Determinism, Realism, and Probability in Evolutionary Theory

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Recent discussion of the statistical character of evolutionary theory has centered around two positions: (1) Determinism combined with the claim that the statistical character is eliminable, a subjective interpretation of probability, and instrumentalism; (2) Indeterminism combined with the claim that the statistical character is ineliminable, a propensity interpretation of probability, and realism. I point out some internal problems in these positions and show that the relationship between determinism, eliminability, realism, and the interpretation of probability is more complex than previously assumed in this debate. Furthermore, I take some initial steps towards a more adequate account of the statistical character of evolutionary theory.

1. Introduction. Probabilistic concepts and statistical reasoning are an integral part of modern evolutionary theory. For example, an organism's fitness does not determine uniquely how many surviving offspring some individual will have, it only provides a statistical expectation. Similarly, only statistical generalizations can be made about the evolution of small populations that are subject to genetic drift. This statistical nature of evolutionary theory raises a number of foundational and philosophical problems. One question is how the concept of probability should be interpreted. Another question one may ask is, *why* is evolutionary theory statistical? Scientists develop statistical theories for different reasons. In physics, this is evident in the contrast between classical statistical mechanics and quantum mechanics. The former treats systems of particles that obey deterministic laws of motion. However, the number of particles in these systems

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is too large to follow them individually. Physicists, in this case, use statistical reasoning in order to reduce the complexity of systems which would otherwise be mathematically intractable. By contrast, quantum mechanics uses probabilistic concepts because there exist states of quantum systems which do not uniquely determine the outcome of measurements. Whereas statistical mechanics is statistical for *epistemic* reasons, quantum mechanics is believed to be (partly) statistical for *ontological* reasons, i.e., because it deals with indeterministic processes.

What about evolutionary theory? In the recent literature in philosophy of biology, two contrary positions have been developed which address this set of issues. The first position holds that the evolutionary process is *deterministic*. Therefore, the reasons for the statistical nature of evolutionary theory are *epistemic*; they lie in our cognitive limitations. Laplace's demon would have no need for evolutionary theory in its current, statistical forms; in other words, it is *eliminable*. Adherents to this position typically adopt a *subjective* or "ignorance" interpretation of probability. In addition, they are *instrumentalists* with respect to evolutionary theory, i.e., they claim that evolutionary theory falls short of representing the real causes of evolutionary change, although it may be useful for other reasons. This position has been defended by Horan (1994), Rosenberg (1994), and Graves et al. (1999), and will henceforth be referred to as GHR.

The second position that has been rigorously defended holds that the evolutionary process itself is *indeterministic*. Thus, like in quantum mechanics, there are *ontological* reasons for the statistical nature of evolutionary theory, which means it is *ineliminable*. Defenders of this position prefer a *propensity* interpretation of probability. For instance, they view fitness values as representations of irreducibly stochastic dispositions of individual organisms. Furthermore, they are *realists* about evolutionary theory. This position is shared by many philosophers of biology, but for simplicity I will refer to it as BC, after a recent defense by Brandon and Carson (1996).

In this paper I want to show that GHR and BC both have internal problems. Even if determinism is true and the statistical character of evolutionary theory is in principle eliminable, neither GHR's instrumentalism nor their subjective interpretation of probability follow (Section 2). BC have also unduly simplified the relationship between determinism, realism, and the interpretation of probability. In addition, I argue that BC's thoroughgoing indeterminism fails to give us a satisfactory account of evolutionary processes as we know them, even if strict determinism is false (Section 3). Finally, I shall take some initial steps towards a more adequate account of the statistical character of evolutionary theory (Section 4).

2. GHR and the Determinism-Instrumentalism Fallacy. Rosenberg's (1994) instrumentalism about biology rests partly on his considerations of reduction (see Weber 1996 for a critique) and partly on his account of probability and the statistical nature of evolutionary theory. The essence of this account is captured by the following claim:

> [T]he only probabilities to which the theory [of evolution] is committed are the subjective probabilities that agents of our cognitive powers require to apply the theory to actual processes among populations of interest to us. If people were a lot smarter, there would be proportionally less reason to appeal to such epistemic probabilities and *mutatis mutandis* less reason to treat the theory as statistical. (Rosenberg 1994, 59)

Subjective probabilities are understood by Rosenberg in the customary (Bayesian) way, namely as degrees of belief (1994, 61). Thus, the theory of evolution does not tell us how nature really is, it merely tells us how much confidence we can have in certain predictions—hence instrumentalism.

How are these rather strong claims, which most practicing biologists would probably reject, justified? A central premise in Rosenberg's argument is his claim that biological processes are deterministic. He claims that, although the universe is fundamentally indeterministic because of quantum-mechanical effects, this indeterminism vanishes asymptotically as we move from the microphysical level (chemical bonds and below) to the macroscopic level of biological processes (1994, 61). For the sake of the present analysis, let us grant Rosenberg this premise, i.e., the determinism of biological processes. What interests me here is how he gets from this premise to his subjective interpretation of probability and, in turn, to his instrumentalist characterization of evolutionary theory, as presented above.

The basic strategy of Rosenberg's argument is to show that an omniscient being would have no need for a statistical evolutionary theory. In a fictional example which is supposed to show this, Rosenberg (1994, 71ff.) considers a population of giraffes from which the individuals with the longest necks are continually removed by poachers. A group of conservation biologists, unaware of the illegal poaching, notes that the population moves away from the adaptive equilibrium in terms of neck length and attributes this change to genetic drift. Now, Rosenberg claims that if these biologists were in possession of the full information concerning the fate of long-necked giraffes, they would not attribute the observed changes to drift. Hence, drift is merely a "useful fiction." A statement that drift has occurred in a population means nothing but the fact that the real causes of evolutionary change are unknown. Some savvy being who has access to these real causes has no need for the theory of genetic drift. This example is generalized by Rosenberg to the effect that evolutionary models (except the principle of natural selection; see below) always merely reflect biologists' ignorance concerning the underlying causes of evolutionary change.

Millstein (1996) has shown that Rosenberg's fictional example is flawed, for his alleged example of genetic drift is not a case of drift at all; it is a case of selection. A group of conservation biologists intelligent enough to notice that they are continually losing long-necked giraffes to poachers would conclude that there has been selection against long-necked giraffes, the selection pressure being exerted by the poachers. Thus in this example, evolutionary theory is not eliminated by the additional causal information. Instead, the case is merely moved from the domain of models of genetic drift into the domain of models of natural selection, which are *also* statistical. In order to show the eliminability of the theory of drift, Rosenberg would have to examine a genuine example of genetic drift. The reasoning behind Rosenberg's odd example, I suspect, lies in the fundamental dichotomy he draws between selection and drift. Selection, in Rosenberg's metaphysics, is not subject to his biological instrumentalism, but is the very *reason* why biology can only be an instrumental science (1994, 127). Therefore, the concept of fitness is exempt from Rosenberg's subjective interpretation of probability; he views it as an indefinable, primitive term. However, this dichotomy seems odd, especially if one considers that selection in finite populations and drift are both stochastic processes which differ only in that the former is discriminate with respect to an organism's physical properties whereas the latter is indiscriminate (Beatty 1984).

Of course, it could still be the case that an omniscient being would have no need for the theory of drift, even if Rosenberg's example fails to demonstrate this. Sober (1984, 126) has argued for the contrary. According to Sober, the statistical approach in evolutionary biology has led to *significant generalizations* about populations of organisms. These generalizations unify a large number of highly heterogeneous phenomena that have very little in common except being instances of the same evolutionary models. They carve out natural kinds that would be invisible to Laplace's demon, who, therefore, wouldn't see the wood for the trees.

Rosenberg (1994, 76ff.) responds to this line of reasoning by arguing that it actually supports his own, instrumentalistic position. Sober's argument, according to Rosenberg, can only establish the indispensability of evolutionary theory *for us* as beings to whom its generalizations *appear* significant. The argument fails to establish that the kinds evolutionary generalizations pick out are *natural* kinds. Furthermore, it fails to establish that the probabilities featured in these generalizations are real in any sense.

I suggest that two issues must be kept separate here. The first issue is whether evolutionary theory in its current statistical form has an *explanatory value* which would be lacking in a non-statistical theory of the kind that Laplace's demon would be able to produce (if determinism is true). The second issue is whether *realism* about current evolutionary theory is justified. The first issue has to do with the nature of scientific explanation, specifically, whether unification has explanatory value. Many philosophers of science think that it does, and if they are right, Sober's point concerning significant generalizations holds true. But this is not what Rosenberg denies, if I understand him correctly. His point is that the kinds of explanations we find significant has something to do with what kind of beings we are. Sober and Rosenberg agree that the statistical generalizations of evolutionary theory are explanatorily indispensable; they differ only in that Sober thinks they are indispensable *in principle* whereas Rosenberg thinks they are only indispensable for us cognitively limited beings. Sober (1984, 127) admits that it is "difficult to bring this science fiction thought experiment to a decisive conclusion." I agree, but fortunately we don't have to bring it to a conclusion. For the main issue at stake is *realism*, and I want to suggest that, with respect to this issue, nothing follows from a theory's explanatory dispensability. A theory may be dispensable in the sense that an omniscient being would be able to understand the phenomena in question at a deeper level, but it is still possible that this theory correctly represents some aspects of reality. To put it differently, a theory may be indispensable merely for *pragmatic* reasons, i.e., for reasons which have to do with our cognitive abilities, but still be open to a realist interpretation. The fact that a theory falls short of giving us a *complete* account of some complex causal processes does not imply that this theory has no representational content whatsoever. A scientific realist is not committed to the thesis that even our best scientific theories provide complete descriptions of reality.[1] Thus, even if Rosenberg is right (*contra* Sober) that smarter beings would have less reason to use a statistical approach, this doesn't imply that our cognitively limited biologists have failed completely in their attempts to provide a description of reality.

This means that Rosenberg has not provided any compelling reasons to accept his instrumentalist account of biology, nor a subjective interpretation of probability, even if we accept his basic premise of determinism.

Let us now have a look at another instrumentalist position, the one given by Horan (1994). Like Rosenberg, Horan starts with the assumption that biological processes are deterministic. On her account, the apparent randomness of processes like genetic drift

> is created by the indiscriminateness of its sampling from the breeding

1. Compare Waters' (1991) notion of "tempered realism."

> populations: Organisms are chosen in a way that is completely independent of how fit they are. If the sampling process is also deterministic, then the statistical perspective introduced by the concept of "sampling" is not necessary. It is convenient and, given limitations in our knowledge of the vagaries of the environment, useful; however, it obscures the essentially deterministic character of evolutionary change. (Horan 1994, 85)

Thus, Horan holds that even events like the establishment of a founder population by a natural disaster—one of the paradigmatic cases of the intrusion of chance in evolution—is a causally fully determined event which would have the exact same outcome under the same conditions. Similar to Rosenberg, Horan infers from this deterministic premise that "the statistical approach is instrumentally motivated but theoretically unnecessary" (1994, 78). I have argued above that whether or not the statistical approach is theoretically necessary, in other words, whether probabilistic theories of evolutionary change are in principle eliminable or not, has no consequences for the question of whether a realist interpretation of evolutionary theory is justified. These are separate issues. However, Horan has provided an additional argument for instrumentalism about evolutionary theory. Specifically, she has argued that population genetics—widely viewed as the core of Neo-Darwinian theory—fails to provide causal explanations of evolutionary processes.

The main thrust of Horan's argument is that the equations of population genetics do not relate causes to their effects. They merely relate sets of effects to one another (1994, 88). For example, typical population genetics equations which give the change in gene frequency from one generation to the next due to selection contain parameters called *selection coefficients*, which are supposed to represent the relative fitness of different genotypes. On the standard interpretation of selection theory, fitness differences are viewed as the cause of natural selection. So why do population genetics equations not relate causes to their effects? Because selection coefficients, according to Horan (1994, 88), are themselves defined in terms of their effects. They specify the proportion of alleles that survive to the next generation.[2]

I think this argument is flawed. To see this, consider the following analogy: Newton's second law of motion relates a force F acting on a body of mass m to the body's acceleration a ($F = ma$). Now consider a simple mechanical model in which this law of motion is used to treat the motion of a mechanical system (say, a harmonic oscillator). With Horan,

2. Curiously, Horan's argument is reminiscent of the old "tautology" objection to the empirical content of selection theory.

we could argue that this model offers no causal explanation of the body's motion because the force F is defined by it's effect, the acceleration a.[3] But surely this would be absurd. The mathematical relations between physical quantities say nothing about whether or not a theory is causal. A theory is causal exactly if its dynamic equations have some causal physical system as a model. Nothing in the mathematical theory of population genetics stops us from giving it a causal interpretation, for instance, by saying that fitness differences cause gene frequency changes by natural selection.[4] Selection coefficients only provide a measure of such fitness differences.

I conclude that neither Rosenberg nor Horan have given us compelling reasons to accept their instrumentalist view of evolutionary theory, even if their deterministic premise is assumed to be true. Nothing follows from determinism for realism about biological theories, even if it is true that a statistical approach is chosen in evolutionary theory merely because human beings lack the cognitive capacities for providing a full description of the complex causal processes which sustain life in every individual of a population. GHR's argument from determinism and eliminability to instrumentalism is a fallacy, perhaps the result of latent reductionistic prejudices according to which only theories which treat phenomena at the most fundamental level can be true. I want to end this section by pointing out that Rosenberg's and Horan's arguments could be used to show that classical statistical mechanics—which deals with fully deterministic systems—cannot be interpreted realistically, or that it is not a causal theory. Foundational problems in statistical physics aside, probably very few physicists would accept such a verdict. So far, there are no reasons to accept such a verdict in evolutionary biology either, even for the determinist. But it is time now to visit the other camp, where determinism is out of fashion.

3. The Fallacy Again, and a Problem in BC. Brandon and Carson (1996) have challenged Horan's and Rosenberg's assumption of an underlying determinism in biological processes. They have offered two different arguments against determinism. The first argument tries to show that quantum mechanical indeterminism can, at least in principle, "percolate up"

3. It could be objected that $F = ma$ is an *empirical* law (which is controversial) whereas the relationship between selection coefficients and gene frequency change is *definitional*. However, it has proven to be difficult to decide which parts of a set of dynamic equations should be viewed as empirical and which parts as definitions of the theoretical magnitudes. On some of the most current accounts of the structure of theories, this question becomes irrelevant, since all dynamic equations are viewed as defining a set of models which are then applied to the world as wholes (Giere 1988, 84).

4. Sober (1984, 88ff.) holds fitness to be causally inert for other reasons. However, he shows how selection theory can be viewed as causal nevertheless.

to the macroscopic level of biological populations. At the same time, Brandon and Carson (1996, 320) claim that the possibility of quantum-mechanical indeterminism with population-level effects is insufficient to ground an "autonomous evolutionary indeterminism" which, on their view, is required if one wants to be a realist about evolutionary theory. For this reason, they present a second argument for biological indeterminism. The basic strategy of this argument is to infer the falsity of determinism from its alleged theoretical unfruitfulness and lack of empirical support (1996, 329–333). Both of these arguments are problematic, as Millstein (1997, Chapter 2) and Graves et al. (1999) have shown. My aim here is not to offer more criticism of Brandon and Carson's argument for indeterminism, nor do I want to take sides on this issue. Instead, I want to show, first, that BC, too, have assumed too simple a relationship between determinism, realism, and the interpretation of probability. Second, I want to point out an internal problem in BC's overall position.

One of the main points of disagreement between GHR and BC is whether the probabilities posited in evolutionary models are "epistemic" or whether they are "real." In other words, do these probabilities merely reflect scientists' ignorance or their subjective degrees of belief, or do they represent some properties which exist in biological organisms and their environment independently of scientists' beliefs? Brandon and Carson (1996, 336) exhibit some modesty in conceding that they have not refuted the instrumentalist view. What they think they have established is the following:

> What we have shown is that if one is a realist in one's attitude toward science—that is, if one thinks that a primary aim of doing science is to develop theories that truly describe the mechanisms producing the phenomena, and if one takes theoretical fruitfulness and experimental confirmation as evidence for the reality of theoretical entities—then one should conclude that ET [evolutionary theory] is fundamentally indeterministic. If, however, one is a metaphysical determinist with respect to ET—that is, one who has decided for reasons outside of science that the process of evolution is deterministic—then one should conclude, along with Rosenberg and Horan, that ET is an instrumental science. (Brandon and Carson 1996, 336)

The first part of this claim, that a realist about evolutionary theory is committed to indeterminism, has already been criticized by Millstein (1997) and Graves et al. (1999). According to Millstein, the only rational attitude for the realist to take towards the question of indeterminism vs. determinism is that of an agnostic. The second part of the claim is once again what I have called the determinism-instrumentalism fallacy.

Brandon and Carson (1996, 326) seem to think that probabilities express either subjective degrees of belief or real, indeterministic propensities. If determinism is true, then probabilities are "epistemic," if it is false, then probabilities are genuinely stochastic propensities. But surely this dichotomy is too simple. For instance, there is a classical interpretation of probability which is neutral with respect to determinism/indeterminism: the frequency interpretation, according to which probabilities represent the actual or limiting frequency of an event in a series of like events. The frequency interpretation, too, makes probabilities real; it is an objective interpretation. Another objective interpretation of probability which is applicable to deterministic systems has been given by Mackie (1973, 181). On Mackie's interpretation, for instance, the probability of a certain outcome in a game of dice represents the number of initial states which, together with the laws which govern the motion of dice, determine this outcome. The propensity interpretation, as it was introduced by Popper (1959), is also intended to be applicable to such deterministic chance setups (although, for Popper, the problem of the interpretation of quantum theory was a main motivation behind the propensity interpretation). Probabilities, thus understood, represent a property of chance setups that may have deterministic laws of working. Thus, contrary to what BC (and GHR) say, a determinist about biological processes *can* be a realist with respect to evolutionary theory and the probabilities it posits. Of course, it is still possible that, although realism about evolutionary theory is compatible with determinism *conceptually*, determinism has been refuted *empirically* by biological research. I did not want to investigate the latter problem here. My aim so far was to show that the relationship between realism, determinism, and the interpretation of probability is more complex than both sides of the debate have assumed.

Thus, it is a mistake to think that probabilities either have to represent subjective degrees of beliefs or irreducibly stochastic propensities. There are other possibilities. Of course, this by itself does not undermine BC's claim that probabilities in evolutionary theory *do* represent genuinely probabilistic propensities. Now I want to show that this is problematic, too.

The main problem with BC's position is that it is committed to the view that *all* applications of the concept of probability in evolutionary theory are manifestations of indeterminism. Even if there exists variation in biological systems which is not explainable by "hidden variables," there can be no doubt that there is also variation which *is* caused by some hidden variables, for example, micro-environmental differences in moisture, nutrient concentration, pH, etc., which affect the growth of plants. Consider a colony of genetically identical plants that share the same environment. An investigation reveals that, in a given year, the individual plants produce different numbers of seeds. On the usual interpretation of the concept of fitness, these differences in seed production are not to be taken as an indication that the plants differ in fitness. Rather, biologists would calculate the average seed production to obtain an estimate of the genotype's fitness in the given environment. Now let us further assume that the variation in the number of seeds is *not* the result of genuinely indeterministic events during the development of the plants. Instead, the differences are caused by an uneven distribution of nutrients in the soil, which is typical for this type of environment. Even if BC (1996, 333) are right in arguing that it is methodologically unsound to assume that there are *always* such hidden variables, surely it is not unscientific to assume that such hidden variables exist *sometimes*. Does this mean that probabilities are rendered epistemic in cases where there are hidden variables? This seems wrong. In my example, one could still say that the probability distribution for the number of seeds produced says something about the relationship between plants of that genotype and their environment; they are therefore not merely "epistemic." However, the probability distribution, in this case, does not represent a genuine stochastic propensity of the kind postulated in quantum mechanics; rather, it expresses the *statistical effect of the action of the hidden variables*. In my hypothetical (but realistic) example, the source of probability is not indeterminism but the heterogeneity of the environment.

The problem is thus not only that BC's account cannot differentiate between cases where biological variation is caused by genuine indeterministic processes and cases where variation is caused by hidden variables. Because they view *all* probabilities featuring in evolutionary theory as expressions of irreducibly stochastic propensities, their position renders many cases of evolution incomprehensible. Even if objective chance exists in biological processes, it is unlikely that it can explain all the variability that renders evolutionary processes stochastic. Evolutionary theory, I maintain, is applicable to intra- and inter-populational variability regardless of whether this variability is a consequence of objective chance or the action of complex hidden variables. Thus, even if strict determinism is false, BC's position fails to account for those applications of evolutionary concepts where biological variability is not caused by genuinely indeterministic events but by some complex hidden variables, which are likely to abound.

4. Outlook. I have shown that both of the recently defended major positions which try to account for the statistical character of evolutionary theory are ridden with problems, regardless of the truth of determinism. The time is ripe to develop alternative accounts that avoid the pitfalls I have pointed out. I suggest that viable alternatives should satisfy the following criteria of adequacy. First, an account of the statistical character of evolutionary theory should be open to a realist interpretation at least to the extent that the best theories of physics and chemistry are. To allow realism about the latter but not about evolutionary theory seems odd, considering that evolutionary theory is one of the most highly confirmed theories in the history of science (Brandon and Carson 1996, 316). Second, a viable alternative should be compatible with determinism. If a non-negligible fraction of biological variability is caused by hidden variables, which is a safe bet, then we need an account which can explain how the combined action of these hidden variables gives rise to the stochastic character of the evolutionary process. Should it then turn out that objective chance plays a role as well (which is far from clear at present; see Millstein 1997), this would not undermine such an account. Clearly, compatibility with determinism is going to be the hard part. But we should do at least as good as philosophers of physics (e.g., Sklar 1993) who have developed realist accounts of the foundations of classical statistical mechanics, which is a fully deterministic theory.

The crux of the matter is going to lie in the concept of probability. Perhaps it is time to admit that the propensity interpretation has outlived its usefulness, because it makes a mess of the distinction between objective chance as it occurs in quantum mechanics and chance as it occurs in deterministic systems. I suggest that the most helpful way to think about probability in evolutionary theory is in terms of *ensembles*, an approach which has also proven to be fruitful in statistical mechanics (Sklar 1993). For example, to say that an allele has a probability of p to go to fixation by random drift means that in a fraction of p in a (fictional) ensemble of populations the allele will go to fixation.[5] Thus, evolutionary probabilities can be viewed as frequencies, though not as frequencies in a series of trials, but frequencies in ensembles of populations. Obviously, the interesting question is going to be how the relevant ensembles are to be individuated. I will deal with this question elsewhere. My goal here is to motivate alternative accounts of the statistical character of evolutionary theory, not to actually present such an alternative. It should be easier now, since we know where the pitfalls are.

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5. This ensemble approach is mentioned by participants of this debate in various places (e.g., Rosenberg 1994, 68; Brandon and Carson 1996, 323). However, they don't seem to be aware of its potential for solving the conceptual problems at hand.

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