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On the Nature of Natural Selection

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ABSTRACT

Some philosophers, known as statisticalists, claim that the concept of natural selection, as it is normally presented in population genetics, is statistical in character and cannot be construed in causal terms. On the contrary, other philosophers, known as causalists, argue against the statistical view and reaffirm the causal interpretation of natural selection. A key element in this debate is the dispute on the nature of drift. If drift is a cause of evolution, uncertainty in population genetics is due to some processes that make a population deviate from predicted outcomes. While causalists see drift as a distinct phenomenon originated by some set of natural processes, statisticalists claim that there is no process that accounts for this uncertainty, since the uncertainty lies not in the events but in the fact that natural selection in population genetics is modeled by a statistical theory. This article aims to illustrate the debate between causalists and statisticalists in order to present a challenge that statisticalists need to address if they wish to maintain a naturalist stance.

KEYWORDS: Causalists; Drift; Natural selection; Population genetics; Statisticalists; Mathematical explanations of natural phenomena.

1. Introduction

The causal nature of natural selection has been a very debated issue in the last years in philosophy of biology, and it is still a controversial issue. Some philosophers, known as *statisticalists*, claim that the concept of natural selection, as it is normally presented in population genetics, is statistical in character and cannot be construed in causal terms (see e.g. M. MATTHEN and A. ARIEW 2009; D.M.

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WALSH *et al.* 2002; D.M. WALSH *et al.* 2017). On the contrary, other philosophers, known as *causalists*, argue against the statistical view and reaffirm the causal interpretation of natural selection (see e.g. E. SOBER 1984; R. MILLSTEIN *et al.* 2009; J. OTSUKA 2016a, 2016b).

Statisticalists started questioning the causal interpretation of natural selection because «most, if not all, principles of evolutionary theory [...] are expressed by purely statistical terms such as variances or covariances» (OTSUKA 2016b, p. 248). In order to avoid any misunderstanding, it is worth specifying that the debate between causalists and statisticalists *is not* about whether genetic variations in a given population are due to causal factors. No one doubts this fact. The debate between causalists and statisticalists is about whether or not the explanations provided by population genetics are genuine causal explanations.

There are many issues involved in the debate between causalists and statisticalists. It is impossible to give here an exhaustive treatment of such debate. We will present just some aspects of the debate between statisticalists and causalists by focusing especially on drift (for a survey on drift, see R. MILLSTEIN 2017). Indeed, a key element in the debate between causalists and statisticalists is the dispute on the nature of drift and whether drift is really distinguishable from natural selection (see e.g. MILLSTEIN *et al.* 2009; M. MATTHEN 2009, 2010; V.J. LUQUE 2016). Drift is supposed to be a sort of measure of contingency in evolution. Thus, drift can be thought as affecting predictability in evolutionary biology. If drift is a cause of evolution, uncertainty in population genetics is due to some processes that make a population deviate from predicted outcomes. But while causalists see drift as a distinct natural phenomenon originated by some set of physical processes, statisticalists claim that there is no process that accounts for this uncertainty, since the uncertainty lies not in the events but in the fact that natural selection in population genetics is modeled by a statistical theory.

This article does not aim at taking side on the debate between statisticalists and causalists. Rather, it aims to illustrate the debate between causalists and statisticalists in order to present a challenge that statisticalists need to address if they wish to take a naturalist stance. Indeed, the debate on the nature of natural selection intersects the more general debate on whether or not non-causal explanations, and more precisely mathematical explanations, are genuine scientific explanations, and so explanations that may be acceptable from a naturalist

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viewpoint. Since evolutionism is essential for a naturalist perspective to be defined as such (R.N. GIERE 2006), and natural selection is central to evolutionism, an inquiry on what kind of explanations is provided by population genetics is crucial to assess the coherence of any naturalist stance.

2. The Force Analogy

To better appreciate the criticisms moved by statisticalists to the traditional view, it may be useful to briefly present one of the most controversial formulation of this view, namely the so-called "Force Analogy" (see LUQUE 2016; C. HITCHCOCK and J. VELASCO 2014). The idea is to present evolution as if it were driven by forces that behave analogously to the forces in Newtonian mechanics. The most developed use of the Newtonian analogy to illustrate evolutionary theory is made by Sober in his famous book *The Nature of Selection* in 1984: «In evolutionary theory, the forces of mutation, migration, selection and drift constitute causes that propel a population through a sequence of gene frequencies. To identify the causes of the current state […] requires describing which evolutionary forces impinged» (SOBER 1984, p. 141).

The force analogy has been widely used to expose the causal structure of the evolutionary theory. More precisely, three main features of evolution have been characterized by using the Force Analogy to interpret population genetics in causal terms: (1) evolution is driven by forces (namely: natural selection, drift, mutation, and migration) which act (and so they are causes) by modifying allele frequencies; (2) the Hardy-Weinberg principle is the "zero-force law" in population genetics; (3) population genetics gives us models that show how evolutionary forces act and combine with each other. The Force Analogy mainly rests on the idea that as forces in mechanics are usually taken to be causes of motion, so evolutionary forces in population genetics should be taken to be causes of change in gene frequencies.

Consider (2), the analogy between the Hardy-Weinberg principle in population genetics and zero-force law in mechanics. The adoption of a zero-force law tells us how the system would behave if forces were not acting on it. For instance, the first law of Newtonian mechanics functions to establish that a body continues in its state of rest, or of uniform motion in a straight line, unless it is compelled to change that

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state by forces impressed upon it. Many authors claim that the Hardy-Weinberg principle can be regarded as the zero-force law in population genetics. According to the Hardy-Weinberg principle, in a diploid and infinite population, where there is random mating, genotype frequencies will remain stable if no cause acts on it, since Mendelian inheritance alone cannot change the allele frequencies. In this view, the equation:

$$p^2 + 2pq + q^2 = 1$$

can be interpreted as representing the Hardy-Weinberg principle. Consider one locus with two alleles, *A* and *a*. *A* has a frequency p, while *a* has a frequency q. The values p^2, 2pq, and q^2 represent the proportions that *AA*, *Aa*, and *aa* will maintain (respectively) in the population from generation to generation (MILLSTEIN, *et al.* 2009).

Luque has clearly summarized how the Force Analogy has been exploited through the following scheme:

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

Fig. 1. Drawn from: LUQUE 2016, p. 398.

But the Force Analogy implies some disputable consequences. Two of the most relevant difficulties that the supporters of the Force Analogy have to face are the following: (a) if we take the Force Analogy seriously, we have to consider evolutionary forces as *distinct* forces, i.e. forces amenable to be separately defined and investigated; (b) if evolutionary forces are regarded as causes of change in gene frequencies, then they should be able to *directly* modify gene frequencies.

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3. Statisticalists' Criticism on the Force Analogy

Let us consider firstly the second difficulty described above, i.e. (b) proving that evolutionary forces modify gene frequencies directly. The difficulty of supporting such a claim derives from the fact that such claim seems to imply a disputable ontological commitment. For example, Sober holds that natural selection is evolution due to heritable variation in fitness. In this line of reasoning, an evolutionary force such as selection would be not merely the sequence of events that lead from variation in heritable fitness to a new gene frequency, but a force that appears when organisms have heritable differences that lead to differential reproductive success (MATTHEN and ARIEW 2009). In this view, evolution does not occur merely because types of organism reproduce and die in differing amounts. Rather evolution is driven by natural selection. If selection is a force in the same way in which a Newtonian force is a force, then we should assume that it is natural selection that *acts* on gene frequencies.

According to the statisticalists, this construal of selection is unacceptable, since it implies a sort of reification of the concept of natural selection, which illegitimately leads to an inflation of our ontology. Matthen and Ariew make clear this point by illustrating how the causal diagram of evolution by natural selection diverges depending on whether one adopts Sober's or their own interpretation of natural selection. According to Sober, evolution by selection would go something like this: «heritable variation in trait $T \rightarrow$ selection of magnitude proportionate to variance in heritable fitness due to heritable variation in $T \rightarrow$ birth and death of animals $\rightarrow$ evolution» (MATTHEN and ARIEW 2009, p. 206). On the contrary, according to Matthen and Ariew, the causal diagram goes like this: heritable variation in trait $T \rightarrow$ birth and death of animals $\rightarrow$ evolution. No extra cause is needed to account for how gene frequencies change at the population level besides those natural events that are responsible for the survival or the death of organisms at the individual level.

So, according to the statisticalists, the Force Analogy is unacceptable because natural selection in population genetics does not really cause any variance in gene frequencies, it is just a statistical abstraction of the events that are the real causes of gene frequencies, i.e.: births, deaths, and matings, which occur at the individual level. Natural selection «is ontologically derivative on individual-level events such

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as births, deaths, and mutations [...]. It occurs in ensembles as a mathematical consequence of events that involve members of those ensembles» (*ibidem*, p. 216). In this view, natural selection in population genetics should be merely regarded as an abstract mathematical description of the accumulation of reproduction events.

4. Drift

Let us now consider the first difficulty mentioned above (section 2) that causalists have to face, i.e. (a) proving that evolutionary forces are distinct forces. The difficulty of supporting such claim becomes particularly evident if one considers drift. The question is: Is drift *really* an independent cause of evolution? More precisely: Can drift be really distinguished from natural selection? This issue is deeply related to the criticism moved to the causalist view illustrated in the previous section. Indeed, if one accepts the traditional view, each evolutionary force has to be regarded as an independent "fact of nature". On the contrary, if one adopts statisticalism, one cannot neatly distinguish natural selection from drift. To see this, it may be useful to recapitulate what drift is. In population genetics, drift is usually understood as departures from expected gene frequencies that arise in finite populations. Briefly, when one kind of individuals is better endowed than another for reproduction, from a statistical viewpoint, one might expect that the better endowed kind will increase, but this expectation can be frustrated by actual outcomes. Departures from expected values are what population geneticists call "drift" (MATTHEN 2010).

An analogy with coin tossing may be of use to illuminate random drift. If one has a fair coin and one tosses it ten times, the expected outcome is 5 heads and 5 tails; but it well may be the case that one gets 6 heads and 4 tails or 8 heads and 2 tails. If one increases the number of tosses (say one tosses the coin 1,000 times), the frequencies obtained will approximate to the expected outcome. If one increases further the number of tosses (say one tosses the coin 1,000,000 times), the frequencies obtained will approximate to the expected outcome even better.

So, we can say that the magnitude of this sampling error (i.e. drift) is inversely proportional to sample size: the smaller the population, the bigger the deviation from the expected outcome.

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Coming to population genetics, the basic model of drift is the Wright-Fisher model, a binomial sampling process in a diploid population in which a new generation is formed as a sample of 2*N* alleles. The transition matrix for *i* copies of allele *A* at generation *t* to *j* copies of allele *A* at generation *t* + 1 is given by:

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

It is easy to see that the transition matrix is determined only by the initial allele frequencies and the population size *N*. Since in population genetics scientists are usually interested in allele frequencies, we define:

$$f_t = \frac{i}{2N}$$

to be the frequency of *A* in generation *t*. Using the properties of the binomial distribution, we see that:

$$\mathbb{E}\left[f_{t+1}|f_t = f\right] = f$$

$$\mathrm{Var}\left(f_{t+1}|f_t = f\right) = \frac{f(1-f)}{2N}$$

So, according to this model, while average allele frequencies will remain constant from one generation to the next one ($\mathbb{E}$), since there are no other evolutionary forces at work, the actual allele frequencies will change at a rate that is inversely proportional to population size (Var). These fluctuations in allele frequencies constitute drift. As the Wright-Fisher model suggests, drift is stronger in smaller populations. And this explains why drift is often compared with coin tossing (LUQUE 2016).

Turning back to the issue at stake, i.e. how drift should be interpreted, for the causalists drift is a natural fact or process in which heritable differences between entities are causally irrelevant to differences in reproductive success. For instance, C. STEPHENS (2004) suggests that drift acts on populations, causing sampling error. In this view, drift is a force with a greater strength in small populations. Consider

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again the coin tosses example: according to Stephens, drift «plays a larger role in flipping a fair coin 10 times than it does in flipping a coin 10,000 times» (STEPHENS 2004, p. 556). On the contrary, according to the statistical interpretation, drift is a departure from expected values attributable to the statistical uncertainty that is inherent in any series of births, deaths, and matings. It is not a separate natural process over and above the individual-level causes of such events. The only relevant feature in drift explanations is population size. And, in this perspective, it is just this feature that distinguishes selection explanations from drift explanations.

5. Drift and Predictability

It is important to appreciate the different consequences that these two interpretations of drift imply with respect to the issue of predictability in evolution. Drift is usually supposed to be connected to the uncertainty of evolutionary outcomes (MATTHEN 2009). Indeed, genetic drift is often associated with randomness (A. WAGNER 2012), and randomness is deeply related to unpredictability (A. EAGLE 2005). Nevertheless, despite in both causalists' and statisticalists' interpretations of drift, drift can be regarded as deviation from prediction, causalists and statisticalists provide radically divergent answers to the following question: What, in the ultimate analysis, is the source of drift? In other words, if drift is deviation from predictions, then «a fundamental understanding of drift requires one to give an account of the source(s) of this deviation» (RAMSEY 2013, p. 3912).

According to the causalists there are natural facts or processes that are responsible for the deviation of actual frequencies from predictions. Drift, in this view, is an objective feature of the world, and the source of drift are objective (i.e. independent from the epistemic subject) worldly processes or facts that make frequencies deviate from their expected values. Thus, the source of drift should be amenable to scientific inquiry as any other natural phenomenon. On the contrary, according to the statisticalists, drift is a merely statistical fact, i.e. it is a mathematical consequence of the mathematical tools that we use to model genetic dynamics. This means that in this view the source of drift is in some sense

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epistemic. Epistemic here does not imply "subjectiveness" or "arbitrariness". Mathematics is widely held to be objective. Nevertheless, in natural sciences mathematics is usually seen as a tool used by the epistemic subject to model a worldly phenomenon. So, epistemic here has to be understood as implying that the source of drift is not the worldly phenomenon itself, but the tool used to model such phenomenon. Drift is in a sense a feature of the model, not of the world. For instance, according to Walsh, causalist models aim at «carving evolutionary change at its causal joints», while in the statisticalist view «one and the same episode of population change could conceivably be explained exclusively as selection *or* exclusively as drift», depending on how we choose to describe such episode, since selection and drift are «ways of characterising population level change *relative to a description*» (D.M. WALSH 2013, p. 303).

These different ways to construe drift have implications also for how one explains one's failure to predict evolutionary outcomes. If one takes the causalist view, then one can see deviation from prediction as due to a lack in one's knowledge of some relevant aspects of the population one wishes to model. If actual frequencies deviate from predictions, there must be somewhere in the world a process which is responsible for such deviation. Obviously, we are not denying that lack of knowledge of some relevant aspects in actual observations or experiments may be unavoidable *in practice*. What we are focused on here is what *in principle* can be regarded as the source of predictability or unpredictability in population genetics. In the causalist view, predictability or unpredictability in evolution would be a matter of complete knowledge or lack thereof. On the contrary, if one takes the statisticalist view, there is no way to fill in the gap between predictions and actual frequencies by enlarging one's knowledge of relevant aspects of a given population, because such deviation derives from the fact that one compares a finite actual population with predictions made by using models that deal with infinite quantities to calculate their outcomes, i.e. predictions. In infinite populations drift cannot occur (RAMSEY 2013). For instance, Strevens states that «in an infinite population, there is no drift», and this is the reason why biologists so often develop their models assuming infinite populations. Indeed, drift «cannot be set to zero directly, […], but it can zeroed indirectly by taking population size, another parameter in stochastic models, to be infinitely large» (M. STREVENS 2017, p. 6). Since there is wide consensus that there cannot be actual

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infinite worldly elements of any kind, it will not be the case that drift will fail to emerge when one deals with actual populations. Predictability or unpredictability in this view is not merely a matter of complete knowledge or lack thereof, neither is it a matter of developing better, i.e. more accurate, models; rather, it is a matter deeply related to some intrinsic feature of the very tool that allows us to make predictions in the first place, i.e. mathematics.

6. Population Genetics and Non-Causal Explanations

It is important to clarify some points in order to avoid any misunderstanding. First of all, it is worth stressing that statisticalists do not deny that population genetics models explain some relevant and objective aspects of the modeled population. They agree those models do that. The point is that statisticalists deny that population genetics explanations are *causal* explanations. As we already noted above, this claim is mainly motivated by the fact that most, if not all, «principles of evolutionary theory […] are expressed by purely statistical terms such as variances or covariances» (OTSUKA 2016b, p. 248).

To better see this crucial point, consider Price's Equation and Fisher's Fundamental Theorem of Natural Selection (FTNS). Price's Equation is a central result in population genetics, and can be written in the following form:

$$\Delta\bar{z} = \mathrm{Cov}\,(\omega, z) + \mathrm{E}_w(\Delta z)$$

where $\Delta\bar{z}$ is the change in average value of a given character from one generation to the next; $\mathrm{Cov}\,(\omega, z)$ represents the covariance between relative fitness (ω)[1] and the value character (z), i.e. the action of selection; and $\mathrm{E}_w(\Delta z)$ represents the fitness-weighted average of transmission bias Δz, which is defined as the difference between the character value of the i^{th} entity (z_i) and the average for its offspring ($\bar{z}$) (S. OKASHA 2006, sec. 1.2). The FTNS can be regarded as a special case of Price's Equation. Indeed, Price's Equation tells us exactly how much of a

[1] The relative fitness of the i^{th} entity (ω) is defined as the fitness of the i^{th} entity (w_i) divided by the average fitness of the population ($\bar{w}$).

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character will exist in the population in the next period. If we let the character equal fitness itself, then we get Fisher's theorem:

$$\Delta\bar{w} = \mathrm{Var}_{\mathrm{add}}(g)/\bar{w}$$

which can be read as: the change in average fitness from one generation to another ($\Delta\bar{w}$) equals the additive genetic variance in the first generation ($\mathrm{Var}_{\mathrm{add}}(g)$), divided by mean fitness ($\bar{w}$). The additive genetic variance, i.e. $\mathrm{Var}_{\mathrm{add}}(g)$, measures the fitness variation in the population that is due to the additive, i.e. independent, action of the genes. In other words, it measures any gene's effect on fitness which is independent of its "genetic background". Indeed, in this perspective, it is possible to see the total genetic variance as the sum of the additive genetic variance and the non-additive genetic variance.

Since its formulation, the FTNS has received different interpretations. This is mainly due to the unclear formulation of the FTNS given by Fisher in his writings (S. OKASHA 2008). Fisher himself describes the FTNS as follows: «the rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time» (R.A. FISHER 1930, p. 35). This formulation of the FTNS induced many authors to compare the FTNS to the second law of thermodynamics, according to which entropy, on average, can never decrease. In this interpretation, the FTNS is able to give a formal representation (and explanation) of the directionality of evolution, i.e. to give a proof of the fact that fitness, on average, will never decrease. If such interpretation were correct, the FTNS would have been able to explain the course of evolution and the development of forms ever more complex without any reference to any kind of design or teleological explanation. This last point clarifies why the analogy between the FTNS and the second law of thermodynamics is relevant to the issue of whether or not the explanations provided by populations genetics are causal explanations. Indeed, if the analogy between the FTNS and the second law of thermodynamics holds, the FTNS would be able to account for a relevant asymmetry in evolution, i.e. complexification of living forms, in a way which is analogous to the way in which the second law of thermodynamics is able to account for relevant asymmetries in physics.

Thus, the reasoning goes, as statistical mechanics, although it is cast in statistical terms, may be understood as bearing on the causal structure of the

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physical world, so the FTNS, despite it is cast in statistical terms, can be understood as bearing on the causal structure of biological evolution. For instance, French says that one could take Price equation (of which, as stated, the FTNS can be regarded as a special case) «as characterizing a certain fundamental—if, perhaps, abstract—and 'high-level' feature of biological structure» (S. FRENCH 2014, p. 338). According to French, this covariance equation can be regarded as able to represent the «modal, relational structure of the evolutionary process […]. Just as the laws and symmetries of physics 'encode' the relevant possibilities, so Price's equation encodes how the average values of certain characters changes between generations in a given biological population» (*ibidem*).

The problem with the analogy between the FTNS and the second law of thermodynamics is that «it is *simply untrue that the average fitness of a population undergoing natural* selection never decreases, so the rate of change of average fitness *cannot always* be given by the additive genetic variance» (OKASHA 2008, p. 328). Okasha clarifies that «Fisher was not talking about the rate of change of average fitness at all, but rather the *partial rate of change which results from* [the direct action of] *natural selection* altering gene frequencies in the population, *in a constant environment*» (*ibidem*, p. 329)[2]. This means that it is more adequate to say that according to the FTNS when natural selection is the only force in operation, average fitness can never decrease. The problem is now that «by Fisher's lights, natural selection will almost never be the *only force in operation; for by causing gene frequencies to change, selection* almost always induces environmental change, which is itself a force affecting average fitness» (*ibidem*, p. 344). In fact, «the environment in Fisher's sense will *not remain fixed, for selection itself alters it*» (*ibidem*, p. 347). Details are not relevant here, the basic idea is that for Fisher, when natural selection operates, this fact directly alters both the mean fitness $\bar{w}$, and the "environment", which in its turn alters the mean fitness $\bar{w}$. Thus, if the FTNS holds only when natural selection is the only force to operate in a constant environment, and if when natural selection operates, the environment cannot remain constant, then we should conclude that the FTNS can never hold. For example, Okasha states that the «theorem tells us that in a constant environment,

[2] To understand Fisher's understanding of the FTNS, we have to accept Fisher's view of "environment": any change in the average effects constitutes an environmental change.

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selection can only drive average fitness up; but since the environment, in Fisher's sense, is always changing, nothing follows about whether average fitness will actually increase or not» (*ibidem*, p. 345). Thus, the analogy between fitness and entropy seems to fail.

The biological import of the FTNS is still controversial. G.R. PRICE (1972) and W.J. EWENS (1989) felt that the FTNS, though mathematically correct, did not have the biological significance that Fisher claimed for it. On the contrary, A.W.F. EDWARDS (1994) and A. GRAFEN (2003) are much more sympathetic to Fisher's view. We cannot develop this issue here for reasons of space. What we wish to point out here is that, despite no-one doubts that the FTNS is a sound mathematical theorem, the possibility of interpreting the explanations provided by such theorem in causal terms in analogy with how explanations provided by certain equations are interpreted in physics, has been fiercely disputed by the statisticalists.

Matthen and Ariew, for instance, state that the reason «for reifying natural selection [...] lies in a[n] […] analogy between equations of population genetics—such as Fisher's Theorem—and certain equations of physics» (MATTHEN and ARIEW 2009, p. 208). But in their view this analogy is not well founded, because, unlike that in physics, the description of natural selection «rendered by population genetics models are in general neither predictive nor explanatory», since «population genetics models are, in general, noncausal models» (B. GLYMOUR 2006, pp. 369, 383). Moreover, as we have seen, in this view natural selection itself is not a genuine feature of the world, it is just «ontologically derivative on individual-level events such as births, deaths, and mutations» (MATTHEN and ARIEW 2009, p. 216).

In this perspective, the FTNS does not tell us anything about the causal structure of the evolutionary process, firstly because such theorem refers to something which, being ontologically derivative, is not a causal concept (i.e. natural selection), and secondly, because such theorem itself is not intrinsically related to anything which is biological in character. For example, Matthen and Ariew state that natural selection «is not even a biological phenomenon as such. It holds in any history in which the terms of the theory can be jointly interpreted in a way that accords with the abstract requirements of the theory» (*ibidem*, p. 222).

As already noted, our aim here is not to take side on the dispute over the nature of natural selection, rather we just wish to point out a possible difficulty for the

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statisticalists which has so far (at least to the best of our knowledge) gone quite unnoticed, a difficulty which might derive from their claim that population genetics explanations are non-causal explanations.

7. Mathematical Explanations and Naturalism

A possible challenge that the statisticalists may have to address is the following: if the explanations provided by population genetics are regarded by statisticalists as non-causal explanations of a certain kind, then statisticalism risks being incompatible with a naturalist stance. This may be a relevant problem because many statisticalists view themselves as naturalists. Moreover, as evolution is central to naturalism in general, for all that proclaim themselves naturalists it is of relevance what kind of explanations population genetics provides.

According to a widespread view, scientific explanations need to be causal explanations in order to be genuinely scientific (for a survey see J. WOODWARD 2017). This is mainly due to the fact that models of scientific explanation which made no reference to causation, because they were developed by positivists «motivated by the apparent appearance within legitimate science of explanations that didn't seem causal in nature» (SKLAR 2009, p. 661), were shown to count various non-explanations as explanatory, i.e. they were unable to account for the so-called explanatory asymmetry. Indeed, if A is correlated with B, and A explains B, we usually think that it cannot be the case that B explains A. There is an asymmetry between the explanans and the explanandum, despite their being correlated. And an adequate account of scientific explanation must be able to account for such asymmetry. To face the asymmetry problem, in the last decades philosophers thought that causal notions should be introduced in our models of scientific explanations to distinguish between regularities that are genuinely explanatory and those that are not. So, despite issues as what is the metaphysical nature of causality, or whether causality finds room in fundamental physics, are very debated issues in philosophy of science and metaphysics (for a survey see T. BLANCHARD 2016), there is still a wide consensus that causation is relevant when dealing with a philosophical account of scientific explanations in order to account for the explanatory asymmetry.

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In recent years, the debate on the nature of non-causal scientific explanations flourished. Some philosophers maintain that there are several genuinely scientific non-causal explanations, while other philosophers either deny that those explanations are genuine explanations, or they deny that those explanations are genuinely non-causal explanations (see A. REUTLINGER 2017 for a survey).

For our purposes, it is not relevant to take side on this debate. We just wish to underline that, given that statisticalists claim that natural selection and drift are not really causes of evolution, the statisticalist faces a sort of dilemma: (1) either she maintains that population genetics explanations are not genuine instances of scientific explanations; (2) or she maintains that scientific explanations can also be non-causal, and that populations genetic explanations are non-causal explanations. Obviously, the first horn of the dilemma, i.e. (1), is unacceptable, and, as we have already stressed, no statisticalist would be interested in taking it, since no statisticalist denies that population genetics *do* provide explanations. So, the statisticalist seems to be committed to the claim that (at least some) non-causal explanations are genuine scientific explanations, and that explanations provided by populations genetics are explanations of that kind.

The problem now is to determine what kind of non-causal explanations the explanations provided by populations genetics are. Apparently, several kinds of non-causal explanations can be distinguished (REUTLINGER 2017). It is beyond the scope of this paper to investigate whether every kind of non-causal explanations is problematic from a naturalist point of view. What is less contentious and easiest to show is that at least one kind of non-causal explanations, namely Mathematical Explanations of Natural Phenomena (MENP), is potentially highly problematic for those who wish to take a naturalist stance. So, as we will try to show, if the explanations provided by population genetics are regarded MENP, statisticalists have to face the challenge described above.

Briefly, MENP are those non-causal scientific explanations in which an indispensable explanatory role is played by a mathematical result (see e.g. A. BAKER 2009). As an example, consider the following question: Why do hive-bee honeycombs have a hexagonal structure? Part of the explanation depends on evolutionary facts. But the explanation is completed by pointing out that the hexagonal tiling is optimal with respect to dividing the plane into equal areas and minimizing the perimeter. This geometrical fact, known as the honeycomb

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conjecture, was finally proved by Hales in 2001 (T.C. HALES 2001). Thus, the supporters of MENP claim, the explanation of the biological fact that hive-bee honeycombs have a hexagonal structure seems to depend *essentially* on a mathematical result. Such a dependency on mathematical results makes MENP non-causal explanations, since mathematical results/facts/objects are usually regarded as non-causal, better they are usually regarded as non-spatiotemporally located and causally inert (M. BALAGUER 2009). This last point is crucial: it is indeed the causal inertness of the explanans in a non-causal explanation of the MENP-kind that is at the core of the difficulty of making this kind of explanations compatible with a naturalist stance.

Two clarifications are in order here: (1) it is important not to confound alleged instances of MENP with scientific explanations that merely use mathematics for representational purposes, i.e. explanations where mathematical results are not playing an *indispensable* explanatory role; (2) MENP are not non-causal explanations in the mere sense that they do not explicitly cite causes. Indeed, there are abstract explanations which do not explicitly cite causes, or which do not clearly specify any mechanism or process responsible for the explanandum, but which, despite their "abstractness", cannot be regarded as genuine MENP (see A. REUTLINGER and H. ANDERSEN 2016).

Another example of MENP is provided by M. LANGE (2013b): a mother tries to divide twenty-three strawberries evenly among three children without cutting any strawberry and fails. What explains her failure? According to Lange, the explanation of her failure involves crucially the following assumption: it is a mathematical fact that twenty-three cannot be divided evenly by three. In this view, this mathematical fact is both non-causal and explanatory, so this explanation can be regarded as a genuine MENP. According to Lange, mathematical explanations explain in virtue of the extra modal force they have compared to the necessity associated with causal laws, i.e. ordinary physical laws.

As regard the compatibility between MENP and naturalism, the main problem derives from the difficulty of giving a justification of the claim that mathematical facts constrain natural phenomena which can be acceptable for a naturalist. We will not be concerned here with any specific view of naturalism, nor we will survey the many criticisms that have been moved to this view so far. For the purpose of this paper, naturalism can be understood as the metaphilosophical stance according to

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which we should refuse explanations that appeal to non-natural entities, faculties or events, where "non-natural" has to be understood as indicating that those entities, faculties or events cannot *in principle* be investigated and accounted for in the way we usually do in science (for a survey, see D. PAPINEAU 2016).

Although such a characterization of naturalism is quite broad, it nevertheless retains the idea that every naturalist view requires both (1) an ontological and (2) an epistemological commitment. This means that, in order to naturalize a domain D, it is insufficient to merely specify what kind of entities we can admit in our ontology of D. We have also to provide a naturalistic (i.e. a scientific adequate and reliable) account of how we can acquire knowledge of those D-entities. In other words, one needs to justify the claim that there is a sort of connection between the mathematical domain and the worldly domain.

The difficulty of providing a naturalist account for mathematics and modality derives from the fact that both mathematics and modality have to face the access problem. The access problem, first raised in the philosophy of mathematics by (P. BENACERRAF 1973), is now thought to arise in many other domains (see e.g. S. JONAS 2017). It is the problem of justifying the claim that our D-beliefs align with the D-truths of a given domain D, if D is regarded as an a priori domain, i.e. a domain whose objects cannot *in principle* be empirically investigated. Both mathematics and modality are usually regarded as a priori domains, i.e. inaccessible domains, or better *in principle* empirically inaccessible domains, domains which cannot be investigated by the means of empirical sciences. Since naturalism claims that we should regard as knowledge only what is knowable by the same means by which we acquire scientific knowledge (M. DEVITT 1998), it is easy to see why there are no satisfactory naturalist accounts of how it is that we can have knowledge of those a priori domains.

Turning to the issue at stake, the point now is: If one adopts statisticalism, is one committed to accept the claim that the explanations provided by population genetics are genuine MENP? This issue is controversial. As already said, if a statisticalist embraces the idea that population genetics explanations are genuine MENP, she has to face a dilemma: either she tries to reconcile her view with naturalism, a goal which might be very difficult to reach, or she has to submit to an anti-naturalist stance, an option which might be unpalatable to many statisticalists.

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To avoid this dilemma, the statisticalist should deny that the explanations provided by population genetics are genuine MENP. But, obviously, she should also maintain that such explanations are nevertheless non-causal explanations, since statisticalists deny that population genetics provides us with causal explanations. It is not clear whether the statisticalist may find a way out. However, this seems not an easy task. Indeed, in order to achieve this goal, since supporters of MENP usually claim that the explanations provided by population genetics are genuine instances of MENP, the statisticalist has to prove that (at least some of) the claims made by the supporters of MENP are ungrounded or do not apply to the explanations provided by population genetics.

Consider, for instance, how Lange conceives of drift explanations. According to Lange, drift explanations in population genetics are what he calls Really Statistical (RS) explanations. In Lange's view, an RS explanation «does not proceed from the particular chances of various results […]. It exploits merely the fact that some process is chancy, and so an RS explanation shows the result to be just 'a statistical fact of life'» (M. LANGE 2013a, p. 173). RS explanations are instances of MENP, since it can be shown that they are both (1) genuine non-causal explanations, i.e. they are not explanations that merely fail to cite causes; and (2) genuine mathematical explanations, i.e. they are not explanations that merely use mathematics for representational purposes.

As regard (1), in order to explain why RS are non-causal explanations, Lange considers explanations by regression to the mean. Regression to the mean is, roughly, the phenomenon that if a variable is extreme on its first measurement it will tend to be closer to the average on its second measurement. This kind of explanations «is not causal. It depicts the result as fallout from the statistical character of the case» (*ibidem*). Indeed, the point of this kind of explanation is «to exhibit the result as arising from the fact that successive runs have a statistical relation – regardless of that precise relation or its […] causes or, indeed, whether it has any causes at all» (*ibidem*, p. 177).

As regard (2), in order to explain why RS are genuine mathematical explanations, Lange points out that RS explanations do not appeal to any particular aspects of what needs to be explained, «but merely to the fact that there are chances. Consequently, instead of subsuming the result to be explained under a statistical law of nature, an RS explanation exploits a theorem of the probability

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calculus» (*ibidem*). This last point is crucial, since insofar as «mathematical facts alone are emphasized as doing the explaining, the explanation is properly characterized as distinctively mathematical» (LANGE 2013b, p. 507), i.e. as a MENP. So, if RS explanations depend indispensably on theorems of probability calculus, i.e. on mathematical results, then such explanations are genuine MENP.

Lange's line of reasoning, although may be disputable to many, seems sound and so worth being taken seriously. Thus, if a statisticalist wishes to deny that drift explanations in population genetics are RS explanations, and so can be regarded as genuine MENP, she has to provide reason for either (a) the claim that drift explanations are not really non-causal, or (b) the claim that in drift explanations it is not some mathematical result that is really indispensably doing the explaining. Both options may be problematic for the statisticalist. As regard (a), it is easy to see that a statisticalist cannot take it, since statisticalists claim precisely that drift explanations in population genetics are non-causal explanations. So (b) appears to be the only option that a statisticalist can take in order to deny that drift explanations are MENP. Now, the problem is that taking (b) may be impervious. Indeed, denying that in a scientific explanation mathematics is indispensably doing the explaining amounts to claim that such explanation is an ordinary scientific explanation which uses mathematics for representational purposes. But when one deals with an explanation in which mathematics is used for merely representational purposes, it is more difficult for one to claim that such explanation is non-causal. It is hard to say whether it is merely difficult or rather impossible. Certainly, it is a big issue to deal with. It seems fair to conclude by saying that the statisticalist who wishes to take a naturalist stance should at least clarify whether she thinks that the explanations provided by population genetics are genuine MENP, and, in the affirmative case, whether she thinks that MENP are compatible with a naturalist stance.

References

BAKER A. 2009, *Mathematical Explanation in Science*, in «The British Journal for the Philosophy of Science», 60, pp. 611-633.

In Ceccarelli, D.; Frezza, G. (eds.), *Predictability and the Unpredictable. Life, Evolution and Behaviour*, Roma, CNR Edizioni, p. 51–70. ISBN: 978-88-8080-236-5.

BALAGUER M. 2009, *Realism and Anti-Realism in Mathematics*, in *Handbook of the Philosophy of Science. Vol. 4. Philosophy of Mathematics*, ed. by D. Gabbay, P. Thagard, J. Woods, Elsevier, Amsterdam, pp. 117-151.

BENACERRAF P. 1973, *Mathematical Truth*, in «The Journal of Philosophy», 70, pp. 661-679.

BLANCHARD T. 2016, *Physics and Causation*, in «Philosophy Compass», 11, pp. 256-266.

DEVITT M. 1998, *Naturalism and the A Priori*, in «Philosophical Studies», 92, pp. 45-65.

EAGLE A. 2005, *Randomness is Unpredictability*, in «The British Journal for the Philosophy of Science», 56, pp. 749-790.

EDWARDS A.W.F. 1994, *The Fundamental Theorem of Natural Selection*, in «Biological Reviews», 69, pp. 443-74.

EWENS W.J. 1989, *An Interpretation and Proof of the Fundamental Theorem of Natural Selection*, in «Theoretical Population Biology», 36, pp. 167-80.

FISHER R.A. 1930, *The Genetical Theory of Natural Selection*, Clarendon Press, Oxford.

FRENCH S. 2014, *The Structure of the World*, Oxford University Press, Oxford.

GIERE R.N. 2006, *Modest Evolutionary Naturalism*, in «Biological Theory», 1, pp. 52-60.

GLYMOUR B. 2006, *Wayward Modeling: Population Genetics and Natural Selection*, in «Philosophy of Science», 73, pp. 369-389.

GRAFEN A. 2003, *Fisher the Evolutionary Biologist*, in «The Statistician», 52, pp. 319-329.

HALES T.C. 2001, *The Honeycomb Conjecture*, in «Discrete and Computational Geometry», 25, pp. 1-22.

HITCHCOCK C., VELASCO J. 2014, *Evolutionary and Newtonian Forces*, in «Ergo», 1, pp. 39-77.

JONAS S. 2017, *Access Problems and Explanatory Overkill*, in «Philosophical Studies», 174, pp. 2731-2742.

LANGE M. 2013a, *Really Statistical Explanations and Genetic Drift*, in «Philosophy of Science», 80, pp. 169-188.

LANGE M. 2013b, *What Makes a Scientific Explanation Distinctively Mathematical*, in «The British Journal for the Philosophy of Science», 64, pp. 485-511.

LUQUE V.J. 2016, *Drift and Evolutionary Forces: Scrutinizing the Newtonian Analogy*, in «Theoria», 31, pp. 397-410.

In Ceccarelli, D.; Frezza, G. (eds.), *Predictability and the Unpredictable. Life, Evolution and Behaviour*, Roma, CNR Edizioni, p. 51–70. ISBN: 978-88-8080-236-5.

MATTHEN M. 2009, *Drift and "Statistically Abstractive Explanation"*, in «Philosophy of Science», 76, pp. 464-487.

MATTHEN M. 2010, *What Is Drift? A Response to Millstein, Skipper, and Dietrich*, in «Philosophy and Theory in Biology», 2:e102.

MATTHEN M., ARIEW A. 2009, *Selection and Causation*, in «Philosophy of Science», 76, pp. 201-224.

MILLSTEIN R. 2017, *Genetic Drift*, in *The Stanford Encyclopedia of Philosophy*, ed. by E.N. Zalta, URL = <https://plato.stanford.edu/archives/fall2017/entries/genetic-drift/>.

MILLSTEIN R., SKIPPER R.A.J., DIETRICH M.R. 2009, *(Mis)interpreting Mathematical Models: Drift as a Physical Process*, in «Philosophy and Theory in Biology», 1:e002.

OKASHA S. 2006, *Evolution and the Levels of Selection*, Oxford University Press, Oxford.

OKASHA S. 2008, *Fisher's Fundamental Theorem of Natural Selection – A Philosophical Analysis*, in «The British Journal for the Philosophy of Science», 59, pp. 319-351.

OTSUKA J. 2016a, *A Critical Review of the Statisticalist Debate*, in «Biology & Philosophy», 31, pp. 459-482.

OTSUKA J. 2016b, *Causal Foundations of Evolutionary Genetics*, in «The British Journal for the Philosophy of Science», 67, pp. 247-269.

PAPINEAU D. 2016, *Naturalism*, in *The Stanford Encyclopedia of Philosophy*, ed. by E.N. Zalta, URL: <https://plato.stanford.edu/archives/win2016/entries/naturalism/>.

PRICE G.R. 1972, *Fisher's "Fundamental Theorem" Made Clear*, in «Annals of Human Genetics», 36, pp. 129-140.

RAMSEY G. 2013, *Driftability*, in «Synthese», 190, pp. 3909-3928.

REUTLINGER A. 2017, *Explanation beyond Causation? New Directions in the Philosophy of Scientific Explanation*, in «Philosophy Compass», DOI: 10.1111/phc3.12395.

REUTLINGER A., ANDERSEN H. 2016, *Abstract versus Causal Explanations?*, in «International Studies in the Philosophy of Science», 30, pp. 129-146.

SKLAR L. 2009, *Causation in Statistical Mechanics*, in *The Oxford Handbook of Causation*, ed. by H. Beebee, C. Hitchcock, P. Menzies, Oxford University Press, Oxford, pp. 661-672.

SOBER E. 1984, *The Nature of Selection*, The University of Chicago Press, Chicago.

STEPHENS C. 2004, *Selection, Drift, and the 'Forces' of Evolution*, in «Philosophy of Science», 71, pp. 550-570.

In Ceccarelli, D.; Frezza, G. (eds.), *Predictability and the Unpredictable. Life, Evolution and Behaviour*, Roma, CNR Edizioni, p. 51–70. ISBN: 978-88-8080-236-5.

STREVENS M. 2017, *The Structure of Asymptotic Idealization*, in «Synthese», DOI: 10.1007/s11229-017-1646-y.

WAGNER A. 2012, *The Role of Randomness in Darwinian Evolution*, in «Philosophy of Science», 79, pp. 95-119.

WALSH D.M. 2013, *Descriptions and Models: Some Responses to Abrams*, in «Studies in the History and Philosophy of Biology and the Biomedical Sciences», 44, pp. 302-308.

WALSH D.M., ARIEW A., MATTHEN M. 2017, *Four Pillars of Statisticalism*, in «Philosophy, Theory, and Practice in Biology», 9:1.

WALSH D.M., LEWENS T., ARIEW A. 2002, *The Trials of Life: Natural Selection and Random Drift*, in «Philosophy of Science», 69, pp. 452-473.

WOODWARD J. 2017, *Scientific Explanation*, in *The Stanford Encyclopedia of Philosophy*, ed. by E.N. Zalta, URL = <https://plato.stanford.edu/archives/fall2017/entries/scientific-explanation/>.