Chapter 5

Darwinism and Neo-Darwinism

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1. Introduction

Scientific theories are historical entities, and like every historical entity, they undergo change through time. Indeed, a scientific theory might undergo such significant changes that the *only* point of continuing to name it after its source is to identify its lineage and ancestry. This may seem obviously true in the case of the theory of evolution by natural selection, still often referred to as Darwinism or neo-Darwinism. For when one looks at an advanced text on evolutionary biology today, especially one that stresses the centrality of mathematical population genetics to the theory, one might wonder what the point would be of applying to such a theory the name of a confessed mathematical illiterate with no clear ideas about the mechanisms of variation and inheritance. Nevertheless, there is merit to the view recently expressed by Jean Gayon, one of Darwinism's most thoughtful narrators:

> The Darwin–Darwinism relation is in certain respects a causal relation, in the sense that Darwin influenced the debates that followed him. But there is also something more: a kind of isomorphism between Darwin's Darwinism and historical Darwinism. It is as though Darwin's own contribution has constrained the conceptual and empirical development of evolutionary biology ever after. (Gayon, 2003, p.241)

Darwinism identifies a core set of concepts, principles, and methodological maxims that were first articulated and defended by Charles Darwin and which continue to be identified with a certain approach to evolutionary questions.[1] This is so *despite* the radical changes that this approach has undergone since the 1920s. One very important reason for this continuity has to do with the fact that most of its concepts, principles, and methods have been continuously challenged, not by those opposed to evolution,

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[1] So described, Darwinism denotes not so much a theory as a "research tradition" (Laudan, 1976) or a "scientific practice" (Kitcher, 1993); that is, at any given time in its history Darwinism consists of a family of theories related by a shared ontology, methodology, and goals; and through time, it consists of a lineage of such theories. I am using "theory" above in the very broad sense in which, from early on in his notebooks, Darwin kept referring to "my theory."

but by evolutionary biologists who portray themselves as *non-Darwinian* in one or more ways.[2]

For that reason it is worthwhile to begin with Darwin's Darwinism as formulated in *On the Origin of Species* in 1859. Charles Darwin was not, as we use the term today, a philosopher, though he was often so described during his lifetime.[3] If the concept of Darwinism has legitimate application today, it is due to a set of principles, both scientific and philosophical, that were articulated by Darwin and that are still widely shared by those who identify with "Darwinism."

2. Darwin's Life

Charles Darwin was born on February 12, 1809 and died on April 18, 1882. It was a time of radical changes in British culture, and his family background put him in the midst of those changes. Both of his grandfathers, physician/poet/philosopher Erasmus Darwin and pottery manufacturer Josiah Wedgwood, were members of an informal group of free thinkers that met regularly in Birmingham to discuss everything from the latest philosophical and scientific ideas to the latest advances in technology and industry. The members of the self-styled Lunar Society,[4] which included James Watt and Joseph Priestly, shared a "non-conforming" religious inclination. Robert Darwin, Charles's father, followed in his father's footsteps and became a doctor, and married Josiah Wedgwood's favorite offspring, Susannah. Charles was the youngest of five children she bore, but she died when he was but eight years old, and much of his upbringing he owed to his three sisters and brother, Erasmus, with whom he shared an early passion for chemistry, and with whom, at the age of 16, he went off to Edinburgh for the best medical education Great Britain had to offer.

Privately, Charles early on decided he could not practice medicine. But his already serious inclination toward science was considerably strengthened both by some fine scientific lectures in chemistry, geology, and anatomy, and by the mentoring of Dr Robert Grant, a Lamarckian who introduced Darwin to marine invertebrates and the use of the microscope in their study. This interest became a lifelong obsession, climaxing in his massive study of fossil and living Cirripedia or "barnacles" (Barrett & Freeman, 1988, vols. 11–13).

Eschewing medicine, he enrolled to take a degree in Divinity at Christ College, Cambridge University, from which he graduated in January of 1831. While in Cambridge, he befriended two young men attempting to institute a serious program of natural science at Cambridge, Rev. John Henslow, who was trained in botany and mineralogy, and Rev. Adam Sedgwick, a leading member of the rapidly expanding community of geologists. Through Henslow, to whom he shipped all his collections

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[2] Some of those biologists considered "non-Darwinian," such as Stephen Jay Gould, insist that in some respects they are closer to Darwin than defenders of the Synthesis. (Cf. Gould's forward to Dobzhansky, 1937/1982, p.xix.)

[3] The word "scientist" was coined by William Whewell during Darwin's lifetime, but very few of Darwin's contemporaries owned up to it.

[4] An entertaining account of the culture of the key members of this group can be found in Uglow (2002).

during the *Beagle* voyage, Darwin was introduced to leading figures in geology and natural history, as well as to Sir John Herschel and Rev. William Whewell, both serious students of the history and philosophy of science. Adam Sedgwick took Darwin on extended geological tours of England and Wales. Darwin's cousin, William Darwin Fox, a year ahead of him at Cambridge, helped convert his amateur passion for bug collecting into serious entomology. All of these influences built on those of Robert Grant, so that despite the lack of science required by his Divinity degree, Darwin graduated a very well-trained naturalist.[5]

3. Darwin's Darwinism

Darwin's mentors decisively shaped his philosophical attitudes and scientific career. Henslow was the final link in securing his position on the H. M. S. *Beagle*. The combination of meticulous field observation, collection, experimentation, note taking, reading, and thinking during that five-year journey through a wide cross-section of the earth's environments was to set the course for the rest of his life. During the voyage, he read and reread Charles Lyell's newly published *Principles of Geology*, which articulated a philosophical vision of rigorously empirical historical science, oriented around four key ideas:

(1) Geology includes the study of the history of life as evidenced by the fossil record and the past and present geographic distribution of species.
(2) It must also search for the causes of the extinction, introduction, or changing distribution of species.
(3) That search must be limited to causes of the same kind and intensity as those "now in operation."
(4) Lamarck's attempt to explain the introduction of new species by the hypothesis of "indefinite modification" of their ancestors fails on both methodological and empirical grounds.

Lyell's vision influenced Darwin profoundly. By the time of Darwin's return to England, likely influenced by conversations with Sir John Herschel in South Africa, he was convinced that the fossil record and current distribution of species were best explained by some form of species transformation. He set out to articulate a causal theory that measured up to Lyell's standards. He struggled to formulate a theory that would account for such transformations by referring only to "causes now in operation," causes that could be investigated empirically. The problem and the methodological constraints were those established by Lyell and received their philosophical defense from Herschel.

Darwin, of course, expected, and got, outraged reactions from religiously conservative colleagues, such as his old geology teacher Sedgwick, who, in a review, expressed his "deep aversion to the theory; because of its unflinching materialism; – because it has deserted the inductive track, – the only track that leads to physical truth; – because

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[5] For an expanded sketch of Darwin's early years see my entry, "Darwinism," for the *Stanford Encyclopedia of Philosophy* at http://plato.stanford.edu/entries/darwinism. The best biography is that by Janet Browne (Browne, 1995, 2002).

it utterly repudiates final causes, and therby [sic] indicates a demoralized understanding on the part of its advocates." What he had not expected was Lyell's refusal to openly endorse his theory and Herschel's decisive (if polite) rejection of its key elements. After setting out the theory in its Darwinian form, we can consider these reactions from those who apparently shared Darwin's philosophical norms about scientific theory, explanation, and confirmation.

The theory can be set out as three fundamental truths about species (1–3); four consequences of these truths that give rise to "natural selection" (4–7); and then three extrapolations from these consequences that will result in the origin and extinction of species (8–10).

(1) Species are comprised of individuals that vary ever so slightly from each other with respect to their many traits.
(2) Species have a tendency to exponentially increase their numbers over generations.
(3) This tendency is held in check by limited resources – as well as disease, predation, and so on – which creates a constant struggle for survival among the members of a species.
(4) Some individuals will *by chance* have variations that give them a slight advantage in this struggle, variations that allow more efficient or better access to resources, greater resistance to disease, greater success at avoiding predation, and so on.
(5) These individuals will *tend* to survive better and leave more offspring.
(6) Offspring *tend* to inherit the variations of their parents.
(7) Therefore, favorable variations will *tend* to be passed on more frequently than others, a tendency Darwin labeled "Natural Selection."
(8) Over time, especially in a slowly changing environment, this process will cause species to change.
(9) Given a long enough period of time, the descendant populations of an ancestor species will differ enough to be classified as different species, a process capable of indefinite iteration.
(10) There are, in addition, forces that encourage both divergence among descendant populations and the elimination of intermediate varieties.

Clearly every aspect of the mechanism of natural selection is capable of empirical investigation – indeed the published confirmatory studies of this process would fill a small library.[6] One can understand why devout and orthodox Christians would have problems; but why did Darwin's philosophical and scientific mentors? It would seem to be the model of Herschelian/Lyellian orthodoxy.

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[6] A more recent phenomenon than is usually appreciated. In Dobzhansky (1937/1982), after describing Ronald Fisher's "extreme selectionism," he quotes, as a "good contrast," the following remark of selection skeptics G. C. Robson and O. W. Richards (1936): "We do not believe that natural selection can be disregarded as a possible factor in evolution. Nevertheless, there is so little positive evidence in its favor . . . that we have no right to assign to it the main causative role in evolution."

4. Philosophical Problems with Darwin's Darwinism

The answer lies in five philosophically problematic elements of the theory.

[i] *Probability and Chance*. Note the language of "tendencies" and "frequencies" in the above principles. Privately, Darwin learned, Herschel had referred to his theory as "the Law of higgledy-piggledy," likely a reference to the probabilistic character of Darwin's claims. His theory is, as we would say today, a "statistical" theory, about what *tends* to happen due to clearly articulated causes. It allows us to make accurate predictions about *trends*, at the level of populations, but not to predict with certainty what will happen in each and every case. The proper philosophical understanding of this aspect of Darwinism is still elusive.

[ii] *The Nature, Power, and Scope of Selection*. For many people, natural selection is the core of Darwin's theory. And yet, even Darwin's strongest supporters and closest allies had problems with it. Some saw it as an "intermediate cause" instituted and sustained by God, others as a purely materialist and aimless process, and thus utterly incapable of dealing with adaptation. Some denied that it could originate species, seeing selection as a negative force eliminating what has already been created by mutation. Many felt that "selection" inappropriately imported into natural history an anthropomorphic vision of Nature choosing purposefully between variants. In a devastating review of *On the Origin of Species*, Fleeming Jenkin happily accepted the principle of natural selection but argued that it must be limited in scope to the production of varieties. [SEE POPULATION GENETICS]. All of these issues re-emerge during the resurgence of Darwinian principles in the creation of the evolutionary synthesis.

[iii] *Selection, Adaptation, and Teleology*. Because Darwin was fond of describing natural selection both as a natural process and one that worked for the good of each species, Darwin's followers seemed to have diametrically opposed views as to whether his theory *eliminated* final causes from natural science or breathed new life into them. In either case, there was serious disagreement on whether this was a good thing or a bad thing.[7]

[iv] *Nominalism and Essentialism*. There is a fundamental philosophical problem with the idea that a species can undergo a series of changes that will cause it to become one or more other species. The problem is well illustrated by the first question faced in the second volume of the *Principles of Geology*:

> . . . first, whether species have a real and permanent existence in nature; or whether they are capable, as some naturalists pretend, of being indefinitely modified in the course of a long series of generations. (Lyell, 1831, II, p.1)

Lyell assumes that a "real" species must have "permanent existence in nature," or ". . . fixed limits beyond which the descendants from common parents can never deviate from a certain type . . ." (Lyell, 1831, II, p.23). For Lyell, evolutionism implies a variety of nominalism about species, i.e., it implies that species names do not refer to types or kinds but only to collections of similar individuals. Darwin sometimes seems to agree.[8]

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[7] On which see Beatty (1990) and Lennox (1993).

[8] Darwin was examined as an undergraduate on John Locke's *Essay on Human Understanding*. As far as I know he never discusses whether this had any impact on his willingness to articulate the views expressed in this quote.

> . . . I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms. (Darwin, 1859/1964, p.52)

Given enough time, the individual differences found in all populations can give rise to stable varieties, these to subspecies, and these to populations that systematists will want to class as distinct species. Moreover, Darwin concludes the *Origin* with very strong words on this topic, words bound to alarm his philosophical readers:

> In short, we will have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species. (Darwin, 1859/1964, p.485)

Lyell, Herschel, Whewell, and Sedgwick certainly would not find this a cheering prospect, since they were unrepentant essentialists about species.[9] Members of a species possess a "type" established in the original parents, and this type provides "fixed limits" to variability. Lyell provided evidence for this view in *Principles* Vol. II; and it was canvassed again in Jenkin's review of the *Origin*. Such fixed limits to a species' ability to track environmental change easily explain extinction. But a naturalistic account of species origination is more difficult, since those "fixed limits" must somehow be transgressed.

Yet, adopting the sort of nominalism advocated above by Darwin has undesirable consequences as well. How are we to formulate objective principles of classification? What sort of a science of organisms is possible without fixed laws relating their natures to their characteristics and behaviors? In chapter 2 of the *Origin*, Darwin sought to convince the reader that, in practice, botanists and zoologists accepted a natural world organized as he described:

> It must be admitted that many forms, considered by highly competent judges as varieties, have so perfectly the character of species that they are ranked by other highly competent judges as good and true species. (Darwin, 1859/1964, p.49)

This is a predictable consequence of the fact that the organisms we wish to classify are products of a slow, gradual evolutionary process. In a given genus some naturalists may see ten species with a few varieties in each; others may rank some of the varieties as species and see twenty species. [SEE SYSTEMATICS AND TAXONOMY]. Both classifications may be done with the utmost objectivity and care by skilled observers. Some systematists are "lumpers," some are "splitters." Reality is neither.

[v] *Tempo and Mode of Evolutionary Change*. Whether or not Darwin's views entailed nominalism about natural kinds, they seem to reflect a belief that the evolutionary process is slow and gradual. I stress slow *and* gradual, for it is clear that one could have a *slow but non-gradual* evolutionary process (perhaps the geologically rapid periods of speciation postulated by Eldridge and Gould's "punctuated equilibrium model" are such

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[9] There is a very important, and underexplored, tension here, at least in Lyell and Herschel, both of whom seem to be in many other respects orthodox followers of Scottish empiricism.

[SEE SPECIATION AND MACROEVOLUTION]), and one could have a *rapid but gradual* one (for example the process George Gaylord Simpson labeled "adaptive radiation").

One of the strongest arguments for insisting that "Darwinism" and "neo-Darwinism" as they are used today are isomorphic to Darwin's Darwinism, as Gayon puts it, is that each of these questions is still hotly debated, and has been throughout the theory's history. Despite the changes wrought by the genetic, biochemical, and molecular revolutions [SEE MOLECULAR EVOLUTION]; the development of mathematical population genetics and ecology; and cladistic analysis in systematics, many evolutionary biologists still adhere to Darwinism, and are recognized as doing so by both themselves and their critics. We may thus organize the discussion of the "evolution" of Darwin's Darwinism into "neo-Darwinism" around these themes.[10]

5. The Core Problems and Darwinism

The philosophical problems of *Darwin's* Darwinism arise from questions concerning: [i] the role of chance as a factor in evolutionary theory and the theory's apparently probabilistic nature; [ii] the nature of selection; [iii] whether selection/adaptation explanations are teleological; [iv] the ontological status of species and the epistemological status of species concepts; and [v] whether evolutionary change is invariably slow and gradual. One dominant approach to evolutionary biology, represented by the so-called "neo-Darwinian Synthesis," sides with Darwin on these issues (and on many less fundamental ones, besides). That in itself is remarkable, given the radical transformations that the theory has undergone since the infusion of mathematics and Mendelian genetics that took place in the period from 1915 to 1930. [SEE POPULATION GENETICS]. But, it is the more remarkable because the Darwinian position on each issue has been continuously under pressure from non-Darwinian evolutionary biologists from Darwin's death to the present.

A full understanding of the underlying philosophical disagreements on these questions requires a historical study of how the "Synthesis" positions on these various issues, and those of their critics, arose. That cannot be done here; but it will be helpful to have a historically accurate summary of that theory.

The use of the term "synthesis" seems to have been suggested by the title of Julian Huxley's account, *Evolution: The Modern Synthesis*. What he intended is not entirely clear. In his chapter on natural selection he emphasizes the need for "facts and methods" from virtually every domain of biology as well as a number of related disciplines. But he immediately admits that most of these disciplines have developed in relative isolation. The synthesis he discusses is in the future and will be greatly aided by a "re-animation of Darwinism" (cf. Huxley, 1942, p.13).

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[10] I will use "neo-Darwinism" to refer to an explanatory framework created by the founders of the evolutionary synthesis of natural selection and population genetics and who hoped to bring a wide spectrum of biological subdisciplines within that explanatory framework. It was, of course, used much earlier to characterize a related framework defended by August Weissman in the 1880s and 1890s.

Among the fields he mentions, embryology and comparative anatomy played no significant part in the "neo-Darwinian synthesis." Huxley focuses most of his attention on the synthesis of Mendelian genetics and Natural Selection forged by R. A. Fisher, J. B. S. Haldane, and Sewall Wright; he also discusses its empirical support in both laboratory and ecological genetics (his book is dedicated to T. H. Morgan).

Thus, in standard accounts of the synthesis one can discern two stages: in the first stage (say, 1912–31) we see the growth of the laboratory genetics associated with T. H. Morgan, H. J. Muller, and A. H. Sturtevant, and the formulation of the mathematical theory of the genetics of populations developed by Fisher, Haldane, and Wright; in the second stage we see the publication of the books of Theodosius Dobzhansky, Ernst Mayr, George Simpson, and Huxley. In these latter works, all published between 1937 and 1944, the implications for paleontology, systematics, and *natural* selection of experimental laboratory genetics and the theoretical models of population genetics were explored.

This picture leaves out a number of important elements, two of which will be briefly noted. The "ecological genetics" exemplified in the work of E. B. Ford, A. J. Cain, P. M. Sheppard, and H. B. D. Kettlewell was critical both to the understanding and the acceptance of the power of selection in natural populations. And, while it is true that many evolutionary biologists tended to ignore development as irrelevant to their interests, two embryologists, C. D. Darlington and G. De Beer, were considered serious contributors to the synthesis.[11]

Nevertheless, after allowance is made for these and a number of other corrections, there is a profound truth in the claim that "the Evolutionary Synthesis" is, at its core, a brilliant integration. Experimental and mathematical genetics are wedded to those subjects that dominate *On the Origin of Species*: natural selection acting on chance variation as the principal mechanism of evolutionary change; the fossil record as the principal historical evidence of the evolutionary process; and biogeographic distribution providing overwhelming evidence that current populations are the products of an evolutionary process. A few key quotations make this clear:

> Since evolution is a change in the genetic composition of populations, the mechanisms of evolution constitute problems of population genetics. (Dobzhansky, 1937/1982, p.12)

> The paleontological record is consistent with the usual genetical opinion that mutations important for evolution, of whatever eventual taxonomic grade, usually arise singly and are small, measured in terms of structural change. (Simpson, 1944/1984, p.58)

> . . . the variability within the smallest taxonomic units has the same genetic basis as the differences between the subspecies, species and higher categories. . . . selection, random gene loss, and similar factors, together with isolation, make it possible to explain species

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[11] See, for example, the extensive citations of Darlington's work in cytology in Huxley (1942), Dobzhansky (1937/1932), and Simpson (1953). De Beer's *Embryos and Ancestors* is Simpson's primary source on the subject of how developmental genetics can play a role in determining the extent of a mutation's effect on the phenotype (Simpson, 1953, p.97). Darlington is cited as often as Fisher in Huxley's *Evolution: the Modern Synthesis* and in Dobzhansky's *Genetics and the Origin of Species*.

> formation on the basis of mutability, without any recourse to Lamarckian forces. (Mayr, 1942/1982, p.70)

The element of the synthesis that, in the minds of all three men, makes it *Darwinian* is the central role of natural selection on the small, genetically based variations studied by the geneticists and modeled mathematically by Fisher, Haldane, and Wright. At the time Dobzhansky, Mayr, and Simpson were writing their seminal works, it was easy for them to cite a large body of evidence skeptical of any significant role for natural selection in the production of evolutionary change. And even within this group, Wright's papers written between 1930 and 1932, which had a significant impact on Dobzhansky, restricted selection's importance to small, relatively isolated populations (cf. Dobzhansky, 1937/1982, p.191). In fact Dobzhansky closes his chapter on "Selection" by quoting Wright's 1932 statement of the view that evolution is due to a "shifting balance" of mutation, selection, inbreeding within colonies, and cross-breeding between them.

We will now turn to some philosophical problems the theory faced during its elaboration between 1930 and 1960. I will discuss only the first four of the five I mentioned at the beginning of this section.

5.1. *The roles of chance in neo-Darwinism*

In evolutionary theory, "chance" plays a key role both in discussing the *generation* of variation and the *perpetuation* of variation (a distinction I owe to John Beatty; see also Sober, 1984, ch. 4). Consider the following *variation grid*, created by asking whether the *contribution to fitness* of a variation does or does not bias its chances in favor of being *generated* or of being *perpetuated*:

	Variations	
	Generation	**Perpetuation**
Fitness biased	Lamarck	Darwin
Not fitness biased	Darwin	Lamarck
	Neutralism	Neutralism

The uniquely Darwinian position is that a variation's future contribution to fitness does not produce a bias in favor of its generation (as it would for Lamarckian theories), but contribution to fitness does produce a bias in favor of its perpetuation. Neutralism, to be discussed shortly, claims that a significant amount of evolutionary change, particularly at the molecular level, is due to randomly generated variation that is also perpetuated by chance. [SEE MOLECULAR EVOLUTION].

The above grid might lead one to conclude that both in the case of the generation of variation and the perpetuation of variation, "chance" will refer to the absence of a bias created by fitness differences. We get to the heart of the problem of the concept of "chance" within neo-Darwinism by seeing why that conclusion is, at best, misleading.

As we have seen, it was Darwin's view that advantageous variations occasionally arise "by chance," and have a "better chance" of being perpetuated than those that are not advantageous (cf. Darwin, 1859/1964, pp.80–1).

On this issue, orthodox neo-Darwinism agrees whole-heartedly with Charles Darwin. Fisher, Wright, and Haldane all start with the Hardy–Weinberg equilibrium principle [SEE POPULATION GENETICS] that represents the current state of a biological population in terms of the *relative frequencies* of alleles which "in a relatively large, closed population remains constant in the absence of any unbalanced pressure due to mutation or selection" (Wright, 1939/1986, p.285; he cites Haldane as the first to put the issue of evolutionary change in these terms; cf. Fisher, 1930/1999, pp.9–10). It is the *presence* of such pressures that is viewed as the principal mechanism of evolutionary change.

Thus understood, fitness differences must be understood in terms of increasing or decreasing the likelihood of the perpetuation of a trait (or gene) above (or below) what might be called "chance" levels. To take a simple case: if there are three possible combinations of alleles at a given locus in a population, we can characterize the outcome of a reproductive cycle as "chance" if, given a certain frequency distribution, each of the three possible combinations occurs at a frequency determined strictly by the laws of probability. Neo-Darwinism conceives of natural populations as "gene pools," and thinks of evolution as long-run changes in the frequencies of different combinations of genes from generation to generation. Thus, even when one factors in natural selection, being relatively better adapted merely increases an organism's "chances," i.e., its probability of leaving viable offspring; it does not guarantee it. Since natural selection is itself a stochastic process, Darwinians from Darwin to the present rightly characterize it in terms of selection influencing the "chances" of a given outcome, in interaction with other variables such as population size, population structure, or mutation rate.

Conceptual confusion arises from the fact that neo-Darwinians often, even typically, contrast the generation of variation due to "chance" and "randomness" with alternative theories that claim the generation of variation is "guided along beneficial lines" (to borrow a phrase from Asa Gray). Darwin defined natural selection as the preservation of variations that *happen* to be beneficial. This was in sharp contrast with the view of variation both of his botanist friend Asa Gray, who at least hoped it was due to design, and of Lamarck and his followers, who saw variation as a direct response to adaptive demands. Against this background, "chance" or "random" variation contrasts with variations arising by design or in response to a need.

The concept of "random variation" is today often used as a synonym for "chance variation" in precisely this latter sense. One of the founding fathers of the Synthesis puts it this way:

> . . . mutation is a random process with respect to the adaptive needs of the species. Therefore, mutation alone, uncontrolled by natural selection, would result in the breakdown and eventual extinction of life, not in the adaptive or progressive evolution. (Dobzhansky, 1970, p.65)

At least a significant amount of confusion concerning the role of chance in evolution can be avoided by determining whether, in a given case, "chance" or "randomness" is being used to characterize the *origins* or *generation* of variation or the *perpetuation* or *spread* of a variation.

Because of the stochastic character of natural selection, neo-Darwinians occasionally characterize it so as to make it almost indistinguishable from random drift. (For a presentation of the problem and various solutions cf. Beatty, 1984; Brandon, 1990, 2005; Lennox & Wilson, 1994; Millstein, 2002, 2005). The fitness of a genotype is characterized as its relative contribution to the gene pool of future generations – the genotype increasing in frequency being the fitter. But, of course, that could easily be the result of a "random" – non-fitness biased – sampling process; which organisms would be declared "fitter" by this method might have nothing to do with natural selection.

In order to provide a proper characterization of the role of chance in evolutionary change, then, we need a more robust and sophisticated account of fitness. But even with such an account there remains a substantial empirical question of what role indiscriminate sampling of genotypes (or phenotypes) plays in evolutionary change. Sewall Wright's work in the 1930s defended the possibility that genes neutral with respect to fitness could, due to the stochastic nature of population sampling, increase their representation from one generation to the next, with the likelihood increasing as effective population size decreases. Wright believed that species were typically subdivided into relatively small, relatively isolated, populations (or "demes") with significant in-breeding, and thus that it was likely that "neutral genotypes" becoming fixed at relatively high levels was significant. Though he gradually toned down this aspect of his work, a significant school of mathematical population geneticists in the 1960s and 70s developed these ideas into the "Neutralist" approach to evolutionary change mentioned earlier. Whether or not such a process plays a significant role in evolution is not a philosophical issue, but it is highly relevant to whether evolutionary biology is seen as predominantly Darwinian. For if any view is central to Darwinism, it is that the evolutionary process is guided predominantly by natural selection preserving randomly generated variation. It is to natural selection and related concepts that we now turn.[12]

5.2. The nature, power, and scope of selection

Darwin consistently refers to natural selection as a *power of preserving* advantageous, and eliminating harmful, variations. As noted in the last section, whether an advantageous variation *arises* is, in one sense of that term, a matter of chance; and whether an advantageous variation is actually *preserved* by selection is, in another sense of the term, also a matter of chance, but selection increases the chances of some variations relative to others. For Darwinism, selection is the force or power that favors advantageous variations, or to look ahead to the next section, of adaptations. It is this that distinguishes selection from drift.

As Darwinism developed in the mid-twentieth century, the expression "survival of the fittest" has essentially been eliminated from any serious presentation of the theory.

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[12] This is in fact the Synthesis view: see Mayr in Mayr and Provine (1980, p.3); Simpson (1984, p.xvii); Eldridge in Mayr (1982, p.xvi); Huxley (1942, pp.26–7).

On the other hand, the concept of "fitness" has played a prominent, and problematic, role. How that came about is a puzzle.[13]

R. A. Fisher's famously perplexing "Fundamental Theorem of Natural Selection" states that "the rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time" (Fisher, 1930/1999, p.35). However, none of the four classic proponents of the "Synthesis" we have discussed (Dobzhansky, Huxley Mayr, Simpson) even mention the term "fitness." Even in Dobzhansky's long discussion of Fisher's work, he uses "differences in viability" where Fisher will use "fitness differences," and he uses mathematical formulae borrowed from Wright's work rather than Fisher's. How and why the concept of fitness becomes central to textbook presentations from the 1950s on is an interesting question for which I have no answer. Nevertheless, from that point on, the mathematical models used in population genetics use "fitness" to refer either to the abilities of the different genotypes in a population to leave offspring, or to the measures of those abilities, represented by the variable $\boldsymbol{W}$. Here is a rather standard textbook presentation of the relevant concepts:

> In the neo-Darwinian approach to natural selection that incorporates consideration of genetics, fitness is attributed to particular genotypes. The genotype that leaves the most descendants is ascribed the fitness value $W = 1$, and all other genotypes have fitnesses, relative to this, that are less than 1. . . . Fitness measures the relative evolutionary advantage of one genotype over another, but it is often important also to measure the relative penalties incurred by different genotypes subject to natural selection. This relative penalty is the corollary of fitness and is referred to by the term **selection coefficient**. It is given the symbol s and is simply calculated by subtracting the fitness from 1, so that: $s = 1 - \mathrm{W}$. (Skelton, 1993, p.164)

The dual senses of fitness (as capacity and measure) are instructively conflated in this quotation. When fitnesses are viewed as differential *abilities* (or propensities) of organisms with different genotypes to leave different numbers of offspring, we are encouraged to suppose that "fitness" refers to the relative selective advantages of genotypes. But if "fitness" refers to a *measure* of reproductive success, it is a quantitative representation of small-scale evolutionary change in a population, and it leaves entirely open the question of the *causes* of the change – in which case the assumed connections among the concepts of fitness, adaptation, and natural selection are severed. "Selection coefficients" may have nothing to do with selection; what W represents may have nothing to do with selective advantage.

Fisher would have been unhappy with treating "fitness" as a measure. In a fascinating comparison between his fundamental theorem and the second law of thermodynamics he notes that both are statistical laws, dependent upon measurable constants, ranging over populations (Fisher, 1930/1999, p.36). Nevertheless, he goes on to note five "profound" differences, including that, though there is a standardized method for *measuring* fitness, *what is measured* is qualitatively different in every population; whereas entropy is presumed to be a measure of the same property for all physical systems (Fisher, 1930/1999, p.37).[14]

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[13] The pre-history of this puzzle is interestingly explored in Gayon (1992, 1995).

[14] It is also likely that Fisher, as well as Haldane, saw these models as experimental or as ways of demonstrating possibilities (cf. Lennox, 1991; Plutynski, 2004).

For Fisher then, fitness, the "measurable property," though always measured in terms of relative increases and decreases in gene frequencies, must not be identified with this measure. Fitness is a relationship between population members and their environments, and that relationship will differ depending on the nature of the population and the nature of the environment.

Following out Fisher's insight, we can formulate the theory in its "synthesis" guise without collapsing the common method of *measuring* fitness with the *heterogeneity* of instantiations of fitness. Since there are a number of confirmed ways in which natural populations can evolve in the absence of natural selection, and since stabilizing selection may prevent a population from evolving in its presence, measuring changes in the genetic make-up of a population does not establish natural selection and failing to detect such changes does not establish its absence. Population genetics and its associated models provide ways of establishing that a population either is or is not in equilibrium, and sophisticated tools for predicting subtle differences in expected trajectories depending on the values of the various variables in the models. Moreover, like the kinematics of any physical theory, if we see cross-generational change in a population of the sort predicted by a certain population model, it not only suggests that there are causes to be found – the detailed contours of those measures may suggest what sorts of causes to look for. What such models cannot do *on their own* is provide knowledge of the actual forces at work. To use language introduced by Elliott Sober, fitness, unlike natural selection, is *causally inert*. As I understand it, this is simply recognition of Fisher's point that the uniformity of the fitness measure hides the very different causal interactions that underlie it.

If we suppose that the standard neo-Darwinian view shares with Darwin a view of natural selection favoring certain organisms in virtue of their phenotypic variations, we can see two challenges to today's Darwinism with respect to *levels* of selection. There are those, such as G. C. Williams and Richard Dawkins, who argue that selection is always and only of genes. Here is a clear statement:

> These complications [those introduced by organism/environment interactions] are best handled by regarding individual [organismic] selection, not as a level of selection in addition to that of the gene, but as the primary mechanism of selection at the genic level. (Williams, 1992, p.16)

Dawkins refers to organisms – or interactors – as the *vehicles* of their genes, in fact, as vehicles constructed by the genome for its own perpetuation.

This view has been extensively challenged by philosophers of biology on both methodological and conceptual grounds, though there are, among philosophers, enthusiastic supporters (cf. Dennett, 1995). Oddly, defenders of this view claim to be carrying the Darwinian flag (an oddity noted by Gayon, 1998; Gould, 2002). Dawkins, for example, regularly refers to himself as a neo-Darwinian (e.g., Dawkins, 1982, pp.50–1). Yet, advocates of the "neo-Darwinian synthesis" invariably gave causal primacy to the interaction between organisms in populations and ever-variable ecological conditions; changes in the gene pools of those populations are viewed as the quantifiable and measurable *effects* of natural selection. On the other hand, both Dawkins and Williams are defenders of the adaptationist program; and at least part of their defense of genic selectionism is that it seems like a plausible interpretation of kin-selection explanations of so-called "altruistic" behavior. After all, if an animal behaves in a way that slightly lowers its individual fitness while increasing its "inclusive fitness," does that not suggest that it is the genes that are in the driver's seat?

Darwinism also faces challenges from the opposite direction. In the 1970s a number of biologists working in the fields of paleontology and systematics challenged the neo-Darwinian dogma that you could account for "macroevolution" by simple, long-term extrapolation from microevolution. Gould, in particular, opens Part II of *The Structure of Evolutionary Theory* (*Towards a Revised and Expanded Evolutionary Theory*), with a chapter entitled "Species as Individuals in the Hierarchical Theory of Selection." That chapter title combines two conceptually distinct theses: first, the thesis defended by Michael Ghiselin (Ghiselin, 1997) and championed and refined by David Hull (Hull, 2001), that species are, in a robust sense of the term, "individuals"; and second, that there may well be selection among groups of organisms, *qua* groups. [SEE SYSTEMATICS AND TAXONOMY; SPECIATION AND MACROEVOLUTION]. Gould's title exemplifies one approach to group selection – the unit of selection is always the individual, but there are individuals at various ontological levels, any of which may be subject to selection. A very different result emerges if one assumes that groups of organisms such as demes, kin-groups, or species, though not individuals, are nevertheless, under tightly specified conditions, subject to selection. Adding to the conceptual complexity, some researchers propose that "group selection" be restricted to the process whereby group-level traits provide advantages to one group over another, in which case there are strict conditions delimiting cases of group selection. Others define group selection primarily in terms of group level *effects*. Thus, a debate analogous to that earlier discussed regarding the definitions of "fitness" emerges here – by group selection do we mean a distinct type of causal process that needs to be conceptually distinguished from selection at the level of individual organism or gene, or do we mean a tendency within certain populations for some well-defined groups to displace others over time? (For further discussion, see Sterelny & Griffiths, 1999, pp.151–79; Hull, 2001, pp.49–90.)

5.3. Selection, adaptation, and teleology

Early in the introduction to *On the Origin of Species*, Darwin observes that the conclusion that each species had descended from others "even if well founded, would be unsatisfactory, until it could be shown how the innumerable species inhabiting this world have been modified so as to acquire that perfection of structure and co-adaptation which most justly excites our admiration" (Darwin, 1859/1964, p.3). One might say that this was the central promise of Darwinism – to account for both phylogenic continuity *and* adaptive differentiation by means of the same principles.

The nature of "selection explanations" is a topic to which much philosophical attention has been devoted in recent years. (Distinctive book-length treatments can be found in Brandon, 1990, and Sober, 1984.) Here, I want to focus on only one important question – to what extent is the teleological appearance of such explanations simply an appearance masking a causal process in which goals play no role?

The *appearance* of teleology is certainly present in Darwinian explanations, and has been since Darwin spoke of natural selection *working solely for the good* of each being (Darwin, 1859/1964, p.84). The appearance of teleology stems from the ease with which both evolutionary biology and common sense take it for granted that animals and plants have the adaptations they do *because* of some benefit or advantage to the organism provided by those adaptations.

Virtually every biologist identified with the neo-Darwinian synthesis has felt the need to address this issue. Haldane is reported to have compared teleology to the biologist's mistress: he cannot live without it but he doesn't want to be seen in public with it (Mayr, 1976, p.392). Dobzhansky stated that "some modern biologists seem to believe that the word 'adaptation' has teleological connotations, and should therefore be expunged from the scientific lexicon," a view with which he "emphatically disagreed" (Dobzhansky, 1937/1982, p.150). In a collection of papers edited by G. G. Simpson and A. Roe, C. S. Pittendrigh acknowledged that the evolutionary biologist cannot get along without references to ends and functions, but recommended replacing the word "teleology" with "teleonomy," a recommendation sometimes endorsed by Simpson, Mayr, and G. C. Williams (Williams, 1966, p.258). Perhaps the best survey of Synthesis views on this topic is to be found in Ernst Mayr's "Teleological and Teleonomic: A New Analysis," which includes a footnote in which a letter from Pittendrigh is quoted at length on why he coined the term "teleonomy." The clearest analysis from an "orthodox" neo-Darwinian of the teleological nature of selection explanations is that by Francisco Ayala (Ayala, 1970).

Whatever term one uses, the serious philosophical issue is whether the functions provided by adaptations (i.e., selected traits) play a central and irreducible role in their explanation. Only if the answer is "yes" are the explanations teleological.[15] [SEE FUNCTIONS AND TELEOLOGY].

Let us begin with a simple, yet realistic, example. In research carried out over many years, John Endler was able to demonstrate that the color patterns of males in the guppy populations he studied resulted from a balance between mate selection and predator selection. To take one startling example, he was able to test and confirm a hypothesis that a group of males with a color pattern that matched that of their river beds except for bright red spots have that pattern because a common predator in those rivers, a prawn, is color blind for red. Red spots provided no selective disadvantage and attracted mates (Endler, 1983, p.173–90). This pattern of coloration is a complex *adaptation* that serves the functions of predator avoidance and mate attraction (Williams, 1966, p.261; Brandon, 1985; Burian, 1983). Do those functions explain why these male guppies have the coloration they do?

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[15] I need to stress here that this discussion is restricted to explanations of adaptation within the Darwinian framework, i.e., by reference to natural selection. Whether other sorts of explanation in other aspects of biology are teleological or not, and whether, if they are, the explanation would take the same form, I leave entirely open. For a good survey of this question, and a defense of a distinct understanding of biological function in the domain of comparative morphology, see Amundson and Lauder (1998).

In order for it to be a product of natural selection, there must be an array of color variation available in the genetic/developmental resources of the species wider than this particular pattern but including this pattern. In popular parlance (and the parlance favored by Darwin), this color pattern is present in the population because it is *good for* the male guppies that have it, and for their male offspring (Binswanger, 1990; Brandon, 1985; Lennox, 2002). That is why natural selection favors this coloration. The analysis offered here is more robust than standard accounts in terms of "selected effects" or "consequence etiologies" in stressing that selection ranges over *value* variation. The reason for one among a number of color patterns having a higher fitness value has to do with the *value* of that pattern *relative to the survival and reproductive success* of its possessors (Lennox, 1993, 1999, 2002).

A commitment to a strong role for natural selection in the evolution of life is certainly central to neo-Darwinism, a commitment sometimes referred to as "adaptationism" or the "adaptationist program." Explanations by reference to selection are a particular kind of teleological explanation, an explanation in which a trait's *adaptive functions, its valuable consequences*, account for its differential increase or maintenance in the population. Given neo-Darwinism's commitment to selection as the source of adaptation, then, it is not surprising that all the central figures in the Synthesis felt it necessary to address this question. Their ambivalence is also understandable. Teleology was closely associated with two discredited biological research programs, natural theology and vitalism. A great deal of work by philosophers of biology over the past 30 years has obviated the need for such ambivalence.

5.4. Species and the concept of "species"

In listing the topics under which I would discuss neo-Darwinism, I distinguished the question of the ontological status of species from the epistemological status of the species *concept*. Though they are closely related questions, it is important to keep them distinct. As will become clear as we proceed, this distinction is rarely honored. Moreover, it is equally important to distinguish the *species concept* from the categories of features that belong in their *definitions*. Advances in our theoretical understanding may lead us to reconsider the sorts of attributes that are most important for determining whether a group of organisms is a species, and thus whether it deserves to be assigned a name at that taxonomic level. It should not be assumed that such changes constitute a change in the species concept, though at least some such changes may lead us to restrict or expand the taxa within that category.

In his contribution to the Synthesis, *Systematics and the Origin of Species*, Ernst Mayr titled chapter five "The Systematic Categories and the New Species Concept." Recall that Darwin made a point of treating the species category as continuous with "well-marked variety" and "sub-species," and made the radical suggestion that its boundaries would be just as fluid. Without explicitly acknowledging Darwin, Mayr takes the same tack, discussing "individual variants" and "sub-species" as a preliminary to discussing the species concept. Mayr notes that for someone studying the evolutionary process, speciation is a critical juncture; ". . . his interpretation of the speciation process depends largely on what he considers to be the final stage of this process, the species" (Mayr, 1942/1982, p.113). With this in mind, he offers the following definition, the now infamous "biological species concept" (BSC):

> Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups. (Mayr, 1942/1982, p.120; 1976, p.518)

Mayr was well aware of the limitations of this definition, and treated it somewhat as a "regulative ideal." Dobzhansky in 1937 gave what he claimed to be a definition of species, but which seems, as Mayr noted (Mayr, 1976, p.481) much more a definition of *speciation*:

> . . . that stage of evolutionary process at which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding. (p.312)

Simpson (1944/1984) and others built even more historicity into the concept. These are all, of course, intended as *definitions* of the species *category*, and they attempt to provide a test (or a "yardstick": Mayr, 1976, p.479) that in principle will permit a researcher to decide whether a group of individuals should all be identified by a single species-level concept such as "homo sapiens." The test for species membership is the *capacity* to interbreed; the test distinguishing two species is *incapacity* to interbreed. Dobzhansky makes the importance of this test transparent – the transition from a single interbreeding population to two reproductively isolated ones is the process of speciation. [SEE SPECIATION AND MACROEVOLUTION].

Now in each of these cases, little attention is paid to the actual methods used by taxonomists and systematists in differentiating between varieties of a species and distinct species, something to which Darwin gave a great deal of attention. Darwin's nominalism regarding the species concept likely stemmed from his close attention to his own taxonomic practices and those of other specialists. But nominalism typically combines a view about the *ontology* of species with one about the epistemological status of the species *concept*. On the first question, the nominalist insists that there are no species – there are more or less similar individuals. On the second question, the nominalist typically insists that the species *concept* is, at best, a useful or convenient grouping of similar individuals or, at worst, an *arbitrary* grouping of similar individuals.

In his work, Mayr relates different approaches to the species concept to the philosophical distinction between essentialism and nominalism. He associates essentialism with the view that a species *concept* refers to a universal or type. This view of the referent of the concept leads to the Typological Species Concept, which he traces from Linnaeus back to Plato and Aristotle and claims "is now universally abandoned" (1976, p.516). At the opposite extreme is nominalism, which combines the view that only individuals exist in nature and that species are concepts invented for the purpose of grouping these individuals collectively.

Mayr claims that his Biological Species Concept (BSC) is an advance on both; individual species members are objectively related to one another not by a shared relation to a type but by causal and historical relationships to one another. Notice, however, that this is, from an ontological perspective, nominalism. Mayr's position can be understood as arguing for a new way of understanding the epistemological grounds for grouping individuals into species. This new way of grouping stresses historical, genetic, and various ecological relationships among the individuals as the grounds for determining species membership. His claim is that this is more reliable and objective than similarities of phenotypic characteristics. This makes sense of the importance he eventually places on the fact the BSC defines species relationally:

> . . . species are relationally defined. The word species corresponds very closely to other relational terms such as, for instance, the word *brother*. . . . To be a different species is not a matter of degree of difference but of relational distinctness. (Mayr, 1976, p.518)

Brothers may or may not look alike; the question of whether two people are brothers is determined by their historical and genetic ties to a common ancestry. Notice, however, that this is a claim about which, among the many characteristics that they have, should be taken most seriously in determining the applicability to them of the concept "brother." That is, it is a defense of a sort of essentialism.

A number of critics have pointed out that essentialism need not be committed to "types" understood as *universalia in re*; and on certain accounts of essences any species taxon that meets the standards of BSC does so in virtue of certain essential (though relational and historical) properties. At one extreme Michael Ghiselin and David Hull (and Mayr [1987] acknowledges this as an extension of his ideas) have argued that this causal/historical structure of species provides grounds, at least within evolutionary biology, for considering species to be individuals. Organisms are not members of a class or set, but "parts" of a phylogenetic unit.

A critical issue in this debate over the account of the species concept most appropriate for Darwinism is the extent to which the process of biological classification – taxonomy – should be informed by advances in biological theory. Besides those already discussed, the moderate pluralism associated with Robert Brandon and Brant Michler or the more radical pluralism defended by Philip Kitcher argue that different explanatory aims within the biological sciences will require different criteria for determining whether a group constitutes a species. Cladists, on the other hand, employ strictly defined phylogenetic tests to determine species rank.

Unlike many of the other topics that define the history of Darwinism, there is no clear-cut position on this question that can be identified as "Darwinian" or "neo-Darwinian." In a recent collection of papers defending most of the viable alternatives (Ereshefsky, 1992), my suspicion is that virtually every author would identify himself as Darwinian. This may be because many of the positions defended could plausibly be traced to roots in Darwin's own theory and practice (see Beatty, 1985; reprinted in Ereshefsky, 1992).

6. Conclusion

In this essay I have built a case for the claim that a certain stance within evolutionary biology today is legitimately referred to as "Darwinism" or "neo-Darwinism," despite the remarkable changes that the theory of evolution by natural selection has undergone since *On the Origin of Species* was first published. The case consists of identifying core principles of Darwin's original theory (with their associated philosophical problems) and tracing the development of those principles through the neo-Darwinian synthesis. I have argued that, despite the radical changes brought about by the fusion of the theory with Mendelism via mathematical population genetics, those core principles survive, and serve to differentiate a "Darwinian" approach to evolutionary biology from other approaches. Moreover, the development of the theory has resulted from a continuous history of philosophical pressure on each of those principles.

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Further Reading

Three excellent, but quite different, perspectives on the historical development of Darwinism are:

(1) Depew, D. J., & Weber, B. H. (1995). *Darwinism evolving: systems dynamics and the genealogy of natural selection*. Cambridge, MA: MIT Press.
(2) Gayon, J. (1998). *Darwinism's struggle for survival: heredity and the hypothesis of natural selection*. Cambridge: Cambridge University Press.
(3) Shanahan, T. (2004). *The evolution of Darwinism: selection, adaptation, and progress in evolutionary biology*. Cambridge: Cambridge University Press.

Three studies focused on different aspects of the "modern synthesis" are:

(4) Mayr, E., & Provine, W. B. (Eds). *The evolutionary synthesis: perspectives on the unification of biology*, Cambridge, MA: Harvard University Press.
(5) Provine, W. B. (1971). *The origins of theoretical population genetic*s. Chicago: Chicago University Press.
(6) Sarkar, S. (Ed.). (1992). *The founders of evolutionary genetics: a centenary reappraisal*. Dordrecht: Kluwer.

And finally, the classic that coined the term “modern synthesis” for the attempt to base diverse biological disciplines on a “genetical” theory of evolution by natural selection:

(7) Huxley, J. (1942). *Evolution: the modern synthesis*. London: George Allen & Unwin.

A website devoted to making all of Darwin’s published works and unpublished notebooks available online, and with links to many other valuable sites is: http://darwin-online.org.uk.