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Is genetic drift a force?

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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 as analogous to "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. I go on to diagnose the reasons for the stubborn persistence of this problem, considering two open philosophical issues and offering some preliminary arguments in support of the force metaphor.

Keywords Evolutionary theory · Genetic drift · Force · Causation · Brownian motion

1 Introduction

Evolutionary theory can, as we all know, be decomposed into multiple components or factors. It characterizes change in populations over time, that is, as the result of natural selection, genetic drift, mutation (Mani and Clarke 1990; Merlin 2010), migration (Shpak and Proulx 2007), linkage disequilibrium (Lewontin and Kojima 1960; Lewontin 1964), meiotic drive (Lyttle 1993), extinction (Lynch et al. 1995; Jablonski 2005), increase in complexity (McShea 1996, 2005; Carroll et al. 2001), and so on.

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A natural philosophical question to ask of the evolutionary process, then, is this: what is the relationship between these "component" theories and the overall trajectory of evolution?

One common approach to answering this question has been to draw an analogy between evolutionary theory and Newtonian mechanics—in particular, to describe these elements of evolution as component forces, and overall, observed evolutionary change as the effect of the "net" or "resultant" force that is their "sum." This analogy, despite its ubiquity, has come in for serious criticism over the last decade.

In this paper, I will evaluate two arguments against the force interpretation of evolutionary theory—in particular, arguments that genetic drift cannot be considered as a force, and hence that the entire force metaphor fails. The first is the (by now, well-trodden) claim that genetic drift, though its expected magnitude may be determined by the effective population size, lacks a direction specifiable or predictable in advance.[1] 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 real-world evolving populations will drift, and thus to describe drift as an "external" force is misleading. Both of these critiques, I will show, miss the mark—if the force metaphor is untenable, it is not for either of these reasons.

This claim, in turn, raises another important question: how ought we evaluate the force metaphor as a whole, after these two arguments are set aside? I will not offer a complete evaluation of this issue here, but as a first step toward a solution I will describe two philosophical issues central to the debate over the use of the Newtonian metaphor in evolutionary theory, and offer some preliminary support for the force interpretation.

2 The force metaphor

Philosophical work on the relationship between evolution's component factors and resulting overall evolutionary change has recently focused on the *causal* picture implied by the structure of evolutionary theory. Where are we to find the causes in evolutionary theory? Do any of the component theories describe independent causes? If so, which ones? And if there are such component causes, how do they combine to produce the resultant trajectory of populations through time? Two broad 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 these components—in particular, natural selection and genetic drift—are not causal. Rather, the causes at work function at the level of individual organisms and their biochemistry: individual instances of survivals, deaths, predations, mutations, and so forth. All these "higher-level" theories, then, constitute quite useful, but *not* causal, ways in which

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[1] Note that, *contra* the claim of Filler (and many others) that the magnitude of drift is represented by population size (Filler 2009, p. 777), population size only determines the distribution of drift outcomes, and hence the expected magnitude of drift. I thank an anonymous reviewer for pointing out this fact.

we may statistically combine events to enable us to grasp interesting trends within populations of causally interacting individuals.[2]

The other view, the "causalist" interpretation (e.g., Millstein 2002, 2006; Shapiro and Sober 2007), considers all of these factors to be genuinely causal. Evolution causes changes in populations, and selection, mutation, migration, genetic drift, etc. do so as well. How exactly we specify these causes varies (about which more later)—for example, as different varieties of "sampling" (Hodge 1987), as population-level causal processes (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.[3] It is a common pedagogical trope in the teaching of biology to describe all of these factors as *component forces,* each of which propels a population in a different direction through some space (of morphologies, phenotypes, genotypes, etc.) with a different strength, combining, 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 secondary 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 the 'force' metaphor at all levels of biological pedagogy. But what of it? Why is this particular biological turn of phrase of philosophical interest? Depew, for example, argues rather persuasively that this should, at best, be seen to be deployed for *rhetorical* purposes—part and parcel of an attempt to couch the optimizing and maximizing effects of natural selection in language which avoids "the ascription of intentions and rational choice" (2013, p. 138).

Writing off the force interpretation this quickly, though, is a mistake. In his original introduction of what would become the causalist interpretation, Sober (1984) influentially described evolutionary theory as a *theory of forces.* Sober's invocation of Newtonian mechanics is not merely semantic—it is intended to carry some genuine explanatory weight. Allowing, of course, that the analogy here is not entirely precise,

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[2] I have described the statisticalist position in a univocal way here, though I suspect that there is as great a diversity of positions among those in the "statisticalist" camp as that in the "causalist" camp which I will describe later. Compare, for example, the positions reflected in Lewens (2010), Walsh (2010), and Matthen and Ariew (2009).

[3] I should also pause to set aside another facet of this debate: the distinction between the processes and products of evolution (the classic source here is Millstein 2002). In the following, I mean to refer only to the *processes* of evolution, as it is clear that this is the feature to which the force interpretation is directed.

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 only 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)

On this picture, which I have interchangeably called the "force metaphor" and the "force interpretation," we draw an analogy between the structure of Newtonian mechanics and the structure of evolutionary theory. As has been repeatedly emphasized, however—most recently and thoroughly by Hitchcock and Velasco (2014)—this is not to say that the two theories are perfectly analogous. Indeed, the question, as Lewens has aptly phrased it, is "in what respects selection and drift resemble Newtonian forces, and in what ways they differ, paying attention all the time to the dangers of a seductive metaphor" (2010, p. 316). To at least some extent, then, proponents of the force interpretation hold that the force "metaphor" is no metaphor at all—at least some components of evolutionary theory really can be described as forces. The force interpretation's detractors hold that such language is at best merely suggestive, if not entirely devoid of value.[4]

If true, the force interpretation 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.[5]

There are many reasons why such a 'force' picture of evolutionary theory might be interesting or useful (even those as mundane as the subjective preference noted by Maudlin), but I want to draw out one in particular. If the statisticalist picture is the correct way to understand evolutionary theory, then the original question with which we began—how to explain the manner in which the various component parts of evolutionary theory combine to produce observed evolutionary change—may be answered in a straightforward manner. The standard tools of statistics are aimed, at least in part, at resolving precisely this problem: we know how different statistical distributions combine to produce resultant distributions, and in the absence of any invocation of causation, this mathematical story is the only story required.

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[4] I will continue using "the force interpretation" and "the force metaphor" interchangeably in the following, recognizing throughout that the question up for debate is the extent to which force language can be said to truly describe evolving systems.

[5] A very similar explanation of the general structure of 'force'-theories is offered by Ellis (1963, 1976), who divides states of a system between "natural" states of affairs that do not require "a continuing causal explanation" and "unnatural" states which do require such explanation—and this separation is a matter of a domain-specific demarcation of the relevant "natural" states.

But the case is different when we turn to the causal interpretation. If all these components of evolution—natural selection, genetic drift, mutation, migration, etc.—are independently theorized, described separately from one another, and yet are all supposed to invoke *causal* processes that act on the same system, the question of how this combination is to proceed becomes more relevant. Of course, we know what the result of such a combination will be (it is specified by the equations of population genetics, or life-history theory, or evolutionary ecology, etc.). But how ought we to think about multiple independent causal influences combining together into a single "resultant" cause? The force metaphor can provide us with an answer. For if the pieces are independent and causal in the same way as Newtonian forces, then we have a ready understanding of the concept of overall evolutionary change by analogy with net or resultant force.[6]

3 What is genetic drift?

If the invocation of quasi-Newtonian forces is a natural way to analyze theories, gives us a handle on how the various components of evolutionary theory might work together, and has been frequently invoked by biologists, then what is the issue? To begin, it is clear that the use of force language in the more substantive, causally loaded sense of Sober opens the force-theorist to an additional line of argument that would not be germane to other varieties of the causal view.[7] 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 the next two sections, I will evaluate two arguments for this claim (and find both lacking), but we should begin with a brief synopsis of what sorts of evolutionary influences are commonly subsumed under the label of 'genetic drift'.

In his helpful review of its history and scope within biology, Beatty (1992) notes that surprisingly little unifies the phenomena known as genetic drift. While "most of the phenomena so designated have in common … one or another biological form of random or indiscriminate sampling," this will not even suffice to demarcate its complete scope, as "there are phenomena sometimes included in the category of random drift

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[6] This point, as with all issues in the causalist/statisticalist debate, is also a matter of some debate. Importantly, if this analogy is to hold, a suitable analogue of "vector addition" must be found for the evolutionary case. Matthen and Ariew (2002, pp. 66–68) push this point forcefully, framing it in terms of the inability to compare different values of "vernacular fitness." Considering the debate over fitness would take us too far afield here; the causalist can, however, respond by providing a new model of fitness which *can* be compared across different biological contexts (Pence and Ramsey 2013), or elucidating a non-additive model of force composition (Stephens 2010).

[7] 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).

that have nothing to do with random sampling" (Beatty 1992, p. 273). We have little choice but to work by example.

Perhaps the most common use of genetic drift among philosophers refers to what Hodge called "fortuitous differential reproduction in the accumulation of random or indiscriminate errors of sampling" (1987, p. 233), an invocation of *indiscriminate sampling processes,* sampling processes which do not take into account differences of fitness between organisms. Often, philosophers instantiate this indiscriminate sampling by invoking "a natural catastrophe that kills all the nearby members of a species indiscriminately, resulting by chance in a change in frequency of the various types within the species" (Beatty 1992, p. 274).[8] Natural selection, on such a view, consists of those drivers of population change that *are* sensitive to differences in fitness values, while genetic drift consists of those causes (like, presumably, natural disasters) for which fitness differences are irrelevant.[9]

Another process responsible for genetic drift is to be found in *Mendelian segregation.* In sexually reproducing, diploid organisms like humans, each individual carries two copies of each gene. In sexual reproduction, offspring receive one copy from each of their parents. Parents will therefore pass only one of their alleles on to each of their offspring. This entails that, merely as a matter of chance, it is possible for an allele to change frequency or even disappear entirely from a population in a single generation: if all parents carrying one allele (call it 'A') also carry a second, different allele (call it 'a'; we call such organisms 'heterozygous'), and all happen to pass the 'a' allele to their offspring, the 'A' allele will vanish. Since this dramatic population change comes about without the influence of natural selection or any other evolutionary factors, this is a clear instance of genetic drift.

Whichever of these (and other) evolutionary factors we choose in the end to call 'genetic drift',[10] we can discern enough common threads to move forward—genetic drift is intended to encompass stochastic or random influences on populations whose effects do not depend on differences in the fitnesses of individual organisms or their traits. And this is enough of a handle on genetic drift to motivate our two objections to the reading of genetic drift as a force.

4 The direction of drift

It is by now an old chestnut in this debate that genetic drift lacks a specifiable or predictable direction. To cite only two examples, Matthen and Ariew (2002, p. 61)

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[8] This conception of genetic drift as indiscriminate, lethal natural disaster is pervasive in the philosophy of biology (see, e.g., Beatty 1984; Millstein 2002; Sterelny 2003; Gildenhuys 2009), and unfortunate insofar as biologists are often much more concerned with many of the other notions of drift mentioned here, as these are more frequently found in natural populations.

[9] This view comes, of course, from one side of the causalist/statisticalist debate, and hence is a matter of significant controversy. The characterization of drift it provides, however, is well known, and serves as an example of the general trend I identify below.

[10] Beatty (1992) also mentions neutral mutations, the founder effect, and even (though such a view is now outmoded) the causes of *any* non-adaptive characters as factors which have, at various historical moments, been considered to be varieties of drift.

note as an 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. As we have already seen, genetic drift is a stochastic process. Consider once again a population which is uniformly heterozygous for some trait 'Aa'—all members of the population possess one copy of the 'A' allele and one copy of '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 is because the states in which all members of the population are homozygous for either 'AA' or '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 which will be its eventual fate is a matter of chance. In this sense, at least, the population-level outcome of genetic drift is random.[11] It is obvious, the argument concludes, that drift cannot act as a Newtonian force, because Newtonian forces have determinate directions. Consider natural selection. The direction in which selection will drive a population is indeed specifiable in advance: selection drives 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.[12] 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, i.e., it "tends to remove variation from natural populations" (Stephens 2010, p. 721; see also 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. Imagine, for example, a slightly modified version of 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).

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[11] This means that, at a minimum, there is a subjective sense of "chance" and "randomness" at work here (i.e., we are unable to predict the outcome of the process of drift). Whether or not there exists a stronger type of "chance" 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).

[12] Though see Pigliucci and Kaplan (2006, Chap. 8) for some of the difficulties with the adaptive landscape metaphor.

Given a particularly broad concept of force, there is thus a continuum of possible force explanations, ranging from entirely vacuous or circular to quite informative. Lacking any argument about the location of genetic drift on this continuum, we don't know whether or not "heterozygosity-space" gives us vacuous, empty force explanations, or genuinely useful explanations—if the former, then the "toward homozygosity" response to this objection fails.

Second, "toward homozygosity" appears to be a direction in the wrong sort of state-space for descriptions of genetic drift.[13] Selection, by comparison, drives trait frequencies in the direction of some particular trait (or genotype), the one with the highest fitness immediately reachable from the population's present state. In such a space, "toward homozygosity" is *more than one direction* at once—in a population of hybrid 'Aa' organisms, say, it is a "direction" toward *both* 'AA' and 'aa'. It is only a unitary direction in some higher-level or second-order space, with a single axis running from homozygosity to heterozygosity.

Finally, another worry about "toward homozygosity" as a direction for drift is that it seems to confuse the question of which phenomena drift is intended to describe. As mentioned above, drift has a direction toward homozygosity predictable in advance insofar as (in the absence of mutation and migration) homozygosity constitutes a set of absorbing barriers for the state of a population. That is, the population tends toward homozygosity in the long run only because once one of the alleles is removed from the population, there is no way for it to be reintroduced. Were this not the case, drift would simply be a random walk. The phenomena that are genuinely "due to" drift, that is, are not the homozygous states (which it would be more natural to say are "due to" the absence of mutation and migration). Drift, rather, accounts for the behavior of the population *between* these barriers, and the behavior it *would have* were the barriers absent—namely, the random walk. Thus, to describe drift as directed "toward homozygosity" incorrectly takes an incidental claim about the absence of mutation and migration to be a central feature of drift itself.[14]

We have several independent reasons, then, for suspecting that the defense of the force view by defining drift as directed "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.[15] Could we discard this requirement *without* discarding the 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

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[13] I thank an anonymous reviewer for pointing out this objection.

[14] Another way to see this is to note that in a population with only selection acting (with a non-zero selection coefficient), in the absence of mutation and migration, we could *also* equally well predict that the population will arrive at an absorbing barrier and stay there. The existence of the barriers has nothing to do with the process driving the population change. I thank an anonymous reviewer for pointing me toward this analogy.

[15] The claim that forces must have specifiable directions appears, at least, in Matthen and Ariew (2002); Stephens (2004); Brandon (2005, 2006); Wilson (2007); and Massin (2009).

(criteria argued for by Bigelow et al. 1988): 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 cases like 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 tactic 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 be added to that of directionality, in general? Such an argument would, it seems, be best phrased in the context of an understanding of what exactly the use of ‘forces’ is to do for us, and when explanations utilizing a force metaphor are useful or perspicuous. I will come back to this issue in Sect. 6.1, but for now it will suffice to note that we do not possess such an account. Second, Filler does not offer a direct argument that genetic drift satisfies these criteria, so we can’t yet be sure that the argument he provides gives us the result that we’re looking for.[16]

I believe both of these deficits can be remedied by comparing genetic drift to a different force that is often invoked in Newtonian dynamics: Brownian motion. If, that is, we cannot in general describe when force metaphors have utility, we may profitably turn to the physicists themselves as arbiters of a “successful” use of force-explanations. The use of a stochastic force in physics would, then, give us a reason—though a defeasible reason, to be sure—that this argument against considering genetic drift to be a force fails.

4.1 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—and as an example, we can consider 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 what we need to block the objection that genetic drift cannot be considered to be a force thanks to its stochastically specified direction.

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[16] Though it is certainly the case that the argument in favor of mathematical unification is relatively straightforward, given that “drift” explanations unify a wide variety of empirical/causal phenomena. Thanks to an anonymous reviewer for pointing this out.

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 Fig. 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):

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

This is a stochastic differential equation, with x representing the location of the particle within the fluid, m its mass, 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 differen-

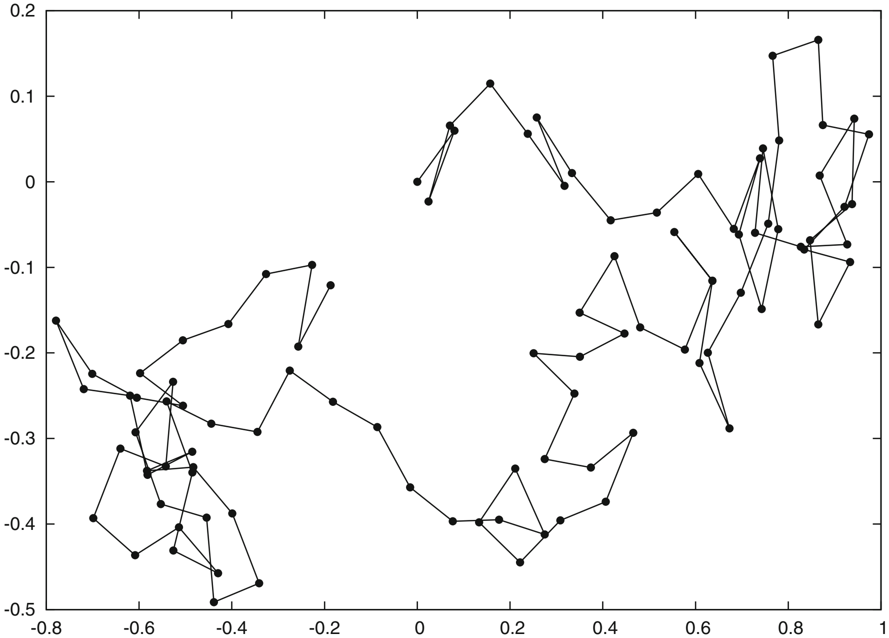

Fig. 1 A simulation of a particle released at (0, 0) undergoing Brownian movement. Inspired by Perrin’s drawing of the Brownian motion of colloidal particles in water, viewed under the microscope (Fig. 6 of Perrin 1909, p. 81)

tial 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 (at least on the simplest models of drift) an allele's 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 (or systems experiencing Brownian motion)—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 their directions cannot be described 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). What matters, that is, is that we are able to (1) describe the causal structure of evolutionary theory in general, and (2) when needed, predict (using the "resultant force") the future trajectory of a given population. Stochastic forces cause no problem for either of these requirements.

Finally, it seems that many authors in the debates over the causal structure of evolution either explicitly tolerate or make room for stochastic forces such as these. Stochastic forces are, therefore, already present in many accounts of the structure of evolution (whether explicitly or implicitly).[17] 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 objective features of the natural world can settle what causal influences are at work in a given system, they cannot, according to McShea and Brandon, settle how we choose to partition these causal processes into "forces"—an element of this latter decision is and must remain subjective.[18] 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.

Of course, this is not to say that deterministic-directional forces and stochastic-directional forces such as Brownian motion are identical, or that there are not interesting and relevant differences between deterministic and stochastic forces. The dynamics of systems in which stochastic forces play a role, for example, will be much more difficult to describe over the long run, and it has recently been argued that such long-run descriptions are sometimes required to adequately account for some features of evolution (Pence and Ramsey 2013). Metaphysical accounts of forces as either dispositions (Hüttemann 2009) or causal powers (Massin 2009) will need to take account of the fact that those dispositions or causal powers are probabilistic for these stochastic forces.

But it is important not to overstate these differences. Deterministic chaos makes trouble for dynamical prediction even in complex systems with deterministic forces (Werndl 2009), and, as I argued above, the dynamics of evolutionary systems are made no more difficult to predict by thinking of genetic drift as a force than they are if we choose not to think of genetic drift as a force.

5 Drift as "constitutive" of evolutionary systems

Another line of attack on the force view, marshaled by Brandon and expanded in his work with McShea, 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

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[17] Notably, if evolutionary forces may be stochastic, then it is likely that selection is best considered as a stochastic force as well. While I lack the space here to pursue all the consequences of this claim, it sharpens the debate between Millstein and Brandon over the distinction between natural selection and genetic drift (Brandon and Carson 1996; Millstein 2002, 2005; Brandon 2005), as it no longer becomes possible to simply sort evolution into its "deterministic" and "indeterministic" components. I thank an anonymous reviewer for noting this implication.

[18] Such conventionalism about what is to count as a force is echoed in several places in the literature (e.g., Ellis 1976; Stephens 2010); see Forster (1988) for opposition.

found in any set of circumstances in which evolution is possible.[19] “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).[20]

To help elucidate this argument further, return to Maudlin’s discussion of “quasi-Newtonian” systems as mentioned in Sect. 2 (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 describe the behavior of a body when, in some particularly relevant sense, *nothing is happening to it.* As is familiar from the Newtonian case, inertial or zero-force conditions can only be observed when they aren’t being overwhelmed by external, second-law forces. Thus the definition of a relevant or appropriate sense of what it is for “nothing to be happening” to a system is intimately tied up with the definition of its inertial or zero-force states.

This sense of “nothing happening,” however, will assuredly be domain-relative, and a matter of the structure of each theory which we wish to consider in a quasi-Newtonian manner. McShea and Brandon, then, claim that placing drift on the side of the force laws—as a second-law, external force—and declaring the Hardy-Weinberg conditions to constitute the times when “nothing is happening” to a biological system results in a poor definition of “nothing happening.” When nothing is happening to a biological system, they argue, *it drifts.* Drift is thus the zero-force or inertial state of evolutionary systems, revealed by the removal of all external forces (like selection, mutation, migration, etc.).

To respond, let’s turn again to an analogy with classical mechanics. Recall from above that a significant part of Brandon and McShea’s evidence that genetic drift serves as the zero-force condition for evolutionary theory rests on drift’s nature as a constitutive, pervasive, or universal characteristic of all real-world evolving systems. Classical mechanics, in turn, has its own set of highly pervasive forces, such as gravitation. Following Stephens (2010, p. 721), if this pervasiveness is to count as evidence that genetic drift features in the zero-force condition for evolution, it should equally well serve as evidence that gravitation ought to feature in the zero-force condition for Newtonian mechanics. If this is right, then Newton’s first law itself is incorrectly formulated, as it fails to incorporate gravitational interaction. 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.

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[19] Or, to be precise, *almost* any—McShea and Brandon define drift as a certain kind of population-level outcome, and it is logically possible (though practically impossible) that drift could produce precisely the outcomes expected of pure natural selection, over and over again. Any real-world evolving population, however, will drift in almost all circumstances.

[20] I should note that my argument against Brandon and McShea’s objection in this section does *not* extend to the coherence or utility of their own, positive ZFEL view. As part of their defense of ZFEL, however, McShea and Brandon (Brandon 2006; McShea and Brandon 2010) argue that Sober’s traditional view, on which genetic drift is considered as a second-law force, is incoherent. It is that argument alone which I claim fails. It has also been briefly evaluated (and rejected) by Stephens (2010, p. 721); the approach I offer here goes farther, I believe, toward telling us *why* this “default-cause” argument fails.

I suspect, however, that the supporter of this objection has a ready reply—there is, one might claim, 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 *conceptually necessary* for the description of a Newtonian system in the way that drift is for an evolutionary system. This, I take it, is the explanation for the emphasis of authors like McShea and Brandon (as well as, e.g., Matthen and Ariew 2002) on the biological and biochemical "substrates" of evolution—if evolution *cannot be conceptualized* without drift, because it cannot be conceived except as acting within a substrate that entails the presence of drift, then this, as the reply goes, suffices as a sufficient difference between drift and gravitation.

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 long run, the population will consist of roughly half A organisms and half B.[21]

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. For that matter, the way in which the expected behavior of both systems is inferred seems to be identical: just as the physicist imagines the limiting case of smaller and smaller values of G, the biologist imagines larger and larger population sizes. There is nothing any more "constitutive" about drift for evolutionary systems than there is about gravitation for Newtonian systems.

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[21] With a small, but predictable, fraction of newly-arisen mutants. Strictly speaking, this discussion concerns behavior in the *limit* as population size approaches infinity, as an actually infinite population cannot be divided into proportions in this way. This example was benefited by the discussion of drift in Ramsey (2013).

6 Moving forward on forces

In the last two sections, then, I have argued that two prominent objections to considering genetic drift as a force do not succeed. But this raises an equally important issue: what should we do with the force metaphor now? Does the removal of these two objections suffice to declare the force metaphor rehabilitated? Such a conclusion would be too hasty.[22] In this section, I will consider two philosophical problems—the overall structure of force explanations and the varying conceptions of the causalist interpretation of evolutionary theory. I offer some preliminary support for the force interpretation here, and I hope that focusing the debate in this way may make a more general appraisal of its merits possible.

6.1 When are force explanations useful?

Let's begin by turning back to an issue that I raised while considering the question of forces with stochastic directions. Resolving this problem by simply adding more criteria to our concept of 'force', such as mathematical specifiability, runs the risk of being an ad hoc modification. The most consistent way to determine whether or not such additions are ad hoc, it seems, would be to embed them within a clear understanding of when an explanation that makes reference to forces is useful and when it is not—that is, to describe the circumstances in which a force explanation gives us genuine purchase on the structure of systems in the world and when such an explanation fails to do so.[23]

There does exist, of course, an extensive literature considering the appropriate role and metaphysical character of forces *within Newtonian mechanics itself* (e.g., Wilson 2007; Bigelow et al. 1988).[24] We see discussions, for example, of whether or not a realist interpretation of forces is justified (for realism, see Hesse 1959; Wilson 2007; Massin 2009; for anti-realism, see Jammer 1957; Fraassen 1980), whether it is individual component forces or the resultant force that ought to be interpreted realistically (Creary 1981; Rupert 2008; Wilson 2009), or whether forces are causally intermediate entities, standing between individual objects and the motions that those objects experience (Bigelow et al. 1988; Wilson 2007).

This literature has not, however, extensively evaluated the legitimacy or usefulness of what Maudlin called 'quasi-Newtonian' theories—theories which are phrased in terms of inertial conditions and deviations *other* than Newtonian mechanics. In his

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[22] For one, there exist further objections to the force metaphor in the literature—Stephens (2010), for example, considers an objection due to Walsh (2007).

[23] Notably, this is a different enterprise than attempting to search for forces as a project lying within the metaphysics of science. I believe considerations like those raised by McShea and Brandon's conventionalism and Maudlin's characterization of quasi-Newtonian theories are fairly decisive that the appropriate question concerns not the existence or ontology of forces, but the explanatory utility of different *types* of force explanations in different *circumstances.*

[24] Wilson (2007, pp. 179–184) raises the interesting possibility that forces in Newtonian mechanics are *not* a fundamental depiction of the world, but rather are elements posited by Newtonian mechanics insofar as it is a *special science,* just as biology is. This would be yet more evidence closing the analogical gap between forces in Newtonian theory and forces in biology.

incisive *Concepts of Force,* Jammer notes, in terms that might well be amenable to us here, that the usefulness of the concept of ‘force’ “is that it enables us to discuss the general laws of motions irrespective of the particular physical situation with which these motions are situated” (Jammer 1957, p. 244).[25] But even this sophisticated treatment brings under the heading of “Concepts of Force in Contemporary Science” only the legacy of Newtonian forces in quantum mechanics, nuclear forces, and special and general relativity.

One notable exception to this general silence on quasi-Newtonian theories is the work of Ellis (1963, 1976). While his examples still come entirely from physics, Ellis phrases his approach to forces in a manner general enough to apply outside the physical sciences. He proposes the following as criteria for a successful use of the concept of ‘force’:

> At its best, a force explanation involves the use of laws of distribution, combination and action of force. Laws of distribution … are laws that enable us to calculate the magnitude of at least some component of the resultant force that is acting upon a system…. Laws of combination, like the vector law for addition of forces, are ones that enable us to calculate the magnitude of the resultant force acting upon a given system from the magnitudes of its various components. Laws of action of force are ones that determine the magnitude of the effect to be explained from a knowledge of the magnitude of the resultant force and of a certain quantity (the inertial factor) that we say provides us with a measure of the system’s resistance to the action of that force. (Ellis 1976, p. 175)

But even this, the best the literature has to offer us for a general discussion of the applicability of ‘force’ explanations, doesn’t clearly weigh in one way or the other in the biological case. While proponents of the force metaphor have offered distribution laws (e.g., the distribution of fitness for natural selection, or the size of populations for genetic drift), combination laws (though these are non-additive, as stressed by Stephens 2010), and laws of action (specified by population genetics, for example), these are not enough to give us a complete evaluation of the force interpretation.

Ellis’s criteria thus fall short, and we may trace this failure to two sources. First, a significant part of what is at issue in the debate over the force metaphor can be seen to be, in these terms, whether or not the evolutionary laws of distribution, combination, and action (particularly the non-additive law of combination) are good enough to serve in the roles demanded of them by Ellis’s understanding of force. To complicate matters, it’s not obvious *which* of the various candidates for the laws of distribution one ought to utilize—consider, for example, the diversity of mathematical analyses of fitness (Jong 1994). Second, we haven’t at all engaged with the broader question of the overall utility of an explanation phrased in terms of forces. That is, even if we can write down laws of distribution, combination, and action, we haven’t yet laid down any criteria as to when and whether such an explanation is beneficial, or provides us with genuine insight into the system being thus explained, as opposed to being nothing more than a syntactic variant of a non-force-based theory.

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[25] Sober (1984, p. 126) invokes a very similar reference to generality in his defense of the separation of natural selection from genetic drift.

The resolution of these sorts of questions would take us far too afield here. But I do claim one thing is obvious: some steps toward answering these kinds of questions about theory structure will be crucial if we are ever to make genuine advances beyond the current state of the debate on the force interpretation. This is the first major piece of open philosophical work forestalling genuine contributions to our understanding of the force picture.

6.2 The causalist interpretations

The second significant issue to be resolved lies in the framing of the causalist/statisticalist debate itself. While it is often presented as a simple, two-sided question, there are in fact an impressive diversity of ways in which one might adopt a causalist understanding of evolutionary theory. More importantly for the project here, the force interpretation is only one of many ways in which one might advocate for the causalist position. An important and long-overdue ingredient, then, in our evaluation of the overall success or failure of the force metaphor should be a comparison between these distinct ways of understanding the causalist project.

At the very least, we need to distinguish between (1) the force interpretation, as discussed here; (2) the *causal process* approach (elaborated most notably by Millstein 2002, 2006, 2013); (3) the *causal mechanism* approach, first deployed for natural selection by Barros (2008) and building on the work of Machamer et al. (2000); (4) the *manipulationist* approach, discussed by Reisman and Forber (2005), Forber and Reisman (2007), and Shapiro and Sober (2007), building on the work of Woodward and Hitchcock (2003); and (5) the *counterfactual* approach, deployed for natural selection by Glennan (2009) and Huneman (2012) and utilizing a notion of counterfactual causal dependence or "relevance."[26] Of course, it is possible—or even likely—that these are not mutually exclusive. A force may equally well be a manipulable cause, capable of counterfactual description, or description as a causal process, or of being more thoroughly explicated by a mechanism. But each of these ways of approaching the problem will come with its own advantages and will guide our theorizing about evolution in particular directions—thus leaving us with a choice about which framework is the most perspicuous way of understanding evolutionary theory.

While I certainly will not settle the issue here, the force interpretation has several advantages with respect to some of these other positions. In particular, I claim that the force approach can salvage one of the key advantages of the mechanistic view while not falling prey to one of its most significant problems.

One distinct advantage that the mechanistic approach has relates to the ability of mechanisms to cut across ontological levels. For the process, manipulationist, and counterfactual approaches, the ontological level at which natural selection and genetic drift operates is a difficult question which depends not only on empirical input, but also on conceptual clarification—for example, just what sorts of entities can participate in

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[26] Of course, I have likely left off—or unduly lumped together—further ways in which one could adopt the causalist position. The relevant, and I believe underappreciated, claim remains, however: that there is a massive variety of "causalist interpretations" on offer in the literature.

causal processes, or what kinds of interventions can legitimately be performed on populations of individuals? Further, the question is taken to have a univocal answer: either selection and drift can both be located at the population level, or they can both be located at the individual level.[27]

The mechanist has more resources at her disposal to resolve this problem. In their seminal paper on mechanisms, Machamer et al. (2000, p. 13) write that "[t]he levels in these hierarchies should be thought of as part-whole hierarchies with the additional restriction that lower level entities, properties, and activities are components in mechanisms that produce higher level phenomena." That is, mechanisms can readily integrate events that occur at multiple causal levels, and the architecture of the mechanism is a question to be resolved by empirical input. The mechanistic approach thus has one fewer purely conceptual problem to resolve than the process, manipulationist, or counterfactual approaches.

The force theory, however, shares this advantage. Return to our general understanding of Newtonian or quasi-Newtonian theories. Earman and Friedman (1973, p. 337) note that one common approach to the interpretation of the first law is as a definition—that is, Newton's laws hold in inertial frames, where "an inertial frame is a frame relative to which the 'law of inertia' holds, i.e. relative to which a particle free of impressed forces either remains at rest or else continues in a state of uniform rectilinear motion." What would such a reinterpretation do for the evolutionary force theorist? In short, it renders the domain of applicability of evolutionary forces an empirical question, just as it is for the mechanist. We interrogate biological systems to see to what extent they approximate the structure required to instantiate the zero-force state of Hardy-Weinberg equilibrium—and if the approximation is reasonably close enough, it may profitably then be asked whether such systems are affected by forces like selection and drift.[28]

This levels the tables between the force and mechanist approaches. But a nod can be given toward the force view by considering one problem with the mechanistic interpretation. A central feature of mechanisms, on the Machamer–Darden–Craver view, is their *regularity:* mechanisms are defined as "entities and activities organized such that they are productive of regular changes from start or set-up to finish or termination conditions" (Machamer et al. 2000, p. 3). And regularity in this sense is defined such that mechanisms "work always or for the most part in the same way under the same conditions" (Machamer et al. 2000, p. 3). A "stochastic mechanism"—or, at

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[27] To cite a few particular instances, Millstein (2006) spends a significant amount of time defending the claim that the causal processes of selection and drift ought to be located at the population level, Huneman (2012) takes it as assumed that both selection and drift are population-level phenomena, while Ramsey (2013) situates both at the individual level. Of course, there are manifold problems inherent in 'ontological-levels' talk (Batterman 1995; Kim 2002; Heil 1999, 2003), but we lack any better way to make reference to the issues I describe here.

[28] The fact that there are no real populations which are actually in Hardy-Weinberg equilibrium parallels the well-known fact that there are no inertial frames in real-world Newtonian systems, only approximations thereto. Also, while I lack the space to pursue the matter here, I believe this dovetails nicely with biological practice on the units/levels of selection problem. See, for illuminating discussion and analysis, Pigliucci (2010).

least, a mechanism which is as stochastic as genetic drift—is a contradiction in terms, for it fails outright to satisfy the regularity criterion.[29]

Genetic drift, therefore, does not count as a mechanism, making for a genuine difference in kind between genetic drift and natural selection. For the force interpretation, on the other hand, these two are both forces, and this difference in kind disappears. On this score, I argue, the force interpretation better matches biological practice. Drift is certainly interesting, for the reasons discussed here, but in evolutionary theorizing itself we lack the kind of difference between drift and selection that such a profound metaphysical distinction would seem to entail.

While these considerations don't suffice to close the case in favor of the force interpretation, I believe they show, taken together with the refutation of the arguments against its coherence above, that the force interpretation deserves its place among the ways in which we might adopt a causalist picture of evolutionary theory.

7 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 misunderstanding of the relationship between the classic Newtonian cases of gravitation and inertia.

We then turned to a broader question: what are we to do with the force interpretation, overall? These two particular arguments having been set aside, is it the most appealing way to understand the structure of evolutionary theory? I explored this in the context of two larger problems, the resolution of each of which would, I claim, be a boon to this evaluative project. First, in which circumstances does an explanation phrased in terms of 'forces' offer helpful insight into the system being explained? And second, what are the virtues of the (at least) five different ways in which we might approach the causalist project? Neither of these questions has been satisfactorily considered in the literature, though I offered here some considerations weighing in favor of the force picture.

I have, of course, done nothing here to resolve the overall debate between the causal and statistical interpretations of evolutionary theory. But the force metaphor, as we have seen, does have conceptual utility, is among the (several) plausible explanatory approaches for understanding evolution, and it continues to survive the host of objections raised against it. Determining whether or not it is the best way to understand the causal structure of evolutionary theory, on the other hand, is a larger problem—but one to which it is time to devote our efforts.

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[29] Alternatively, one might modify the account of mechanism, making room for stochastic mechanism, as recently and persuasively advocated by DesAutels (2015).

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