Chapter 9

Drift as a Force of Evolution: A Manipulationist Account

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Abstract Can evolutionary theory be properly characterised as a "theory of forces", like Newtonian mechanics? One common criticism to this claim concerns the possibility to conceive genetic drift as a causal process endowed by a specific magnitude and direction. In this article, we aim to offer an original response to this criticism by pointing out a connection between the notion of force and the notion of explanatory depth, as depicted in Hitchcock and Woodward's manipulationist account of causal explanation. In a nutshell, our argument is that, since force-explanations can be consistently reframed as deep explanations and vice versa, and the notion of drift can be characterised in manipulationist terms as constitutively intervening in evolutionary deep explanations, then drift-explanations can be consistently reframed as force-explanations, and drift can be properly considered as a force of evolution. Insofar as similar considerations may be extended also to other evolutionary factors – chiefly selection –, our analysis offers an important support to the claim that evolutionary theory is a theory of forces.

9.1 Introduction

Wondering about the explanatory structure of evolutionary theory – that is, roughly, the way in which it provides patterns of explanation applicable to a wide set of phenomena (Kitcher 1989) –, many authors have depicted it as a *dynamical* theory or, in other words, as a *theory of forces*. According to Elliott Sober (who popularised this conception in the philosophy of biology):

> A theory of forces begins with a claim about what will happen to a system when *no* forces act on it. The theory then specifies what effects each possible force will have when it acts alone. Then the theory progresses to a treatment of the pairwise effects of forces, then to triples, and

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> so on, until all possible forces treated by the theory are taken into account. Since most objects in the real world are bombarded by a multiplicity of forces, this increase in complexity brings with it an increase in realism (Sober 1984, p. 31; emphasis in the original).

Taking Newtonian mechanics as the paradigmatic example, we could say that a theory of forces must include:

- a first law – the zero-force law – describing how the system behaves when no forces act on it (i.e., in the case of Newtonian mechanics, the principle of inertia);
- a (or a set of) consequence law(s) that describe the direction, the magnitude and the outcome of the forces acting in the system (exemplified in classical mechanics by Newton's second law);
- a causal characterisation of the acting forces (e.g., the laws of gravitation, buoyancy etc.).

Likewise, we might consider the Hardy-Weinberg principle as the zero-force law of evolutionary theory, the equations calculating the effects of selection, drift, mutation, recombination and migration in population genetics as its consequence laws, and specific ecological configurations instantiating these laws as the causal characterisation of the theory (Caponi 2014). According to a common conception, in Newtonian mechanics the notion of force is explanatory because it subsumes the possible causes of change in motion under specific theoretical/nomological descriptions. Analogously, according to the dynamical interpretation of evolutionary theory, evolutionary forces would conceptually subsume sets of ecological factors according to their effects, thus allowing unified causal explanations of the changes in genotypic and phenotypic distributions. In spite of its apparent plausibility (many textbooks of evolutionary biology and population genetics adopt the force analogy; see, for instance, Gillespie 2004; Rice 2004; Futuyma 2005; Hartl and Clark 2007), this view has been nonetheless repeatedly questioned. On the one hand, the so-called *statisticalists* (Matthen and Ariew 2002; Walsh et al. 2002) have argued that a clear-cut causal characterisation of selection and drift is unviable. Since, as we have just seen, a well-defined notion of force depends on the identification of the specific kind of causal process instantiating it, if the statisticalists were right, the dynamical interpretation would be untenable. On the other hand, Brandon (2006), who defends a heterodox version of the dynamical interpretation, has more specifically denied that drift may be considered as a force because – differently from Newtonian forces – it lacks predictable and constant direction.

In this paper, we aim to defend a rather standard version of the dynamical interpretation from these criticisms by showing that genetic drift can be genuinely characterised as a force. Many authors have attempted to do this before. On the one hand, against the statisticalist view, Reisman and Forber (2005) and Shapiro and Sober (2007) have argued – by invoking Woodward's (2003) manipulationist (or interventionist) theory of causation – that it is possible to offer a clear causal characterisation of drift as the process that, depending on the size of a population, may produce proportional fluctuations in genetic and phenotypic distributions. On the other hand, Stephens (2004, 2010), Filler (2009), Hitchcock and Velasco (2014), Pence (2016) and Roffé (2017) have defended the directional features of drift against Brandon's criticism. Stephens (2004, 2010), Filler (2009) and Roffé (2017) have championed the view that drift has a direction because it "pushes and pulls" populations towards homozygosity. Hitchcock and Velasco (2014) and Pence (2016), by contrast, have argued that, differently from Newtonian traditional forces, drift has a stochastic direction, like Brownian motion.

These two sets of solutions are in our opinion only partially satisfactory. Reisman, Forber, Shapiro and Sober may have well succeeded in defending the causal character of drift, but they do not clearly defend the thesis that it can be considered as a force[1]; while the authors who focused on directionality do not provide an explicit characterisation of the causal features of drift. Our goal is to offer a synthesis of the two approaches, in order to overcome their limitations: we aim to argue that drift is a force *because* it is a cause of a certain kind. In a nutshell, we shall support this claim by pointing out a connection between the notion of force and the notion of explanatory depth interpreted in manipulationist terms (see especially Hitchcock and Woodward 2003). Our argument is that, since the notion of force in Newtonian mechanics is what allows this theory to provide deep explanations, and given that the notion of drift plays an analogous role in evolutionary theory, then drift can be considered as a force of evolution. Insofar as our analysis applies to other evolutionary factors – e.g., selection and mutation –, it offers overall support to the dynamical interpretation.

The plan of the chapter is as follows. In section 1, we spell out in more detail the statisticalists' and Brandon's criticisms to the interpretation of drift as a force. In section 2, we outline the replies to these criticisms and situate our proposal within this context. In section 3, we introduce the manipulationist account of explanatory depth. In section 4, we discuss in what

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[1] Shapiro and Sober (2007) are nominally committed to the force analogy. Yet, besides their manipulationist argument for considering drift as a cause, they do not provide any further strong reason to conceive it, in addition, as a force.

sense the notion of force endows Newtonian mechanics' explanations with explanatory depth. In section 5, we show how to apply our analysis to drift. In the conclusion, we sketch out how our approach can be generalised to other evolutionary forces.

9.2 Drift as a force and its enemies

The dynamical interpretation of evolutionary theory has been under attack particularly in the last two decades (a notable exception is Endler 1986). The disagreement between dynamicalists and statisticalists covers quite a broad set of issues, but here we shall focus, for obvious reasons, just on those which concern the possibility of considering genetic drift as a force. As we have seen in the introduction, a force is a cause that, in the context of a theory, is usually characterised as acting with a certain magnitude and direction. Statisticalists are sceptical about both the claim that drift is a cause (or, more precisely, that it is a cause clearly differentiable from selection) and the claim that it has a predictable and constant direction. We shall start by introducing the criticisms levelled by statisticalists against the former claim while reserving the criticisms concerning the latter for later in the section in connection with Brandon's criticisms.

Arguments against the causal interpretation of drift can be found in a number of statisticalists' papers, but we shall mainly refer to the articles by Walsh, Lewens and Ariew (2002) and Matthen and Ariew (2002). In their view, drift is nothing more than sampling error, thus a *purely* statistical (as opposed to causal) concept. In order to illustrate their point, the statisticalists compare evolutionary processes to series of coin tosses. If we toss a fair coin for a large number of times, it is overwhelmingly likely that we will obtain a ratio of heads and tails very close to 50:50 (albeit not necessarily 50:50). Likewise, in an infinitely large and panmictic population an advantageous allele will, over a certain number of generations, almost certainly reach fixation by natural selection. Nonetheless, if we reduce, in the first case, the number of the tosses and, in the second, the size of the population, these outcomes will become increasingly less likely: "the law of large numbers tells us that the likelihood of significant divergence from these predictions is an inverse function of the size of the population. The small size of a population increases the chances of error" (Walsh et al. 2002, p. 459). If we toss the coin just, say, four times, any distribution of heads and tails is almost equally likely. Analogously, the change of allelic distributions in a small population over a certain number of generations will not necessarily reflect the differences in fitness between them. From the statisticalist standpoint, it is precisely this deviation from the expectation what evolutionary biologists usually call genetic drift.

Now, the statisticalists stress that, although there obviously are physical factors that *cause* each single toss of the coin to land either head or tail, they are irrelevant to *explain* the differences in the expected outcome in short or large series of tosses. As a matter of fact, the *same* kind of physical factors cause a coin to land head or tail in different series of tosses. What explains the differences in the expected outcomes is the number of tosses, which is not – properly speaking – a causal but rather a structural feature of the experimental setup. This conclusion can be easily extended to drift. Although an evolutionary outcome is obviously instantiated by a set of births, deaths and reproductions, what explains the fact that in a small population the expected allelic distributions over a certain number of generations diverges from the outcome predicted by differences in fitness is not that set of causal factors, but the size of the population. The latter, in its turn, does not properly play a causal role, but just define – to use a phrase by Anya Plutynski – "a *condition on the possibility* of sampling error" (2007, p. 165; emphasis in the original). Since, moreover – as in the case of the coin – the causal factors supposedly acting when the sample is small or large are exactly the same (i.e., myriads of births, deaths and reproduction), it is impossible to distinguish in any intermediate case if the evolutionary process is due to drift or selection. But, if drift and selection are not clearly differentiable at a causal level – the statisticalists conclude – then they cannot count as distinct forces: instead, they both just denote statistical outcomes.

Against the dynamical interpretation, the statisticalists also observe that, due to its non-deterministic nature, differently from Newtonian forces, drift lacks a predictable and constant direction. To be fair, Sober himself acknowledged this point, although he simply drew the moral that, when compared to selection and other evolutionary forces, drift "is a force of a different colour" (1984, p. 117). Of a different opinion is Stephens (2004), who first pointed out – in the context of the present debate – that, relying on elementary population genetic models (basically the classic Wright-Fisher model), it is possible to say that drift's direction is homozygosity. Given a two-gene locus not subject to selective pressure, these mathematical models predict that, after a certain number of generations, one of the two alleles eventually reaches fixation, while the other disappears – albeit we cannot predict which one. The main argument against this characterisation of drift's direction has been provided, as anticipated, by Brandon (2006; see also Brandon 2010). Differently from the statisticalists, Brandon is not critical of the dynamical interpretation as a whole: in a sense, he also believes that evolutionary theory is a theory of forces. His point is rather that drift is equivalent to the principle of inertia of evolutionary dynamics instead of a force. Drift cannot be a force in the sense defended by Stephens because, if we take seriously the Newtonian analogy, the supposed directionality of drift (towards homozygosity) is nonsensical. To claim that, due to drift, *either* one homozygous genotype *or* the other will, in the long run, predominate in a population (that is, without saying which of them will predominate) is problematic. Since Newtonian forces are vectors, it is not possible to simply say that a force is acting on an object, without any other qualification. The statement that drift is acting on a population, without specifying its direction, is analogously meaningless or incomplete.

9.3 Causes and forces

As sketched out in the introduction, two main strategies have been deployed in order to defend the dynamical interpretation of drift: against the statisticalists, Reisman and Forber (2005) and Shapiro and Sober (2007) have argued that the size of a population has not just statistical relevance but that it is a genuine causal factor too; against Brandon, some authors have insisted on the correctness of Stephens' analysis (Filler 2009; Stephens 2010; Roffé 2017), while others have attempted to liberalise the Newtonian analogy, so as to include "non-canonical" forces too (Hitchcock and Velasco 2014; Pence 2016). We shall not pay much attention to this latter subset of solutions to Brandon's challenge since they do not have much to do with our proposal; nonetheless – as we shall spell out more clearly below – we share with them the spirit of a "liberalisation" of the Newtonian analogy (a position defended also by Luque 2016).

Reisman and Forber's and Shapiro and Sober's attempts to rescue a causal interpretation of drift are grounded on the fact that evolutionary biologists do not refer to drift exclusively as an effect or as an outcome (see Ohta 2012, for instance). Basically, their goal is to show that, contrary to the statisticalists' view, the size of the population is a genuine causal factor and not merely a statistical variable (see also Millstein 2006 for a similar view). In order to do this, they need to neutralise the statisticalists' premise according to which the causes of evolution are located uniquely at the level of individuals' births, deaths and reproductions. To this aim, as anticipated, they adopt Woodward's account of causation and causal explanation (Woodward 2003). According to Woodward, given two variables X and Y, "a necessary and sufficient condition for X to be a direct cause of Y with respect to a variable set V is that there be a possible intervention on X that will change Y or the probability distribution of Y when one holds fixed at some value all other variables in V" (2003, p. 55). Woodward's account allows non-local interactions (i.e., those that – unlike the interactions involved in specific coin tosses, or in specific sequences of births, deaths and reproductions – do not require the transmission of some physical mark or some conserved physical quantity from causes to effects) to be causal. The relevant relation in manipulationist causation is, in fact, counterfactual dependence rather than production (differently from traditional accounts of causation; cf. Salmon 1986; Dowe 2000). In this sense, although the size of a population is clearly somehow determined by the individuals that compose it, it is nonetheless a genuine causal factor on its own. As illustrated by Reisman and Forber through an experiment carried out by Dobzhansky and Pavlovsky (1957), it is possible to intervene on the size of a population – while differences in fitness are held fixed – in order to increase or decrease the random "fluctuations" of allelic distributions.[2] Since random fluctuations are counterfactually dependent on size, there are no reasons – in accordance to Woodward's account – to deny that drift is a cause.

Instead of focusing on its causal features, Stephens (2010) and Roffé (2017) argue that drift is a force on the grounds that it has indeed a specific direction. While Stephens asserts that drift is directed to "remove variation from natural populations" (2010, p. 721) and thus to push populations towards homozygosity[3], Roffé argues that, although one cannot predict the direction which a population evolving by drift will move towards, "when an allele frequency is greater than 0.5, it is more likely that this frequency will go up rather than the reverse, even in the very next generation" (2017, p. 551). According to Roffé, Brandon is wrong in his criticism because, making exception for the case in which – for a two-gene locus – both alleles have exactly the same frequency, the prediction of the Wright-Fisher model when drift is at work is the increased probability of fixation of the most common allele. A different – and, for our purposes, more interesting – defence of drift as a force against Brandon's attack is given by Filler (2009). That a concept may count as a force depends, in his opinion, mainly on the fact that it is able to play an appropriate *unificatory* role concerning a variety of phenomena –

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[2] Dobzhansky and Pavlovsky separated twenty replicate populations of *Drosophila* in two groups of ten populations each. The first group was composed by large populations, while the second by very small populations (10 males and 10 females). Dobzhansky and Pavlovsky aimed to track two allelic types that, initially, were present in each population with a ratio of exactly 50:50. By reducing the size of the second group of populations they intended to simulate a founder effect (which is usually considered as a common cause of drift). After a certain number of generations, they let all the populations grow to the same size. Finally, they let selection act freely and, after a number of generations necessary to reach the equilibrium, they recounted type frequencies in each population. The result was that, while in large populations the degree of variance between frequencies at equilibrium was small, in small populations it was far greater.

[3] Of course, also purifying selection is an eliminative process. Stephens is rather contrasting eliminative forces with forces generating variation (e.g., mutation).

this criterion was already implicit in Sober's (1984) original proposal – and that it has a precisely mathematically specifiable magnitude. When compared with these criteria, the requirement according to which a force must have a specific direction is secondary. Insofar as drift unifies disparate phenomena – parent sampling, gamete sampling, founding of new populations, splitting of populations etc. – and has a specifiable mathematically precise magnitude, the fact that it has not a specific direction (but only a "disjunctive" one; i.e., *either* dominant homozygosity *or* recessive homozygosity) does not invalidate its status as a force.

Albeit sympathetic with Filler's deflationary attitude, Pence (2016) and Luque (2016) are sceptical about his specific proposal. They suspect that, by focusing exclusively on mathematical magnitude, it weakens too much the criteria for "forcehood", thus making the concept of force trivially applicable and ultimately vacuous. We partly agree with them. In this sense, one of our goals in this article may be interpreted as an attempt to find better criteria for "forcehood". Like Filler, we think that one of the crucial features of the notion of force is its capacity of unifying various phenomena, by focusing on their shared characteristics. Yet, differently from him, we do not believe that the unificatory virtues of the notion of force are merely attained through the identification of its mathematical magnitude or its specific direction. To be sure, these are important features of a Newtonian force: if Stephens and Roffé were right and drift may indeed be conceived as having a specific direction, this would obviously strengthen the analogy between evolutionary theory and Newtonian mechanics. But, from our point of view, the most salient feature of the notion of force in Newtonian mechanics is that it captures certain shared *causal* characteristics of the phenomena that it unifies.[4] In this sense, our analysis should be considered as closer to that carried out by Reisman and Forber or Shapiro and Sober. As a matter of fact, what we want to show is that the manipulationist account of causal explanation provides the conceptual resources to characterise drift not just as a cause of evolution, but as a force as well. Forces are "deep causes", not in the sense that they are ontologically "fundamental" (like, for instance, micro-physical interactions), but because they are constitutively invoked in *deep explanations*, that is, explanations able to support a wide range of counterfactuals.

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[4] Henceforth, except if otherwise specified, we shall use the word "force" to refer to *component forces*, and not to *net forces*. As a matter of fact, we take the expression "net force" to denote a theoretical representation of the combinatorial effects of interacting forces (as represented in the consequence laws of a theory of forces), while only the component forces are causally efficient.

9.4 The manipulationist account of explanatory depth

The manipulationist conception of explanatory depth has been initially developed by Hitchcock and Woodward (2003; see also Woodward and Hitchcock 2003) and later refined by – among others – Woodward (2006, 2010, 2016), Ylikoski and Kuorikoski (2010), Weslake (2010), and Blanchard, Vasilyeva and Lombrozo (2017). It is based on two main assumptions. The first is that to explain means to invoke *invariant* generalisations connecting the explanandum with its explanans. The second is that there are straightforward ways to compare the degree of invariance of two or more generalisations.

An invariant generalisation is a statement that captures the counterfactual dependence between a variable (a property, an event etc.) and its putative causes. In accordance with what we have already seen in the previous section, in the manipulationist framework "a generalisation is invariant if it would continue to hold under an appropriate class of changes involving *interventions* on the variables figuring in that generalisation" (Woodward and Hitchcock 2003, p. 2; emphasis in the original). Notice that (differently from other counterfactual accounts of causation and causal explanation; e.g., Lewis 1986) it is precisely the possibility of intervening on the variables figuring in that generalisation what allows to establish the counterfactual dependence between an effect and its causes and, thus, guarantees the explanatory power of the generalisation. The manipulationist framework does not require that interventions must be "physically possible". Rather, it just requires that they are "logically possible and well-defined" (Woodward 2003, p. 128), in the sense that "we have some sort of basis for assessing the truth of claims about what would happen if an intervention *were* carried out" (p. 130; emphasis in the original). Explanations of the same phenomenon invoking different invariant generalisations can be "more or less explanatory" – that is, they can be *deeper* or *less deep* – depending on the *range of invariance* of the generalisations figuring in them. In order to understand the concept of "range of invariance", it is useful to think of an invariant generalisation as a linear regression equation:

$$(1)\ \mathrm{Y} = a_1\mathrm{X}_1 + a_2\mathrm{X}_2 + \ldots + a_n\mathrm{X}_n + \mathrm{U}$$

While a_x represents fixed coefficients, U is a placeholder for other possible causal influences not explicitly taken into account in the equation – that is, background conditions. Interventions on the values of Xs determine corresponding changes in the value of Y. By showing how Y covaries with Xs in non-actual situations, invariant generalisations allow to answer a class of so-called *what-if-things-had-been-different* questions. The *range of invariance* of a generalisation is the property of the generalisation that determines, so to speak, “how many” what-if questions the generalisation is able to answer.

The second assumption of the manipulationist conception of explanatory depth is that the range of invariance of a generalisation is mainly determined by what different authors call *insensitivity* (Woodward 2006; Ylilkoski and Kourikoski 2010) or *stability* (Woodward 2010; Blanchard et al. 2018).[5] An explanatory generalisation is less sensitive, or more stable, than another if and only if it makes explicit the counterfactual dependence of the explanandum on variables treated as background conditions by the other generalisation. In order to illustrate these concepts, let us consider an example proposed by Woodward and Hitchcock (2003). Imagine we want to explain why a plant grew up to a certain height and that we know that the variable “plant height” is counterfactually dependent on the amount of water and fertiliser the plant received. We may represent this invariant generalisation as:

$$(2)\ Y = a_1X_1 + a_2X_2 + U$$

Y is the variable “plant height”, a_1X_1 is a certain amount of water, a_2X_2 is certain amount of fertiliser, and U is a set of background conditions. (2) explains the actual height of the plant by supporting a certain class of counterfactuals: if the plant had received a different amount of water or fertiliser, it would have reached a different height. In this way, (2) allows answering a non-trivial set of what-if questions. Nonetheless, according to Hitchcock and Woodward (2003), explanations invoking (2) are quite shallow. The reason is that (2) can be easily *disrupted*:

> [2] would fail if we were to spray the plant with weed killer or heat it to a very high temperature. Less dramatically, there are many possible conditions that will not destroy the plant, but which will alter the effect of water and fertiliser on plant height. There may be physical changes in the root system of the plant or the surrounding soil that would change the way in which given amounts of water affect plant height (Woodward and Hitchcock 2003, p. 5).

The problem with (2) is, in brief, that it makes plant height counterfactually dependent on

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[5] Blanchard et al. (2018) think that stability should be better characterised as denoting two distinct explanatory virtues, that is, breadth and guidance. We do not need to enter into such details here.

factors (the amount of water and fertiliser) that are extremely sensitive to a change in the background conditions. Alternatively, imagine that we have a theory that describes the details of the physiological mechanisms governing plant growth by referring to a series of biochemical reactions. Such a theory would allow deriving an invariant generalisation like

$$(3)\ Y = a_1X_1 + a_2X_2 + \ldots + a_nX_n + U'$$

where Y is the plant's height and the Xs denote a set of variables relative to the physiological features of the plant, while U' is a subset of U. (3) might be thought as "unpacking" U in a set of known variables such that, being manipulable, explicitly spell out how they interfere in the causal outcome (i.e., plant height). In making explicit those variables, (3) allows explaining, for instance, how the composition of the soil, temperature, air or noise pollution, presence of pests etc. can, in terms of types of biochemical reactions, make a difference to Y. Since it is difficult to imagine a generalisation about plant height that takes into account *all* background conditions (consider logically possible metaphysical scenarios such as drastic changes in the physical structure of the universe – for instance, a change in the composition of matter or in the structure of space), (3) still must include a variable for background U'. Nonetheless, (3) is *more stable than* (2), because it is insensitive to many of those circumstances that disrupted (2). Accordingly, an explanation invoking (3) is deeper that an explanation invoking (2) because (3) "enable[s] inferences to more counterfactual situations" (Ylikoski and Kuorikoski 2010, p. 209) than (2).

Explanatory depth is not just related to the stability of the explanatory generalisations, but also to the choice of the variables taken into account. In this respect, Hitchcock and Woodward observe that "ideally, one would like to formulate generalisations that are not sensitive at all to the ways in which the values of the variables figuring in them are produced" (2003, pp. 186-7). Remember that, in the manipulationist framework, it is precisely the (logical) possibility of interventions what allows establishing the counterfactual dependence between an effect and its causes. Importantly, variables that can be manipulated independently from the specificity of the scenario under study make the generalisation in which they appear *portable* to other scenarios. (2), besides being shallow in the sense that it does not take into account potentially disrupting background conditions, is also shallower than the explanation invoking (3) because it relates Y to variables quite sensitive to the way in which they are manipulated. Amount of water and fertiliser are certainly relevant to explain the height of many plants, but are not relevant in all cases (think about, for instance, aquatic plants): the explanation invoking (2) is thus not easily portable to other scenarios relatively analogous to the specific one taken into consideration, but different in some important respect. On the contrary, (3), which makes reference to certain types of biochemical reactions, captures features of the process of growth common to all plants and, therefore, is extremely portable. The reason for this high degree of portability is precisely that the conditions of manipulability of the invariant relation are abstracted away from the specific growth pattern of the actual plant under study, so as to cover analogous phenomena as well. In its turn, portability is achieved because the choice of variables concerning biochemical reactions, so to speak, *carves nature at its joints* by spelling out what all phenomena concerning plant growth share.

Stability and portability of a generalisation are strictly related. Although, as far as we can see, not every stable generalisation is also portable, portable generalisations are generally stable. We suggest that highly stable and portable generalisations provide the deepest possible explanations of a natural phenomenon. This characterisation relates explanatory depth to *unification*. As a matter of fact, stability and portability together account for the ability of a generalisation to cover a broad set of phenomena. Differently from Kitcher's classic account of explanatory unification (Kitcher 1989), which makes a generalisation explanatorily deep insofar as it is derived from a set of theoretical statements or inferential patterns, the manipulationist account derives the unificatory virtues of a class of invariant generalisations mainly from their causal features (Woodward 2016). Stable and portable generalisations are more frequently encountered in the fundamental sciences, in which phenomena are explained by invoking physical properties assumed to be shared by all physical objects (positions, velocities, masses, charges etc.). Nonetheless, this is not necessary (Weslake 2010). On the contrary, it is precisely the possibility of finding stable and portable generalisations in different disciplines what permits, as we shall see starting from the next section, to transpose the notion of force to them.[6]

9.5 Force-explanations as deep explanations

In the last section, we have seen that, in order to be deep, an explanation must contain stable

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[6] Quite clearly, the criteria for explanatory depth here adopted are not metric, i.e., they do not allow arranging distinct explanations of a given phenomenon on a univocal scale ranging from the shallowest to the deepest. Rather, they have to be interpreted, more modestly, as comparative criteria. This does not mean, as we shall see in the next sections, that they cannot be useful as analytic tools.

and, possibly, portable generalisations. In this section, we aim to argue that, to the extent that they invoke generalisations maximally integrating background conditions, Newtonian mechanics explanations allow providing very deep explanations of changes in motion. We moreover want to argue that this is precisely *because* they employ the notion of force, which permits to understand the counterfactual dependence between physical effects and its causes regardless of how the interventions on the causes are performed. We therefore shall conclude that, besides the fact of having a certain direction and magnitude, one of the main characteristics (in our opinion, the most fundamental) of the notion of force is the extreme portability of the generalisations in which it appears. We believe that this is the characteristic that we have to take into account when we assess the possibility of transferring the notion of force to other theoretical contexts.

Let us illustrate our claim with the help of another example presented by Hitchcock and Woodward (2003, p. 187-8). Imagine that you drop an object from a certain height and that you want to know why it takes a certain time to fall. One way to do this is by invoking the invariant generalisation between (X) – the height from which the object has been dropped – and (Y) – the time it takes to fall –, also known as Galileo's law of free fall. This would provide a perfectly acceptable explanation of the phenomenon at stake. Nonetheless, the invariant relation described by Galileo's law has a limited range of invariance: "it would fail to hold if the object were dropped from a height that is large in relation to the earth's radius or if it were dropped from the surface of a massive body of proportions different from those of earth (such as Mars)" (Hitchcock and Woodward 2003, p. 187). Alternatively, we may explain Y by invoking Newton's second law along with his law of gravitation, which describe the behaviour of the dropped object in a way that is insensitive to the above-specified potentially disrupting background conditions. As a matter of fact, Newton's law of gravitation remains invariant under changes in the mass and radius of the massive object upon which the object is dropped: "an intervention that increases the mass of earth would count as an intervention on *background conditions* with respect to Galileo's law, but as an intervention on a *variable explicitly figuring in* Newton's laws" (p. 188; emphases in the original). Leaving aside relativistic considerations, we could say that, since Newton's laws are able to take into account all variables relevant to explain the behaviour of the dropped object, the explanation invoking Newton's laws is a very deep explanation of the phenomenon.[7] No matter which potentially perturbing conditions are

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[7] In the last section we noticed – regarding our hypothetical generalisations concerning plant height – that some background conditions are ineliminable. This is possibly true also of generalisations dealing with more fundamental features of the physical world, but we shall not discuss this issue here.

made explicit, Newtonian laws are able to show how they are related to the outcome, thus enabling inferences concerning *any* counterfactual situation.

This, of course, does not apply just to the behaviour of falling bodies. Similar considerations can be extended to the behaviour of any material object in a Newtonian universe: planets, colliding objects, pendulums, springs etc. The explanations invoking Newton's laws are so deep not just because they are stable but also – and, perhaps, mainly – because they are portable. In its turn, they are portable arguably *in virtue* of the fact that they employ the notion of force. As the historian of physics Max Jammer has noticed "the usefulness of the concept of 'force' is that it enables us to discuss the general laws of motions irrespective of the particular physical situation with which these motions are situated" (Jammer 1957, p. 244; see also Sklar 2013, chap. 6). Within a manipulationist framework, this claim can be interpreted as stating that forces are variables that are maximally insensitive to the concrete circumstances in which they are manipulated. That is, while the degree of invariance of hypothetical pre-Newtonian generalisations relating – without mentioning universal forces – the motion of planets, the period and length of a pendulum, the behaviour of a billiard ball after a collision, and so forth, would be limited to changes in the specific variants appearing in them (as illustrated by less portable generalisations like, besides Galileo's law, Kepler's law of planetary motion or Huygens' law of elastic collision), the possibility of conceiving all these phenomena as the product of the same forces allows to capture their causes in a highly portable form. Any change in motion, in a Newtonian world, can be causally explained by invoking generalisations virtually neglecting the specificity of physical bodies (excluding mass, which is a property shared by all of them) that we need to manipulate in order to account for the relevant phenomena. Any change in motion is simply counterfactually dependent on the specific component forces represented by the values of the manipulated variables.

Differently from Filler and other authors cited in section 2, we think that it is the high portability of force-explanations, rather than the fact that forces have magnitude and precise direction, what should be taken as the characteristic unificatory feature of the notion of force. Again, we do not reject the idea that magnitude and direction are important in the characterisation of a force (of course, they are crucial in the *representation* of Newtonian forces), and certainly Stephens and Roffé are right in the claim that if drift had a precise direction this would reinforce the analogy between Newtonian mechanics and evolutionary theory. In spite of that, our account aims to point out what is a more fundamental feature of forces: their ability to provide very deep causal explanations – in the manipulationist sense – of a class of phenomena. Surely, the fact that the notion of force allows Newtonian laws to provide such deep explanations of changes in motion does not obviously entail that any concept playing an analogous role with respect to another class of phenomena is, *ipso facto*, a force. We think, nonetheless, that it would be reasonable to accept that a concept able to play an analogous role *may* be considered as a force. Even though it seems to us that not many concepts can satisfy the conditions to be a force outside physics, we still shall argue that genetic drift is one of them.

9.6 Drift as a force

Following our argument in the last two sections, we think that the minimal requirement for a concept to play the role of a force within a theory is to allow deep explanations of a certain class of phenomena. This requirement, in its turn, is satisfied just by those concepts permitting to formulate generalisations that are highly stable (thus answering a broad range of what-if questions) and portable (i.e., insensitive to the specific ways in which the variables denoted by the concept are manipulated). According to this latter criterion, drift would – or, at least, might – be reasonably considered as a force if we had a concept able to identify all the causal processes that are characteristically and systematically related to stochastic evolutionary outcomes.[8]

As we have seen in section 2, Reisman and Forber (2005) and Shapiro and Sober (2007) rescue the causal character of drift against statisticalists' criticisms by showing how, by adopting a manipulationist framework, the *effects* of drift, Y – that is, random fluctuations in allele frequencies and, possibly, removal of genetic variation and homozygosity – are counterfactually dependent on X, the size of the population under study. We may manipulate the size of a population by shrinking it, thus increasing the effects of drift, or *vice versa* we may diminish the effects of drift by increasing the size of the population indefinitely, allowing selection to act increasingly undisturbed. We think that this characterisation, albeit valuable, does not capture the features for which drift can be considered as a force. This is, at least partially, because it leaves aside cases in which the effects of drift are not *caused* by a change in the size of the population.

Many phenomena commonly associated to drift – like parent sampling, gamete sampling,

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[8] Even though also mutation might be considered as a stochastic process, in traditional population genetic models it is commonly conceived as a deterministic one (see, for instance, Hartl and Clark 2007).

founding of new populations, splitting of populations, bottlenecks – are indeed often related to a reduction of the size of the population. In all such cases, there is a difference between the potential and actual reproducers that is captured by the distinction between census and effective population size.[9] For instance, gamete sampling is the process by which only a percentage of the gametes produced is represented in the next generation because some individuals over-reproduce and others do not at all. So, for example, given a census population size N, the idea of gamete sampling is that only the genetic contribution of the effective population size N_e is represented in the next generation. Thus, the passage from N to N_e clearly involves a reduction in the size of the population. However, significantly, other potential cases might not involve reduction of the size of the census population. Suppose for instance that in a small population of 10 organisms with equal fitness (e.g., clones) reproducing by parthenogenesis, 9 have one offspring but one has mono-ovum twins: in this case, all potential reproducers do as a matter of fact reproduce, so all members of the census population do, but one of them reproduces more. In this case, there is no reduction of the census population to the effective population as the two coincide: in fact, there are 10 potential and 10 actual reproducers. In spite of this, because all organisms have equal fitness, we are inclined to consider the evolutionary outcome as an instance of drift. Still other cases might involve the expansion of the effective population size. For instance, in vitro fertilization allows infertile organisms (i.e., members of the census population who are not potential reproducers) to have offspring.

As a consequence of these considerations, even though population size reduction is undoubtedly a good proxy to test drift hypotheses in many cases, it cannot, in our opinion, be considered as the cause of drift outcomes. As a matter of fact, we think that population size reduction is an effect, rather than a cause, of drift.[10] In order to clarify this *prima facie* unintuitive statement, let us introduce what we think are the causes of drift. They are, as a first approximation, *chance events* (in our examples, for instance, the spontaneous division of the ovum in two embryos and the availability of a certain technology). With this expression we do not refer to indeterministic events (even though they might sometimes be), but rather to the

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[9] Effective population size can be conceptualized in a variety of ways. When it is estimated that human effective population size is around 10.000 individuals (Yu et al. 2004) even though current census size is over 7 billions, reference is to the genetic variability in sampled genes. The reason for this discrepancy – already highlighted by Wright (Ohta 2012, p. 2) – is that a bottleneck in the history of the lineage drastically reduces effective population size. Another, more general and less refined, conceptualisation of effective population size merely draws on the difference between potential and actual reproducers. While both ways of conceptualising effective population size are legitimate (indeed there are many more, see note 11), the vernacular conceptualisation is sufficient to ground our argument.

[10] This is not to say that the size of a population cannot play a causal role in evolutionary dynamics, but just that it is not because of the causal role that population size plays that drift can be considered as a force.

environmental circumstances (like lightning strikes, floods, droughts, forest fires etc.) and reproductive phenomena (like meiosis) instantiating what Millstein (2002, 2005; relying on Beatty 1984, 1992; Hodge 1987) calls “indiscriminate sampling”. This characterisation has been more or less explicitly endorsed by many population geneticists (e.g., Fisher 1921; Wright 1932; Dobzhansky 1937; Fisher and Ford 1947). The rationale of this view is that drift, as well as natural selection, is an iterative and inter-generational process of sampling of parents or gametes in a population. While selection is a process of discriminate sampling – since parents, and thus gametes, are sampled according to their differential fitness – drift is indiscriminate insofar as the differences in fitness are irrelevant to the sampling process. In an attempt to improve Millstein’s proposal, Gildenhuys suggests to consider chance events as *non-interactive*, *non-pervasive* and *indiscriminate* causes, that is, *NINPICs*:

> [NINPICs] 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 (Gildenhuys 2009, p. 522; emphases in the original).

Thus, for instance, a forest fire is usually considered as a chance event – and, therefore, as a cause of drift outcomes – because: (i) potentially, it has the same reproductive effects on each type of organism in a population (combustion is virtually lethal for any organism); (ii) in most actual cases, it does not affect all population members, but only a subset of them (i.e., those that incidentally happen to live in the geographical area affected by the fire); (iii) the chances of a population member being affected by the fire are independent from the fact that she has any specific genomic or phenotypic property (except, of course, the property of being spatially proximal to the geographical area affected by the fire).

Taking for granted that this is a satisfactory characterisation of the notion of chance events, we can ask in what sense NINPICs are causes of the characteristic drift effects. The key to understand this is the so-called Kolmogorov forward equation of diffusion theory (Hartl and Clark 2007, p. 106 ff.). The equation describes the diffusion of an allele as the sum of two functions M(x) and V(x), such that M(x) denotes the effects of systematic forces like selection (but also mutation and migration) and V(x) the variance in allele frequency due to binomial sampling (that is, drift, as considered in the Wright-Fisher model). Following Gildenhuys

(2009, p. 528 ff.), the equation that determines V is $p(1-p)/2N_{ev}$, where N_{ev} is variance effective population size. For simplicity, we shall equate, in our discussion, N_{ev} to N_e.[11] Since p (the allele frequency) is a kind of background condition, it is N_{ev} (or N_e) the variable that we need to know in order to solve Kolmogorov forward equation.

Let us now turn our attention to what we call a "drift generalisation"; that is – as we said at the beginning of this section –, a generalisation able to identify all the causal factors that are characteristically and systematically related to stochastic evolutionary outcomes. In manipulationist terms, the "stochastic evolutionary outcome" is the Y of a linear regression equation of which we need to find the Xs, its causes. If the stochastic evolutionary outcome in the Kolmogorov forward equation is V, and N_e is what determines V values, then Y is N_e. This is why, as mentioned before, the size of a population – more precisely, the effective size of a population – is the effect rather than a cause of drift. It is the variable that, when plugged in the Kolmogorov forward equation, amplifies or reduces the stochasticity of the overall evolutionary dynamic of the allele under study. Nonetheless, when we consider drift as a cause – that is, when we want to know the Xs that produce a change in N_e – we are referring to NINPICs, that is, the set of chance events materially responsible for such a change.

We can make this claim clearer as follows. One way to understand N_e – both in the Wright-Fisher model and in diffusion theory – is as a variable that tracks the amount of actual variance in progeny number per parents (Charlesworth 2009). Without entering into excessive technicalities, we could say that a large amount of variance normally implies a reduced N_e, while a small amount implies a large N_e. In other words, variance in progeny number is large in the case in which there is a great difference between the number of offspring of the members of a population, while in the case in which each parent in a generation has a single offspring we have no variance, i.e., the effective population is identical to the census population. Nonetheless, the latter is an ideal case; in the real world this rarely, if ever, happens. The variance in progeny number may be due to natural selection, but we shall here focus exclusively on the variance due to non-selective factors (as usual in population genetics models). These are the "chance" events that constitute the causes of drift. The idea is that the NINPICs characterisation captures the shared features of all of them in a way that, necessarily, if we manipulate NINPICs, the variance in progeny number correspondingly increases or is reduced

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[11] There exist at least three ways in population genetics to conceptualise effective size: besides variance effective population size, they are inbreeding effective population size and eigenvalue effective population size. Although they have different functions within population modelling, they all represent the number of actual reproducers in contrast with the number of potential reproducers denoted by census population (see note 9).

and this, in its turn, stochastically biases the evolutionary dynamics. A small amount of NINPICs yields less variance in progeny number and allows maintaining a large N_e, with the effect that – in accordance to the Kolmogorov forward equation – (putatively) deterministic forces, like selection, act relatively undisturbed. On the contrary, a large amount of NINPICs increases the variance in progeny, thereby reducing N_e and – in the case in which the differences in fitness between the members of the population are small – producing the fluctuations in allele frequencies characteristic of drift.

Generalisations counterfactually relating effective population size with NINPICs are maximally insensitive to background conditions insofar as they leave no potentially disrupting factors unconsidered. Although, quite obviously, in a specific situation it is impossible to enumerate all the ecological and reproductive factors counting as non-interactive, non-pervasive and indiscriminate causes, this is an epistemic limitation that does not affect the explanatory depth of the invariant generalisation. The invariant generalisation relating effective population size to NINPICs just says that, independently from our ability to identify and enumerate all these factors, if they have NINPICs characteristics, they are thus causally responsible for the fluctuations in effective population size and, if not, they are not. The generalisation is nonetheless stable because a change in the NINPICs would necessarily lead to a change of effective population size, in any specific evolutionary scenario. The stability of such generalisation is, in turn, guaranteed precisely by the availability of a causal notion of drift like NINPICs. NINPICs confers the manifold causes of drift the status of a force because, paraphrasing Jammer, *they enable us to discuss the general effects of drift irrespective of the particular physical situation with which these causes are situated.*

9.7 Conclusion

In this chapter, we have defended a notion of force grounded on the manipulationist interpretation of explanatory depth. According to this interpretation, an explanation is deep if it contains in its explanans an invariant generalisation that is stable (i.e., it is not easily disrupted by background factors) and portable (i.e., it contains a description of the causes of the explanandum that is highly insensitive to the specific circumstances in which they occurred). We have argued that a "force" may be any unitary set of causes of a certain class of phenomena such that, when invoked to explain a phenomenon pertaining to this class, it is able to provide a very deep explanation. Hence, we have shown that both Newtonian forces and drift (this latter considered as NINPICs) satisfy this condition and, thus, may be properly considered as forces. We have suggested that characteristic features of Newtonian forces such as mathematical magnitude and direction, albeit important for the formal representation of a force, are secondary with respect to its specific explanatory role within the theory. Accordingly, although a characterisation of drift as a directional force would surely strengthen the Newtonian analogy, a cause may be an instance of a force even without specific direction. This liberalisation of the notion of force is, in our opinion, the first step towards a refinement of the dynamical interpretation of evolutionary theory free of the burden of having to be completely isomorphic to Newtonian theory (in the spirit of authors like Filler 2009; Pence 2016 and Luque 2016).

The crucial characteristic of a force is its unificatory causal role. In the case of drift, this is achieved by individuating all those causal factors that act unsystematically to perturb the (putatively) deterministic evolutionary dynamic of an allele through the fluctuations of the effective size of the population under study. We do not intend here to attempt an analysis of the other forces of evolution, but it is easy to imagine how it could be extended, for instance, to mutation and natural selection. Mutation might be considered a force if stable and portable generalisations concerning its evolutionary role were formulated. The intuitive problem at this stage is that the processes of genomic change instantiating mutation are multifarious (ranging from point mutations to chromosome duplications), even though this variability is somehow analogous to the variability of the NINPICs instantiating drift as a process. Mutation affects evolutionary dynamics in a way that is clearly conceptually different from that of selection and drift for the reason that the focus is on the causal role of genomic change in evolution. Interestingly, it has been argued that mutation might bias the evolutionary process (Stoltzfus and McCandlish 2017). Consider for instance the preponderance of transitions (i.e., a mutation from one purine to another or from one pyrimidine to another) compared to transversions (i.e., mutations from a purine to a pyrimidine or vice versa). It has been calculated that transitions are three times more common than transversions. If this bias generates a systematic evolutionary effect – for instance in the form of a predictable and constant direction –, then we can consider mutation as a force.

Selective causes have the effect of increasing or reducing, in a population, the frequency of an allele depending on its overall contribution to the survival and reproduction of the individual organisms expressing it phenotypically. Such causes may be instantiated, as in the case of drift, in an impressive variety of ecological and developmental ways. It is arguably difficult to provide a satisfactory definition of the notion of ecological fitness that could be used to characterise the "discriminateness" of selection against the "indiscriminateness" of drift; nonetheless, it is precisely to this shared feature of selective factors that biologists refer to when they talk about selection as a cause.

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