

# **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 and other evolutionary equations could be diverted. This move also links Price's equation with Newton's second law of motion, and therefore vindicates the Newtonian analogy.

**KEYWORDS:** Price equation, generalization-sketch, abstractness, unification, Newtonian analogy.

### **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 (see section 4)

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”<sup>1</sup>.

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 explains the key concepts it contains. Section 4 develops the idea of interpreting the Price equation as a generalization-sketch and its key features (abstractness, unifying power, invariance), explaining what special role play these sort of generalizations inside scientific theories. Section 5 exposes, firstly, the recent controversy surrounding the interpretation of Hamilton’s rule, and secondly how understanding the Price equation as a generalization-sketch helps to overcome the dispute. Section 6 argues that the Price equation follows a fundamentalist approach to theorizing, links it with Newton’s second law of motion, and therefore vindicates the Newtonian analogy.

## **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. 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<sup>2</sup>. The Hardy-Weinberg law

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<sup>1</sup> Structuralists (Diez and Lorenzano 2012) use the term “guiding principle”. I am not committed to the structuralism program and its formal apparatus.

<sup>2</sup> The allele and genotype frequencies must add to 1, respectively:  $p + q = 1$ , and  $p^2 + 2pq + q^2 = 1$ .

(Wakeley 2005) postulates six-dimensional space<sup>3</sup>: diploid organisms ( $D = 2$ ), infinite population size ( $N = \infty$ ), no mutation ( $u = 0$ ), no migration ( $m = 0$ ), no selection ( $s = 0$ ), and random mating ( $r = 1$ ).

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, that is, modifying the zero value for  $s$ , 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

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

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<sup>4</sup>. The transition matrix for  $i$  copies of  $A_i$  to  $j$  copies of  $A_j$  is given by:

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

And 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

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<sup>3</sup> Actually, Wakeley (2005) claims that there are five parameters, but I think migration should be also considered. So I introduce migration and I change parameters notation.

<sup>4</sup> The model make 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.

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 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. So diffusion theory makes a transition from discrete to continuous models when the population size tends to infinite ( $N \rightarrow \infty$ ). 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

$$\hat{\Psi} = C e^{-2N_e s p^2} (1-p)^{4N_e u_1 - 1} p^{4N_e u_2 - 1}$$

where  $C$  is a constant,  $s$  the selection coefficient,  $u$  the mutation rate, and  $N$  the 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 2012).

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 2012, 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  $i$ th 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:

$$\begin{aligned}
\Delta \bar{z} &= \bar{z}' - \bar{z} \\
&= \sum q'_i z'_i - \sum q_i z_i \\
&= \sum q'_i (z'_i - z_i) + \sum q'_i z_i - \sum q_i z_i \\
&= \sum q'_i (\Delta z_i) + \sum (\Delta q_i) z_i
\end{aligned}$$

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

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

This is the Price equation in its usual form in evolutionary literature. 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, it says nothing about what causes this covariance and, therefore, it applies equally to drift (Rice 2004). The second term on the right-hand side is the expected value (the average) of the quantity  $\Delta z$  weighted by fitness, that 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 are in our derivation, but we just stipulated a particular mapping between sets and their relationships. 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. 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, migration, etc.

What makes the Price equation so powerful is its abstract nature and that we can derive from it the relevant mathematical equations found in the last century. For example, the covariance term for quantitative traits was found 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,  $\bar{w}\Delta\bar{z} = Cov_{add}(w, z)$ . 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  $\bar{w}\Delta\bar{w} = Cov_{add}(w, w) = Var_{add}(w)$ .

It seems that the Price equation has a special status, different from the other equations used in evolutionary theory. I will argue in the next section that the Price equation is a “generalization-sketch”, in Kuhn’s terms (1970).

#### 4. THE PRICE EQUATION AS A GENERALIZATION-SKETCH

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  $f = ma...$ ] 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  $\frac{m_1 d^2 s_1}{dt^2} + k_1 s_1 = k_2 (d + s_2 - s_1)$ . 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).

Structuralists follow this idea as guiding principles and develop it with the notions of *specialization* and *theory-net* (Díez and Lorenzano 2012). It is quite natural that both philosophical traditions resort to classical mechanics and consider the second law of motion as the fundamental schema. 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 value of these generalization-sketches is to be 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. Thus, Newton's second law guarantees that if we have any mechanical problem, there are some dynamical equation for it based on forces, masses and accelerations; and push us to work hard to find them. So generalization-sketches play a heuristic role and work as an abstract formalism awaiting for empirical application. I claim that the Price equation possesses these features and plays this role in evolutionary biology.

#### **4.1. Abstractness**

All authors stress abstractness as the fundamental feature of the Price equation. This characteristic allows it to be applied to any population (from bacteria to humans), no matter their specific features. The Price equation works as a schema, or in Okasha's words: "So [the Price equation] it is not a model, but rather a schema that may be used to understand all other evolutionary models. [It is in recognition of this point that Rice (2004) deliberately talks about Price's *theorem*, rather than Price's *theory* (p. 68)]" (Okasha 2010, p. 426). More precisely, as a theorem the Price equation represents the consequence of particular mapping between sets and their relationships. The Price equation is a mathematical result or, in other terms, it is a mathematical identity. 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 and, therefore, not even considering it as a model. 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 (Sklar 2013, Barbour 2001). Some authors claimed that it should be considered a description of empirical situations while others, like d'Alembert and Mach, argued that



the second law was simply a definition of force (as we can find in some textbooks, see Corben and Stehle 1994, p. 28).

In this case, there is no doubt that the Price equation is a theorem and, therefore, a mathematical identity. But it should be noted that, although the Price equation is a mathematical identity and therefore it follows from the definitions of the terms (it is a mathematical result), its underlying concepts are empirically grounded. Rice (2004, p. 169) summarizes these concepts as: 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.

If I am right about the Price equation as a generalization-sketch, my approach may solve the problem set out by van Veelen and colleagues when they claim that the Price equation is not a model on its own. Actually, the Price equation is not a model, but a schema that provides a unifying framework in order to develop specific models. 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 exist, 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 arise only how to compute them when they are in a system.

#### **4.2.Unification**

From the Price equation we can obtain a great amount of important results in theoretical biology in the past century: Robertson and Fisher's theorems, the breeder's equation, etc. More important, if the Price equation play a role as a generalization-sketch, new forms could be found in order to resolve new specific problems. Actually, that is exactly what happens 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 elaborating specific models. In other words, the Price equation has become a generalization-sketch, a puzzles solver tool if the researchers are audacious and skilled enough to find some specific form for it. The Price equation has been applied for several disciplines briefly summarized<sup>5</sup> (for equations based on Price's equation see Tab. 1):

- *Selection processes.* Since its first formulation by Price, the Price equation has been directly connected and developed for natural selection models. In section 3 we have 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 2012); replicator-mutator equation, adaptive dynamics and evolutionary game theory (Page and Nowak 2002, Rice 2004); multilevel selection (Okasha 2006, Frank 2012, Gardner 2014); kin selection theory, inclusive fitness and Hamilton's rule (Frank 2013, Rice 2004, McElreath and Boyd 2007); and so on. Special mention deserves Grafen's long term work (Grafen 2007, for an outline), called "The formal Darwinism project". Grafen's 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 Papadopoulos 2009; but see also Grafen 2000) have developed a stochastic version of the Price equation that can deal with random

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<sup>5</sup> The most relevant bibliography is reviewed but not intended to exhaust it.

variables as stochastic fitness and stochastic migration, demographic stochasticity or random environmental change. Following this path, Engen and Saether (2013) 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.). 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, analyzing how cultural and genetic evolution interact but also differentiating each other.

These are some of the most important and interesting investigations, but not unique<sup>6</sup>, using the Price equation as cornerstone.

### **4.3. Invariance**

The Price equation shares with other scientific principles the feature of invariance or symmetry, the property of remaining unchanged under some transformation. For instance in Cartesian axes, for Newton’s laws of motion, we can shift a coordinate system to a new point or change the orientation of the axes, and the bodies motion will stay the same. Therefore Newton’s laws are invariant “with respect to translations (shifting of the origin) and rotations” (Barbour 2001, p. 30).

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 Fisher information (a measure of distance between two probabilities distributions) and Shannon information (entropy) with the properties of natural selection, and gives an

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<sup>6</sup> Other works are: Kerr and Godfrey-Smith (2009, extending the Price equation for migration); Gardner et al. (2007, relating multilocus population genetics and social evolution); Coulson and Tulkjapurkar (2008, extending the Price equation for 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.

expression of the Price equation in terms of Fisher information (see tab. 1). More recently, Frank (2012) 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 2012 for mathematical details). 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 2012, 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. All this infinite number of combinations equals the total quantity of selection, remaining unchanged, and so they are invariant. 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, therefore, being applied also for nonlinear processes.

Price equation in terms of Fisher information (Frank 2009)	$\dot{z} = \dot{z}_P + \dot{z}_{E P}$
Selection identities (Frank 2012)	$\begin{aligned} \Delta_s \bar{z} &= Cov(w, z) / \bar{w} \\ &= \bar{w} \beta_{zw} Var(w / \bar{w}) \\ &= \Delta \mathbf{q} \cdot \mathbf{z} \\ &= \ \Delta \mathbf{q}\  \ \mathbf{z}\  \cos \phi \\ &= \bar{w} \beta_{zw} (\Delta \hat{\mathbf{q}} \cdot \Delta \hat{\mathbf{q}}) \\ &= \bar{w} \beta_{zw} F(\Delta \hat{\mathbf{q}}) \end{aligned}$
Robertson's theorem	$\bar{w} \Delta \bar{z} = Cov_{add}(w, z)$
Fisher's theorem	$\bar{w} \Delta \bar{w} = Var_{add}(w)$
Breeder's equation (Frank 2012)	$R = Sh^2$
Path analysis (Frank 2012)	$\bar{w} \Delta \bar{z} = \beta_{wz} Var(z) + \beta_{wy} Cov(y, z)$
Replicator-mutator Price equation (Page and	$\dot{E}(p) = Cov(f, p) + E(\dot{p}) + E(f \Delta_m p)$

Nowak 2002)	
Hamilston's rule (Birch 2014)	$rb - c > 0$
Stochastic evolution (general equation) (Rice 2008)	$\widehat{\Delta\phi} = cov(\widehat{\phi^o}, \widehat{\Omega}) + \overline{cov}_l(\phi^o, \Omega) + \bar{\delta}$
Demographic stochasticity (Rice 2008)	$\hat{S} \approx \frac{cov(\phi, \widehat{w})}{H(\bar{w})} - \frac{cov(\phi, var(w))}{N\widehat{w}^2} + \frac{cov(\phi, \mu_3(w))}{N^2\widehat{w}^3}$
Random environmental change (Rice 2008)	$\hat{S} \approx \frac{cov(\phi, \widehat{w})}{H(\bar{w})} - \frac{cov(\phi, f_\phi var(\tilde{w}))}{\widehat{w}^2} + \frac{cov(\phi, f_\phi^2 \mu_3(\tilde{w}))}{\widehat{w}^3}$
Stochastic fitness and stochastic migration (Rice and Papadopoulus 2009)	$\widehat{\Delta\phi} = \left[ \left[ \overline{^a\phi^o}, \overline{^a\Omega} \right] + \ll \overline{^a\phi^o}, \overline{^a\Omega} \gg + \overline{^a\delta} + \ll \gamma, \bar{E} \gg + \bar{E}(\hat{\gamma} - \overline{^a\delta}) \right]$
Fluctuating selection and drift (Engen and Saether 2013)	$R = GP^{-1}ES + GP^{-1}\Delta S_e + GP^{-1}\Delta S_d$
Difference Ecosystem Function (Fox 2006)	$\Delta T = \bar{z}\Delta s + Sp(w, z) + \sum_i w_i \Delta z_i$
Collins/Gardner equation (2009)	$\Delta \bar{z} = E_l \left( E_{j_i}(\Delta z_{ij}) \right) + E_l \left( cov_{j_i}(w_{ij}, z'_{ij}) \right) + cov_l(w_i, z'_i)$
Genotype-Phenotype-Environment equation (Ellner et al. 2011)	$\frac{dX}{dt} = \frac{\partial X}{\partial z} \left( \frac{d\bar{z}}{dt} - E[\Delta z] \right) + \frac{\partial X}{\partial z} E[\Delta z] + \frac{\partial X}{\partial k} \frac{dk}{dt}$
The Price equation with mutation (Day and Gandon 2006)	$\dot{x} = cov(x, r) - \mu(\bar{x} - \bar{x}_m)$
The Price equation to multiple habitats (Day and Gandon 2006)	$\dot{x}^A = cov_A(x, r^{AA}) - \mu(\bar{x}^A - \bar{x}_m^A) + \frac{N_T^B}{N_T^A} cov_B(x, r^{BA}) + \frac{N_T^B}{N_T^A} r^{-BA}(\bar{x}^A - \bar{x}^B)$
Nongenetic inheritance Price equation (for overlapping generations) (Day and Bonduriansky 2011)	$\bar{W}\Delta \bar{h} = Cov(W, h) + E(b\Delta h^b) + E(p\Delta h^p)$
Interactions genetic and nongenetic inheritance (Day and Bonduriansky 2011)	$\Delta \bar{g} = \sigma_{gg}\beta_g(\bar{g}, \bar{h}) + \sigma_{gh}\beta_h(\bar{g}, \bar{h}) + \frac{1}{\bar{W}} E(b\Delta g^b) + \frac{1}{\bar{W}} E(p\Delta g^p)$
Epigenetic inheritance (Otsuka 2015)	$\Delta \bar{Z} = \frac{1}{\bar{W}} \beta [\sigma_A^2 + \sigma_{epi}^2] + v(\bar{E}_c - \bar{C})$
Maternal effects (Otsuka 2015)	$\Delta \bar{Z} = \frac{1}{\bar{W}} \beta [\sigma_A^2 + \sigma_m^2] + m(\bar{Z}_{GP} - \bar{Z})$
Niche construction (Otsuka 2015)	$\Delta \bar{Z} = \frac{1}{\beta \bar{Z} + R} (\beta + \lambda_2) \sigma_A^2$

Cultural Price Equation (El Moulden et al 2014)	$\Delta \bar{z} = cov(c, z) + E_c(\Delta z)$
The Price equation with migration (Kerr and Godfrey-Smith 2009).	$\Delta \bar{X} = cov(\tilde{C}_*^a, X^a) + ave((\Delta X)_d^a) - cov(\tilde{C}_d^*, X_d)$
Age-structured Price equation (Coulson and Tulkapurkar 2008)	$\Delta \bar{Z}(t) = \frac{Cov(D, R)(a, t)}{\bar{R}(a, t)}$

Tab. 1. Identities, derivations and extensions of the Price equation, respectively.

## 5. HAMILTON'S RULE AS A CASE

Hamilton's rule is an inequality developed by William Hamilton 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). Notwithstanding, Hamilton's rule and kin selection theory in general are recently under dispute because some authors like Nowak et al. (2010, p. 1059) claim that Hamilton's rule "almost never holds", while evolutionary biologists like Gardner et al. (2011) maintain a strong position for the correctness and the unrestricted applicability of Hamilton's rule.

In a recent paper, Birch (2014) argues that discussions about Hamilton's rule arise because there are two possible versions of it. One version comes from evolutionary game theory, and is based on the one-shot two-players Prisoner's Dilemma (van Veelen et al. 2012). Birch labels it as the special version of Hamilton's rule (HRS), and is characterized by its simplifying assumptions. A consequence of these simplifications is that the applicability of HRS is constrained to very specific cases and cannot handle more complicated ones (for example, when the frequency of cooperators matters). Is in this sense that Nowak and collaborators claim that Hamilton's rule "almost never holds". The other version comes from the Price equation (Frank 1998). It is not tied to any simplifying assumption and fits to any social behaviour system because it follows a priori from the Price equation. Birch labels it as the general version of Hamilton's rule (HRG). It is this version that Gardner and collaborators have in mind when they defend the generality of Hamilton's rule. Here is the problem: if HRG is always true then it is difficult to see how Hamilton's rule keeps its explanatory power (Gardner and

colleagues' aim); and if we are content with HRS then we lose predictively power because it is not widely applicable.

Nevertheless, thinking of the Price equation as a generalization-sketch may clarify this issue. The question is how HRG, which derives directly from an abstract mathematical theorem, can give us any details about which particular social behaviour will evolve by natural selection. The answer is clear: it cannot. The reason is that HRG is a derivation of the Price equation and plays the same role as a generalization-sketch, except that in this case it is applied to social behaviour. In other words, no empirical information is supplied by HRG, only says that a social behaviour will be favoured by natural selection when  $rb - c > 0$ . Put another way: if there is some social trait in a population, look for the genetic relatedness of the recipient to the actor, the benefits to the recipient, and the costs to the actor. If these relations are greater than zero (they are positive) then natural selection favoured this trait in the population. This is how a consequence law works. But the source of these relations will be related to specific populations (paper wasps, meerkats, ground squirrels, prairie dogs, etc.), and concrete predictions will be provided by specific models and, therefore, subject to simplifying assumptions. HRS is precisely a specific model subject to simplifying assumptions and then it only makes valid predictions in particular situations. Birch detects these two different roles played by HRG and HRS when he says: "We therefore face a trade-off. By construing Hamilton's rule as HRG rather than HRS, we buy generality at the expense of predictive power" (Birch 2014, p. 400). On the other hand, other HRG's characteristic, detected by Birch but omitted by Nowak and colleagues, is the explanatory value of unification: "HRG constitutes a unifying principle: a means of bringing together results from disparate models under a single conceptual framework".<sup>7</sup> This unifying power of the Price equation, and then also of HRG, has been stressed in the present article as one of its key features.

However, the problem is that, if we are seeking the most general framework for all the processes of social evolution under natural selection, it seems that it would be better to use Robertson's theorem of natural selection. My reply is different from Birch and is based on the hierarchical structure view of the theory. HRG is derived from the Price equation firstly by leaving aside the second term, and resting only the covariance term. As we have seen in section 3, the covariance term was developed by Robertson

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<sup>7</sup> Birch 2014, p. 401. Kitcher (1993, chap. 2) underlined the unifying power of the theory of natural selection as its greatest explanatory value.



and it is known as the secondary theorem of natural selection. So it is true that Robertson's theorem is more general than HRG, but HRG is a special form of this theorem focused on the evolution of social behaviour. Robertson's theorem tells us when a trait, in general, will be favoured by natural selection, whereas HRG tells us when a social trait will be favoured by natural selection. Thus, if we are focused on social behaviour, using HRG is sufficient to produce specific models.

## **6. A FUNDAMENTALIST APPROACH**

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 Papadopoulos (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)<sup>8</sup>. 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.

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. When a special model is formulated, simplifying assumptions are necessary for acquire predictive power or dynamic sufficiency, but these simplifications come at the end of the theoretical work, and not at the beginning.

### **6.1. The Newtonian analogy vindicated**

Textbooks and most of the evolutionary literature talk about evolutionary forces acting on a population (Gillespie 2004, Templeton 2006). Sober (1984) developed this

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<sup>8</sup> The aim of Water's article is to show that Okasha's book (2006) favours a "toolbox view" (which aim is finding partial descriptions and denies a unique correct description) based in his analysis on multi-level selection and the appropriateness of the Price equation versus Contextual analysis, although Okasha devoted the first chapter of his book to the benefits of Price's equation (Okasha 2011 for a reply). However, there is no confrontation between the Price equation and contextual analysis because the latter is a form of path analysis which "follows as a natural extension of the Price equation (...) It does not make sense to discuss the Price equation and path analysis as alternatives" (Frank 2012, p. 1014).

point of view according to which evolutionary theory is a theory of forces in the same way that different forces of Newtonian mechanics cause changes in the movement of bodies, because evolutionary forces cause changes in trait frequencies. A lively debate about the appropriateness of the forces analogy has been developed in the last decade (Matthen and Ariew 2002, Hitchcock and Velasco 2014). I think that most of these attacks to the Newtonian analogy have been positively answered so, I will not go into detail about them. Rather I want focus on a particular contention on the force interpretation since Sober formulated it: that evolutionary theory does not contains any law or equation comparable with Newton's second law of motion. Thus, only two years after the publication of Sober's book, John Endler wrote:

“First, if natural selection is a “force,” what is it acting on? (A force is meaningless without an object). If natural selection were a force, it should be possible to decompose it into a mass and an acceleration. In this case “acceleration” is phenotypic selection, but what is the “mass”? The “mass” could be a frequency distribution or the genetic system (condition c, inheritance), but this is tantamount to assuming that natural selection applies only to groups. Natural selection arises from biological differences among individuals (condition b, fitness differences); therefore to make a proper analogy, the “mass” is the genetic composition of an individual. This is reasonable because it also allows mutation to be a “force”. But the “mass” in the physicist's  $F = ma$  is a class of objects with defining properties and not an individual, so the analogy either breaks down or restricts natural selection to group selection” (Endler 1986, p. 31).

And most recently,

“[T]he Newtonian analogy does not work (...) We do not build evolutionary models by beginning an analog of the force equation expressing Newton's second law of motion ( $\vec{F} = m\vec{a}$ , where  $\vec{F}$  is the force,  $m$  is the mass, and  $\vec{a}$  is the acceleration) and substituting for the force term” (Sarkar 2011, p. 464).

Nevertheless, the present article demonstrates that evolutionary theory counts with an equation comparable to Newton's second law of motion. Both equations share several key features like abstractness, unifying power, and invariance. In turn, the Price equation and the second law of motion work as consequence laws, computing all possible causes in a common framework in evolutionary theory and in Newtonian mechanics, respectively. Actually both equations share a family resemblance, for example in cases of equilibrium. When two evolutionary forces, represented by the

covariance term and the expected term respectively, are acting upon a population with equal magnitude but opposite sign, we obtain  $\bar{w}\Delta\bar{z} = 0$ , i. e.  $-E(w\Delta z) = Cov(w, z)$ . In the same way, when two forces ( $F1$  and  $F2$ ), are exerted on a body with the same magnitude but opposite sense, we have  $0 = m \cdot a$ , i. e.  $F2 = -F1$ . This shows that, contrary to Endler and Sarkar's claim, evolutionary forces can be expressed by covariance and expectations and not as a clumsy copy of Newton's second law through masses and accelerations. It is fair to say that this kind of model building with the Price equation, in a way analogous to the second law of motion, is relatively recent<sup>9</sup>. In this line, the effort of Steven Frank (1995, 1997) to spread Price's work was crucial. This shift is an issue for sociology of science and that question goes beyond the purview of this paper, but I guess that the initial dismissal of the Price equation lies probably in the reluctance of many (field) biologists on mathematical works (a complaint supported by Grafen (2007)). Be that as it may, the present article and the works cited show that many evolutionary biologists have taken the Price equation as a unifying framework, in a similar way as physicists in the eighteenth century took Newton's second law of motion. van Veelen and colleagues (2010, 2012) repeatedly complained that the Price equation is usually considered by many evolutionary biologists as  $E = mc^2$  is considered by physicists; rather the Price equation is like Newton's second law.

## 7. 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, and also with other related equations like Hamilton's rule. 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

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<sup>9</sup> Although, early approaches were developed by Hamilton (1970, 1975), Seger (1981), Grafen (1985), and Wade (1985), among others.

generalization-sketches like Newton's second law of motion. This is a case, in the end, for vindicating the Newtonian analogy.

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