

Drift and Evolutionary Forces: Scrutinizing the Newtonian Analogy¹ *

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ABSTRACT: This article analyzes the view of evolutionary theory as a theory of forces. The analogy with Newtonian mechanics has been challenged due to the alleged mismatch between drift and the other evolutionary forces. Since genetic drift has no direction several authors tried to protect its status as a force: denying its lack of directionality, extending the notion of force and looking for a force in physics which also lacks of direction. I analyse these approaches, and although this strategy finally succeeds, this discussion overlooks the crucial point on the debate between causalists and statisticalists: the causal status of evolutionary theory.

Keywords: Evolutionary forces, causation in Biology, genetic drift, Newtonian analogies, Brownian motion.

RESUMEN: El presente artículo analiza la visión de la teoría evolutiva como una teoría de fuerzas. La analogía con la mecánica newtoniana se ha puesto en duda debido a las diferencias entre la deriva y el resto de fuerzas evolutivas. En tanto que la deriva genética no tiene dirección, varios autores han tratado de proteger su estatus de fuerza: negando su falta de direccionalidad, extendiendo la noción de fuerza y buscando una fuerza que también carezca de dirección en física. Analizo estas aproximaciones y aunque esta estrategia finalmente tiene éxito, argumento que esta discusión pasa por alto el punto crucial en el debate entre causalistas y estadísticos: el estatus causal de la teoría evolutiva.

Palabras clave: Fuerzas evolutivas, causalidad en Biología, deriva genética, analogías newtonianas, movimiento browniano.

1. Introduction

Textbooks and most of the evolutionary literature talk about *evolutionary forces* acting on a population. In that way, Gillespie says: “Population geneticists spend most of their time doing one of two things: describing the genetic structure of populations or theorizing on the evolutionary forces acting on populations” (2004, 1). Hartl and Clark reiterate: “there are many forces in population genetics that act in opposition to one another, and it is this tension that makes for interesting behaviour at the population level” (1997, 294). Similarly, we can find chapters entitled “Interactions of Natural Selection with other evolu-

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tionary forces” (Templeton 2006, chap. 12) or the vector representation of different forces (Rice 2004, chap. 5). Supposedly, the analogy with Newtonian mechanics has been successful in both mathematical modeling and the structuring of evolutionary theory. It was firstly proposed by Elliott Sober (1984) as follows: “In evolutionary theory, the forces of mutation, migration, selection and drift constitute causes that propel a population through a sequence of gene frequencies. To identify the causes of the current state (...) requires describing which evolutionary forces impinged” (Sober 1984, 141)

Sober argues that evolutionary theory is a theory of forces because, in the same way that different forces of Newtonian mechanics cause changes in the movement of bodies, evolutionary forces cause changes in gene and/or genotype frequencies. As a result, selection, drift, mutation and migration would be the main forces or causes of evolution².

The force metaphor is intended to expose the causal structure of the evolutionary theory. This is what Maudlin (2004) calls “quasi-Newtonian” theories. These are characterized by shaping them in a similar form to Newtonian mechanics whose main axis is the adoption of a zero-force law which tells us how the system would behave if forces were not acting on it. The main purpose of building quasi-Newtonian theories is to identify the causes that affect a particular system.³ Thus, the first law of Newtonian mechanics functions to establish that a body continues in its state of rest, or of uniform motion in a straight line, unless it is compelled to change that state by forces impressed upon it. Evolutionary theory usually takes for granted the Hardy-Weinberg law (Sober 1984, Gillespie 2004, Templeton 2006) as its zero-force law counterpart. According to the Hardy-Weinberg law a diploid and ideal infinite population, where there is random mating (panmictic population) and whose individuals are viable and fertile, will remain or return to equilibrium (i.e. gene and genotype frequencies will remain stable) if no force acts on it, since Mendelian inheritance alone cannot change the allele frequencies. Thus, both the law of inertia and the Hardy-Weinberg law, tell us how the system would behave if nothing disturbed it, assuring a neutral substrate where we can introduce forces. Table 1 makes a comparison between Newtonian mechanics and Evolutionary theory:

Table 1

	Newtonian mechanics	Evolutionary Theory
Forces as causes	Forces cause changes (or maintenance) in bodies position	Natural selection, drift, mutation and migration are forces (causes) which change allele frequencies.
Zero-Force Law	Newton’s first law (inertia)	Hardy-Weinberg law
Models of combination and resolution of forces	Vectorial combination	Population Genetics provides models which represent the action of that forces and their combination

² These vary in number, sometimes introducing other factors such as recombination, population structure, etc., but the four above are canonical. It is not my aim to elaborate a complete list here.

³ It should be noticed that there are causal approaches to evolutionary theory which are not committed to the Newtonian analogy. See Millstein (2006), Reisman and Forber (2005), Rosenberg and Bouchar (2005), Brandon and Ramsey (2007), Gildenhuis (2009). For a new approach committed with the Newtonian analogy, although it deviates from the traditional view argued by Sober, see Brandon (2006), and McShea and Brandon (2010).

Nevertheless, the appropriateness of the dynamical view, and particularly the Newtonian analogy, has been challenged in the last decade. Several authors (Walsh *et al* 2002, Matthen and Ariew 2002 and 2009, Pigliucci and Kaplan 2006) argued for a new view, the *statistical view*, where the evolutionary process and its parts (selection, drift, etc.) are mere statistical outcomes, inseparable each other. They would be pseudo-processes without causal power (as shadows on a wall). Thus, unlike Newtonian mechanics, it is not possible to separate the different *forces* which act upon populations. The so called *evolutionary forces* should be conceptualized as statistical population-level tendencies, abandoning any causal role for them. In other words, they would be simple mathematical aggregates of individual-level events (births, deaths and reproduction). Table 2 summarizes both views:

Table 2

Dynamical View	Statistical View
Forces as causes	Evolutionary forces are pseudo-processes or outcomes
Zero-force law: Hardy-Weinberg law	There is no zero-force law
Models of combination and resolution of forces	Evolutionary forces cannot be combined

I think that most of these attacks to the dynamical view have been positively answered (Abrams 2007; Stephens 2004, 2010; Brandon and Ramsey 2007; Millstein *et al.* 2009; Hitchcock and Velasco 2014; Sarkar 2011) so, I will not go into details about them. Rather I will focus on genetic drift, an evolutionary force less similar to the others which has created the greatest problems to the force interpretation. I analyse three options in order to save drift's status as a force. I argue that only one of them succeeds. I claim, however, that the discussion around the force-talk have lost sight of what is the crucial point on the debate between causalists and statisticalists, that is, the causal status of evolutionary theory.

The structure of the paper is as follows. Section 2 analyses the different definitions and properties of drift. Section 3 explores the lack of directionality of drift and how some authors have attempted to mitigate this problem in order to maintain the forces analogy. Section 4 is devoted to conclusions.

2. Drift: Definitions and Properties

Definitions of drift in evolutionary literature are ambiguous. Sometimes drift is defined as a process or cause that produce random fluctuations: "One of the most important random processes in evolution is random fluctuation in the frequencies of alleles or haplotypes owing to "sampling error": the process of random genetic drift" (Futuyma 2013, 258). But other times drift is defined as an outcome by equating it to the random fluctuations themselves: "The term random genetic drift (or just genetic drift) refers to fluctuations in allele frequency which occur by chance, particularly in small subpopulations, as a result of sampling process" (Conner and Hartl 2004, 52).

Among philosophers, Millstein defines drift as “an indiscriminate sampling *process*, in which physical differences between organisms are causally irrelevant to differences in their reproductive success” (Millstein 2002, 37). A more detailed definition is suggested by Gildenhuis: “Drift’ is used to refer to causal influences over a population with variant members of different types, causes that have three features: they are non-interactive, non-pervasive, and indiscriminate causes” (Gildenhuis 2009, 522)⁴. These definitions are variations on the same idea, that is, drift causes changes in allele or trait frequencies in a population no matter what kind of differences exists among individuals –in contrast, specific variation is crucial for natural selection in order to work upon a population. This characteristic is stressed by Millstein and Gildenhuis when they said that drift is indiscriminate.

The issues around the definition of drift, nevertheless, are harmless as long as biologists and philosophers aforementioned (i.e. those who consider drift a cause of evolution) refer to a process that produces a concrete effect⁵, and there is no ambiguity in the mathematical apparatus used to model drift. The basic model is the Wright-Fisher model (Gillespie 2004), a binomial sampling process in a diploid population in which a new generation is formed as a sample of $2N$ alleles⁶. The transition matrix for i copies of A_1 to j copies of A_1 is given by:

$$P_{ij} = \binom{2N}{i} \left(\frac{j}{2N}\right)^i \left(1 - \frac{j}{2N}\right)^{2N-i}$$

The transition matrix is determined only by the initial allele frequencies and the population size N . This explains why drift usually is compared with tossing a coin (Templeton 2006) or sampling balls from an urn (Brandon 2005). If you have a fair coin and you toss it ten times, the most likely expected outcome is 5 heads and 5 tails; but it would not be surprising that you get 6 heads and 4 tails or 7 heads and 3 tails. Increasing the number of tosses will approximate the frequencies obtained to the expected outcome. The magnitude of this sampling error is inversely proportional to sample size, i.e. the smaller the population the bigger the deviation from the expected outcome. As you increase the population

⁴ More specifically: “They are (i) *non-interactive* insofar as they have the same sort of causal influence on the reproduction of individuals of each type in the population (most are deadly for individuals of all types); (ii) *non-pervasive* insofar as they affect only some population members in any given generation or time slice; and (iii) *indiscriminate* insofar as they are just as likely to affect one population member as any other population member, regardless of what variant types they are” (Gildenhuis 2009, 522).

⁵ There is some philosophical debate concerning whether drift is conceptualized as a process (Millstein 2005) or a product (Brandon 2005), in other words, as a cause or an effect. Nevertheless biologists conceptualize drift as a causal influence on population dynamics and here I am just referring to philosophers who consider drift as a cause. Even Brandon (2006), and also McShea and Brandon (2010), consider drift as a cause of evolution despite being, in their terms, an effect (see Gildenhuis (2009) for a discussion on the process-product/cause-effect ambiguity of drift). Thanks to a referee for drawing my attention to this point.

⁶ The model takes for granted some assumptions: there are non-overlapping generations; the population size is constant; there is no selection, mutation or migration; adults make an infinite number of gametes and every parent contributes equally to the gamete pool; all members breed; all members mate randomly.

size deviations become smaller, decreasing the fluctuations across generations. That is why drift is usually linked to population size (Reisman and Forber 2005) and introduced in our mathematical models through its different versions –the population size N or, in more realistic models, the effective population size N_e and the variance effective population size N_{ev} (Rice 2004)⁷.

The main features of drift can be summarized as follows (Templeton 2006, 87-88):

- *Drift has no direction.* If we simulate a large number of identical populations, the overall allele frequency remains equal. Genetic drift is a non-directional process “since the expected change at every point is zero” (Rice 2004, 131). Correlated with this, we cannot predict the direction of change. Drift is a random walk.
- *Evolutionary change via drift accumulates with time.* Drift, as a Markov process, is determined by its actual state, but not by its previous history, deviating from the initial conditions as generation time increases.
- *Drift causes the loss of genetic variability within a population.* As generations pass, drift changes allele frequencies until one allele is fixed or lost. As a random walk, drift goes somewhere and these places are called “absorbing boundaries”. Once the process has reached such a state, it will stay there forever (barring reintroduction via mutation or migration).
- *Drift causes an increase of genetic differences between populations.* If we simulate a large number of identical populations, they will deviate not only from the ancestral condition but also from each other.

For our interest, the most important feature is the first one: the lack of directionality. So, the forces analogy seems to face a big problem when it deals with genetic drift. Directionality seems an essential property for Newtonian forces. However, although we can specify a magnitude to genetic drift —as aforementioned, the population size N , the effective population size N_e and the variance effective population size N_{ev} (but it should be noticed footnote 7)— we cannot assign a direction to it. Nevertheless, several authors still think that drift is an evolutionary force inasmuch as it is an essential causal factor in evolutionary phenomena. The next section is devoted to exploring such proposals.

3. *Drift as a Force*

3.1. STEPHENS’ APPROACH

Contrary to the commonest view among population geneticists about drift’s lack of directionality, Stephens (2004 and 2010) argues that “Drift does have a direction –it serves

⁷ Clatterbuck (2015) points out other models of drift (Eldon-Wakely model, Canning models, etc., see Der et al. 2011 for a technical purview) that have the same characteristics than the Wright-Fisher model, but differ from it in their higher moments (skew, heavy-tailedness, etc.). So, if we intervene in these higher moments we can change the evolutionary outcomes. This undermines the statisticians’ view that drift is only a mathematical relationship, because concrete biological properties are crucial in order to model drift processes accurately. That is, mathematical models on their own do not exhaust the ontological status of drift (Millstein et al. 2009).

to eliminate heterozygosity” (Stephens 2004, p. 563). We saw in section 2 that drift may cause the loss of genetic variability within a population. The consequence of this is that a population under drift will become homozygous at a locus. Stephens claims that “march to homozygosity” supports the claim that drift has a direction, even though it does not have direction with respect to allelic frequencies. We can see that Stephens is focused on change in genotype frequencies rather than in allelic ones. Brandon (2006) replies to Stephens that this is a false directionality. It cannot be specified since it does not say which genotype will increase or decrease: “In physics that would be like saying that a 20-Newtons force is acting on an object A. Such statement either make no sense (the magnitude, but not direction has been specified) or is incomplete (oops, I meant a 20-Newton downward force)” (Brandon 2006, 325). Nonetheless, despite Brandon’s critique, Stephens keeps maintaining drift’s directionality in terms of variation: “there is an important sense in which drift does have a direction. Drift tends to remove variation from natural populations” (Stephens 2010, 721).

Keeping in mind Brandon’s critique, this position is problematic because when direction for natural selection, mutation and migration, is presented, it is not in terms of homozygosity and heterozygosity. It is true that all textbooks talk about how different evolutionary forces affect variation (and variation is usually measured in terms of the amount of heterozygosity present in a population⁸), but not in terms of directionality. There is only one book —as far as I know— that could be interpreted as making that leap, *A Premier of Ecological Genetics* (2004) by Jeffrey Conner and Daniel Hartl, where they show the effects on genetic variation of the four evolutionary forces that change allele frequency. The authors use two levels of variation: variation within subpopulations, and variation among subpopulations⁹. The former is measured by the amount of heterozygosity (H_I), whereas the latter is measured by the fixation index or F-statistics (F_{ST}). The authors summarize all this in the following table:

Table 3. Adapted from Conner and Hartl (2004)

	Level of variation	
	Within subpopulations: Heterozygosity (H_I)	Among subpopulations: Differentiation (F_{ST})
Mutation	↑	↑
Gene flow (migration)	↑	↓
Drift	↓	↑
Selection	↑↓	↑↓

Up arrows (↑) indicate an increase in variation; down arrows (↓) indicate a decrease in variation; dual arrows (↑↓) indicate both an increase and a decrease in variation

⁸ Other measures are the proportion of polymorphic loci, and the number of different alleles at the locus (Charlesworth and Charlesworth 2010).

⁹ Subpopulations are local populations connected each other by gene flow (migration), creating a meta-population.

For the sake of Stephens' argument, let's read table 3 in terms of directionality following the arrows. Mutation tends to increase variation within subpopulations, and also tends to increase variation among subpopulations. Migration tends to increase variation within subpopulations, but tends to decrease variation among subpopulations. Drift works exactly in the opposite way, decreasing variation within subpopulations and increasing variation among subpopulations. So, it seems that Stephens has found a direction for genetic drift—even though drift does not have direction by definition—at two different levels of variation: drift tends to eliminate heterozygosity (decrease in variation) within subpopulations, and also tends to increase variation among subpopulations. However, if we look at the row where selection is located, we notice that there are two arrows with different direction in each column. Selection within subpopulations may increase or decrease variation, and selection among subpopulations may increase or decrease variation too. That is, selection may decrease, but also increase variation at both levels. Taking all of this into account, what kind of directionality can we assign to natural selection? The answer is 'none'. Selection can increase or decrease variation, so there is no clear tendency. If we locate directionality at the level of variation, as Stephens claims, we could assign directionality to drift but then selection loses its directionality.

In the debate about evolutionary forces, directionality of natural selection was undisputed; it seemed obvious. But now directionality, at this variation level, is absent. That is the dilemma that Stephens has to face: attributing directionality to genetic drift and losing it for selection, or maintaining selection's directionality but then drift's directionality disappears¹⁰.

3.2. FILLER'S APPROACH

Despite that genetic drift lacks a direction, Filler (2009) is in favour of maintaining the *force-talk* although he is aware that abuse of it could turn the concept of force into an all-encompassing concept with no real explanatory value. Newtonian mechanics uses vector representation to describe the forces which occur in space and time. Likewise, evolutionary theory uses the evolutionary space—represented by a genotypic space, phenotypic, etc.—to represent the evolutionary dynamics of a given population. But we can imagine an admirer of Molière who would explain the sleep-inducing properties of opium as a result of its dormitive virtue. Thus, the admirer could create a fatigue-space where opium has a direction, pushing it up to the top of the fatigue-space, due to its dormitive power. This is not an explanation of the efficient cause of why opium is sleep-inducing, but an explanation devoid of content. Shortly, there is a real danger of trivializing the concept of force and its representation unless further constraints were specified. Therefore, Filler postulates two criteria. Firstly, the concept must unify diverse phenomena, allowing us to see what they all have in common. Secondly, it must have a mathematical specific magnitude. If these crite-

¹⁰ Another criticism is that the force interpretation is usually related with adaptive landscapes (Pigliucci and Kaplan 2006, Pence 2016). Adaptive landscapes are usually presented as a diagram with one or two axes representing the mean fitness of a population and the frequencies of certain alleles. Thus, in this picture we found hills and valleys, and populations go through the surface, reaching adaptive peaks or falling into valleys. Nevertheless, heterozygosity does not appear on adaptive landscapes, and is not easy to see how somebody could build an adaptive landscape based on the claim "toward homozygosity".

ria were not enough to cast aside the dormitive virtue of our force-talk definitely, at least the existence of a continuum of forces could be established which allows us to distinguish forces which have great explanatory strength (greater mathematical precision and unifying power) from those which are really poor explanations (for instance, the dormitive virtue). In this continuum, although drift does not exhibit specific directionality, in contrast to the other evolutionary forces, it carries out both the previous requirements, so it would be closer, in that continuum, to the rest of evolutionary forces than to dormitive virtue.

Nevertheless, Filler's approach is not completely convincing. Filler assumes that genetic drift possesses the two features that any force must accomplish in order to be a *force* (unifying power and mathematical specificity), but never gives an explicit example. This is strange since one might say that drift fulfils both criteria to the extent that it unifies diverse phenomena (founder effects, Wright effect, Hedges effect, etc.) and has a precise mathematical magnitude (the population size N , the effective population size N_e or the variance effective population size N_{ev}). At the same time, Filler's continuum of forces does not specify where drift should exactly be located. He just claims that drift is closer to the other evolutionary forces than to other *forces* like the dormitive virtue.

Mostly important, it is not clear why the problem of directionality disappears. Filler defends that claims like a "population under genetic drift can reduce the allelic variability in it and, eventually, one type will be fixed in the population" (or in other words, genetic drift leads diploid populations to homozygosity), are not empty. However, no one defends that that is an empty claim. Of course drift affects variation in natural populations. This shows that drift has a causal role but not necessarily a direction. As a random walk, the next state of any type in a population under genetic drift is determined by its actual state but not by its previous history—that's why we can model drift as a Markov process—and so the type has the same probability of increasing or decreasing. Filler is ambiguous about accepting "toward homozygosity" as a legitimate directionality. He admits that talk about population secondary properties as homozygosity and heterozygosity is a weaker claim than talk about specific genotypes, but in some cases it may count as a direction (see section 3.1. for a reply). Nevertheless, this is an unstable position because Filler develops the two criteria (mathematical precision and unifying power) and "the continuum of forces" in order to overcome drift's lack of directionality. If there is a clear directionality for drift, why stressing mathematical precision and unifying power as the key criteria for being a force? Again, drift has no direction by definition (see above section 2).

The lack of directionality turns drift into a problem for the defenders of force-talk and brings about a mismatch between forces in evolutionary theory and in Newtonian mechanics (Hitchcock and Velasco 2014). In addition, it is really questionable that we can extend the term "force", in a Newtonian sense, beyond classical mechanics since it is connected to notions like masses, accelerations and the second law of motion (I will discuss this in section 3.3). Summing up, Filler's criteria are not enough precise to univocally classify something as a "force" and, consequently, they do not avoid the risk of an excessively loose use of the concept.

3.3. PENCE'S APPROACH

As Pence (2016) recognizes, there is a real danger to be facing an *ad hoc* argument in order to fit drift in the force-talk, because Filler never confronts his criteria with drift or any other evolutionary force. Pence is aware of these problems and develops a new strategy.

Are any phenomena in physics similar to those brought about by drift which could be considered as a Newtonian force? Pence maintains that such a phenomenon is Brownian motion¹¹ which is the random motion of particles suspended in a fluid resulting from their collision with the atoms or molecules of that fluid. Brownian motion is stochastically modelled by the following Langevin's equation:

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

where x represents the location of the particle within the fluid, m is its mass, $-6\pi\mu a$ characterises the damping coefficient (fluid viscosity that slows the movement of the particles), and X denotes a random "noise term" which describes the effect of the collisions between fluid atoms or molecules. On the left side of the equation we can find the mass m and the term $\frac{d^2 x}{dt^2}$ which represents second space derivative respect to time twice. Thus, the left side of the equation can be rewritten as ma , and following Newton's second law of motion, $F = ma$. Hence, the entire equation can be rewritten as $F = -6\pi\mu a \frac{dx}{dt} + X$. In other words, we have found a physical phenomenon, Brownian motion, represented by an equation with an explicit force formulation.

Nevertheless, such phenomenon lacks a precise directionality on account of the stochasticity produced by the noise term X . The analogous elements between Brownian motion and genetic drift are clear. Brownian motion can be combined with gravity to predict, with a margin of error, the vertical distribution of particles. In the same way, drift can be combined with the rest of evolutionary forces to predict probabilistically, with a margin of error, the evolution of a given population¹². One of Pence's main sources is Lemons and Gythiel (1997), the first English translation of Langevin's 1908 work. In the introduction, Lemons claims: "Langevin applied Newton's second law to a representative Brownian particle. In this way Langevin invented the "F=ma" of stochastic physics now called the "Langevin equation." (...) In particular, Langevin introduced a stochastic force (his expression actually is "complementary force") pushing the Brownian particle around in velocity space" (Lemons 1997, 1079). Stochastic or random force is a concept which is not found in Newton's work. Newton exposes the parallelogram law and defines forces as vector quantities with magnitude and direction. A stochastic force lacks of directionality so it cannot be represented as a vector. Newton's world is a deterministic one; there is no place for probabilities and random variables. Nevertheless, the concept of force and physicists language has changed since Newton's age. Today is not unusual to find "stochastic force" or "random force" in the physics literature (see, for instance, Fuchs 2013, Huang 2010, Schuss 2010).

¹¹ This comparison between genetic drift and Brownian motion also appears in Futuyama (2013, 330).

¹² For instance, the probability of fixation of a favourable allele due to the interaction of selection and drift comes from the equation $u = \frac{1 - e^{-2(N_e s)}}{1 - e^{-4N_e}}$, where N_e is the variance effective size, N is the population size, and s is the selection coefficient (Templeton 2006, 381).

A reply to Pence's claim could be: it is hard to believe that physicists really consider that the Brownian motion is caused by a force, in a Newtonian sense, or that it is a force in itself precisely because it is a standard example in statistical physics. Rather, the equation does not include a detailed description of the single force acting on each point —that is because the term “noise” X is necessary—, so it is not possible to describe the motion of a particle individually and deterministically in classical terms. The left side of the equation, far from being a force, is just the acceleration of a particle multiplied by its mass. The first term of the equation's right side is a force, a friction force, and its direction is opposite to motion; the second term is a term whose magnitude and direction are unknown, usually called “random force” for convenience.

In short, the argument would say that the noise term encompasses all the interactions between the Brownian particle and fluid atoms or molecules, but is not itself a force. Nevertheless, this is similar to that we find when we talk about friction forces. A friction force occurs at the interface of two rough surfaces (for instance, a block and a ramp), and friction coefficients will depend on their materials. But friction emerges from the aggregate behaviour of the components of these materials (atoms, etc.). Friction is a *bona fide* Newtonian force (Goldstein et al. 2000, Radi and Rasmussen 2013), but it is the result of different forces acting at lower level (essentially electromagnetic interactions and Pauli's exclusion principle). It could be said that we get the same picture in Langevin's equation, where Brownian motion is produced by forces which sum up micro-level interactions. There is a particle which is bombarded by fluid molecules in its surrounding, bumping it to different directions. Langevin's equation represents this as a complementary or random force. When the particle is moving it faces more energetic collisions in the direction it moves, and slows down (Fuchs 2013). Langevin's equation represents this as a frictional force. As Huang says (2010, 183): “The total force that the medium is exerting on the particle is split in two [a random force and a frictional force]. These forces represent different aspects of interactions with the medium, one representing fluctuation, the other dissipation”. In other words, there is a total force that emerges from collisions between the Brownian particle and the fluid molecules (the medium). If we accept that friction is a Newtonian force in situations like the block and the ramp, then it is hard to deny that the Brownian particle is under the influence of a total (random) force exerted by the medium (where one component force is friction indeed)¹³.

I think it is clear that Brownian motion is not a force, and Pence is wrong when he uses this term. Brownian motion —like circular motion, simple harmonic motion, and so on— is an outcome or effect produced by forces (a frictional force and a random force) but it is not a force itself. I propose to call *Langevin force* (following Mahnke et al. 2009) to this total (random) force that acts on Brownian particles¹⁴.

¹³ Pence quotes an endorsement of this sort of argument by statisticians: “The expectation for the trajectory of the feather is generated by summing those forces known to be acting on the feather. The feather is 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.*” (Walsh et al. 2002, 454, *emph. added*).

¹⁴ The stochastic part in the Langevin's equation it is also called Brownian force (Kim and Zydney 2004). Maybe this explains why Pence calls force to Brownian motion.

There is an interesting connection between Pence's article and Hitchcock and Velasco (2014), where the aim is to clarify the heterogeneity nature of Newtonian forces. Thus, in the same way that Pence presents an especial kind of Newtonian forces (a stochastic force), Hitchcock and Velasco show that there is heterogeneity among Newtonian forces, where not all of them share the same features. In this way, statisticians' criticism on the forces analogy is based on a misconception: they do not realize about this heterogeneity. Statisticians think that all Newtonian forces are such as gravity or electrostatic forces, and that all evolutionary forces are such as natural selection or genetic drift. Some of the main arguments against the analogy¹⁵ rest on this misconception indeed. When we think about Newtonian forces, gravity probably is the first force that comes to mind, and perhaps electrostatic forces are also considered. Nevertheless, even these *canonical forces*, in Hitchcock and Velasco terminology, satisfy many but not all the criteria established by the advocates of the statistical view¹⁶ (see Hitchcock and Velasco 2014 for details). In this line, other Newtonian forces such as friction forces or spring forces, i.e. *non-canonical forces* in Hitchcock and Velasco terminology, hardly satisfy some of these criteria. The debate about the analogy of forces is fueled because of this overlooked heterogeneity. In fact, canonical evolutionary forces such as natural selection are more closely analogous to non-canonical Newtonian forces such as elastic and friction forces. On the other hand, mutation and migration are more similar to canonical forces such as gravity or electrostatic forces. "Thus the analogy between forces in evolutionary theory and Newtonian mechanics exhibits a kind of mismatch, where the canonical forces of one theory are not matched up with the canonical forces of the other." (Hitchcock and Velasco 2014, 51). In the same line, Pence's work presents another non-canonical Newtonian force, a stochastic or random force, partially undermining the criticism raised by statisticians.

If the debate is simply a terminological one, then it seems that Pence has a counterexample for people who deny the word "force" to genetic drift. However, this victory is not clearly relevant if we intend a clarification of the structure of evolutionary theory and its concepts. Filler explicitly intends to create a broader concept of force, while Stephens and Pence are dealing with a semantic issue (solving the directionality problem and not extending the concept of force beyond classical mechanics). Stephens (2004) establishes that natural selection, drift, and so on are causes of evolution (being "force" just another way to call them causes); and this seems quite clear too in Pence's previous paper title ("It's Okay to Call Genetic Drift a 'Force'") despite Pence's sympathy for Filler's attempt to develop a broader concept of force.

Having said this, however, on my view the debate has largely deviated from the original point. There are no evolutionary biologists who would claim that evolutionary forces are, strictly speaking, forces like Newtonian ones. First of all, a force in a Newtonian sense

¹⁵ Hitchcock and Velasco summarize all this in four arguments: Isolability (forces can act in isolation), Source Laws (these describe the circumstances that produce forces), Composition of forces (Newtonian forces have an addition law to combine them) and Tertium Quid (Newtonian forces are causes that appear in a causal chain).

¹⁶ For example, gravitational force is not a *tertium quid* in a causal chain because it "comes into existence simultaneously with the appearance of the massive objects; so, if causes must precede their effects, we shouldn't view the relation as causal" (Sober 1984, 50, footnote 38). Hitchcock and Velasco (2014, 69-74) strengthen this position showing that this *tertium quid* criteria for gravity fails Woodward's manipulability test of causation.

is something that produces the change of motion of a mass and is calculated through the second law of motion, but in evolutionary biology we are not dealing with masses and it is not used the second law (Endler 1986, Sarkar 2011; for another approach see Luque 2016b). Sober was aware about this, claiming that any causal theory must discover its own way to combine the causes that it describes (see Sober 1984, 31-32), to solve its compositional problems. Furthermore, Sober postulated the force interpretation because he wanted to emphasize the causal role played by different evolutionary factors¹⁷. But a theory can be a causal theory without resorting to forces. However, statisticalists built their argumentation focusing on the forces analogy in order to attack evolutionary theory as a causal theory. Again, to show that evolutionary forces are not forces do not undermine them as causes (Millstein 2006, Brandon and Ramsey 2007).

4. Conclusion

The view of evolutionary theory as a theory of forces has been challenged due to the mismatch between drift and the other evolutionary forces. On account of genetic drift and its lack of direction, several authors tried to protect its status as a force. Denying its lack of directionality is one option. Extending the notion of force and looking for a force in physics which also lacks of direction is an alternative strategy. I tried to argue firstly that: (i) Stephens has to face a crucial dilemma in order to accept some kind of directionality for drift; and (ii) Filler's attempt to extend the concept of force is not fully convincing since it is exposed dangerously to be an *ad hoc* argument. Then we found a new move, i.e., appealing to a random force in physics in order to keep alive the analogy (Pence). Supposedly, then, there is no problem after all in considering drift as a force.

However, this is not very rewarding provided that we are interested in a clarification of the structure of evolutionary theory and its concepts. My impression is that the debate on the force interpretation in the last decade has improved our understanding of Newtonian mechanics, but not necessarily our understanding of evolutionary theory. Hitchcock and Velasco's article is a very good example of this (distinct kinds of forces, etc.). The background of the debate was the causal structure of evolutionary theory but since then some causal approaches have been developed without appealing to the force interpretation (see footnote 3). It must be acknowledged, nevertheless, that the forces analogy seems to capture something important. That is the reason for the extended use of the force-talk among biologists and the primacy of the force interpretation among philosophers for the last three decades. However, it is highly desirable a unifying approach to all causal arguments which could explain what exactly the force interpretation captures. That could be a third way in the causalist stance on evolutionary theory (Luque 2016a).

¹⁷ Sober was indeed very careful regarding genetic drift: "I have chosen to describe random genetic drift as a 'force' of evolution to emphasize the causal role it plays. Nothing much hangs on this terminology, however. In any case, it is clear that drift is a very different kind of force from its deterministic counterparts (...) If drift is an evolutionary force, it is a force of a different color" (Sober 1984, 117).

REFERENCES

- Abrams, Marshall. 2007. How Do Natural Selection and Random Drift Interact? *Philosophy of Science* 74: 666-679.
- Brandon, Robert. 2005. The Difference Between Selection and Drift: A Reply to Millstein. *Biology and Philosophy* 20: 153-170.
- . 2006. The Principle of Drift: Biology's First Law. *Journal of Philosophy* 103: 319-335.
- Brandon, Robert and Grant Ramsey. 2007. What's Wrong with the Emergentist Statistical Interpretation of Natural Selection and Random Drift? In *Cambridge Companion to the Philosophy of Biology*, eds. David Hull and Michael Ruse, 66-84. Cambridge: Cambridge University Press.
- Charlesworth, Brian and Deborah Charlesworth. 2010. *Elements of Evolutionary Genetics*. Colorado: Roberts and Company Publishers.
- Clatterbuck, Hayley. 2015. Drift Beyond Wright-Fisher. *Synthese* 192: 3487-3507.
- Conner, Jeffrey and Daniel Hartl. 2004. *A Primer of Ecological Genetics*. Sinauer, Sunderland.
- Der, Ricky, Charles Epstein and Joshua Plotkin. 2011. Generalized Population Models and the Nature of Genetic Drift. *Theoretical Population Biology* 80: 80-99.
- Endler, John. 1986. *Natural Selection in the Wild*. Princeton: Princeton University Press.
- Filler, Joshua. 2009. Newtonian Forces and Evolutionary Biology: A Problem and Solution for Extending the Force Interpretation. *Philosophy of Science* 76: 774-783.
- Fuchs, Armin. 2013. *Nonlinear Dynamics in Complex Systems*. Berlin: Springer.
- Futuyma, Douglas. 2013. *Evolution* (3rd edition). Sunderland: Sinauer.
- Gildenhuys, Peter. 2009. An Explication of the Causal Dimension of Drift. *British Journal for Philosophy of Science* 60: 521-555.
- Gillespie, John. 2004. *Population Genetics: A Concise Guide* (2nd edition). Baltimore: The John Hopkins University Press.
- Goldstein, Herbert, Charles Poole and John Saffo. 2000. *Classical Mechanics* (3rd edition). New York: Allison Wesley.
- Hartl, Daniel and Andrew Clark. 1997. *Principles of Population Genetics* (3rd edition). Sunderland: Sinauer.
- Hitchcock, Christopher and Joel Velasco. 2014. Evolutionary and Newtonian Forces. *Ergo* 1: 39-77.
- Huang, Kerson. 2010. *Introduction to Statistical Physics* (2nd edition). London: Taylor and Francis Group.
- Kim, Myung-man and Andrew Zydny. 2004. Effect of Electrostatic, Hydrodynamic, and Brownian Forces on Particle Trajectories and Sieving in Normal Flow Filtration. *Journal of Colloid and Interface Science* 269: 425-431.
- Lemons, Don and Anthony Gythiel. 1997. Paul Langevin's 1908 Paper "On the Theory of Brownian Motion" ["Sur la théorie du mouvement brownien," C. R. Acad. Sci. (Paris) 146, 530-533 (1908)]. *American Journal of Physics* 65 (11): 1079-1081.
- Luque, Victor J. 2016a. The Principle of Stasis: Why drift is not a Zero-Cause Law. *Studies in History and Philosophy of Biological and Biomedical Sciences* 57: 71-79.
- Luque, Victor J. 2016b. One equation to rule them all: a philosophical analysis of the Price equation. *Biology and Philosophy*. doi:10.1007/s10539-016-9538-y
- Mahnke, Reinhard, Jevgenijs Kaupuzs and Ihor Lubashevsky. 2009. *Physics of stochastic processes*. Weinheim: Wiley-VCH.
- Matthen, Mohan and André Ariew. 2002. Two Ways of Thinking About Fitness and Natural Selection. *Journal of Philosophy* 99: 55-83.
- . 2009. Selection and Causation. *Philosophy of Science* 76: 201-224.
- Maudlin, Tim. 2004. Causation, Counterfactuals, and the Third Factor. In *Causation and Counterfactuals*, eds. John Collins, Ned Hall and L. A. Paul, 419-443. Massachusetts: The MIT Press.
- McShea, Daniel and Robert Brandon. 2010. *Biology's First Law: The Tendency for Diversity and Complexity to Increase in Evolutionary Systems*. Chicago: The University of Chicago Press.

- Millstein, Roberta. 2002. Are Random Drift and Natural Selection Conceptually Distinct? *Biology and Philosophy* 17: 33-53.
- . 2005. Selection vs. Drift: A Response to Brandon's Reply. *Biology and Philosophy* 20: 171-175.
- . 2006. Natural Selection as a Population-Level Causal Process. *British Journal for Philosophy of Science* 57(4): 627-653.
- Millstein, Roberta, Robert Skipper and Michael Dietrich. 2009. (Mis)interpreting mathematical models: drift as a physical process. *Philosophy and Theory in Biology* 1: 1-13.
- Pence, Charles. 2016. Is Genetic Drift a Force. *Synthese*. doi:10.1007/s11229-016-1031-2
- Pigliucci, Massimo and Jonathan Kaplan. 2006. *Making Sense of Evolution: The Conceptual Foundations of Evolutionary Biology*. Chicago: University of Chicago Press.
- Radi, Hafez and John Rasmussen. 2013. *Principles of Physics*. Berlin: Springer.
- Reisman, Kenneth and Patrick Forber (2005). Manipulation and the Causes of Evolution. *Philosophy of Science* 72: 1113-1123.
- Rice, Sean. 2004. *Evolutionary theory: mathematical and conceptual foundations*. Sunderland: Sinauer.
- Rosenberg, Alexander and Frederic Bouchard. 2005. Matthen and Ariew's Obituary for Fitness: Reports of its Demise have been Greatly Exaggerated. *Biology and Philosophy* 20: 343-353.
- Sarkar, Sahotra. 2011. Drift and the Causes of Evolution. In *Causality in the Sciences*, eds. Phyllis McKay, Federica Russo and Jon Williamson, 444-469. Oxford: Oxford University Press.
- Schuss, Zeev. 2010. *Theory and Applications of Stochastic Processes*. London: Springer
- Sober, Elliott. 1984. *The Nature of Selection*. Cambridge: MIT Press.
- Stephens, Christopher. 2004. Selection, Drift, and the 'Forces' of Evolution. *Philosophy of Science* 71: 550-570.
- . 2010. Forces and Causes in Evolutionary Theory. *Philosophy of Science* 77: 716-727.
- Templeton, Alan. 2006. *Population Genetics and Microevolutionary Theory*. New Jersey: Wiley.
- Walsh, Denis, Tim Lewens and André Ariew. 2002. The Trials of Life: Natural Selection and Random Drift. *Philosophy of Science* 69: 452-473.

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