ONE EQUATION TO RULE THEM ALL

A philosophical analysis of the Price equation

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ABSTRACT

This paper provides a philosophical analysis of the Price equation and its role in evolutionary theory. Traditional models in population genetics postulate simplifying assumptions in order to make the models mathematically tractable. On the contrary, the Price equation implies a very specific way of theorizing, starting with assumptions that we think are true and then deriving from them the mathematical rules of the system. I argue that the Price equation is a generalization-sketch, whose main purpose is to provide a unifying framework for researchers, helping them to develop specific models. The Price equation plays this role because, like other scientific principles, shows features as abstractness, unification and invariance. By underwriting this special role for the Price equation some recent disputes about it could be diverted.

KEYWORDS: Price equation, generalization-sketch, abstractness, unification, invariance.

1. INTRODUCTION

The Price equation, first presented by George Price at the beginning of the 1970s, is one of the key equations in evolutionary theory. Price believed that he had found an equation so special that it could describe any evolutionary situation and any evolutionary problem –in other words, Price developed an abstract way of theorizing and thinking about evolution. Nevertheless, this equation has been involved in a great dispute the last decade due to its special nature, after a long period of oblivion when it was used by very few researchers. Some authors (van Veelen 2005, van Veelen et al. 2012, Nowak and Highfield 2011) claim that Price's equation is not more than an identity and, therefore, is not even a model, so that its scope and power should be significantly reduced. On the other hand, a large number of researchers have been using the Price equation in their theoretical and empirical work, developing models and

analysing empirical data through it. In this paper, I offer a philosophical analysis of the ongoing controversy on the interpretation and significance of the Price equation. I argue that critics are right when they claim that the Price equation is not a model on its own. But at the same time, defenders of the Price equation are right when they use it in their research. I argue that this special character of the Price equation is due to what Thomas Kuhn (1970) called a "generalization-sketch"[1].

I follow a particular view in order to shed light on Price's equation and, in general, on theoretical biology work. This view is based on comparing physicists and biologists' methodologies, analysing their tasks and goals, and trying to find out a common ground. Some advantages of this methodology are quite obvious. Physics is the most advanced science from a theoretical point of view –in terms of abstractness and mathematization– so trying to find help and/or inspiration on it seems reasonable. Actually, the architects of the Modern Synthesis conceptualize their own theoretical work influenced by how physicists work. Ronald Fisher (1930) stressed the dynamics of gene frequencies and how different *forces* might change these frequencies. Fisher also likened his "Fundamental theorem of natural selection" to the second law of thermodynamics. Sewall Wright introduced diffusion theory in the study of population dynamics which basic equation –Kolmogorov forward equation– is a general form of the Fokker-Plank equation in physics (Rice 2004). In addition, the main example of a generalization-sketch by Kuhn, as we will see in section 6, is Newton's second law of motion. So, our comparatives will be focused on seminal and central equations in physics such a Newton's second law. Needless to say, this approach is not "physics envy" neither obligates a perfect isomorphism between physics and biology. Rather this approach is a methodological pathway that has been fruitful in the past and I think it still is. The goal of this paper is to approach to the Price equation in two ways: descriptive and prescriptive. First, I show how the Price equation has been used by researchers from the past until our days. This is a descriptive task. After, I argue that researchers, in general, *should* adopt the Price equation in their investigations and this use will be rewarded. This is clearly a prescriptive claim.

The structure of the paper is as follows. Section 2 explores the traditional way of theorizing in population genetics and the use of diffusion theory. Section 3 introduces the Price equation and its different expressions. Sections 4 and 5 explain the key

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[1] Kuhn also called "law-sketch" (Kuhn 2000). Structuralists (Diez and Lorenzano 2015) use the term "guiding principle".

concepts it contains: abstractness, unifying power, and invariance. Section 6 develops the idea of interpreting the Price equation as a generalization-sketch, its key features, and gives some examples. Section 7 analyses some critiques on the Price equation and how understanding the Price equation as a generalization-sketch helps to overcome these critiques. Section 8 concludes.

2. POPULATION GENETICS AND DIFFUSION THEORY

Population genetics studies the genetic structure of populations and the causal factors, i. e. evolutionary forces, which act on populations changing allele and/or genotype frequencies (Gillespie 2004). Population genetics textbooks usually start formulating the Hardy-Weinberg law: a diploid and ideal infinite population, where there is random mating (panmictic population) and whose individuals are viable and fertile, will remain or return to equilibrium (i.e. allele and genotype frequencies will remain stable) if no force acts on it. In other words, the Hardy-Weinberg law assumes: random mating, discrete generations, no mutation, no migration, no random genetic drift, and no natural selection. Its simplest formulation says that for one locus with two alleles, A and a, with frequencies p and q respectively, the frequencies for the three genotype (AA, Aa and aa) are p^2, $2pq$ and q^2 respectively[2]. Therefore relaxing these assumptions we can elaborate dynamic models in order to predict the allele frequencies provided that one or more evolutionary forces are acting on populations. For differences in fitness –natural selection– one of the simplest examples is one locus with two alleles, A and a, with frequency p and q (respectively), non-overlapping generations, and with constant genotypic fitnesses w_{AA}, w_{Aa}, w_{aa}. The model deals with viability selection, where w is the average probability of survival from zygote to reproductive age. Assuming Hardy-Weinberg equilibrium before selection, the frequency of A in the next generation is

$$p' = \frac{w_{AA}p^2 + w_{Aa}pq}{\bar{w}}$$

where $\bar{w}$ is the mean population fitness ($w_{AA}p^2 + 2w_{Aa}pq + w_{aa}q^2$). The expected change in the frequency of A is

$$\Delta_p = p' - p = p\left(p\frac{w_{AA}}{\bar{w}} + q\frac{w_{Aa}}{\bar{w}} - 1\right)$$

We can reduce the portion of the brackets as

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[2] The allele and genotype frequencies must add to 1, respectively: $p + q = 1$, and $p^2 + 2pq + q^2 = 1$.

$$\Delta_p = p\left(\frac{w^* - \overline{w}}{\overline{w}}\right)$$

where w^* is the marginal fitness of allele A, i.e., a measure of its average fitness, taking into account the frequencies of the other alleles present in the genotypes in which A is present (Charlesworth and Charlesworth 2010).

In the same way, if we relax the infinite population size assumption postulating a finite population we can include drift. The basic model is the Wright-Fisher model (Gillespie 2004), a binomial sampling process in a diploid population in which a new generation is formed as a sample of $2N$ alleles[3]. The transition matrix for i copies of A_1 to j copies of A_1 is given by:

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

And the variance in frequency (p') is:

$$Var(p') = \frac{pq}{2N}$$

Thus, we might continue relaxing some other assumptions in the Hardy-Weinberg law, including mutation, migration, etc. The difficulties arise when we want to see how different evolutionary forces interact together upon a population. As far as we introduce more interacting forces, the complexity of the model increases, turning their mathematics less tractable. The basic problem is that we are dealing with deterministic processes as selection, migration, mutation and recombination, and also with stochastic processes like drift (here I follow Rice 2004). The consequence is that we cannot calculate with certainty the changes in a particular population, but only the probability distribution of populations. In order to do this we need, instead of using a discrete time model (like Wright-Fisher model), a continuous time model (continuous allele-frequency approximation). The appropriate method is, then, *diffusion theory* that allows us to combine deterministic and stochastic processes. *Diffusion equations*, used originally in physics to describe the behaviour of molecules diffusing by random motion (Charlesworth and Charlesworth 2010), allow us to determine the change in the density probability using the mean and the variance of change in the allele frequency per

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

generation. In order to make the model mathematically tractable, the diffusion approximation makes some simplifying assumptions: very large pool of gametes (large population size); mutations occur at the time of gamete production; selection operates on a large pool of the diploid offspring; selection, mutation, and migration are weak.

The problem is that finding solutions for discrete models, like the Wright-Fisher model, is not easy and resolution of partial differential equations is much more advanced than discrete equations. Thus, diffusion theory makes a transition from discrete to continue models when the population size tends to infinite ($N \longrightarrow \infty$). The Kolmogorov forward and backward equations are the basic mathematical models in diffusion approximations. The Kolmogorov forward equation characterizes population dynamics as

$$\frac{\partial \Psi(p, t)}{\partial t} = -\frac{\partial}{\partial p}[\Psi(p, t)M(p)] + \frac{1}{2}\frac{\partial^2}{\partial p^2}[\Psi(p, t)V(p)]$$

where $\Psi(p, t)$ is the probability density of populations with allele frequency p at time t, M represents the probability distribution governed by deterministic forces (selection, mutation, migration), and V represents the variance in allele frequency due to non-directional forces (drift). From this equation we can obtain specific equations combining several evolutionary factors, especially for equilibrium distribution (see Rice 2004, chap. 5 for mathematical details). For example, for the equilibrium probability distribution of allele frequency under selection, mutation, and drift we obtain

$$\widehat{\Psi} = Ce^{-2N_e sp^2}(1 - p)^{4N_e u_1 - 1}p^{4N_e u_2 - 1}$$

where C is a constant, s the selection coefficient, u the mutation rate, and N_e the effective population size. Nevertheless, the diffusion approach has limitations, and these limitations are tied to the simplifying assumptions. When evolutionary forces as selection, mutation or migration are not weak, the quantity of gametes is low, and so forth, these models lose a great deal of their reliability, requiring computer simulations (Charlesworth and Charlesworth 2010).

3. THE PRICE EQUATION

All models exposed in the previous section, including all models in population and quantitative genetics in general, make a number of assumptions in order to simplify the target system under study. Nevertheless, there is another way, a simplifying-assumptions-free model way to constructing theories. According to this approach, instead of starting with an idealized model containing deliberate simplifications, we begin by asking what is actually going on in the system, what are its basic properties and its appropriate mathematical principles. In evolutionary biology, the Price equation, also labelled as Price's theorem, plays this role (Rice 2004, Frank 2012a).

Developed originally by George Price (1970, 1972), the Price equation describes the evolution of a population from one generation to another in a simple algebraic language. Price's theorem is expressed in terms of covariances and expectations for describing evolution. There are equivalent derivations of the Price equation (Rice 2004, Frank 2012a, McElreath and Boyd 2007, Okasha 2006) with slightly different notations, so I follow Frank's standard derivation: think of a population where each entity is labelled by index i and each one has the character z_i, where i can be instantiated by different elements (alleles, genotypes, phenotypes, group of individuals, etc.). The frequency of i elements in the overall population is denoted q_i, and the average value of z in the population (the arithmetic mean) is $\sum q_i z_i$. So, if a descendant population has the traits z_i' and frequencies q_i', then the change in average character value is $\Delta \bar{z} = \sum q_i' z_i' - \sum q_i z_i$. Let q_i' be the frequency in the descendant population, as the fraction of the descendants of the elements i in the parent population. Let w_i be the contribution of each i parent to the descendant population, i.e. the fitness of the ith type. Therefore we can express q_i' as $q_i' = \frac{q_i w_i}{\bar{w}}$ where $\bar{w} = \sum q_i w_i$ is the average fitness. In a similar way, z_i' refers to the average measurement of the property z of the descendants from ancestors with index i, and the average trait value in the descendant population is $\bar{z}' = \sum q_i' z_i'$. Finally, we represent $\Delta q_i = q_i' - q_i$ as the change associated with differential survival and reproduction and $\Delta z_i = z_i' - z_i$ as the property value change. Following these definitions, the Price equation expresses the total change in the average property value as $\Delta \bar{z} = \bar{z}' - \bar{z}$. Now we can substitute and derive:

$$\Delta \bar{z} = \bar{z}' - \bar{z}$$
$$= \sum q_i' z_i' - \sum q_i z_i$$
$$= \sum q_i'(z_i' - z_i) + \sum q_i' z_i - \sum q_i z_i$$

$$= \sum q_i'(\Delta z_i) + \sum (\Delta q_i)\, z_i$$

Switching the order of the terms and substituting and rearranging:

$$\Delta \bar{z} = \sum q_i \left(\frac{w_i}{\bar{w}} - 1 \right) z_i + \sum q_i \frac{w_i}{\bar{w}} (\Delta z_i)$$

Applying the standard definitions of covariance and expectation we obtain

$$\bar{w}\Delta \bar{z} = Cov(w, z) + E(w\Delta z) \qquad (1)$$

This is the Price equation in its usual form in evolutionary literature, and defines evolutionary change as the sum of two terms. We can reduce equation 1 dividing both sides by $\bar{w}$ so the absolute fitness w becomes the relative fitness ω:

$$\Delta \bar{z} = Cov(\omega, z) + E_w(\Delta z) \qquad (2)$$

where $Cov(\omega, z)$ is the covariance between z and relative fitness ω, and $E_w(\Delta z)$ is the fitness-weighted average of the quantity Δz (Okasha 2006). The Price equation decomposes total evolutionary change in two terms, changes in frequency and changes in property values. These total effects are attributed to different factors –actually, causes– as selection, drift, mutation, etc. The first term on the right-hand side is the covariance between fitness w and character z, so is the change due to differential survival and reproduction. Usually this term is used as representing natural selection because give us an intuitive view of selection: if some entities in a population have a positive association between a character and fitness because that character gives them more chances to survive and reproduce to a certain selection pressure, the covariance will be positive. However, as the covariance term only measures the statistical association between the character and fitness –the number of descendants, also called absolute fitness or realized fitness–, it says nothing about what causes this covariance and, therefore, it applies equally to drift (Rice 2004)[4]. The second term on the right-hand side is the expected value (the average) of the quantity Δz weighted by fitness, that

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[4] There are ways to separate the actions of natural selection and drift. Averaging over uncertainty eliminates drift, so the action of natural selection can be taken to be the expectation of this covariance (Gardner and Grafen 2009, Gardner 2015). Okasha (2006, pp. 32-33) also argues that if we separate the realized fitness w_i in two parts –the expected fitness w_i^* and its deviation δ_i– we can add it in the Price equation, assuming that there is no transmission bias for simplicity, as $\bar{w}\Delta \bar{z} = Cov(w^*, z') + Cov(\delta, z')$, being the first part of the right side of the equation the change due to selection and the second part the change due to drift.

is, the change due to processes involved in reproduction. In other words, this term measures the relationship between parents and offspring, also called the *transmission bias* (Okasha 2006). This bias can be caused by mutation, recombination, selection at a lower level of organization, and so on.

We can see that we have not specified what kind of entities –mode of reproduction, mechanism of inheritance– are in our derivation, but we just stipulated a particular mapping between sets and their relationships[5]. So there is no simplifying assumption or idealization of any kind in the Price equation. It is an abstract representation of entities in a population changing in time. Only one assumption, but not a simplifying one, restricts Price's theorem scope. In our derivation all entities in a population at time $t + x$ must either be descendants of entities present at time t, or entities present at time t who survive to time $t + x$ (the latter is a case of differential persistence, where an entity is an ancestor at time t and the same entity is a descendant at time $t + x$). In other words, we have a closed population where all entities have ancestors, and therefore there is no migration. This restriction has been overcome by Kerr and Godfrey-Smith (2009) and expanded by Rice and Papadopoulos (2009). Moreover, although is usually presented in terms of one generation time interval (parents–offspring relationship), Price's theorem holds for any time interval. This is useful in cases like Fisher's sex ratio model, which is framed in terms of reproductive value, i.e. concerning an individual's or class's asymptotic genetic contribution on a very large number of generations.

Several equivalent forms of the Price equation can be obtained (tab. 1). The previous equations express Price's theorem in discrete time. For continuous time, the Price equation is of the form (Page and Nowak 2002; notation has been adapted)

$$\dot{E}(z) = Cov(w, z) + E(\dot{z}) \tag{3}$$

The dot denotes differentiation, the rate of change of the variable against time. Returning to the discrete form of Price's equation, we may want to remove the variable ω from the second term on the right side of equation 2 in order to capture all the effects of fitness by the first term on the right side, the covariance. So we obtain:

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[5] Notice that the Price equation is a categorization of the ancestors, connecting all the descendants to their ancestors through this categorization, i.e. "The focus is entirely on the categories of ancestors, *not* on which categories the descendants are in" (Walsh and Lynch 2013, p. 123).

$$\Delta \bar{z} = Cov(\omega, z') + E(\Delta z) \qquad (4)$$

where now $Cov(\omega, z')$ is the covariance between an entity's relative fitness and the average character value of its offspring, and $E(\Delta z)$ it is simply the difference between the mean character in the parent generation and the mean character in the offspring generation (Rice 2004, Okasha 2006). Although equations 2 and 4 are equivalents expressions, mathematically speaking, Okasha (2006, pp. 25-31) argues in favour of equation 4 because this equation, supposedly, gives us the *correct* decomposition from a causal point of view. As now all the effects of fitness are located in the covariance term, $Cov(\omega, z')$ represents the total action of natural selection; while $E(\Delta z)$ represents the change due to transmission bias. So both processes, natural selection and transmission bias, are represented separately and their effects independent from each other. Nevertheless this is only true when both terms interact additively. But if they do not, the total change is not equal to sum of the covariance and the expectation term, despite being natural selection and transmission bias the only two causes in action. In order to represent this non-additively interaction, the Price equation can be partitioned as

$$\Delta \bar{z} = Cov(\omega, z) + Cov(\omega, \Delta z) + E(\Delta z) \qquad (5)$$

where $Cov(\omega, z)$ represents fitness differences only, $E(\Delta z)$ represents transmission bias only, and $Cov(\omega, \Delta z)$ combines both (Godfrey-Smith 2007). If selection and transmission do not interact, $Cov(\omega, \Delta z)$ can be added to the first term (recovering equation 4) or added to the last term (recovering equation 2). All these partitions show the usefulness of decomposition.

$$\Delta \bar{z} = \sum q_i'(\Delta z_i) + \sum (\Delta q_i) z_i$$
$$\bar{w}\Delta \bar{z} = Cov(w, z) + E(w\Delta z)$$
$$\Delta \bar{z} = Cov(\omega, z) + E_w(\Delta z)$$
$$\dot{E}(z) = Cov(w, z) + E(\dot{z})$$
$$\Delta \bar{z} = Cov(\omega, z') + E(\Delta z)$$
$$\Delta \bar{z} = Cov(\omega, z) + Cov(\omega, \Delta z) + E(\Delta z)$$

Table 1. Different equivalent expressions of the Price equation

4. ABSTRACTNESS AND UNIFICATION

As a fully general description of evolution, Price's theorem is a fundamental principle that relates different things that we study, and that might not be obvious from our basic definitions. Thus, Price's equation contains two important properties: abstractness and unification. These two characteristics have been stressed by Andy Gardner as follows:

> "(…) because of its generality and simplicity, Price's equation has been used to uncover fundamental processes in evolution and, as a meta-model, it allows comparisons and contrasts to be drawn between different models and methodologies. As such, it is an important conceptual aid that has led to the discovery of unexpected connections between different bodies of theory, has settled long running controversies, and has helped to resolve semantic confusion" (Gardner 2008, R199).

Due to its abstract nature, we can derive from it the relevant mathematical equations found in the last century in evolutionary biology. For example, results in population genetics and quantitative genetics that were originally derived from different simplified models can all be derived from Price's theorem; showing relationships between those results that were not clear when they were originally derived. As Price himself stated (Price 1970), a classical population genetics model as the viability selection model –one locus, diallelic population genetics model with non-overlapping generations (see section 2)– can be obtained straightforward from his equation[6]. Recall that we have two alleles, A and a, with frequency p and q (respectively), and with constant genotypic fitnesses w_{AA}, w_{Aa}, w_{aa}. We index alleles A and a as $i = 1$ and $i = 2$, respectively, coding their associated values as $z_1 = 1$ and $z_2 = 0$. Therefore R_z represents the change in p because the mean value of z is $\bar{z} = (1 \cdot p) + (0 \cdot q) = p$. Remember that this model ignores the transmission bias term, thus $\Delta_p = R_z = \frac{Cov(w_i, z_i)}{\bar{w}}$. In this model of viability selection, the population is under random mating, so the fitness w_1 of an A allele is its marginal fitness, $w_1 = pw_{AA} + qw_{Aa}$. In the same way, the fitness w_2 of an a allele is $w_2 = pw_{Aa} + qw_{aa}$. Additionally, $E(w_i) = \bar{w} = pw_1 + qw_2$. From the definition of covariance, we obtain

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[6] Here I follow Walsh and Lynch (2013). For another source, see Michod (1999, p. 57).

$$\Delta_p = \frac{Cov(w_{i,}z_i)}{\overline{w}} = \frac{1}{\overline{w}}\left(E(w_iz_i) - E(w_i)E(z_i)\right)$$

Note that $E(w_i) = \overline{w}$, $E(z_i) = p$, and

$$E(w_iz_i) = \sum_{i=1}^{2} W_iz_i\, frequency\, (category\, i) = (w_1 \cdot 1 \cdot p) + (w_2 \cdot 0 \cdot q) = pw_1$$

Now, we can recover the allele frequency change equation for diploid over a generation:

$$\Delta_p = \frac{1}{\overline{w}}(pw_1 - \overline{w}p) = p\left(\frac{w_1 - \overline{w}}{\overline{w}}\right)$$

For quantitative genetics, the covariance term for quantitative traits was found earlier by Robertson (1966) and is known as the Secondary Theorem of natural selection. It says that the rate of change in a character equals the additive genetic covariance between fitness and character, $\overline{w}\Delta\overline{z} = Cov_{add}(w,z)$. Also, we can obtain Fisher's Fundamental Theorem of natural selection, which states that the rate of change in mean fitness equals the additive genetic variation in fitness. As fitness can be another character, we substitute the character z for fitness w in the covariance term, and then $\overline{w}\Delta\overline{w} = Cov_{add}(w,w) = Var_{add}(w)$. This is the classical interpretation of Fisher's Fundamental Theorem[7].

Thus, from the Price equation we can obtain a great amount of important results in theoretical biology in the past century. In several branches of evolutionary biology (multilevel selection, epidemiology, non-genetic inheritance, biodiversity, etc.) many researchers employ the Price equation as a unifying framework for analysing and, also, elaborating specific models (see section 6). The Price equation has been applied for several disciplines briefly summarized[8] (for equations based on Price's equation see tabs. 2 and 3).

- **Selection processes.** Since its first formulation by Price, the Price equation has been directly connected and developed for natural selection models. We have

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[7] Nevertheless, the exact version of Fisher's Fundamental Theorem only applies to the partial evolutionary response caused by natural selection, $\partial R_\omega = \sigma^2(A_\omega)$, (Lynch and Walsh 2013). See Frank (2012a), and Lynch and Walsh (2013), for detailed derivations of Robertson and Fisher's theorems, and the breeder's equation.
[8] The most relevant bibliography is reviewed but not intended to exhaust it.

seen how key equations of natural selection, Robertson and Fisher's theorems, can be derived directly from the Price equation. Other follow the same path: breeder's equation (Frank 2012a); replicator-mutator equation, adaptive dynamics and evolutionary game theory (Page and Nowak 2002, Rice 2004); multilevel selection (Okasha 2006, Frank 2012a, Gardner 2015); kin selection theory, inclusive fitness and Hamilton's rule (Frank 2013, McElreath and Boyd 2007); species selection (Rankin et al. 2015); and so on. Special mention deserves "The formal Darwinism project". This is a long term work carried out by several researchers (Gardner and Grafen (2009), Gardner and Welch (2011), Gardner (2014a and 2014b), Grafen (2002 and 2006); see Grafen 2007 and 2014 for an outline). Their aspiration is to establish a mathematical link between population genetics and optimization programs, in other words, between see natural selection as a mechanism that change gene frequencies and conceptualizing natural selection as a fitness-maximisation mechanism that produces *design*. For this task of linking, Price's equation plays a crucial role due to its generality, and because "The Price equation places individuals at the center of its technical apparatus" (Grafen 2007, p. 1245).

- **Stochastic evolution.** The Price equation, in its classic form, is a total description of evolutionary change because takes both present and future states as given or, in other words, is a deterministic description of evolutionary change. Nevertheless, sometimes all the parameters cannot be specified exactly, before reproduction (or any future state) has taken place. In this case, evolution turns out a stochastic process and then, some parameters should be changed to random variables. Thus, Rice and collaborators (Rice 2008, Rice and Papadopoulus 2009; but see also Grafen 2000) have developed a stochastic version of the Price equation that can deal with random variables as stochastic fitness and stochastic migration, demographic stochasticity or random environmental change. Following this path, Engen and Saether (2014) analyse how demographic and environmental stochasticity generate random genetic drift and fluctuating selection.

- **Ecology.** Fox and collaborators (Fox 2006, Fox and Haporle 2008, Fox and Kerr 2012) extend and use the Price equation as a general framework for biodiversity and ecosystem function, analyzing differences in ecosystem function between sites. Collins and Gardner (2009) develop a new form of the Price equation in

order to express the total change at the community level as the sum of the separate effects of physiological, evolutionary and ecological change, providing a way for integrating and linking these three different levels. Ellner et al. (2011) study how evolution, non-heritable phenotypic change and environment affect ecological dynamics, developing a continuous-time version of the Price equation that they call "Genotype-Phenotype-Environment equation".

- **Epidemiology.** Day and Gandon (2006 and 2007) deal with the evolutionary and epidemiological dynamics of host-parasite interactions focusing on a continuous model of pathogen evolution, providing a continuous-time derivation of the Price equation with mutation. This can be generalized to multiple habitats and as a formalism to model the evolutionary dynamics of pathogen populations (for example, S-I-R model). Thus, using the Price equation as a framework, Day and Gandon offer a way to integrate different theories of host-parasite interactions. Based on this approach, Alizon (2009) develops a framework that combines within-host population dynamics models, population genetics, theory and data, to study disease intrahost evolution for any parasite trait. Alizon argues that "This Price equation framework has four advantages: (i) it helps to identify how (and which) trade-offs can affect within-host evolution; (ii) it allows for predicting the short-term evolutionary dynamics of a trait from the genetic composition of the parasite population in the host; (iii) it helps link theory and data; and (iv) it can be applied to most existing models of within-host population dynamics" (Alizon 2009, p. 1124).

- **Non-genetic inheritance and proximate causes.** Modern Synthesis based their mathematical and empirical results on genetic inheritance. However, other non-genetic systems of inheritance may have a causal role on evolution. Halenterä and Uller (2010) use the Price equation for analysing and gathering four different inheritance systems (genetic, epigenetic, behavioral, and symbolic) on a common framework. Day and Bonduriansky (2011) developed several evolutionary models based on the Price equation that unifies the effects of genetic and non-genetic inheritance (nontransmissible environmental noise, indirect genetic effects, transgenerational epigenetic inheritance, RNA-mediated inheritance, etc.). Gardner (2011) applies the Price equation to blending inheritance, showing that Hamilton's rule can be derived under the assumption of blending inheritance. Otsuka (2015) develops a unified framework to translate

"proximate causes" (such epigenetic inheritance, maternal effects, niche construction) into "ultimate evolutionary response" based on the Price equation and causal graph theory. El Moulden et al (2014) explore how cultural transmission can be conceptualized as evolutionary systems, using the Price equation as a unifying framework, analysing how cultural and genetic evolution interact but also differentiating each other. Particularly on linguistics, Jäger and colleagues (Jäger 2008, Gong et al. 2012) use Price's equation to model various aspects of cultural evolution of language.

Price's theorem has also been used in economics (Andersen 2004), and cosmology (Gardner and Conlon 2013). These are some of the most important and interesting investigations, but not unique[9], using the Price equation as cornerstone.

5. INVARIANCE

Invariance or symmetry is the property of remaining unchanged under some transformation. This property has become one of the most important in the field of physics for several reasons. The presence of symmetries make easier to solve the equations in a theoretical model. Also, invariance under translations in space and time guarantees experimental repeatability. The importance of this property lies in the core of scientific research which is, basically, to distinguish between what changes and what does not. If everything changed in the world (or our target system), we would not do science because we would not be able to say nothing interesting about it since we would not compare any magnitude. There must be something that remains in order to talk about changes.

The Price equation shares with other scientific principles the feature of invariance or symmetry. More precisely, there is invariance on the Price equation contained in the term $Cov(w, z)$. Steven Frank has been the first author to show what kind of invariances contains the Price equation. For that he connects the Price equation, written in covariances and expectations, with information theory, overcoming the problem of representing nonlinear processes with statistic language. Thus, Frank (2009) relates

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[9] Other works are: Gardner et al. (2007, relating multilocus population genetics and social evolution); Barfield et al. (2011), Coulson and Tulkjapurkar (2008) extending the Price equation for stage- and age-structured; and Gardner 2015, Grafen 2015, Taylor 2009, Rebke 2012, for study populations composition (class-structured populations, decomposition, etc.) expressed with the Price equation.

Fisher information (a measure of distance between two probabilities distributions) and Shannon information (entropy) with the properties of natural selection, and gives an expression of the Price equation in terms of Fisher information (see tab. 2). More recently, Frank (2012a, 2012b) developed these ideas demonstrating different identities for the evolutionary change caused by selection in the Price equation, relating the covariance term with notions as information and geometry, where covariance is taken as a measure of distance (see Frank 2012a and 2012b for mathematical details). Thus, the fundamental expression for the change in mean character value caused by selection is:

$$\Delta_s \bar{z} = \bar{w} \beta_{zw} F(\Delta \hat{q})$$

where $\bar{w} \beta_{zw}$ is the scaling β that describes the amount of the potential information that the population captures, and $F(\Delta \hat{q})$ is the total Fisher information in the frequency fluctuations. In this way, Frank claims:

> "for any particular value for total selection, there is an infinite number of different combinations of frequency changes and character measurements that will add up to the same total value for selection. All of those different combinations lead to the same value with respect to the amount of selection. We may say that all of those different combinations are *invariant* with respect to the total quantity of selection" (Frank 2012a, p. 1007).

In other words, the covariance term allows us to evaluate selection completely since it does not matter how frequency changes and character measurements are combined. The basic idea is that the total quantity of selection does not depend on concrete individual values of the sum. The key point is that both terms, $\bar{w} \beta_{zw}$ and $F(\Delta \hat{q})$, can have the same overall value although their own values change, i.e. $F(\Delta \hat{q})$ value can be small and β_{zw} big, and vice versa, and give us the same total value. You can combine them in different ways an always obtain that same quantity of selection. The specific values of w and z are not important if we are concern only with the covariance term. In addition, this evaluation is complete because the covariance is taken as a measure of distance (i.e. as a measure of information) and not as is usually used in statistics and, consequently, being applied also for nonlinear processes. Therefore, "the distance $\Delta_s \bar{z}$ measures the informational gain by the population caused by natural selection" (Frank 2012a, p. 1009).

Someone might object that symmetries are important because they contribute to our understanding of our target systems[10]. For instance, Newtonian systems are invariant to Galilean transformations, and this seems an empirical assertion that characterizes the system. And we know it is empirically false because, according to the general relativity, physical systems are invariant not to Galilean but to Lorentz transformations. But the point is that this is all empirical matter. Now, turn to the invariance of the Price equation. It is invariant to some transformations, but these invariances seem to stem from the mathematical form of the equation, but not empirical matters of facts. If this is correct, how the symmetry of the Price equation contributes to our understanding of evolution? The answer is that is not an empirical question if Newtonian or general relativity systems are invariant. This is a *mathematical* question. Newtonian systems are invariants to Galilean transformations. This is not an empirical assertion but a mathematical one. If this distinction is not clear we run the risk of confusing the physical system with the model. A Newtonian model is invariant to Galilean transformations, and a general relativity model is invariant to Lorentz transformations. Invariances, precisely, stem from the mathematical form, and they cannot come from nowhere else. Another question is whether the invariances of our model, which come from our equations, have physical consequences. For example, the orbits of the planets of our Solar System are in a plane because, as Newtonian models are invariants under rotations, the angular momentum is conserved (positions and velocities are coplanar). This is a claim about a physical system due to the mathematical features of the model. If our model is (approximately) correct, it will have consequences regarding to the system under study.

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[10] I am grateful to Jun Otsuka for drawing my attention to this objection.

$$\dot{\bar{z}} = \dot{\bar{z}}_P + \dot{\bar{z}}_{E\|P}$$
Price equation in terms of Fisher information (Frank 2009)
$$\Delta_s\bar{z} = Cov(w,z)/\bar{w}$$ $$= \bar{w}\beta_{zw}Var(w/\bar{w})$$ $$= \Delta\boldsymbol{q} \cdot \boldsymbol{z}$$ $$= \|\Delta\boldsymbol{q}\| \|\boldsymbol{z}\| \cos\phi$$ $$= \bar{w}\beta_{zw}(\Delta\hat{\boldsymbol{q}} \cdot \Delta\hat{\boldsymbol{q}})$$ $$= \bar{w}\beta_{zw}F(\Delta\hat{\boldsymbol{q}})$$
Selection identities (Frank 2012a)
$$\bar{w}\Delta\bar{z} = \beta_{wz}Var(z) + \beta_{wy}Cov(y,z)$$
Path analysis (Frank 2012a)
$$\bar{w}\Delta\bar{z} = Cov(W,Z) + E(Cov_k(w,z))$$
Multi-level Price equation (Okasha 2006)
$$\bar{w}\Delta\bar{z} = Cov_{add}(w,z)$$
Robertson's theorem (Walsh and Lynch 2013)
$$\bar{w}\Delta\bar{w} = Var_{add}(w)$$
Fisher's theorem (Walsh and Lynch 2013)
$$R = Sh^2$$
Breeder's equation (Frank 2012a)
$$\Delta\bar{z} = GP^{-1}S$$
Lande's equation (Rice 2004)
$$rb - c > 0$$
Hamilton's rule (Hamilton 1970)
$$\Delta_p = p\left(\frac{w^* - \bar{w}}{\bar{w}}\right)$$
Viability selection equation (Rice 2004)
$$var(\Delta p) = \frac{p(1-p)}{2N}$$
Drift equation (Rice 2004)

Table 2. Identities and derivations of the Price equation, respectively.

$$\dot{E}(p) = Cov(f,p) + E(\dot{p}) + E(f\Delta_m p)$$
Replicator-mutator Price equation (Page and Nowak 2002)
$$\widehat{\Delta\bar{\phi}} = cov\big(\widehat{\phi^o},\hat{\Omega}\big) + \overline{cov_\iota(\phi^o,\Omega)} + \bar{\delta}$$
Stochastic evolution (general equation) (Rice 2008)
$$\widehat{\Delta\bar{\phi}} = \Big\|\Big[\![\,\overline{^d\phi^o},\,^d\hat{\Omega}\,]\!\Big]\Big\| + \overline{\ll \,^d\phi^o,\,^d\Omega \gg} + \widehat{\,^d\delta} + \ll \gamma,\Xi \gg + \bar{\Xi}\big(\hat{\gamma} - \widehat{\,^d\delta}\big)$$
Stochastic fitness and stochastic migration (Rice and Papadopoulus 2009)
$$R = GP^{-1}ES + GP^{-1}\Delta S_e + GP^{-1}\Delta S_d$$
Fluctuating selection and drift (Engen and Saether 2014)
$$\Delta T = \bar{z}\Delta s + Sp(w,z) + \sum_i w_i\Delta z_i$$
Difference Ecosystem Function (Fox 2006)
$$\Delta\bar{z} = E_I\Big(E_{Ji}\big(\Delta z_{ij}\big)\Big) + E_I\Big(cov_{Ji}\big(w_{ij},z'_{ij}\big)\Big) + cov_I(w_i,z'_i)$$
Collins/Gardner equation (2009)
$$\frac{dX}{dt} = \frac{\partial X}{\partial z}\Big(\frac{d\bar{z}}{dt} - E[\Delta z]\Big) + \frac{\partial X}{\partial z}E[\Delta z] + \frac{\partial X}{\partial k}\frac{dk}{dt}$$
Genotype-Phenotype-Environment equation (Ellner et al. 2011)
$$\dot{x}^A = cov_A(x,r^{AA}) - \mu(\bar{x}^A - \bar{x}_m^A) + \frac{N_T^B}{N_T^A}cov_B(x,r^{BA}) + \frac{N_T^B}{N_T^A}r^{-BA}(\bar{x}^A - \bar{x}^B)$$
The Price equation to multiple habitats (Day and Gandon 2006)
$$\bar{W}\Delta\bar{h} = Cov(W,h) + E(b\Delta h^b) + E(p\Delta h^p)$$
Non-genetic inheritance Price equation (for overlapping generations) (Day and Bonduriansky 2011)
$$\Delta\bar{Z} = \frac{1}{\beta\bar{Z} + R}\,(\beta + \lambda_2)\sigma_A^2$$
Niche construction (Otsuka 2015)
$$\Delta\bar{X} = cov\big(\tilde{C}_*^a,X^a\big) + ave((\Delta X)_d^a) - cov\big(\tilde{C}_d^*,X_d\big)$$
The Price equation with migration (Kerr and Godfrey-Smith 2009)
$$\Delta\bar{z} = \frac{Cov(\bar{z}_j,\bar{w}_j)}{\bar{w}} + \frac{Cov(\bar{d}_j,\bar{w}_j)}{\bar{w}} + \frac{E[Cov_j(z,w)]}{\bar{w}} + \frac{E[Cov_j(d,w)]}{\bar{w}} + E(\bar{d}_j)$$
Stage-structured Price equation (Barfield et al. 2011)
$$\Delta\bar{z} = \frac{cov(C_*^a,z^a)}{(C_*^*/n^a)} - \frac{cov(C_d^*,z_d)}{(C_*^*/n_d)} + ave((\Delta z)_j^i)$$
Macroevolutionary Price equation (Rankin et al. 2015)

Table 3. Several extensions of the Price equation.

6. THE PRICE EQUATION AS A GENERALIZATION-SKETCH

Until now, Price's equation has been considered a meta-model (Gardner 2008), a useful tool (Frank 2012a) for the analysis of multiple biological phenomena and

different models. As it was explained in previous sections, the generality of the Price equation and its capacity of encompassing different biological phenomena is something recognized by researchers. However, abstractness and unifying power are also present in other scientific generalizations, usually laws, but their importance inside a particular theory is generally rather limited. Thus, laws like Hooke's law for spring movements abstracts from particular cases and unifies them, yet its importance inside classical mechanics is quite limited with other classical mechanics law such as Newton's second law of motion.

Thomas Kuhn suggested the existence of some generalizations in scientific theories which are "schemes" rather than simple laws, and these schemes should be specified for particular problems. These generalizations are usually expressed in mathematical form and play a programmatic role inside the theory:

"generalizations [like $f = ma$, or Schrödinger's equation] are not so much generalizations as generalization-sketches, schematic forms whose detailed symbolic expression varies from one application to the next. For the problem of free fall, $f = ma$ becomes $mg = md^2s/dt^2$. For the simple pendulum, it becomes $mg \sin \alpha = -md^2s/dt^2$. For coupled harmonic oscillators it becomes two equations, the first of which may be written $m_1 d^2s_1/dt^2 + k_1 s_1 = k_2(d + s_2 - s_1)$. More interesting mechanical problems, for example the motion of a gyroscope, would display still greater disparity between $f = ma$ and the actual symbolic generalization to which logic and mathematics are applied" (Kuhn 1970, p. 465).

We can see that Newton's second law takes different forms in order to solve specific problems, the puzzles with every physicist has to deal in her day-to-day work. These specific forms, as Kuhn claims, may change Newton's second law in such a way that we cannot even capable to recognize it. This is what the paradigmatical examples (simple pendulums, pulleys, inclined planes, etc.) are for, they are used to familiarize physicists with the second law and hence, when they face a new problem, be able to find out a specific new form of Newton's second law in order to compute any phenomena based on forces, masses and accelerations. This characteristic gives to the second law its power and makes it so fruitful.

The idea here is that, much as Newton's second law of motion is not supposed to provide a full description of the workings of physical systems but rather emphasises that a (potentially quite complicated) description of that system can be provided in terms of force, mass and acceleration, the proper use of the Price equation is to motivate the

development of more detailed evolutionary equations that use its same basic language and logic. Thinking about the Price equation in these terms seems to be very similar to Price's aspirations. Thus, Price claimed:

> "Recognition of covariance... is of no advantage for numerical calculation, but of much advantage for *evolutionary reasoning and mathematical model building*" (1970, 521; emphasis added).

> "The mathematics given here applies not only to genetical selection but to selection in general. It is intended mainly *for use in deriving general relations and constructing theories*, and to clarify understanding of selection phenomena, rather than for numerical calculation." (1972, 485; emphasis added).

The use of the Price equation as a generalization-sketch implies a very specific way of theorizing: we start with postulates or assumptions that we think are true and then derive the mathematical rules of the system. Rice and Papadopoulus (2009) call theories that follow this way of theorizing "axiomatic theories", where postulates or assumptions are the axioms of the theory. Philosophers of science conceptualize this kind of thinking as "fundamentalism" (Cartwright 1999) where "scientists [are] guided by a commitment to find fundamental concepts and principles sufficient for providing a universal and unified account of nature" (Waters 2011, p. 232). For the fundamentalist approach universality is the goal, and according to Cartwright one clear example of this approach is Newton's second law of motion and the aspiration to encompass all dynamical processes through all forces acting upon bodies or, in other words, that there is a mechanical model for any dynamical situation[11]. A fundamentalist approach seeks generality, finding the mathematical expressions that encompass all the special models and allow us to produce more special ones. At the core of an axiomatic theory lies a unifying framework and, at the same time, a formula in order to produce specific models. That is, generalization-sketches are not models but sketches or schemas that provide a unifying framework in order to develop specific models. This schematic nature has been partially noted by Okasha: "So [the Price equation] it is not a model, but

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[11] This is not entirely accurate. There are trajectories that Newton's second law does not aim to apply to; "for instance the movement of a pen in somebody's hand at will" (Díez and Lorenzano 2015, p. 802). Likewise, there are biological problems that the Price equation may not be applied.

rather a schema that may be used to understand all other evolutionary models" (Okasha 2010, p. 426). These generalization-sketches constrain, in a certain way, our modelling possibilities. Thus, the Price equation requires to a biological system: change over time, ancestor/descendant relations, and phenotypes (Rice 2004). Therefore, it demands that researchers clarify the entities and characters, their relationships and partitions, the time step, etc., in any model. That is, Price's equation requires clarity to modellers (Jäger 2008).

The Price equation alone cannot play any empirical role if it is not supplied by a specific model. In the same way, Newton's second law tells nothing about what forces act on bodies, and needs to be supplied by specific models setting the forces and empirical information (masses, velocities, etc.). The Price equation works as a consequence law (Sober 1984). Sober describes two types of laws: source laws, which describe the circumstances that produce forces (such as Coulomb's law or the law of gravitation), and consequence laws, which describe how forces, once they exist, produce changes in the system (such as Newton's second law of motion). Thus, the Price equation describes how evolutionary forces produce changes in a population, but do not determine how many causes exists, how these causes are, and so on. In the same way, Newton's second law works as a consequence law, it tells nothing about how forces arises only how to compute them when they are in a system. In considering the Price equation as a generalization-sketch does not invalidate it as a meta-model. Actually, one feature of a generalization-sketch is that it works in that way. As is well known, Newton's work unified celestial and terrestrial motions under one theoretical framework. Newton's second law of motion provided a common language –forces, masses, and accelerations– adopting various forms such as the law of gravity. In Newton's words:

> "In the third book we give an example of this in the explication of the System of the World: for by the propositions mathematically demonstrated in the former books, we in the third derive from the celestial phenomena the forces of gravity with which bodies tend to the sun and the several planets. Then from these forces, by other propositions which are also mathematical, we deduce the motions of the planets, the comets, the moon, and the sea. I wish we could derive the rest of the phenomena of nature by the same kind of reasoning from mechanical principles; for I am induced by many reasons to suspect that they may all depend upon certain forces" (Newton 1846[1687], xviii).

The value of these generalization-sketches is to be, in some sense, a "promise", a driving principle for scientists whose work will be based on the abstract character of the principle and in their ability to transform an abstract schema into a concrete expression for particular cases. I use, following Kuhn's terminology, a "promise" because generalization-sketches are not algorithms that can be applied mechanically; rather they are like a language (Wilczek 2005).Thus, Newton's second law promises that if we have a mechanical problem, there are some dynamical equations for it based on forces, masses and accelerations; and push us to work hard to find them. Likewise, the Price equation tells us that if we have a biological problem, there are some equations for it based on convariances, expectations, or regressions. What Price's equation stresses is that, from an evolutionary point of view, those terms are the only important thing, "they are exactly what matters in determining the dynamics of evolution" (Rice 2004, p. 170)[12]. So generalization-sketches play a heuristic role and work as an abstract formalism awaiting for empirical application.

As generalization-sketches are not algorithms, a learning period is necessary in order to become confortable and competent, like a native speaker. It is not enough with knowing the meaning of the terms in the equation. That is why Kuhn did so emphasis in the exemplary problem solutions, the "exemplars". Thus, "doing problems is learning the language of a theory and acquiring the knowledge of nature embedded in that language" (Kuhn 2000, p. 169). Researchers need to be able to use the generalization-sketch in new situations, be able to create new forms of that sketch. William Hamilton was one of the first in glimpsed the importance of Price's equation. He used it to derive his rule –Hamilton's rule– and understand crucial concepts in social evolution theory[13]. Moreover, he understood the importance of learning the Price equation. As supporting

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[12] Van Veelen (2005) argues that the covariance term in the Price equation is not a real covariance because there is no sample measure (i.e. sample statistics). Nevertheless, as Frank (2012a) has stressed, Price (1972) was considering the total population and not a sample population (i.e. the covariance it is not an estimate but a mathematical function (Rice 2004), so there is no statistical corrections associated with sample statistics (Rice and Papadopoulos 2009)). There are different, but legitimate, uses of the term "covariance" (Frank 2012a, Gardner et al 2011).

[13] Hamilton's rule is an inequality inside kin selection theory. Its aim is to explain the evolution of social behaviour in populations. Hamilton's rule states that a social behaviour will be favoured by natural selection if and only if $rb - c > 0$, where r represents the genetic relatedness of the recipient to the actor, b the benefits to the recipient, and c the costs to the actor (Davies et al. 2012). Hamilton derived his rule in two different ways, so there are two possible versions of it. The first version (Hamilton 1964) is characterized by its simplifying assumptions, and as a consequence of these simplifications, the applicability of this version is constrained to very specific cases and cannot handle more complicated ones (for example, when the frequency of cooperators matters). The other version comes from the Price equation (Hamilton 1970, Frank 1998), it is not tied to any simplifying assumption, making it a general statement of social behaviour systems (Birch 2014).

information for his article, Frank (2013) provides Hamilton's class notes for his graduate course at the University of Michigan, Fall 1979. These notes start with the Price equation and indicate several tasks: use the equation to expand its second term, replace covariances by product of regressions and variance, etc. Hamilton's students were faced with sex ratios for group structured populations through the language of the Price equation[14].

Although some researchers are already using the Price equation as a generalization-sketch, I argue that researchers, in general, *should* adopt the Price equation in their investigations –as physicists in the eighteenth century took Newton's second law of motion– and this use will be rewarded. If the Price equation plays a role as a generalization-sketch, new forms could be found in order to resolve new specific problems. In other words, the Price equation is a puzzles solver tool as long as researchers are audacious and skilled enough to find some specific form for it. Let see some of these audacious researchers.

6.1. Genetic and non-genetic inheritance

Day and Bonduriansky (2011) have developed several evolutionary models based on the Price equation that unifies the effects of genetic and non-genetic inheritance. They postulate a population of replicating individuals, discrete time and overlapping generations. In addition, they denote g and h as the value of a genetic and non-genetic component, respectively; and define fitness as $w = b + p$ where b is the number of offspring of an individual, and p the probability of survival of the parent itself. Then, Day and Bonduriansky derive a version of the Price equation with overlapping generations, obtaining

$$\overline{w}\Delta\bar{g} = Cov(w, g) + E(b\Delta g^b) + E(p\Delta g^p) \quad \text{(6a)}$$

$$\overline{w}\Delta\bar{h} = Cov(w, h) + E(b\Delta h^b) + E(p\Delta h^p) \quad \text{(6b)}$$

The first terms represent the effect of natural selection on the genetic (6a) and non-genetic (6b) components. The second terms represent the "reproductive transmission", the change in genetic (6a) and non-genetic (6b) values that occur during transmission

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[14] Frank remembers this learning period as follows: "I took up the empirical study of fig wasp sex ratios in 1981. At that time, I also began to study Hamilton's notes and to learn how to extend Price's hierarchical multilevel selection analysis to apply to my empirical work" (Frank 2013, p 1174).

from parent to offspring. The third terms represents the "survival transmission", the change in genetic (6a) and non-genetic (6b) values that occur in parental individuals as they survive from one time step to the next. We can see how both types of inheritance interact with each other splitting the covariance term, visualizing frequency-dependent selection. Assuming that fitness w is a function of genetic and non-genetic components, that g and h are quantitative characters and their variation is relatively small[15], gives

$$\Delta\bar{g} = \sigma_{gg}\beta_g(\bar{g},\bar{h}) + \sigma_{gh}\beta_h(\bar{g},\bar{h}) + \frac{1}{\bar{w}}E(b\Delta g^b) + \frac{1}{\bar{w}}E(p\Delta g^p) \quad (7a)$$

$$\Delta\bar{h} = \sigma_{gh}\beta_g(\bar{g},\bar{h}) + \sigma_{hh}\beta_h(\bar{g},\bar{h}) + \frac{1}{\bar{w}}E(b\Delta h^b) + \frac{1}{\bar{w}}E(p\Delta h^p) \quad (7b)$$

where σ denotes covariance and β is the selection gradient. Thus, selection acts directly (first term eqn 7a) and indirectly (second term eqn 7a) on genetic components, as well as selection acts directly (first term eqn 7b) and indirectly (second term eqn 7b) on non-genetic components. Day and Bonduriansky use this model, and the mathematical framework (the Price equation), in order to develop several models focused on the evolutionary consequences of non-genetic inheritance. Assuming, for simplicity, non-overlapping generations –the third term, the "survival transmission", is zero–, one- or two-trait systems, and others simplifying assumptions, the Price equation takes different forms. For environmental noise, the Price equation becomes $\Delta\bar{z} = \sigma_{gg}\beta_g(\bar{g},\bar{h}) + \sigma_{gh}\beta_h(\bar{g},\bar{h})$. For maternal effects, it becomes two equations $\Delta\bar{g} = (\sigma_{gg} + \sigma_{gh})\beta_z$ and $\Delta\bar{h} = m\sigma_{zz}\beta_z + m\bar{z} - \bar{h}$. For indirect genetic effects there are also two equations, the second of which is $\Delta\bar{h} = m(\sigma_{gg} + \sigma_{gh})\beta_z + m\bar{g} - \bar{h}$. For transgenerational epigenetic inheritance, the Price equation becomes $\Delta\bar{g} = \sigma_{gg}\frac{s_g + k_h s_\varepsilon}{2\bar{b}} + \sigma_{gh}\frac{s_h}{2\bar{b}}$ and $\Delta\bar{h} = \sigma_{gh}\frac{s_g}{2\bar{b}} + \sigma_{hh}\frac{s_h + k_g s_\varepsilon}{2\bar{b}} + (1-\tau)(M - D)$.

Previously, Halanterä and Uller (2010) used the Price equation for classify different inheritance systems. Thus, they used the Price equation in a narrow way, as a meta-model, allowing comparison between different inheritance mechanisms and as a conceptual aid, discovering that different inheritance systems share features that are

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[15] Day and Bonduriansky use a first-order approximation for fitness as $w(g,h;\bar{g},\bar{h})/\bar{w} \approx 1 + \beta_g(\bar{g},\bar{h})(g - \bar{g}) + \beta_h(\bar{g},\bar{h})(h - \bar{h})$, where $\beta_j(\bar{g},\bar{h}) = (\partial w(\bar{g},\bar{h};\bar{g},h)/\partial j)/\bar{w}$ is the selection gradient on j.

conceptually very similar. On the other hand, Day and Bonduriansky used the Price equation in a more general way, as a generalization-sketch.

6.2. Stochastic evolution

Rice and collaborators (Rice 2008, Rice and Papadopoulus 2009) have developed a stochastic version of the Price equation. This new version treats individual fitness w, mean population fitness $\bar{w}$, and Δz (the difference between the mean phenotype of an individual's offspring and that individual's phenotype), as random variables, and expresses the expected change in mean phenotype as follows (Rice 2008; notation has been adapted)

$$\widehat{\Delta \bar{z}} = Cov(z, \widehat{\omega}) + Cov(\widehat{\Delta z}, \widehat{\omega}) + (\overline{Cov_\iota(\Delta z, \omega)} + \widehat{\widehat{\Delta z}}$$

$Cov(z, \widehat{\omega})$ is the covariance between the phenotype of an individual and the expected value of relative fitness[16]; $Cov(\widehat{\Delta z}, \widehat{\omega})$ is the covariance between the expected value of Δz in the population and the expected value of relative fitness; $(\overline{Cov_\iota(\Delta z, \omega)}$ is the average value of the covariance, across all possible outcomes, between random variables Δz and ω; and $\widehat{\widehat{\Delta z}}$ is the expected mean value of Δz in the population. If $\Delta z = 0$, we have the selection differential $Cov(z, \omega)$. Rice shows all moments of the individual fitness distribution since $\widehat{\omega}$ can be written as an infinite series. Substituting this result into the selection differential, for the first three terms in the expansion, gives:

$$\hat{S} \approx \frac{Cov(z, \widehat{w})}{H(\bar{w})} - \frac{Cov(z, var(w))}{N\widehat{w}^2} + \frac{Cov(z, \mu_3(w))}{N^2\widehat{w}^3}$$

where H is the harmonic mean and N the actual population size. This correspond to demographic stochasticity in a constant environment (i.e. the fitness values of different individuals are independent). These moments contribute to directional evolution: there is selection (first right-hand side term), a force pulling the population towards phenotypes with minimum variance in fitness (second term), a force pulling the population toward phenotypes with maximum skewness in fitness (third term). If environment change over time (random environmental change), then the expected

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[16] However, as $\bar{w}$ is a random variable correlated with w, ω does not scale like typical relative fitness.

fitness of individuals with a particular phenotype will itself vary over time. In a very large population, that yields this formula

$$\hat{S} \approx \frac{cov(z, \hat{w})}{H(\overline{w})} - \frac{cov\left(z, f_z var(\widetilde{w})\right)}{\widehat{\overline{w}}^2} + \frac{cov\left(z, f_z{}^2 \mu_3(\widetilde{w})\right)}{\widehat{\overline{w}}^3}$$

where f_z is the frequency of phenotype z in the population, and $\widetilde{w}$ is the expected fitness in the current environment of individuals with the same phenotype. Rice is able to predict new evolutionary processes with directional stochastic effects, because $\overline{w}$ is treated as a random variable, where the selection differential is very influenced by variations in the values of $\overline{w}$ (even in large populations). Previous studies, based on diffusion approximation, assumed that higher moments could be ignored. Rice's works shows, in contrast, that all moments contribute to directional evolution. Rice and Papadopoulus (2009) extend this approach considering an open population and treating migration as a random variable and not as a parameter. Following this path, Engen and Saether (2014) analyse how different forms of stochasticity –demographic and environmental stochasticity–, affects the selection differential. They develop different equations based on the Price equation. For example decomposing the selection differential in different parts (the mean value, environmental stochasticity, and demographic stochasticity) as $S = ES + \Delta S_e + \Delta S_d$; or deriving the vector response with fluctuating selection and random genetic drift, $R = GP^{-1}ES + GP^{-1}\Delta S_e + GP^{-1}\Delta S_d$. Engen et al. (2014) also provide an age-structured extension of the stochastic Price equation.

These different investigations (genetic and non-genetic inheritance, stochastic evolution) are good examples of how a generalization-sketch works. All these researchers started with a problem or question: How genetic and non-genetic inheritance can interact with each other and what are the evolutionary consequences? How stochasticity, in its many forms, affects the evolutionary trajectory of populations? Instead of appealing to a simplifying model, we start with the Price equation, and then we derive new equations. Subsequently, we develop different models in order to predict how a population would behave under different (simplifying) assumptions: non-overlapping generations, one- or two-trait systems, constant genetic variance, constant environment, large (infinite) population size, one-dimensional character, normally distributed phenotypes, Gaussian distribution, approximately linear terms, very small values, constant noise, and so on. Finally, we can also confront our theoretical results

with previous empirical research (Day and Bonduriansky 2011), computer simulations (Rice 2008, Rice and Papadopoulus 2009), or natural populations (as house sparrows from Norway; Engen and Saether 2014, Engen et al 2014). These researchers did not use the Price equation only as mathematical exercise in order to obtain, and unify, old results. In fact, they found previous results: Lande's work on expected fitness and fluctuating selection (Lande 2007); or Gillespie's results about stochastic variation among generations and within-generation variation (Gillespie 1974, 1977). Of course, these new alternative proofs for the same results indicate their validity and also their limitations. However, that was not the main goal. All these researchers used the Price equation as a generalization-sketch, as a starting point for the development of more detailed evolutionary equations.

7. CRITICAL VIEWS ON THE PRICE EQUATION

In this section I address some critiques on the Price equation pointed out by van Veelen (2005) and other authors (van Veelen et al. 2012, Nowak and Highfield 2011).

7.1. Tautologies and mathematics

Usually the Price equation is defined as a mathematical tautology. For instance:

"The Price equation did not, however, prove as useful as [Price and Hamilton] had hoped. It turned out to be the mathematical equivalent of a tautology" (Nowak and Highfield 2011, p. 100).

"[T]his equation [the Price equation] is simply a mathematical tautology for the relationship among certain quantities of populations. (…) the Price Equation is derived from, and is no more than, a set of notational conventions. It is a mathematical tautology" (Frank 1995, pp. 378–379).

"the [Price] equation is simply a mathematical tautology whose truth follows from the definition of the terms" (Okasha 2006, p. 24).

A tautology is a proposition represented by a tautological formula. Tautologies are universally true or logically true formulas. Although classical logic has several levels and we are able to define tautologies in all of them, propositional logic is where the

basic notion of tautology is founded. The components of a proposition are called atoms. A proposition is tautological if the truth values of their atoms make the proposition always true. There are various techniques for testing tautologies: truth tables, Beth's semantic tableaux. Therefore, tautologies are all those propositions that can be proved through logical procedures. For decades, logicians and mathematicians tried to prove that all mathematical truths were actually logical. Nevertheless, Gödel's incompleteness theorems proved that this was false. Roughly, Gödel's incompleteness theorems prove the impossibility of a complete formalization of arithmetic in an axiomatic consistent system and inference rules (Raatikainen 2015). Thus, mathematical propositions are not tautologies in a strict sense[17].

The term tautology highlights that the Price equation emerges directly from notational definitions rather than from model assumptions. It adopts a particular notation, and defines the resulting terms in such a way that the quantity on the left hand side is necessarily equal to the quantity on the right. This is the sense in which the term tautology is used by some researchers[18]. Van Veelen (2005) and other authors (van Veelen et al. 2012, Nowak and Highfield 2011) have stressed this feature as a drawback for the Price equation. This controversy has echoes of those disputes about the meaning of Newton's second law. Since it was formulated, Newton's second law produced a long term discussion among physicists and philosophers about its empirical value and ontological status (Sklar 2013, Barbour 2001). Some authors, like Daniel Bernoulli, claimed that it should be considered a description of empirical situations, being the second law a "contingent truth". Leonard Euler went further, trying to prove that this principle was a "necessary truth". Immanuel Kant tried to show that Newton's laws are a priori necessary truth. On the other hand, physicists like Pierre-Louis Maupertuis or Jean d'Alembert argued that the second law was simply a definition of force, since we cannot define forces independently of the law. Therefore, "if force was *defined* as the change of momentum that it produced, then Newton's second law would mean only that a change of momentum was proportional to a change of momentum –an obvious tautology" (Hankins 1990, p. 184). Hence accelerative force and motive force were just a name for acceleration and change of momentum, respectively. This line of thinking

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[17] Oddly, van Veelen et al (2012, p. 73) claim that any theorem is a tautology because they are analytical. However, that is not correct. Mathematical theorems are not tautologies, and not every analytical statement is a theorem or a tautology. Actually, Putnam (1975, chap. 4) argued that not all truths in mathematics are analytical as a result of Gödel's incompleteness theorems, so there must be synthetic truths in mathematics.

[18] Andy Gardner (personal communication), Samir Okasha (personal communication).

continued into the nineteenth century, where Gustav Kirchhoff and Ernst Mach defended the definitional or *tautological* status of Newton's second law because force is simply the product of the mass and the acceleration. Henri Poincaré, at the beginning of twentieth century, also defended that the second law was a definition, a *convention*, as concepts like force and mass were intrinsically linked. More recently, Frank Wilczek (2004, 2005) continues this approach, describing the second law as formally empty, since the force term has no independent meaning. Thus, there has been a long-term debate around the status of Newton's second law, if it is an analytic proposition or a synthetic one, necessary or contingent. One possible way to solve this conundrum is appealing to a Ramsey-Quine theoretical holism (see Sklar 2013, chap. 19, for details). This states that non-observational terms, like force, acquire their meaning in virtue of the role they play in the theory. This theoretical holism claims "that is theories that are the units of scientific meaning –not words and not individual sentences of the theory" (Sklar 2013, p. 227). Newton's second law needs to be embedded in a theoretical framework and therefore being interpreted, in order to acquire meaning[19].

The necessity, in general, of an interpretation for mathematical equations has been stressed by Millstein et al. (2009, p. 4): "it is a mistake to derive definitions from mathematics alone (…) since *many*, very different definitions can be derived from the same equation. Moreover, it is problematic to think that ontological questions about the causality (or lack thereof) of terms appearing in equations can be gleaned from the equations alone". Millstein et al. offer the following equation as an example: $(p + q)^2 = p^2 + 2pq + q^2 = 1$. This equation could represent the Hardy-Weinberg law. Recall (see section 2) that this law postulates a diploid and ideal infinite population, where there is random mating. For one locus and two alleles, *A* and *a*, with frequencies p and q respectively, the frequencies for the three genotype (*AA*, *Aa* and *aa*) are p^2, $2pq$ and q^2 respectively. However, the same equation could represent the area of a square with sides of length $p + q$, so its area is $(p + q)^2$. As the Hardy-Weinberg law, the equation represents a biological causal process: the consequence of a diploid sexual population under random mating. On the other hand the same equation represents a non-causal, purely mathematical, geometrical relationship[20].

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[19] "I've indicated how $F = ma$ acquires meaning trough interpretation –that is, additional assumptions about– F" (Wilzek 2005, p. 10).

[20] Actually, equation $(p + q)^2 = p^2 + 2pq + q^2$ is simply a *special product*, the square of a sum. Why mathematical truths, such as the square of a sum or Price's theorem, can represent a biological process?

In a similar line of argumentation, the Price equation acquires its meaning by virtue of the role it plays in a particular theoretical framework. We derived the Price equation in section 3 postulating a population. However, they do not have to be biological entities. Price himself emphasized that his equation could be used to describe the selection of radio stations with the turning of a dial (Gardner 2008). Actually, they do not have to be empirical objects or entities. We just stipulated a particular mapping between sets and their relationships. The Price equation takes (empirical) meaning when it is interpreted in a particular theory. A biological interpretation stipulates that our set is composed of individuals (a population) with particular traits, each with a value z, and these individuals have offspring with particular traits, each with a value z'. Rice (2004, p. 169) summarizes this biological interpretation through the following concepts: change over time, ancestor/descendant relations, and phenotype. In our world a population changes over time, it is possible to assign relations between ancestor and descendant, and we can identify the property of an individual (a phenotype) and represent it as a number. There is nothing a priori on these features. These concepts are empirically grounded. It is really no important if we arrive to the Price equation through a mathematical derivation, but how we interpret the symbols in the equation[21].

7.2. Predictive power

A repetitive critique to the Price equation is that lacks of dynamic sufficiency (Grafen 2000). A model is dynamically sufficient if it is capable of being iterated, predicting the state of the system at any time in the future (Lewontin 1974). In the case of evolutionary dynamics, knowledge of higher moments is required in order to make

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This is a metaphysical question. However, it is beyond the scope of this paper to solve this issue. An interesting proposal is French (2014).

[21] We can also derive mathematically, in a Price's equation way, Newton's second law as follows: Let the change of quantity of a body be Δb. This change is equal to an impulse I, where I is equal to a force F multiplied by the change of time Δt. Therefore, $\Delta b = I = F \cdot \Delta t$. We define the change of motion of body b as the product of its mass m and its velocity v, so $b = m \cdot v$. Now we can substitute, switching the order of the terms, and derive:

$$F \cdot \Delta t = \Delta b$$
$$F = \frac{\Delta b}{\Delta t}$$
$$F = \frac{\Delta(mv)}{\Delta t}$$

This is actually Newton's original formulation. It states that the change in motion is proportional to the motive force impressed. If the mass is constant, then $\Delta v / \Delta t = a$, where a is the acceleration. Therefore we obtain the familiar form, due to Euler, $F = ma$. Physics textbooks (Corben and Stehle 1994, p. 28; Goldstein et al 2000, pp. 1-2) introduce the second law in a very similar way (except they read it as the rate of the change in motion).

our model dynamically sufficient. Gardner and colleagues call this the *moment closure*, "where higher-order moments must be expressed in terms of lower-order moments" (Gardner et al 2007, p. 209). Since fitness in the Price equation is defined in terms of changes in frequency, we cannot use it in order to predict evolutionary trajectories beyond a single time step because we have not enough information of the next time step in order to iterate, i.e. applying the Price equation again –except if the entire distribution is defined only by the mean (Rice 2008). Nevertheless, as Steven Frank and other authors (Frank 1995, Frank 2012a, Gardner et al 2007) have already said in repeated occasions, dynamic sufficiency is a property that can be ascribed to the assumptions of particular models rather than the Price equation itself.

Van Veelen et al (2012) agree that the Price equation itself cannot be dynamically sufficient or insufficient, but models can be dynamically sufficient or insufficient. The core of the problem lies elsewhere. Van Veelen (2005) argues that there are two types of questions that theoretical biologists are interested in. Type 1 questions are top-down questions, starting with (simple) modelling assumptions and deducing the implications of the model. Type 2 questions are bottom-up questions, starting with an actual population and trying to figure out what model fits better to our data. Van Veelen claims that the Price equation cannot be used as a tool to response Type 1 questions, although many researchers use it in this way. The problem is not that the Price equation is a tautology –actually, it is not (see previous subsection)– but that it lacks of predictive power by itself, since it has no assumption in, and needs to be supplied by a model to produce predictions, so it cannot predict or explain anything. Therefore, if we can formulate a predictive model without the Price equation, in what sense this equation is helpful remains unsolved.

First of all, it is worth noting that predictive power is not the only possible explanatory value. Several philosophers of science (for example, Philip Kitcher (1993)) have claimed that there is also the explanatory value of unification, the systematization of different phenomena under common theoretical principles. In doing so, we usually "buy generality at the expense of predictive power" (Birch 2014, p. 400). In previous sections it has been showed that Price's equation fulfils this criterion. Turning to the subject of predictive power, van Veelen and colleagues are demanding too much to the Price equation. Generalization-sketches are, by themselves, empty in their predictive content. Take Newton's second law as an example. If you want to predict the trajectory of one or several bodies, you need to specify (with actual data, or assume if it is a

theoretical model) the features of the system, its constraints, the values of particular forces and masses, etc. In other words, it is necessary to specify a system with initial conditions (specify initial positions and initial velocities) as solutions of differential equations need to satisfy some boundary conditions, generally called initial conditions because time is usually the parameter. Without this additional information –specific system, initial conditions and particular forces, i.e. model assumptions– Newton's second law is useless from a predictive point of view, empty of any predictive power.

The Price equation is helpful because it works as a generalization-sketch. The advantages of working with a generalization-sketch have been explained in previous sections –unifying power, abstractness, theoretical common framework, theoretical progress, etc.– and it lead us to insights that special case models would not.

8. CONCLUSION

My aim in this paper was to show the special nature of the Price equation and the role it plays in evolutionary theory. I have argued that the Price equation has all the characteristics of a generalization-sketch: (i) it is a schema that allows for elaborating specific models with concrete symbolic expressions, (ii) it shares with other scientific principles such features like abstractness, unifying power and invariance, and (iii) many researchers are actually using it as a generalization-sketch. Understanding Price's equation in this way solves many problems stated by van Veelen and colleagues on the supposed role it plays in evolutionary theory. Furthermore, attributing this role to the Price equation –i.e. a generalization-sketch– favours a specific way of theorizing (an axiomatic or fundamentalist approach) in evolutionary biology and relates it with other generalization-sketches like Newton's second law of motion.

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