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The Principle of Stasis: Why drift is not a Zero-Cause Law

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Abstract
This paper analyses the structure of evolutionary theory as a quasi-Newtonian theory and the need to establish a Zero-Cause Law. Several authors have postulated that the special character of drift is because it is the default behaviour or Zero-Cause Law of evolutionary systems, where change and not stasis is the normal state of them. For these authors, drift would be a Zero-Cause Law, the default behaviour and therefore a constituent assumption impossible to change without changing the system. I defend that drift's causal and explanatory power prevents it from being considered as a Zero-Cause Law. Instead, I propose that the default behaviour of evolutionary systems is what I call the Principle of Stasis, which posits that an evolutionary system where there is no selection, drift, mutation, migration, etc., and therefore no difference-maker, will not undergo any change (it will remain in stasis).

Eliminate all other factors, and the one which remains must be the truth.
Sherlock Holmes, in Arthur Conan Doyle's The Sign of the Four

1. INTRODUCTION

Since Darwin's times, through the authors who constructed and moulded the Modern Synthesis, until our current days, evolutionary theory has been conceptualized as a causal theory. Darwin considered natural selection as a *vera causa* (Gould 2002) and the causal-talk has been pervasive in all authors after him. In order to emphasize this causal view, textbooks and most of the evolutionary literature talk about e*volutionary 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, p. 1). Similarly, we can find chapters entitled "Interactions of Natural Selection with other evolutionary forces" (Templeton 2006, chapter 12) or the vector representation of different forces (Rice 2004, chapter 5). The analogy with Newtonian mechanics has been successful in both mathematical modeling and the structuring of evolutionary theory. The analogy was proposed by Elliott Sober (1984) as follows:

> All possible causes of evolution may be characterized in terms of their “biasing effects”. Selection may transform gene frequencies, but so may mutation and migration. (…) All this is merely to locate evolutionary theory in a familiar territory: it is a theory of forces (Sober 1984, p. 31).

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 evolution[1].

Nevertheless, the appropriateness of the causal view, and particularly the Newtonian analogy, has been challenged in the last decade. Several authors (Walsh *et al* 2002, Matthen & Ariew 2002 and 2009, Pigliucci & Kaplan 2006, Walsh 2007 and 2010) have argued for a new view, the *statistical view*, where the evolutionary process and its parts (selection, drift, etc.) are mere statistical outcomes, inseparable from each other. The so called *evolutionary forces* should be conceptualized as statistical population-level tendencies, abandoning any causal role for them. Inside the causal view of evolutionary theory, its advocates have taken two different ways in order to response to this challenge: to strengthen the force interpretation (Filler 2009, Hitchcock & Velasco 2014, Pence 2016, Stephens 2004 and 2010, Shapiro & Sober 2007) or elaborate a causal view not committed to the Newtonian analogy (Reisman & Forber 2005, Rosenberg & Bouchard 2005, Brandon & Ramsey 2007, Gildenhuys 2009 and 2014, Millstein 2006, Millstein et al. 2009, Sarkar 2011). Authors committed to the Newtonian analogy capture the common theoretical structure between evolutionary theory and Newtonian mechanics. On the other hand, causalists not committed to the Newtonian analogy share statisticalists’ concern about some important problems in the force interpretation (the most important being the mismatch in the analogy produced by the lack of directionality of genetic drift).

[1] 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.

In this article, I argue for a third way to defend the causal view. The aim of the force interpretation was to expose the causal structure of the theory. This is what Maudlin (2004) calls "quasi-Newtonian" theories. These are characterized by shaping them into a similar form to Newtonian mechanics whose main axis is the adoption of a default behaviour which tells us how the system would behave if external factors were not acting on it. I call Zero-Cause Law (henceforth ZCL) this default behaviour. The main purpose of building quasi-Newtonian theories is to identify the causes that affect a particular system. That is why the ZCL is necessary. The question about the proper ZCL of evolutionary systems has been implicit in the vast majority of discussions between causalists and statisticalists but never has the concept been made explicit, only a narrow sense of the ZCL such as zero-force law has been used.

In this paper, I argue that the main point in the debate about the structure of evolutionary theory as a quasi-Newtonian theory is the establishment of a ZCL. Some authors agree to give drift such a role. I offer a critical analysis of the role played by drift within the structure of evolutionary theory. I defend that (i) theoretical and empirical reasons reject this claim; and (ii) drift's causal and explanatory power (for instance, in the increasing of eukaryotes' genome size) prevents us from considering it as a ZCL, because it does not correspond to the features of ZCLs.

The structure of the paper is as follows. Section 2 explains in detail the features of ZCLs and the causal account adopted in this paper. Section 3 analyses the points of view of some authors who attribute a special character to drift. They envisage drift as the ZCL of evolutionary systems, where change and not stasis is the default behaviour of them. Section 4 explains why drift does not work as a ZCL. Section 5 develops what I consider to be the proper ZCL in evolutionary theory which I call "The Principle of Stasis". Section 6 concludes.

2. ZERO-CAUSE LAW'S PROPERTIES AND CAUSALITY

The force interpretation was proposed to help identify evolutionary causes. Nevertheless not all causes are forces. Situations like "She has lung cancer because she smokes", "Sherlock Holmes died because Moriarty poisoned him", or "I came late to work because my car broke down", are conceptualized as causal claims but they are not forces in a Newtonian sense –they are not represented, for example, as vectors with magnitude and direction. When we say that smoking causes lung cancer, we are saying that smoking makes a difference (for example that the probability of cancer is greater if you smokes than it is if you do not). I argue for a difference-making account of causation (Menzies 2004). According to this approach, then, a cause is conceptualized as a *difference-maker*, disturbing the normal behaviour of the system. In other words, a cause is "what makes the difference in relation to some assumed background or causal field" (Mackie 1980, p. xi). The system is defined by a number of background conditions, and among these conditions the ZCL tells us how the system behaves before the intervention of external factors, what the *normal course* of the system is like. Some authors (Brandon 2006 and 2010, McShea and Brandon 2010) call a *default state* the normal course of the system. However, I think that *default behaviour* is preferable because a default state of a system is shaped not only by the ZCL, but also by other default settings or background conditions –for example in Newtonian mechanics the default state, before forces are included in the system, encompasses notions like absolute space, absolute time or the law of inertia, but the only ZCL is the law of inertia. Thus, difference-making factors "are seen as intrusions into the system that account for the deviation from the normal course of events" (Menzies 2004, p. 170). How to elaborate a particular system is crucial but, at the same time, it is tied to a context-relativity in the sense of relativity to the "context of inquiry" and the "context of occurrence"[2] (where this not only depends on our why-questions but also on our instrumental capacity, data availability, historical moment, computing capacity, etc., but these obstacles never stopped scientific research). The same fact can be explained in different ways depending on our "why-questions", which depends on our research field, and that is why causal statements are relative to certain contextual parameters.

This kind of theorizing is found in Population Genetics textbooks by, firstly, establishing the background conditions of the system and, secondly, by introducing factors against this background. Evolutionary theory usually takes for granted the Hardy-Weinberg law (henceforth H-W law) (Sober 1984, Gillespie 2004, Templeton 2006) as its ZCL counterpart. According to the H-W 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

[2] In Menzies words: "One form of relativity might be called relativity to the context of occurrence. If a forest is destroyed by fire, the presence of oxygen would be cited as a mere condition of the forest's destruction. On the other hand, if a fire breaks out in a laboratory where oxygen is deliberately excluded, it may be appropriate to cite the presence of oxygen as a cause of the fire. The second form of relativity might be called relativity to the context of enquiry. For example, the cause of a great famine in India may be identified by an Indian farmer as the drought, but the World Food Authority may identify the Indian government's failure to build up reserves as the cause, and the drought as a mere condition" (Menzies 2014).

frequencies will remain stable) if no external factor acts on it. The best historical example following this way of theorizing is Newtonian mechanics (Menzies 2004, Maudlin 2004) –that is why Maudlin call them quasi-Newtonian theories and, very likely, the reason for the rise in force-talk**.** Thus, the first law of Newtonian mechanics functions to establish that every body continues in its state of rest, or of uniform motion in a right line, unless it is compelled to change that state by forces impressed upon it (Newton 1846 [1687]). Thus, both the law of inertia as well as the H-W law, tell us how the system would behave if nothing disturbed it, and so assuring a neutral substrate where we can introduce external factors (i.e. causes). In addition, both laws are idealizations because there are always forces applying on real objects and some H-W conditions are always violated in real populations (Toulmin 1961, Gouvêa 2015).

Since Sober proposed the Newtonian analogy, this default behaviour has been called *zero-force law* until now. Nevertheless, it is easy to see that the zero-force law is a special case of ZCL: it tell us how the system behaves if there is no difference-maker acting on it, except than in this case the difference-makers are forces. That is, the zero-force law works as a ZCL on a system where causes are forces. In addition, the difference-making account allow us to avoid the problems associated with the extension of the concept of "force" beyond classical mechanics; this account does not require that a cause has an explicit and predictable directionality, only that it makes a difference, so drift can still be considered an evolutionary cause without dealing with all the properties that a force must have (see Luque 2016). Another advantage of this difference-making account of causation is that it encompasses different causalists approaches. The vast majority have followed Woodward (2003)'s manipulationist account of causation (Reisman & Forber 2005, Abrams 2007, Shapiro & Sober 2007, Gildenhuys 2009 and 2014, Ramsey 2012, Clatterburk 2015, Otsuka 2016), while others have followed a counterfactual account of causation (Glennan 2009, Huneman 2012; Millstein 2006 uses both accounts) or a probabilistic account of causation (Razeto-Barry & Frick 2011). Difference-making is a general form of all these accounts of causation (manipulationist, counterfactual and probabilistic).

Within the background conditions, ZCLs play a crucial role because they tell us how the system behaves before the intervention of external factors and what the normal course of the system is like[3]. Since the ZCLs are part of the background conditions, they

[3] Here we are not dealing with the realism-antirealism debate. The notion of *normal world* is specified by the model; but it is obvious that many authors thought that the background conditions postulated to their

are the basis to explain the unexpected. They are what is expected (the default behaviour), but because of that, they are required to identify what must be explained (Toulmin 1961). That is the role that Newton gives to the law of inertia. It tells us that when no force is operating, the body will continue at a constant velocity. In addition, Newton's First Law is the link between the background conditions and difference-makers in any Newtonian system, since it puts us in a position to appreciate the effects of different forces and is the only background condition which plays that role. The law of inertia presupposes the following features: absolute space, absolute time and the existence of one body (Maudlin 2012; see table 1). The first two give us a topology, a structure, a metric and a vacuum where the body and its state of motion can be located, measured and continued in a straight line (if it is not at rest). At the same time, the law of inertia requires the inclusion of external forces (difference-makers) in order to explain why a body is not in uniform motion (in a straight line or at rest).

	BACKGROUND CONDITIONS	**DIFFERENCE-MAKERS**
NEWTONIAN MECHANICS	Absolute space Absolute time Body The Principle of Inertia	Gravity Electromagnetism Spring forces Friction forces Etc.

Table 1.

Aristotle (1983) established in a narrative way –since he lacked the tools and mathematical notations– that the constant force applied to an object was equal to the velocity of the object times its mass, so two horses move a car with double speed than one. What Aristotle understood was that bodies are always subject to a resistance –as Aristotle denies the existence of a vacuum– so always the action of a force is required to keep a body in motion[4]. In other words, for Aristotle "change" in the physical sense

normal world specify how the world really is (Newton is a clear example where absolute space, absolute time, etc. were *the structure of the world* and not only of his model).

[4] Brandon (2006 p. 320) writes in a Newtonian way, the dynamic formula of Aristotle as $F = m \cdot v$. However, this formula is not exact because it requires an additional term, resistance r, since denying a vacuum implies that there is always a resistance. Consequently $F = m \cdot v \cdot r$. This modern formulation of Aristotelian dynamic shows why Aristotle denies the existence of vacuum. If a body's velocity is $v = \frac{F}{m \cdot r}$

means displacement, “change of place”. The Scientific Revolution of the sixteenth and seventeenth centuries brought about a radical change in this view. The principle of inertia, formulated in a restricted way by Galileo (uniform circular motion) and with all its generality by Descartes and Newton (Barbour 2001, Sklar 2013), posits that “change” means “change of velocity”. It implies that what needs to be explained is the change with respect to that default behaviour which could also be an effect of operating forces. These forces will be calculated by means of the second law of motion. What is normal is that a body keeps its constant velocity (at rest or in motion) and what needs to be explained is the change in its default behaviour (see Gouvêa 2015 for a recent discussion)[5].

Several authors thought that its supposed futility made it unnecessary, arguing that it could be deduced from the second law of motion: if none impressed force exist, the acceleration is zero and therefore the velocity is constant (uniform and rectilinear or null). However, its existence seems difficult to deny because it works as a ZCL –it tells us what has to be explained. Even if relativistic mechanics totally rejected the second law –on which, according to some authors the principle of inertia depends–, the law of inertia still remains both in the special theory of relativity (the law of inertia is invariant under Lorentz’s transformations) and in the general theory of relativity (according to which, geometrically, the cosmoline of a free particle is a geodesic).

2.1. The persistence of ancestral forms

The importance of the ZCLs is shown more clearly when two of them, in the same way as was done above with Aristotle and Newton, are opposed. The ZCL defended by pre-Darwinian authors –especially Cuvier– and by Darwin (1859), are antagonistic, and their opposition is illuminating. Cuvier thought that the normal state of nature was exuberance, that is, the emergence of the greater number of varieties of living forms. Four Cuverians’ physiological types (verbrata, mollusca, articulata, and radiata) exhaust all living beings and circumscribe nature’s propensity to generate spontaneous variety. He seeks to explain the persistence of form regularities –the living being organization–,

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then the time it needs to go over a space S will be $T = \frac{S \cdot m \cdot r}{F}$. If resistance is zero, then the body goes over such a space in time 0, in infinite velocity. But to Aristotle this is absurd and consequently he denies the existence of vacuum.

[5] Thanks to a referee for drawing my attention to Gouvêa’s paper. Gouvêa claims that the law of inertia is a sufficient cause of certain events (constant velocity), but is not necessary because it is the second law that explains how forces can cancel each other (another way to maintain constant velocity). Nevertheless, a difference-making account of causation invalidates inertia as a cause, because a cause is defined as a difference-maker that alters the default behaviour (i. e. inertia). In addition, the second law is conceptually parasitic on the first law (Maudlin 2012). I will go into detail in section 4.

in other words, the limits on variation, because what does not need to be explained is the creation of variation which "always keeps within the limits of the prescribed conditions of existence, nature becomes free in its fecundity in so far as those conditions do not limit it" (Cuvier 1805, p. 58, my translation). Rather, what must be explained is the permanence of some regularities in living beings (Caponi 2004). Unlike him, Darwin pointed out that the bodies' normal state is the persistence of its ancestral form and what needs explanation is the change of that normal state, i.e. the diversification of forms. This contrasts with the Cuverian's world in which the coordination of the parts, their integrity and harmony are essential to produce a functional living being, whose *conditions of existence* are conceptualized, not from an ecological Darwinian perspective, but from a physiological one (Grene 2001). However, in the Darwinian world what becomes important is the struggle for existence which occurs between individuals and the environment –the ecological conditions (Collins 1986). This could change the ancestral form, natural selection being the cause of such a change.

In the pre-Darwinian world where Cuvier or Lamarck lived, change is not a legitimate explanandum. "Contrary to the world of Lamarck, the Darwinian world is not *naturally* or *spontaneously* prone to change." (Caponi 2004, p. 10, emphasis in original; my translation).

3. DRIFT AS A ZERO-CAUSE LAW

The forces analogy seems to be faced with a big problem when it deals with genetic drift. Drift lacks a direction by definition: it is a non-directional process "since the expected change at every point is zero" (Rice 2004, p.131). Genetic drift is the only one of the so-called evolutionary forces which lacks a direction and is stochastic, the other ones are directional and deterministic. Its special role could be explained by considering it not as a force but as the ZCL counterpart in all evolutionary systems.

3.1. The Principle of Drift.

McShea and Brandon (2010; Brandon 2006 and 2010) defend that drift is not a force; indeed it would be the default state or zero-force law (in Brandon's and McShea's terminology, see section 2; in my terms, the ZCL) instead of the H-W law. Their reasoning is based on a *reductio ad absurdum*. They give two definitions of the H-W law:

H-W_1: If a population exists with two alleles, A_1 and A_2, with frequencies p and q respectively, then in a single generation the population will settle into genic and genotypic equilibrium with gene frequencies *p* and *q*, and genotypic frequencies of $A_1A_1 = p^2$; $A_1A_2 = 2pq$; and $A_2A_2 = q^2$—provided that there is no selection, mutation, migration, non-random mating, or *drift.*

H-W_2: If an *infinite* population exists with two alleles, A_1 and A_2, with frequencies *p* and *q* respectively, then in a single generation the population will settle into genic and genotypic equilibrium with gene frequencies *p* and *q*, and genotypic frequencies of $A_1A_1 = p^2$; $A_1A_2 = 2pq$; and $A_2A_2 = q^2$—provided that there is no selection, mutation, migration, or non-random mating (Brandon 2006 p. 324; McShea & Brandon 2010 pp. 100-101).

We can observe that the only difference between them is that the first one considers a finite population –and therefore is subject to drift– which is in H-W equilibrium, while in the second formulation the population is in H-W equilibrium, but it is infinite and, by definition, there is no drift in it. In H-W_1 drift would be a force which alters population's equilibrium. In H-W_2 there is no drift but it faces the problem of the non-existence of infinite populations. In H-W_1 drift is understood as a force but McShea and Brandon point out the difficulties of considering drift as a force because of its lack of direction. Instead, these authors defend that drift, far from being a special force which is introduced in the population, is the default behaviour of the population and, hence, a ZCL in the same way that inertia is the bodies' default behaviour in Newtonian mechanics. The sampling process which finite populations are subjected to is constitutive of them, not something that can be added to them after. Then, the H-W law, both in its H-W_1 and H-W_2 form, cannot be the ZCL because it confuses constitutive elements (drift) with elements which are introduced –selection, mutation, migration, mating system, etc.– (H-W_1), and when it does not (H-W_2), its formulation is false because infinite populations do not exist. The authors do not dispute the use of idealizations whenever it can be used in a concrete reality. What they say is that the H-W_2 is not useful because if we wanted to introduce drift to it, we would come back to H-W_1 and, therefore, we would face the problem of confusing drift with a force. This claim contrasts with the standard view among population geneticists, who consider the H-W law as a robust model to many violations (see Conner & Hartl 2004). This special status is called by Brandon (2006) "The Principle of Drift" (PD) and is formulated as follows:

(A) A population at equilibrium will tend to drift from that equilibrium unless acted on by an evolutionary force. (A population at rest will tend to start moving unless acted on by an external force)

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

Drift, such as inertia in Newtonian mechanics, is the default behaviour or ZCL of populations but at the same time it is a non-Newtonian model of evolution. That is because the principle of inertia establishes stasis or lack of change as the default behaviour of bodies. The PD however, as is noted in clause (B), resembles the Aristotelian principle of movement because it requires the action of a constant force to keep the population in the same state of motion. One of the utilities of the PD versus the H-W law would be its universality, since it does not depend on the need of diploid sexual organisms, and therefore it can be applied to any form of life that could be found. Thus, evolutionary biology would have two universal laws: the PD and the Principle of Natural Selection. It must be highlighted that the causal conception favoured by Brandon (Salmon's model of causal-mechanical explanation) requires the conceiving of inertia and drift as causes because they are a fundamental part of the causal structure of our world, but none of them are forces. Therefore, McShea and Brandon consider drift-based explanations as having a different status than selection-based explanations. So Brandon calls them *default causal explanations*, while explanations that appeal to Newtonian and evolutionary forces are, respectively, called *special causal explanations*. Imagine we have an apple at rest on the ground. As two opposing forces of equal magnitude (Earth gravitational field and surface friction) are acting on it, the net force is zero. So the apple is obeying Newton's first law. McShea and Brandon argue that this is a causal explanation because "Newton's laws describe the causal structure of a Newtonian world and that apple is behaving accordingly" (McShea & Brandon 2010, p. 107). This is an important claim in so far as I will defend (see section 4) that a ZCL cannot be a cause due to its own nature –it does not matter if this ZCL takes the form of a zero-force law.

A concept related to the PD is the so called "Zero-Force Evolutionary Law" (henceforth ZFEL) which posits that "In any evolutionary system in which there is variation and heredity, there is a tendency for diversity and complexity to increase" (McShea & Brandon 2010, p. 4). The ZFEL is presented as the default behaviour of evolutionary systems, which leads them towards diversity and complexity (complexity is used in the sense of non-functional complexity or pure complexity) in the absence of forces, especially natural selection. The ZFEL, like the PD, is analogous to the law of inertia and at the same time, is non-Newtonian because it follows the same slogan: If no force, then change (McShea & Brandon 2010, p. 6). Also the ZFEL, like the PD, despite being the default behaviour of evolutionary systems, has causal power[6].

Although its scope and empirical value are questionable (Bromham 2011), there is a possible structural problem in McShea and Brandon's position. It is not clear whether both, the ZFEL and the PD, are distinct things or simply that the ZFEL is an extension of the later –for example, Brandon (2010, p. 703) says "Dan McShea and I (McShea and Brandon 2010) generalize the Principle of Drift into what we name the Zero-Force Evolutionary Law (ZFEL)". Although the authors try to show their distinction by claiming that the two laws apply to two different phenomena[7], the Principle of Drift is on most occasions what underlies the ZFEL (see McShea & Brandon 2010, p. 95). This dichotomy could not be more than two forms of a common principle (see Ramsey 2012)[8] establishing a single default behaviour with possible different instantiations (in this case, means and variances). Even if the ZFEL and the PD become fused or not, I will attempt to show in section 4 that the major problem in their position is the causal import of the PD and the ZFEL**.**

3.2. Constitutive and facultative assumptions

In a similar line of argumentation, Sarkar (2011) locates drift as ZCL (although he never uses the term) but with different connotations from those defended by McShea and Brandon. Sarkar builds a haploid model with a closed population (it doesn't have migration), taking into account only selection, mutation and drift. An equal probability

[6] In their book, the ZFEL is described as a cause. For instance: "we claim to have identified is a background tendency, one that acts everywhere and always" (McShea and Brandon, p. 7); "And the resulting increase in complexity is the ZFEL in action" (ibid., p 55). This causal import has been confirmed by McShea (personal communication).

[7] McShea (personal communication): "The principle of drift is about means. It says that in the absence of forces, the mean will tend to drive. The ZFEL is about variances. It says that in the absence of forces, the variance will tend to increase".

[8] Ramsey creates the concept of "driftability" which would be what underlies the PD and the ZFEL. I will not go into detail here.

of reproduction is assumed –which is produced at the same time– and also that all the fitness differences between the two types –*A* and *a*– are due to viability differences, and not as a consequence of fertility differences, such as probabilities remaining constant over time. Population size, when it is finite, is fixed by resource constraints (it has reached the maximum carrying capacity of the environment). Then, Sarkar calculates how populations would behave when there is selection and when there is not (equal fitness) if the population were finite or infinite. In the case of a finite population, the probability of fixation of one of the types in the absence of selection is equal to the initial number divided by the population size. In an infinite population, if there is no selection, the result is the same as before; the difference appears when selection is introduced. In this case, the probability that the type with greatest fitness would be fixed is equal to 1, regardless of the initial frequencies, unlike what happened in the previous finite population model where the result of the selection depends on the initial frequencies.

Sarkar points out that drift is not mentioned in the model. However it is included in the model through the population size when it is finite. Population size actually is a *constitutive assumption* of the system. Constitutive assumptions are those privileged conditions which cannot be changed without changing the identity of the system. Facultative assumptions, on the other hand, are those which may vary without changing the identity of the system. Concerning this distinction, Sarkar follows the work of Mackie (1980) and Menzies (2004) adopting a difference-making account of causation –the same adopted in this paper. Constitutive assumptions are the *assumed background*, and the facultative assumptions are *what make the difference in relation to some assumed background*. Therefore, the facultative assumptions would be the relevant causes which operate against the background conditions stipulated by the constitutive assumptions. Thus, selection and mutation expressed in the model would be the causes of evolutionary change. However, drift would not be a cause of evolutionary change but a constituent part of the system; so Sarkar agrees with advocates of the statistical view that drift is not a cause, although he gives different reasons for that. Nothing causes the constant change in finite populations by a sampling process; it is its default behaviour and the reason of the stochastic nature of finite population's models. Here, we are facing a stochastic dynamical model of evolution.

Despite the similarity between McShea and Brandon's position and Sarkar's one, there is a fundamental discrepancy between them: the first considers drift –and its related concept, the ZFEL– a cause, despite being the ZCL counterpart in evolutionary biology, while Sarkar considers that drift is not a cause precisely because it is the ZCL.

4. DRIFT AS A ZERO-CAUSE LAW, AGAIN

The main question is: Is drift a good ZCL? McShea, Brandon and Sarkar suggest that drift must be the ZCL of evolutionary systems because it is the default behaviour (McShea and Brandon) of all real populations, a constitutive assumption of the system (Sarkar). Universality plays in favour of considering drift as a ZCL. But this feature is not enough. Think about the force of gravity. Newton formulated it as a universal law and, in fact, it operates anywhere in the universe where bodies are interacting. We could say that it is a constituent part of the universe, its default behaviour and because of that, it should be considered a ZCL. In other words, following the reasoning of the authors cited earlier in this paragraph, Newton was wrong when he put the law of inertia as ZCL since gravity, due to its universal character, would be the true default behaviour of the system (Pence 2016, Stephens 2010). However, we can imagine situations, although they cannot be physically feasible for real systems, where it is possible to eliminate from the system both gravity and drift**.** Many models in physics remove forces of whose existence physicists are aware, like in electromagnetic models where the action of gravity is ignored or models without friction (as a pulley with two masses and no friction, frictionless planes, simple pendulum, etc.). In these scenarios, not including gravity or friction do nothing to alter the nature of the system, so they are not constitutive but facultative assumptions that we can introduce and remove without altering the model. In the same way as gravity can be removed from a Newtonian system[9], it is possible to model a system where there is no drift postulating an infinite population size and where only selection and mutation would be acting (as Sarkar does). Neither situation, a universe without gravity nor a population without drift, seems plausible in the world we live; nor their constitutive character neither.

Following Sarkar's distinction between constitutive and facultative assumptions, we can see why drift is not the default behaviour. The distinction implies identifying the features that cannot be removed without changing the essence or the identity of the system. Establishing a definitive list of constitutive assumptions for evolutionary

[9] For example, Pence (2016) defends gravity could be removed from the system if we postulate that the gravitational constant, G, has value 0; or by imagining the behaviour of a mass which had been sent to an infinite distance from any other body.

systems is utopic because it depends on several issues (see section 2). But this long philosophical debate has been played out within a precise framework (in a precise context): Population Genetics. It was in this area where Sober said that evolutionary theory was like a theory of forces, and why he postulated the H-W law as a ZCL. Therefore my analysis will focus on these models. However, I defend that the notion of the permanence of ancestral forms shows that this privileged status for stasis has been pervasive in evolutionary theory from Darwin to our days, by embracing higher-level entities and not being constrained to a gene's eye view. For that reason, McShea and Brandon talk about a gestalt shift –they are changing a constitutive assumption– admitting that stasis, not only in Population Genetics, but also in evolutionary theory in general has been the common view.

So, the relevant question here is what the constitutive assumptions of standard evolutionary theory are[10]. I propose that its default settings can be summarized as follows (see table 2): a population, variation, an environment, ancestor/descendant relations, and what I call The Principle of Stasis (see section 5). Evolution requires a population of individuals because individuals, themselves, do not evolve; only populations evolve. Evolution also requires non-identical individuals, the existence of variation in a population. In other words, for any evolutionary process we need a population of non-identical individuals. The environment is where the population is located, the action space where the population develops its activities. Ancestor/Descendant relations give to the population a time line and it is not committed to any particular form of heredity; but in this context, Earth ancestor/descendant relations are instantiated by particulate inheritance (clonal and Mendelian)[11]. The Principle of Stasis tells us how the system will behave if there are no facultative assumptions. In other words, it tells us what the default behaviour is. It is the ZCL that connects constitutive and facultative assumptions. We can see that the Principle of Stasis depends on the Ancestor/Descendant relations, in the same way that the Principle of Inertia depends on absolute space (the vacuum), or the existence of a body. If the inheritance was blending, change and not stasis would be the ZCL. What all this shows

[10] I called "standard" in order to not limit the existence of other approaches, like McShea and Brandon's approach, on evolutionary theory.

[11] Evolutionary theory is capable of dealing with other forms of inheritance, from blending inheritance (Gardner 2011) to other none genetic ones (epigenetic, behavioural, symbolic) through the Price equation (Halenterä & Uller 2010). This feature links the current theory with its beginning in Darwin's time, where the inheritance system was unknown, and it is not limited by the kind of inheritance which is the contingent result of evolution on Earth. That is why it would be able to deal with other kind of organisms different to those on Earth.

is that constitutive assumptions are not statics and depend on the available data in any historical time.

	BACKGROUND CONDITIONS	DIFFERENCE-MAKERS
STANDARD EVOLUTIONARY THEORY	Population Variation Environment Ancestor/Descendant relations The Principle of Stasis	Natural selection Genetic drift Mutation Migration Etc.

Table 2.

On the other hand, facultative assumptions (i.e. evolutionary causes or difference-makers) can be removed without changing the identity of the system. We could devise a prototypical standard evolutionary theory system without natural selection by postulating no fitness variation. Also we could think of an evolutionary system without mutation by postulating a perfect replication mechanism or without migration by postulating a closed population. In all these cases, the absence of the processes does not affect the nature of the system –actually Sarkar's model does it. And, finally, the mathematical models in Population Genetics allow us to see why drift is not a constitutive assumption. In any Population Genetics textbook drift is introduced by postulating a finite population size. In order to make the calculus easier, models start with an infinite population to construct a deterministic process. Thus, we can perfectly model an evolutionary system with an infinite population size and the system will remain within standard evolutionary theory's framework. What it shows is that we can model an evolutionary system without drift. What is a constitutive assumption is the population itself and not its size. Therefore, against Sarkar's claim, drift is not a constitutive assumption because its absence does not change the identity of the system. So Sarkar, and also McShea and Brandon, when locating drift inside the constitutive assumptions, are breaking the evolutionary scheme or the research program initiated by Darwin, i.e. a gestalt shift, because change and not stasis would be the ZCL (see table 3).

	ZERO-CAUSE LAW	EVOLUTIONARY CAUSES
STANDARD EVOLUTIONARY THEORY	The Principle of Stasis*	Natural selection Genetic drift Mutation Migration Etc.

McShea and Brandon	The Principle of Drift The ZFEL**	Natural selection Mutation Migration Etc.
Sarkar	Drift	Natural selection Mutation Migration Etc.
* A particular form is the H-W law ** In fact, for McShea and Brandon, both ZCLs are causes too		

Table 3

Thus, from a theoretical point of view, following the standard mathematical models in Population Genetics, drift is not a constitutive assumption, so it cannot be a ZCL. Another problem that appears when we consider drift as a ZCL, and maybe this is the main one, is that it has a central role in the explanation of a large number of evolutionary phenomena**.** Focusing on what would be one of the most important of such phenomena, but not unique (see Millstein 2009), Lynch (2007a, 2007b) has suggested that the increase in genome size occurred in the transition from prokaryotes organisms – a few kilobases in viruses– to eukaryotes organisms –megabases in plants, mammals, etc.– has been due to genetic drift which fixed in genomes, along lineages, elements with little or no advantage, and even mildly deleterious, such as introns, transposable elements, noncoding DNA, amino acid substitutions, etc. Drift would be the main factor because the eukaryotes effective population size was smaller than the prokaryotes one. Thus, bacterial species have an effective population size so large that selection quickly fixed any beneficial mutation and its ability to eliminate the deleterious one is huge. On the other hand, in eukaryotic species, the effective population size is much smaller so that natural selection is not as effective in eliminating those elements. Thus, drift is shown as a crucial factor in explaining the increase of organisms' complexity. This apparently agrees with McShea and Brandon who think that drift, in line with their ZFEL, generates diversity and complexity[12]. However, its important explanatory and

[12] McShea and Brandon claim that molecular tests show that molecular biologists (like Lynch) are already postulating drift as the default behaviour. The molecular tests compare substitutions rates between nonsynonymous and synonymous nucleotide sites, there being neutral expectation at the starting point (i.e. under genetic drift) (Charlesworth & Charlesworth 2010). What these tests do is to postulate a system with background conditions and one factor (drift) in the system before it sees the consequences of *extra factors* (in this case, natural selection) –an equivalent example in physics would be the case of a simple pendulum, which starts with one factor (gravity) and after we introduce an extra factor (friction). In other words: "Even when a system already possesses an array of causal forces, it makes sense to ask about the causal significance of additional causal forces. The condition for difference-making provides us with a test of the causal significance of these extra factors" (Menzies 2004, p. 161).

causal role is what makes it impossible to understand drift as a ZCL. ZCLs are not the cause of anything or the explanation of anything, but they provide a sort of framework which stipulates what needs to be explained and what is a cause in the system. Inertia does not explain why a body remains at rest or in uniform motion. The default behaviour of bodies is constant velocity. Inertia, as a constitutive assumption cannot be the cause of the default behaviour of the bodies. Because of that Sarkar postulated, quite rightly, that if drift was a constitutive assumption of the system it could not be a cause. But drift seems to play a causal and explicative role, as in the case of the increasing size of the genome, which is so crucial that it cannot be reduced to a constitutive, non-causal, element. Therefore, McShea and Brandon (see also Brandon 2006) are forced to provide both drift and inertia, as causal powers. But, following Maudlin reasoning (2004, p. 430): "If a body is at rest at one time, and nothing acts on it (i.e., no force acts on it), then it sounds odd to ask what causes it to remain at rest. It sounds odd to say that the body's own inertial mass causes it to remain at rest, since there is no force that the mass is resisting, and the inertial mass is just a measure of a body's resistance to force. And it sounds odd to say that the law of inertia itself causes the body to remain at rest".

ZCLs, like the law of inertia, do not have causal power because they are inside the background conditions. The law of inertia sets the boundaries of an explanation in Newtonian mechanics because it is an ideal (Toulmin 1961, Gouvêa 2015), theoretically prior to inclusion of forces in the system. Remember the example in section 3 about the apple at rest. We have two opposing forces of equal magnitude, and therefore the apple at rest. McShea and Brandon claim that this empirical experience shows that inertia can be conceptualized as a causal explanation. Nevertheless, this is not correct because the law of inertia can never be achieved by experience[13]. The law states that in the absence of forces, a body will continue its state of rest, or of uniform motion in a straight line. However, the apple is at rest due to the action of two forces, not because the absence of them. It is a state of simulated inertia because we cannot ever achieve a world without any force. It is incorrect to say that the apple's own inertial mass causes it to remain at rest, but it is still a legitimate question to ask what forces are acting on the apple in order to produce its being at rest on the ground.

[13] "[The] law of inertia cannot be derived directly from experiment, but only by speculative thinking consistent with observation. The idealized experiment can never be actually performed, although it leads to a profound understanding of real experiments" (Einstein & Infeld 1938, p. 8). Gouvêa (2015, p. 375) agrees: "Newton's first law is not known from empirical examples".

So ZCL cannot have any causal role. However, it is not unusual for biologists to consider drift as the cause of some changes in populations. If drift were considered a ZCL it could not be a cause of anything. Nevertheless, experimental research shows that it is a key factor in the increase of complexity. Thus, if we accept that drift is a ZCL, consequently, complexity would have neither explanation nor cause. Complexity just appears (as it is appealed to in the ZFEL). This does not seem an acceptable position. Complexity must be explained, not only be found.

The ZFEL faces the same problems as the PD. Its causal role in the formation of complexity prevents it from being a ZCL. Furthermore, the similarity between the tendency of increasing complexity and diversity of ZFEL and the pre-Darwinian position is clear. In both "nature becomes free in its fecundity in so far as those conditions do not limit it" (Cuvier 1805, p. 58). If there were no constraints and other forces, complexity would spontaneously emerge. Therefore, McShea and Brandon appeal to the causal power of the ZFEL, but in doing so they invalidate it as a ZCL. Complexity, however, demands explanation.

5. THE PROPER ZERO-CAUSE LAW

To sum up, drift cannot be a ZCL because it is not more constitutive for populations than gravity is for the Newtonian's system. Furthermore, its causal and explanatory power exceeds what a ZCL would require. Then, if drift is not a good ZCL, what could be a good one for evolutionary biology? The H-W law has traditionally played this role. However, critics point out its restricted application to diploid sexual organisms and its nomological slack due to being a consequence of evolution (Beatty 1995; see Barrett et al. 2012, p.731, for a reply). Another problem faced by the H-W law is that it allows two formulations, one for allelic frequencies and another for genotypic frequencies. Sober himself (1984, p. 36) recognizes this dual way of formulating the H-W law as a ZCL because, indeed, a diploid sexual population may be changed in its genotypic frequencies without changing its allelic frequencies (Sober 2000, Stephens 2004). For this reason, sometimes the mating system is included among the evolutionary causes because it could change the genotype frequencies but not the gene ones. In favour of H-W law, it describes how a diploid sexual population would behave were it disturbed by some external factor, a fundamental characteristic of a ZCL. The population, when there are no difference-makers operating on it, will remain in equilibrium; its default behaviour will continue unchanged. In this situation, the explanatory power of the H-W law within population dynamics is minimal or non-existent[14]. Moreover, the H-W law has a heuristic value −while drift lacks it when it is considered as a ZCL. That allows us to know for sure when one or more factors are acting upon a population (Stephens 2010). Loss of H-W equilibrium is a sufficient condition to detect a difference-maker, but it is not enough for McShea and Brandon's PD or ZFEL.

If the genetic system is itself the product of evolution, then there should be a ZCL that is not genetic. So there is a necessity to develop a ZCL that is not tied to any genetic system. I consider the H-W law –in its two possible formulations: allelic and genotypic– as well as *the persistence of the ancestral form* of Darwin, as special cases of a more general principle –the *Principle of Stasis*– which could be formulated as follows:

> *Principle of Stasis*: An evolutionary system where there is no selection, drift, mutation, migration, etc., so there is no difference-maker, will not undergo any change (it will remain in stasis).

This applies to asexual organisms (see Charlesworth & Charlesworth 2010 p. 34) overcoming the limitations of the H-W law, in so far as mathematical models of asexual populations (e.g., bacteria) start with models of population growth but not with models of change in gene frequencies. That is because asexual populations reproduce themselves through cloning and because of that, gene frequencies cannot change. This apparently obvious remark is the characteristic feature of the ZCLs and the causes of evolutionary change in biology –both in asexual populations (Elena and Lenski 2003) and sexual ones (Gillespie 2004, Templeton 2006, Charlesworth & Charlesworth 2010)– and so correspond to those postulated in the Principle of Stasis.

Only one equivalent principle has been formulated recently. It is the *zero cause evolutionary law* developed by Barrett et al (2012), which states that "If there is no selection and no drift (and no mutation or migration, either), then trait frequencies will remain the same; this is a 'law of stasis'." (Barrett et al. 2012, p. 733). Both principles stipulate the same ZCL and our views are similar. However, Barrett et al. (2012),

[14] However, as we are building upon a Mendelian genetic background, the H-W law plays an explanatory role at such a level. It explains why genetic variation, based in a Mendelian genetic, persists indefinitely because inheritance is particulate rather than blending (Templeton 2006).

although they do not use the word “force” in stating their principle, they still think in terms of the force interpretation and search for a possible directionality to drift. On the other hand, I postulate a broader causal framework that avoids this issue, unifying different causalists approaches. In addition, the distinction between background conditions and difference-makers (or in Sarkar’s terms, constitutive and facultative assumptions) clarifies the features that any ZCL must accomplish and why drift does not work in that way. My formulation is not entirely new but it intends to show clearly the principle that follows the research program which comes from Darwin to modern evolutionary biology. This ZCL has a universal character and it remains in the framework initiated by Darwin –unlike orthogenetic proposals like McShea and Brandon’s (2010, p. 127). At this point one should be reminded that, "contrary to the world of Lamarck, the Darwinian world is not *naturally* or *spontaneously* prone to change" (Caponi 2004, p. 10). The proper ZCL is the Principle of Stasis.

6. CONCLUSION

The structure of evolutionary theory as a quasi-Newtonian theory involves the establishment of a ZCL or default behaviour which indicates how the system would behave if there are no difference-makers. Several authors have claimed the special character of drift within evolutionary theory, postulating it as the ZCL of evolutionary systems. It has been shown that such approach is not well-grounded since drift is not a good ZCL. Instead, I propose a ZCL which includes the H-W law and the persistence of the ancestral form of Darwin, the Principle of Stasis, which postulates that an evolutionary system, if it is not influenced by a difference-maker, will remain unchanged. Its advantages are: (i) it keeps drift as a cause of evolution: (ii) it remains itself within the research program initiated by Darwin encompassing different special formulations of the Principle of Stasis (H-W law, persistence of the ancestral form), and (iii) it demands a causal explanation for the increase in complexity.

Despite my sympathy for the force-talk and the Newtonian analogy in general, my approach somehow deflates part of the issues with the use of the concept “evolutionary forces” because, in my analysis, they are causes (difference-makers). But there is no need to extend the metaphor excessively. So drift can still be considered an evolutionary cause without dealing with all the properties that a *force* must have (in short, without commitment to all the features of Newtonian forces). Nevertheless, the Newtonian analogy is illuminating insofar as it is helpful in revealing the causal structure of evolutionary theory. In other words, the theory is constructed from a ZCL that stipulates a default behaviour and arises by introducing factors which alters that behaviour. That is the reason why the force metaphor was formulated in the first place and why it still continues in evolutionary literature.

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