am referring to what Dobzhansky's conceptual vocabulary implies about the entities and processes countenanced by his evolutionary theory. For the larger cosmological, metaphysical, and religious dimensions of Dobzhansky's evolutionary theory, see Delisle (2009, this issue).

6 It is intriguing that in the 1st edition of Genetics and the Origin of Species we read: "That adaptations exist is so evident as to be almost a truism" (Dobzhansky, 1937, p. 150). That is the only time this location occurs in the entire book, and even here it is so closely associated Fisher's "extreme selectionism" that, Fisher having been critiqued, it never comes back. In the 3rd, 1951 edition of this text the paragraph in which this sentence occurs is rewritten in such a way that neither pluralized "adaptations" nor the singular "an adaptation" are mentioned. Nor are they to be found anywhere else in the book. What replaces the sentence just quoted is: "The theory of natural selection is primarily an attempt to account for adaptation of organisms to their environment" (Dobzhansky, 1951, p. 77). Emphasis immediately shifts in the following pages to a concept used at times informally in 1937, but now made central: "adaptive value" (Dobzhansky, 1951, pp. 77-78). Adaptive value is the "capacity," as Dobzhansky defines it, "of carriers of a given genotype to transmit their genes to the gene pool of the following generations" (Dobzhansky, 1951, p. 78; see Burian, 1983, p. 303). "Adaptive value" is closely linked to "adaptive norms" or "norms of reaction." Since genotypes generally enable their carriers to maximize the adaptive value of their traits if a range of different phenotypes can be elicited quickly from the same genotype when environments change, natural selection is said to have a tendency to evolve not static adaptations in the design sense, but "adaptive norms" or "norms of reaction" (Dobzhansky, 1970, p. 401). The greater distance expressed here from stereotypical adaptations that can be identified prior to and independently of evolutionary theory, as in principle they can be in design Darwinism, is expressed by intensified use of a processive vocabulary in Dobzhansky's later work, as witness the title of Dobzhansky (1970).
argued, Dobzhansky hoped in this way to secure consent from two different kinds of readers, naturalists and geneticists, fusing them into a single, if bifocal, discipline (Ceccherelli, 2001). This is, however, no more than Dobzhansky’s own preferred interpretation of his theory. Unsurprisingly, it has been a source of contestation among his heirs. Francisco Ayala imports a certain amount of design talk into his account of consequence-etiological natural teleology, thereby bringing the adaptations that individual organisms come to possess in the course of ontogeny into the range of Dobzhansky’s theory of the genetic adaptedness of populations (Ayala, 1970). By contrast, Richard Lewontin has always been reluctant to treat statements of the form “X is an adaptation for Y” as part of the science of genetic Darwinism, believing that such locations are contaminated by an adaptationist ideology that is little more than a secular, free-market offsporing of pre-evolutionary creationism (Gould & Lewontin, 1979; Lewontin, 1991).

3.1. Adaptationism and the British Synthesis

It is unlikely that Julian Huxley’s 1942 Evolution: The Modern Synthesis would have been written were it not for the fact that Huxley was lecturing in the United States in the period when Dobzhansky’s Genetics and the Origin of Species was being disseminated. He also knew about the work of Sewall Wright. In general, Huxley can be construed as bringing the news about American genetic Darwinism, especially its application to natural populations, to his British colleagues. One might expect, accordingly, that he was affording Dobzhansky a bully pulpit, much as his grandfather had given Darwin’s Origin of Species—the book on which Dobzhansky modeled his own—some amplification.

From the start, however, Huxley’s primary aim in writing his book differed from Dobzhansky’s in writing his. The news Huxley brought home bore on his British colleagues’ ongoing debate about whether traits used by naturalists and systematists to identify species are or are not adaptations. Huxley was out to rebut the dominant opinion of British naturalist-systematists in the wake of early 20th century mutationism that key diagnostic traits are non-adaptive. By contrast, the question that animated Dobzhansky was the relationship among the processes of selection, adaptation, and speciation. It was for this reason that Wright’s work on genetic drift figured so differently in Dobzhansky’s and Huxley’s respective uses of it. What Huxley called “the Sewall Wright effect” was made to bear on the role of chance, and hence non-adaptive traits, on speciation. Wright protested (though perhaps a bit too much) that his major concern was with its role in promoting the adaptedness of demes between which there is gene flow (Provine, 1986). He made no such complaint against Dobzhansky.

At the outset of Evolution: The Modern Synthesis, Huxley was emboldened to claim that states of relative adaptiveness are “pervasive” and “omnipresent” (Huxley, 1942, p. 37; see also p. 420). As a reader of Dobzhansky, one might expect him to be moving away from seeing organisms as bundles of discrete adaptations and moving instead toward seeing successful lineages as having evolved integrated systems of co-adapted genes possessing adaptedness and, through wide norms of reaction, phenotypic abilities to adjust to changing environments. But in the long, culminating chapter of the book Huxley transforms his claim about the pervasiveness of adaptedness into “an enumeration of various classes of adaptations” in order to answer his driving question about systematics. So many discrete adaptations does he catalogue that by the end of the chapter we find him affirming that “every organism cannot be other than a bundle of adaptations” (Huxley, 1942, p. 420). This is the very claim that at the beginning of his book he had seemed to doubt and at which Dobzhansky would continue to balk.

This is not an inconsequential difference. As Gould correctly notes, Huxley’s counting exercise encouraged British naturalists such as Arthur Cain, David Lack, and Bernard Kettlewell to discover, throughout the 1950s, more and more adaptations (Gould, 1982). Much of this work was done under the aegis of the Oxford School of Population Genetics, which took off when the Cantabrigian Fisher made common cause with the Oxonian E.B. Ford, creating a research program in which natural theological issues long dear to the neo-Paleyan Oxford School founded in the later 19th century by Aubrey Moore, Frederick Dickey, and Edward Poulton were reworked against a Fisherian—and decidedly not a Dobzhanskyan—population genetical background. In this way, older forms of British adaptationism gave way to new articulations that sprang up on both sides of the Atlantic after the empirical validation in the late 1960s (in the case of social insects) of W.H. Hamilton’s theory of inclusive fitness. In this succession of research programs, adaptations are the primary objects of investigation. The genetic adaptedness of populations is merely presumed to lie in their etiology.

3.2. Gould’s Hardened Synthesis

Stephen Jay Gould claimed that adaptationism of the sort I have just described simultaneously and permanently affected both American and British evolutionary biologists from the 1950s onward (Gould, 1983). I think, however, that his way of framing the question—are traits adaptations or not?—tilted too far toward Huxley’s British framing to make it perspicuous. Gould failed to notice or perhaps to think significant that Dobzhansky’s theoretical vocabulary, both early and late, did not toggle from one side of that dichotomy to the other, as Gould himself did, but threw cold water on this way of framing things itself.

Gould’s emphasis is understandable in light of the fact that the focus of his own training was systematics. We know from his recollections of his years as a graduate student that Gould was taught to look for adaptations in diagnostic traits that earlier naturalists took to be non-adaptive (Gould, 1983). In this respect, I do not deny that British adaptationism has been influencing American evolutionists ever since the 1950s. What is more telling and more questionable, however, is that when Gould turned against his adaptationist training he did so by conjuring up a vision of an original Synthesis—again presupposed to be the same on both sides of the Atlantic—that pitted chance against adaptations rather than, like Dobzhansky, pitting enumerated adaptations against the genetic adaptedness and adaptability of populations. In the name of an early Synthesis that was presumed to be “pluralistic” about evolutionary “forces” such as genetic drift and the different hierarchical levels at which these forces might operate (Gould, 1982), Gould retrojected onto a mythic past ideas that were not only framed in terms more Huxleyan than Dobzhanskyan, but reflected

7 In the same way that Bohm’s interpretation of quantum mechanics, for example, differed from the so-called Copenhagen interpretation.

8 A few points about the Oxford School. Its uptake of Fisher deleted his eugenical enthusiasms, as did the American version of the Synthesis. Both research communities were questing for scientific legitimacy (Ruse, 2001). Because legitimacy in science seems to rest on marginalizing and privatizing values and on professing agreement on matters of fact, professionalized evolutionary scientists have long had a standing interest in stressing that they all adhere to the same Synthetic Theory. In many books, Michael Ruse has defended this interest (see Ruse, 2001 in particular.) I call it into question. A relevant question is why under the leadership of Dawkins the Oxford school should have turned from the ardent neo-Paleyan theism that lies at its foundation to a no less ardent atheism rather than to scientific neutrality toward religion is a question worth investigating (Dawkins, 2008). As Ruse correctly notes, this is a very poor way of protecting the scientific objectivity of “the Synthesis” from religious obscurantism.
disputed questions—about the discovery of neutral molecular mutations, for example—that had arisen in Gould’s own, not Dobzhansky’s, Mayr’s or Simpson’s, heyday.

By doing so, Gould screened from view the contrast between discrete adaptations and the relative adaptedness of populations that had been central to Dobzhansky’s approach from the start. By veiling what actually divided Dobzhansky from the adaptationist tendency of the British Synthesis, Gould gave the impression that there was an unhardened, “pluralistic” view of the Synthesis at work in Britain as well as in America before it turned adaptationist on both sides of the Atlantic. But there never was such a pre-hardened pluralistic Synthesis in Britain. In America, moreover, the pluralism that did obtain was not a matter of favoring accidents over adaptation as the cause of evolutionary pattern. To say either of these things is to give a false impression that the Synthesis was more unitary than it was. It also makes it difficult to understand the spontaneity, unanimity, and argumentative creativity that Dobzhansky’s followers brought to the critique of British-style adaptationism as soon as it appeared in America in the 1970s. His ideas were clearly alive and well at the time.

My point might be dismissed as historical nitpicking were it not for the widespread opinion of supporters of adaptationism, including evolutionary psychologists and philosophers of mind, as well as many of its critics, that contemporary genocentric adaptationism represents the high point of a continuously advancing, unitary Modern Synthesis. This claim can be true only if the diversity of conceptual frameworks and the intensity of debates about them among genetic Darwinians can be downplayed or relegated to the dustbin of history. I have never seen an argument to this effect, however, that is persuasive enough to discount the fact the Modern Synthesis had and indeed still has several warring tendencies, or interpretations, and that in point of fact the wing that most properly deserves the name “The Modern Synthesis,” if any does, was advanced from 1937 to 1951 by Dobzhansky, Simpson, and Mayr through the auspices of Columbia University and the New York Museum of Natural History.

Gould did recognize conceptual diversity. Still, I do not think his account of the pluralism of the Modern Synthesis, early or late, captures the nature of that diversity. His way of characterizing it toils, as we have seen, within a simple binary in which either adaptations or accidents are the primary causes of evolutionary pattern. This binary is not only insufficiently pluralistic, but is itself characteristic of only one of the competing tendencies. It is not enough to say that the early Synthesis included several warring tendencies, or such as Wright, whose fallen mantle Gould wished to don. The adaptationist Daniel Dennett recognized that this account is false enough on its face to be discounted, thereby giving himself permission to throw the accent onto the adaptationist side of the same binary. By doing so he gave himself permission to recycle precisely the sort of overly cumulativist and adaptationist historiography that Gould wished to challenge (Dennett, 1995).

Admittedly, after 1937 Dobzhansky moved away from the element of chance in Wright’s “shifting balance” theory and was drawn progressively toward whatever ‘adaptationism’ was implicit in his own theory of “balancing selection.” But if one chooses to call post-1937 Dobzhansky an adaptationist one is obliged to acknowledge, as Gould does not, that his adaptationism differed so qualitatively from that of the Oxford School that there is no evidence for Gould’s claim that under the influence of Cairn’s, Lack’s, Kettlewell’s, and others’ discoveries, Dobzhansky, or perhaps even Mayr or Simpson, ever became adaptationists in the British sense.

To get the story right one must treat Gould as an involuntary witness against himself.

4.1. Conceptual frameworks in the Darwinian research tradition

In making my argument, I have put much stress on distinctions between the terms ‘adaptation,’ ‘adaptive,’ ‘adaptedness,’ ‘adaptability,’ and ‘an adaptation.’ One might assert, however, that the progressive advance of adaptationist genetic Darwinism is a matter of accumulated facts rather than of different ways of expressing them. Beneath diversity in style, it might be alleged, lies the common commitment of all professional genetic Darwinsians to a single theory that explains a growing body of facts. If different vocabularies have served individual scientists as instruments for learning the facts these can be assigned to the “mode of discovery” congenial to each scientist or his or her shared professional network, not to the confirmed outcomes of their labor.

Since Thomas Kuhn’s Structure of Scientific Revolutions, philosophers of science have found many ways to make conceptual framing play a more constitutive role in the production of scientific knowledge than it does in the view I have just summarized. Typically, these analyses make language choice the key to different conceptual frameworks. My point at present is not to adopt one or another of these philosophies of science, but to argue that without some such view it is impossible to tell an even remotely accurate story about the history of Darwinism.

Darwinism is not a theory, but a research tradition (Depew & Weber, 1995). This research tradition has never been, is not now, and probably never will be smoothly cumulative. It has gone through reformulations in which conceptual change has played as prominent a role as empirical discovery. So true is this that David Hull assigns to the term ‘Darwinism’ a processive, historicist rather than a fixed, essentialist meaning (Hull, 1988). If the Darwinian rather than other evolutionary traditions—neo-Lamarckism, for example, or neo-Geoffroyian structuralism—still dominates evolutionary inquiry it is primarily because its adherents have invented, sometimes in the nick of time, new conceptualizations of its core notion, natural selection, that have restored the continuity of the research tradition after periods in which the threat of failure has loomed large. Darwinism’s most innovative thinkers—Darwin, Wallace, Galton, Weismann, Fisher, Wright, Dobzhansky, Mayr, Hamilton, Maynard Smith, Dawkins—have been fertile in developing the mathematical means to apply the novel frames they invent. Discoveries that could not be coded in older frameworks have thus been accommodated and understood in new ones.

Novel conceptual frameworks have also revealed, if only in retrospect, where older versions of Darwinism were spinning their wheels in factual voids that, precisely because they were data free, could be as ideologically contaminated as they in fact have been. It is very easy for a conceptual framework to exceed the conditions of its applicability as its owners and operators quest for a general theory of evolution that will also apply to human beings and their doings. If popular Darwinism differs from scientific it is because ideological contamination of this sort plays the starring role. But even in Darwionic science shared facts are at best precipitates from controversies that depend at least as much on conceptual frames as on observational or experimental results and are liable to the same excesses. They depend on frames because without those facts are invisible and unintelligible. As knowledge grows by way of controversy-driven criticism almost as many supposed
selection as craftsman shapes organic form to meet environmental problems. But adaptedness is not always produced by selection acting in this ‘shaping mode.’ One alternative is that members of a population slowly migrate until they find a habitat in which some preexisting unchanged trait enhances fitness. This is a natural selection explanation of sorts, for the relational trait of ‘being in a better habitat’ increases in frequency as the members of this population change their environments. But it is nonetheless misleading to say that the fact of adaptedness indicates selective design in this scenario (Lewens, 2007, p. 13).

Darwinians who work within the design-without-a-designer paradigm must strain mightily to accommodate cases such as the one Lewens hatches up. Small wonder that Lewens, like Dobzhansky, cannot quite bring himself to use the location ‘an adaptation’ to describe scenarios in which biogeographical population shifts, perhaps in response to trophic scarcity, temperature change, or invasion by predators and competitors, enhance the adaptedness of a population without much, or perhaps any, morphological change. From a design perspective these phenomena don’t look much like paradigmatic adaptations. Such cases call for a conceptual framework in which relative adaptedness is predicated of populations in dynamically changing environments. They are just the sorts of cases that Dobzhansky’s conceptual framework was meant to handle.

Disagreements about adaptation, or if you prefer pseudo-disagreements, are common among those who work in the competing design-without-a-designer and population-dynamical frameworks. Here is an example. “Adaptations,” write Leda Cosmides and John Tooby, two of the principal promoters of evolutionary psychology, “will usually exhibit low heritability… because adaptations are in most cases universal and species-typical” (Cosmides & Tooby, 1992, p. 180). The thought is as follows. Genetic variation for traits such as the ability of human children to acquire syntactical language is minimal or even absent. Whatever differences exist must be due to developmental or environmental injury. Since heritability is a measure of the variance or statistical spread of genetic variation low or absent variance implies low or absent heritability. The philosopher of biology Robert Richardson, however, thinks that both Cosmides’s and Tooby’s claim and argument are exceedingly odd (Richardson, 2007, p. 100). That is because he works in a different conceptual framework.

For one thing, writes Richardson, paradigmatic adaptations such as lactose tolerance in human populations whose ancestors followed milk-producing herds or the partial resistance to malaria conferred by the heterozygous form of hemoglobin have high, not low heritability. Second, where genetic variance is altogether absent the concept of heritability does not apply at all. One is simply not dealing in that case with an issue that arises in population genetics. Nor, for that matter, is one dealing with the concept of adaptation, which in Richardson’s meaning is a technically defined term within the population-genetical theory of natural selection. Cosmides and Tooby, he concludes, have made “a remarkable mistake” (Richardson, 2007, p. 100).

My judgment is that this conflict reveals clashing conceptual frameworks at least as much as simple mistakes. Where my own sympathies lie the reader will inevitably have divined. I should note, accordingly, that writers like Cosmides and Tooby do, in fact, take themselves to be presupposing standard population genetical Darwinism as their explanatory background theory as much as Richardson does. But theirs is a version of population genetic Darwinism that secures reference to the adaptations that are its explananda by common sense criteria that are as readily available to creationists as they are to Darwinians. Having hatched up a plausible narrative about the evolutionary rationales of an adaptation thus identified, they tend to adopt a rather hand-waving attitude toward the population and molecular genetics that they presume undergirds the tale they tell about language. That is Richardson’s complaint about Evolutionary Psychology more generally (Richardson, 2007).

In Richardson’s own approach reference to the explananda of genetic Darwinism can be secured only by adopting an ontology that departs from common sense narrativism by constituting its objects statistically and operating on them mathematically. I note, however, that Richardson is as willing as his opponents to use the location ‘an adaptation’ of lactose intolerance in populations that depend on herd animals and of the spread of heterozygotes that protect against malaria, albeit by elevating the risk of sickle cell anemia. I think Dawkins was on sounder grounds by evading that location altogether as complicit with the very design talk that he opposed. Lewontin, I presume, agrees. Still, in Richardson’s analysis the adaptation in question is a population-level trait, heterosis, that may or may not be adaptive in a given environment. This is far less problematic than identifying the adaptation in question as “for protection against malaria,” since in non-malarial environments the same trait would seem to be “for” life-threatening sickle cell anemia. In the commonsense, narrative language that dominates most forms of adaptationism this is a hard saying, since in that framework adaptations are presumably as good-making and value-laden as they were for Paley and, if truth be told, for Darwin.

4.2. Toward evolutionary developmental Darwinism

Difficulties posed by the very notion of an adaptation led Dobzhansky to move increasingly toward a process-centered conceptual framework. Process-oriented conceptual schemes treat states of

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10 I see little substantive conflict between this paragraph’s claims about Darwinism’s history and Massimo Pigliucci’s claim that the Darwinian paradigm has not changed since Darwin (Pigliucci, 2007). Pigliucci is using ‘paradigm’ to refer to the notion of natural selection. His work actually reveals as much conceptual shifting since Darwin as Weber and I see. Indeed, he thinks that developmental evolutionary studies are now midwife to a kind of developmentalism that Pigliucci, like Weber and myself, thinks will displace or limit the range of the Modern Synthesis while remaining within the generous boundaries of what he calls the Darwinian paradigm and we call the Darwinian research tradition.
systems as more transient than substance ontologies such as Aristotle’s. As temporalized, often self-organizing wholes, processes stand at an even greater distance from the prevalence of parts over (assembled) wholes that characterizes our way of talking about machines and other artifacts. In this connection, it cannot be accidental that the title of the book in which Dobzhansky stressed adaptive norms as the proper objects and outcomes of the process of adaptation is Genetics of the Evolutionary Process.11

Dobzhansky’s emphasis on process was not restricted to treating the adaptive natural selection of populations as a process. It implied treating organisms themselves as developmental processes. When Dobzhansky contrasted design with development in the opening pages of Genetics of the Evolutionary Process he was not thinking of evolution as itself developmental (Dobzhansky, 1970, pp. 4–5). After all, the whole point of the Modern Synthesis was to eliminate any suggestion that phylogeny is ontogeny writ large or that ontogeny is phylogeny writ small. He meant that the outcomes of selection are beings that come to be by developing toward a viable adult state. The process of adaptive natural selection can be as consequence teleological as Dobzhansky takes it to be only if organisms themselves are as goal-oriented as Aristotle, for one, took them to be (Depew, 2008). Dobzhansky denies that natural selection applies to anything other than organisms so considered (Dobzhansky, 1970, p. 2). Natural selection is not what Dennett calls it: an algorithm that can range over any substrate that varies in ways that can be amplified in successive trials (Dennett, 1995).

Dobzhansky’s stress on norms of reaction entails that his theory of adaptive natural selection remains much closer to the developmental biology that the Synthesis displaced than design-without-a-designer versions. A norm of reaction is what natural selection at its most creative evolves: genotypes that have spread through populations because they can produce a range of phenotypes in individuals. Which phenotypes are expressed depends on interactions between embryos and environments. That is why Lewontin, writing with Richard Levins, remarks that “norms of reaction are the proper object of study for developmental biologists” (Levins & Lewontin, 1985, p. 94). A very strong presumption is at work here that ontogenetic processes enable embryos to maintain their trajectories by adjusting to environmental contingencies and that a primary object of natural selection is to evolve the capacities to do so.12 Although adaptation, contra Lamarckism, is necessarily a trans-generational process that depends on genetic change, Dobzhansky held that among the most important phenomena that any adequate theory of natural selection must explain are the abilities of organisms actively to adjust to contingencies (and so in the colloquial meaning of the term to ‘adapt’) on which Lamarckians focused. The fact that Lamarckians wrongly took these abilities to be explanatory rather than phenomena that need to be explained does not belie their importance (Dobzhansky, 1970, p. 32).13

The various modes of natural selection postulated by Dobzhansky testify to the developmentalist nature of his expansanum as well as the expansanata to which he appeals in explaining them. “Directional selection” is the scenario to which design-without-a-designer theories are overwhelmingly, if not exclusively, devoted. Over trans-generational time it evolves traits that are markedly better than their predecessors at dealing with environmental challenges. This sort of situation arises for Dobzhansky, however, and especially for his conceptual heirs only under conditions in which environments are rendered stable in large part by the heritable activities of organisms themselves (Lewontin, 1983; Odling Snee et al., 2003). To produce active beings of this sort—the sort that Lamarckians noticed, but misread—requires what Dobzhansky called “balancing selection,” which “maintains genetic heterogeneity or polymorphisms, that is, the continued presence in a population of two or several alleles of some genes or chromosomal structures” (Dobzhansky, 1970, p. 96). The idea is simple: Phenotypic responsiveness requires genotypic diversity, and hence a balance between using up variation and maintaining it in populations. We have already familiarized ourselves with this distinctively Dobzhanskyan contribution.

But neither directional nor balancing modes of selection can be effective unless they are complemented by what the developmental geneticist Ivan Schmalhausen called “stabilizing selection,” which keeps embryos on track as they develop. (The concept of ‘norm of reaction’ that informs Dobzhansky’s theory of balancing selection was itself taken from Schmalhausen.) Dobzhansky concurred with C.H. Waddington that stabilizing selection has at least two forms, normalizing and canalizing selection (Dobzhansky, 1970, p. 96). Normalizing selection trims away non-viable embryos, usually early in development. It is what remains of the negative, eliminative, or “fly swatter” natural selection that dominated Darwinism in the mutationist era, thereby giving natural selection the bad name it still has in popular culture. As Dobzhansky points out, this insufficiently population account, considered as a general theory, stood in the way of seeing natural selection as “creative.” It implies that what “survives” after the elimination of the “unfit” are at most a few variants that because they just happen in the first generation to be adapted to an external environment remain in later generations little more than frozen accidents (Dobzhansky, 1970, pp. 430–431). Still, the slippery relation between genes, organisms, and environments means that in fact there is selection against non-viable organisms and that adaptive evolution itself has ensured that this occurs as nearly as possible at early stages of ontogeny.

The complementary form of stabilizing selection is “canalizing selection,” an evolved capacity that ensures that whatever possible embryos that are viable will stay on a path toward flourishing. It pushes the restart button in the development process. Canalizing selection was taken from Waddington’s notion of developmental canalization. This and other appropriations of developmentalist themes have sometimes been cast in a negative light by writers who complain about how the makers of Modern Synthesis marginalized up-to-date developmental biology in order to make a new, developmentally insensitive paradigm out of population thinking (Gilbert, 1994). It is possible, however, to view the same facts in a more positive light. Rather than casting development aside, as Fisher did, or co-opting it, as he is sometimes accused of doing, Dobzhansky was paying a compliment to Schmalhausen and Waddington by favoring precisely what he is often accused of undermining. He was attempting to integrate development with genetic Darwinism.

Contemporary evolutionary developmentalists might claim with some justice that, good intentions aside, Dobzhansky’s integrative impulses could never overcome the stubborn fact that what can be seen in a populational framework screens off what is visible
from a developmentalist point of view as much as the opposite. Among phenomena thought to be inconsistent with or at least insufficiently explainable by population genetical Darwinism are the following discoveries, hypotheses, and implications, none of which was even on the horizon in the early days of molecular genetics, let alone in the pre-DNA days when Dobzhansky did his basic theorizing.

Genes are not (primarily) arrays of alleles, but highly conserved gene complexes that since early in the history of life have served as a “tool kit” for ontogeny. What makes organisms, species, and higher clades differ are changes in the cellular milieu, and even the external environment, that affect when, where, how, and to what extent regulatory gene sectors are expressed (Alperch, 1991; Newman, 2002; Newman & Müller, 2000, 2005). To the extent that natural selection is responsible for phylogenetic differentiation, much of the variation on which it works consists of changes in the intensity, placement, and timing of gene products thus generated in the developmental cycle (Blumberg, 2009; Gilbert &Epel, 2009). With respect to the trans-generational retention, recurrence, or reconstruction of variants generated in this way it is often environmental changes that are dispositive. When, for example, stickleback fish migrate from saltwater seas to freshwater lakes they no longer express gene products that produce the spiny pelvic plates that presumably conferred on them a selective advantage against predators in the open seas. This occurs invariably in disconnected freshwater lakes and in stickleback populations between which there is no gene flow whatsoever. So in this case ecological change, not a continuous selective history, is in the driver seat (Gilbert & Epel, 2009).

In such cases there is little or no gap between ontogenetic adapting in the Lamarckian sense and population-level adaptation in the Darwinian sense. Each generation is adapted because it responds adaptively to the same environmental factors (Walsh, 2006). Populations, accordingly, do not typically evolve over many generations from unfitness to fitness by the fixation of an adaptation. Rather, the presumed adaptive fit between populations and changing environments is retained or, if lost, quickly restored by the adaptive qualities of the self-organizing, ecologically-embedded beings we call organisms. In this way, the “arrival of the fittest” is of greater causal importance in any theory of adaptive change than the “survival of the fittest.” Perhaps negative natural selection is the most prevalent phenomenon thought to be inconsistent with or at least undermined by evolutionary genetical Darwinism. The change in freshwater and saltwater sticklebacks, for example, is associated with a 1000 base pair regulatory region of the genome. Typically, however, it is not allelic mutation, but phenotypic plasticity—the capacity to react to an internal or external environmental input—change in a form in state, movement, or rate of activity,” as Mary Jane West-Eberhard defines it (West-Eberhard, 2003, p. 33)—that is the leading edge of adaptation and speciation, with genes following behind as stabilizers of ontogeny in environments rendered relatively constant by the active adjustments of organisms (West-Eberhard, 2003). Genes exerted much less control in the evolution of early, less complex forms of life than they do in forms whose complexity requires more ontogenetic stabilization. But even today the variation that selection uses to evolve useful traits can be produced as part of the cycle of adjustment to environmental contingencies, as Darwin himself surmised by reflecting on ontogeny.

I do not vouch for the precision, generalizability, or even factuality of all the components in this composite picture of the new evolutionary developmentalism. My aim is only to point out that much of this picture, even if it is not technically inconsistent with the ascendant genocentric adaptationism, is not very well explicable by it. By contrast, the picture stands in far less tension with Dobzhansky’s legacy. It is true that Dobzhansky and his followers take many of the phenomena to which evolutionary developmentalists point to be expressions of genotypes already well-entrenched in populations. The black morph of the pepper moth was not created out of whole cloth when smog arrived in England, as even genocentric adaptationists will admit. Dobzhansky might be right, too, in thinking that the phenotypic plasticity that makes organisms so responsive to environmental change is itself an adaptive product of past natural selection. Yet it would seem that not much correction is needed for his admirers to agree with West-Eberhard that the process of adaptive change typically begins with accommodations at the phenotypic level. These take the lead in an ongoing, cyclical process that over vast periods of time embeds genotypes in ontogeny and distributes them in populations. After all, Dobzhansky himself denied that allelic mutation is anything more than the most remote source of the variation on which selection works. Changes in the timing, placement, and intensity of development are as admissible as proximate sources of the variation on which selection works as Dobzhansky’s stress on chromosomal rearrangements.

To make room for developmental Darwinism I have been arguing that Darwinism today should not be identified with genocentric adaptationism. To do so would be to consign Darwinism to its deathbed in much the same way that early 20th century mutationists did. Now as then this would be to ignore sources of vitality, both conceptual and empirical, that can reconcile population genetical Darwinism with evolutionary developmentalism. What stands in the way, above all, is dogmatic adherence to what was, after all, only a dogma to begin with: Francis Crick’s Central Dogma of Molecular Biology, according to which information flows from DNA to the environment but never the other way around. This stipulative proclamation had the intended effect of constituting research communities in molecular genetics with a built-in bias toward explanation at the level of DNA itself, thereby undermining not only the hierarchical structure of biological systems, as Dobzhansky, Mayr, and Simpson saw early on, but also the ontogenetic nature of the organic processes that are the proper subject of biology. More than anything else this dogma is responsible for the rise of genocentric adaptationism, which has generated gene-centered varieties of Darwinism tailored to its specifications. In taking a generally “genes-first” approach to adaptive natural selection, Dobzhansky and some of his successors have not themselves been immune to the unwarranted influence of the Central Dogma. By relinquishing it they may put themselves and their philosophical defenders in a position to solve the apparent conflict between population-level natural selection and individuals who develop, vary, and adapt much as the founders of population genetics themselves found ways to solve what turned out to be only an apparent contradiction between mutation and natural selection.

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14 In this connection, West-Eberhard defends the so-called “baldwin effect,” which treats the ability of organisms to adapt to their environments over multi-generational time frames as prior to the spread over no less long time frames of genotypes favorable to the activities in question (West-Eberhard, 2003). Mayr, Dobzhansky, and Simpson minimized or declared incoherent this process in the belief that it is insufficiently committed to the primacy of genetic change that they regarded as definitive of genetic Darwinism. But in saying so they frequently mischaracterized as crypto-Lamarckian a phenomenon that actually seems to be at work in, for example, the spread of lactose tolerance in pastoral human populations. See Deacon (1997) and Weber & Depew (2003).
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