Dialogue

What is the price of using the Price equation in ecology?

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The Dialogue series is intended to promote critical thinking and the expression of contrasting or even opposing viewpoints on important ecological topics. Here, seven researchers debate the use of the Price equation, a framework that has long been used in evolution to analyze temporal changes in the frequency of traits and alleles. This Dialogue describes different philosophical and mathematical perspectives on the application of the Price equation to ecological questions such as the relationship between biodiversity and ecosystem functioning (BEF). The hope is that the broader scientific community will benefit from these contrasting viewpoints.

Keywords: biodiversity and ecosystem function, community ecology, partitioning, Price equation

The Price equation in evolution

The Price equation is a mathematical identity that was first introduced in evolutionary biology to track changes in the frequency of traits or alleles from a parent generation to an offspring generation (Price 1970). If each individual i in the parental generation has a trait value z_i and a fitness w_i determined by the number of offspring produced, then one can write what Price (1970, 1972) called the *covariance* form of the equation:

$$\overline{w}\Delta\overline{z} = \underbrace{\text{Cov}[w,z]}_{\text{selection}} + \underbrace{\text{E}[w\Delta z]}_{\text{transmission bias}} \qquad (1)$$

where $\overline{w}$ is the average fitness in the parent population and $\Delta\overline{z} = \overline{z}' - \overline{z}$ is the change in average trait in the population across generations. The 'selection' term $\text{Cov}[w,z]$ is the covariance between an individual's trait and its fitness, and the 'transmission bias' term $\text{E}[w\Delta z]$ is the weighted average of the difference between the trait of a given

parent and the average trait of its offspring (or the average allele frequency in its successful gametes).

In evolutionary biology, the original Price equation and its variants are regularly used to make theoretical claims, but are rarely applied to data (Rice 2004, Okasha 2006, Frank 2012, Marshall 2015, Queller 2017, Luque 2017, Gardner 2020, Bourrat 2021). There is however some dissent by those that question its usefulness for either purpose (van Veelen 2005, 2020a, van Veelen et al. 2010, 2012).

An extension of the Price equation in ecology

In ecology, the original and most prominent extension of the Price equation is the additive partitioning scheme developed by Loreau and Hector (2001) to study the relationship between biodiversity and ecosystem functioning (BEF). Specifically, the Loreau–Hector (LH) scheme partitions the 'net biodiversity effect', defined as the difference between the total amount of ecosystem functioning (yield) observed in an n-species mixture, O, and the amount expected based on the average of the monocultures, $\bar{M}$, as follows:

$$\underbrace{O - \bar{M}}_{\text{net biodiversity}} = \underbrace{n\mathrm{E}\left[M\Delta p\right]}_{\text{net biodiversity}} = \underbrace{n\mathrm{Cov}\left[M, \Delta p\right]}_{\text{Selection effect}} + \underbrace{n\bar{M}\overline{\Delta p}}_{\text{Complementarity effect}} \quad (2)$$

where Δp represents the difference between the proportion of monoculture yields *observed* in mixtures minus the proportion of yields *expected* based on initial species densities. The 'net biodiversity effect' is partitioned into the 'selection effect', which represents the relationship between each species' yield in monoculture and its relative yield in mixtures due to 'dominance by species with particular traits affect[ing] ecosystem processes', and the 'complementarity effect', which represents changes in the average relative yield of the mixture that can be positive due to 'resource partitioning or positive interactions' or negative due to 'physical or chemical interference' (Loreau and Hector 2001).

However, some have argued that the LH additive partitioning scheme produces inflated estimates of the 'net biodiversity effect' and incorrect estimates of both the 'selection effect' and the 'complementarity effect' when species' ecosystem properties scale nonlinearly with their densities in monocultures (Pillai and Gouhier 2019a, see also comments by Loreau and Hector 2019, Wagg et al. 2019, and responses by Pillai and Gouhier 2019b, c, 2020).

Overture – contributors independently explore their views on the Price equation

The Price equation is a contentious topic in evolutionary theory. Some regard it as a great tool to deepen our understanding of evolutionary theory (Rice 2004, Okasha 2006, Frank 2012, Luque 2017). Others view it as misleading if not used in combination with model assumptions (van Veelen et al. 2012, van Veelen 2020a). More recently, it has been applied in community ecology (Loreau and Hector 2001, Fox 2006). I believe this development would have seemed quite natural to George Price since he was working on a general theory of selection – that is, applicable to any domain – before his tragic death (Price 1995). Unsurprisingly, similar 'camps' have arisen in this field.

Before being able to take a stance on the usefulness of the Price equation, whether in evolutionary theory or community ecology, it is important to understand what one can legitimately expect from it. Progress in science rests on at least two pillars: a desire to understand and a desire to predict. These two desires crystallize in the Price equation as what Frank (2012) calls an inductive and a deductive interpretation, respectively (see also Frank and Fox 2020). It has long been recognized that the Price equation, in and of itself, cannot be regarded as a tool for prediction (Frank 1995, 2012, van Veelen et al. 2012) as it is a mathematical identity that does not contain any assumption required for making predictions about– or in other words, deducing – the state of the population after a certain period from some initial values and rules of change.

Therefore, it would be incorrect to use the Price equation as a tool for prediction. If one were to commit this mistake, it would instead reveal that one has implicitly made a number of assumptions about the rules of change in the population. However, it would also be wrong to argue that the Price equation cannot be legitimately used to help understand objects of scientific investigation, including ecological communities, through induction. When the rules of change are not known, but only data is available, one way to begin investigating is from the basic partitioning of the Price equation, and then make it more complex (i.e., partitioning it into more terms) it if it does not fit with the data. As the complexity increases, the links with the basic terms of the equation become more tenuous. Nonetheless, the Price equation can be regarded as a placeholder for both unifying different models through a common language (Bourrat 2021) and assessing how far a particular situation is from the implicit idealized model elicited by the Price equation.

Only by exploring the conceptual space of the aims of science will it be possible to set the Price equation within its proper bounds.

P. Bourrat

Many ecological problems amount to linking the attributes of individual organisms (such as birth rates, death rates and dispersal) to overall descriptions of change (Sutherland et al. 2013). Ecology has emphasized reductionist approaches, starting with the attributes of individual organisms and working forward to overall descriptions of change (MacArthur 1972, Kot 2001, Hastings 2011, Vellend 2016). By comparison, the Price equation is holistic, starting with an overall description of change then working backwards to individual attributes. This point is made by George Price's noted collaborator John Maynard Smith, as quoted in Okasha (2005).

In principle, the Price equation should lead to the same answers as traditional approaches to biological theory. For example, Lion (2018) translates textbook ecological models of population growth (Lion 2018, Eq. 7) into models for change in traits. This approach allows for analyses of many familiar ecological models such as exponential growth, consumer resource dynamics or species interactions mediated by a Lotka–Volterra model. The Price equation is just the final step allowing 'one to translate population dynamics into phenotypic change' (Lion 2018, Eq. 12). This derivation does not need additional ecological assumptions, meaning that interactions between species may be mutualistic, non-zero sum, or non-linear.

In practice, no approach is perfect, and we should expect a healthy tension between the Price equation and other approaches. We rarely obtain the data to test reductionist approaches in nature (Miller et al. 2005, Rees et al. 2012, Urban et al. 2016), and these approaches can furnish poor predictions (Socolar et al. 2016, Hillebrand et al. 2018). While the Price equation is quite general (Queller 2017), it was derived as a tool to better understand evolutionary theory. The goals, tastes and requirements of evolutionary theory differ from those of ecology (Vellend 2016). There is substantial opportunity for dialogue with the Price equation providing tools for ecologists and ecologists providing new tests for the Price equation.

W. Godsoe

Although often venerated as the 'algebra of evolution' (Rice 2004), we contend that the evolutionary Price equation is a trivial, near-tautological identity (van Veelen 2020a) that simply decomposes the property of a system into the *expected* quantity of change arising from variation in the growth of the system's individual parts when on their own (*variational* change; or more specifically, the covariance component of this variational change), and the residual difference left over between the observed value and the expected variational growth (*transformational* change; Pillai and Gouhier 2018).
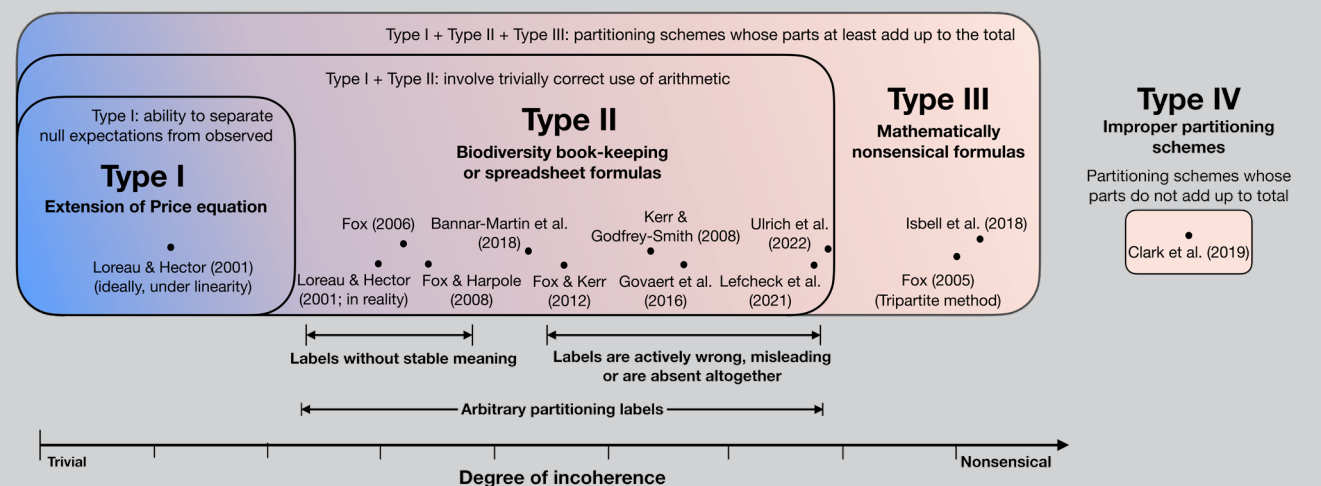

Figure 1. Taxonomy of ecological partitioning methods inspired by the Price equation.

In biodiversity studies, formulas analogical to the Price equation have been adopted for compartmentalizing the total change observed in biodiversity datasets. These so-called 'Price equation partitioning' methods fall into three broad categories. Type I methods, represented exclusively the Loreau and Hector (LH) partitioning scheme, are, at least mathematically or structurally, congruent with the original Price equation in that they compare observed and expected variational changes in a system (Pillai and Gouhier 2018). Type II and III methods, however, are unable to separate out expectations due to variational change from total observed changes and are thus not properly isomorphic to the evolutionary Price equation. Type II and III methods are instead represented by a set of partitioning formulas that are either arithmetically trivial and biologically meaningless (Type II; e.g. Fox 2006, Fox and Kerr 2012, Lefcheck et al. 2021, Ulrich et al. 2022), or both biologically and arithmetically nonsensical (Type III; e.g. Fox 2005, Isbell et al. 2018).

Type II (pseudo-Price) methods are often meaningless, or at least ambiguous in that they involve dividing some total observed change into arbitrary parts that are then affixed with labels lacking any stable or meaningful ecological referent. As such, Type II methods represent a 'phenomenological trap': they produce raw empirical quantities devoid of biological meaning. The subcomponents in Type III methods are even worse because they are constructed with nonsensical arithmetic operations that make them incapable of measuring any real quantity (Pillai and Gouhier 2018). Furthermore, Type II and III methods are almost never properly justified – whether mathematically, biologically, or conceptually – aside from the use of numerical simulations to demonstrate that the parts always sum up to the observed total in case studies (Fox 2005, Isbell et al. 2018, Ulrich et al. 2022, see Fig. 1). Only the Type I method (i.e. the LH additive partitioning scheme) is formally and logically set up to, at least in principle, measure some real form of ecological change. However, as we recently demonstrated mathematically (Pillai and Gouhier 2019a), the LH method falls apart in nearly all real-world biological systems, rendering this partitioning scheme a de facto Type II method in all but the most rare and special cases.

In the end, Type II and III methods represent little more than bookkeeping operations for curating and compartmentalizing biodiversity datasets. Despite claims to the contrary, these methods display no real mathematical relationship to the Price equation in evolutionary biology aside, perhaps, from some tenuous family resemblances based on the occasional use of the covariance operator. Hence, the biodiversity class of 'Price partitioning' methods involve taking an already trivial but at least conceptually sound formula from evolutionary biology and rendering it both arithmetically trivial and biologically suspect.

<div align="right">P. Pillai and T. C. Gouhier</div>

Ecological insights from a Price partition? A cautionary note. The Price equation of evolutionary biology describes the change in character expression within a population in terms of average character values and the covariance of character values and fitness (Price 1970). Loreau and Hector (2001) and Fox (2006) first applied the Price partition to quantify the contributions of diversity (complementarity) and dominance (competition/composition) to trait variation. This approach has been controversial (cf. Luque 2017, Loreau and Hector 2019), and critics have argued that that Price partitions are not statistically independent (Pillai and Gouhier 2019a) and lack a simple, unequivocal interpretation, or even become meaningless (van Veelen 2020a), making functional inferences challenging (Barry et al. 2019).

Non-independence of data is a serious problem in statistical analyses, but this is a different issue from the non-independence of a statistical partitioning. Like the partitioning of the sum of squares in an analysis of variance, the Price partition is a tautological, additive partitioning based solely on the definitions of arithmetic means and covariances (Gardner 2020). Because these partitions must sum to a fixed total, they are not linearly independent, but the relative sizes of the different partitions still can provide meaningful insights.

Previous partitions within the biodiversity – ecosystem functioning debate (Loreau and Hector 2001, Isbell et al. 2018) initially focused on a single functional interpretation of the partitions and their parameters. Such an argument is similar to the competition-based interpretation of observed patterns in the analyses of community assembly (Ulrich and Gotelli 2013). Recent advances in the null model literature have provided explicit logic-trees that can be used in conjunction with additional statistical analyses to address the relative strength or frequency of different mechanisms (Blois et al. 2014, Ulrich et al. 2017, D'Amen et al. 2018). We suggest a similar strategy for a deeper understanding of Price partitions.

<div align="right">W. Ulrich and N. J. Gotelli</div>

There are three reasons why the Price equation is so incredibly popular. The first is that it borrows words and formulas from statistics. That gives the Price equation credibility by association. Even if 'covariances' and 'regression coefficients' are used in ways that go against everything that your statistics professor taught you, it sounds as if the Price equation is part of the serious department. The second ingredient of the success formula is that it is a tautology. Anytime anyone points out that there is a problem, one of the standard defenses is: it is a tautology, and therefore it cannot be wrong. That

provides a real good excuse not to listen to the actual, more complex argument. The last element is its generality. The unique selling point of the Price equation is that it does not make any assumptions whatsoever. While most scientists are restricted by the rules of philosophy of science (no assumptions in, no predictions out), others have apparently moved beyond these narrow Popperian bounds and produce theoretical claims without making any modeling assumptions whatsoever, just by writing the Price equation. If that sounds too good to be true, you are right. It is.

The problem with the Price equation approach, and with 'partitioning' in general, is that it is not a well-defined scientific activity (van Veelen 2005, 2020a). What is typically missing is an understanding that there are a million tautological ways to rewrite or partition change, and that just being a tautology is not good enough. What we need is a tautology with a meaningful interpretation. And that is where the lack of assumptions makes itself felt. You cannot have tautological, general (i.e. assumption-free), and meaningful. Tautological and meaningful, yes. Tautological and general, also possible. All three, however, is too much to ask.

What is possible is that under one set of assumptions there is a partition for which the terms in it have a meaningful interpretation. One and the same partition, however, can typically be written for *any* change, whether this change satisfies the assumptions that would give the terms in it meaning or not. That implies that an approach that takes a partitioning as its point of departure is almost bound to make *general* theoretical claims, that might have been true under a certain set of assumptions, but are just untrue in general (van Veelen et al. 2012).

A symptom of this problem is that there can also be competing partitionings (Fig. 2). It may be that there is a model A that would make partitioning A have a meaningful interpretation, and a model B that would do the same for partitioning B. Not acknowledging that no partitioning is ever universally meaningful then leads to an impossible to settle debate about which one is the right partitioning.

Partitionings are general. Deciding when partitionings are also meaningful requires that we go back to the 'normal' scientific approach after all, with model assumptions, when doing theory, and with normal, proper statistics, when deciding whether our data fit the assumptions that would make a partitioning meaningful.
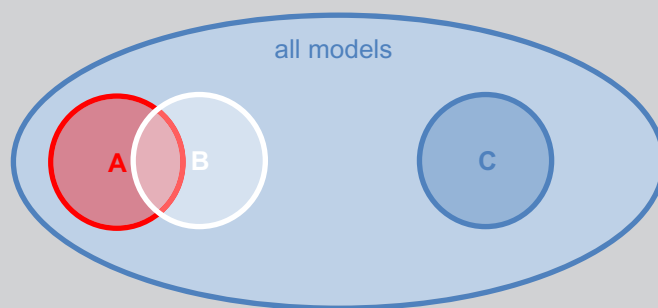

Figure 2. Partitionings are general, but not generally meaningful. Within a set of models A (or B, or C) partitioning A (or B, or C) has a meaningful interpretation. Partitionings however lose their meaning outside their set of models. One should therefore never just write a partitioning, which typically is a formula that is not restricted to the set of models for which they are meaningful. Instead, for theory, one should begin with specifying model assumptions. After this one might, but does not have to, produce a partitioning with terms in it that have meaning under the model assumptions (van Veelen 2020a).

M. van Veelen

Dialogue – contributors elaborate their views on the Price equation based on the overtures

P. Bourrat

Both Godsoe and Ulrich and Gotelli see some promise in the use of the Price equation. In contrast, van Veelen and Pillai and Gouhier take issues with the equation's usefulness in general and in community ecology in particular, respectively.

I believe that this difference in opinion lies precisely in the fact that the two camps have different implicit expectations about what the Price equation is for and what it can do, which map the distinction I made in my overture. For the 'pro camp,' roughly, it seems that the Price equation might generate new insights into the ways one can understand and measure changes in ecological communities. Here, the term 'Price equation' is understood loosely, and the expectation is not that, as such, it will make predictions similar to a dynamical model. Rather, it is expected merely that adopting a 'Price approach' might help explain things that would otherwise be more difficult to understand, or make connections

between different parts of science, used as a guiding principle or in combination with some assumptions. According to some philosophers (Kitcher 1989), and I agree with them, there is room in science for such unification principles. The Price equation is a good contender for being one such principle (Luque 2017, Luque and Baravalle 2021). For the 'against camp,' the equation has a very specific form and ought to represent something akin to a dynamical model yielding predictions that can be refuted.

Thus, it appears that both camps have vastly different expectations. How shall we adjudicate their disagreement? For one thing, it is clear that prediction and data are crucial parts of science. Equally clear, however, is that science does not reduce to pure empiricism and Popperian falsificationism. If it is recognized that the Price equation is not a dynamical model but rather something looser that can be used as a placeholder in explanations, it becomes unproductive to treat it as a dynamic model. Second, because the term 'Price equation' can refer to a number of partitionings that only bear some family resemblance and, further, are used in a broad range of contexts for different purposes, one might lament that using this term uncritically renders it meaningless. I agree with this complaint, which is expressed in different forms by both van Veelen and Pillai and Gouhier. When using the term 'Price equation,' one should clarify the precise form used, including all the assumptions made, as well as the exact context and purpose. If it is wielded as a magical tool and regarded as a solution to all evolutionary biology and community ecology problems, it becomes specious.

W. Godsoe

All of us want an interpretable description of change in ecology. I sympathize with Pillai and Gouhier's desire to clarify the applications of the Price equation to biodiversity experiments, and van Veelen's mathematical analyses. However, the critiques focus whether the Price equation fits into a tightly circumscribed view of science, what van Veelen calls 'narrow Popperian bounds'. This represents a small fraction of normal science, a point made forcefully by Hull (1999) who shows how many of Popper's suggestions have been ignored by biologists, in part because Popper initially claimed that much of evolutionary biology was tautological, then subsequently reversed his position. Science includes a broader array of tools including theoretical frameworks designed as an aide to thinking and to unify approaches to major classes of ecological phenomena (Grainger et al. 2022), such as the Price equation.

Simply adding historical context emphasizes the need for a broad view. Van Veelen claims that the Price equation 'borrows words and formulas from statistics', he cites as an example regression coefficients. The concept of regression was developed by a Galton to understand problems of heredity posed by Darwin (Galton 1886). The 'borrowing' critique amounts to criticizing biologists for using a concept developed by… biologists.

Van Veelen claims '*The unique selling point of the Price equation is that it does not make any assumptions whatsoever.*' If that sounds too bad to be true, you are right. It is. To quote Luque (2017): '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.' Similar statements are found in Frank (2012), Lion (2018), Luque and Baravalle (2021) and Queller (2017).

By focusing just on the Price equation, we miss the fact that plenty of mathematics is deeply odd, even when it is insightful (Strogatz 1994). Consider for example a basic description of population growth for a species with a population density N:

$$\Delta N = N(t+1) - N(t)$$

In other words, the change in population density is equal to the population density at time $t+1$ minus the population density at time t. This seemingly innocuous formula shares many of the properties of the Price equation that critics claim are harmful. It is a 'near tautological identity', it represents 'little more than bookkeeping', it is not dynamically sufficient (i.e. it does not make assumptions about how a population changes). I agree with these mathematical observations, but in my view, critics have yet to show how these mathematical observations imply stern to judgment that the equation is 'meaningless'. More pointedly van Veelen states that the Price equation is not a 'well-defined scientific activity' and cites himself as the authority (van Veelen 2005, 2020b), why does he get to decide?

P. Pillai and T. C. Gouhier

Bourrat, Godsoe and Ulrich and Gotelli suggest that the application of the Price equation in ecology holds great promise, but we maintain that every 'Price equation' inspired approach published over the last twenty years has been foundationally flawed. The only plausible exception (at least on first appearance) is the LH Type I method (2001), which can be seen as a tool to partition the residual transformational component of the original Price equation. As such, the LH method should, ideally and unlike the Type II and Type III methods, be able to successfully parse out different types

of biological phenomena. In reality, however, the LH Type I method is no more able to meaningfully partition ecological phenomena than the Type II methods (for proofs see Pillai and Gouhier 2019a).

Yet, because of the inability of biodiversity researchers to follow or address any of the mathematical proofs demonstrating the flaws in the LH Type I method (e.g. Loreau and Hector 2019, see Pillai and Gouhier 2019b, c for a discussion), the mathematical critique ended up serving as a kind of Rorschach Test wherein each reader simply projected onto the formal proof a purely subjective interpretation stitched together from a limited repertoire of elementary concepts and poorly understood technical terms (for example, see Loreau and Hector 2019's inability to understand the meaning of 'linearity' as described in Pillai and Gouhier 2019b, or Ulrich and Gotelli's incorrect use in this Dialogue of terms like 'tautological' or 'linearly independent', and their misrepresentation of the Pillai and Gouhier 2019a critique as being grounded in 'statistical non-independence').

Incomprehension and subterfuge aside, the *mathematical* results of Pillai and Gouhier (2019a) still hold: the LH Type I method, in general, does *not* work, and its compartments labeled 'selection' and 'complementarity' have no coherent biological meaning. This effectively brings the LH Type I method in line with the Type II methods in ecology, which involve taking an observed change after-the-fact, and then restating it as a set of differences in some underlying state variables (Fig. 3). This approach produces arithmetic terms without any value for predicting, categorizing, or understanding biological phenomena. Instead, Type II methods merely provide an opportunity for researchers to shuffle and rewrite the total change in a potentially infinite number of ways (e.g. Fox 2006, Fox and Harpole 2008, Kerr and Godfrey-Smith 2009, Fox and Kerr 2012, Govaert et al. 2016, Bannar-Martin et al. 2018, Fig. 1).

Canonical form of the pseudo-Price equation
(biodiversity book-keeping formula)

The ecological pseudo-Price equation can be seen as a simple arithmetic application of the discrete analog of the product rule in infinitesimal calculus, i.e., $\Delta Y = \Delta(fg) = \Delta f \cdot g + f \cdot \Delta g + \Delta f \Delta g$.

For example, if we assume that for species i the total property is $Y_i = x_i \, \varphi_i$, where x is number of individuals and φ is *per capita* property value, then across all species we get:

$$\Delta Y_{\text{total}} = \sum_i^n \Delta x_i \cdot \varphi_i + \sum_i^n x_i \cdot \Delta \varphi_i + \sum_i^n \Delta x_i \Delta \varphi_i$$

Simple canonical form

$$\Delta Y_{\text{total}} = \sum_i^n \Delta x_i \cdot \varphi_i + \sum_i^n x_i' \cdot \Delta \varphi_i$$

Any number of trivial extensions obtained by rewriting (e.g., Fox, 2006)

$$(\mathbb{E}[W] - 1) \times \sum_i x_i \varphi_i + n \, \text{Cov}[W, \phi] + n \, \mathbb{E}[W \Delta \phi]$$

"Random effects"   "Selection"   "C.D.E"

Figure 3. Canonical form of the pseudo-Price or biodiversity book-keeping equation. All Type II formulas can be seen as a simple arithmetic restating of total change. Note that the prime notation used in x' within the canonical equation indicates the final number of individuals in species i, as opposed to the initial number, x. In the final equation W and ϕ are random variables for both the growth, and the total (not per capita) property value of a given species, respectively.

As such, Type II methods allow a form of book-keeping/spreadsheet partitioning without any purpose, aside from the need to fill in the terms of the formula itself ('measurement for measurement's sake'; e.g. Ladouceur et al. 2022, Ulrich et al. 2022). Arbitrary labels such as 'selection/S.C.E.' and 'C.D.E' then give a scientific veneer to arithmetic terms that do not map onto any defined or coherent biological phenomena (e.g. Lefcheck et al. 2021).

However, for labels to be *inferentially* meaningful they require 1) an appropriate experimental set-up and *controls* for teasing out effects and 2) the structure provided by a scientific theory to provide meaning to the measurements, entities and categories being demarcated – both of which are absent in the Type II methods. As a result, the arbitrary

labels ascribed to the partitions in Type II equations range from ambiguous (e.g. Fox 2006) to outright misleading (e.g. Lefcheck et al. 2021). The only way to avoid such issues is to abjure the use of labels altogether and thus not venture any biological interpretation (e.g. Ulrich et al. 2022). Unfortunately, when devoid of any biological or ecological interpretation, the scientific value of a partitioning scheme becomes nil (e.g. Ulrich et al. 2022).

In contrast, statistical methods like ANOVA avoid the issues associated with the arbitrary nature and infinite number of partitioning schemes possible with Type II methods because their partitioning of the response variable is based on external constraints in the form of explanatory variables. When these external explanatory variables are uncorrelated, they typically yield a limited number of partitioning schemes whose labels are inferentially meaningful.

In the absence of external constraints, both the original Price equation and Type I methods avoid the pitfalls of Type II approaches because they do not partition an observed response variable in an ad hoc manner. Instead, these methods make use of 'internal constraints' based on null expectations. Indeed, the real – albeit weak – inferential claims that are possible under ideal conditions with the original Price equation and Type I method are due to their ability to measure a difference between expected and observed changes.

Type III methods represent a set of formulas concocted with a novel mix of logical non-sequiturs and nonsensical arithmetic, yielding a series of biologically senseless expressions (Fox 2005, Isbell et al. 2018). For instance, in lieu of proper mathematical derivations or proofs, Type III partitioning schemes are fabricated using a patchwork of eccentric techniques ranging from arguments based on verbal and visual analogies, to the inappropriate use of elementary arithmetic operations (see Pillai and Gouhier 2018 for an analysis). The end result is the creation of components that either have no physical interpretation, or that are completely inscrutable, as for example, the mysterious 'squared biomass' quantities that were inadvertently produced by Isbell et al. (2018) while attempting to partition biomass (Pillai and Gouhier 2018). These formulas represent a new absurdist phase in the ecological and evolutionary fetishism of the Price equation. Ultimately, the only thing Type III methods have in common with Type I and Type II methods is that the parts sum up to the total, a necessary (though not sufficient) condition for any numerical scheme to be characterized as a partition. Yet the novel Type IV method recently introduced by Clark et al. (2019) somehow fails to meet even this basic requirement by introducing a scheme whose parts do not properly sum up to the total (see Pillai and Gouhier 2020 for an analysis).

W. Ulrich and N. J. Gotelli

In his overture, Bourrat emphasizes that progress in science rests on at least two pillars: a desire to understand and a desire to predict. We agree that the Price partitions can be helpful in understanding mechanisms of ecological or evolutionary change because they decompose a single metric into meaningful components. In statistics, the partitioning of a sum of squares is useful because it decomposes variance into additive and interactive components of the factors in the model. These components can then be used to infer the relative strength of different processes for both experimental and correlative data. Calling the Price equation a 'tautology' is simply asserting that the whole is the sum of the parts. What is of interest is the size of those different parts. We agree that the Price equation does not provide explicit predictions, but that does not negate its utility in generating new patterns, especially for understanding the role of abundance in BEF relationships. In a similar fashion, logical inference alone cannot inform us about reality, but helps to formulate useful hypotheses. In this respect we agree with Godsoe that the Price equation mainly provides a tool for a better understanding of ecological theory.

Pillai and Gouhier reiterate their claim (Pillai and Gouhier 2019a) that Price partitions in ecology are arithmetically trivial and biologically meaningless and nonsensical; these are strong assertions that others have already addressed (Loreau and Hector 2019, Wagg et al. 2019). Pillai and Gouhier criticize the inability of Price partitions 'to separate out our expectations', but this refers only to predictive power and neglects the utility of empirical partitions to generate new patterns and thereby help to construct predictive theories.

Similarly, van Veelen's philosophical complaint is that Price partitions are not assumption-based. But we do not need explicit lists of assumptions for useful ecological interpretations of partitions that can be reasonably based on the strength of the additive and interactive components. Such interpretations also do not depend on the specific form of the partitioning; alternative interpretations for a particular pattern of the component parts may be possible and would help to clarify the precise details of the underlying mechanisms, which can yield new predictions. We note that the same argument would apply to any partitioning of a correlative model. In conclusion, we maintain that partitioning of composite variables, such as in Ulrich et al. (2022), is a beneficial tool for generating hypotheses and understanding complex ecological processes.

M. van Veelen

The central question of the dialogue is: if we use the Price equation, does that give us a correct result with a meaningful interpretation? This question is rather well-defined. In community ecology: we have a bunch of data, we partition them, does the partition mean anything? In evolutionary theory: we write the Price equation, with or without model assumptions, do we get a correct theoretical claim? The contributions of Bourrat, Godsoe, and Ulrich and Gotelli almost make one forget that these are math and stats questions, and create an elusive impression of what using the Price equation is.

P. Bourrat

Bourrat discusses inductive versus deductive interpretations, the desire to predict versus the desire to understand, and describes the Price equation as '*a placeholder for both unifying different models through a common language and assessing how far a particular situation is from the implicit idealized model elicited by the Price equation.*' I don't really know what any of that means. That might very well indicate that I am a limited thinker with no talent for philosophy, but it is also possible that this paints a needlessly complicated picture of what really is a rather well-defined activity, of which we would just really like to figure out if it produces correct and meaningful answers or not. Bourrat ends with '*Only by exploring the conceptual space of the aims of science will it be possible to set the Price equation within its proper bounds*', but for finding those bounds I am betting on the more prosaic approach in Pillai and Gouhier's contribution for community ecology, and my own for evolutionary theory.

W. Godsoe

The second contribution is also more abstract than I would think is necessary, with many statements that are at non-zero distance from full accuracy.

'*By comparison, the Price equation is holistic, starting with an overall description of change then working backwards to individual attributes. This point is made by George Price's noted collaborator John Maynard Smith, as quoted in* Okasha (2005).'

Godsoe suggests that the difference between the Price equation and other approaches is one of direction; reductionist approaches go one way, the Price equation works backwards. I don't think this is a correct description of what the Price equation does. Also, John Maynard Smith was indeed a 'noted' collaborator of George Price, but not on the Price equation. As a matter of fact, the paper that Godsoe cites, tells us that John Maynard Smith was '*never a fan of Price's equation and did not employ it in his own work.*' In a video that is the source for this, John Maynard Smith prefaces his discussion of the Price equation with '*I am not going to tell you what Price's Theorem is, because I don't actually understand it*'. What follows is a gentleman being very respectful to a coauthor, by describing the contrast between their two approaches as microscopic versus macroscopic (and not so much as forwards versus backwards), but we should perhaps also be open to the possibility that there might have been a good reason why he didn't follow.

Godsoe's contribution ends with '*There is substantial opportunity for dialogue with the Price equation providing tools for ecologists and ecologists providing new tests for the Price equation.*' This sounds vaguely positive and generally constructive, but it is also incorrect, and I would like to maintain that that matters too. The Price equation is a tautology, and tautologies do not need to be tested. Predictions do, but the Price equation does not produce predictions. And the whole question at hand is whether the Price equation is a useful tool or not, so just stating that it is, does not make it so (and formulating it as there being substantial opportunity for the Price equation *providing* tools is a bit weird, because the Price equation is itself supposed to be the tool).

W. Ulrich and N. J. Gotelli

Instead of addressing the arguments that have been made against the unstructured use of the Price equation, and partitioning in general, Ulrich and Gotelli pull a switcheroo, by pretending that the suggested problem is non-independence of data. That is just not what Pillai and Gouhier (2018, 2019a) claimed the problem was, and neither did I in any of my papers. And even if it were, their statements about it would still just be super weird. They describe non-independence of data as a serious problem in statistical analyses, but a different issue from the non-independence of data in what they call statistical partitioning. Apparently statistical partitioning is not the same as doing statistics, and to Ulrich and Gotelli, that closes the matter. They do not specify what kind of scientific activity 'statistical partitioning' is, if not statistics, nor do they give a reason why what is a problem for normal statistics would not be a problem here. The fact of the matter is that for them, partitioning is a free-for-all activity, without well-defined restrictions on when terms in it can be given

meaningful interpretations. To them, that provides an escape from the criticism, while it really is the root of the problem, as both Pillai and Gouhier and I described in our contributions to the dialogue.

<div align="right">Price and Popper</div>

Without a real link to theory or statistics, just partitioning away is not a meaningful scientific activity. It can be useful on the drawing board, but after the inspirational phase of sketching and just trying stuff out, there should be a more rigorous phase with scrutiny of whether any of this means anything, and, when applied to data, if that meaning survives statistical testing. It seems to me that some contributions to this dialogue prefer to skip that part of the job and defend that choice with a retreat into mysticism.

Epilogue

When suggesting the writing of this Dialogue, we were surprised to find out how divided ecology was on the usefulness of the Price equation in ecology; and how far the field seems from converging toward a consensus on its use and utility. Tautologies such as the Price equation should have a clearly defined purpose, and it has yet to be apparent what this purpose is. The 'desire to explain' is a good motivation for many scientific endeavors; however, explaining based on a movable, non-unique way of partitioning quantities, using 'labels without stable meaning', makes us feel like ice-skating without actual skates – a perilous journey. At the very least, presenting a change of any quantity as the sum of sub-quantities should be relatable to a null model, which would give some predictions about the relative contributions of these sub-quantities. This aspect does not seem to be the norm when using the Price equation in ecology. As such, additional work is needed on this front if the goal is to converge toward a consensus on using the equation.

From a sociology of science viewpoint, the debate developed in this Dialogue was also interesting because it illustrates some potential pitfalls when trying to reconcile 'opposite sides' around a common issue. Ecologists may or may not use the Price equation, and among the ones that have tried it, some may have perceived and acknowledged issues regarding its interpretation and usefulness, and just stopped using it. In contrast, others may have continued to use it without much questioning, as it helps them fulfill some academic obligations, such as publishing. These natural reactions can bias the general perception in the field in a status quo-preserving way:

1. The Price equation might be generally thought of as being useful just because a significant fraction of ecologists does not care – if they have never used it, they do not have an informed opinion and perceive this method based on the 'publication cue' (some colleagues use the Price equation in their published work);
2. Ecologists who have successfully published work based on the Price equation might be enticed to continue using it and to defend the method, because some reviewers have found it to have merits (but if the majority of ecologists do not use the Price equation, this appreciation might not be worth exactly what it should be);
3. Adversaries to the use of the Price equation are mechanically going to be a minority, whatever the veracity of their statements. The standpoint that a method does not work is less promising for colleagues searching for a solution than promoting it.

As curious spectators that never really got involved in this debate, what we wish for the future is an attempt to find the 'good null models' to generate predictions for the different fractions of trait-partitioning through the Price equation, and how these different null models can be related to ecological mechanisms. As for the inclusive fitness/direct fitness literature, we would like to see how the Price equation can move the field by reformulating model predictions in new terms rather than just applying it to 'raw data'. To finish this Epilogue with what it seems a good example of partitioning, our wish is that if the Price equation is indeed useful, it could be as theoretically and empirically justified as the responsiveness/inconsistency partitioning of the genotype × environment interaction variance introduced by Bell in the 1990's (Bell 1990, see also Venail et al. 2008 for a more recent application of the partitioning).

<div align="right">F. Massol and P. Peres-Neto (editors of Oikos)</div>

Author contributions

Pierrick Bourrat: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **William Godsoe**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Pradeep Pillai**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Tarik C. Gouhier**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Werner Ulrich**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Nicholas J. Gotelli**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Matthijs van Veelen**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

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