

The Propensity Interpretation of Fitness and the Propensity Interpretation of Probability

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Abstract The paper provides a new critical perspective on the propensity interpretation of fitness (PIF), by investigating its relationship to the propensity interpretation of probability. Two main conclusions are drawn. First, the claim that fitness is a propensity cannot be understood properly: fitness is not a propensity in the sense prescribed by the propensity interpretation of probability. Second, this interpretation of probability is inessential for explanations proposed by the PIF in evolutionary biology. Consequently, interpreting the probabilistic dimension of fitness in terms of propensities is neither a strong motivation in favor of this interpretation, nor a possible target for substantial criticism.

1 Introduction

The propensity interpretation of probability relies on the claim that physical set-ups give rise to natural tendencies toward the production of singular events. Popper calls these tendencies “propensities” and he claims that each one is measured by the probability of the event it tends to produce. The propensity interpretation, therefore, explicates the idea that probabilities of singular events are grounded in physical

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facts. It was the first interpretation to do so, it still is one of the few that does among the major received interpretations, and we see this as the main reason why the propensity interpretation has remained appealing and regularly discussed in spite of the important criticisms it has had to face.¹ One important domain where the propensity interpretation of probability has been considered useful is the philosophy of evolutionary biology. Relying on the propensity interpretation of probability, a “propensity interpretation of fitness” appeared at the end of the 1970s, which has been much debated in the 1990s² and still has proponents today.

Although proponents of the propensity interpretation of fitness (PIF) explicitly refer to the propensity interpretation of singular probabilities, it is unclear what the relationship between the two propensity interpretations exactly is. This is what the present paper aims at elucidating. We shall focus here on Mills and Beatty’s 1979 paper, where the PIF was explicitly advocated for the first time.³ Indeed, the questions we tackle concern the very foundations of the PIF and, as a consequence, we can stick to Mills and Beatty’s paper, independently of the way the interpretation they suggest has been developed and refined afterwards. As far as the propensity interpretation of probability is concerned, we will focus on Popper’s position as expounded in particular in the 1959 paper. No later development differs from this orthodoxy in a way that would make the propensity interpretation of singular probabilities either significantly less problematic, or openly more in line with the PIF.⁴

2 The Propensity Interpretation of Fitness

Biologists appeal to the notion of fitness in order to explain evolutionary changes: differences in fitness between types in a given population, where a type corresponds to a certain allele or trait, are invoked to explain differences in the average offspring contribution of these types, and thus to account for changes in the proportions of these types in the population over time.

The most traditionally used definition of fitness in biology is in terms of actual survival and reproductive success: fitness corresponds to the actual number of offspring left by an individual or by a type, usually relative to the actual contribution of some reference individual or type. This implies that, the higher the number of offspring left by an individual or a type, the fitter this individual or this type. This traditional definition, however, raises two problems.

¹ Major criticisms are developed in: Humphreys (1985), Kyburg (2002), Eagle (2004), Humphreys (2004). For discussion of such objections, see Berkovitz’s paper in this volume.

² See Richardson and Burian (1992), Brandon and Carson (1996).

³ Brandon (1978) is also an early paper in the PIF tradition. Yet, even though he mentions propensities in connection with fitness and cites Popper (1959), this paper deals neither specifically, nor explicitly with the claim that fitness is a propensity.

⁴ We cannot use Coffa (1977), that is cited by Mills and Beatty, as our reference concerning propensities because it is not about probability and does not define or support a version of the propensity interpretation of probability.

First, it makes explanations invoking fitness differences circular. Indeed, under the traditional definition of fitness, that type A is fitter than type B means that type A leaves a higher number of offspring than type B. But clearly, then, we cannot say that the difference in fitness between type A and type B *explains* the difference in the actual offspring contribution of types A and B. Accounting for type frequency differences by fitness differences between types provides just a description, not an explanation, of the observed changes in the population over time.

Second, the actualist conception of fitness leads to counter-intuitive analyses of some situations. For instance, let us imagine that two genetically and phenotypically identical twins are standing in a forest (Scriven 1959): one of them is struck by lightning and dies, while the other one is spared and reproduces. In this case, differing reproductive success is explained by the fact that the lightning strikes one twin but not the other one. However, being struck by lightning is not a property that can be invoked in evolutionary biology explanations. More generally, because there is no physical difference between the two organisms, they should have the same fitness. Nevertheless, according to the actualist conception, we are committed to say that the lucky twin is fitter because she reproduces more than the other one. More generally, the traditional definition of fitness makes it possible that an individual or a type which intuitively is not the fittest (or, even, which intuitively is the less fit) should be considered the fittest just because by chance it has left more offspring than the other individuals or types of the same population.

By introducing the PIF, Mills and Beatty (1979) wanted to solve these two problems, while providing an analysis of fitness “which reveals the empirical content implicit in evolutionary biologist’s explanations” (1979, p. 264). They believed that fitness should not be defined in terms of actual survival and reproduction, but rather in terms of the organisms’ physical properties that cause them. Nevertheless, it is impossible to define fitness merely as some function of physical properties (or traits) of individuals or types both because these properties are very diverse and because fitness crucially depends on the particular environment where an organism is embedded and on the natural population it belongs to.

The PIF is a sort of compromise between on the one hand the traditional definition of fitness and on the other hand a definition of fitness in terms of the physical properties of organisms that would make fitness independent of their actual survival and reproductive success. Individual fitness (“fitness₁”) is defined as the propensity (or the disposition, the ability, the tendency, the capability) of an individual organism to survive and reproduce in a particular environment and a particular population (Mills and Beatty 1979, p. 270–3). So, fitness is a dispositional property of individual organisms in a given environment and it is a function of their physical properties. Indeed, following the propensity interpretation of probability, propensities depend on physical conditions (Popper 1959).

Mills and Beatty argue that conceiving fitness in this way makes it explanatory. The strategy, here, is to ground the explanatoriness of evolutionary explanations invoking fitness in the explanatory power of dispositions with respect to their manifestations. More precisely, since fitness is conceived as a dispositional property of individual organisms, fitness differences are supposed to explain differences concerning the manifestations of fitness, that is differences in actual survival and

reproductive success. Finally, Mills and Beatty suggest that the fitness₁ of a given individual organism is measured by this organism's expected number of offspring (Mills and Beatty 1979, p. 274–5).⁵

Mills and Beatty also provide a definition of the fitness of types—“fitness₂”. The fitness₂ of a type is defined as the average fitness₁ of the members of this type, where being a member of a type means having a certain gene allele or trait (Mills and Beatty 1979, p. 276). Explanations of evolutionary changes primarily appeal to fitness₂, or rather to relative fitness₂, that Mills and Beatty define as follows (1979, p. 277): the relative fitness₂ of a type in a given environment equals the ratio of its fitness₂ to the maximum fitness₂ of a type in this environment (i.e. the fitness₂ of the fittest type in this environment). Given the relative fitness₂ of different types in a given environment and some information about the mechanisms of inheritance, we can predict and explain how the frequencies of these types in the population change over time. Mills and Beatty (1979, p. 272) explicitly claim that, when the notion of fitness refers to types, it cannot be a single-case propensity. Fitness₂ is just derivative from individual fitness propensities.

In order to explicate the relationship between the PIF and the propensity interpretation of probability, we will have to deal with two questions. First, Mills and Beatty's paper is characterized by ambiguities about how one should understand the claim that fitness₁ is a disposition or a propensity, and we will try to understand this claim (Sect. 3). Second, we will consider whether the PIF needs the propensity interpretation of probability in order to provide a non-circular account of explanations of differences in reproductive success in terms of fitness differences (Sect. 4). We shall conclude that, for the PIF to satisfactorily solve the problems raised by the traditional definition of fitness, it is in fact not necessary that singular probabilities be given a propensity interpretation.

3 Fitness₁ as a Propensity

How should one understand the claim that fitness is a propensity? Is it a propensity in the sense that was introduced by Popper? In Mills and Beatty's paper, one finds two hints at how one may answer these questions. First, an analogy is drawn between fitness and the solubility of salt, suggesting that the claim that fitness is a propensity should be understood quite literally (1979, p. 270–2). Second, the authors characterize the fitness of an organism as “the entire distribution of its reproductive propensities” (1979, p. 274). The two characterizations are not meant to be separate from each other. Rather, the second one is taken to specify the first one, for the particular case of fitness₁. Focusing on this case, we shall now try to make precise sense of each characterization and confront the two of them.

⁵ The expected number of offspring is certainly not a good measure of fitness: other parameters, like variance, are relevant too. However, we shall not enter the debate concerning the statistic(s) that should enter measures of fitness: the initial suggestion to the effect of defining fitness in terms of expectation suffices to raise the questions we are interested in. For a critical discussion of the idea that fitness is measured by the expected number of offspring, see Beatty and Finsen (1989), Richardson and Burian (1992), Sober (2001).

The analogy between the solubility of salt and the fitness₁ of an individual organism that is explored by Beatty and Mills is grounded on the fact that both have to do with a capacity: they are dispositional properties. Accordingly, both can be manifested and can fail to be manifested. The solubility of salt is manifested when salt actually dissolves. Analogously, the fitness₁ of an organism is manifested when this organism actually survives and, most importantly, reproduces: fitness₁ is a “*propensity to survive and reproduce*” (1979, p. 270; italics in the original).

There are at least two reasons why the analogy with solubility is rhetorically important for Mills and Beatty. First, it highlights the fact that the PIF makes fitness refer to physical properties of individual organisms—a point which is also emphasized by Brandon (1978). Indeed, however one conceives of dispositions, it is usually granted that they have a physical basis. Thus, in the same way as “the propensity of salt to dissolve in water [...] consists in (i.e., ‘water solubility’ *refers to*) its ionic crystalline character [...], the fitness of an organism consists in its having traits which condition its production of offspring in a given environment” (1979, p. 271). Second, the analogy with solubility makes it clear why considering fitness as a disposition makes it explanatory: “the fitness of an organism explains its success at survival and reproduction in a particular environment in the same way that the solubility of a substance explains the fact that it has dissolved in a particular liquid” (1979, p. 270).

This, however, points to the fact that the analogy, if taken seriously, goes further. It suggests an analogous status for the “particular environment” an individual organism lives in and the “particular liquid” a soluble substance may be plunged in. Both should be seen as “triggering conditions” (p. 271), that cause the corresponding disposition to be manifested. Moreover, all this works only in “the absence of disturbing factors” (ibid.). Disturbing factors are factors that interfere with the manifestation of a disposition and block it even when the triggering conditions are present. Concerning solubility, “the salt’s having been coated in plastic before immersion” (ibid.) would be such a factor. Concerning fitness₁, disturbing factors are factors that have an impact on the reproductive success of individual organisms but do not have to do with physical differences between them. Mills and Beatty cite “environmental catastrophes (e.g., atomic holocausts, forests fires, etc.) and human intervention” (ibid.). The analogy with solubility strongly suggests that, in a given particular environment, fitness₁ is manifested unless such factors interfere: “the propensity of salt to dissolve in water [...] consists in [...] its ionic crystalline character, which causes salt to dissolve *whenever* the appropriate triggering condition—immersion in water—is met” (1979, p. 271; our emphasis).

One can take the difference between dispositions and propensities to be that propensities are dispositions of a particular type: stochastic dispositions that get manifested only with a certain probability, even when the triggering conditions are present and the disturbing factors are absent. Following this (standard) terminology, the analogy between fitness₁ and solubility as it is drawn by Mills and Beatty clearly suggests that fitness₁ is not a propensity, but rather a deterministic disposition.⁶ Accordingly, the stochastic element which is central to propensities in the context of

⁶ Strictly speaking, the disposition of salt to dissolve in water is not deterministic: the probability of dissolution is not 1. However, this probability is extremely close to 1 and the quotation above (p. 271) clearly shows that Beatty and Mills take it to be deterministic.

interpreting probabilities is absent. A probabilistic dimension may be reintroduced if one considers that different triggering conditions (that is, different environments) lead to different manifestations and that one can assign probabilities to the various possible environments. This reading, though, does not make fitness₁ as paralleled to solubility any more a propensity than solubility is. If it is a propensity, then it is trivial in the sense that it cannot take values different from 0 and 1.

Let us now turn to the second characterization of fitness₁: the fitness₁ of an organism is “the entire distribution of its reproductive propensities” (1979, p. 274). Here, the idea is that, in a given environment, there are different numbers of offspring that an individual organism may leave, that one can define a probability distribution over these possible numbers, and that the corresponding probabilities should be given a propensity interpretation. A consequence is that “there are many such propensities [propensities to reproduce]. There is an organism’s propensity to leave zero offspring, its propensity to leave 1 offspring, 2 offspring, ..., n offspring (during its lifetime)” (1979, p. 273). Even though the set of propensities may well be determined by the environmental conditions, these are propensities properly speaking, that is stochastic dispositions (and they are non-trivial). Still, under this reading, fitness₁ is not a propensity. At best, it can be considered as a set of propensities, each corresponding to a number of offspring the organism can leave.

All in all, none of the characterizations used by Mills and Beatty makes fitness₁ a propensity in the sense this would have in the context of interpreting singular probabilities. The propensity interpretation of probability that is developed in Mellor (1971), according to which “the display of a propensity is the chance distribution over the possible results of the appropriate trial” (1979, p. 70), may be able to do justice to the intuitions underlying both of these characterizations. However, Mellor’s position has remained heterodox in the field of propensity interpretations of probability. Moreover, even though Beatty and Mills refer to Mellor, this is only in a footnote and they never explicitly cite Mellor’s 1971 book. Most importantly, the characterizations of fitness₁ that actually appear in the 1979 paper are *not* in line with Mellor’s views, strictly speaking. As a consequence, we conclude that the claim that fitness₁ is a propensity can be understood only in a very loose way, by reference to one or the other of the two characterizations that we have discussed.

This claim must be understood all the more loosely since the two characterizations that are used alternatively by Mills and Beatty are incompatible. Most significantly, the first reading implies that whatever probabilistic element there may be to fitness₁ is reducible to probabilities on the various possible environments and/or on the presence of disturbances, while the second reading makes fitness itself probabilistic, by making it a stochastic disposition. One has to choose between these two characterizations, implying that the relationship between them is not the relation of specification that is suggested by Mills and Beatty.

4 Does the Propensity Interpretation of Fitness Need Propensities?

Let us now try to understand whether the propensity interpretation of probability is required for Mills and Beatty to account for evolutionary biology’s explanations invoking fitness.

These explanations are mostly explanations of differences in actual reproductive contribution between types in terms of fitness₂ differences between them. Therefore, the question we address concerns the explanatory power of differences in fitness (conceived according to the PIF) with respect to differences in reproductive success. Note that this is not the same thing as the explanatory power of fitness with respect to reproductive success.

4.1 The Propensity Interpretation of Fitness₁ and the Propensity Interpretation of Probability

Before discussing explanations whose explanans are fitness₂ differences, we want to clarify a point concerning the fitness of individual organisms. This should make clear what is at stake in fitness explanations.

Mills and Beatty seem to take for granted that a disposition explains its manifestations because, be it deterministic or probabilistic, it has a causal productive value with respect to them. There is little agreement about the causal relevance of dispositions, the explanatory power of disposition ascriptions, and the kind of explanations dispositions can ground.⁷ But our point is independent from this controversy: even though we take for granted that dispositions causally explain their manifestations and we consider fitness as a dispositional property of individual organisms—as Mills and Beatty do—this does not entail that fitness₁ differences explain differences in reproductive success between individual organisms.

The figure below represents the set of propensities of two individual organisms, *x* and *y*, to leave different numbers of offspring. For instance, it indicates that *x*'s propensity to leave 3 offspring has value 0.5. *E* represents the measure of *x*'s and *y*'s fitness₁, i.e. the expected number of offspring for each of the two individuals. In the last column (italicized), the number of offspring left by each of them represents its actual reproductive success:

individual	P(N=1)	P(N=2)	P(N=3)	P(N=4)	P(N=5)	<i>E</i> (N)	<i>Na</i>
<i>x</i>			0.5		0.5	4	3
<i>y</i>	0.6		0.3		0.1	2	5

If we assume that dispositions cause their manifestations and so explain them, the figure justifies the following claims: *x*'s propensity to leave 3 offspring explains that, actually, *x* has left 3 offspring and *y*'s propensity to leave 5 offspring explains that, actually, *y* has left 5 offspring. Nevertheless, we cannot make similar claims in terms of differences. More precisely, nothing in the figure above explains the difference in reproductive success between the individual organisms *x* and *y*. In

⁷ In particular, some authors argue that disposition ascriptions are just a way of talking about intrinsic properties of objects (Quine 1974; Boyle 1666/1979). Others claim that, although dispositions are more than just names we use to refer to categorical properties, they are causally impotent (O'Shaughnessy 1970; Prior et al. 1982). For a complete review of objections to the view that dispositions are causally efficacious, and for an argument in favour of this view, see Mumford (1998, chapter 6).

particular the difference in fitness₁, that is the difference between x 's and y 's expected numbers of offspring, does not.

This becomes clearer if we understand that the values of propensities, given by probabilities, do not make any difference concerning their explanatory power with respect to their manifestations. x 's propensity to leave 3 offspring, whose value is 0.5, explains that x left 3 offspring exactly as well as y 's propensity to leave 5 offspring, whose value is 0.3, explains that y left 5 offspring. Probabilities, here, do not measure anything like explanatory power.⁸ They only stem from the probabilistic nature of propensities: as already said, propensities are stochastic dispositions that get manifested only with a certain probability, even when the triggering conditions are present and the disturbing factors are absent. This means that even if we take for granted that dispositions causally explain their manifestations, clearly, the only relations figuring in the table above that are relevant with respect to the explanation of differences in individual reproductive success are between propensities and their manifestations (for instance, between the propensity of x to leave 3 offspring and its actual reproductive success). In particular, the values of propensities—that is, probabilities—and therefore their differences, have no explanatory relevance here.⁹

4.2 The Propensity Interpretation of Fitness₂ and the Propensity Interpretation of Probability

We already mentioned that Mills and Beatty's 1979 paper defines the fitness₂ of a type as the average fitness₁ of the individuals belonging to this type. The fitness₂ of T , then, is the average expected number of offspring for the individuals belonging to T . Yet, in a later paper (1989), Beatty and Mills (then Beatty and Finsen) expound their initial definition as follows: "Fitness, then, is probable offspring contribution" (1989, p. 18), meaning that the fitness₂ of T is the expected number of offspring for T , computed out of type probabilities that "represent average descendant-contribution probabilities" (1989, p. 23). Thus, the 1989 paper suggests that the propensity interpretation of fitness₂ requires to first averaging over individual probabilities in order to get type probabilities and second taking the expectation for type probabilities, while the initial paper suggested to first considering individual expectations and then averaging over them.

The two definitions are mathematically equivalent. Moreover, both rely on the idea of getting magnitudes concerning a type through averaging over the corresponding magnitudes for the individual organisms belonging to the type.

⁸ More generally, the idea that events with higher probabilities are better explained has been discarded by critics of the inductive-statistical account of explanation (e.g., Salmon 1971, Coffa 1977, Railton 1978).

⁹ It is true that differences in probabilities could appear in the explanation of differences in relative frequencies of various offspring contributions. Think about repeating similar circumstances. Then, the larger the number of repetitions, the higher the probability that the actual amount of offspring will correspond to the expectation. Moreover, the larger a population of similar individuals, the higher the chance that the average number of offspring will be close to the expectation. Those explanatory relations, however, are irrelevant as far as the explanation of differences in *individual* reproductive success are concerned.

This, however, is problematic. First, it is unclear what one should average on: the actual individual organisms belonging to the type? Or rather on (some particular combination of) possible individuals of the type? Second, averaging on individual magnitudes in order to obtain type magnitudes is inadequate: it disregards the possibility of accidental correlations. For instance, consider two traits T and S and an environment E such that, in E , T is advantageous and S is disadvantageous. Moreover, imagine that, by chance, in the population under consideration T and S happen to be strictly associated. Using the average in order to get type magnitudes out of individual magnitudes, it cannot be the case that the fitness_2 of T and the fitness_2 of S are different, even though T is assumed to be fitter than S . Averaging, therefore, is problematic. Consequently, we shall rely on the 1989 definition and remain silent about how type probabilities are defined or computed (implying that we do not define them as averages of individual probabilities).

How do the explanations mentioning fitness_2 thus defined work? Or: how do differences in fitness_2 explain differences in actual reproductive success? As far as we can see, the only way they can is through the law of large numbers. More precisely, evolutionary biology explanations pertain to the type level and they rely on the law of large numbers for type probabilities. This means that individuals are considered only as members of a type, disregarding possible differences within the same type. In this explanatory context, probabilities of various numbers of offspring are the same for all individuals of the same type, as if they were identical.

In order to see how the law of large numbers does the job of explaining differences in actual reproductive success by differences in fitness_2 , let $E(T)$ be (the value of) the fitness_2 of type T and $S(T)$ be (the value of) its actual reproductive success of T . We assume that $S(T)$ is the average actual number of offspring for the individuals belonging to T . Averaging is unproblematic here, since we are seeking to measure something that, unlike fitness_2 , is plain and only actual. By definition, $S(T)$ equals the total number of offspring left by the individual organisms belonging to T , $O(T)$, divided by the total number of these organisms, $N(T)$:

$$S(T) = \frac{O(T)}{N(T)}$$

Now, $O(T)$ is a weighted sum: each possible number of offspring, i , receives as a weight the number of individual organisms that leaves i offspring

$$S(T) = \frac{\sum_i i \cdot N(i)}{N(T)} = \sum_i i \cdot \frac{N(i)}{N(t)} = \sum_i i \cdot F(i)$$

where each $F(i)$ is the actual frequency of individual organisms that leave i offspring. Here comes the law of large numbers: when the number of individuals belonging to T tends to infinity, each $F(i)$ tends in probability to the type probability to leave i offspring, $P(i)$ —meaning that the probability that $F(i)$ tends to $P(i)$, when the number of individuals tends to infinity, is 1. Therefore, $S(T)$ tends in probability to

$$\sum_i i \cdot P(i)$$

But, following our initial assumptions, this sum is nothing but the fitness₂ of T. Therefore, the law of large numbers implies that the actual reproductive success of T tends in probability to the fitness₂ of T when the number of individual organisms belonging to T tends to infinity. A consequence is that differences in actual reproductive success tend, in probability, to reflect fitness₂ differences. Thus, one can consider that differences in fitness₂ explain differences in actual reproductive success. We contend that this is how fitness₂ explanations work according to the PIF.

Whatever the kind of explanation at work here exactly,¹⁰ it is clear that there is no circularity: differences in actual reproductive success are not explained by differences in actual reproductive success, but rather by differences in expectation of reproduction. Moreover, one should notice that it is only in very idealized circumstances that fitness₂ explanations thus conceived work. For the law of large numbers to work in the envisaged way, one must consider a big population of individuals of type T that are independent and identical, which entails in particular that the environment is stable. This means that our analysis has to be made more complex if it is to account for less idealized cases.

This, however, would not alter our main point: fitness₂ explanations construed as above do not depend on how one interprets probability. Especially, they do not require a propensity interpretation. Even though one interprets probabilities in terms of propensities and grants that propensities explain actual relative frequencies, none of these does the explanatory job in evolutionary biology. The law of large numbers does. It accounts for the fact that, in large sample limits, differences in actual reproductive success tend to differences in fitness₂. The explanation provided by the law of large numbers is not causal and, in this respect, it differs from explanations that specifically rely on propensities and the explanatory power of dispositional properties. The fact that proponents of the PIF do not need the propensity interpretation of probability shows that most discussions of the PIF should not and, as a matter of fact, do not deal with the very point of interpreting fitness as a propensity. Rather, they most generally pertain to the statistical measures used to define and evaluate fitness.

An objection to our conclusion would have it that probabilities still have to be given a propensity interpretation if fitness₂ is to be something objective, rather than mere expected credence. We agree that fitness₂ differences are legitimate scientific explanans only if fitness₂ is somewhat objective, and that this requires an objective interpretation of probabilities. Yet we do not think that this compels to propensities. First, the line of reasoning we are examining most directly justifies a propensity interpretation of the type probabilities that enter the definition of fitness₂, while the propensity interpretation of probability is usually characterized at the individual level and it is not completely clear what a propensity interpretation of type probabilities would be. Second, the propensity interpretation is not the only objective interpretation of probabilities: frequentism and, more recently, objective Bayesianism and best system analyses of chance also are. Consequently, it is false

¹⁰ Such an explanation, in any case, is not causal. Among the main kinds of explanation, inductive statistical seems to be the closest.

that fitness₂ and its value are objective only if type probabilities are given a propensity interpretation.

But, our objector may reply, frequentism and objective Bayesianism (although arguably not best system analyses of chance) do not convey the idea that probabilities are grounded on physical properties of individuals. This is true, and we also acknowledge that proponents of the PIF appeal to the propensity interpretation of probability because they want probabilities, and fitness with them, to be grounded on physical properties. But they do this explicitly only at the individual level, not at the level of types that evolutionary biology's explanations concern. Here, our objector may give a definition of type probabilities, explain what the relationship between individual and type probabilities is under this definition, and show that it is such that type probabilities cannot be objective unless individual probabilities are given a propensity interpretation. Or she may claim that (maybe for coherence sake) proponents of the PIF should also require that type probabilities depend on physical properties, construct a propensity interpretation of type probabilities, and show that this interpretation is required for type probabilities to depend on physical properties. This, however, would not alter our main claim: in evolutionary biology, what makes fitness explanations explanatory is neither the explanatory power of dispositions, nor the explanatory power of propensities with regard to frequencies—but the law of large numbers.

In conclusion, the relationship to the propensity interpretation of probability is inessential to the PIF. First, fitness is not a propensity in the sense that “propensity” has in the Popperian interpretation of singular probabilities, and the claim that fitness is a propensity can be understood only loosely. Second, the PIF's account of evolutionary biology explanations does not rely on probabilities being interpreted in terms of propensities. Consequently, interpreting the probabilistic dimension of fitness in terms of propensities is neither a strong motivation in favor of the PIF, nor a possible target for substantial criticism.

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