Synthese (2013) 190:3909–3928
DOI 10.1007/s11229-012-0232-6

Driftability

Grant Ramsey

Received: 30 May 2012 / Accepted: 3 December 2012 / Published online: 14 December 2012

Abstract In this paper, I argue (contra some recent philosophical work) that an objective distinction between natural selection and drift *can* be drawn. I draw this distinction by conceiving of drift, in the most fundamental sense, as an individual-level phenomenon. This goes against some other attempts to distinguish selection from drift, which have argued either that drift is a population-level *process* or that it is a population-level *product*. Instead of identifying drift with population-level features, the account introduced here can explain these population-level features based on a property that I label driftability. Additionally, this account shows that biology's "first law"—the Principle of Drift (Brandon, J Phil 102(7):319–335 2006)—is not a foundational law, but is a consequence of driftability.

Keywords Drift · Fitness · Selection · Evolution · Population · Individual

1 Introduction

There is a heated debate amongst philosophers over whether central notions in the theory of evolution by natural selection—fitness, selection, and drift—can be given a coherent causal construal; whether, that is, it can ever justifiably be said that a population's evolution was *caused by selection* or *caused by drift*. The positions in this debate vary from Matthen and Ariew (2002), who argue that drift and selection cannot be distinguished (either as distinct processes or as distinct outcomes) and that neither is a cause of evolution, to Brandon (2006), who not only holds that drift and selection are

G. Ramsey (✉)
Department of Philosophy, University of Notre Dame, 100 Malloy Hall, Notre Dame,
IN 46556-4619, USA
e-mail: grant.ramsey@nd.edu
URL: http://www.grantramsey.com

conceptually distinct, but argues that drift is a fundamental law of biology, biology's first law. Among those who argue for a distinction between drift and selection, there is no univocal view on how this distinction can be made. Some (e.g., Brandon 2005) argue that the distinction should be made in terms of evolutionary *outcomes*, while others (e.g., Millstein 2002) argue that the distinction instead should be made in terms of *causal processes*.[1] One thing that unites these accounts is that drift is taken to be a strictly population-level phenomenon. In what follows, I will argue against this received view of drift. I will make the case that drift in the most fundamental sense is an individual-level phenomenon, which I will label *driftability*. Driftability, as we will see below, allows us to understand the drift-as-cause and drift-as-effect distinction, paralleling the classic distinction between selection and the evolutionary response to selection (see Haldane 1954). Locating drift at the individual level provides a way of causally explaining the population-level phenomena often equated with drift, as well as providing a foundation for biology's first law, the Principle of Drift (Brandon 2006), and McShea and Brandon's (2010) related zero-force evolutionary law.

2 The case against drift

In his 1994 book, Rosenberg argues that drift is not only not a process or force in evolutionary change, it is not even an objective feature of evolution. Drift enters the stage only when we are ignorant of the causes of this change. He holds[2] that "evolutionary phenomena are…deterministic, or at least as deterministic as underlying quantum indeterminism will allow" (p. 82), and in the absence of indeterminism, there is no drift. Matthen and Ariew (2002) take a similar position, though their motivation and arguments differ significantly from Rosenberg. For Matthen and Ariew, fitness is "a statistical measure of evolutionary change" (p. 56) and "natural selection is not a process driven by various evolutionary factors taken as forces; rather, it is a statistical 'trend"' (p. 57). Similarly, drift is not a cause of evolutionary change: "Suppose that over a period of time a population stays exactly the same, or changes in some determinate way. The proposition that drift was involved to degree p in this history generally has no determinate truth value" (p. 65). Furthermore, "there is, in general, no objective, as opposed to epistemic, apportioning of causal responsibility to selection as against drift in a concrete evolutionary history" (p. 68). This final quote shows their allegiance with Rosenberg's position. In historical reconstructions of evolutionary scenarios, drift

---

[1] These do not exhaust the possibilities. For example, Bouchard and Rosenberg (2004) place drift in the initial conditions, "drift—the departure of these initial conditions from equality in proportion among all physically possible initial conditions" (p. 352); Pfeifer (2005) understands drift to be both a cause of evolution and a result of ignoring or abstracting environmental features; Abrams (2007) takes (one kind of) drift to be understood in terms of the properties of population-level probability distributions: "Natural selection is the aspect of the distribution which is under the control of fitness differences, and drift is the aspect of the distribution which is under the control of population size" (p. 677). I do not have the space in this essay to challenge all of these and other positions. It should be clear in what follows, however, that the position argued for here is not identical to any of these positions.

[2] This view, it should be noted, is not one Rosenberg currently holds.

arises only from ignorance—it is a property of our knowledge (or lack thereof) of the world, not an objective property of the world.[3]

But to hold that drift consists in ignorance is to give up on the idea that drift occurs independently of our epistemic state, and it is difficult to reconcile with our knowledge of population dynamics: It is not just that our ideas about drift are undermined by understanding drift in terms of ignorance, it seems that they violate empirical observations. Biologists have long observed that populations will undergo change in the frequency and distribution of its traits in the absence of selection, migration, or mutation, and that this change (which is an instance of drift-as-effect) tends to occur more rapidly and more frequently in smaller populations. This seems difficult to reconcile with the epistemic view of drift, since more, not less, is generally known about small populations. In an attempt to make sense of these observations, I will argue here that not only can selection and drift be distinguished from each other as objective features of the world, drift-as-cause is properly understood at the level of the individual organism. To motivate this argument, let's first examine the ways in which others have attempted to mark the selection-drift distinction.

3 Drift: process or product?

Evolution by natural selection clearly *seems* to be a process. And so, it appears, is drift. Millstein (2002) has thus attempted to distinguish selection and drift as two kinds of processes. Millstein follows Beatty (1984) in distinguishing *discriminate sampling* from *indiscriminate sampling*. Although there are many kinds of sampling, Millstein focuses on parent sampling, which Beatty defines as "*the process of determining which organisms of one generation will be parents of the next, and how many offspring each parent will have*" (1984, p. 188, italics in the original). Millstein illustrates this distinction with an example of gray and brown varieties of squirrels. She posits that the two squirrel morphs are equally fit, i.e., being gray or brown acts neither as a hindrance nor as a benefit in procuring food, avoiding predators, etc. If it happens, then, that more brown squirrels have offspring (i.e., are sampled) than the gray ones, this difference in squirrel type reproduction will be indiscriminate with respect to the features of the squirrel type: "the physical differences between the two types of squirrels do not play a *causal* role in the differences in reproductive success" (Millstein 2002, p. 35, italics in the original). Discriminate sampling, on the other hand, is sampling "with regard to fitness differences" (p. 39). Under this account, drift is identified with indiscriminate sampling and selection is identified with discriminate sampling.

Although identifying selection with discriminate sampling and drift with indiscriminate sampling appears to be a very elegant way of making this distinction, there are a number of difficulties with this account. As Brandon (2005) points out, in any real example, organisms of one type will almost always bear at least a small fitness difference from those of the other type. Indiscriminate sampling, then, represents an endpoint on a continuum ranging from fully-discriminate to fully-indiscriminate

---

[3] They note that while this is true of historical reconstructions, such is not the case for "evolutionary *theory*, which abstracts away from individual causes" (2002, p. 64).

sampling. Selection is necessary and drift impossible at one end of this continuum, and drift is possible at all other points.[4] If Brandon is right, then drift can occur *along with* (and not exclusively in the absence of) discriminate sampling. For Brandon, “there is a single process, sampling” (2005, p. 167)—and any attempt to draw a distinction between discriminate and indiscriminate sampling that corresponds with the drift-selection distinction will fail.

If drift as indiscriminate sampling is problematic, what alternative does Brandon suggest? Brandon argues that the solution is to understand drift in terms of *outcomes*, not *processes*. For Brandon, “*drift is any deviation from the expected result due to sampling error*” (2005, p. 158, italics in the original).[5] For him, fitness values provide us with expectations of what will occur and drift is deviation from these expectations. This approach bears a resemblance to the view of drift argued for by Walsh, Lewens, and Ariew (2002).[6] They argue that “[d]rift is manifested as a difference from the outcome predicted by the fitnesses in the population […] Drift, in any of its forms, is a statistical property of an ensemble of trials or events: *drift is statistical error*. A series of births, survivals, deaths, and reproductions manifests drift just if the outcome—measured as changes in trait frequencies—diverges from that predicted by differences in fitness” (459, italics in the original). Under this statistical error account, drift is only a property of ensembles, not individuals, and is an outcome, not a kind of process or force.

There are two problems with considering drift to be only a population-level deviation from prediction. First, it leaves unanswered the question *what, fundamentally is the source of drift?* Without answering this question, it is difficult to know how to answer Rosenberg’s (1994) assertion that drift consists in ignorance. Drift as deviation from prediction (the position of Walsh et al. (2002)) fails to answer Rosenberg’s challenge because if drift is a difference from *predictions*, this difference could be due to the fact that the predictions do not take into account all of the details of the population under consideration (predictions can fail, that is, for epistemic reasons). And if drift is deviation from mathematical expectation,[7] then, again, a fundamental understanding of drift requires one to give an account of the source(s) of this deviation.

The second problem is that even those who define drift in terms of outcomes often end up at least implicitly endorsing a causal concept of drift. Brandon, for example, speaks of the “effects” of drift: “Everything else being equal, the greater the selection differentials, the smaller the expected *effect of drift*” (2005, p. 159, italics added). Similarly, Brandon and Nijhout (2006) note that “[o]nce *drift moves the population* sufficiently, selection will tend to move it back toward equilibrium” (p. 280, italics

---

[4] See Fig. 1 from Brandon (2005, p. 162).

[5] See also Brandon and Carson (1996).

[6] Though the positions of Brandon and Walsh et al. differ quite radically in other ways, such as their characterization of natural selection and fitness.

[7] Deviation from *mathematical expectation* should be sharply distinguished from deviation from *prediction*. Brandon identifies drift with the former, but others, like Walsh et al. (2002) fail to sharply distinguish between prediction and expectation—as their quote at the end of the previous paragraph evinces, they cash out statistical error in terms of predictions in some places, but they also base drift on deviations from expectation in other places, e.g., “because the outcome diverges somewhat from expectation, there is drift too” (p. 464).

added). Those who identify drift as an effect, while nonetheless speaking of the *effects of drift*, are using 'drift' in a polysemous manner: drift in one sense of the term is an outcome, but in another is a cause of this outcome. I will maintain that drift-as-cause and drift-as-effect are coherent and related concepts—neither should be discarded. Instead, I argue that we should sharply distinguish between them and provide an account of how the former brings about the latter. In maintaining this sharp distinction, I will henceforth use 'drift_c' for drift-as-cause and 'drift_o' for drift-as-outcome. The view of drift_c that I will be arguing for, as mentioned in the introduction, will be labeled 'driftability'.

In what follows, I will argue against both of the central claims of the statistical error account, i.e., that drift is only a property of ensembles, not individuals, and that it is merely an outcome, not a kind of process or cause. I will argue for the conclusion that drift_o is an evolutionary response to driftability. Driftability can bring about a deviation from expectation, but is not itself identical to this deviation. But before this argument can be made, we first need to be clear on the nature of fitness and natural selection.

4 The nature of fitness and selection

Just as there are multiple possible outcomes that a particular kind of coin might realize when flipped in some coin-flipping device (landing heads or tails, say), there are multiple possible outcomes that a particular kind of organism might realize when it interacts with some environment (producing many or few offspring, dying young or old). This point is not controversial and has long been recognized. Darwin made it repeatedly—he argued, for example, that "if any slight innate change of habit or of structure benefited an individual wolf, it would have the *best chance of surviving and of leaving offspring*" (1859, p. 91, italics added). A change of habit does not (directly) increase the number of offspring an individual produces. Instead, it increases the *chance* of producing offspring. There is a strong theoretical motivation for not equating fitness and actual reproductive output. Biologists and philosophers alike (e.g., Ariew and Ernst 2009; Krimbas 2004) generally hold that citing the greater fitness of type A individuals can help explain why the As outcompeted the Bs. For these explanations to be possible (i.e., for fitness to play some role in explaining evolutionary outcomes), fitness must not be identical with (or be a mere function of) these actual outcomes.

If fitness is not identified with actual outcomes, what is it to be identified with? Brandon (1978) and Mills and Beatty (1979) introduced the *propensity interpretation of fitness* in order to answer this question. They hold that fitness should be understood as a probabilistic propensity to produce offspring. This propensity can help explain evolutionary outcomes and seems to be the implicit idea behind (at least some of) Darwin's (1859) evocations of "chance." Furthermore, many contemporary biologists have adopted the propensity interpretation of fitness. For example, Wagner (2010) argues that "[a]n important step in the conceptual clarification of the fitness concept was the realization that fitness refers to a propensity (i.e., a potential ability) of an individual to leave offspring rather than the actual number of offspring produced"

(p. 1359). And as biologists McGraw and Caswell argue, "[t]he resolution of the paradox that fitness is the 'population growth rate of the individual' requires the philosophical basis provided by the propensity fitness concept combined with classical demographic tools" (1996, p. 49). Although there is a considerable controversy surrounding attempts to specify the nature of this propensity (see Beatty and Finsen 1989; Sober 2001; Pence and Ramsey *forthcoming*), these debates will not concern us here. All that is needed is the rather weak claim that there is more than one way that an individual of a particular type in a particular environment can live its life.[8] Let's now draw out the implications of this claim.

Consider an organism O with genome G in environment E. Assuming that O's fitness is non-zero, there are a number of distinct ways that such an O with G can interact with its environment. It might be eaten by a predator early in life and die without leaving behind any progeny, or it might live a long life and leave behind a large number of progeny. Let's designate each of these possible ways O could live its life in E (henceforth O's *possible lives*) with L. Thus O has a large set of possible lives, $L_1, L_2, \ldots, L_n$. Each of these possible lives will have a probability associated with it.[9] The understanding of fitness as a propensity, then, can be explicated in terms of the properties of this set of possible lives (with their associated probabilities). Holding E constant, a change from one G to a different genome G^* will change the properties of the L_i (i.e., different genes can lead to differences in fitness). We now can understand both fitness and selection in terms of this set of possibilities: The fitness of O consists in the properties of O's set of possible lives (with their associated probabilities). Fitness is thus quantified via a function[10] on O's probability-weighted possible lives. Similarly, selection consists in the differential weighting of the L_i for O with G in E, relative to the other L_i for the other conspecifics in E. In other words, selection is the inter-organismic heterogeneity in the L_i and is quantified via a function on this heterogeneity.[11] This way of understanding fitness and selection,[12] derived from the simple premise that an organism has many possible ways to interact with its

---

[8] This is not a denial of determinism (though I take it that there is good scientific support for fundamental indeterminism). Instead, this is possible because 'environment' refers to a broader set of factors than those that happen to determine a particular outcome of a particular life. This is analogous to the observation that it is not inconsistent to hold that the (conditional) probability of a fair coin landing heads in a coin flipping machine is 0.5, whether or not the world is deterministic. See Sober (2010) for a discussion of this point.

[9] Strictly speaking, the set of possible lives is infinite and the probability of each of the L_i is zero. Thus it does not make sense to speak of differences in the probabilities of the various L_i. But because some of these lives will be effectively equivalent in terms of their outcomes, they can be bundled together in such a way that there is a finite number of bundles and each bundle has a non-zero probability. To not overly complicate the following discussion, I will simply speak of probabilities associated with particular possible lives, even though it is only the bundles that differ in their probabilities.

[10] Describing this function precisely is a deep and difficult question, and one beyond the scope of the current discussion (see Pence and Ramsey *forthcoming*).

[11] Under the label of 'heterogeneity' fall such things as differences in the timing, quality, and quantity of the offspring produced. The function on this heterogeneity will thus need to incorporate all of these facets of L_i heterogeneity.

[12] Note that I am here explicating *organismic* fitness and selection, not the fitness and selection of *traits*. These notions of fitness and selection are distinct (though related) and, for the sake of simplicity, I will not here discuss trait fitness/selection.

environment, has some profound implications for our understanding of the distinction between selection and drift$_c$. As we will see, it will allow us to understand drift$_c$ in terms of individual organisms, something that has previously not been considered possible.

5 Locating drift in the individual

Selection appears to be a population-level phenomenon *par excellence* (Millstein 2006), and if there were a coherent notion of drift$_c$, it would seem to be a population-level cause. Supporting this idea, the possibility of locating drift at the individual level has been challenged. Walsh, Lewens, and Ariew put the point quite forcefully, claiming that "it is a category mistake to suppose that drift is to be found in an individual instance of a birth or death" (2002, p. 459). They are representing a majority opinion: drift is fundamentally a population-level phenomenon. And they are certainly right that it is individual organisms that are being sampled *from a population* in order to compose the next generation. But this, it will be argued here, is not drift$_c$ in the most fundamental sense; rather, it is a result of individual-level drift$_c$, which is what I am labeling driftability.

To see how driftability can be located in the individual, consider again the L_i. Two immediately obvious, though crucially important facts about the L_i are, first, that the L_i will be a heterogeneous set (not all ways an organism can live its life have the same outcomes), and second, an organism can live only one life (only one L can be realized for any particular O). Because of this, the life that any particular O lives will probably not be a representative sample of the L_i (i.e., the realized L will tend not be an average of the L_i, say). And distinct Os in the population will have a variety of outcomes, even if they are of the same type. These observations lead us to the conclusion that differences in the heterogeneity of the L_i will lead to differences in evolutionary outcomes.[13] Driftability, then, can be identified with intra-organismic heterogeneity in the L_i and can be quantified by a function on this heterogeneity.[14] Thus while selection is heterogeneity in the L_i *across organisms*, driftability is heterogeneity in the L_i *within organisms*. Defining driftability in this way, does five important things: it (1) makes driftability an objective property of individuals (it is a property of organisms, not our ignorance of them), (2) provides a framework for quantifying the causal notion of drift (since higher heterogeneity will tend to result in the population deviating from expectation—i.e., exhibiting drift$_o$—to a greater degree), (3) places selection and driftability in the same ontological arena,[15] (4) shows that driftability and selection are both conceptually distinct and that their quantities can change independently from one

---

[13] Similarly, flipping a set of coins with a '2' on each side will tend to lead to a different tally from that of the same size set of coins with a '1' on one side and a '3' on the other, even though the expected tally is the same.

[14] As with fitness, the task of specifying the nature of this heterogeneity and this function will be left to another paper.

[15] By claiming that selection and driftability are in the same "ontological arena" I mearly mean that they are structurally the same, that they both consist in heterogeneity in the L_i.

another, and (5) accounts for why population size matters to drift$_o$. Although (1)–(3) are clear from the preceding discussion, I will now show why (4) and (5) are the case.

To see how driftability and selection can be distinguished and how they can lead to population-level change, let's return to Millstein's (2002) example of the gray and brown squirrels. Let us grant for now Millstein's assumption that the brown and gray squirrels are equally fit. What this means is that being brown (as opposed to gray) does not change the properties of the L_i (or, more precisely, does not change the value of the fitness function on these properties). How, then, can driftability increase the proportion of brown squirrels in the population over time? Under the framework introduced here, the answer is that the realization of an organism's life is a sampling process (the sampling of one L from among the L_i), and that it happened that the sum of the successful reproductive events for the sampled Ls for the brown individuals (divided by the number of brown individuals in the population) is greater than the corresponding sum for the gray individuals (divided by the number of gray individuals in the population). These population-level effects, then, are a result of an individual-level sampling process, a process that allows the population to drift$_o$ only if there is non-zero driftability. And the higher the driftability, the more (and more rapidly) the population will tend to deviate from expectation.

It is thus clear that driftability is able to explain population-level changes in trait frequency in the absence of selection. But, as Brandon (2005) convincingly argues, there is more to drift$_o$ than this. Drift$_o$ can also occur along with selection and is manifested as a deviation from expectation. The brown squirrels, for example, could be fitter than the gray ones. Under the driftability framework, this means that the properties of the L_i for the brown morphs results in them having a higher fitness than gray ones. This does not mean that for any particular brown individual (or the set of brown individuals in a population) that the number of successful reproductive events for the realized L will in fact be higher. Instead, it merely means that the brown individuals will tend to reproduce more than the gray ones. If the selection pressure is only moderate, we would expect that there would be a fluctuation in the gray-brown ratio in the population, but that in the long run, the brown ones will probably drive the gray ones to extinction.

Driftability can clearly operate in the absence of, as well as in conjunction with, selection. But are driftability and selection truly distinct? Can one change each of them independently of the other? Because driftability is intra-organismic heterogeneity and selection is inter-organismic heterogeneity, the question to be answered is whether these two kinds of heterogeneity can be changed independently of one another. To see that this is possible, consider this simplistic model: the fitness of each O will simply be taken to be the weighted average offspring production for the L_i, selection will be the variance in the fitness values of the Os in the population, and the driftability of each O will be the variance in offspring production for its L_i. If this is how driftability and selection are quantified, it is easily seen that these quantities can vary independently: consider two organisms, O and O^*, each with a 0.5 probability of producing one offspring and a 0.5 probability of producing three offspring. Here the driftability of each is one and there is no selection coefficient between them. We can easily alter driftability without altering selection by, for example, changing the possible outcomes for O and O^* to zero and four instead of one and three. There is still no fitness difference between O and O^*, but driftability has increased from 1 to 4.[16] And we can similarly vary selection without altering driftability by adding one to each L in O^*'s L_{i}., while keeping O's L_{i} unmodified.

Driftability and selection, then, can vary independently and driftability can account for evolution in the absence of selection (drift *sensu* Beatty 1984; Millstein 2002) as well as deviation from expectation (drift *sensu* Brandon 2005). But driftability can also make sense of the predictable features of drift$_{\mathrm{o}}$ as well. As discussed above, it is recognized, for example, that small populations tend to exhibit more drift$_{\mathrm{o}}$ than large populations. In the case where the brown and gray squirrels are equally fit, a population that begins with 50 % brown individuals will be expected to retain a roughly 50 % proportion (from generation n to generation $n + 1$) if the population is large, but it is expected to deviate from 50 % if the population is small. The reason for this, according to the driftability framework, is that in a large population, the set of realized Ls for the brown individuals has a higher probability of being a representative sample of the L_{i} for that type than in a smaller population. And if it is a representative sample, then we would predict little deviation from the expected outcome of the brown type (i.e., that they do not change in proportion to the gray type). But in a small population, the set of realized Ls for the brown individuals is probably *not* a representative sample of the L_{i} for the brown type. The smaller the population, the smaller the probability that any new generation will have of being a representative sample of the L_{i}. Therefore, small populations will tend to drift$_{\mathrm{o}}$ more than large ones, and infinite populations will not drift$_{\mathrm{o}}$. This framework thus provides a basis for the standard population-genetic models of allele dynamics in which smaller populations tend to lead to greater deviations from expectation as well as a decrease in genetic diversity.

In addition to showing why population size matters for drift$_{\mathrm{o}}$, the framework presented here shows that drift$_{\mathrm{o}}$ is quantified by two things, population size and driftability. It is well known that population size quantifies drift, but I have shown that driftability quantifies it as well. With zero driftability, the populations cannot drift$_{\mathrm{o}}$, no matter what their size. And if the population is infinite in size, then drift$_{\mathrm{o}}$ cannot occur, independent of driftability values.[17] But for any non-zero driftability values in a finite population, the population will tend to drift$_{\mathrm{o}}$, and the quantity of this drift$_{\mathrm{o}}$ will be modulated via both population size and driftability.

---

[16] I am here ignoring the complicating factor of the effect of the variance in possible offspring on fitness (Beatty and Finsen 1989). See Sect. 10 for more on variance and fitness values.

[17] Because driftability includes germline mutations (such a mutation can be understood as a heritable transformation occuring along part of an L), the claim that drift$_{\mathrm{o}}$ cannot occur in an infinite population requires the assumption that the individuals in the population are not sui generis. Instead, each type in the infinite population must be represented by an infinite number of individuals. If this were not the case, there could be drift$_{\mathrm{o}}$ even in an infinite population. To see how this is possible, consider the probability of surviving extinction for a particular allele that arises in an individual. This probability is approximately $2k$, where k is the advantage conferred by the allele (Haldane 1927). And since k is (or can be) constant over changes in population size, drift$_{\mathrm{o}}$ is not eliminated by an infinite population size (this requires the assumption that the offspring are drawn from a Poisson distribution—see Haldane 1927).

6 But is it a cause?

At this point, the proponents of the non-causal interpretation of selection, fitness, and drift have two ways to challenge the view just presented. They could argue that it is illegitimate to understand fitness/selection/drift in terms of L_i or that while fitness/selection/drift are justifiably characterized in terms of the L_i, the relationship between evolution and the L_i is not a causal one. In this section I will attempt to show that one cannot make these challenges without more generally challenging the causal efficacy of dispositional properties.

There are of course long-standing debates in metaphysics over the nature of dispositional properties, their relationship to their categorical bases, and whether (and how) dispositions have causal efficacy. By characterizing driftability as a dispositional property, the cogency of driftability and the justification for the claim that driftability causes evolution therefore rests on particular views of dispositional properties. I will try to remain as neutral as possible about these debates and point out that all that my view needs is for dispositions to be causally efficacious with respect to their manifestations. Thus, I need it to be true that glasses can break because they are fragile, where 'because' is understood causally. For the purposes here, it does not matter whether one thinks that dispositions are type- or token-identical to their bases, or if one holds that there is a more complicated relationship. What is required is the claim that dispositions can at times (correctly) be said to cause their manifestations.[18]

Furthermore, the way in which I characterize and quantify fitness/selection/driftability is not unique, but works for other dispositional properties as well. Let's continue with the example of fragility to see how it can be quantified. The fragility of a glass, like other dispositions, is characterized in terms of its possible states (remaining in one piece or being broken this way or that). Now consider the possible outcomes of the life of a glass, where the length of a life could be defined as 10 years. A glass can end its life in one piece or it can end its life in many shards. For each type of glass, then, we could construct a histogram of the possible outcomes of the lives of the glasses. For example, 80 % of these lives could end with the glass in one piece, 5 % in two shards, 7 % in three shards, etc. The resultant histogram gives us a detailed picture of the fragility of the glass. And we could compare this histogram to that of, say, a mug to see which of the two is more fragile. Of course, in order to construct a rank ordering of the levels of fragility, one needs to collapse the histogram into a single number. One way to do this would be to take the arithmetic mean of the distribution. This would be the expected number of pieces that the object would end up in at the end of its life.[19] The value of this number could be obtained for the glass and the mug and the

---

[18] This implies that a rejection of the causal efficacy of dispositional properties would allow one to accept the definition of driftability and selection in terms of L_i heterogeneity without holding that driftability or selection can cause evolution. Thus, a statisticalist could hold that the driftability framework is the right way to think about drift, but that while driftability quantifies and correctly locates the basis of drift in features of individual organisms, driftability is not a cause of drift$_o$.

[19] This way of quantifying fragility will have some odd implications. A glass that will almost certainly not break over its life but, if broken, will shatter into a billion pieces, will obtain a higher fragility value than a mug that always breaks, but always does so into a few pieces. If one is perturbed by these results, there are different ways to reduce the distribution to a single value. For example, using the mode of the

higher number would indicate higher fragility. This is analogous to what is done in the case of fitness—the "outcomes" are offspring instead of shards and the histograms are similarly collapsed into single values, which can be compared to determine relative fitness.[20]

Fitness and fragility are thus directly analogous, and so is driftability. Driftability consists in the heterogeneity of the possible outcomes. Unless the glass is unbreakable, it has multiple possible outcomes and can realize only one. A small number of glasses of the same kind will be predicted to deviate significantly from the expected number of shards; a large number of such glasses will be predicted to deviate less from the expected number. This shows that if one is arguing against the characterization of driftability in terms of L_{i}, then one must also argue that fragility, and other dispositional properties as well, cannot be characterized in terms of possible future outcomes and their associated properties. Although such an argument could perhaps be made, it is difficult to know how it could be accomplished without forming an argument against dispositional properties in general.

One possible strategy of separating ostensibly causal dispositions from the sort that underlie drift or fitness was taken by Sober (1984). Sober argues that fitness is like life expectancy—it gathers together a set of heterogeneous causes to produce a single value. But just as life expectancy is not a cause, so, he argues, fitness is not a cause. Instead, he argues that although fitness does not cause outcomes, it *explains* them. Fitness explains without causing by articulating the causal structure of the situation without pointing out particular actual causes. If one agrees with Sober on this point, then one might hold that driftability can be used to causally explain drift$_{\mathrm{o}}$ without driftability actually causing drift$_{\mathrm{o}}$. I lack the space here to fully engage with this critique, but I will merely point out that in order for it to work, properties like fitness and driftability must form a class distinct from the causal dispositional properties. Furthermore, because selection and driftability are both based on heterogeneity in the L_{i}, one might argue that if driftability is not a cause, than selection is not either. And since for Sober selection—and in particular *selection for*—is causal, there is reason to think that driftability should also be considered causal.

Setting aside the Sober worries, the above discussion implies that if dispositional properties are causal, driftability and selection can be causes of evolutionary change. And in the previous section, we saw that driftability and selection can change independently of one another: intra- and inter-organismic heterogeneity in the L_{i} can vary independently. Driftability can be non-zero without any selection (when there is heterogeneity within, but not between, organisms) and this can cause populations to drift$_{\mathrm{o}}$ (the example of this above is the proportion of brown squirrels changing in the absence of selection). And selection values can be non-zero even when driftability is zero. An example of the latter would be the following. Say that the brown and gray squirrels each had only one L in their L_{i}. Each brown one had a probability of 1.0 of having

---

Footnote 19 continued
distribution (instead of the mean) would reverse the rank ordering of the fitness values for the glasses and mugs, avoiding this counterintuitive result.

[20] Arithmetic mean, it has been shown, is not a good metric for fitness in all situations. But more sophisticated metrics are available that are much more general (Pence and Ramsey, *forthcoming*).

three offspring and each gray one had a probability of 1.0 of having two offspring. In this case, the brown type would be selected for and because there are no distinct Ls (i.e., no Ls having distinct outcomes) to sample from, there is zero driftability and drift$_\mathrm{o}$ is therefore impossible (regardless of population size). (The fact that nature will never produce organisms with only one possible L shows that we should expect drift$_\mathrm{o}$ to always occur. This feature of driftability, as we will see below, allows it to ground what Brandon (2006) identifies as biology's first law.)

It follows from this that selection and driftability are distinct causes, and that one could (at least ideally) intervene on a population and modify driftability values independently of selection values, and vice versa.[21] The identification of driftability as an independent, individual-level cause undermines some previous arguments against drift$_\mathrm{c}$, since these have been against drift as a *population-level cause*, the sort argued for by Stephens (2004, p. 556), when he asserts that "drift is a *population level* cause. One sees the differential causal impact of drift *only* by comparing populations of different sizes. Drift plays a larger role in flipping a fair coin ten times than it does in flipping a coin 10,000 times." Walsh (2007) argued against this position by suggesting that it implies that the strength of the force is a function of how the situation is described—whether we are interested in, say, the whole population, or only a portion of it. Similarly, Matthen (2009) suggests that it is a peculiar force: "How can strong nondirectional (and therefore noncancelling) forces operating on parts of a population give rise to a weak force operating on the whole?" (p. 469). Upon recognizing that drift$_\mathrm{c}$ is based at the individual-level, all of these worries evanesce. Driftability is *not* stronger in small populations, it is simply that in small populations, driftability has a stronger effect on drift$_\mathrm{o}$. And driftability remains the same however we decide to carve up the population.

7 Putting it all together: a sanctuary, a hawk, and a road

We have seen that driftability and selection are independent causes of evolution. In this section I will use the above framework to provide a brief sketch of how selection and driftability can operate independently in ecological settings.

Case 1: A sanctuary free of predators If we ask of two squirrel types in a sanctuary whether they differ in fitness, this question amounts to asking whether the L_i in the two types of O are differentially weighted so that the function on the L_i that constitutes the O's fitness produces different values for the individuals of the two types (I am of course assuming here that this is the only trait that varies between these two types). We can then ask whether or not we should anticipate the trait frequencies deviating from what we would expect given these fitness values. The answer to this question is based on the heterogeneity among the L_i.[22] If

---

[21] Because selection and driftability could be independently intervened upon, the manipulability construal of causal explanation (Woodward 2005) would hold that selection and driftability can form the basis of independent, causal evolutionary explanations.

[22] Direct access to the L_i is of course impossible. But the heterogeneity in outcomes can be inferred either from (developmental, environmental, etc.) features affecting the organism's life history, or from observing a sample of like organisms.

there is significant heterogeneity, then is the population of squirrels great enough that each generation will form a representative sample of the L_i? If the answer to the latter question is no, then we will expect to see an evolutionary response to driftability.

Case 2: The introduction of a road Now consider a road that is opened in the heart of the sanctuary. Vehicles on the road kill squirrels, but squirrels of each type are equally likely to meet their fate under the wheel of a vehicle. This introduction of the road increases heterogeneity among the L_i, with a new class of the L_i ending as road kill. This (assuming a finite population) will tend to increase the evolutionary response to driftability.

The fact that the cars act indiscriminately with respect to coat color makes this a case of drift in the Millstein/Beatty sense of drift as an indiscriminate process. If all cases of drift were like this, then I would have no quibbles with the Millstein/Beatty view. But, as the next case will make clear, drift$_o$ can also be induced via a discriminate cause.

Case 3: The introduction of a hawk If a hawk makes its home in the sanctuary and begins to prey on the squirrels—and is disposed to prey on the gray individuals over the brown ones—then the brown individuals will be fitter than they previously were relative to the gray ones. This is because more of the L_i for the gray than the brown individuals are truncated by predation. We should expect the population to respond to this selection (assuming, of course, that coat color is heritable). Will the population also exhibit a greater response to driftability? This depends on the degree to which the presence of the hawk increases the heterogeneity in the intra-organismic L_i. If there is already a large heterogeneity in the L_i—if, therefore, there is a great diversity in the lifespan and number of offspring produced by members of the population—then the presence of the hawk will precipitate little additional response to driftability. If, on the other hand, the L_i are relatively homogeneous, then the hawk could have a large effect on driftability, which should lead to increased drift$_o$, especially if the population is small in size.

These three cases show how selection and driftability can be understood as objective features of the world, that they have their foundation in individual-level properties, and that driftability can act along with, and not merely in the absence of, selective (i.e., discriminate) forces. If this is correct, then the arguments that drift is not an objective feature of the world (and therefore not a cause of evolution) are mistaken, as is the argument that drift is based (always or merely) on indiscriminate sampling. It should be noted, however, that the emphasis on the individual does not mean that individual-level events can be partitioned into drifty and non-drifty ones. It is not part of this view that the squirrels who met their fate on the road have died "because of drift." These "chance events," like the squirrel being flattened by the wheel of a car, may be part of what explains the evolutionary response to driftability, but they are not necessary for driftability.

In the remains of this paper, I will draw out the relationship between driftability and some recent accounts of drift, Brandon's (2006) Principle of Drift, McShea and Brandon's (2010) zero force evolutionary law, and Gildenhuys's (2009) NINPICs.

8 Biology's first law, explained

Brandon (2006) introduced the Principle of Drift (PD), which he characterized as *biology's first law*. Is the PD really a universal law of biology? If so, is it a basic law or do even more fundamental laws or features underlie it? One of the payoffs of the driftability framework is that it is able to answer these questions. As we will see below, the answer driftability provides is that the PD is in fact a true universal generalization about evolutionary systems, but it is not basic. Instead, it is a result of driftability plus a few other generic features of evolutionary systems. The PD is defined in the following way:

> *The Evolutionary Principle of Drift*:
> (A) A population at equilibrium will tend to drift from that equilibrium unless acted on by an evolutionary force.
> (A population at rest will tend to start moving unless acted on by an external force.)
> (B) A population on evolutionary trajectory t, caused by some net evolutionary force F, will tend to depart from the extrapolated path predicted based on F alone (in either direction or magnitude or both) even if no other evolutionary force intervenes, unless F continues to act.
> (A population in motion will tend to stay in motion, but change its trajectory, unless continually acted on by an external force.)
> (Brandon 2006, p. 328)

Is this principle a universal law, as Brandon claims? If so, is there something more basic than the principle that explains both its truth and its universality? I will argue here that it is driftability that underlies the principle and shows it to be true and universal. To see why this is the case, lets explore the consequences of driftability.

In all real populations, individuals will possess a heterogeneous set of possible lives. And because the populations are not infinite in size, the lives that are sampled in each generation will have a high probability of not being a representative sample of the L_i. This provides us with two premises: (I) the L_i are heterogeneous and (II) the sampled lives are not generally a representative sample of the L_i for each type. If we add the additional premise that (III) there are multiple types (or trait differences) in the population, this leads to the conclusion that the population's trait distribution from one generation to the next will tend to differ and, if evolution is taken to be trans-generational trait differences, evolution will tend to occur.

This brings us to part (A) of the PD: a population at equilibrium will tend to drift from that equilibrium unless acted on by an evolutionary force. This is tantamount to the conclusion of the previous paragraph that evolution will tend to occur. I did not mention the possibility of a countervailing force that can keep the population from evolving, but Brandon is correct to make this explicit. Thus, driftability leads directly to the conclusion that populations, unless acted on by a evolutionary force,[23] will tend

---

[23] There is, however, one possible point of tension between the driftability framework and the PD, since the PD explicitly excludes drift from being an evolutionary "force." I will not here lay out what I consider to be the necessary and sufficient conditions for something to qualify as a force, but the argument for

to drift_o. Part (A) of the PD thus directly follows from driftability, but does part (B) follow as well?

Before I discuss the relationship between driftability and (B), I should mention one caveat about (B). While (A) is couched in ontological terms, (B) is couched in epistemic terms. This is problematic because since populations are so complex and because fitness values are so difficult to determine, we would expect that the trajectory of a population would deviate from what we would predict *even if there were no drift*. Furthermore, in predicting the future states of a population, one might predict several states at a given future time and associate a probability value with each. Thus, there might be no unique "predicted path." These problems, however, are not fatal to the PD, since one can easily couch it in ontological terms. One could, for example, recast (B) into something like: A population on evolutionary trajectory t, caused by some net evolutionary force F, will tend to depart (in either direction or magnitude or both) from this trajectory, even if no other evolutionary force intervenes, unless F continues to act. This caveat aside, let's now turn to the question of how driftability can underwrite (B).

Part (B) of the PD says that if a population is evolving in response to a selection pressure, the path one will predict that the population will take will tend not to be the one that the population realizes. Driftability underlies (B) just as it does (A) and we can see this if we reformulate (B) into the framework described above. The "evolutionary force, F" referred to by Brandon is a difference in organismic fitness values for different individuals, and this fitness difference is underlain by differences in the L_i amongst the individuals. These fitness differences will change the probabilities associated with the evolutionary outcomes of the population. But premises (I)–(III) still obtain. And these premises lead to the conclusion that the population should depart from its predicted path.

Driftability is thus the basis for the PD: The driftability account shows that drift_o will (for any real population) always tend to occur.

9 Driftability and the ZFEL

We have seen that driftability underlies and explains the PD, but it also underlies a related concept, McShea and Brandon's (2010) "zero-force evolutionary law," or ZFEL. The ZFEL is defined in the following way:

> ZFEL (general formulation): In any evolutionary system in which there is variation and heredity, there is a tendency for diversity and complexity to increase, one that is always present but may be opposed or augmented by natural selection, other forces, or constraints acting on diversity or complexity. (p. 4)

---

driftability does take driftability to be a *cause* of evolutionary change. And, as suggested in Sect. 9 below,
Footnote 23 continued
since driftability and selection are in the same ontological arena, it seems that if selection is a force, drift is too. If driftability were to be understood to be a force, then one could simply amend the PD by, for example, inserting 'additional' or 'counterveiling' before 'evolutionary' in condition (A).

Just as driftability is the basis of the PD, it is also the basis of the ZFEL. If we take premises (I)–(III) from the previous section and add the additional premise that (IV) there is variation across L_i, not just in the number of offspring, but also in the heritable traits of the offspring, then it follows that a population of relatively homogeneous organisms should increase in diversity from one generation to the next. The phenotypic and genotypic space occupied by the population will tend to increase via driftability, and will do so unless curtailed by selection or another evolutionary cause. The ZFEL, then, is a direct consequence of driftability plus four rather innocuous premises.

Driftability serves as a foundation for the ZFEL, but it also says something about how the ZFEL should be characterized. McShea and Brandon are adamant that the ZFEL is a background condition, not a force. As they put it, "the ZFEL tendency is to be understood as a background state that is present prior to and during the imposition of any constraints or forces" (p. 4). Similarly, "[i]n the ZFEL view, increase is the background condition, with natural selection in the role of superimposed force, augmenting or opposing the background increase" (p. 6). The driftability framework challenges this background/foreground partitioning. As argued for above, selection consists in inter-organismic heterogeneity in the L_i, while driftability consists in intra-organismic heterogeneity. Selection and driftability are thus in the same ontological arena (both consisting in L_i heterogeneity), if one is background or foreground, the other must be as well. If this is true, then driftability and selection are both omnipresent and structurally isomorphic—they are distinct causes of evolution, but are part of the same ontological category.

10 Driftability and NINPICs

This paper has been concerned with introducing a novel account of drift, explicating and defending this account, and showing that it is superior to views of drift as population-level process and population-level product. I will now consider an additional account of drift that has goals similar to mine (explicating drift_c and its relationship to drift_o), one recently argued for by Gildenhuys (2009). Gildenhuys does an excellent job pointing out some of the problems with the various concepts of drift discussed above (the Beatty/Millstein view and the Brandon view as well as Bouchard and Rosenberg's (2004) account). Although I agree with many of Gildenhuys's critiques of other accounts of drift, I do not find his positive account of drift to be satisfactory. In what follows, I will compare his account to driftability and I will show that it fails as an explication of the causal dimensions of drift.

> For Gildenhuys, 'drift' denotes:
> noninteractive, non-pervasive, and indiscriminate causes (NINPICs). They are (i) *non-interactive* insofar as they have the same sort of causal influence on the reproduction of individuals of each type in the population (most are deadly for individuals of all types); (ii) *non-pervasive* insofar as they affect only some population members in any given generation or time slice; and (iii) *indiscriminate* insofar as they are just as likely to affect one population member as any other population member, regardless of what variant types they are. (2009, p. 522).

He takes most instances of drift to be deadly and uses a lightning strike as an exemplar: Lightning strikes one squirrel and kills it. This is *non-interactive* since the lightning strike would have killed any squirrel, independent of its type; it is *non-pervasive* since the lightning did not strike all of the squirrels; and it is *indiscriminate* since the squirrel's being of a particular type did not make its being struck by lightning more probable.

Gildenhuys goes on to justify the claim that "NINPICs are the causal influences responsible for drift, because," as he claims, "any causal influence that is interactive, pervasive, or discriminate cannot have a non-directional influence over population dynamics" (p. 543). A counterexample to his view, then, would be a cause that is interactive, pervasive, or discriminate, yet nonetheless adds a non-directional influence over population dynamics. I will now construct such an example.

Consider, again, our population of gray and brown squirrels. Let's assume that all squirrels are equally fit, and that all have a probability of 1 of having two offspring. Drift$_o$, in such a case, is impossible. The only way to introduce a cause that leads to the population drifting would, according to Gildenhuys, be to introduce a NINPIC. But consider a virus that subsequently spreads through the individuals in the population. The virus has the following effect: For brown infected individuals, it changes them from having $P(2) = 1$ (i.e., a probability of one of having two offspring), to having $P(1) = 0.5$ and $P(3) = 0.5$. And for the gray infected individuals, the new probabilities are $P(0) = 0.5$ and $P(4) = 0.5$. This virus is interactive, since it acts differently depending on the type affected: Only gray individuals have zero or four offspring and only brown individuals have one or three offspring. The virus is pervasive, since it affects all of the individuals of each type. It is thus both interactive and pervasive. All that is needed for a counterexample is for one of Gildenhuys's conditions to fail to obtain and for the effect to have a non-directional influence over population dynamics. In this example, two of the conditions fail to obtain, and it is thus clear that the viral infection is not a NINPIC. But how does the virus infection change our predictions about population-level change? Since $((1\times 0.5)+(3\times 0.5)) = ((0\times 0.5)+(4\times 0.5)) = 2$, the expected number of both types (infected or not) is the same, and they are thus equally fit. However, if the population is of finite size, it will tend to change in the proportion of brown and gray types because of the virus. This thus serves as an effective counterexample to the NINPIC view of drift$_c$. NINPICs are one—but not the only—way to achieve drift$_o$.

One could object to this attempt at a counterexample to the NINPIC understanding of drift in the following way: expected number of offspring is not (in all cases) equivalent to fitness (Ariew and Lewontin 2004; Beatty and Finsen 1989; Sober 2001). In particular, fitness values can change in the absence of a change in expected number of offspring if the variance in offspring number changes. The gray individuals have a larger variance in their expected number of offspring and are thus less fit. The virus, therefore, causes a directional change. The conclusion of this objection, then, is that because the virus causes a directional change, it does not serve as a counterexample to the NINPIC conception of drift.

This conclusion, however, does not follow. Expectation values were used as proxies for fitness to simplify the example and achieve readily calculable whole numbers for fitness values. One could easily substitute more sophisticated models of fitness to achieve the same counterexample. For example, the geometric mean, unlike the arithmetic mean (i.e., expectation value), is sensitive to changes in variance. Using the geometric mean to calculate fitness values, the counterexample could run like this: The infected brown individuals have a $\Pr(2) = 0.3$ and $\Pr(4) = 0.7$, while the infected gray individuals have a $\Pr(1) = 0.268$, $\Pr(5) = 0.732$. Given these values, the geometric mean fitness for the brown individuals = the geometric mean fitness for the gray individuals = 3.248. The virus therefore precipitates drift$_o$ without causing a directional change. The virus thus successfully counterexamples the NINPIC view of drift.

This counterexample based on geometric mean fitness shows two things. First, it shows that a counterexample can be formed based on a fitness measure sensitive to variance in the distribution of potential offspring numbers. Second, the fact that one can form counterexamples out of both arithmetic and geometric mean fitnesses lends confidence to the idea that a counterexample can be formed based on any standard fitness measure. All one has to do to counterexample the NINPIC view is to take a fitness measure and construct a case where driftability changes in the absence of directional changes, i.e., in the absence of the fitness values of the types changing relative to one another.

The driftability account, in contrast to the NINPIC view, correctly identifies the virus as increasing driftability, since it changes the squirrels from having only one possible life to having a heterogeneous set of possible lives. And this driftability will lead to drift$_o$, changing the proportions of brown and gray types in the population.

11 Conclusions

This paper introduces a novel way of understanding drift$_c$. Drift$_c$ is not to be equated with population-level processes or products, but is instead an individual-level phenomenon. The implications of driftability are substantial: (1) driftability dissolves the paradoxes of drift$_c$, since these paradoxes arise only when identifying the cause at the population-level. (2) Just as there is a distinction between *selection* and the *evolutionary response to selection*, so there is a distinction between *driftability* and the *evolutionary response to driftability*. Driftability is an individual-level phenomenon, but its evolutionary effects, drift$_o$, can be observed at the population-level. (3) One can use driftability to draw a distinction between drift$_c$ and selection—selection consists in inter-organismic heterogeneity in possible lives and driftability conists in intra-organismic heterogeneity in possible lives. Finally, (4) biology's first law, the PD, as well as ZFEL are grounded and explained by driftability.

Acknowledgments This paper was the subject of a symposium at the 2011 meeting of the Pacific Division of the American Philosophical Association. I thank my commentators, Vadim Keyser, Mohan Matthen, and Sarah Roe for their insightful comments. This paper was also presented at the 2011 Workshop on Metaphysics of Microevolutionary Processes at the University of Alabama at Birmingham. I thank the organizer, Marshall Abrams, as well as the other attendees for their input. I also thank Robert Brandon, Yoichi Ishida, Bence Nanay, Charles Pence, and the anonymous reviewers for reading and commenting on earlier versions of this paper.

References

Abrams, M. (2007). How do natural selection and random drift interact? In: C. Bicchieri & J. Alexander (Eds.), *Proceedings of the 2006 biennial meeting of the Philosophy of Science Association. Part I: Contributed papers*. *Philosophy of Science, 74*(5), 666–679.

Ariew, A., & Ernst, Z. (2009). What fitness can't be. *Erkenntnis*, *71*(3), 289–301.

Ariew, A., & Lewontin, R. C. (2004). The confusions of fitness. *British Journal for the Philosophy of Science*, *55*, 347–363.

Beatty, J. H. (1984). Chance and natural selection. *Philosophy of Science*, *51*, 183–211.

Beatty, J. H., & Finsen, S. (1989). Rethinking the propensity interpretation of fitness: A peek inside pandora's box. In M. Ruse (Ed.), *What the philosophy of biology is: Essays for David Hull* (pp. 17–30). Dordrecht: Kluwer.

Bouchard, F., & Rosenberg, A. (2004). Fitness, probability and the principles of natural selection. *British Journal for the Philosophy of Science*, *55*(4), 693–712.

Brandon, R. N. (1978). Adaptation and evolutionary theory. *Studies in History and Philosophy of Science*, *9*(3), 181–206.

Brandon, R. N. (2005). The difference between selection and drift: A reply to Millstein. *Biology and Philosophy*, *20*(1), 153–170.

Brandon, R. N. (2006). The principle of drift: Biology's first law. *Journal of Philosophy*, *102*(7), 319–335.

Brandon, R. N., & Carson, S. (1996). The indeterministic character of evolutionary theory: No 'no hidden variables proof' but no room for determinism either. *Philosophy of Science*, *63*(3), 315–337.

Darwin, C. (1859). *On the origin of species*. London: John Murray.

Gildenhuys, P. (2009). An explication of the causal dimension of drift. *British Journal for the Philosophy of Science*, *60*(3), 521–555.

Haldane, J. B. S. (1927). A mathematical theory of natural and artificial selection, part v: Selection and mutation. *Proceedings of the Cambridge Philosophical Society* (pp. 838–844). Oxford: Oxford University Press.

Haldane, J. B. S. (1954). The measurement of natural selection. *Proceedings on IX International Congress Genetics*, *1*, 480–487.

Krimbas, C. B. (2004). On fitness. *Biology and Philosophy*, *19*(2), 185–203.

McGraw, J. B., & Caswell, H. (1996). Estimation of individual fitness from life-history data. *American Naturalist*, *147*(1), 47–64.

Matthen, M. (2009). Drift and "statistically abstractive explanation. *Philosophy of Science*, *76*, 464–487.

Matthen, M., & Ariew, A. (2002). Two ways of thinking about fitness and natural selection. *Journal of Philosophy*, *99*(2), 55–83.

McShea, D., & Brandon, R. N. (2010). *Biology's first law: The tendency for diversity and complexity to increase in evolutionary systems*. Chicago: University of Chicago Press.

Mills, S. K., & Beatty, J. H. (1979). The propensity interpretation of fitness. *Philosophy of Science*, *46*(2), 263–286.

Millstein, R. L. (2002). Are random drift and natural selection conceptually distinct? *Biology and Philosophy*, *17*, 33–53.

Millstein, R. L. (2006). Natural selection as a population-level causal process. *The British Journal for the Philosophy of Science*, *57*(4), 627–653.

Pence, C., Ramsey, G. (forthcoming). A new foundation for the propensity interpretation of fitness. *British Journal for the Philosophy of Science*.

Pfeifer, J. (2005). Why selection and drift might be distinct. *Philosophy of Science*, *72*(5), 1135–1145.

Rosenberg, A. (1994). *Instrumental biology or the disunity of science*. Chicago: University of Chicago Press.

Sober, E. (1984). *The nature of selection*. London: MIT Press.

Sober, E. (2001). The two faces of fitness. In E. Sober (Ed.), *Conceptual issues in evolutionary biology* (pp. 25–38). London: MIT Press.

Sober, E. (2010). Evolutionary theory and the reality of macro-probabilities. In E. Ellery & J. H. Fetzered (Eds.), *The place of probability in science* (pp. 133–161). New York: Springer.

Stephens, C. (2004). Selection, drift, and the 'forces' of evolution. *Philosophy of Science*, *71*(4), 550–570.

Wagner, G. (2010). The measurement theory of fitness. *Evolution*, *64*(5), 1358–1376.

Walsh, D. (2007). The pomp of superfluous causes: The interpretation of evolutionary theory. *Philosophy of Science*, *74*(3), 281–303.

Walsh, D. M., Lewens, T., & Ariew, A. (2002). The trials of life: Natural selection and random drift. *Philosophy of Science*, *69*(3), 452–473.

Woodward, J. F. (2005). *Making things happen: A theory of causal explanation*. Oxford: Oxford University Press.