

It's Okay to Call Genetic Drift a "Force"

Charles H. Pence

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Abstract

One hotly debated philosophical question in the analysis of evolutionary theory concerns whether or not evolution and the various factors which constitute it (selection, drift, mutation, and so on) may profitably be considered to be "forces" in the traditional, Newtonian sense. Several compelling arguments assert that the force picture is incoherent, due to the peculiar nature of genetic drift. I consider two of those arguments here – that drift lacks a predictable direction, and that drift is constitutive of evolutionary systems – and show that they both fail to demonstrate that a view of genetic drift as a force is untenable.

1. Introduction

The evolution of populations in nature is described in many ways, using a whole host of smaller factors with extensive theories of their own: natural selection, genetic drift, mutation, migration, linkage disequilibrium, meiotic drive, extinction, increase in complexity, and so on. The natural philosophical question, then, is this: what is the relationship between these "component" theories and the overall trajectory of evolution in the broad sense?

Work on this question has recently focused on the *causal* picture implied by this relationship. Is evolution (as a whole) a causal process? Do some of the smaller-scale theories describe causal processes? Which ones? And how do those smaller-scale causal processes combine to produce the resultant trajectory of populations through time? Two positions on these questions have crystallized. One, the "statisticalist" interpretation of evolutionary theory (e.g., Walsh et al., 2002; Matthen and Ariew, 2002), claims that both evolution as a whole and these smaller-scale theories do not describe causal processes. Rather, the causal processes at work exist at the level of individual organisms and their biochemistry: individual instances of survivals, deaths, predations, mutations, and so forth. All these theories, then, constitute quite useful, but *not* causal, ways in which we may statistically combine events to enable us to grasp interesting trends within populations of causally interacting individuals.

The other view, the "causalist" interpretation (e.g., Millstein, 2002, 2006; Shapiro and Sober, 2007), considers all of these processes to be genuinely causal.

Evolution causes changes in populations, as do selection, mutation, migration, genetic drift, and so forth. How exactly we specify these causal processes varies – for example, as different varieties of “sampling” (Hodge, 1987), as population-level causes (Millstein, 2006), or as supervening on lower-level causes (Shapiro and Sober, 2007) – but they are causal nonetheless.

This heated debate has produced much work on an allied problem which will be the topic of my discussion here. It is a common pedagogical trope in the teaching of biology to describe all of these smaller-scale theories as referring to *forces*, each of which propels a population in a different direction through some space (of morphologies, phenotypes, genotypes, etc.) with a different strength, adding together in some sense to produce the population’s overall evolutionary trajectory over time. Crow and Kimura introduce a discussion of equilibrium under selection pressure by noting that “ordinarily one regards selection as the strongest force influencing gene frequencies” (1970, p. 262). Hartl and Clark discuss the possibility of balancing mutation and drift, writing that “there are many forces in population genetics that act in opposition to one another, and it is this tension that makes for interesting behavior at the population level. [...] Merely because these two forces are in opposition, it does not guarantee that there will be a stable balance between them” (1997, p. 294). Strickberger argues that since mutational equilibrium is not reached in many natural populations, “other forces must be responsible for the establishment of gene frequencies” (1968, p. 719). This pedagogical pattern is even common at the high school level: in a chapter titled “The Forces of Evolutionary Change,” Lewis summarizes natural selection, nonrandom mating, mutation, migration, and genetic drift in a force-like diagram (1997, p. 412).

I have quoted from several textbooks to demonstrate the pervasiveness of this ‘force’ metaphor at all levels of biological pedagogy. But what of it? Why is this particular biological turn of phrase of philosophical interest? In his original introduction of what would become the causalist interpretation, Sober (1984) described, influentially, evolutionary theory as a *theory of forces*. Sober’s metaphor is intended to carry some genuine explanatory weight. Allowing, of course, that the analogy here is not entirely precise, he claims that *just as* component, causal forces are summed together to determine the net force acting on a body in Newtonian dynamics, a force-like understanding is the right way to picture not just the metaphorical structure of evolution, but its *causal* structure as well. Sober writes that in addition to work on the history of life,

evolutionary biology has also developed a theory of *forces*. This describes the *possible causes* of evolution. The various models provided by the theory of forces describe how a population will evolve if it begins in a certain initial state and is subject to certain causal influences along the way. (Sober, 1984, p. 27)

This view makes evolution, in the apt terminology deployed by Maudlin, a “quasi-Newtonian” theory (2004, p. 431). “There are, on the one hand, *inertial* laws that describe how some entities behave when nothing acts on them, and then

there are laws of *deviation* that specify in what conditions, and in what ways, the behavior will deviate from the inertial behavior” (Maudlin, 2004, p. 431). This is, Maudlin notes, a very natural way for us to understand the behavior of systems: whether or not the laws of a given system are amenable to such analysis, we *like* to produce quasi-Newtonian theories.

But to deploy force language in this more substantive way brings Sober in for another line of argument in addition to the critiques aimed at the causal view in general.¹ For we now must ask about the soundness of this appropriation of Newtonian force. Should selection and drift be treated in this way, or not? One recurring difficulty with adopting the force metaphor is the issue of genetic drift. A common refrain in this debate claims that considering drift to be similar to a Newtonian force is highly problematic.

In what follows, I will argue in favor of the force metaphor, by taking on two arguments against the tenability of considering drift as a force. The first is the (by now, well-trodden) claim that genetic drift, though its magnitude may be determined by the effective population size, lacks a direction specifiable or predictable in advance. Since all Newtonian forces, it is said, must have specifiable magnitudes *and* directions, drift cannot be considered a force, and the metaphor thus falls apart. The second argument claims that it is a category mistake to consider drift a force which impinges upon populations. It is, rather, the default state in which populations find themselves. All evolving populations *necessarily* drift, and thus to describe drift as an “external” force is misleading. Both of these critiques, I will show, miss the mark.

2. The Direction of Drift

It is by now an old chestnut in this debate that genetic drift lacks a specifiable or predictable direction. Matthen and Ariew (2002, p. 61) note in a dismissive aside that “in any case, drift is not the sort of thing that can play the role of a force – it does not have predictable and constant direction.” Brandon (2006) adopts the same argument, and it is one of the central motivations behind his development of the “zero-force evolutionary law” (Brandon, 2006, 2010; McShea and Brandon, 2010).

The basic outline is straightforward. Genetic drift, often called “random” drift, is a stochastic process. Consider a population which is uniformly heterozygous for some allele Aa – all members of the population possess one copy of the dominant allele (A) and one copy of the recessive allele (a). Assuming no selection, mutation, or other evolutionary forces act on the population, genetic drift will eventually drive this population toward homozygosity, uniformity at either AA or aa, with one of the two alleles removed from the population. This

1. Early in the debate between causalists and statisticalists, this point was often missed – Matthen and Ariew (2002), for example, take it to be a point against *the causal interpretation itself* that genetic drift cannot be described as a force. This entails, at best, that the force metaphor should be discarded, not that the causal interpretation is untenable, a point stressed by Stephens (2004) and Millstein (2006).

is because the homozygous states AA and aa are what we might call “absorbing barriers” – once a population has lost all of its A or a alleles (and again, given that there is no mutation), it is “stuck” at the uniform homozygous state. The “random walk” of genetic drift will, given enough time, eventually arrive and remain at one or the other of these permanent states.

Here, then, is the rub – the population will arrive at *one* of these states, but it is impossible in advance to predict which one will be its eventual fate. In this sense, at least, the population-level outcome of genetic drift is random.² It is obvious, the argument concludes, that drift cannot act as a Newtonian force, because Newtonian forces have directions that may be specified and predicted. Consider natural selection. The direction in which selection will drive a population is obvious, and is indeed specifiable in advance: selection will move populations in the direction of increased fitness. We may even visualize the “adaptive landscape” in the absence of any actual populations, specifying the direction of the selective force prior to any actual population’s experiencing it.³ Such analysis is clearly impossible for drift, and drift cannot therefore be described as a force.

Two responses on behalf of the force metaphor have been offered. In our initial discussion of drift above, drift was described fairly clearly in directional terms: it drives populations toward homozygosity (Stephens, 2004, pp. 563–564). Insofar as this is a *direction*, we may avoid the objection. There are several reasons that we might be worried about this response, however. First, Filler has argued persuasively that if we are *too* liberal with our force metaphor, we run the risk of sapping the notion of ‘force’ of all its explanatory power. Consider, for example, Molière’s classic satire of opium’s “dormitive virtue.” We could construct a “fatigue-space” in which sleep sits at the end of one axis, and then describe a “dormitive force” which drives persons up the sleep axis. Ascribe this “dormitive force” to opium, and we have come close to completing Molière’s folly, providing a nearly empty “explanation” for opium’s causing sleep (Filler, 2009, pp. 779–780). If “heterozygosity-space” resembles “fatigue-space” in Filler’s sense too closely, then the “toward homozygosity” response to this objection fails.

Another worry about “toward homozygosity” as a direction for drift is that it may mischaracterize what it is that drift is intended to describe. As mentioned above, drift has a direction toward homozygosity insofar as (in the absence of mutation and migration) homozygosity constitutes a set of absorbing barriers for the state of a population. What drift is genuinely about, however, is not the existence of these barriers – which are set by the mutation and migration constraints – but rather the population’s behavior *between* these barriers. This “toward homozygosity” direction of genetic drift, therefore, is not a feature of drift itself, but defined by other parts of evolutionary theory; thinking that

2. The sense of “stochastic” and “random” at work here is, therefore, a subjective one. Whether or not there exists a stronger type of stochasticity underlying genetic drift, and what exactly this sense might amount to, seems to hinge in large part on the result of the debate over drift’s causal potency (see Rosenberg, 2001).

3. Though see Pigliucci and Kaplan (2006) for some of the difficulties with the adaptive landscape metaphor.

“toward homozygosity” is a feature of drift thus may be mistaken.

We have several independent reasons, then, for suspecting that the defense of the force view by appeal to drift’s direction “toward homozygosity” is problematic. If this is true, we must look for another way to resolve the trouble with drift’s direction, and the second available response turns to the definition of ‘force’ itself. Perhaps the trouble with the objection lies in its rigorous adherence to the claim that forces must have directions predictable in advance.⁴ Could we discard this requirement *without* discarding the extra explanatory power that the notion of a ‘force’ provides us?

One attempt to do so is offered by Filler (2009, pp. 780–782). He argues that we may harvest two specific criteria for forces from the literature on Newtonian systems: namely, that forces be both *precisely* numerically specifiable in magnitude and able to unify our explanations of a large array of phenomena. Such criteria, it is presumed (though not argued), would forestall the “dormitive force” while permitting genetic drift. Even if they do not, however, Filler notes that “we could still posit a continuum of forces with maximally precise and unifying forces on one end and mathematically vague and weakly unifying forces on the other” (Filler, 2009, p. 781).

What of this attempt to salvage the force view? In general, I am broadly sympathetic with the response of carefully weakening the criteria for ‘force’-hood. I would like, however, to support the same conclusion by a slightly different line of argument. While the literature that Filler cites to establish mathematical specifiability and unifying power as desiderata for forces is valuable, I am concerned about it for two reasons. First, given that these criteria are offered by Filler without providing an analysis of genetic drift or any other forces, they seem dangerously close to being ad-hoc additions to our force concept. Is there a principled argument for why these criteria should replace that of directionality, in general? Second, Filler does not offer a direct argument that genetic drift passes these criteria, so we can’t yet be sure that the argument he provides gives us the result that we’re looking for. I believe both of these deficits can be remedied by comparing genetic drift to a different force that is standardly invoked in Newtonian dynamics: Brownian motion.

2.1. Brownian Motion

My claim, then, is this: whatever our general analysis of a force winds up being, it happens to be the case that we *already* countenance examples of forces that do, indeed, have stochastically specified directions, namely, the force of Brownian motion. This argument is admittedly less ambitious than that of Filler – we do not, for example, wind up with enough theoretical resources to fully specify the continuum from paradigm cases of forces to fringe cases. But we do have precisely what we need to countenance genetic drift as a force, for genetic drift,

4. The claim that forces must have specifiable directions appears, at least, in Matthen and Ariew (2002); Stephens (2004); Brandon (2005); and Brandon (2006).

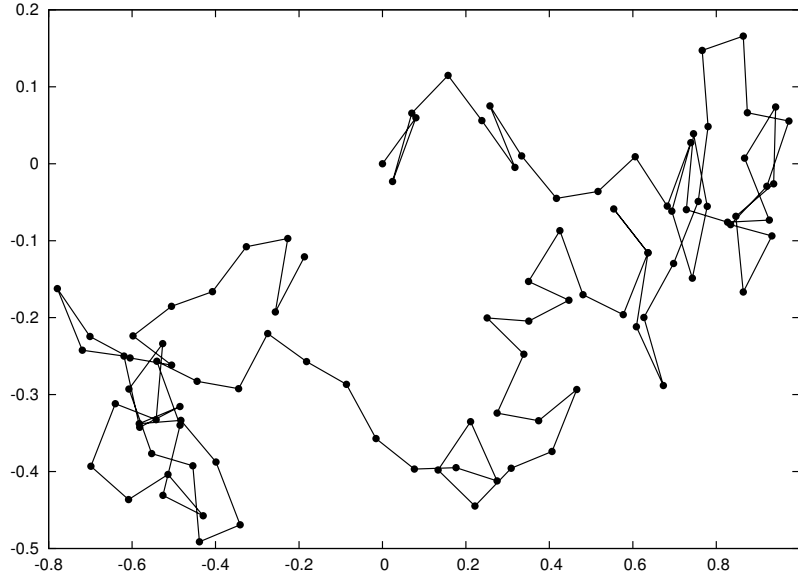


Figure 1: A simulation of a particle released at $(0,0)$ undergoing Brownian movement. Inspired by Perrin’s drawing of the Brownian motion of colloidal particles in water, viewed under the microscope (fig. 6 of Perrin, 1909, p. 81).

it turns out, can be formulated precisely analogously to the force of Brownian motion.

Brownian motion is a common occurrence. The behavior of dust particles as they float through a sunny window or a glass of water is governed in large part by the manner in which they collide with the molecules of the fluid in which they are suspended (see Figure 1). Since the motion of the fluid molecules is itself modeled stochastically (with the tools of statistical mechanics), it is unsurprising that Brownian motion in turn is a stochastic force.

What does the formal representation of a stochastic classical force look like? The now-standard derivation of the mathematics of Brownian motion was provided by Langevin in 1908 (translated in Lemons and Gythiel, 1997):

$$m \frac{d^2x}{dt^2} = -6\pi\mu a \frac{dx}{dt} + X. \quad (1)$$

This is a stochastic differential equation, with x representing the location of the particle within the fluid, m its mass, a a damping coefficient $-6\pi\mu a$ (which describes the manner in which the viscosity of the fluid through which the particle moves slows its travel), and a random “noise term” X , which describes the actual effect of the collisions with fluid molecules.

A few observations about this equation are in order. First, it is written as an equation for a force: $m \cdot d^2x/dt^2$ is just mass times acceleration, so we could equivalently have written $F = -6\pi\mu a \cdot dx/dt + X$. Nor need one quibble that the differential equation specifying this force references the particle’s velocity, dx/dt . Equations for many other forces do so as well, including friction in air or

water (drag). Secondly, the “source” of the randomness here is obvious, coming entirely from the noise term X . About it, Langevin says that “we know that it is indifferently positive and negative and that its magnitude is such that it maintains the agitation of the particle, which the viscous resistance would stop without it” (Lemons and Gythiel, 1997, p. 1081).

Finally, the force described by this equation bears all of the same “problematic” characteristics as genetic drift. Most importantly, its direction can by no means be predicted in advance: nothing about the direction of the force described by equation (1) is “determinate” in this sense. It depends entirely on the noise term which, as Langevin notes, “indifferently” (that is to say, randomly) changes sign and magnitude as the system evolves. The same is, of course, true of genetic drift, under which an allele frequency is equally likely to increase or decrease at each point in time. The example of Brownian motion, therefore, offers us a case in which the notion of ‘force’ is weakened in *precisely* the way required to countenance genetic drift – by admitting forces that vary in direction stochastically over time.

The opponents of the force view still have one obvious way to respond to this argument. They might reject outright the extension of force talk to both Brownian motion and genetic drift. While this is a perfectly coherent choice, I am not certain what the motivation for it would be. Of course, when we introduce a stochastic force, we introduce an element of unpredictability into our system, rendering null one of the primary benefits of a classical, force-based picture: the ability to use information about component force values to make determinate advance predictions about the behavior of systems. But we already lack the ability to make such detailed predictions of individual biological systems – why would we think that a force-based view of evolutionary theory would somehow make them possible? The question, rather, is simply whether it is possible to maintain a “net-force” picture of evolutionary theory which includes the randomness of genetic drift, and the example of Brownian motion shows this to be clearly achievable, should we be inclined to do so.

Further, just because the values are not predictable in advance does not mean that these stochastic forces somehow cannot be taken into account in the development of models. The Wright-Fisher model of genetic drift has spawned much research in population genetics as a computational/mathematical model of the action of genetic drift, and, similarly, Brownian motion can be taken into account in models of fluid dynamics when it is taken to be an important factor (see, e.g., Huilgol and Phan-Thien, 1997).

Finally, it seems that many authors in the debates over the causal structure of evolution either explicitly tolerate or make room for forces of different sorts such as these. McShea and Brandon, for example, when discussing how we might arrive at the “correct” distribution of evolutionary causes into forces, note their skepticism that “there are objective matters of fact that settle what counts as forces in a particular science, and so what counts as the zero-force condition” (2010, p. 102). That is, while facts can settle what causal influences are at work in a given system, they cannot, according to McShea and Brandon, settle how we

partition these causal processes into “forces.” Even the statisticalist analysis of Walsh, Lewens, and Ariew describes as a paradigm case of Newtonian, dynamical explanation the case of a feather, “affected not only by the force of gravity but also by attractive forces from other bodies, electromagnetic forces, *forces imparted by random movements of the air molecules*, etc.” (2002, p. 454, *emph. added*). I claim that without further argument, there is little reason to dogmatically adhere to the requirement that forces have directions specifiable in advance.

3. Drift as “Constitutive” of Evolutionary Systems

Another line of attack on the force view, marshaled by Brandon, doesn’t turn on the appropriateness of stochastic-direction forces. Rather, it claims that it is a category mistake (or something close to it) to consider drift as an *external* force that acts on biological systems. Drift, on the contrary, is “part and parcel of a constitutive process of any evolutionary system,” and is therefore *necessarily* found in any set of circumstances in which evolution is possible. “Force” talk, on the other hand, should be reserved for forces which appear in “special” circumstances. In the biological case, mutation, selection, and migration (among others) are “special” forces, but drift, as a “constitutive” component of evolution, is not – it is part of the “zero-force” state of evolutionary systems (Brandon, 2006, p. 325).

To help elucidate this argument further, return to Maudlin’s discussion of “quasi-Newtonian” systems as mentioned in the introduction (2004, p. 431). Maudlin points out a very valuable psychological or motivational distinction between our inertial or zero-force laws and our deviation or force laws. Namely, the zero-force conditions are supposed to be what influences a body when, in some particularly relevant sense, *nothing is happening to it*. The appropriate sense of “nothing happening” is obviously domain-relative, and Brandon’s claim seems to be precisely that placing drift on the side of the force laws is a poor definition of “nothing happening.” When nothing is happening to a biological system, he argues, *it drifts*.

Again, let’s turn to an analogy with classical mechanics. Classical mechanics has its own set of highly pervasive forces, and for each of these we have made the implicit decision to consider that force not as part of the inertial conditions, but as a deviation from those conditions. Take gravitation, for example. We might reply to Brandon’s objection that gravitation is as universal in Newtonian systems as genetic drift is in evolutionary systems. Applying the logic of Brandon’s objection here, then, Newton’s first law is incorrectly formulated. Gravitation should be considered part of the “default” or “zero-force” state of Newtonian mechanics. While this isn’t an outright *reductio*, it strikes me that any discussion of forces which fails to handle the paradigm case of Newtonian gravitation is seriously flawed.

I suspect, however, that the supporter of this objection would reply that there is an important and salient difference between genetic drift and gravitation.

While there may be no Newtonian system which *in fact* exhibits no gravitational effects, it is possible to describe in Newtonian terms a system that would not be subject to gravitation – either by dialing the gravitational constant G back to zero, or by imagining the behavior of an isolated test mass “at infinity,” infinitely distant from all other mass in the universe. Gravitation therefore is not *necessary* for the description of a Newtonian system in the way that drift is for an evolutionary system.

It is not obvious to me, however, that there is any conceptual difficulty in abstracting genetic drift away from an evolutionary system. Imagine an infinite population with individuals initially equally distributed among four possible genotypes, A, B, C, and D. Parents produce offspring identical to themselves, modulo a small mutation rate. There exists a selective force, which causes types C and D to have a 10% chance of dying before reaching reproductive age. Finally, the reproductive output of each type in the next generation is set in advance: say that all types produce exactly one offspring if they survive to reproductive age, and then die. Here we have an example of a thought experiment on which selection exerts an influence (types C and D will clearly eventually die out), mutation has an influence (due to the non-zero mutation rate), but genetic drift has none. The population is infinite, so we have no bottleneck effects or effects of finite population size. Further, each individual has a guaranteed reproductive outcome from birth, based upon its type – and to the extent that these outcomes are probabilistic, this is the influence of *selection* or *mutation*, not *drift*. Indeed, we can predict that in the infinite limit, the population will consist of roughly half A organisms and half B.⁵

Is there anything more outlandish about this drift-free toy model than an example consisting of a universe containing only one isolated and non-extended point mass, free of gravitation, or a test mass at infinite distance from all other masses? Clearly there are no infinite populations in the real world, but here it seems we have a perfectly tenable thought-experiment on which we may separate the effect of drift from all the other evolutionary forces, and then reduce that effect to zero. There is nothing any more “constitutive” about drift for evolutionary systems than there is about gravitation for Newtonian systems.

4. Conclusion

I have here considered two arguments against the conceptual tenability of considering genetic drift as a “force” like those of Newtonian dynamics. The first asserted that genetic drift lacks a predictable direction. This argument fails by virtue of an analogy with Brownian motion: if Brownian motion is a satisfactory force (and, I have argued, it is), then so is genetic drift. The second argument against drift-as-force proposed that drift is a constitutive feature of evolutionary systems. This argument fails because accepting its premises results in a misun-

5. With a small, but predictable, fraction of newly-arisen mutants. I am indebted to Grant Ramsey’s thoughts on drift for helping me devise this example.

derstanding of the relationship between Newtonian gravitation and inertia.

I have, of course, done nothing here to resolve the overall debate between the causal and statistical interpretations of evolutionary theory. But the utility of the force metaphor in the description of evolutionary systems makes it something worth defending – and it continues to survive the host of objections raised against it.

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