Interpretations of Probability in Evolutionary Theory

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The ubiquitous probabilities of evolutionary theory (ET) spark the question: Which interpretation of probability is the most appropriate for ET? There is reason to think that, whatever we take probabilities in ET to be, they must be consistent with both determinism and indeterminism. I argue that the probabilities used in ET are objective in a realist sense, if not in an indeterministic sense. Furthermore, there are a number of interpretations of probability that are objective and would be consistent with deterministic evolution and indeterministic evolution. However, I suggest that evolutionary probabilities are best understood as propensities of population-level kinds.

1. Introduction. Evolutionary theory is teeming with probabilities. Probabilities exist at all levels: the level of mutation, the level of microevolution, and the level of macroevolution. This raises an interesting philosophical question. What is meant by saying that a certain evolutionary change is more or less probable? In other words, which interpretation of probability is the most appropriate for evolutionary theory?

This question about probabilities in evolutionary theory is related to the longstanding philosophical question that asks whether determinism or indeterminism is the correct characterization of our world. As an ontological claim about the world, determinism can be roughly characterized as follows: Given the complete state of the world at a particular time, for any

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future time there is only one possible state. Indeterminism, on the other hand, suggests that given the complete state of the world at a particular time, a future time may have *more* than one possible state.

Quantum mechanics is often interpreted as implying indeterminism at the microlevel. But what about the macrolevel, the level of evolutionary processes in particular? Is that indeterministic, also? Elsewhere, I have argued that we are not currently able answer this question, and that even scientific realists ought to remain agnostic concerning the determinism or indeterminism of evolutionary processes (Millstein 2000). If this argument is correct, it suggests that, whatever we take probabilities in evolutionary theory to be, they should be consistent with both determinism *and* indeterminism. Two other considerations point to the need for an interpretation of probability that is noncommittal with respect to determinism and indeterminism. The first is that, while the determinism question in evolutionary biology is currently a "hot" topic among philosophers of biology (see, for example, Brandon and Carson 1996; Graves, Horan, and Rosenberg 1999; Stamos 2001; Glymour 2001), it appears to garner little or no attention from evolutionary biologists. This suggests that the conception of probability at work in evolutionary theory is one that is independent of determinism and indeterminism. Second, both determinists and indeterminists agree that evolution is to *some* degree indeterministic, differing only as to the extent of the indeterminism (Millstein 2000); however as Weber (2001) argues, even if evolution is indeterministic, it is not plausible to think that *all* of the statistical behavior is due to indeterminism.

Which interpretations of probability in evolutionary theory are consistent with determinism and indeterminism? Almost any understanding of probability is consistent with indeterminism. However, determinism is the harder case. What sense can be made of probabilities in evolutionary theory if the evolutionary process is deterministic? A number of philosophers have argued that, even if evolutionary processes are deterministic, there still seems to be an important sense in which evolution is objectively probabilistic (Sober 1984; Brandon and Carson 1996; Weber 2001). Yet these arguments, with the exception of Sober's, do not provide fully characterized interpretations of probability under determinism.

In what follows, I contrast "objective" probability with "epistemic" probability. I then examine several candidate interpretations of probability, focusing on understanding probabilities under evolutionary determinism, with a brief discussion of their application under evolutionary indeterminism at the end. I argue that evolutionary probabilities are best understood as objective propensities of population-level kinds.

A few caveats: I am not trying to decide what *the* interpretation of probability is—only which one is appropriate for evolutionary theory. It

may be that certain interpretations of probability are appropriate for certain areas, and different ones for others. Also, my focus here is *not* to address the well-known issue of the propensity interpretation of fitness—I am seeking to understand the use of probabilities in evolutionary theory more broadly, not to define the notion of fitness. I do this through an examination of random drift, on the assumption that this case can be extrapolated to other areas of evolutionary theory.

2. Probability in Evolutionary Theory—An Example of Random Drift. Let us take a simple case of random drift, occurring in the absence of selection. Random drift (hereafter, "drift") is a random sampling process in the sense that it is a process where physical differences between organisms are causally irrelevant to differences in reproductive success (Millstein 2002). For example, suppose a population of red and brown butterflies has a colorblind predator that cannot distinguish between them—i.e., where the color difference between the two types of butterflies is causally irrelevant to any differences in reproductive success.

In a very large population, we would expect the proportion of red butterflies to brown butterflies to remain relatively constant from generation to generation. However, we would *not* expect the proportions to remain constant in a small population.

To see this, imagine an urn filled with colored balls where balls are sampled without respect to color. If a large sample of balls were taken, we would expect the frequencies of colored balls in the sample to be very close to the frequencies in the urn. On the other hand, if we only take a small sample of colored balls, our sample may very well have different proportions of colored balls than the urn does. In the same way that the color difference between the balls is causally irrelevant to which ball gets picked, in a population undergoing the process of drift, the physical differences between organisms are causally irrelevant to differences in their reproductive success. So in large populations, as with large urn samples, we would expect gene frequencies to be representative of the parent generation, but in small populations, as with small urn samples, gene frequencies may or may not be representative. Thus, when drift occurs over a number of generations in a small population, gene frequencies may fluctuate, or drift, randomly from generation to generation. Thus, if our population of red and brown butterflies were small, we would expect that the relative proportions of red and brown butterflies would fluctuate from generation to generation.

Biologists have sought to characterize how probable each of the possible transitions is, from one generation to the next. Given the frequency of an allele A in one generation, we can predict the frequency of A in the next

generation using the following equation, assuming random sampling as described earlier:[1]

$$P_{ij} = [(2N)!/(2N-j)!j!]\ (i/2N)\ j\ (1-i/2N)^{2N-j}$$

This is known as the *transition probability*—the probability that a population of size N (containing $2N$ alleles) will go from i alleles of type A to j alleles of type A. For example, if there are 3 individuals in the population and 3 A alleles in the current generation, the probability of decrease to two A alleles or increase to four A alleles in the next generation is .234, and the probability that the number of A alleles will remain constant is .312. In other words, the equation specifies the probabilities of the various possible increases and decreases (or lack thereof) in the number of alleles from one generation to the next.

This transition probability equation is a simple one that takes into account only two factors: the size of the population and its initial frequency. However, biologists create more complex transition probability equations by incorporating additional causal factors (e.g., selection). The question at hand is, how should we understand the probability used in both simple and complex transition probability equations?

3. Epistemic vs. Objective Probability. Philosophers generally divide interpretations of probability into two basic kinds: (1) epistemic (or epistemological) probability—probability that is concerned with the knowledge or beliefs of human beings, and (2) objective (or ontological) probability—probability that is a feature of the world (like the sun, the earth, etc.), independent of the knowledge and beliefs of human beings (Gillies 2000, 2).

Using these (not entirely uncontroversial) definitions as a starting point, we can now ask whether the transition probabilities in ET are epistemic or objective—keeping in mind that we are temporally assuming evolutionary determinism. Alexander Rosenberg (1994, ch. 4) has argued that determinism implies that an omniscient being would know every causal factor and know for *certain* whether a given event (such as an increase in the frequencies of brown butterflies from one generation to the next) would occur or not. An omniscient being in a deterministic world, so his argument goes, would have no need for probabilities. Thus, he concludes, *we* only use probabilities because we are *not* omniscient, and therefore our use of probabilities just reflects our ignorance.[2]

1. "This formula is simply the jth term in the binomial expansion of $(p+q)^{2N}$ where $p=i/2N$ and $q=1-(i/2N)$" (Roughgarden 1996, 65–66).

2. However, Rosenberg no longer believes that "epistemic probabilities *exhaust* the statistical character of the theory of natural selection" (2001, 541).

However, this "ignorance" interpretation overlooks the fact that we are aware of more causal factors than are included in the transition probability equation; for example, we know things about the predator and the color of the butterflies. Thus, we *choose* to ignore these causal factors, rather than being ignorant of them. In fact, even if we knew *all* the causal factors, we still might choose to use probabilities, as Elliott Sober has argued, because they allow us to compare similar populations to one another, ignoring the "nitty-gritty" causal details of individual populations (1984, ch. 4). Rosenberg, however, insists that Sober's argument shows only that probabilities are explanatorily useful to *us,* not that they have any objective standing.

I believe that Marcel Weber makes a useful distinction that clarifies the disagreement between Sober and Rosenberg. There are really two issues here, according to Weber, one having to do with explanatory value and one having to do with realism (2001). Weber points out that both philosophers seem to agree that the generalizations afforded by evolutionary probabilities are explanatorily useful—even indispensable, differing only as to whether these probabilities are indispensable exclusively to us, or to an omniscient being as well. But, Weber suggests, this disagreement over explanatory indispensability is not the most important issue—the most important issue is one of *realism.* Thus, in order to decide whether evolutionary probabilities are objective or not, we need to consider whether they refer to real, physical features of the world. Weber acknowledges that probabilistic descriptions may not be *complete,* but that is different from saying that they are based on our ignorance. A realist account is not required to be a complete account—no scientific theory is complete. It is enough that the probabilities capture some aspect of reality.

What Weber's arguments illustrate is one sense in which probabilities can be said to be objective: They can be objective in the sense that they refer to real, physical features of the world. Furthermore, I think that part of the problem is that Rosenberg utilizes a different sense of "objective" than Weber (and probably Sober) does, and this is illustrated by his claim that "on the assumption of determinism here in force, the only way probabilities can vary from one is if they are *epistemic*" (Rosenberg 1994, 81). This suggests that on Rosenberg's view, either probabilities are objective in an indeterministic sense (given identical initial conditions, more than one outcome is possible, as with radioactive decay), or they are epistemic. But this dichotomy overlooks the alternative meaning of "objective" as "realist," a meaning that is implicit in frequency interpretations of probability and even some propensity interpretations of probability (more on this below).

So, then, are evolutionary probabilities objective in a realist sense? In other words, does the model underlying the transition probability equation correspond to reality? Here, we can examine the system and see if it is

consistent with the probability assignment. The model that the probability equation rests on presupposes random sampling. So, we can examine the population and try to find evidence that this is so (for example, is the predator really color-blind, or can it somehow distinguish between the types?). The other way that we can decide if the probability represents a real, physical feature of the world is through testing to see if actual frequencies match the transition probabilities. These are tests that can, and have, been done to demonstrate the realism, and thus the objective probabilities, at work in transition probability equations (see, for example, Dobzhansky and Pavlovsky 1957).

4. Interpretations of Probability in Evolutionary Theory. Objective interpretations of probability tend to be of two kinds: frequentist and propensity. Under frequentist interpretations, probability is the (actual) relative frequency of an event in the long run (or in an infinite sequence or as the frequency approaches a limit). Under propensity interpretations, probability is the physical tendency or disposition of a system to produce a certain kind of outcome.

First, let us consider whether a frequency interpretation will work for transition probability equations. A frequency interpretation rests on identifying the probability with relative frequencies. However, with drift, there is no *one* frequency with which to identify the probability, whether the frequencies are actual, in the long run, or in an infinite sequence. That is, drift models cannot predict frequencies for any single population; they can only predict frequencies for an *ensemble* of populations (Hartl and Clark 1989, ch. 2). This is because, as discussed earlier, frequencies may increase, decrease, or remain constant. In an ensemble of populations, eventually each population undergoing drift will go to fixation for *one* of the types, but *which* type cannot be predicted.

That leaves propensity interpretations, unless we are to develop a third alternative.[3] But are propensity interpretations an option, given our (temporary) assumption of determinism? It has sometimes been suggested that propensity interpretations are inconsistent with determinism. This is because the propensity interpretation was developed as a way to account for quantum mechanical probabilities—interpreted as indeterministic probabilities. This *is* one sense of objective probability. Yet such claims overlook the deterministic propensity accounts already extant in the philosophical literature.

3. A possibility I would not want to rule out—Weber (2001), for example, suggests that we define evolutionary probabilities in terms of ensembles. This is an intriguing suggestion that Weber promises to spell out more fully in a future work.

One is Ronald Giere's single-case propensity interpretation. By "single-case," Giere means that propensities adhere to an *individual trial* (1973). On Giere's view, the propensity of a system to exhibit a certain frequency is absolute in the sense that "it is no more relative to any description than any other physical characteristics, e.g. mass, specific gravity, or electrical conductivity" (1973, 473). However, as James Fetzer (1981) argues, this really means that propensity is relative to the complete state of the world at the time of the individual trial. Thus, strictly speaking, on Giere's view deterministic systems exhibit probabilities of 1 or 0 (1973, 475). However, Giere suggests that we treat certain systems (systems that exhibit a distribution of different outcomes in repeated trials even when we have controlled all the variables that we have been able to identify) "instrumentalistically," that is, as if they were indeterministic, even though they are deterministic (1976, 345). Populations undergoing drift, as mentioned earlier, are systems of this kind. This would mean that we consider the probability of the outcome given certain specified properties of the system (in our drift example, the size of the population and its initial frequency), rather than given the complete state of the world. Does relativizing the probability in this way mean that we are abandoning objective probability? Giere denies this, and his denial reflects the characterization of objective probability that was given earlier:

> [I]t is correct to say that the propensities we attribute to macroscopic systems are in some sense relative to our knowledge. Yet these instrumentally assigned values are in no direct way a measure of our knowledge or our ignorance of the systems in question. (1976, 346)

In other words, when Giere says that propensities of deterministic systems are to be understood "instrumentalistically," he means only that they are not "true" (indeterministic) propensities, not that they are epistemic probabilities. In fact, according to Giere, we may "even use the propensity interpretation when we *do* know all the relevant variables, but for some reason do not think it worth the effort to obtain or employ the necessary specific information" (1976, 346). Thus, we may use the transition probability equation, understood as the disposition of a single population to change from one frequency to another in the course of one generation, even when additional information about the butterflies is available, or when we do not think it is worth the effort to obtain the information.

So, rather than being relative to our *knowledge,* these probabilities are relative to a *particular specification*. But this does not make them "unreal," because, as Popper argues, *all* experimentation is relative to specification (Popper 1967). This is because one can never repeat *exactly* the same experiment; there will always be at least slight differences between different trials of a given experiment. When we say we are performing the

"same" experiment, what we really mean is that we are performing an experiment that meets certain specifications—and the results of those experiments are relative to that specification. This relativity to specification holds not just for probabilistic systems, but for nonprobabilistic systems as well, and the results are equally "real" for both kinds of systems. Thus, using Giere's account, transition probabilities can be viewed as instrumental (indeterministic) propensities, but they are objective probabilities nonetheless, in the sense that they refer to real, physical features of the world.

A second possibility for propensity under determinism is to endorse a propensity interpretation that views probabilities as adhering to *kinds* or classes, rather than to the single case, as on Giere's view.[4] On this view, when we say that a population has a certain probability of changing to (or remaining in) a certain state, what we mean is that *this kind* of population (for example, a population of a certain size, having a certain frequency) has a *propensity* to undergo a certain kind of change (for example, to a specified frequency).

This, of course, raises the question: what kind of kind? Is any kind (any level or amount of specification) equally good, or is some way the most preferable? In the terms used in the literature of the philosophy of probability, this is known as the "the problem of the reference class." However, my intent here is not to solve this problem, but rather the much more modest goal of determining which way of specifying a reference class is most appropriate for evolutionary theory. There are a number of different possibilities to consider here.

Karl Popper, the most well known defender of the propensity interpretation, seems to endorse "anything goes" kinds. On Popper's view, propensities are not inherent in individual *things,* rather "they are *relational* properties of the *experimental arrangement*—of the conditions we intend to keep constant during repetition" (1959, 37; emphasis added). The same experimental arrangement, or system, can be characterized in different ways: "Take the tossing of a penny: It may have been thrown 9 feet up. Shall we say or shall we not say that this experiment is repeated if the penny is thrown to a height of 10 feet?" (1967, 38). Here Popper's question is rhetorical; we might choose to say that it is the same experiment, or we might choose to say that it is a different experiment. Either way is

4. Normally, philosophers distinguish between "single-case" propensities and "long-run" propensities. Thus, my contrast between "single-case" and "kind" is somewhat nonstandard. I deviate from the canon here for two reasons: (1) because "kind" seems to be the more natural opposite of "single-case," as in the type-token distinction; and (2) in evolutionary theory, one often wishes to speak not in terms of the outcome of many repetitions of a single experiment, but rather the outcomes of an ensemble of different experiments (or, more appropriately, populations).

equally correct and equally objective. On this kind of view, we could describe populations at many (perhaps infinitely many) different levels of description, being more or less specific (including greater or fewer causal factors), and the resulting probabilities would each be objective, in the sense described earlier—they would capture reality.[5] The one that we choose to use would be a pragmatic matter, depending on the questions that we are trying to answer.

Sober provides a characterization of the propensity interpretation for evolutionary theory that seems sympathetic to the "anything goes" position that I attribute to Popper: in discussing the fact that different characterizations lead to different probability assignments, Sober states that "both [assignments] are correct, and which characterization we use depends on our purposes" (1984, 130). Thus, I will refer to this position as the Popper/Sober view.

The Popper/Sober view has the advantage of flexibility, but perhaps it is too flexible. Are not some ways of describing populations superior to others? For example, would a characterization that left out the size of the population be as adequate as one that included it (even if the former were useful for some purposes)? As the debate between Wright and Fisher illustrates, the effective population size is a key factor in drift, so perhaps any model that fails to include it is deficient.

Other propensity interpretations of kinds would argue for limitations on the kinds of kinds. One possibility is Fetzer's (1981) version of the propensity interpretation where the kind is specified by *all and only the causally relevant factors*.[6] Thus, for the evolutionary case, we would need to figure out which factors were causally relevant to the change from one generation to the next, and which were causally irrelevant. The kind of population would be specified by all and only the causally relevant factors. This would include population size and initial frequency at a minimum, but would include also a host of other causally relevant factors, such as the locations of the individual organisms and their interactions with one

5. It should be noted that my interpretation of Popper's views here is controversial in at least two ways. First, some will argue, Popper's propensity interpretation deals with the single-case, not with kinds—or, to use the more common language, it is a single-case propensity theory, not a long-run propensity theory. Second, it may be argued that Popper's views apply only to indeterministic cases, not to deterministic ones. Yet there is reason to think that Popper was at least ambiguous on these points. See Gillies 2000 for a discussion of Popper's ambiguity on the single-case vs. long-run question, and see Schneider 1994 for an interpretation that supports the view that Popper's arguments do apply to deterministic cases. If the reader still has qualms, he/she can think of these views as being endorsed by the lesser-known philosopher, Popper*.

6. As with Popper, Fetzer claims to be solving single-case propensities, not propensities of kinds (see previous footnote). If so, then I am borrowing his criterion for other purposes.

another. It would exclude causally irrelevant factors such as the positions of the stars during the generational change in question.

Thus, on this view, the simple transition probability equation described earlier would embody an inadequate characterization of a population because it fails to include all causally relevant factors. Yet this normative conclusion seems overly harsh. The transition probability equation is admittedly a simple model. But it is intentionally so, in part for instructional purposes, but also, as Sober argues, to capture significant biological generalizations. Would a more complicated model be preferable? Probably, for most purposes, and to that end biologists have developed additional models with increasing complexity. However, there is a trade-off; the more causal factors you include in the model, the less general it becomes. The more complex models are more predictively accurate, but they apply to fewer cases and overlook aspects that different populations may have in common.[7] In the extreme, where all causal factors are included, the model applies to very few cases; if causal factors like location of organisms are included, the model probably applies to one and only one case.

We might also consider whether there is a distinctively *evolutionary* way of picking out kinds, and I think that there is. The discipline of population genetics is founded, in part, on the realization that selection, drift, and other evolutionary processes are *population-level* processes. That is, it is not individual organisms that evolve (or undergo selection or drift), it is populations. Thus, population geneticists have sought to identify the causal factors that are common across populations, ignoring nitty-gritty causal details particular to one population (such as the relative locations of organisms within the environment). The transition probability equation described earlier illustrates this way of thinking, implying that populations of a certain size and a certain initial frequency are of a kind. Restricting causal factors to those that operate at the population level provides a useful way of balancing the desire for accuracy with the desire for generality.

5. Conclusion. What can we make of these different ways of characterizing propensity-kinds? The conclusion that I want to emphasize is that *any* of the possibilities that I have enumerated (Giere, Popper/Sober, Fetzer, and population genetics) provides us with an interpretation of probability that is objective in a realist sense. Thus, the problem is not that there is no way to do it; the problem is, which way is the most preferable? For those that endorse single-case propensities for other reasons and are looking for a unified account, then Giere's account, or some variant, would be the most desirable. For those who reject single-case propensities or who

7. See Strevens (ms.) and Weisberg (2003) for further discussion of the tradeoff between precision and generality.

are willing to accept that different interpretations may be appropriate in different areas, one of the propensity-kind interpretations provides an objective account. What I have suggested here is that the Popper/Sober view seems too liberal, whereas Fetzer's view is not liberal enough. But these are, perhaps, pragmatic considerations. Still, within an evolutionary context, it is the population-level factors that will make a difference over the long run, not the facts about individual organisms. Thus, understanding evolutionary probabilities as propensities of population-specified kinds provides the long-term perspective on evolutionary processes.

The implications of these arguments are twofold. The first is to urge the point that the use of probabilities in ET does not imply that it is inadequate in some way, or that the probabilities should be dispensed with if we were smarter. The second is to suggest that biologists focus on the causes that operate on the population level. I think, for the most part, that *is* what they do.

Suppose, however, that what we have granted for the sake of argument throughout this essay is false—that evolutionary processes are in fact *indeterministic*. As Weber (2001) argues, it is implausible to think that *all* applications of probability in ET would be the result of this indeterminacy. Rather, some of the observed variance would be due to indeterminacy, and some would be due to the use of probabilities relative to specified kinds (population-level kinds, on my account). Thus, both indeterministic propensity and deterministic propensity would play a role.

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