Darwinism as a Theory for Finite Beings

Darwinism & Metaphysics
University of Notre Dame
March 8-10, 2001

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1. Introduction

In the *Origin of Species*, Darwin wrote:

> I have hitherto spoken as if the variations—so common and multiform in organic beings under domestication, and in a lesser degree in those in a state of nature—had been due to chance. This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the causes of each particular variation (Darwin 1859, 131).

In these lines, Darwin can be interpreted as expressing a *subjective view of chance*—most likely a consequence of a metaphysical doctrine which was held by many 19th century scientists. This doctrine, of course, is *determinism* and was most succinctly formulated by Pierre Laplace. According to this doctrine, our failure to predict or explain a natural event cannot be attributed to probabilistic causes or objective chance. Instead, the reasons for such failures must be sought in our *ignorance* of the real causes determining the event. In other words, for the determinist, chance is merely an appearance or an illusion which arises because of the *finite nature of human reason*.

Was Darwin right about this? Or should we revise our thinking about chance in evolution in light of the more advanced, quantitative models of Neo-Darwinian theory, which make substantial use of statistical reasoning and the concept of probability? Is determinism still a viable metaphysical doctrine about biological reality after the quantum revolution in physics, or do we have to abandon it in favor of an objective indeterminism? In light of such reflections, what is the relevant interpretation of probability in evolutionary theory? Do biologists use the concept of probability because they are finite cognitive agents or because the evolutionary process is fundamentally probabilistic? In this paper, I will show that we do not yet fully understand the nature of chance in evolution.

In the next section, I will review the different evolutionary contexts in which chance and probability appear. In Section 3, I take a brief look at chance and probability in physics, since I believe that there are lessons to be learnt from the philosophy of physics. In Sections 4 und 5 I critically discuss an instrumentalist and a scientific realist account of the statistical nature of evolutionary theory. I show that they are both unsatisfactory. In Section 6, I show that there are viable alternatives to these accounts. I sketch one such alternative, which is compatible with both determinism and realism and which tries to do justice to the scientists' own thinking on this problem. In Section 7, I turn to the question of whether evolutionary processes are deterministic or not. An examination of the arguments presented by indeterminists will lead me to agnosticism about this question. Finally, in Section 8, I show that there are limits to our understanding of the metaphysical foundations of Darwinism.

2. Chance and Probability in Evolution

In the passage from the *Origin* which I have quoted above, Darwin was concerned with the causes of *genetic variation*. Modern geneticists, of course, know much more about the causes of genetic variation than Darwin did. Molecular geneticists have discovered a variety of mechanisms which can cause changes in an organism's genetic material, also known as *mutations*. It is a central tenet of Neo-Darwinism that mutations are *random* in the sense that their probability of occurring is causally independent of their effect on an organism's fitness. In other words, mutations which are beneficial or detrimental for an organism's survival and reproduction are not made more likely *by virtue* of their being beneficial or detrimental. The mechanisms which cause mutations are "blind" to adaptive value. I believe that this is the correct sense in which mutations can be said to be random. However, this account of chance variation leaves an important question unanswered: What exactly do we mean by "probability" or "likelihood" when we say that mutations are not made more probable or more likely by virtue of their adaptive value? Does this probability express an *irreducibly stochastic disposition* of the kind postulated in quantum mechanics? Since the Neo-Darwinian definition of random mutation is also compatible with strict determinism, questions like these are far from being trivial.

I am going to argue that we cannot give a definitive answer to this question, in spite of the fact that molecular geneticists know so much about the mechanisms causing mutations. The reason is that we do not know, at present, whether evolutionary processes are deterministic or not. Thus, we do not know exactly what the nature of chance is in the mechanisms generating genetic variation. For the most part of the present paper, I want to leave the issue of random mutation aside. For the concepts of chance and probability arise in different contexts in Neo-Darwinian theory, and it is these other contexts with which I will be mainly concerned here. The main issues I will be addressing are the following: First, what is the relevant sense of chance and probability in different evolutionary models? Second, why do evolutionary biologists use probabilistic concepts? Is it due to the nature of the evolutionary process or the finite nature of human reason?

Probabilistic concepts occur in different contexts in contemporary models of evolutionary change.[1] First, they appear in the *theory of natural selection*. Unless a population of organisms is infinitely large—which is physically impossible—the outcome of natural selection is not fully determined by the fitness values of all the individuals in the population. In finite populations, there is always a non-zero probability that the fittest do not survive (Beatty 1984). Furthermore, if we focus our attention on individual organisms, we find that the individual's *actual* reproductive success is not fully determined by its fitness value. This fitness value provides only a *statistical expectation*, for example, a probability distribution that the organism has 0, 1, 2, 3, or *n* surviving offspring (Beatty and Finsen 1989, Mills and Beatty 1979). Second, probabilities occur in the theory of *random genetic drift*. Genetic drift is defined as an evolutionary process in which the change of gene frequencies is independent of any gene's contribution to fitness. Drift has also been described as a *random sampling process*, while "random" means that population sampling is *indiscriminate* with respect to phenotypic properties (Beatty 1984, 1987). Third, probabilities are used in certain models of *macroevolutionary change*. Macroevolution can be modeled as a stochastic branching process in order to explain certain long-term phylogenetic patterns (Sober 1988). Fourth and finally, probabilities arise in evolutionary models which consider the effect of new mutations on a population.

As this brief overview demonstrates, modern evolutionary theory is profoundly statistical in nature. Statistical concepts are used by evolutionary biologists not just for data analysis, but as an integral part of most of the theoretical models they advance in order to explain evolutionary change. Like in other scientific disciplines which deal with statistical theories, the use of probabilistic concepts raise a number of difficult foundational, epistemological and metaphysical issues. Let me first relate a general observation, which should be uncontroversial. The *reasons* why scientists resort to statistical theories may differ considerably, depending on the theories' subject domain. This is evident if we take a brief look at modern physics.

3. A Brief Look at Chance and Probability in Physics

Probably the most important physical theories which use statistical reasoning are the theories of *statistical mechanics* and *quantum mechanics*. During the 1960s, it became clear that these theories differ fundamentally with respect to the foundational issues surrounding chance and probability.[2] Classical statistical mechanics assumes that the systems it models are governed by fully deterministic laws of motion, namely Newton's laws. The reason why the theories of statistical mechanics are statistical is that their subject domain consists of systems which are composed of an extremely large number of particles, for example, a macroscopic container filled with gas molecules that interact with each other as well as with the walls of the container. It would be impossible to solve the equations of motion for each of these particles in order to explain the bulk properties of this physical system. For this reason, physicists abstract from the trajectories of each individual gas molecule and investigate *probability distributions*, e.g., the probability that a system composed of N particles is found in a certain region of an abstract state space of $6N$ dimensions. According to the standard interpretation, such probability assignments generalize over hypothetical, infinitely large sets of systems—so-called *ensembles*—which differ only in initial conditions and are otherwise identical. Thus, in statistical mechanics, we find *objective probability statements* even though the systems investigated are fully deterministic. And even though probability is objective, in statistical mechanics, the *reason* why scientists use probabilistic thinking is the finite nature of human reason.

The case is very different in quantum mechanics. There, probabilistic reasoning is used because there exist states of quantum systems which do not fully determine the outcome of measurements. Even though unobserved quantum systems are governed by deterministic laws—namely the time-dependent Schrödinger equation—as soon as a measurement is performed, the dynamics of the system changes radically and it starts to behave unpredictably. However, this unpredictability is fundamentally different from the unpredictability found in classical statistical mechanics, for, as a matter of principle, it cannot be overcome by any amount of additional information and computing power. Quantum mechanics is statistical because of the indeterministic nature of the measurement process, *not* because of the finite nature of human reason. Accordingly, in quantum mechanics, probability statements express irreducibly stochastic propensities of quantum systems.

As these two examples demonstrate, concepts like chance and probability can differ even within a single scientific discipline. If we turn to evolutionary theory—which I will do in an instant—there is thus little reason to expect that the concepts of chance and probability are the same as in physics, or even that they are they same in different biological theories.

4. An Instrumentalist View

In the recent literature in philosophy of biology we find two different accounts of the statistical nature of evolutionary theory. The first account has been developed independently by Alex Rosenberg (1994) and Barbara Horan (1994), and it looks roughly as follows: Rosenberg and Horan hold that all the processes which are relevant for evolutionary change are *deterministic*. They argue that, even though there exist genuinely indeterministic events at the microphysical level, this indeterminism vanishes asymptotically as we move from the micro- to the macrolevel. In other words, indeterminism may play a role at the level of chemical bonds or below, but it plays no role in the macroscopic world of biological organisms. This raises the question of why evolutionary theory uses statistical reasoning and probabilistic concepts.

Rosenberg develops his answer to this question in the context of the theory of genetic drift. To this end, he invented the following fictional example (1994, 71-73): Consider a population of giraffes which, for unknown reasons, shifts away from its adaptive peak in neck length. A team of conservation biologists attributes this change to random genetic drift, in other words, to the chance survival of genotypes which have shorter necks. Rosenberg then assumes that the real reason for the change in neck lengths is illegal poaching. In other words, long-necked giraffes are killed by poachers on a regular basis. The conservation biologists are unaware of this poaching activity, and this is why they attribute the evolutionary change observed to random genetic drift. Rosenberg concludes that the theory of genetic drift, in this fictional example, fails to give us the true explanation of evolutionary change. The theory of drift is merely a way of expressing the biologists' ignorance concerning the real causes of evolutionary change. Rosenberg then generalizes from this example and claims that the same is true for all cases where biologists invoke genetic drift in order to explain evolutionary change. In other words, in all the alleged cases of drift known to biologists, there is a hidden cause or a set of hidden causes which are responsible for the observed changes in gene frequencies. In his fictional example, the hidden cause is given by the poachers. In other cases of drift, the hidden causes may be something else. Rosenberg's claim is that there are always hidden causes when biologists see genetic drift. Thus, he concludes the theory of drift is merely a "useful fiction".

Rosenberg's argument does not stop here, for he eventually arrives at far-reaching conclusions. He concludes that the probabilities which feature in evolutionary theory are *subjective* (1994, 61). According to this view, the probability, say, that a certain allele of gene is fixed in a small population by chance merely expresses a human agent's *degree of belief* in the statement that the allele is fixed. As a consequence, the theory of random genetic drift says nothing about the real causes of evolutionary change. It only says something about what humans can rationally expect to happen in a small population of organisms in the absence of any additional causal information. Thus, Rosenberg is an *instrumentalist* about the theory of genetic drift.

Roberta Millstein (1996) has shown that Rosenberg's example which is supposed to demonstrate the instrumentalist nature of drift theory is fundamentally flawed. The way he has set up his example, it is really an example of *selection* rather than drift. What is actually going on in his fictional example is that the poachers select for short-necked giraffes. The example is ill-chosen for making any claims about genetic drift, because it simply does not qualify as a case of random drift. Furthermore, it is unlikely that biologists would invoke genetic drift in a case where there seems to be a systematic bias in the survival rate towards short-necked giraffes. They would rather look for a cause for this bias in survival rate. Thus, Rosenberg's fictional example fails to support his subjective account of probability and the resulting instrumentalist view of genetic drift theory. Of course, this does not yet mean that such an account is incorrect. It could still be that Rosenberg is right and that the theory of genetic drift fails to give us true explanations of certain cases of evolutionary change. In the next Section, I will offer additional criticism of this view. Before I come to this, I would like to critically review a similar account of the statistical character of evolutionary theory, namely the account given by Barbara Horan.

Like Rosenberg, Horan is a determinist with respect to evolutionary processes (Horan 1994). Furthermore, she has also argued that the probabilities which appear in evolutionary models are subjective or "epistemic" and that, therefore, only an instrumentalist account of evolutionary theory is justified. However, her argumentation is sufficiently different from Rosenberg's to merit special consideration.

Horan wants to dissolve a potential problem for instrumentalist accounts of evolutionary theory. The problem is the following. If evolutionary models are merely instruments telling a rational agent what evolutionary outcomes she should expect, how can evolutionary theory provide *causal explanations* of evolutionary change? Her strategy of dissolving this problem is by rejecting the premise that evolutionary models are causal. Horan argues that the models of population genetics—widely seen as the core of Neo-Darwinian theory—fail to give us causal explanations. The main gist of her argument is that population genetic equations do not relate *causes* to their *effects*; they merely relate *effects* to *one another*. Take, for example, models for selection at a single genetic locus. Such models contain a theoretical quantity called *selection coefficients*. Such coefficients specify the proportion of alleles that survive to the next generation. Horan argues that these coefficients are defined by their effects, namely the rate of transmission of alleles into the next generation.

I think that this argument proves too much, for it could be used to show that *Newtonian mechanics* fails to give us causal explanations. On some interpretations of classical mechanics, force is defined by acceleration, i.e., by its effect. Thus, Horan's argument could be applied *mutatis mutandis* to Newtonian mechanics. Thus, the argument, if taken at face value, does not only undermine the causal nature of evolutionary theory, it undermines the causal nature of *all* dynamical theories. Surely, this is against Horan's intentions, because her argument seems to be directed at evolutionary theory *specifically*. Of course, she could argue that there is a substantial difference between Newtonian mechanics and population genetic models in that force is not *defined* by acceleration. The relationship between force and acceleration could be *contingent* or *empirical*. But this defense invites the question of why the relationship between selection coefficients and gene frequency changes cannot be viewed as empirical. On the standard view of population genetic models, selection coefficients represents the *fitness* of the genotypes involved. What stops us from saying that fitness differences are a *cause* of gene frequency changes? If viewed this way, the relationship between selection coefficients and gene frequency changes is not definitional, it is causal. Thus, population genetics comes out as a causal theory after all. Of course, Horan could argue that it is inappropriate to view fitness as a causal disposition. But such an argument is lacking in her account. Her attack on the causal nature of population genetic theory thus reduces to the old "tautology objection" to the empirical status of selection theory, an objection which has been rejected by several authors (e.g., Mills and Beatty 1979, Hodge 1987).

So far, we have seen that Rosenberg's and Horan's arguments for a subjective view of probability and a resulting instrumentalist view of evolutionary theory are deficient. It must be emphasized again that this does not imply that their views are incorrect, it only means that they have failed to produce positive arguments in their support. It is therefore worth examining whether their position could be strengthened.

It is important to realize that Rosenberg's and Horan's arguments fail *even if determinism is true*. Let me come back to Rosenberg's attempt to show that the theory of genetic drift is merely a "useful fiction". Is it possible to reject this conclusion without rejecting the deterministic premise on which it rests? I suggest that this is possible, and we don't even have to construct any new arguments to show this. In his influential book *The Nature of Selection*, Elliott Sober (1984, 126) has argued that even if evolutionary processes are assumed to be deterministic, there are reasons to believe that the statistical models of evolutionary theory provide genuine causal explanations. In order to show this, Sober imagines a Laplacian demon who can calculate the fate of any population of organisms. Sober then asks whether such a Laplacian supercalculator would have any need for statistical models of evolutionary change. The answer is yes, according to Sober, for the following reasons. Statistical evolutionary models, such as the models for random genetic drift, abstract from the specific causal details which determine survival and reproduction in particular populations and arrive at *significant generalizations* which hold for a large class of very different populations which have nothing else in common. These significant generalizations define *natural kinds* which are invisible in the Laplacian demon's convoluted calculations. The knowledge of these higher-level natural kinds—formulated in the language of probability—contributes to our understanding, thus the statistical generalizations are genuinely explanatory. Laplace's demon, on his part, simply wouldn't see the wood for the trees.

Rosenberg, of course, is aware of this argument. However, he can reject it by denying that the generalizations of evolutionary theory pick out natural kinds. Sober's significant generalizations, according to Rosenberg (1994, 76), only *appear* as significant to cognitively limited beings such as humans. Sober's only argument for the reality of these kinds seems to be that if we don't allow such higher-level natural kinds, then other special sciences such as psychology are doomed as well. For example, the psychological concept of *intentional states*, according to Sober, is analogous to the concept of probability in evolutionary theory in that it provides us with natural kinds which are invisible at the micro-level. Rosenberg finds this unconvincing, because the existence of natural kinds in the realm of psychology is far from established. And even if it were established, Sober would only have an argument from analogy for the reality of natural kinds of evolutionary processes.

The question is where the *burden of proof* lies in this argumentative standoff. Does Sober has to show that the statistical generalizations of evolutionary theory pick out genuine natural kinds, or does Rosenberg have to show that they fail to do so? I think this is largely a matter of one's greater metaphysical predilections. For those of us who do believe that special sciences such as biology or psychology are in the business of discovering natural kinds and that they succeed at least sometimes, Sober's arguments carry some weight. For someone like Rosenberg, for whom the epistemological status of special sciences is more precarious, the argument appears weak.

I find myself on Sober's side in this question, that is, I would not want to confine natural kinds to the micro-physical level. At the end of the day, Rosenberg's and Horan's instrumentalist accounts of evolutionary theory rest on nothing but an extremely strong and problematic reductionistic assumption, namely that only theories which treat phenomena at the most fundamental level can be true. If this assumption is rejected, determinism about biological processes does not imply instrumentalism about evolutionary theory (Weber, forthcoming).

5. A Realist View

Robert Brandon and Scott Carson (1996) reject the view that biological processes are deterministic. In their account of the statistical character of evolutionary theory, the source of probability is not the finite nature of human reason, but objective chance events in the development of individual organisms. They have offered two independent arguments in support of this contention. I will review these arguments in Section 7. Right now, what I want to do is point out some internal difficulties in their account of the statistical nature of evolutionary theory.

The starting point of Brandon's and Carson's analysis is their belief that the processes and relations postulated in evolutionary theory are *real*. Thus, in contrast to Rosenberg and Horan, Brandon and Carson are *realists* with respect to evolutionary theory. Their justifying reason for this belief is the fact that evolutionary theory is "one of the most highly confirmed theories in the history of science" (1996, 316). Thus, Brandon and Carson think that a high degree of empirical confirmation of a scientific theory provides reasons to believe that the processes and relations postulated in the theory are real, and they think, in addition, that contemporary evolutionary theory qualifies as a highly confirmed theory. I am not going to argue this point, since this position is certainly respectable. What I want to take issue with are the conclusions they draw from these starting assumptions.

Brandon and Carson want to reject the view defended by Rosenberg and Horan that the probabilities which appear in evolutionary models are subjective probabilities or degrees of belief. Their approach of undermining this account is by rejecting the central premise from which Rosenberg and Horan started out, namely that biological processes are deterministic. If evolutionary theory provides us with true descriptions of reality, they argue, it *must* be assumed that the concept of probability represents stochastic dispositions of individual organisms. For example, fitness is such a stochastic disposition. Fitness does not uniquely determine how many offspring a biological individual will have, and the reason for this is that indeterminism prevents that the organism's physical properties fix exactly how many offspring the organism will produce. Thus, Brandon and Carson prefer a *propensity interpretation of fitness* (first developed by Mills and Beatty 1979). Probabilistic propensities are thought of as real properties of individual organisms, therefore, realism about evolutionary theory is saved from the instrumentalists' attack.

My first objection to this line of reasoning is the following. Brandon and Carson jump to the conclusion that the realist about evolutionary theory must accept a propensity interpretation of probability too quickly. Although they are right that realism requires an objective interpretation of probability, the propensity interpretation is not the only objective interpretation conceivable. There are other objective interpretations, for example, the *limiting frequency interpretation* of probability. Frequency interpretations are neutral with respect to the question whether the events on which probability is measured are deterministic or not. There also exist interpretations of probability which are not neutral with respect to this question. Attempts have been made to introduce a concept of probability which applies to deterministic systems (e.g., von Plato 1982). Popper's original formulation of the propensity interpretation (Popper 1959) suggests that it is also applicable to deterministic systems, even though, for Popper, the main motivation for introducing the propensity interpretation was quantum mechanics. Let us also remember that statistical mechanics, which treats fully deterministic systems, conceives of probabilities as objective features of ensembles (see Section 3). Thus, Brandon and Carson are mistaken in thinking that objective *probability* implies objective *chance*. Especially statistical mechanics is living proof that this is not so, for—as I have pointed out earlier—it combines objective probability with subjective chance.

It is clear that nothing in what I have said so far is an argument against Brandon's and Carson's view that evolutionary probabilities *do*, in fact, represent genuine stochastic propensities. Now I want to show that this is problematic, too.

To see this, consider the following thought experiment. A colony of genetically identical plants is found, in a given year, to produce different numbers of seeds. A biologist samples the numbers of seeds produced by each individual plant and calculates the probability distribution that a plant of this genotype produces 0, 1, 2, 3, ..., or n seeds. For most theoretical purposes, the *arithmetic mean* of this distribution:

$$\frac{1}{n}\sum_{i=1}^{n} ip_i$$

(where p_i is the probability that an individual plant produces i seeds) will provide an estimate of the genotype's fitness.[3] Now let us make the following assumption: Let the variation in seed number be result of some *objective chance events* during the plants' development. Under this assumption, the probabilities p_i could be interpreted as representing an irreducibly stochastic disposition of plants of that genotype to produce i seeds. In other words, the probabilities could then be read as expressing genuine probabilistic propensities. It is Brandon's and Carson's view that *all* applications of the concept of probability in evolutionary theory are to be interpreted in this manner.

But now let's change our hypothetical example only slightly. Let us now assume that the variation in seed production is not the result of objective chance events. Instead, there is a set of *hidden variables* which determines the number of seeds produced. This could be any set of causal variables which influence the growth of the plant and which we do not know. In this case, we could not read the probabilities p_i as *irreducibly* stochastic propensities. The stochasticity observed is now a mere illusion created by our ignorance of the hidden variables. However, the probabilities p_i would not be rendered subjective or "merely epistemic" in this scenario—contrary to what Brandon and Carson as well as Rosenberg and Horan would make us believe. It is still possible to interpret the probabilities p_i as expressing a property that plants of this genotype actually posses, a property which is determined by the plant's physical properties and their environment and which is *invariant* with respect to the different values of the hidden variables.

It is clear that both of my hypothetical scenarios—the one with and the one without the hidden variables—are compatible with current evolutionary theory. In fact, in most theoretical contexts, it will not matter at all for using the probability values in question in order to predict or explain what will happen to these plants, for example, if they have to compete with plants of a different genotype. However, I believe that my two scenarios demonstrate the inadequacy of Brandon's and Carson account of the statistical nature of evolutionary theory. The reason is that their account can only treat the first scenario—the one without the hidden variables. But surely, the second scenario—the one with the hidden variables—also occurs in nature. I do not know whether objective chance events exist in the biological domain, nor how frequent they are *if* they exist. I will come back to this question in Section 7. All I want to claim right now is that it is a safe bet that a substantial proportion of biological variation which we observe is a result of some hidden variables. If this is true, then Brandon's and Carson's account of chance and probability in evolution has to be rejected because it sees objective chance as the *only* source of probability. Their account does not apply to cases where there are evolutionarily relevant hidden variables in biological processes, and yet the existence of such variables is highly likely regardless of whether the biological domain is strictly deterministic or not (Weber, forthcoming).

I therefore conclude that Brandon's and Carson's account of the statistical character of evolutionary theory fails to give us an adequate account of evolutionary processes as we know them. Since the same is true about Rosenberg's and Horan's account, we urgently need an alternative. This is what I turn to now.

6. Are There Alternatives?

The following table summarizes the two accounts of the statistical nature of evolutionary theory that I have examined so far:

	Rosenberg, Horan:	Brandon & Carson:
Determinism:	yes	no
Eliminability:	yes	no
Source of probability:	cognitive limitation	objective chance
Interpretation of Probability:	subjective	propensity
Realism:	no	yes

This table contains various epistemological and metaphysical claims which do not necessarily imply each other. For example, I have argued—*contra* Rosenberg and Horan—that determinism about biological processes does not imply instrumentalism about evolutionary theory, and—contra Brandon and Carson—that a scientific realist is not committed to indeterminism or a propensity interpretation of probability. This suggests that, by playing around with this table, we can easily generate alternative accounts of the statistical character of evolutionary theory and check them for coherence. In theory, we could try all possible combinations of positions with regard to the different claims that are included in the table. Some of these combinations will clearly be incoherent or even self-contradictory, while others might be consistent, coherent, and metaphysically plausible. However, I do not want to bore the reader with such a systematic exercise. Instead, I will present the combination of claims which I find most promising. It is summarized in the following table:

	Rosenberg, Horan:	Brandon & Carson:	Weber:
Determinism:	yes	no	mostly
Eliminability:	yes	no	don't care
Source of probability:	cognitive limitation	objective chance	hidden variables
Interpretation of probability:	subjective	propensity	?
Realism:	no	yes	yes

Determinism: I think that a viable interpretation of evolutionary models that use probabilities should at least be consistent with determinism. To the extent that biological variability which is relevant for evolution is caused by hidden variables, the evolutionary process *is* deterministic, even if this does not necessarily exclude the occasional intrusion of objective chance events. As we have seen in the previous section, Brandon's and Carson's account fails because it cannot adequately explicate the relationship between such hidden variables, which are likely to exist, and evolutionary probabilities. Therefore, an adequate interpretation of probability in evolutionary theory should proceed *as if* evolution was a deterministic process.

Eliminability: This is the question of whether an omniscient being (e.g., Laplace's demon) could produce a theory of evolutionary change which does not require any probabilistic reasoning. All we can say about this question is that, presumably, the statistical character of evolutionary theory is eliminable *in principle* if the evolutionary process is fully deterministic. By contrast, such elimination is clearly impossible of the evolutionary process is indeterministic. However, such considerations are strictly counterfactual since, to my knowledge, there are no omniscient beings. The crucial point to note here is that *in principle*-eliminability does not imply instrumentalism. It is not incoherent to believe that evolutionary theory is eliminable *in principle* (i.e., for an omniscient being) and, at the same time, to accept a realist interpretation of current evolutionary theory. All we have to assume is that special sciences like biology can have some access to reality even if they fail to produce *complete* accounts of the processes in their domain. The scientific realist is not committed to the thesis that true theories are complete in the sense that they incorporate the maximally possible causal information concerning the phenomena they treat. Thus, the question of eliminability can be dissociated from the realism issue and therefore pushed into the realm of science fiction.

Source of probability: The main issue in this debate, so far, has been whether the source of probability, i.e., the reason(s) why evolutionary models use probabilities have to be sought in the nature of the process itself (as indeterminists hold) or in our ignorance of the real causes of evolutionary change (as some determinists maintain). On my account, the source of probability is located in the hidden variables. To be precise, the source of probability lies in the fact that the hidden variables *are* hidden. Basically, this amounts to the same as saying that the source of probability is ignorance or cognitive limitation, but I prefer this way of speaking because it is more precise.

Interpretation of probability: This is clearly the crux of the matter and will therefore be discussed separately (see below).

Realism: The position that I am advocating is a realist one. Obviously, a defense of scientific realism in general or of realism about evolutionary theory specifically is beyond the scope of this essay. All I would like to claim here is that realism about current evolutionary theory is at least as justified as realism about other mature scientific theories. *If* it is all justifiable, on metaphysical and epistemological grounds, to be a realist about the entities and causal processes postulated by well-tested scientific theories, *then* it is reasonable to assume that current models of natural selection and genetic drift represent the causal structure of evolving populations of organisms at least approximately. The issue at stake here is how to maintain this realism in the face of the challenge leveled specifically at evolutionary theory by Rosenberg and Horan, namely that determinism implies that statistical evolutionary models are mere predictive devices and not representations of biological reality. In the previous Sections, I have shown that they have not established this conclusion, and that Brandon's and Carson's attempt to rescue realism with the help of a thoroughgoing indeterminism fails. The question, then, is how realism about statistical evolutionary models can be defended on the basis of a positive account.

The centerpiece of such a positive account, clearly, will have to be an *objective interpretation of probability*. Is there an interpretation of probability which is compatible with—but not necessarily committed to—determinism, and which is objective and therefore able to sustain a realist stance? Such an interpretation does exist for some domains of the physical world, for example, the domain of statistical mechanics. We have seen (Section 3) that the probabilities that appear there can be interpreted as objective properties of so-called ensembles, that is, fictional sets of systems which differ only in initial conditions. Clearly, this interpretation cannot be uncritically transferred to biological contexts because biological systems differ considerably from the idealized physical systems treated in statistical mechanics.

But perhaps there are some interesting analogies to statistical mechanics which could be fruitfully explored. Indeed, one of the pioneers of population genetics—R.A. Fisher—was quite fond of such analogies and has likened his "fundamental theorem of natural selection" to the second law of thermodynamics (Fisher 1930, 36), but I think this is mostly of historical interest. What I would like to suggest is that certain models of evolutionary change in finite populations bear an interesting analogy to the ensemble approach in statistical mechanics.

Population geneticists, when they are treating populations of finite size, are unable to predict exactly what will happen to a particular population. The reason is the intrusion of chance factors like random sampling of gametes in small populations. The first quantitative theory of evolutionary change to systematically take such effects into account was developed by Sewall Wright. He wrote in 1931:

> The gene frequencies of one generation may be expected to differ a little from those of the preceding merely by chance. In the course of generations this may bring about important changes, although the farther the drift from equilibrium the greater will be the pressure to return. The resultant of these tendencies is a certain frequency distribution, or probability curve, for gene frequencies in place of a single equilibrium value (Wright 1986, 93).

Wright derived the following general formula for the probability distribution of gene frequencies at a single genetic locus:

$$y = Ce^{4Nsq}q^{4N(mq_m+v)-1}(1-q)^{4N[m(1-q_m)+u]-1}$$

In this model, y is the probability that an allele will reach a gene frequency of q from an initial frequency of q_m in a population of size N. s represents the selection coefficient of the allele, while u and v are the mutation rates from and to the allele, respectively. m is the rate of migration. Figure 1 shows some of the properties of Wright's model graphically. The four charts represent probability arrays for relative gene frequencies, i.e., for any given gene frequency between 0.0 and 1.0, the graph gives the probability that the population will end up at this frequency. If the population is very small (Chart I), the gene will either be lost or fixed by random drift. By contrast, a very large population (Chart III) will hold the gene frequency at an equilibrium value that is determined by natural selection, mutation, and migration. In an intermediately sized population (Chart II), the gene frequency will draft at random about their equilibrium values. Chart IV shows a situation of a large species with partially isolated subgroups, i.e., a high migration pressure and intermediately sized populations (thought to be most favorable for evolution by Wright).

How should we interpret the probabilities that feature in this model? According to Rosenberg's subjective interpretation, we should read these probabilities as expressing degrees of belief, for example, belief in the proposition that an allele will be fixed by random drift. Alternatively, if we were to follow Brandon and Carson and several other philosophers of biology, we should interpret these probabilities as irreducibly stochastic dispositions (propensities) that each individual in the population possesses. However, I suggest that there is an interpretation which is more in line with Sewall Wright's own thinking than both the subjective and propensity interpretations. Namely, we can interpret these probabilities as measuring the *frequency* of populations with a given gene frequency in a hypothetical, infinite set of populations which contain the same number of individuals and the same initial gene frequencies. In other words, we can interpret probability as a property of an *ensemble*.

That Wright conceived of his probability distributions in this manner is supported, for example, by the following passage from the Galton Lecture which Wright gave at University College, London, in 1950 (explaining the results of his theoretical calculations on evolution in natural populations under the combined action of various evolutionary forces including fluctuations due to random sampling):

> The resultant is a probability distribution of *frequencies of gene frequencies* which applies to any one strain in the long run, or to an array of strains, subject to the same conditions, at any one time (Wright 1986, 586, my italics).

When Wright says "frequencies of gene frequencies", what he means is the proportion of populations with a given gene frequency in an *ensemble* of populations which are identical in all respects but the unique chance events that cause gene frequencies to fluctuate randomly.

A look at contemporary textbooks in population genetics shows that scientists still think of probability distributions for gene frequencies in this way. For example, the eminent population biologist Joan Roughgarden writes:

> Because any specific population shows a random amount of sampling error, we cannot hope to predict exactly what any given population will do. But we can combine the results of several populations and observe the properties of a *group of populations* (Roughgarden 1996, 58, my italics).

Roughgarden then goes on to calculate probability distributions for gene frequencies under various conditions. The approach taken is still basically Sewall Wright's, except that Roughgarden uses more advanced mathematical theory, namely stochastic theory. In Roughgarden's presentation of the models, the probability that a system is in a certain state at a given time is interpreted as a frequency of systems in that state in an infinite set of systems called the ensemble. He even explicitly draws the analogy to the ensemble approach in statistical mechanics (p. 61).

What I would like to show with this short excursion into population genetic theory is that theoretical biologists, at least when developing certain models of evolutionary change, interpret probability in a similar way like physicists do in statistical mechanics. In these models, probability assignments *are* intended to have representational content with respect to real biological systems, contrary to what Rosenberg and Horan think. Probabilities represent frequencies in the limit to infinitely large ensembles of populations. Yet, like in statistical mechanics, these applications of the concept of probability are fully *compatible with determinism*. The differences between the individual populations in the ensemble that cause random fluctuations could be entirely due to hidden variables rather than objective chance. Thus, in these models, probability does not necessarily represent irreducibly stochastic propensities, as Brandon and Carson and other philosophers of biology believe.

I think I have at least made it plausible that alternatives to both the Rosenberg/Horan and Brandon/Carson account of the statistical character of evolutionary theory exist. I have sketched how an alternative which combines determinism with objective probability and realism about evolutionary theory might look like in the context of some models of evolution in finite populations. However, I am not sure whether the approach I have taken could be transferred to other applications of the concept of probability in evolutionary theory, for instance, macroevolutionary models, or the origin of mutations. We must be open to the possibility that there is no single account of chance and probability which would cover all of modern evolutionary theory.[4]

In the next Section, I would like to address a question which I have neglected so far: Are biological processes deterministic or not?

7. The Determinism Question

Brandon and Carson (1996) have produced two independent arguments that are intended to support indeterminism about biological processes. The first argument purports to establish that quantum indeterminism can have population-level effects. Brandon and Carson imagine a population which is at an unstable equilibrium point, such that one newly arising mutation can make the difference which one of two alleles will be fixed by natural selection. They then argue that, since mutation is a microphysical process which could, in theory, be caused by quantum events, it is at least conceivable that the fate of an entire population is subject to quantum indeterminism. The way they put this is by saying that quantum events could "percolate up” all the way to the level of biological populations. Another locution they use is that quantum indeterminism could “infect” the population level.

I do not think that, at present, this kind of scenario can be ruled out altogether. Brandon and Carson do admit that their argument does not amount to a strict “no hidden variables-proof” of the kind which has been produced in quantum mechanics. However, I would like to sound some words of caution about such a recourse to the indeterminism of quantum mechanics.

Brandon and Carson’s talk about quantum effects “percolating up” or “infecting” the population level is misleading. It does not fit with the orthodox interpretations of quantum mechanics. One of the many remarkable features about quantum mechanics is that, so long as a system is not observed, it evolves according to deterministic laws. Thus, there is, in this case, no indeterminism which could “percolate up” or “infect” anything. Quantum indeterminism does not arise simply because systems are very small. It only arises once a microphysical system is subjected to *measurement*. In other words, indeterminism arises when some measurement device is coupled to the system, which collapses its wave function. In such situations, the outcome of the measurement can be uncertain in the strong sense of objective chance. To my knowledge, this is the only form of objective chance which is recognized by modern physics. Note that this indeterminism is a feature which emerges at the *macroscopic* level under certain conditions—namely measurement conditions—and not something which “percolates up” from the microlevel unpredictably. It is a property of a whole quantum system coupled to a measurement apparatus.

The problem is thus that Brandon and Carson seem to take it for granted that quantum mechanics has shown that we live in a fundamentally indeterministic universe, and that the question in biology can only be whether its domain partakes in this indeterminism. However, no such conclusion is warranted. What quantum mechanics shows is that the universe is fundamentally *deterministic*—unless measurements are performed. But does evolution perform measurements? I do not believe that anyone can answer this question at present. This ought to be a question for scientific research rather than metaphysical speculation. At present, no strong claims should be made about the relevance or irrelevance of quantum mechanics to biological processes.

How about Brandon's and Carson's second argument for indeterminism? This argument does not make any use of quantum mechanics. In fact, it purports to demonstrate an *autonomous* form of indeterminism for biology.

Brandon's and Carson's autonomous argument is an argument from empirical evidence. In other words, these authors think that experiments in evolutionary biology support indeterminism in the same way in which experiments can be said to support a theory. The evidence they have in mind comes from, e.g., experiments with cloned plants, which show a considerable amount of variation even if environmental conditions are kept highly homogenous.

There is an obvious reply by the determinist to this empirical argument for indeterminism. She could defend her position by arguing that if cloned plants show variation, then the environment was not homogenous after all. Or perhaps there are some internal hidden variables responsible for this variation, something like "developmental noise". Brandon and Carson are aware of this possible refutation of their argument by determinists. However, they think that they can defuse this objection with a methodological argument. They proceed by asking what *theoretical purpose* the postulate of deterministic hidden variables may serve. In their view, the only purpose that this postulate serves is to rescue determinism from empirical refutation. These variables, therefore, are not theoretically fruitful; they must be removed on methodological grounds. Brandon and Carson, thus, apply a methodological rule that reads "never postulate hidden variables unless they are theoretically fruitful".

Roberta Millstein (2000) has criticized this argument against determinism. According to her, the indeterminist who attributes any variation which is yet unexplained to objective chance runs the risk of overlooking some important causal variables. Far from being theoretically unfruitful, thus, the postulate of hidden variables may lead to the discovery of yet unknown biological processes[5]. Therefore, we are once again faced with the question of where the burden of proof lies: Does the determinist have to show that hidden variables do more theoretical work than merely saving determinism, or does the indeterminist have to show that there are no hidden variables? Determinists and indeterminists are equally at risk of committing an error; the former risk the error of dogmatically sticking to a metaphysical doctrine with the help of the *ad hoc*-postulate of hidden variables, while the latter are at risk of missing some important causal information. How should these cognitive risks be balanced?

If this question cannot be rationally answered, Brandon and Carson have not established indeterminism. Millstein concludes that the only rational attitude for a scientific realist to take is *agnosticism*. In other words, there are, at present, no strong reasons for preferring either determinism or indeterminism about evolutionary processes.

In the final Section, I will show that this conclusion limits our ability to understand the metaphysical foundations of Darwinism.

8. Agnosticism and the Limits of Metaphysics

If we cannot decide, at present, whether evolutionary processes are deterministic or indeterministic, any account of the statistical nature of evolutionary theory is bound to be incomplete. We are here reaching the limits of metaphysical inquiry. Only empirical science can tell us whether quantum mechanics is relevant for evolutionary theory, or whether there is an autonomous biological indeterminism, as Brandon and Carson have suggested. But without this knowledge, we cannot give a universally valid interpretation of chance and probability, i.e., an interpretation which will cover all the instances of probabilistic models of evolutionary change. Clearly, these models work just as well regardless of whether the processes they represent are deterministic or indeterministic. For all explanatory purposes of evolutionary theory, and for all current methods of testing evolutionary models in the field, determinism and indeterminism are *empirically equivalent*.

In conclusion, I suggest that there are at least two senses in which Darwinism (and Neo-Darwinism) is, indeed, a theory for finite beings. If we accept that evolutionary processes are effectively deterministic (in the sense explained in Section 6), then we must admit that the statistical nature of evolutionary models is a manifestation of human cognitive limitation. However, I have shown that this conclusion does not commit us to instrumentalism, provided that we can come up with an objective interpretation of probability which is compatible with determinism and, at the same time, applicable to evolutionary theory or parts thereof. I have sketched such an interpretation for a certain class of models of evolution in finite populations by using the ensemble concept. But, on a more skeptical note, a critical examination of Brandon's and Carson's argumentation for indeterminism shows that there are no strong reasons for preferring either a determinist or indeterminist position with regard to the nature of chance in evolution. What this means is that evolutionary theory reveals the finite nature of human reason by using concepts like chance and probability in a fruitful way, yet without us fully understanding what exactly they mean.

Acknowledgments

Special thanks to Paul Hoyningen-Huene for many helpful suggestions.

Footnotes

[1] An excellent analysis of the different roles of chance in evolution has been given by Roberta Millstein (1997).

[2] For the following, I am relying on Sklar (1993).

[3] Beatty and Finsen (1989) point out that, in some instances, other parameters of the distribution, e.g., variance or skew, will be relevant for the genotype's fitness. However, this is of no relevance for my thought experiment.

[4] I owe this insight to Kenneth Waters.

[5] My favorite example is the ground-breaking research of Barbara McClintock. She would never have discovered mobile genetic elements had she attributed the yet unexplained variations in her maize plants to an ineliminable indeterminism or objective chance.

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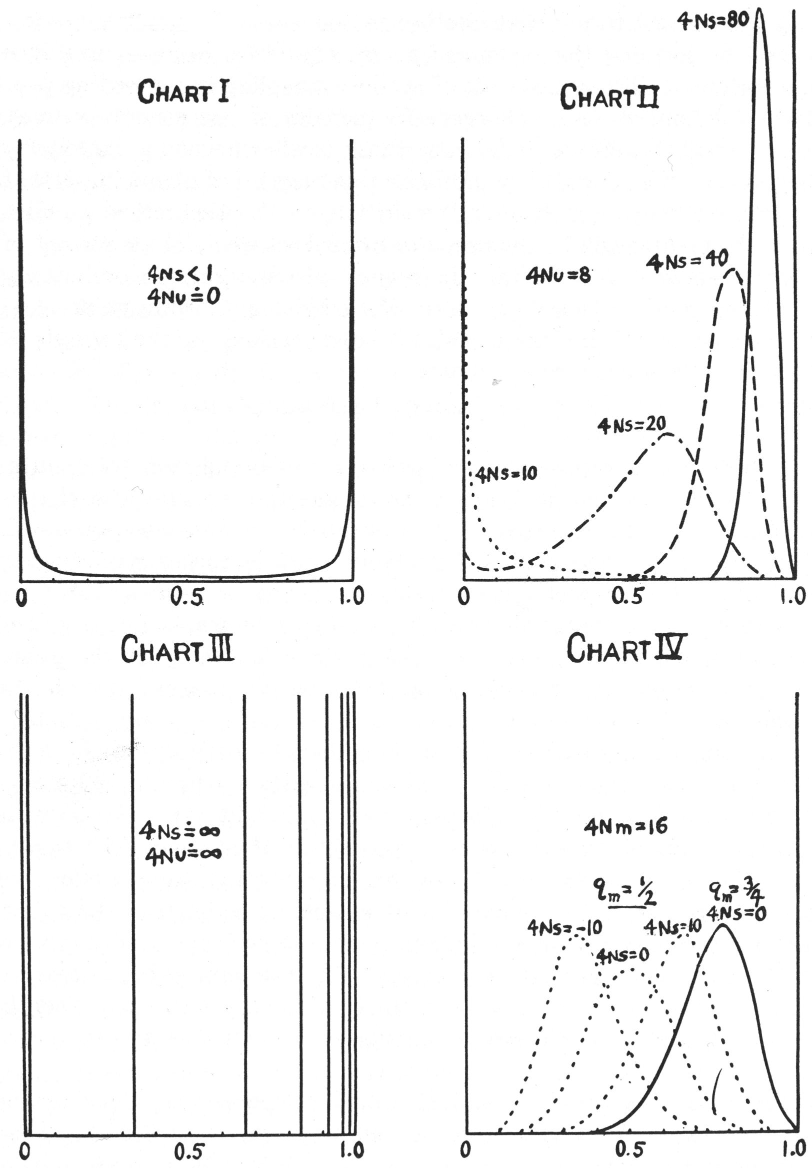

Figure 1. Sewall Wright's one-locus model of evolution in finite populations (1931). The four graphs show the distribution of probability that a population of size *N* will reach a gene frequency of *q*. Gene frequencies are shown on the abscissa. Chart I shows the result for a population in which the product of size and selection coefficient (4*Ns*) is small. Such populations are most likely to either lose (*q* = 0) or fix (*q* = 1) the allele by random drift. Chart III shows the extreme case of an infinite population. In this case, the variance of the distribution approaches zero: that is, the population will reach an equilibrium state deter- mined by the selection coefficients and the mutation rates (*u*) with a probability of 1. Charts II and IV show intermediate cases with various values for population size, selection coefficients, initial frequencies (*q*), and mutation rates (m). The probability values (*y* axis) can be interpreted as fre-

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