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Selection vs. Drift: A Response to Brandon's Reply

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Introduction

Due to constraints on space, I will not spend time on 'exegetical matters' except to say that I believe that I made no substantial misrepresentations of Brandon and Carson's (1996) conceptions of drift and selection. Brandon's current clarification of his position is: *'Drift is any deviation from the expected levels of reproduction due to sampling error'* whereas *'Selection is differential reproduction that is due to (and in accord with) expected differences in reproductive success'* (this issue; emphasis in original). This position is implicit in Brandon and Carson (1996), as Brandon notes. I characterized their position as follows: 'natural selection is a process whereby organisms achieve their expected reproductive success (based on their fitness in a given environment), random drift is a process which probabilistic ally deviates the population from those expectations' (2002, p. 48).

It is this position that generates the genuine philosophical disagreement between Brandon and myself. In contrast, I argue that selection is a discriminate sampling process in which physical differences between organisms are causally relevant to differences in reproductive success, whereas random drift is an indiscriminate sampling process in which physical differences between organisms are causally *irrelevant* to differences in reproductive success (a position derived from Beatty 1984 and very much in sympathy with Hodge 1987). My definitions of drift and selection are, in Brandon's terms, 'purely process-oriented,' whereas his own definitions include outcome as well as process. One of my motivations for these purely process-oriented definitions is that an indiscriminate sampling process can produce what looks like a directed outcome (mimicking the most likely outcome of a discriminate sampling process). On the other hand, a discriminate sampling process can produce little or no change, or change in different directions if the environment is fluctuating (mimicking the most likely outcomes of an indiscriminate sampling process). This, I argued, could lead to confusion unless one were careful to distinguish process from outcome (2002, pp. 39-50).

The difference in our positions will result in our labeling certain cases differently. It is my impression that, in biological studies, observed frequencies seldom match expected frequencies. Let's assume that in a particular case these deviations from expectation are not due to a miscalculation of fitness values. If

the deviation from fitness expectations is due to the 'sampling error' of a finite population and not to indeterministic processes, Brandon would attribute the deviation to drift. I, on the other hand, would label the deviations from expectations as drift if and only if there were no physical differences that were causally relevant to the change in frequency. If there were causally relevant physical differences, then I would attribute the change to selection.

Response to criticisms

Brandon states that my view is a 'non-starter.' I identify the following three objections to my position in Brandon's reply: (1) it 'does not map well onto the ways biologists differentiate drift from selection;' (2) selection and drift are the same process - sampling; and (3) the large majority of biological cases are not cases of indiscriminate sampling. I will respond to each of these criticisms in turn.

1.

Brandon's first criticism is that my definitions are not consistent with the way these terms are used by biologists, in spite of my argument (2002, pp. 4445) that my definitions make sense of studies such as Grant and Grant's (1989). The quote cited above, stating that my definitions do not map well onto those of biologists, is immediately followed by an abstract discussion of sampling balls from an urn rather than an actual biological example. More to the point, in a footnote, Brandon states that his definition of drift is consistent with textbooks such as Roughgarden's. I do not deny that biologists (and philosophers) sometimes use definitions close to those of Brandon's. Rather, my claim was that biologists and philosophers also sometimes use the definitions that I identify, leading to confusion when one changes between the different sets of definitions (2002, pp. 39-50).1

I also claim that the definitions that I endorse make better sense of the neutralist/selectionist debate (2002, pp. 50-51). (Brandon correctly identifies making sense of the debate as my primary motivation and says that he shares this motivation as well). That is, my definitions make better sense of biologists' attempts to determine whether, for example, 'the great majority of evolutionary mutant substitutions at the molecular level are caused by random fixation through sampling drift, of selectively neutral (i.e., selectively equivalent) mutants under continued mutation pressure' (Kimura 1991, p. 5956). To a large extent, the debate between neutralists and selectionists is couched in terms of the prevalence of drift vs. the prevalence of selection in just the way that I have specified; the concern is whether variants are 'neutral' or

1 Robert Skipper has suggested to me (personal communication) that the situation with regard to the concept of 'drift' may be analogous to the situation with regard to the concept of 'gene' with different usages for different circumstances.

not (i.e., causally irrelevant to differences in reproductive success or not), not over the extent of deviation from expectation.

2.

Brandon's second criticism is that selection and drift are the same process - sampling. Brandon further elaborates on this claim by arguing that there is no qualitative difference between discriminate and indiscriminate sampling, only a quantitative one. With respect to Brandon's urn examples 1 and 3, Brandon states that 'Both setups will regularly lead to *results* that deviate from the expectation; the difference between them is quantitative, not qualitative' (this issue; emphasis added). My claim was that the *processes* of indiscriminate and discriminate sampling are distinct, not that the *outcomes* (i.e., the results) of discriminate and indiscriminate sample are distinct (2002, pp. 42-46). It is true that using outcome-oriented definitions, the differences look purely quantitative (in Brandon's example 1, approximately 37% of the outcomes will achieve the expected result in the long run, whereas in example 3, approximately 42% of the outcomes will achieve the expected result in the long run); but, as discussed above, my definitions are purely process-oriented, excluding outcome entirely. So, it would appear that Brandon's claim that there is no qualitative difference between discriminate and indiscriminate sampling is achieved by begging the question against me.

Brandon's claim is puzzling in light of his assertion that 'distributions of MPD are qualitatively distinct with respect to drift' because 'drift *cannot* occur with such a distribution' (this issue). Under my definition of drift, *selection* cannot occur; there are physical differences, but no fitness differences, for selection to act on. There seems to be no reason why the one case should count as a qualitative difference between selection and drift but not the other.

Moreover, the case can easily be made for a qualitative difference between discriminate and indiscriminate sampling. There is a qualitative difference between a population of finches under 'typical' conditions in which 'adult survival was generally unrelated to phenotype' (Grant and Grant 1989, p. 218) and a population of finches under post-EI Nino conditions in which 'presumed mortality' was 'nonrandom with respect to phenotype' and 'relatively longbilled birds were at a selective disadvantage' due to the absence of their favored food (Grant and Grant 1989, p. 221). Or, to use Brandon's hypothetical urn example, there is a qualitative difference between choosing where all balls have an equal chance of being picked because all are equally smooth and choosing where some balls are easier to pick than others because some are stickier.

3.

Brandon's third objection is that:

> From a mathematical point of view, the equiprobable distribution and the finite set of MPD distributions represent an infinitesimally small fraction of the possible probability distributions. Were we to categorize sampling with an equiprobable distribution as drift and sampling with an MPD distribution as selection, we would be leaving all but an infinitesimally small fraction of cases uncategorized. Biologically things are probably worse still for this sort of strategy. Has any real biological

> population in the history of life on Earth ever realized one of these two extremes? I will not pretend to know the answer to that question, but I would not be surprised if it were no (this issue).

I do not discuss MPD distributions in my article and I share Brandon's intuition that there are probably no such populations in nature. However, evidence does exist for 'equiprobable distributions' in nature (to use Brandon's phrase). Certainly many biologists think that they have demonstrated, for example, molecular differences that have no phenotypic effect. As Kimura notes, 'The first definitive evidence supporting the neutral theory was the discovery that synonymous base substitutions, which do not cause amino-acid changes, almost always occur at much higher rate than nonsynonymous - that is, amino-acid altering - substitutions' (1991, p. 5970). Of course, these claims can be controversial - perhaps there is a selective difference between variants that we are unaware of - and that is why there is a neutralist/selectionist debate.

On Brandon's view, there is nothing to debate (he suspects there are no 'equiprobable distributions'), yet he says that he wants to do justice to the neutralist/selectionist debate. More to the point, my article and Brandon's reply address whether or not the *concepts* of drift and selection are distinct. If it were to turn out that the concept of drift has no applications in the real world, there would be no impact on the clarity of the two concepts. The criticism misses its mark.

Conclusion

In sum, Brandon's three criticisms fail to overturn my position, and his own definitions do not do justice to the neutralist/selectionist debate. Nonetheless, Brandon's definitions are a viable alternative to my own. Moreover, he makes explicit and mounts a defense of definitions that are implicit in some biological and philosophical literature. The problem is that more than one set of definitions are implicit, and that has led to confusion. Given the prevalence of his definitions. I do not pretend to think that I can change the way that people use the terms 'drift' and 'selection.' Rather, I hope only that they are more careful when they do so.

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