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ORIGINAL ARTICLE

The Value of Price

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Abstract

The Price equation provides a comprehensive representation of evolutionary processes. Since its original formulation by George Price, it has been used to model a variety of phenomena in quantitative genetics and related fields. However, there is no consensus on the explanatory power of the equation. In this article we aim to clarify its place within modern evolutionary theory. To this end, we first state the basic concepts from which the Price equation can be derived as a theorem. From this axiomatization, we conclude that the Price equation is not explanatory in itself. It merely provides a phenomenological description of evolutionary processes. We argue that its role is analogous to that of Galilean kinematics in classical mechanics. Both the Price equation and Galilean kinematics function as conceptual frameworks that define the basic features of the behavior of a class of systems. Practitioners are encouraged to theorize further on these frameworks to find the possible explanation of this behavior in various specific scenarios. Thus, despite its phenomenological character, the Price equation integrates different fields of evolutionary biology by providing a common formalization of their shared explanandum.

Keywords Explanation · Kinematics · Price equation · Population thinking · Theorization

Introduction

In recent years, the Price equation has been widely used in a number of fields, including, of course, evolutionary theory (e.g., Rice 2004; Frank 2012; Walsh and Lynch 2018) and especially social evolution theory (e.g., Frank 1998; Marshall 2015; Lehtonen 2020), but also ecology (e.g., Fox 2006; Govaert et al. 2016), epidemiology (e.g., Alizon 2009; Day et al. 2020), cultural evolutionary theory (e.g., El Mouden et al. 2014; Aguilar and Akçay 2018), behavior and individual learning (Borgstede and Luque 2021), evolutionary computation (Altenberg 1995), and even economics (Andersen 2004) and physics (Gardner and Conlon 2013).

Given this wide range of applications, it is perhaps surprising that there is no consensus on the theoretical and explanatory value of the Price equation. On the one hand, there are a number of authors who welcome the Price equation as the missing keystone in the edifice of evolutionary biology (Frank 2012; Luque 2017; Queller 2017; Lehtonen 2018; Luque and Baravalle 2021; Baravalle and Luque 2022). These authors emphasize, among other things, that the Price equation is a fundamental equation from which we can derive all the most important equations of evolutionary biology, such as Fisher's fundamental theorem, the breeder's equation, Robertson's theorem, mutation and recombination equations for haploid and diploid models, and so on. According to this view, the Price equation would be both the most general way of representing evolutionary processes and a valuable tool for discovering the causes of evolution in specific scenarios. On the other hand, there is a group of authors (van Veelen 2005, 2020; Nowak and Highfield 2011; van Veelen et al. 2012) who are very skeptical about

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both of these claims. For them, the Price equation is merely a mathematical identity or a tautology, devoid of empirical meaning and ultimately useless for explaining or predicting evolutionary dynamics.[1]

Some of those who defend the theoretical and explanatory value of the Price equation (Frank 2012; Luque 2017; Luque and Baravalle 2021; Baravalle and Luque 2022) argue that "empirical emptiness" is something that most fundamental laws in science—such as Newton's second law, Schrödinger's equation, or Einstein's equations of special and general relativity—have in common. The abstractness of such principles makes them a kind of "conceptual precondition" for research in the field in which they are considered fundamental laws, even if their empirical content is limited. According to Luque and Baravalle (2021), the abstractness and partial emptiness of the Price equation are qualities rather than defects. It is precisely because of these features that the equation can be applied in such a versatile way in different contexts and evolutionary scenarios. Price's formalism provides a unifying framework for all theoretical projects that aim to describe a dynamical process in evolutionary terms. It provides a general partition of the possible causes of evolution (i.e., sorting processes and transmission biases) by statistically characterizing their effects on the composition of a population. The explanatory power of the Price equation stems from its ability to serve as a basis for deriving additional equations that offer more concrete and accurate descriptions of evolutionary dynamics within specific domains. These "Price-like equations" modify the original equation to make explicit, in statistical or causal (probabilistic) terms, the influence of particular evolutionary causes (e.g., different types of selection, genetic drift, alternative inheritance channels) in real-world populations.

Despite the above, van Veelen (2020) raises doubts about the explanatory value of most applications of the Price equation to concrete scenarios. In his view, the equation is empirically meaningful only under very restrictive conditions. This requires the Price equation to be combined with other models that can be derived independently. According to van Veelen, these models can describe evolutionary change just as well *without* the Price equation. This would be evidence that the equation, due to its putative tautological status, adds little or nothing to our theoretical knowledge of evolutionary processes. Moreover, van Veelen argues that when the Price equation is taken to have empirical content, as when it is used to derive Hamilton's rule to demonstrate that group selection and inclusive fitness are equivalent, it performs poorly in accounting for empirical data and provides a misleading picture of evolutionary processes.

The debate seems to have reached a stalemate in which the proponents of the Price equation—strengthened by the recent boom in the use of the equation to represent and model a variety of evolutionary phenomena—seem to have a prima facie good case for its importance, while the skeptics deploy new arguments to undermine their optimism. In our view, a conciliatory solution necessarily involves clarifying the allegedly tautological nature of the Price equation. Is the Price equation really "devoid" of empirical meaning? If not, what is its empirical content? What exactly do we mean when we say that we "derive" other equations from it? Only by answering these preliminary questions, will we be able to reconsider the theoretical and explanatory value of the Price equation. One of the goals of this article is, therefore, to make the metatheoretical language we use to speak about the Price equation more precise. We will talk about notions like tautologicity, derivability, and so on using their precise technical meanings. Since much misunderstanding has arisen from the vague use of these notions, our hope is that these clarifications can move the discussion forward.

To this end, we proceed as follows. First, in the second section, we provide a formal reconstruction of the conceptual framework from which the Price equation can be derived as a theorem. We call this framework the "Pricean framework." By itself, the Pricean framework has little explanatory power, although it is not tautological in the precise sense of logic (i.e., it is not a set of logical truths). In the third section, we draw an analogy between the Pricean framework and Galilean kinematics. We argue that they play similar roles in their respective domains. Both provide phenomenological descriptions of a particular domain of phenomena. Both are explanatorily weak in the sense that they need to be supplemented by further assumptions in order to explain the causes of concrete phenomena. Nevertheless, both are conceptually invaluable because they provide a solid basis for *theorization*. Theorization is, in formal terms, the enrichment of an existing set of axioms or definitions with new concepts. These new concepts are intended to provide an explanation of the behavior of the system described by the original set of axioms or definitions. Thus, Newtonian mechanics enriches Galilean kinematics with the concepts of mass and force, and in this way it enables causal explanations of motion (i.e., it endows Galilean kinematics with *dynamical* properties). Similarly, as we argue in the fourth section, Price-like equations theorize on the Pricean framework by introducing new concepts intended to explain the behavior of populations represented by the original Price equation.

From this picture we can draw a number of interesting considerations, which we discuss in detail in section five. First, we can reassess some of the positions involved in the

[1] Van Veelen (2020, p. 3), for instance, states: "The two aspects of the Price equation that are usually appreciated the most are its generality, and the fact that it is a tautology.".

debate over the value of the Price equation in evolutionary biology. On the one hand, the defenders of the equation are right to stress its importance, but wrong to give it the status of a fundamental law. The skeptics, on the other hand, are wrong to portray it as trivial or tautological, but they are right to denounce that without a proper interpretation of its formalism it can lead to misleading results. Second, as a result of our analysis, we can better understand the role of the Price equation within evolutionary biology. In a sense, we argue, the Price equation is a rigorous characterization of what some authors have called "population thinking" (e.g., Mayr 2004; Sober 1980; Ariew 2008). Since it is not an explanatory principle, it is probably incorrect to characterize it as capable of "unifying" all evolutionary theories. Nevertheless, because of its kinematic features, it can be praised for its integrative role.

A Formal Reconstruction of the Price Equation

A classical way to clarify the metatheoretical status of a scientific hypothesis, model, or theory is to provide a formal reconstruction of it. There are already several (formal and informal) accounts of the Price equation in the literature (see, for example, Rice 2004; Okasha 2006; Frank 2012; Luque 2017; Walsh and Lynch 2018).[2] However, none of them aims to show precisely how the equation can be derived as a theorem from a given set of axioms. Since a proposition deductively derived from others has no more empirical content than the set of propositions from which it is derived, understanding what this derivation consists of is fundamental to discussing the nature of the Price equation. Moreover, once we have a formal representation of the basic Price equation and some Price-like extensions, it will be easier to determine the precise kind of relation that exists between them—later we will argue that "derivation" is not the correct term to describe this relation. Thus, in the remainder of this section, we offer a sketch of a formal reconstruction of the basic Price equation.

To begin this task, it is crucial to specify the formal language we will be working with, along with the intended interpretations of the vocabulary items. The most basic form of the Price equation works by considering two generations of the same population. Thus, we have two non-empty sets, P and O, representing the parent and offspring populations.[3] These populations are linked such that members of the offspring population are descendants of individuals in the parent population. To represent this, we introduce a function a, which takes an offspring as argument and returns its immediate ancestor (i.e., its parent; for simplicity, we assume that each child has exactly one parent). Formally, $a: O \to P$.

We also need to consider a character or trait type, which we denote by a set Z whose members ($z_1, \ldots, z_n$) are the possible states of that character—as usual, we represent states by real numbers (i.e., $Z \subseteq \mathbb{R}$). Each individual (in both the parent and offspring populations) is assigned a state in Z via a function z. That is, formally, $z: P \cup O \to Z$. So, for example, if the trait Z (say, flower color) has two possible states 0 and 1 (say, purple and white flowers, respectively) and parent p_1 has white flowers, we would express this by saying that $z(p_1) = 1$.

These are all our primitive concepts, namely P, O, a, Z, and z. We will also need some mathematical and defined concepts on top of them. First, we can define a function $d: P \to \wp(O)$ that, for a given parent, returns the set of its immediate descendants (i.e., a descendant o belongs to $d(p)$ if and only if $a(o) = p$). This allows us to define the *realized* fitness of an individual in the parent population as the number of offspring the individual has (it is important not to confuse this with the explanatory concept of *fitness* from the theory of natural selection; see section four below). Formally, we represent this by a function w, defined as follows: $w: P \to \mathbb{N}$ such that $w(p) = |d(p)|$. We will also use various averages; for example, $z\Delta(X) = \frac{\sum_{x \in X} z(x)}{|X|}$ will be the average value of trait Z for a set X of individuals. Similarly, $\overline{w}(X) = \frac{\sum_{x \in X} w(x)}{|X|}$ will denote the average realized fitness (i.e., the number of children) of a set of parents X.

For a given parent p, the difference between the average trait of its offspring and its own trait is denoted by $\Delta z(p)$, which is equal to $\overline{z}(d(p))$—$z(p)$. Finally, at the population level, the difference between the average offspring trait and the average parent trait is denoted by $\Delta\overline{z} = \overline{z}(O)$—$\overline{z}(P)$.

[2] A generalized version of the Price equation that takes into account open populations has been derived by Kerr and Godfrey-Smith (2009). In this article, we focus on the original Price equation because it has been at the center of the disputes between its defenders and critics. Our main results also apply to Kerr and Godfrey-Smith's equation.

[3] For simplicity's sake, we assume that the populations are finite. However, the framework and the derivation seem to work equally

Footnote 3 (Continued)

well with at least some cases of infinite populations. Andy Gardner (personal communication, 18 September 2023) suggests the following example. Let us assume that we have an infinite number of parents. All odd-numbered parents have trait value 0 and fitness 0 and all even-numbered parents have trait value 1 and fitness 2. Then we can apply Price's equation to see that selection will act so as to increase the average trait value by 1/2 between parent and offspring generations.

To recapitulate, we have a language which (including the defined terms) consists of $\langle P, O, a, Z, z, d, w, \overline{z}(X), \overline{w}(X), \Delta z(x), \Delta\overline{z}\rangle$, and the following axioms (including the defined concepts, from 6 on)[4]:

(1) P is a non-empty set [parent population]
(2) O is a non-empty set [offspring population]
(3) $a: O \rightarrow P$[immediate ancestry function]
(4) Z is a non-empty subset of $\mathbb{R}$ [character and its states]
(5) $z: P \cup O \rightarrow Z$[state of an individual]
(6) $d: P \rightarrow \wp(O)$, such that $o \in d(p)$ iff $a(o) = p$ [descendants function]
(7) $w: P \rightarrow \mathbb{N}$, such that $w(p) = |d(p)|$ [realized fitness]
(8) $\overline{z}: \wp(P \cup O) \rightarrow \mathbb{R}$, such that $z\Delta(X) = \frac{\sum_{x \in X} z(x)}{|X|}$ [average character of a set]
(9) $\overline{w}: \wp(P) \rightarrow \mathbb{R}$, such that $\overline{w}(X) = \frac{\sum_{x \in X} w(x)}{|X|}$ [average realized fitness]
(10) $\Delta z: P \rightarrow \mathbb{R}$, such that $\Delta z(p) = \overline{z}(d(p)) - z(p)$[parent–offspring change in trait]
(11) $\Delta\overline{z} = \overline{z}(O) - \overline{z}(P)$[population-wide change in trait]

Note that axioms (6)–(11) are explicit definitions—again, in the technical sense of statements that provide both necessary and sufficient conditions for the application of some term. Syntactically, this can be seen from the fact that they are either biconditionals or equalities (depending on whether the definiendum is a sentence or a term). So, for instance, if the denotation of P is given, then axiom (7) restricts the possible interpretations of w to a single one. In this sense, w, like all defined concepts, is eliminable, since one can replace each of its occurrences with its definiens (though it may still make sense to keep it for pragmatic reasons). This is not the case with axioms (1)–(5), which are not definitions. Take for example, axiom (3). It states that a is a function from O to P; that is, that a is a relation that satisfies the existence and uniqueness requirements (i.e., each member of O is assigned one and only one member of P). This excludes, for example, that a member of O has no member of P assigned by a (under the intended interpretation, that an organism is spontaneously generated in the offspring population). But given an interpretation for the sets P and O, there are (formally) multiple ways to satisfy that criterion. This means that a (and the concepts that we called primitive above) is not eliminable without loss.

As can be seen from the above, this is a phenomenological theory in the sense that it does not introduce explanatory concepts, but simply provides tools for describing variations in the frequency of a trait state. This is done by focusing on a population of token individuals (usually organisms), rather than on types of traits (as it is usually the case in more traditional population genetics approaches; see Gardner 2020, p. 4). Moreover, the theory imposes almost no empirical constraints on the phenomenon being modeled, since it is compatible with any distribution of traits between successive generations. We can express this point by saying that the set of axioms 1–11 is "empirically weak."

What we want to emphasize here is that the above axioms, although phenomenological and empirically weak, are all that is needed to derive the Price equation. The derivation of the equation from these axioms is as follows. First, note that O is nothing more than the union of subpopulations composed of the offspring of each parent in P (Okasha 2006, p. 20). The average trait in each subpopulation is $\overline{z}(d(p))$. The contribution of each subpopulation to the average trait in O is given by $\frac{w(p)}{\overline{w}(P)}$. So we have that:

$$\overline{z}(O) = \frac{\sum_{p \in P}\left(\frac{w(p)}{\overline{w}(P)}\overline{z}(d(p))\right)}{|P|}$$

This states that the average offspring trait is equal to the contribution that each parent makes to that trait average through the set of its children.

The rest are simple mathematical transformations. By axiom 11 we have that:

$$\Delta\overline{z} = \overline{z}(O) - \overline{z}(P)$$

Applying the above result on the first term of the right side and the definition of $\overline{z}(P)$ on the second term (axiom 8):

$$\Delta\overline{z} = \frac{\sum_{p \in P}\left(\frac{w(p)}{\overline{w}(P)}\overline{z}(d(p))\right)}{|P|} - \frac{\sum_{p \in P} z(p)}{|P|}$$

If we multiply both sides by $\overline{w}(P)$, we get:

$$\overline{w}(P)\Delta\overline{z} = \frac{\sum_{p \in P} w(p)\overline{z}(d(p))}{|P|} - \frac{\sum_{p \in P} \overline{w}(P)z(p)}{|P|}$$

Using the equality $\overline{z}(d(p)) = z(p) + \Delta z(p)$ (derived from axiom 10):

$$= \frac{\sum_{p \in P} w(p)(z(p) + \Delta z(p))}{|P|} - \frac{\sum_{p \in P} \overline{w}(P)z(p)}{|P|}$$

Separating the sum on the left:

$$= \frac{\sum_{p \in P} w(p)z(p)}{|P|} - \frac{\sum_{p \in P} \overline{w}(P)z(p)}{|P|} + \frac{\sum_{p \in P} w(p)\Delta z(p)}{|P|}$$

Taking $z(p)$ as the common factor in the two terms on the left:

[4] Axioms (8) and (9) (i.e., the definitions of the averages) belong to the underlying mathematical apparatus and are thus not strictly necessary in the presentation of the Pricean framework. We choose to include them in order to make explicit what concepts are necessary for deriving the Price equation.

$$= \frac{\sum_{p\in P} z(p)\big(w(p) - \overline{w}(P)\big)}{|P|} + \frac{\sum_{p\in P} w(p)\Delta z(p)}{|P|}$$

And this is the Price equation in algebraic form, which in its usual statistical notation looks as follows[5]:

$$\overline{w}(P)\Delta\overline{z} = Cov(w(p), z(p)) + E(w(p)\Delta z(p))$$

As mentioned in the introduction, we will sometimes refer to the above set of axioms as the Pricean framework, while reserving the terms "equation" and "theorem" for the usual Price equation (the proposition derived from the axioms).

The Value of Kinematics

Since the Price equation follows from the axioms presented in the previous section, the question about the metatheoretical nature and empirical content of the equation should be transferred to questions about the metatheoretical nature and empirical content of the axioms. And that is why it is useful to have such axioms clearly reconstructed.

Of course, taken in isolation—that is, purely formally, without any indication of their intended interpretations—these axioms have no empirical content. But this is trivially true of the axioms of any formalized hypothesis, model, or theory. If one takes the formalization of the axioms of, say, classical mechanics, and strips the concepts of their intended interpretations, then one is left with a formalism that says nothing about any part of the empirical world. It is precisely the fact that the axioms *have* intended interpretations that makes them empirical. The fact that the Price equation talks about what happens to *members of two populations* which are *related by reproduction and/or persistence*, and which *have states of a certain character*, means that it is an empirical claim (however weak it may be; more on this below). Those who point out the lack of empirical content of the Price equation cannot simply be arguing that mathematical equations by themselves (without their intended interpretations) have no empirical content. Otherwise, no mathematized theory in the empirical sciences would have empirical content.

Something similar must be said about the claim that the Price equation is tautological. A tautology, in the technical sense, is a statement that is *logically* true, that is, derivable from the axioms of logic alone.[6] One can immediately see that none of the above axioms is tautological, since none of them is a logical truth, derivable from the axioms of logic. Nor are they theorems of some mathematical theory—i.e., the Price equation is not simply applied mathematics. Since the usual charge is about tautologicity, let us expand a bit more on this.

That the axioms of the Pricean framework are not tautologies does not mean that the Price equation itself is not a tautology, since one can derive tautologies from non-tautological propositions. But notice two things. First, if the axioms were tautologies, then this would imply that the Price equation would necessarily be a tautology, since one can only derive tautologies from other tautologies. The fact that they are not eliminates a possible argument for the tautologicity of the Price equation. Second, tautologies can be derived without any premises (other than the axioms of logic), which is not the case here. If the Price equation were a tautology, no non-tautological premise would be required for its derivation. The axioms we have presented (or some equivalent) are necessary to derive the result, which means that the Price equation cannot be tautological.

The axioms of a theory can be considered stipulative in the sense that they characterize a system or set of systems by specifying how it behaves (this is what all axiom systems do). But a logical truth and this type of characterization are two different things. While a logical truth trivially holds in every possible scenario, the systems characterized by axioms either do or do not represent specific real-world cases. Accordingly, the Pricean framework specifies a set of conditions that a set of entities and their relations must satisfy—e.g., be divisible into parental and filial generations, have an ancestry relation between individuals that is constrained in certain ways, and so on. It will make sense for *some* empirical phenomena to be represented as instances of the above framework (e.g., biological populations, paradigmatically), when they satisfy those conditions, but not for others. This is something to be determined empirically. The half-factual

[5] According to some authors (van Veelen 2005, 2020; van Veelen et al. 2012), this last step involves not only an algebraic manipulation, but also the introduction of further—possibly unwarranted—statistical assumptions. Whether or not this is the case in other formalizations of the Price equation is a matter on which we take no position. Note, however, that in our present characterization, *Cov* and *E* are merely notational abbreviations that do not imply any conceptual enrichment. Additional statistical assumptions might be actually at play when the covariance term is interpreted—as it usually is—as identifying the effects of selection in concrete scenarios (see sections below). Whether or not these assumptions are warranted should be judged on a case-by-case basis, depending on the specific applications, consistent with the piecemeal approach to theorization that we present in the following sections.

[6] Note that mathematical statements such as "2 + 2 = 4" or "the internal angles of a triangle sum to 180°" are not tautological in this sense (at least if the logicist project in the foundations of mathematics is considered to have failed). Different questions are whether they are analytic (if one accepts that distinction), whether they have empirical content, or whether they are useful in general. We believe that when critics like van Veelen call the Price equation tautological, they are referring to this last question, and we will turn to this issue later on. Here, since (as said in the introduction) we are trying to be maximally precise with our use of metatheoretical language, we refer to the precise logical notion of tautologicity.

and half-stipulative character of scientific laws has been pointed out countless times (Nagel 1961; Balzer et al. 1987; Friedman 2001; Kuhn 2022). The factual character of these statements arises from the empirical constraints they impose on the relevant phenomena, while their stipulative character stems from their role in defining the meaning of certain concepts by providing criteria for their application. If the Price equation has any peculiarity, it cannot be this.

In our view, the most noticeable aspect of the Price equation as we have presented it is that it is very close to a description. That is, it arises from the mere presentation of the relations between the phenotypic composition of an offspring generation and a parental generation, without any explanation of what causes the parents to reproduce as they do, or the traits to be inherited as they are (or are not). This is in tension with the role that many have assigned to the Price equation as a very general law that provides the backbone for much of evolutionary biology. From our point of view, it is necessary to reconsider this position. This can only be done by first gaining a better understanding of the role that phenomenological theories can play within a discipline. As we anticipated in the introduction, our main thesis is that the Pricean framework is similar to Galilean kinematics, which can be seen as another example of a phenomenological theory. The reason why the Pricean framework and the Price equation seem trivial to some authors is the same reason why any kinematics, taken in isolation, seems so. Galilean kinematics tells us that certain particles move in space with certain velocities, accelerations, and so on, but it does not tell us *why*. Similarly, the basic Price equation tells us that changes in a population trait are due to differential reproduction (or persistence) and transmission biases, but it does not specify the causes of these phenomena.

Nevertheless, the availability of Galilean kinematics was a condition of possibility for Newton to conceive classical particle mechanics as he did. It would have been impossible to formulate the explanandum of classical particle mechanics under Aristotelian kinematics, or equivalent frameworks.[7] This is because Newtonian mechanics aimed to explain accelerated motion, while Aristotelian physics idealized all motion as uniform or quasi-uniform (Kuhn 1977). Thus, the Galilean description of motion contributed to Newton's explanation by allowing a different way of looking at the world. This shows that kinematics can be crucial to the development of a scientific field, even if it does not provide an explanation of the phenomenon under study. The analogy with Galilean kinematics cannot be taken further in this sense, because it cannot be said that the Price equation was actually fundamental to the formulation of Darwinian evolutionary biology in the same sense that Galilean kinematics was fundamental to Newtonian mechanics. This is obvious, since the Price equation postdates many theories in evolutionary biology. But this does not diminish the power of the analogy. Since its original formulation, the Price equation has been adopted by many practitioners as a standard representation of evolutionary processes and has thus become a common tool for model building in evolutionary biology. Thus, despite their idiosyncrasies, both Galileo and Price provided frameworks that other theories have adopted as their explananda.

To clarify this point and the whole analogy, we need to introduce the notion of "theorization." This will help us better understand the relationship between kinematics, or phenomenological theories, and dynamical theories, which aim to explain the behavior of the systems represented in the phenomenological theories. This, in turn, will allow us to properly characterize Price-like equations as examples of theorization over the original Pricean framework.

From Kinematics to Dynamics

The concept of theorization is related to the question of scientific explanation. Some have argued that theorization is a necessary (but not sufficient) condition for genuine explanations (Díez 2014). As is well known, providing an account of scientific explanations is one of the most enduring challenges in the philosophy of science. Fortunately for us, we do not need to provide that full account here. Rather, we are interested in an aspect of explanation that can be seen as transversal to almost any approach. Scientific explanations typically redescribe explanandum phenomena by introducing new concepts, as well as new statements or laws formulated using these new concepts, which serve to make the explanandum "expectable" (Hempel 1965). In the context of metatheoretical structuralism—a formal approach that aims, among other things, to make the structure of scientific theories explicit (Balzer et al. 1987)—this redescription is called "theorization" (Balzer et al. 1987, pp. 250–252).[8]

More precisely, if a theory T_1 has a language $\mathscr{L}_1 = \langle t_1, \ldots, t_n \rangle$ and a set of axioms $A_1, \ldots A_i$, then a second theory T_2 theorizes over T_1 if it extends its language (i.e., $\mathscr{L}_2 = \langle t_1, \ldots, t_n, t_m, \ldots, t_r \rangle$) and adds axioms $A_j, \ldots, A_k$ that establish links between the old and the new language. In this way, T_2 conceptually enriches T_1. The new language and the new axioms make it possible to establish new systematic connections between statements formulated exclusively with the vocabulary of the old language. To illustrate this procedure,

[7] We will use "explanandum" in a global sense, referring not to the conclusion of particular explanations, but to the kind of phenomena a theory is intended to explain.

[8] See Alleva et al. (2018); Díez and Suárez (2023); Lorenzano and Díez (2022); and Olmos et al. (2020) for some applications of this idea to concrete reconstructions of empirical theories.

suppose that T_1 is a purely phenomenological theory—in the sense discussed above—describing some observed regularity in a particular domain of phenomena. Thus, a theory T_2 that theorizes over T_1 introduces an extension of the language of T_1, containing new terms that allow us to infer such (and possibly other) regularities from the new axioms. We can say that the statements inferred from the new axioms are *explained* in some relevant sense, insofar as the new language makes them logical consequences of more basic/primitive statements in T_2.[9] Theorization can be iterative. For example, a theory T_2 may theorize over the theory T_1, another theory T_3 may theorize over T_2, and so on. This leads to a "layered" view of science in which there are theories at different levels, rather than just theories and facts. In each theorization we add new vocabulary and axioms to the theory below. In this way, a theory can explain (or at least make expectable and/or predictable) some things that other theories take as brute/postulated facts and/or regularities.

Returning to the analogy above, classical particle mechanics theorizes over Galilean kinematics insofar as it enriches its vocabulary (describing motion in terms of particles and accelerations) with new concepts (i.e., mass and force) and axioms formulated through the extended vocabulary (e.g., Newton's second law). To make this idea more rigorous, let us offer a brief formal reconstruction of how Newtonian mechanics builds on Galilean kinematics (slightly modified from Suppes 1957; Díez and Moulines 1999). As mentioned above, Galilean kinematics provides an overall description of how particles move in space, with given velocities and accelerations. To formulate such descriptions, the following language is sufficient:

(I) P is a non-empty finite set[particles].

(II) T is an interval of real numbers[time].

(III) $s: P \times T \to \mathbb{R}^3$, twice differentiable on T[position, velocity, and acceleration].

Newtonian mechanics enriches this framework with new concepts:

(IV) $m: P \to \mathbb{R}^+$[mass].

(V) $f: P \times T \times \mathbb{N} \to \mathbb{R}^3$ (where the index $i \in \mathbb{N}$ represents the type of force at play)[force].

These new definitions, in turn, allow us to formulate new statements, such as Newton's second law:

(VI)

$$\forall p \in P, \forall t \in T : m(p)\left(\frac{d^2}{dt^2}(s(p,t))\right) = \sum_{i \in N} f(p,t,i)$$

Now, with the extended language of Newtonian dynamics, we are able to explain why a given particle is moving with a given velocity or acceleration, and even to predict its motion. Note that Newton's second law is not derived from the axioms (I)–(V), but is postulated on top of them. Newton's second law is an axiom of the new theory that, together with other new statements, allows one to deduce certain states of affairs that previously, in the context of Galilean kinematics, could only be taken as brute facts.

As we have shown, the Price equation can be derived as a theorem from a phenomenological description of two generations and their filial relationships. Its explanatory power is limited by the fact that the vocabulary of the Pricean framework does not include any reference to concepts aimed at explaining the changes described by the equation. However, this does not mean that it is useless for the development of theories/hypotheses/models aimed at explaining such changes. The best way to understand the value of the Price equation for explanatory purposes is to consider the principles, models, hypotheses, or theories that theorize on it. To illustrate this point, we will consider two examples of theorization, both of which lead to the formulation of new "Price-like" equations. In both examples, new concepts are introduced into the existing framework in order to make the concept of fitness explanatory.

An Explanatory Concept of Fitness

There is a large literature on the polysemy of the term "fitness" (e.g., Sober 1993; Ariew and Lewontin 2004; Rosenberg and Bouchard 2009; Abrams 2012; Pence and Ramsey 2013; Ginnobili 2016; Walsh et. al. 2017). We cannot review this literature in detail here, but it is possible to point out at least three senses of the term fitness: realized fitness, statistical fitness of population genetics, and ecological fitness (the latter being of a more qualitative or comparative nature, referring to the ability of organisms to survive and reproduce by relating their traits to some features of the environment).

As discussed above, the notion of fitness present in the basic Price equation is realized fitness. The Pricean framework does not show why some individuals have greater/less reproductive success than others, nor what types of factors should be considered to explain these differences. In addition, as noted above, the basic Pricean framework is not predictive, in the sense that it does not tell us what trait frequencies we should expect to find in the offspring population.

[9] Note that the idea that new vocabulary serves to establish new connections between previously established statements by adding new axioms dates back to logical empiricism (see, for example, Hempel 1958, pp. 40–41). For this reason, Díez (2014) calls his account of explanation neo-Hempelian. In the classical account, the new vocabulary consists of *theoretical* terms (see Ginnobili and Carman 2016 for some discussions around this point in a more contemporary setting), and new laws (including mixed statements) allow one to infer (either deductively or inductively) new *observational* statements. Since these early writings, the project of eliminating theoretical concepts from science has been abandoned, along with the theoretical–observational distinction. However, the core idea behind the concept of theorization can be maintained without this problematic distinction.

One way to enrich this framework conceptually, then, is to add an explanatory concept of fitness. We will not discuss whether this should be interpreted statistically or ecologically (see the references at the beginning of this subsection for a detailed discussion of this topic). Suffice it to say that both statistical and ecological fitness can be used to explain differences in realized fitness.

Okasha (2006, Sect. 1.4.1) shows a way to do this. We follow his exposition but adapt and formalize it with our previous framework in mind. If the language of the basic framework consists of $\mathscr{L}_1 = \langle P, O, a, Z, z, d, w \rangle$ (plus a few averages and deltas, which we can think of as defined concepts), we will enrich this language with three additional elements: a binary function n and two unary functions f and δ, so that the following holds:

(12) $n: P \times \mathbb{N} \to \mathbb{R}$.

(13) $f: P \to \mathbb{R}$.

(14) $\forall i \in P, f(i) = \sum_{y \in \mathbb{N}} y \cdot n(i, y)$.

(15) $\forall i \in P, \delta(i) = w(i) - f(i)$.

Informally, $n(x, y)$ is a function that returns the probability that an individual x has y children. Thus, in this extended framework, the number of offspring y is a random variable and n must satisfy the basic requirements of a probability mass function. Therefore, $f(i)$ will represent the (weighted) expected number of children for individual i. (15) defines the deviation δ between the actual and the expected outcome.

We then have an extended framework with a language $\mathscr{L}_2$ consisting of $\langle P, O, a, Z, z, d, w, n, f, \delta \rangle$ and the four additional axioms above. With this in place, Okasha (2006, pp. 32–33) shows how to derive a Price-like equation by substituting $w(i)$ for $f(i) + \delta(i)$ in the basic Price equation (which still holds).[10] In our terms, this new equation is:

$$\overline{w}(P)\Delta\overline{z} = Cov\big(f(p), \overline{z}(d(p))\big) + Cov\big(\delta(p), \overline{z}(d(p))\big)$$

According to Okasha, this decomposes the change in the average trait in the population into two causal factors related to natural selection (first term on the RHS) and drift (second term on the RHS) through the notions of expected fitness and deviation from expectation, respectively. Our intention here is not to discuss Okasha's philosophical reading of this equation, but only to show how, by adding new vocabulary and axioms to a framework, one can derive new principles that (can be taken to) explain what, in the original framework, were brute facts.

Before moving on to a more interesting example, note two additional points. The first is that this new Price-like equation is not, as is sometimes assumed, derived from the basic Price equation, but only from that equation *plus* axioms (12)–(15), which contain new vocabulary. The second noteworthy point is that, if we wanted, we could decompose $f(i)$ (or $n(i, y)$) into even more causal factors by finding out which factors affect the probability of an individual having y children. To do this, we would need to add even more vocabulary and new axioms that relate this new vocabulary to n and f. In other words, the exercise we did in this section can be done recursively. One can theorize over frameworks that have already been theorized (see the fourth section, above).

Inclusive Fitness Theory and Hamilton's Rule

The previous example involves a very specific model within population genetics. Our next example, however, involves the development of an entire theory that extends the classical theory of natural selection. Since Darwin's time, biologists have wondered how social traits (especially those that affect an individual's own fitness, such as altruistic behavior) evolved. William Hamilton provided an answer to this puzzle by developing the so-called "inclusive fitness theory," and its fundamental principle: Hamilton's rule. The first step was to broaden the traditional concept of fitness. Instead of relying on the classical conceptualization of fitness as the direct reproductive success of an individual due to (or caused by) its own traits (including its behavior), Hamilton argued that the fitness of an individual is best understood as "neighbor modulated fitness" (as he called it). This can be written as a function of the individual's traits and their correlations with the traits of its neighbors.[11] The second step in Hamilton's development of inclusive fitness theory was the rule that bears his name, which formalizes social evolution through the concepts of *actors* (the individuals who perform the social behavior), *recipients* (the individuals who receive the action of the actors), *costs* and *benefits* of these behaviors, and *relatedness* (the degree of genetic relatedness between actors and recipients). It is well known that the first presentation of Hamilton's rule (1964) was a model with a limited scope, although Hamilton rapidly expanded it using Price's work (Hamilton 1970).

Here we present a partial formalization of the extended Pricean framework used to derive Hamilton's rule. In addition to the axioms (1)–(11), we need some other axioms, i.e.:

(16) $S \subseteq P \backslash \{p\}$ is the set of social partners of p.

[10] Okasha uses a slightly modified form of the basic Price equation. He also assumes that characters are transmitted without bias from the ancestor to the descendant population, so the following result can be thought of as the consequent of a conditional that begins with "if $E(\Delta z(p)) = 0$, then …". See Okasha (2006, Sect. 1.4) for more details.

[11] For a more detailed discussion of the relationship between inclusive fitness and neighbor-modulated fitness, see Birch (2017, Chap. 5).

(17) $\hat{z} : S \to \mathbb{R}$, such that $\hat{z}(p) = \frac{\sum_{s \in S} z(s)}{|S|}$[average character in the set of social partners of p].

(18) α is the non-social component of fitness.

(19) β_1 is the partial regression of $w(p)$ on $z(p)$ controlling on $\hat{z}(p)$

(20) β_2 is the partial regression of $w(p)$ on $\hat{z}(p)$ controlling on $z(p)$.

(21) ε_w is the residual of the regression

$$w = \alpha + \beta_1 z(p) + \beta_2 \hat{z}(p) + \varepsilon_w \quad (22)$$

where (22) is the Lande–Arnold regression model of fitness (Lande and Arnold 1983). Note that in many classical derivations of Hamilton's rule, such as Queller (1992; see also Marshall 2015 and Birch 2017), what is tracked between generations are changes in allele frequencies. Here, we prefer to stick with our original framework and, like Lande and Arnold (1983), refer to an unspecific/abstract trait z. Hamilton's rule is primarily concerned with how natural selection favors social behavior; therefore, the second term on the right-hand side of the original Price equation (the expectation term) is assumed to be 0. This yields this formula:

$$\overline{w}(P)\Delta\overline{z} = Cov(w, z(p))$$

By substituting w for (22), we obtain

$$\overline{w}(P)\Delta\overline{z} = Cov(\alpha, z(p)) + \beta_1 Var(z(p)) + \beta_2 Cov(\hat{z}(p), z(p)) + Cov\left(\varepsilon_w, z(p)\right)$$

Simplifying and rearranging, this yields:

$$\overline{w}(P)\Delta\overline{z} = \left(\beta_1 + \beta_2 \frac{Cov(\hat{z}(p), z(p))}{Var(z(p))}\right) Var(z(p))$$

which states that a social behavior will be favored by natural selection if and only if $\frac{Cov(\hat{z}(p), z(p))}{Var(z(p))}\beta_2 > -\beta_1$, where $\frac{Cov(\hat{z}(p), z(p))}{Var(z(p))}$ represents the relatedness of the recipient to the actor, β_2 the benefits to the recipient, and $-\beta_1$ the costs to the actor. This is the so-called Hamilton's rule, which in its usual form is expressed as $rb > c$, where $r = \frac{Cov(\hat{z}(p), z(p))}{Var(z(p))}$, $b = \beta_2$, and $c = -\beta_1$.[12]

Two important points need to be made. First, it is crucial to recognize the key role that the Pricean framework plays in the above derivation of Hamilton's rule. In order to develop the inclusive fitness theory in its complete and modern form, we assumed the kind of kinematics provided by the Price equation, and then we theorized about the causes of evolutionary change, the types of traits, and the mechanisms of inheritance in the system. This led to further assumptions/modeling procedures about the ways to parameterize fitness, and the types of dynamics that can cause social traits to evolve through natural selection. Second, we can see that Hamilton's rule plays a fundamental role within inclusive fitness theory, establishing the basic concepts of the theory: inclusive fitness, actors, recipients, cost, benefit, relatedness, genes, and so on.[13] The task of evolutionary biologists, according to proponents of this theory, is to find the specific causal settings that affect the three terms (r, b, and c) in the inequality (Rousset and Lion 2011; Bourke 2014). In any case, alternative theories and models can be developed to explain social evolution based on different assumptions and principles (Lehtonen 2020; van Veelen 2020). Some of these alternative theories and models can, as van Veelen (2020) correctly notes, be formulated without explicitly using the Price equation or Hamilton's rule. However, as we will argue in the next section, there is a sense in which any theory or model in evolutionary biology presupposes the Pricean framework, because of its kinematic character. As mentioned in the introduction, van Veelen (2020) also emphasizes that Hamilton's rule can, under certain circumstances (particularly when it results from a theorization over the Price equation), give a misleading picture of evolutionary processes. This may be the case, but we do not enter into that debate here. Our point is simply that even if van Veelen were right, this would only show that *certain assumptions* about a particular scenario are wrong. In other words, while the application of a specific Price-like equation may lead to incorrect conclusions or predictions, this does not invalidate the metatheoretical scheme that we are developing here.

Both examples from the previous two subsections show that when evolutionary biologists use the Price equation to generate new equations, they are theorizing (in the technical sense of this article) and not just deriving theorems. They are trying to develop a dynamical picture from a kinematic one, postulating possible explanatory factors/causes that account for the regularities found in other more basic theories. In other words, this task is not a purely mathematical exercise of deriving theorems, but a scientific, theoretical, and empirical endeavor.

[12] Both representations depend on the condition that Var(z(p)) ≠ 0.

[13] Birch (2017) portrays it, in a similar way, as an *organizing framework*.

Price, Population Thinking, and the Integration of Evolutionary Biology

In the third and fourth sections, we pointed out some similarities between the conceptual framework deployed by Price and Galilean kinematics. Both provide a general *description* of the behavior of a particular domain of phenomena (i.e., evolving populations and bodies in motion, respectively), and both serve as explananda for dynamical theories (synthetic Darwinian theory—or some extension of it—and Newtonian mechanics, respectively), aimed at explaining the causes of such behaviors. We also noticed an important difference between the Pricean framework and Galilean kinematics. Unlike Galilean kinematics, which predates the Newtonian theorization of the laws of motion in terms of forces, the Price equation was formulated more than 100 years after the publication of the *Origin*, and 50 years after the work of Haldane, Fisher, and Wright inaugurated the Modern Synthesis.

This "historical accident" explains, in our view, some of the misunderstandings about the role of the Price equation in evolutionary biology. Evolutionary biologists typically fail to conceptualize the difference between kinematic and dynamical aspects of their models because—unlike physicists—they first learned the dynamical theory of evolution (i.e., traditional population genetics and its extensions: Kimura's neutral theory, Gould and Eldredge's theory of punctuated equilibrium, etc.; Futuyma 2013) and only recently the corresponding formal framework of its kinematics (i.e., the Pricean framework). In most cases, the kinematic aspects of the theory are implicitly assumed and conflated with the dynamical aspects. As a result, some of those who have praised the Price equation as the fundamental law of evolution (e.g., Luque 2017; Queller 2017; Luque and Baravalle 2021; see section one) have tended to think of the original Price equation (as depicted in the second section) as endowed with dynamical features, like Newton's second law. In the previous sections, we have argued that this comparison is not entirely accurate. Although some Price-like equations do indeed aim to provide a dynamical characterization of a class of evolutionary phenomena, the original Pricean framework itself is not dynamically sufficient.[14] Thus, while the former dynamical forms of the Price equation may be somehow comparable—in their respective domains of application (e.g., social evolution theory, in the case of Hamilton's rule; Birch 2017)—to Newton's second law or some of its versions (such as the Cauchy momentum equation in fluid mechanics; Luque and Baravalle 2021), the latter cannot.

Although historically the Pricean framework was not a condition of possibility for the formulation of Darwinian theory (as was supposedly the case with Galilean kinematics for Netwonian mechanics), this does not mean that it cannot be fundamental for future developments. To begin with, we can think of the Pricean framework as a rigorous, mathematical expression of so-called *population thinking*—which is often presented as one of the pillars of the Darwinian tradition (e.g., Godfrey-Smith 2009). Population thinking has received a number of different formulations over the past 60 years or so (e.g., Mayr 2004; Sober 1980; Ariew 2008). Beyond the differences between these accounts, however, we can identify two common assumptions. The first is that populations are the fundamental evolving entities (Hull 1980; Futuyma 2013; Akçay and Van Cleve 2016). The second assumption is that variation among individuals endowed with traits is the core feature of biological populations (Futuyma 2013). Consequently, evolutionary change is a change in a population over generations due to a change in its composition—in terms of the traits of individuals. Evolutionary theory is called upon to explain the causes of this change. In modern Darwinian theory, these causes are associated with the environment in which the population is found (i.e., selective pressures) or with the peculiarities of the system that allows the transmission of traits from one generation to the next (e.g., genetic inheritance). Both of these features (that evolution is something that happens to populations rather than to organisms, and that populations are thought of as consisting of varieties distinguished by the possession of certain traits) are presupposed in Darwin's own selectionist explanations, even if this kind of kinematics is not made explicit by Darwin.

The Pricean framework—and thus the Price equation itself—formalizes both of the previous assumptions and makes explicit what evolutionary change is (Gardner 2020). First, it depicts evolutionary change as involving populations that are linked by an ancestral–descendant relationship, thus potentially forming lineages. Second, it characterizes populations in terms of individuals with different traits. To formalize the idea that evolutionary change involves a change in the composition of populations, the Pricean framework posits that there is intergenerational differential transmission of traits between parental and offspring populations, based on reproductive differences between individuals belonging to the parental generation. It further suggests that intergenerational changes in population composition are due to factors that relate individuals' traits to their reproductive success. These factors are presumably related to the environment in which the population occurs (this is typically

[14] By "dynamically sufficient" we mean here that the Pricean framework does not account for the actual causes of evolution. This notion should not be confused with the notion of "dynamic sufficiency," which refers to a model's capability to predict the future states of the system under study (Lewontin 1974; Frank 2012). Both Newton's second law and the Price equation, by themselves (i.e., without additional information about the target system), lack predictive power (Luque 2017).

expressed in the covariance term of the Price equation), or to the transmission system itself (this type of factor is represented by the expectation term). Again, the Price equation does not directly account for what makes a trait increase an individual's chance of reproduction, or for how the traits are transmitted (nor does population thinking, per se).[15] What elements of the environment or reproductive system cause a trait to increase or decrease its frequency is, as we have seen, something that further theorizations on the Pricean framework are called upon to explain. Nevertheless, to the extent that population thinking is often seen as a landmark achievement of modern evolutionary theory, the Pricean framework should be celebrated for its ability to properly formalize it.

It is important to emphasize this last point, because by recognizing the kinematic role of the Pricean framework, we are not only able to better understand the current practices of modelers in various areas of evolutionary biology (as we have shown in the fourth section). Our analysis of the Pricean framework also sheds light on the *structure* of much of evolutionary biology. Recent advances in the field, particularly those motivated by proponents of the Extended Synthesis (Pigliucci and Müller 2010; Laland et al. 2015), have pointed to the need to include within the scope of the discipline previously neglected causes of evolution and nongenetic inheritance systems that cannot be accounted for by traditional population genetics. This has led some scholars to be skeptical about the conceptual unity of evolutionary biology (e.g., Mitchell and Dietrich 2006; Love 2010). It is worth noting, however, that the Price equation has been widely used to model these previously overlooked evolutionary factors and inheritance channels (see, for example, Otsuka 2015 on niche construction; Smith 2007 on symbiosis; Helanterä and Uller (2010) and Day and Bonduriansky (2011) on nongenetic inheritance—transgenerational epigenetic inheritance, RNA inheritance, etc.; Edelaar et al. 2023 on adaptive evolution via inheritance of parental responses; and so on). While new models can add considerable complexity to the picture we have of evolutionary processes, it is surprising how consistently they adopt the Pricean kinematics and theorize on it in a manner similar to Hamilton (1970), Queller (1992), or Okasha (2006) in their attempts to explain social or drift dynamics. From a metatheoretical point of view, we see this as evidence that the Pricean kinematic has the power to *integrate* (if not unify) large areas of research. This integration may not be identical to the one we observe in classical mechanics, where specific theorizations (e.g., celestial mechanics, particle mechanics, aero- and hydrodynamics, etc.) assume not only Galilean kinematics but also a specific dynamic, i.e., that provided by Newton's second law. In contrast, some recent models tend to downplay the role of what are traditionally considered the main causes of evolution (mainly natural selection). That is, some recent models disagree about the dynamical features of some specific evolutionary processes. However, even in these cases, a certain degree of integration is guaranteed by the identification of a common phenomenon and a method for approaching its possible causes. This integration is made possible by the widespread use of the Pricean framework as a common framework for analyzing and parameterizing evolutionary phenomena.

Conclusions

In this article, we have tried to clarify some misconceptions about the role of the Price equation in evolutionary biology. On the one hand, we wanted to emphasize that there is nothing trivial about the Price equation. Although it cannot by itself explain the causes of evolution in specific scenarios, it perfectly *describes* the conditions that any system must satisfy in order to be considered an evolving system, at least according to modern evolutionary theory. On the other hand, we wanted to nuance the claim that the Price equation is something like the "fundamental" law of evolutionary biology. If we think of a fundamental law as a statement that contributes to explaining all phenomena in a given field (like, for instance, Newton's second law in classical mechanics), then the Price equation is not a fundamental law. Its descriptive nature precludes it from playing that role. Rather than being the end result of evolutionary biology, the Price equation is more like a canvas on which practitioners are called to continue to work. The Pricean framework from which the Price equation is derived is a starting point for formulating more definite explanatory models.

This is not to say that the Price equation is only of heuristic value. Throughout our article we have emphasized that the Pricean framework is the kinematics of evolution. Thus, its value lies not only in "suggesting" ways to explain evolutionary dynamics, but also, similar to what happened in modern physics with the advent of Galilean kinematics, in *enabling* rigorous formalizations of these processes. By *theorizing* over the Pricean framework in the technical sense that we have discussed throughout this article, practitioners enrich it with new concepts and distinctions that gradually make evolutionary phenomena more understandable and predictable. The value of the Pricean framework is that it provides a common grammar and basic description of

[15] This is one reason why the Price equation, but not traditional population genetics, is a proper formalization of population thinking. Traditional population genetics assumes genetic inheritance as the only possible channel of inheritance. But neither population thinking nor the Price equation requires this. Traditional population genetics can be derived (by theorization) from the Pricean framework, and is only one specific application of population thinking among others (see the reminder of this section for other applications assuming alternative channels of inheritance).

evolutionary processes upon which a web of more specific and interrelated theories and models can be built.

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Declarations

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