Putting Process and Product Conceptions of Natural Selection and Genetic Drift to the Test

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Abstract

This paper argues for two claims. First, despite a persistent appearance to the contrary in the philosophy of biology literature, the question of whether natural selection and genetic drift should be defined as processes or as the products (or outcomes) of those processes is independent of the question of whether natural selection and genetic drift are causally efficacious (the debate between the 'causalist' and 'statisticalist' interpretations of evolutionary theory). Second, there exist biological cases – cases which are quite prevalent in natural populations – that can be used to drive apart process and product notions of selection and drift, and hence which could provide evidence useful in determining which of these two classes of definitions is in line with biological practice. Two cases presented here weigh in favor of process definitions, though this does not suffice to resolve the question.

1. Introduction

One of the most common debates in contemporary philosophical literature on the foundations of evolutionary theory concerns whether natural selection and genetic drift are *causal.* This issue, in turn, has touched on several other core questions in the philosophy of biology. Are we right to describe selection, drift, mutation, migration, and so on as analogous to Newtonian forces, each of which drives a population in a given direction? If we are, which of these should be considered part of the "inertial" state (analogous to Newton's first law), and which should be considered "special" forces (analogous to Newtonian gravitation and described by the second law)? What is the role of fitness

in natural selection? If selection is causal, is fitness causal as well? Or is fitness merely a non-causal property of organisms, tallied for biological convenience?

Broadly, two positions in this debate have solidified. The "causalist" picture, canonically stated by Sober (1984), considers selection and drift to be causal processes, which in many cases can profitably be compared with Newtonian forces. The "statisticalist" interpretation, inaugurated by Walsh et al. (2002) and Matthen and Ariew (2002), disagrees. On this interpretation, selection, drift, and fitness are all non-causal, statistical summaries of the genuinely causal events that occur at other ontological levels (such as the individual, genetic, or biochemical). The analogy with Newtonian forces, the statisticalists argue, cannot be sustained, particularly in the case of genetic drift (e.g., Walsh, 2007).

A survey of the relevant articles here would constitute a paper in its own right, so let's narrow the focus to one issue commonly discussed in the context of this debate. Are natural selection and genetic drift to be defined as *processes,* or as the *products* or *outcomes* of those processes?

This question demands an answer in order to clarify our philosophical understanding of evolutionary theory, for it has bearing on several core interpretive issues. Are selection and drift objective, mind-independent features of the biological world, or are they merely useful theoretical tools – that is, should we adopt a realist interpretation of these aspects of evolutionary theory? If selection and drift are processes, this seems to lend credence to a realist interpretation, while a product conception might more readily support an anti-realist reading.[1] A process view of selection and drift also entails that there is a metaphysical story to be told about the relationship between the lower-level events which constitute selection and drift (births, deaths, matings, and the like), and the

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[1]. The correlations mentioned in this paragraph are only that – there is nothing logically inconsistent about an anti-realist process reading of selection and drift, for example. But the relationships between these positions indicates why resolving this issue is so important for our philosophical approach to evolutionary theory.

processes of selection and drift themselves (see, e.g., Shapiro and Sober, 2007). If selection and drift are outcomes, then, as Walsh has argued, "in deploying the *modern synthesis* theory of evolution we are *not* engaged in the project of articulating causes" (Walsh, 2007, p. 301), opening an interesting philosophical avenue for the study of the nature of explanations that invoke selection and drift (see, e.g., Matthen, 2009).

Finally, it is commonly held that the question of process versus product definitions of selection and drift is central to the resolution of the causalist/statisticalist debate more broadly: that is, if selection and drift are processes, then they are *causal* processes, and if they are outcomes, then selection and drift are decidedly *non-causal.* On this view, the question about process and product definitions is a proper part of the causalist/statisticalist debate.

It is this last claim that I will critique in this paper, by arguing for two theses. First, the question of whether selection and drift should be defined as processes or products stands *entirely separate* from that of whether selection and drift are causal – that is, the process/product question should *not* be considered to be a mere part of the causalist/statisticalist debate, and the mistaken belief that it is so has only obscured the issue. Second, there are *biological cases* – indeed, biological cases which are commonplace in the natural world – that can be brought to bear to help us determine which of process or product definitions of selection and drift passes the test of consistency with biological use. I will describe two such cases here, each of which offers evidence in favor of process definitions, but which are, taken together, still far from sufficient to resolve the debate. More engagement with the biological literature is required, and I hope to show one form that such engagement might take.

2. Distinguishing Process and Product Definitions

We should begin by sketching, at least in general, the difference between process and product concepts of selection and drift.[2] These are only outlines of some of the more common definitions – we will return them in more detail below. Initially, though, we might characterize these positions as follows:

> *selection (process):* a process of sampling that discriminates between individual organisms based on differences in fitness (or merely any physical or causally-relevant differences whatsoever)
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> *selection (product):* a change (result, outcome) which is predicted (or explained, or both) by differences in the fitnesses of traits
>
> *drift (process):* a process of sampling that does *not* discriminate between individual organisms
>
> *drift (product):* a change (result, outcome) which is *not* predicted (or explained, or both) by differences in the fitnesses of traits

As I mentioned above, it is often taken that these classes of definitions can be straightforwardly associated with sides in the causalist/statisticalist debate. It is not difficult to see why this would be so. The process view of selection tends, indeed, to be most often associated with the causalists. Beatty defines natural selection as "a sampling process that discriminates, in particular, on the basis of *fitness* differences" (1984, p. 190). Hodge defines it as "what is occurring when and only when there is the nonfortuitous differential reproduction of hereditary variants" (1987, p. 251). Bouchard and Rosenberg describe it as "a contingent causal process in which individual fitness differences are the causes and subsequent population differences are the results" (2004, p. 710). Millstein argues that natural selection is a process that acts on populations of organisms, on the basis of "differences in abilities to survive and reproduce" (2006, p. 643).[3]

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2. This distinction has also been laid out by (among others) Matthen and Ariew (2009) and by Millstein (2002), who describes it as a difference between process and outcome notions of selection and drift.

3. For another instance of this view, see Filler (2009, pp. 774–775).

Much the same is true of the process view of genetic drift, which is also associated with the causalists. Beatty defines drift as "indiscriminate" sampling, on which "any physical differences between the entities in question are irrelevant to whether or not they are sampled" (1984, p. 189). Millstein describes it as "an indiscriminate sampling process whereby physical differences between organisms are causally irrelevant to differences in reproductive success" (2006, p. 640). Slightly differently, Bouchard and Rosenberg define drift as occurring in cases where "the initial conditions in the divergence [are] rare, improbable, and unrepresentative of the whole population of initial conditions" (2004, p. 708).[4]

The product view of natural selection, on the other hand, is associated with the statisticalists. Walsh has defined selection in several slightly different ways, always consistent with a product-based view – as "the consequence [elsewhere, an 'effect'] of the differential rates of distinct causal processes occurring within individuals" (2000, p. 141), as that which "explains the changes in the structure of a population by appeal to differences in trait fitness" (2003, p. 289), and as "a change in population structure predicted and explained by variation in trait fitness" (2004, p. 351). Walsh, Lewens, and Ariew describe selection as what occurs "only when the relative frequency of trait types changes in a population as a consequence of differences in the average fitnesses of individuals in different trait-classes" (2002, p. 464). Matthen and Ariew describe it as "a statistical trend emerging from events that occur in these 'substrates' [chromosomes, reproductive systems, body plans, developmental sequences, etc.]" (2002, p. 68).[5]

And again, for genetic drift, we see the product view often adopted by statisticalists. Walsh defines drift as "a change in the structure of a population that is not predicted or explained by trait

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4. For more instances of this process view of drift, see Hodge (1987), Millstein et al. (2009, p. 1) and Filler (2009, pp. 774–775).
5. And yet more: see Brunnander (2006, p. 245), Walsh (2007, p. 282), Matthen (2009, p. 484), and Matthen and Ariew (2009, p. 222).

fitnesses" (2004, p. 351), and elsewhere claims that "what it is for a change in relative trait frequencies to constitute selection (or drift) is merely for it to be susceptible to a certain kind of statistical description" (2007, p. 282). Matthen argues that genetic drift is best described as the "uncertainty associated with" the "spread of possible outcomes" in a finite series of trials of a specific sort of probabilistic process (2009, p. 484).

3. The Independence of the Process vs. Product Question

As a general rule, then, we can see that causalists argue from process definitions of drift and selection, while statisticalists argue from product definitions. Why not, then, just refer to these as, respectively, the causal and statistical notions of selection and drift, and consider the process/product question to be an alternative way of phrasing the debate between causalists and statisticalists? Three arguments may be offered that such an identification would be mistaken.

3.1. Mismatched Definitions

First, one prominent definition of genetic drift adopted by some causalist authors is clearly a product-based notion, breaking the straightforward connection between causalists and process concepts. Beatty notes that one of the few things uniting all the phenomena that are standardly described as 'genetic drift' is that they all involve "one or another biological form of random or indiscriminate sampling, and consequent sampling error" (Beatty, 1992, p. 273). If genetic drift is thus simply defined *as this sampling error,* then this is clearly an outcome-based notion of drift – and it is occasionally adopted by causalist authors.[6]

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6. For example, see Glymour (2006, p. 388), Barros (2008, p. 309), or the discussion of this definition in Forber and
    Reisman (2007, pp. 622–623). A plausible explanation for the prevalence of this definition among causalist authors is

3.2. Hybrid Definitions

Second, some authors – in particular, and most prominently, Brandon – have adopted *hybrid* definitions of selection or drift that cut across the divide between process and product. While Brandon at times refers to drift as "any deviation from the expected result due to sampling error" (2005, p. 158), and several authors have interpreted him as therefore holding an outcome-based notion of genetic drift (e.g., Pfeifer, 2005, p. 1136; Gildenhuys, 2009, p. 525), his position is in fact more nuanced.[7] Immediately following the statement above connecting drift to product-level deviation from expectation, Brandon writes that "I label this approach 'outcome-oriented' to differentiate it from Millstein's [process-based definition], but notice that it does refer to a process, viz. sampling, and so here *drift is defined in terms of both process and outcome*" (Brandon, 2005, pp. 158–159, emph. added). Brandon thus aims to define drift as not merely a process, but a process that *also* generates a certain kind of product. Only when we consider both, he argues, do we correctly encapsulate the phenomena of drift.[8]

Despite adopting a hybrid definition of drift, Brandon's position on the causalist/statisticalist debate is no hybrid: he is most certainly a causalist (Brandon and Ramsey, 2007). Yet again, we have a case which challenges the connection between causalist interpretations and process definitions of selection and drift.

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that it arises as a result of the misreading of Brandon that I describe below.

7. I thank Roberta Millstein for making Brandon's view, and her opposition to it, much clearer.

8. I am not, notably, considering here the relationship of this hybrid definition to those offered in Brandon's more recent work (2006; McShea and Brandon, 2010).

3.3. Orthogonal Questions

Third, and most importantly of all, whether one accepts process or product definitions of selection and drift is *logically independent* of whether or not one takes them to be causal. These are therefore two entirely separate, orthogonal questions in the interpretation of evolutionary theory. It is worthwhile to defend this claim in some detail, as the relatively strong alignment of causal/statistical with process/product may make it rather surprising.[9]

Consider, as an exemplar of the process view of selection and drift, Hodge's indiscriminate and discriminate sampling processes, briefly defined above. Indiscriminate sampling (i.e., sampling which does not take fitness differences into account) can certainly be non-causal. Imagine shuffling a deck of cards and then spreading them out on a table in a line. After the fact, we choose the first five or last five cards, and call this a "sampling" event. Nothing about the card selection process causally impinged on the cards. Indeed, the fact that a central element of the process was entirely subjective seems to provide paradigmatic evidence for its being "non-causal" in this sense (a point that is often made by the statisticalists in the context of genetic drift). And discriminate sampling (sampling which *does* involve fitness differences) could be non-causal as well – we simply choose instead the first five red cards, or the last five black cards (making color analogous to fitness), and we have discriminate, non-causal (again, subjective) sampling.

Of course, these processes could also be causal. Spread out the same deck of cards, then fire a very large dart with a suction cup on the end at the line. Say the suction cup isn't perfectly sticky, so it grabs only eighty percent of the cards it touches. Now we have two causal processes that have, together, resulted in indiscriminate sampling – the firing of the dart gun, clearly causal, and the

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9. Some language in Walsh (2007) seems to indicate that he may have noticed this feature of these two classes of definitions, though I cannot say for certain.

precise physical details of the stickiness of the suction cup, also causal. We can make the sampling discriminate by making some of the cards stickier than others – these sticky cards are more likely to be picked up by the suction cup, so they will be overrepresented in our random sample.[10]

For the product view of natural selection, we need only consider the outcomes from the cases already considered. In the non-causal, discriminate case above, if we choose the first five red cards, then their being chosen is (partially) explained by (and would have, before-the-fact, been predicted by) the fact that the cards are red (the higher "trait fitness" of red against black). This, then, is a non-causal product view of selection. And the example of the sticky cards and dart gun is causal product-selection – the cards that are chosen are again (partially) explained and predicted by the fact that some of them are sticky (the higher "trait fitness" of sticky against non-sticky).

As a token example of the product view of genetic drift, the "sampling error" definition of drift is also amenable to both causal and non-causal analysis. We have already seen a causal example – the 80% success rate of our suction cup counts as a causal sort of sampling error. But it could be non-causal as well, in a manner noted by Brandon and Carson (1996). Let's say we spread out our deck of cards and want to select one third of them. Of course, we can't successfully grab 17 1/3 cards, so we will by necessity be off by a fraction of a card. This seems to be a paradigm case of non-causal sampling error – the "error" in our sample is merely a result of mathematics.[11]

This, then, establishes the first of our two theses. The distinction between process and product notions of genetic drift and natural selection has little to do with whether drift and selection are

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10. This example is similar to one involving colored balls in an urn developed by Brandon and Carson (1996, pp. 321–325), though they take this case as evidence that selection and drift are both causal and "stochastic" in their sense of the term. The claim that selection and drift must be causal because of this example is refuted by the analysis here. Brandon and Carson's notion of stochasticity lies outside the scope of this article.
11. Again, this case is very similar to one that Brandon and Carson (1996) describe, although the conclusion they draw from it – that genetic drift is "inevitable" in certain types of populations – only follows if one adopts their process/product hybrid definition of genetic drift. A process-only notion of genetic drift, as we have seen, might or might not be operating in such an instance.

causal or statistical and, hence, the process/product question should be viewed as an independent interpretive issue in the philosophy of biology, *not* as a proper part of the causalist/statisticalist debate.[12]

4. Getting an Empirical Handle on Process and Product

It might be thought that only *a priori* philosophical work could adjudicate the question of which class of definitions of selection and drift we should adopt. The argument would go something like this: If we've done our jobs as philosophers of biology correctly, the *extensions* of scientific concepts like natural selection and genetic drift are set by the scientists themselves – biologists, that is, are in charge of telling us which cases count as natural selection and which count as genetic drift. The *intensions* of these concepts would then vary, as philosophers work to determine the best conceptual interpretation of these scientific theories, but it is unlikely that empirical evidence could weigh strongly one way or the other.

In one sense, such an argument gets things right – in the biological literature, selection and drift are not exclusively defined in terms of either processes or products. For the case of drift in particular, Plutynski notes that "drift is spoken of interchangeably as effect and cause, pattern and process" (2007, p. 157). Further, historically, she argues that the fact "[t]hat drift is referred to as both effect and cause is not new," dating back to foundational figures like Wright and Fisher (Plutynski, 2007, p. 161). Biological practice, then, cannot resolve our issue by a mere census.

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12. In the limited context of genetic drift, Plutynski has stressed a similar point, indicting the debate over drift for conflating the "metaphysical" question of the existence of a population-level process of drift with the "epistemological" question of the relative assessment of the importance of drift and selection (Plutynski, 2007, p. 162). I agree, and argue further here that Plutynski's metaphysical question can be disentangled into two separate questions: should we adopt a process or product definition, and *further,* are drift and selection genuinely causal?

But in another, more important sense, there *is* a way in which biological practice can be brought to bear on the question of process versus product definitions of selection and drift. For while the extensions of process and product definitions are *nearly* identical, as it turns out, they are not *precisely* identical. There do exist cases, then, where the extensions can be driven apart – and to this extent, biological evidence can be made relevant. Let's consider this, in turn, in conceptual terms and by invoking examples.

4.1. The Abstract: Differing Extensions

First, then, let's explore in more detail some of the process and product definitions on offer in the literature, with an eye toward describing places where their extension can be seen to come apart in the abstract.[13] One strange feature of the argument in this section should be noted at the outset. We are focusing here on the definitions of selection and drift deployed by both process and product advocates in the debate – *not* on whether selection and drift should be conceived of as causes, for reasons discussed in the last section. Thus, I will, for the moment, drop all reference to the causal or non-causal character of these processes or products.[14]

Further, in what follows I will only introduce one process definition and one product definition of each of natural selection and genetic drift. There are, however, more than only these four definitions found in the philosophical literature. Natural selection has at least one more process definition on offer,[15] and I am aware of at least two other process definitions of genetic drift[16] and one other

13. If the reader is interested in cutting to the empirical chase, he or she may skip to section 4.2.
14. Relatedly, it is important to note that when I use the term 'process' in the following, I do *not* mean to imply that such a process is causal – I intend only to refer to something like a temporally ordered sequence of states of a system. Salmon, for example, notes that 'process' in this broad sense "can reasonably be regarded as a primitive concept that can be made sufficiently clear in terms of examples and informal descriptions" (1994, p. 297).
15. Ramsey (2012) gestures at this view, which has yet to be described in detail; it ascribes natural selection to a probability distribution over the possible paths of an evolving system, and is intended to be interpreted causally.
16. Bouchard and Rosenberg (2004) define genetic drift as a population's initial conditions being unrepresentative of the full space of possible initial conditions, which is a property of the processes responsible for genetic drift. Gildenhuys

product definition.[17] The important fact for us, however, is that process and product definitions *can* be extensionally separated from one another, and that they can be so separated using plausible, even commonplace, biological examples. Extending this analysis to further definitions of selection and drift is a project for future work.

Case 1: Genetic Drift and Indiscriminate Sampling Processes.   A tradition in process definitions of genetic drift, beginning with Hodge (1987; see also Beatty, 1984; Millstein, 2006), defines drift as an *indiscriminate sampling process* – sampling that does not discriminate based on fitness differences. The most common product definition of drift, on the other hand, defines drift as *any change in a population that cannot be predicted or explained by variation in fitness* (Walsh, 2004, 2007; Matthen, 2009).

It is clear that, as expected, these two definitions will be extensionally equivalent in almost all cases. Any process that does not discriminate on the basis of fitness differences (satisfying this process definition of drift) will produce outcomes that do not need to be explained by reference to fitness differences (satisfying this product definition). And if we have a change in a population that does not require any reference to fitness differences for its explanation, then it is reasonable to assume that this change was the result of some process (in the minimal sense described in footnote 14) that itself does not take fitness differences into account. But the precise details are made more complicated by the details of this product definition of drift, primarily because it requires us to demonstrate a negative – that the change at work *cannot* be explained by reference to trait fitness differences.

As Millstein points out, "an indiscriminate sampling process can produce what looks like a

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(2009) proposes a definition of NINPICs, a precise class of causal influences which he claims includes all and only those causes responsible for genetic drift.

17. As mentioned above, genetic drift is occasionally defined as any outcome which deviates from the outcome that we expected to obtain (see Glymour, 2006; Barros, 2008).

directed outcome (mimicking the most likely outcomes of a discriminate sampling process)" (2005, p. 172). That is, it is possible that a population which is actually being altered by a process which does *not* take fitness differences into account (i.e., which is undergoing genetic drift according to the process definition) produces the same result that would have been expected were offspring produced according to fitness differences (i.e., it is *not* undergoing genetic drift according to the product definition). The product definition, then, might well lead us to infer that it was natural selection that was responsible for the population change at issue. Walsh has precisely this characteristic in mind when he notes that "[i]t is an unfortunate consequence of [the conjunction of these two definitions] that drift-the-process [drift as indiscriminate sampling] causes selection-the-effect [the absence of drift as outcomes not explained by trait fitness]" (Walsh, 2010, p. 154).[18]

At a more general level, consider what it would take to prove that these two definitions of genetic drift were extensionally equivalent. We take as a premise that a population has undergone a change which cannot be explained or predicted by reference to fitness differences. But how can we really infer further that the process responsible for that change did not discriminate at all with respect to fitness differences? Perhaps the process has fitness differences as a core feature, but combines these with a substantial stochastic element, altering the results significantly enough that the best *explanation* of the change no longer requires any reference to those fitness differences. Following van Fraassen's (1977) seminal work on the pragmatic dimensions of explanation, most philosophers of science argue that explanations have a subjective element that the existence or non-existence of causal processes does not. In such a case, we would have drift in the sense of this product definition without drift in the sense of the process definition, a failure of extensional equivalence. In the next

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18. Notably, no author in this debate simultaneously accepts both a product definition of selection and a process definition of drift, so it is not clear who is the target of Walsh's argument.

section, we will see a biological example of precisely this kind of case.

Case 2: Process and Product Definitions of Natural Selection.   Turn now to natural selection. On the process side, natural selection has often been defined as a *process that discriminates between organisms based upon differences in their fitness values* (Hodge, 1987; Beatty, 1984; Millstein, 2006). On the product side, it is *any change in a population that can be explained by variation in fitness* (Walsh, 2004, 2007; Matthen, 2009).

As in the case of the two definitions of drift that we considered above, these two definitions will be extensionally equivalent in almost all cases – processes that discriminate based on fitness will require reference to fitness differences for their explanation. But, once again, there is the possibility for a failure of equivalence introduced by the requirement not just that the process at issue is *acting* on a population, but that the *net population change* be identical with that expected on the basis of trait fitness values. As emphasized by Shapiro and Sober (2007, pp. 254–255), any population in which a fitness-discriminating process is acting but which fails to produce the appropriate outcome will, then, exhibit natural-selection-the-process without natural-selection-the-product. Again, in the next section, we will see an instance of exactly such a real-world example.

4.2. The Concrete: Biological Case Studies

One might think that these theoretical cases in which the extensions of process and product definitions of drift differ are, in some sense, marginal. They lie at the fringes of our conceptual space as philosophers of biology, and require precise circumstances in which the various factors of evolution take on precise values or produce very specific outcomes. It turns out, however, that there is nothing at all marginal about such cases. We can find empirical examples of both of these kinds of cases –

and not merely examples of unusual circumstances, but instances that are highly prevalent in natural populations. This means that it will be, at the very least, not at all difficult to find empirical evidence which could help us determine whether process or product definitions are more in concert with biological practice.

Case 1: Fluctuating Selection.   Begin with the first conceptual example mentioned above, on which genetic drift qua indiscriminate sampling process classifies cases differently from genetic drift qua outcomes which can neither be explained nor predicted by differences in trait fitness.

One important open biological area of study invokes precisely this kind of case: fluctuating selection.[19] To take just one instance of the importance of fluctuating selection, Arnold et al. (2001) discuss its role in the connection between the processes of microevolution and macroevolution. The relative stability and homogeneity of selection coefficients is, they note, "a convenient simplifying assumption that can greatly facilitate theoretical work and data analysis," but this assumption likely does not hold for all kinds of traits. Life-history traits, in particular, are likely to "experience strong selection that can fluctuate with nearly any kind of ecological change" (Arnold et al., 2001, p. 21). Notice how prevalent this means that fluctuating selection is. Life-history traits are crucial to an organism's evolution, and include such features as brood or clutch size, the size of young at birth, age at reproduction, investment of child-rearing effort, and the variance of all such traits in future generations (Stearns, 1976; Mayo, 1980). To say that all traits such as these experience fluctuating selection is to recognize it as an incredibly important influence throughout evolving populations. Indeed, Bell even argues that, as a rule in *all* open populations, "selection is generally rather strong and fluctuates on all time-scales such that abrupt changes can occur over short periods of time and

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19. My thanks to Roberta Millstein for bringing this example to my attention.

gradual directional change occurs over long periods of time" (2010, p. 90; see also Leroi, 2000).[20]

Let's return to the connection between fluctuating selection and our two definitions of genetic drift. Arnold et al. (2001) argue that life-history traits have something like the following selective structure. First, their adaptive landscape is almost entirely directional – that is, it is flat and sloped in a single direction, as there is a uniform fitness advantage to producing more offspring at an earlier age. The lack of curvature on such an adaptive landscape means that there is no stability to be found, no local optima at which a population may find some resistance to small perturbations. This entails, secondly, that changes in these traits' distribution will be incredibly sensitive to the current direction of selection pressure. Third, because selection for these traits fluctuates dramatically according to current ecological or environmental conditions, that direction of selective pressure will vary quite dramatically over both space and time.

Any trait that behaves in this way constitutes an example of the sort of evolutionary change that distinguishes our process and product notions of genetic drift. Because the fitness landscape is relatively flat and slopes uniformly in a single direction, there is precisely *one* change in the population that would be predicted by consulting present differences in trait fitness. Any change other than this which does occur (and we have reason, based on the fluctuation in ecological parameters, to think that such change will be frequent) will be described as genetic drift by the product definition. But according to the process definition, this is most emphatically not genetic drift at all – even though environmental conditions fluctuate wildly over time, these are selective processes which *do* take fitness into account. The evolution of life-history traits under fluctuating selection therefore constitutes a case which is (almost always) counted as genetic drift under a product definition, and is

20. For a historically and philosophically sophisticated discussion of one of the founding empirical examples of fluctuating selection, see Millstein (2008).

not counted as genetic drift under a process definition. If we are to take the injunction of the biologist seriously that this constitutes an instance of natural selection, then the product account seems to pass the test, providing the solution for these kinds of empirical examples that lines up with biological practice.

One objection could be raised here on behalf of the product conception of drift, and is worthy of consideration in more detail. The discussion so far hasn't considered the time-scale at which descriptions of selection and drift should be deployed. Selection may well fluctuate enough to "look like" genetic drift over short time periods, but in the long run, as Bell noted above, it is plausible that change in the general direction of the slope of the adaptive landscape will be realized, and hence, over those longer time scales, product definitions will delineate selection and drift in line with empirical practice.

It may well be the case that a change in time-scale provides the product theorist with one way in which to respond to these cases of fluctuating selection. But as many proponents of the product definition of drift have been quick to point out, we should not think that there is a single correct choice of time-scale or context for descriptions of selection and drift – this choice should be set, at least in part, by explanatory context (Walsh et al., 2002, p. 466). If this is true, then it is clearly a virtue of process definitions that they align with practice over *both* short- and long-term explanations of evolutionary change. It seems difficult to establish a motivation for declaring the long-term explanation to be the preferred one, as would be required to support product definitions of selection and drift.

Case 2: Evolutionary Balancing Acts. Another important set of examples are those in which process and product definitions are forced apart by precise cases of evolutionary balance. One

example, as mentioned in the last section, are circumstances in which processes which are sensitive to fitness differences (and constitute natural selection according to a process definition) do not change the population outcome, and hence fail to produce natural selection on a product definition. For genetic drift, we might consider cases in which one of the indiscriminate sampling processes implicated in the product definition of genetic drift considered above are acting, but the action of those processes *fails* to change the population outcomes from the expected result (i.e., fails to produce genetic drift as product).

One obvious source of real-world examples of this sort can be found in mutation-selection balance, originally described by Fisher (1922) and Haldane (1927). If the mutation rate is sufficiently high, even quite deleterious alleles may be retained in a population, as mutation reintroduces them faster than they can be effectively be removed by natural selection. While it is a commonplace to claim that most mutations are deleterious, the extent to which this is true is surprising – Sawyer et al. (2007) report that ≈95% of non-synonymous mutations in 91 genes of *Drosophila melanogaster* are deleterious. It is thus clear that the impact of these deleterious changes on the evolutionary process constitutes an important evolutionary influence – albeit one that is difficult to estimate in natural populations (Mitchell-Olds et al., 2007, pp. 853–854).

One particular case where a detailed argument may be marshaled, however, is that of the persistence in human populations of genetic predispositions for mental illnesses that are both highly heritable and extremely harmful. Keller and Miller (2006) collate data concerning the fitness costs of possessing such mutations, the correlation of such mental illnesses with parental age, inbreeding, and other risk factors for mutation, and the estimated frequency of such alleles in the population, and conclude on this basis that the only adequate explanation is that such alleles are maintained

under (multiple-gene) mutation-selection balance.[21] Schizophrenia, for example, is prevalent at a rate of 1,000 individuals per 100,000 in the population, and has a high heritability value ($h^2 \approx .80$) – that is, around 80% of observed variation in schizophrenia seems to trace to genetic differences.

Why is mutation-selection balance interesting for us here? If such a balance holds for a given allele, the common way of describing the scenario goes something like this. We have no change over time in the frequency of the allele – hence, according to the product definition of selection, no natural selection is acting. But when biologists argue that there is a *strong* influence of natural selection against such mutations (e.g., strong selection against schizophrenia in humans), they seem to mean that there are processes in place that are strongly influenced by the low fitness of these alleles – that is, that there is quite substantial natural selection in the sense of the process definition. Mutation-selection balance, therefore, is both a significant influence in plausible empirical cases, and constitutes an example in which these two definitions offer different characterizations of natural selection. Once again, if we are to take biologists seriously in their claims that mutation-selection balance does indeed involve natural selection, we have empirical cases that weigh in favor of the process definition of natural selection.

I have offered here only two examples of real-world cases that underline the difference between these various definitions, and these only briefly – more can (and should) doubtless be found. But it is precisely in instances such as these, I claim, that profitable engagement with the biological literature can move this debate forward. In both cases, these empirical results support process over product definitions of selection and drift.

Further, one characteristic of these two examples should strike philosophers of biology as

21. Mitchell-Olds et al. (2007, p. 853) argue, however, that some (though not extensive) data available from natural populations of *Drosophila* and the common monkey-flower, *Mimulus guttatus,* are *not* compatible with simplistic mutation-selection balance models, and that more complex models of the influence of deleterious alleles need to be developed. The empirical question thus remains open.

troubling. As I mentioned above, these examples seem "marginal" with respect to the conceptual space of our current definitions of selection and drift – they seem to require precise kinds of conditions that would only be satisfiable in a small fraction of logically possible evolving systems. But as it turns out, such cases are incredibly prevalent empirically. Fluctuating selection is a vitally important evolutionary influence, and mutation-selection balance is also likely to play a major role, though the extent of its impact is more difficult to estimate. Considerations of length prevent me from pursuing this line of thought here, but it is worth noting that this disconnect between the structure of our conceptual space and the distribution of real-world empirical cases – i.e., cases which are conceptually marginal but empirically common – may well indicate trouble with our overall understanding of selection and drift.

5. Conclusions

I hope to have established two claims in this article. First, the question of whether natural selection and genetic drift should be defined as processes or products is an independent research question worthy of more intense scrutiny. While it is clearly affiliated with the debate between causalists and statisticalists, it is not a proper part of that debate (as it has been treated in the literature).

Second, and more importantly, there are a host of quite common empirical cases that can help us discriminate between process and product definitions. In both cases that I have described here, if we are to take seriously the biologist's delineation of cases of selection and drift, then these cases weigh in favor of definitions that make reference to the processes responsible for selection and drift – whether those are exclusively process-based or hybrid definitions. For such an analysis to

be conclusive, more examples need to be found and evaluated, and we cannot therefore declare the issue closed here. But the evidence in favor of process definitions is strong.

Regardless of the end result of an appraisal of these empirical cases, however, it is clear that the focus on the standard formulation of the causalist/statisticalist debate has served to obscure discussion of the proper definitions of selection and drift. This is unfortunate for a variety of reasons. If biological evidence can be applied to the process/product question, then this marks an important difference with the more metaphysically oriented questions concerning theories of causation often broached in the causalist/statisticalist debate. And finally, work toward a resolution of the process/product issue on its own merits might provide the impetus needed to advance the otherwise seemingly intractable debate on the causal potency of fitness, selection, and drift.

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