parent and the average trait of its o spring (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 (Price 2004, Okasha 2006, Frank 2012, Marshall 2015, Queller 2017, Luque 2017, Gardner 2020, Bourrat 2021). ere is however some dissent by those that question its usefulness for either purpose (van Veelen 2005, 2020a, van Veelen et al. 2012, 2020).

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).

Many ecological problems amount to linking the attributes of individual organisms (such as birth rates, death rates a 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 (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. is point is made by George Price's noted col laborator 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. example, Lion (2018) translates textbook ecological models of population growth (Lion 2018, Eq. 7) into models for change in traits. is approach allows for analyses of many familiar ecological models such as exponential growth, co sumer resource dynamics or species interactions mediated by a Lotka–Volterra model. e Price equation is just the n step allowing 'one to translate population dynamics into phenotypic change' (Lion 2018, Eq. 12). is derivation does not need additional ecological assumptions, meaning that interactions between species may be mutualistic, non-z sum, or non-linear.

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

W. Godsoe

Although often venerated as the 'algebra of evolution' (Price 2004), we contend that the evolutionary Price equation is a trivial, near-tautological identity (van Veelen 2020) 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 variational (change; or more speci cally, the covariance component of this variational change), and the residual di erence left o between the observed value and the expected variational transformation (natural change, Pillai and Gouhier 2018).

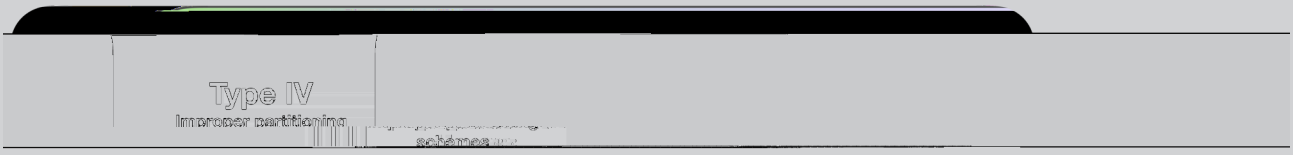

Figure 1. Taxonomy of ecological partitioning methods inspired by the Price equation.

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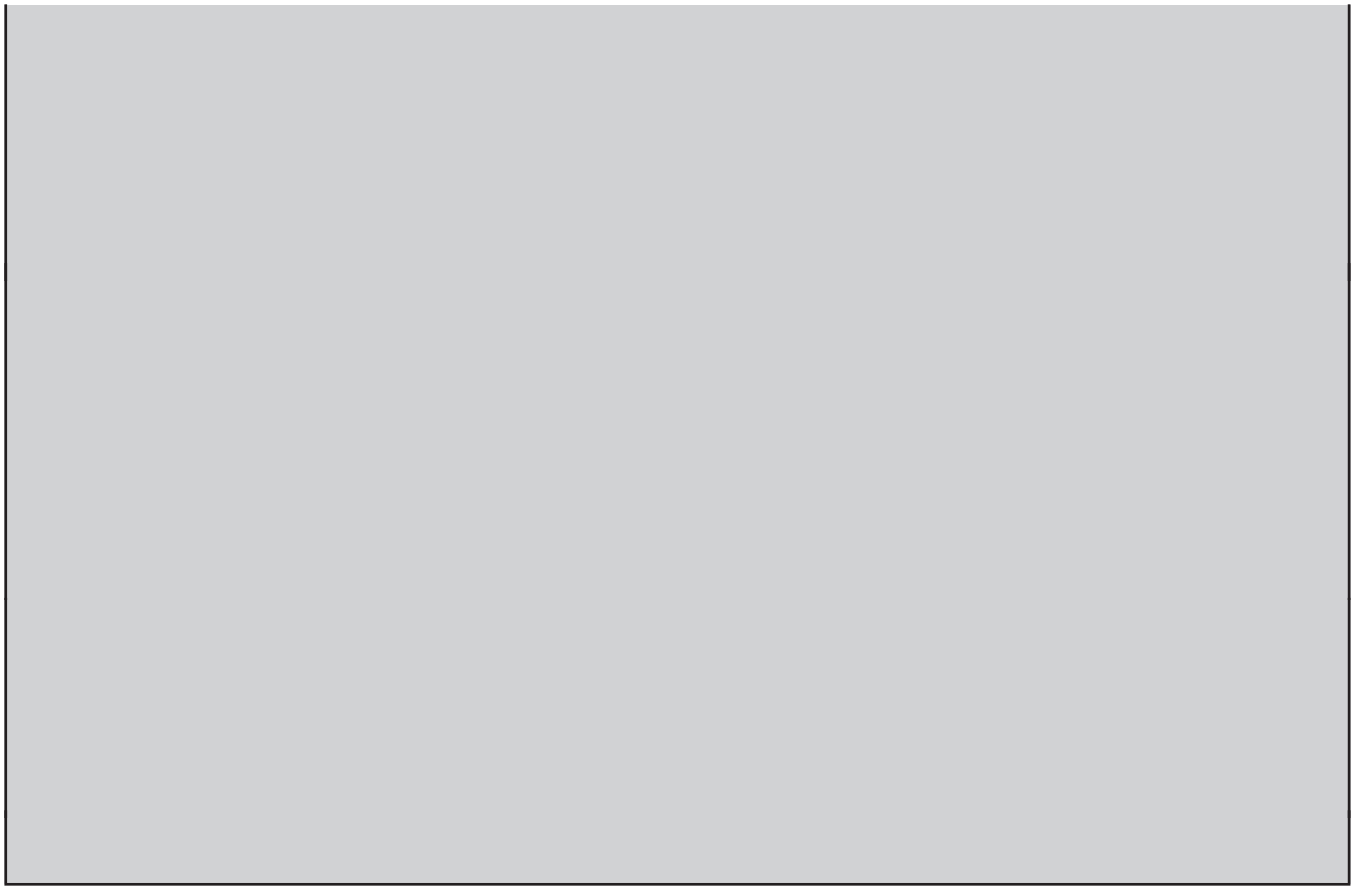

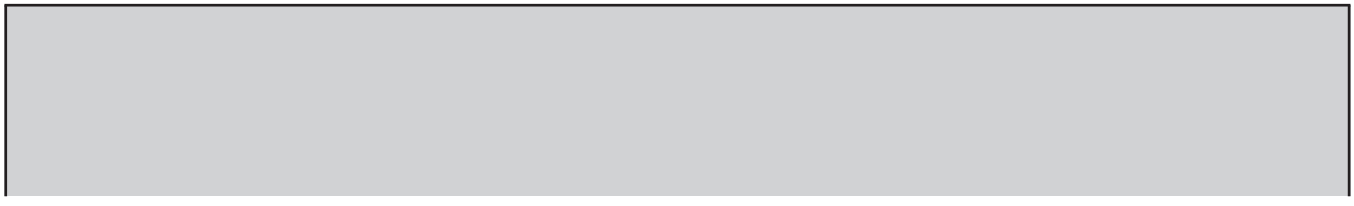

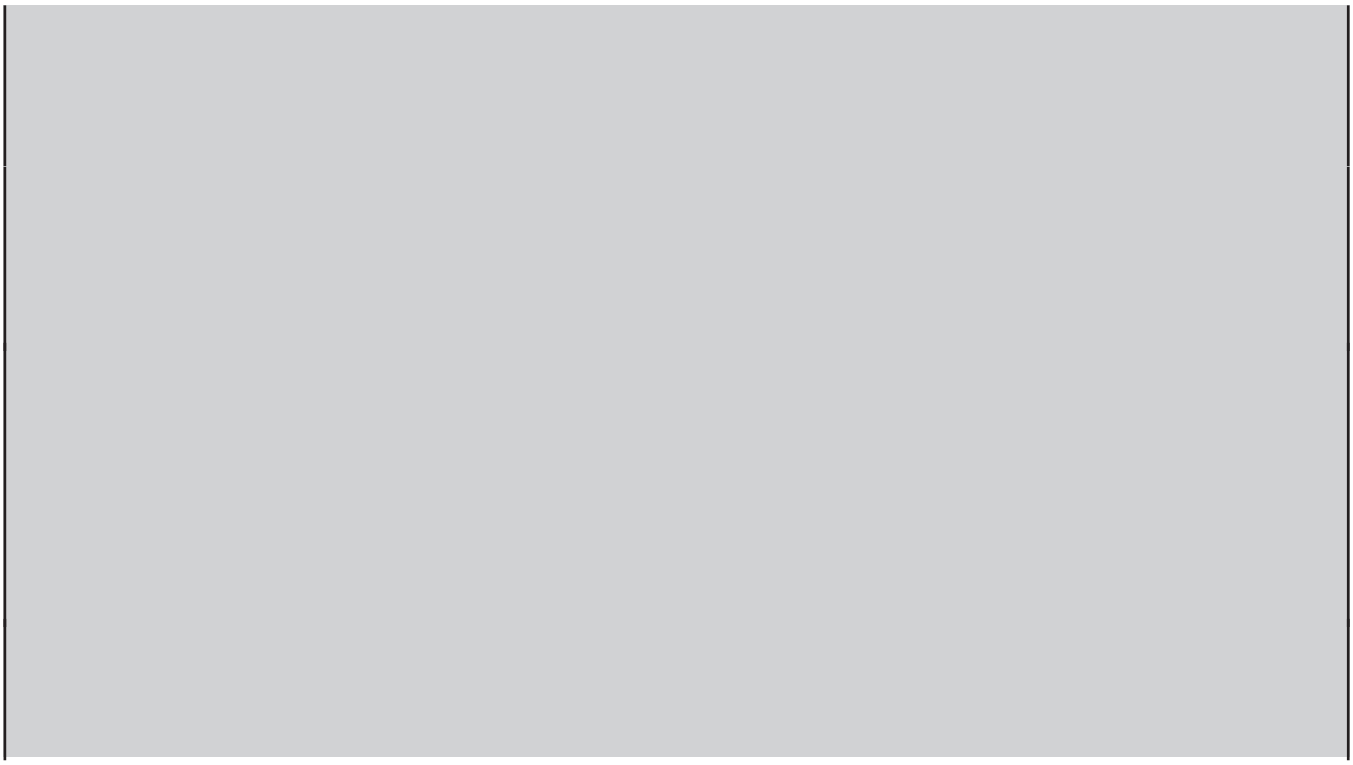

between di erent parts of science, used as a guiding principle or in combination with some assumptions. According to some philosophers (Kitcher 1989), and I agree with them, there is room in science for such uni cation principles. e Price equation is a good contender for being one such principle (Luque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

us, it appears that both camps have vastly di erent 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 reduce to pure empiricism and Popperian falsi cationism. 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 be

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M. van Veelen

e central question of the dialogue is: if we use the Price equation, does that give us a correct result with a meanin ful interpretation? is question is rather well-de ned. 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 mode assumptions, do we get a correct theoretical claim? e 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 equation is.

P. Bourrat

Bourrat discusses inductive versus deductive interpretations, the desire to predict versus the desire to understand describes the Price equation as ‘
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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.

Price and Popper

Without a real link to theory or statistics, just partitioning away is not a meaningful scienti c activity. It can be useful on the drawing board, but after the inspirational phase of sketching and just trying stu 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 nd out how divided ecology was on the usefulness of the Price equation in ecology; and how far the eld seems from converging toward a consensus on its use and utility. Tautologies such as the Price equation should have a clearly de ned purpose, and it has yet to be apparent what that purpose is. e 'desire to explain' is a good motivation for many scienti c 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. is 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 ful ll some academic obligations, such as publishing. ese natural reactions can bias the general perception in the eld in a status quo-preserving way:

1. e Price equation might be generally thought of as being useful just because a signi cant 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 the statements. e 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 nd the 'good null models' to generate predictions for the di erent fractions of trait-partitioning through the Price equation, and how these di erent null models can be related to ecological mechanisms. As for the inclusive tness/direct tness literature, we would like to see how the Price equation can move the eld by reformulating model predictions in new terms rather than just applying it to 'raw data'. To nish 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 justi ed 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).

F. Massol and P. Peres-Neto (editors of Oikos)

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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). Tadeusz 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.

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