The problem of models

Can quantitative evolutionary biology also call for an EES?

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Abstract: The Extended Evolutionary Synthesis (EES) has been presented as an expansion of the Modern Synthesis (MS). A common and parsimonious view maintains that MS's *quantitative evolutionary biology* remains both valid and central within the EES, insofar as the EES primarily introduces a more elaborate *qualitative* research agenda. This article examines the relationship between qualitative and quantitative approaches in the EES debate and argues for a more complex view of how the EES relates to the MS. Its guiding question is whether quantitative evolutionary biology itself might call for an EES. Although no specific answer is supported, the article analyzes the significance of this question and surveys the principal positions in the current literature. Two aims structure the discussion. First, by providing a detailed literature review, I show that, over the past two decades, quantitative research programs have increasingly contributed to modeling the phenomena at the core of the EES. The rationale for the EES is not confined to qualitative considerations; a growing body of work now (re)interprets population-level dynamics through the EES lens. Second, I present the *problem of models*: Is the mathematical framework of the MS sufficient to account for the phenomena emphasized by the EES, or must these models be extended? I identify and discuss four main positions: (1) strong accretionism—standard quantitative evolutionary biology is enough; (2) mild accretionism—the continuous historical expansion implies that current extensions do not constitute a substantive theoretical shift; (3) mild radicalism—population models require EES assumptions and novel applications; and (4) strong radicalism—some biological phenomena demand genuine modifications to the existing modeling framework.

Keywords: Extended Evolutionary Synthesis; Population Genetics; Price Equation; Quantitative Genetics; Philosophy of Biology; Scientific Change.

1. Introduction

The Extended Evolutionary Synthesis (EES) emerged during the first decade of the twenty-first century (Pigliucci, 2007, 2009; Müller, 2007; Pigliucci and Müller, 2010a, 2010b) as a conceptual framework aimed at integrating key aspects of evolutionary processes that were underdeveloped or absent in the Modern Synthesis (MS).[1] Most analyses that justify the EES propose a more complex understanding of the causes and mechanisms of evolution—specifically, how phenotypic variation arises beyond random genetic mutation and recombination, what mechanisms contribute to the transgenerational inheritance of traits, and how organism–environment fit is dynamically constructed throughout the life cycle (Laland et al., 2015). These constitute *qualitative* (Huneman, 2017, 89) analyses of evolutionary change and represent a distinct explanatory approach, a different "problem

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[1] A crucial point related to the historical dimension of the debate concerns the very theory under discussion: the MS. Several authors—most explicitly and recently Svensson (2023)—have argued that criticizing the MS as such is a misleading endeavor, since it represents a specific phase in the development of evolutionary theory (1930–1950) and has undergone continuous refinement and extension ever since. Even more problematic is the critique of so-called "neo-Darwinism," a term that actually predates the MS. To acknowledge the extensions of the MS beyond 1950, the label "Standard Evolutionary Theory" (SET) is sometimes employed instead; however, Svensson contends that this too is conceptually unsound, as evolutionary biology should not be regarded as a single unified *theory*. Acknowledging this important consideration, I will nonetheless continue to treat the MS as the primary point of reference—following the practice of EES proponents—since my discussion will also critically engage with the ongoing theoretical developments that have extended SET beyond the framework of the MS throughout the latter half of the twentieth century (for further discussion, see also Callebut (2010), Griesemer (2019), Fábergas-Tejeda and Vergara-Silva (2018)).

agenda", compared to the primarily *quantitative*[2] evolutionary biology that lies at the core of the MS.

By *quantitative evolutionary biology*, I refer to the suite of mathematical approaches in evolutionary science devoted to analyzing population dynamics across generations and identifying the causes and patterns of changes in population structure. This domain encompasses both population genetics—the first fully developed quantitative framework in evolutionary theory, formulated by R. A. Fisher, J. B. S. Haldane, and S. Wright, and foundational to the formation of the MS—and quantitative genetics, which also traces its origins to Fisher's (1918) work but underwent substantial elaboration throughout the second half of the twentieth century (for historical analysis, see Provine, (2001), Charlesworth and Charlesworth (2016), and Serpico et al. (2023)).

The central guiding question in this article is whether *quantitative* evolutionary biology also calls for an EES. No answer is defended. Rather, I justify that this is indeed a pertinent question, and an elaborated theoretical reconstruction of possible answers is advanced. As such, the aims of this article are twofold. First, it provides a critical and systematic review of research from the past two decades that develops quantitative evolutionary models grounded in the theoretical assumptions and empirical results from the EES—that is, models that integrate the qualitative perspectives of the EES into quantitative evolutionary theory. I conclude that a more elaborated view of the EES and the MS is deserved towards a more comprehensive integration between qualitative and quantitative approaches to evolutionary explanations. Second, it presents the *problem of models* in the EES debate, which regards different interpretations that the literature review might receive: Is the mathematical framework of the MS sufficient to account for the phenomena emphasized by radicals, or must these models be extended? I will analyse different positions on the problem of models to see how the problem of models is entangled, yet differentiated, from other key problems in the EES debate.

I begin by introducing the EES and examining its largely absent relationship with quantitative evolutionary biology. In Section 3, in connection with work by Lewens (2019), I present the *problem of models* as a specific concern that must be analysed within the EES debate. In section 4, I present four possible positions on the problem of models. I end with a series of questions concerning how a genuinely pluralistic view of evolution might integrate

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[2] My reference to quantitative approaches does not encompass all quantitative practices in biology. Instead, it specifically denotes those approaches aimed at mathematical modeling population dynamics in evolutionary processes. See below for details.

diverse evolutionary approaches within a coherent explanatory framework. The Appendix systematizes recent population models in biology from an EES perspective.

2. The Call for an Extended Synthesis

The aim of re-evaluating the foundational pillars of evolutionary theory is not something new (Eldredge, 1985; Gould, 1980; Gilbert et al., 1996; see Svensson (2023, Table 11.1) and Baedke et al. (2020) for further historical analysis). The EES is presented as one, probably the principal, attempt to incorporate recent trends in evolution beyond the MS perspective, highlighting the limits of the MS but being explicit that no "paradigm shift" or "Kuhnian scientific revolution" is needed (Pigliucci, 2007). While more revolutionary views[3] exist (Jablonka & Lamb (2020), Noble (2021); see Fábregas-Tejeda & Vergara-Silva (2018), dos Reis and Araújo (2020) and Gefaell and Saborido (2022) for analysis), and to some extent are connected to the EES framowerk, the EES is an *expansion*, but not an *alternative* to the MS (Pigliucci, 2007; Müller and Pigliucci, 2010b; Nuño de la Rosa, 2017)—the EES lies in-between *extremes*, a *middle-ground* position between revolution and conservatism in biological thought (Pigliucci and Finkelman, 2014).

Following Baedke et al. (2020), the EES motivations are threefold (for recent presentations of the EES, see Laland et al., 2014, 2015; Müller, 2017; Lewens, 2019; Huneman and Walsh, 2017):

1. There is a *growing body of evidence* suggesting that the *central tenets* of the MS[4] are empirically problematic, insofar as several key biological phenomena—now recognized as central to evolutionary dynamics—remain largely unaddressed within the MS framework. Which phenomena are at stake? Critics of the EES sometimes refer to a "laundry list" (Welch, 2017) of processes emphasized by EES proponents, noting that the specific elements in the list vary across authors and over time (see Svensson, 2023, Table 11.1 for a detailed overview of these lists). To avoid the negative connotations of this expression, I refer to these processes more neutrally as *EES-phenomena*, including, for instance, developmental bias, plasticity, non-genetic inheritance, and niche construction, *sensu* Laland et al. (2015), or evolvability, phenotypic plasticity, epigenetic inheritance, complexity theory, and high-dimensional adaptive landscapes, *sensu* Pigluicci and Müller (2010b).

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[3] Albeit nobody so revolutionary as Lynn Margulis was: "It's wrong like phrenology is wrong. Every major tenet of it is wrong" (quoted in Kelly 1994, 470).

[4] For description of these tenets, see Futuyma (2017), Laland et al., (2015) and Müller (2017).

2. Due to the growing body of evidence concerning EES-phenomena, the EES introduces a *new problems agenda* (Love, 2010; Buskell, 2020) in evolution: a deep *qualitative* inquiry into the mechanisms and causes of evolution. The main fields motivating an EES (and producing the growing body of evidence) are entangled with searching for the causes and mechanisms that produce phenotypic change in populations.

3. As a result, a *more pluralist perspective* on evolutionary explanations emerges, in which the strength of quantitative methods central in the MS is enriched by a more rigorous and complex understanding on qualitative aspects of evolution: "Evo-devo [or other disciplines aligned with the EES] does not invalidate the formal framework of the Modern Synthesis, but adds another level of explanation" (Müller, 2007, 6; see Laubichler (2010) and Minelli (2010) for discussion).

One of the most contested issues raised by the EES concerns the explanatory scope of quantitative evolutionary biology. Quantitative evolutionary biology, particularly population genetics, constituted the theoretical core of the MS in at least three major respects (Beatty, 1987; Bowler, 1989; Gould, 2002; Delisle, 2011). I) *Historical*: It emerged in a context where different frameworks—the mutationist and selectionist schools—were in tension, and population genetics proved capable of fostering reconciliation, thereby enabling the unification of diverse biological disciplines within a synthesized evolutionary framework. II) *Theoretical*: The MS adopted the definition of evolution and the main causes of evolutionary change used in population genetic models. III) *Empirical*: Population genetics established the methodological foundation for testing evolutionary hypotheses through quantitative data, and as such, the main labour of the so-called architects of the MS was to link the models with observable patterns in natural and experimental populations, and the knowledge of different disciplines informing evolution.

However, despite the resounding success of quantitative evolutionary biology, the EES proponents state that their motivations (described before) cannot be accounted for under the MS quantitative evolutionary approach. The central problems can be grouped into two main issues. The first point emphasizes that *a qualitative analysis of evolutionary causes and mechanisms should be incorporated into our understanding of evolution to foster a more pluralistic perspective beyond quantitative approaches*. The second point highlights that *such qualitative investigations cannot be fully pursued within the restrictive assumptions of the MS*. Let's describe them:

1. The formal framework of quantitative evolutionary biology abstracts away from the developmental, ecological, and physiological processes that cause phenotypic evolution, and proponents of the EES aim to put these processes at the core of evolutionary research: "The ongoing shift from a population-dynamic account to a causal-mechanistic theory of phenotypic evolution brings with it a significantly expanded explanatory capacity of evolutionary theory. It has become possible to address phenomena of evolution that were untreatable by the MS" (Pigliucci and Müller, 2010b, 12). A comprehensive understanding of evolution requires not only quantitative models of gene frequency dynamics but also qualitative accounts of how evolutionary causes and mechanisms operate across multiple levels of organization: a "shift of emphasis from statistical correlation to mechanistic causation" (Pigliucci and Müller, 2010b, 12). Carroll (2005, 294), elegantly, in one of the most influential books in evo-devo, raises precisely this point: the view (from population genetics) "forces the explanation toward mathematics and abstract descriptions of genes, and away from butterflies and zebras… Instead of 'change in gene frequencies,' let's try 'evolution of form is change in development'." A deep qualitative understanding of development, then, must be a central problem agenda in evolutionary biology.

2. The MS quantitative and mathematical approach to evolution relies on *specific modeling and empirical assumptions* that tend to simplify a qualitative analysis of the causal and mechanistic dimensions of evolutionary change: that variation is random (non-adaptively oriented) and produced by mutations and recombinations, that natural selection is the only cause of adaptation, and that genetic inheritance is responsible for transgenerational transmisión of traits, among others. The empirical and modeling assumptions of the MS quantitative approach represent a limited view of evolutionary causes, processes, and factors: "Many mechanisms now known to influence evolution—such as developmental plasticity, epigenetic inheritance, and niche construction—cannot be adequately represented within the traditional gene-centered framework" (Laland et al., 2015, p. 6). The EES argues that numerous research fields that accumulated notable advances over the past few decades—such as developmental biology, epigenetics, ecology, systems biology—have demonstrated the need to reconceptualize evolution beyond these restrictive assumptions. In this view, the MS captures only a subset of the processes shaping evolutionary dynamics. Consequently, pursuing a deep and adequate qualitative analysis requires moving beyond the assumption of the MS: "The Modern Synthesis was built upon assumptions of random genetic variation and natural selection as the principal

> drivers of evolution, but empirical advances now reveal a much broader landscape of causal factors" (Müller, 2017, 3).

I aim to focus on the specific relationship between the EES and quantitative evolutionary biology—particularly, the interplay between the more deep qualitative analyses of evolution emphasized by the EES and the consequences for the quantitative explanatory framework central to the MS. The pluralist approach of the EES often underemphasizes the implications and consequences of qualitative analysis in quantitative models. This is indeed a topic that did not receive much attention. In particular, the main texts presenting and defending the EES do not engage in a detailed debate concerning how assumptions aligned with the EES are to be included in quantitative models (Pigliucci 2007, 2009; Müller 2007, 2017; Laland et al., 2014, 2015). Comments are limited in seminal presentations of the EES—but see Pigliucci (2008) and Craig (2010). In general, the discussion is largely confined to emphasizing how the EES diverges from traditional quantitative genetics and that a different research agenda, or scientific *perspective* (Walsh and Rupik, 2023), is needed. Central edited volumes on the EES, such as *Evolution: The Extended Synthesis* (Pigliucci and Müller, 2010a) or *Challenging the Modern Synthesis* (Huneman and Walsh, 2017), do not offer[5] a systematic way to relate the effects of the EES's qualitative approach with quantitative frameworks.[6]

For that reason, I concur with Svensson (2023, 290) when he notes that "[t]hese critics failed to deliver any constructive alternative analytical approaches to study evolution", and with Buskell's (2020, 2) remark "that its [EES] most explicit theoretical reflections to date are found in qualitative statements and pictorial representations". The net result is that the EES has become closely associated with qualitative analyses of evolutionary change, whereas MS's traditional emphasis on quantitative modeling remains untouched, part of a different research agenda and scientific perspective. Precisely, the non-revolutionary spirit of

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[5] Specific exceptions are Gavrilets (2010) on high-dimensional landscapes, Uller and Helanterä (2017) on non-genetic inheritance, and Pocheville and Danchin (2017) on genetic assimilation.

[6] Notably, although not always in a fully systematic way, this situation has begun to change, and principally due to the works overviewed in the Appendix. For example, in the final chapter of the recent *Evolution Evolving* (Laland et al., 2024), authors present a "new vision" of "the structure of evolutionary theory" by outlining "a research agenda for the twenty-first century" and note that "formal theory exploring how developmental processes connect genetic to phenotypic evolution becomes important" (p. 242) and, consequently, that "a concerted interdisciplinary effort will be needed for a true understanding of how evolution evolves" (p. 245).

extending (and not abandoning or substituting) the MS theory enables a parsimony with the EES, since the extension does not intervene on MS quantitative foundations. I believe a much more complex image is now needed.

The guiding question in this article is whether quantitative evolutionary biology also calls for an EES. The main motivation for this question is that, over the past two decades, there has been a significant systematization of quantitative approaches to evolution that adopt empirical and modeling assumptions from the EES. In this respect, it is now a *misconception* to rigidly associate the EES with a qualitative view of evolution and the MS with a quantitative one. Many authors argue that there exist—and there will increasingly exist—models of evolutionary change that cannot be fully encompassed within the tenets of the MS. In this sense, this article offers a systematization of recent evolutionary models from those who adopt *EES assumptions* (Laland et al., 2015) or *EES tenets* (Pigliucci and Muller, 2010b; see also Carroll, 2008). Call it *population ontogenetics*, *extended quantitative evolutionary biology*, or any other catchy expression: its *leitmotif* is that the empirical advances in the qualitative analysis of evolution prompted by the EES should, in some form, be reflected in quantitative approaches. After evolution turns its attention to qualitative inquiry, closer "from butterflies and zebras" (Carroll, 2005), how do we come back to mathematics? How can we construct mathematical models in evolution when "evolution of form is change in development" (Carroll, 2005)? EES assumptions must guide population modelling; efforts must be on searching for "transformation of quantity into quality and vice versa" as Engels said (1883, quoted in Svensson, 2018, 3). If "[a]ll models of evolution rely on making the complex tractable" (Helanterä and Uller, 2020, 6), how do we make the complexity underlying EES-phenomena mathematically tractable? From a theoretical standpoint, the key takeaway is that the time has come to approach the relationship between quantitative and qualitative approaches to evolution with greater systematicity.

3. The Problem of Models: Rethinking the EES-MS Relationship

Over the last two decades, there has been a marked increase in research devoted to modelling EES-phenomena. In the Appendix, this literature is organized and presented in relation to specific EES-phenomena and the modelling frameworks employed. Comments on specific cases and general models will be made in Section 4. Of course, attempts to model such phenomena are not entirely new: the EES, as formulated in the twenty-first century, seeks to provide a coherent framework for processes that had been recognized earlier, even if they were not yet robustly supported by empirical evidence or integrated into a unified research program. Influential early examples include Laland et al. (1996, 1999), Wagner

(1988), Gavrilets (2004), Otto et al. (1995), Okasha (2006), Rice (2002), Houle (1992), Cowley and Atchley (1992), and Arnold (2003). However, as the empirical and conceptual foundations of the EES began to solidify, a growing number of researchers turned their attention to the challenge of incorporating insights from qualitative studies into quantitative modelling. Yet, as noted in the previous section, this body of research has not been fully articulated as a constitutive component of the EES.

An immediate question might come to our minds: Do all these models and studies genuinely support the call for an EES, or the other way around? Should they be taken as evidence for the necessity of an EES, or rather as demonstrations of the explanatory power already inherent in the MS? A competing interpretation—one that has been advanced by several authors—holds that mathematical modelling of the EES-phenomena in fact shows that the quantitative framework of the MS is sufficient. The broader the explanatory reach of MS-based quantitative modelling, the smaller the need for any substantive extension. While some models are made by self-declared EES defenders (e.g., Helanterá and Uller, 2010), this is not always the case (e.g., Day and Boundaransky, 2011). This issue is central to what I refer to as the *problem of models*. In what follows, I introduce it and examine the diverse responses it has elicited.

Disputes over the validity of scientific frameworks often gain depth through shedding light on what is truly at stake in such debates. In a recent appraisal of the EES debate, Timothy Lewens (2019) offers incisive conceptual tools for clarifying the many faces of the EES debate. He distinguishes between *accretionists*, who see no need for substantial revisions to evolutionary theory, and *radicals*, EES advocates calling for significant—sometimes sweeping—modifications. I will follow Lewen's terminology. Given the multifaceted nature of the debate, it is unproductive to frame it as a single binary question: "Should evolutionary theory be revised?" Lewens' key contribution lies in disentangling this overarching query into a taxonomy of questions, each reflecting distinct dimensions of the controversy. Within this framework, one can be accretionist or radical in connection to three specific problems under consideration:

1. The *historical problem* concerning reconstruction of the MS: To what extent has evolutionary theory already addressed EES-phenomena in its history?
2. The *empirical problem* regarding the search for evolutionary processes and causes: Addressing empirical questions concerning the mechanism of phenotypic variation, transgenerational inheritance of traits, or organism–environment developmental interactions.

3. The *philosophical problem* about key conceptions and epistemic frameworks in evolution: How should we understand selection and adaptation? What is an evolutionary process?

While this demarcation illuminates the richness and diversity of the EES debate, I propose that a fourth question warrants distinct consideration: the adequacy of mathematical models in evolutionary theory. I refer to this as the *problem of models* (henceforth: PM).

4. PM: Is the mathematical framework of the MS sufficient to account for the phenomena emphasized by the EES, or must these models be extended?

The problem behind PM concerns the interpretation of the literature reviewed in the Appendix. To explain the "neglected" and "ignored" factors in evolutionary theory alleged by EES proponents, is it necessary to modify or extend the population models in standard evolutionary theory? Do changes in the mechanism of inheritance, the units of variation, and the construction of organismal fitness entail modifying population models in our measurements of population change? Despite its significance for the EES debate, this has not been a problem that received detailed discussion (some authors commented on this—e.g., Svensson (2018), Vidya et al. (2023), Villegas (2023), and Rama (2025)).

Lewens does, in fact, analyze this problem by discussing the use of certain "analytical tools" to model EES-phenomena. However, treating the PM separately is motivated by a different set of considerations. First, the literature reviewed here justifies the legitimacy and significance of the PM: there is not merely a handful of isolated cases (as Lewens discusses), but a growing body of work employing analytical tools while endorsing, at least in part, EES tenets. Second, the adequacy of population models constitutes one of the principal arguments deployed by accretionists against radicals. In attempting to downplay the significance of the EES's qualitative approach, supporters of the MS frequently appeal to the explanatory strength of quantitative evolutionary biology—i.e., implicitly, the PM is already under discussion. Third, positions taken on the PM can be maintained with quasi-independence from the stances adopted on the other problems identified by Lewens—one may be an accretionist or a radical with respect to the PM while remaining relatively (though not entirely) independent in one's views on the other issues. Finally, treating the PM as a distinct element within the EES debate serves to highlight the importance of reconsidering the relationship between quantitative and qualitative approaches to evolution, a topic that, as argued, warrants more sustained attention.

Having introduced the PM, let's analyze the ways of being accretionist and radical concerning PM. Firstly, an accretionist on PM states that no modelling extension is needed, that no "extended evolutionary quantitative biology" is in fact required. Alternatively, a radicalist on PM states that the qualitative advances in EES-phenomena also deserve modelling extension in quantitative approaches—that a deepened qualitative agenda affects the quantitative one. Going into details a bit further, I identify four possibilities[7]:

> **(1)** *Strong accretionist*: Standard quantitative evolutionary biology is enough.
>
> **(2)** *Mild accretionist:* Modification of quantitative evolutionary biology represents no drastic change with the foundations of MS, since quantitative evolutionary biology has always been expanding since its beginnings.
>
> **(3)** *Mild radicals:* Due to the explanatory leverage of EES, we must change the application, use, and modelling assumptions of population models to explain EES-phenomena.
>
> **(4)** *Strong radicals:* Some EES-phenomena do deserve modifications of population models, since both population genetics and quantitative genetics are limited frameworks.

As noted, the positions adopted on the PM are quasi-independent of the responses to the other problems identified by Lewens. Lewens (2019, 718) likewise examines the "cross-cutting assessment" of the questions he introduces, illustrating the various ways in which one might adopt accretionist or radical stances. While radical or accretionist stances on the PM are certainly related to corresponding positions on other issues, there remains a degree of independence, allowing for mixed positions. For example, one could adopt a strongly accretionist view on the PM while maintaining more radical positions on the historical problem. Mild accretionists may or may not recognize the empirical significance of the phenomena emphasized by the EES and may remain neutral on many philosophical questions. Conversely, for instance, neither mild nor strong radicals in the PM are obliged to adopt radical positions on the historical problem.

4. Positions on the Problem of Models

In this section, I will present each position of the PM, referring to some cases of their defense, and discussing some of the relevant literature presented in the Appendix.[8]

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[7] A related taxonomy, though not concerned with the PM, is presented in Shan (2024).

[8] A classificatory point must first be made. I will identify specific works as belonging to each position. Some works consist of entirely theoretical defenses of one of these positions (e.g.,

4.1. Strong Accretionism: “No, everything is well.”

Accretionists, following Lewens, have been claiming that the EES has no place in evolution since the alleged revolutionary vibes are out of place. This might be due to different answers to the questions raised by Lewens. Concerning the historical problem, accretionists state that the EES-phenomena have always been under the scope of evolutionary theory, even since Darwin (e.g., Wray et al., 2014). Regarding the empirical problem, some authors argue that the empirical basis of the EES is not sufficiently justified, as Charlesworth et al. (2017) or Dickins and Rahman (2012) analyze in relation to non-genetic inheritance, or Futuyma (2017, 2021) concerning genetic accommodation. As far as the conceptual problem, accretionists reject the idea that there are further causes of adaptation beyond natural selection—that “adaptation without natural selection is an oxymoron” (Svensson, 2023, 262).

The PM enables a different way of being an accretionist. *Strong accretionism* on PM states that the EES poses no relevant changes in the quantitative methods of evolutionary biology because all the phenomena that apparently justify the EES can be explained by the standard quantitative approach in the MS. As Wray et al. (2014, 161) responded in the famous *Nature* article about the EES, a strong accretionist answer to the PM says: “No, everything is well.” No model extension is needed, and the EES does not affect the bases of quantitative evolutionary biology: “Most evolutionary geneticists would agree that the major problems of the field have been solved,” Charlesworth said (1996, 220), since, as Lynch (2007a, 364) reinforced, “the basic theoretical machinery for understanding the evolutionary process is well established”. Indeed, this is a common accretionist response to the EES: while the EES is presented as an effort to get into more details concerning the qualitative analysis of evolution, this qualitative analysis does not provide substantial modifications to the

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Craig 2010; Futuyma 2017). These works reflect the authors’ own self-declared standpoints. In other cases, authors present models that I interpret as belonging to one of the positions defined here. It is important, however, to separate the “art from the artist”—the model from the modeler. The fact that one constructs a model that, for instance, extends beyond standard quantitative evolutionary biology makes the model part of a strong radical position; it does not mean that, if we ask them, the authors themselves should be taken to endorse such a position. This is an interpretation of the model, not a claim about the authors’ theoretical commitments. Similarly, the fact that an EES-phenomenon is modeled using standard methods does not imply that the authors are against the EES. For example, Laland et al. (1996, 1995)—central proponents of the EES (i.e., radicals)—model niche construction using standard population genetics. In this case, the model represents an accretionist position, even though the authors, in other theoretically oriented work (e.g., Laland et al., 2015), defend a radical position.

quantitative approach of evolution, which is, and has been, the core of evolutionary theory. All in all, the EES "poses no challenge to the explanatory and conceptual resources of the MS, which are sufficient" (Dickins and Rahman, 2012, 2913).

A central tenet of radical accretionism on PM is the defense of a gene-centered definition of evolution. In light of the literature presented in the Appendix, there are two possible radical accretionist responses, both ultimately affirming the full adequacy of standard quantitative evolutionary approaches:

1. One response maintains that these models do not demonstrate the pervasive relevance of non-standard modes or causes of evolution. In other words, for instance, while extended modes of inheritance may exist, they are neither sufficiently widespread nor impactful to challenge the centrality of gene-based evolution; still, "[e]volution is a population genetic process" (Lynch, 2007a, 370). More generally, despite the EES call for raising the evolutionary importance of development processes, evolutionary remains, in essence, intact: "it's still genes and selection, all the way down" (Futuyma, 2021, 360).
2. A second, more elaborated possibility is that, even when acknowledging the importance of the EES-phenomena in quantitative approaches, these phenomena are ultimately explained at the genetic level and therefore fall within the explanatory standard approach in evolution. This strategy involves reducing developmental explanations to genetic ones, ultimately accounting for evolutionary change in terms of shifts in genetic composition within populations over phylogenetic timescales (see Rama (2024) for a detailed analysis).

Different EES-phenomena have been treated under this second strategy. Futuyma's (2017, 2021) analysis of the role of plasticity in evolution goes in this line. Opposition to West-Eberhard's theory of phenotypic accommodation, he states that "genes are 'followers' only to the extent that genetic assimilation or accommodation 'fine-tunes' an adaptation that had already evolved by selection and genetic variation" (Futuyma, 2017, p. 6, emphasis added). A similar position is taken by Gupta et al. (2017, p. 495, emphasis added): "Almost from its inception, quantitative genetics has been concerned with what is now called [...] phenotypic plasticity [...] the quantitative genetic notion of genotype × environment interaction reflects an appreciation that there may be genetic variation for the degree and nature of phenotypic plasticity in a population." Indeed, the field devoted to modelling "eco-evolutionary dynamics," which has recently produced several population models (see Appendix), has not entered into a systematic dialogue with niche construction models despite modelling similar phenomena—perhaps precisely because it preserves the tenets of the MS (e.g., Fussmann et al. (2007) and Travis et al. (2014); see Uller and Helanterä (2019) for discussion).

Non-genetic inheritance has also been explained using the second strategy by different authors, rooted in the idea that "epigenetic processes rely on mechanisms that are genetically inherited" (Dickins and Rahman, 2012, 2915). This enables the possibility of viewing non-genetic factors as controlled by genes, and thus tractable from genetic approaches of evolution: "Quantitative genetic evidence shows that epigenetic variation itself is influenced by genetic variation" (Dickins and Rahman, 2012, 2916). Haig (2007, 421, emphasis added) also takes this approach, first noting that the epigenetic state is "a property of the DNA sequence itself" and second that it can be "subject to natural selection on *conventional* mutations." Similarly, after reviewing the evolutionary significance of non-genetic inheritance and the adequacy of the quantitative approach to handle them, Charlesworth et al. (2017, 10) conclude: "Allele frequency change caused by natural selection is the only credible process underlying the evolution of adaptive organismal traits." In direct response to Carroll's evo-devo view of evolution as change in development, Lynch (2007b, 8598) states that "if we are concerned with the process of evolutionary change, then evolution is indeed a change in genotype frequencies." In turn, radical accretionism on PM is strongly based on the preservation of a gene-centered view of evolution.

4.2 Mild Accretionism: Business as Usual

There is another way to be an accretionist on PM. One might argue that, indeed, quantitative evolutionary biology has always been changing since its origins. Mathematical refinements, new niches, adequate generalization, and different applicabilities have been made across the twentieth century. And most notably, none of these modelling extensions demanded an EES. So, even accepting that evolutionary phenomena emphasized by EES proponents are relevant and they can require particular population models, this does not mean that the foundations of the MS are at risk. The expansion of the EES is, according to this position, by no means a controversial hitus in the history of evolutionary theory; it is just business as usual: "Evolutionary theory will continue to be extended, but there is no sign that it requires emendation" (Futuyma, 2017, 1). This position can be represented by Haldane's (1932, emphasis added) book, which closed his mathematical appendix with the following words: "The permeation of biology by mathematics is only beginning, but unless the history of science is an inadequate guide, it will continue" (quoted in Crow, 1987, 19).

This position is probably the one principally adopted by Wray et al. (2014). They are not in opposition to accepting the importance of many of the phenomena raised by EES proponents. However, they identify no special mark in current evolutionary biology that justifies an EES: “We, too, want an extended evolutionary synthesis, but for us, these words are lowercase because this is how our field has always advanced” (Wray et al., 2014, 164). This can be translated to quantitative evolutionary biology: it does not require any specific extension, since it has always been in extension and has adequately encompassed advances in the second half of the twentieth century, such as G-matrices, group selection, or neutral evolution. While Hamilton’s Rule, Kimura’s models of neutral molecular evolution, or Lande’s multivariate Beeder’s Equation can be considered an extension of previous quantitative views, they do not represent any Extension (with a capital letter). If we avoid seeing evolutionary theory “as static and monolithic” (Wray et al. 2014), we will observe a harmonious continuing expansion.

One important justification for the position of mild radicals is that quantitative methods in evolutionary biology are not limited to population genetics, despite it being usually presented as the “*sine qua non* of evolutionary explanations” (Bromham, 2009, 387). Crucially, it also encompasses (evolutionary) quantitative genetics. This point is significant because genetic accounts of evolution—even in multilocus models—often rely on G×P maps that are highly idealized and rarely realistic in natural populations. A key limitation of population genetics, therefore, is its focus on genes rather than on organisms, which are the actual targets of selection. Quantitative genetics, by contrast, emphasizes phenotypic evolution and thereby avoids an exclusively gene-centered approach: “quantitative genetics becomes liberated from the tyranny of genetic details in classical population genetics” (Svensson, 2018, 8). While it is true that population genetics has represented the foundational pillars of the MS, “[s]ome elements of the MS, like quantitative genetics, were actually broader and more nuanced than is often thought to be the case” (Svensson, 2018, 7).

Modelling EES phenomena does not require abandoning the foundational view of quantitative genetics, as the analysis of parental effects shows—see Hadfield (2012) for a review; Uller and Helanterä (2019) for discussion. Advances in quantitative genetics—such as the use of the genetic variance–covariance matrix to model complex genetic architectures, or specific extensions of the Price Equation to account for extended inheritance—can be seen as elaborations of existing models rather than as foundationally novel frameworks. These developments enable the modeling of diverse causal factors affecting phenotypic evolution, including those highlighted by the EES, thus framing a potential “bridge” for EES and MS (Svensson, 2018, 7). Separating the origins of quantitative evolutionary biology from its advances and diversity is key to mild accretionism. For instance, in the analysis of reciprocal causation—one of the two foundational pillars of the EES according to Laland et al. (2015)—, one of Svensson's (2018) arguments points out that reciprocal interaction between organism and environment has been systematically analyzed by quantitative approaches and that "Laland et al. (2015) have underestimated the *flexibility* and *scope* of evolutionary genetics, particularly evolutionary quantitative genetics" and as a result, "evolutionary quantitative genetics can be used to model reaction norm evolution, canalization, and phenotypic plasticity" (Svensson's, 2018, 8). This *flexibility* is precisely what allows one to characterize quantitative evolutionary biology as a "business-as-usual" enterprise—one that has been, and continues to be, extended in ways that readily accommodate the "routine progress of science" (Scott-Phillips et al., 2011, 39).

A specific case concerns the Price Equation (see Frank (2012) and Okasha (2006) for an introduction). While Fisher's Fundamental Theorem may be limited in its ability to model EES-phenomena, the Price Equation has proven to possess greater generality and a broader capacity to model evolutionary processes under diverse parameters: "Selection has been studied mainly in genetics, but of course, there is much more to selection than just genetic selection" (Price, 1995, 389). Indeed, this was Price's explicit aim: to construct "a model that unifies all types of selection (chemical, sociological, genetic, and every other kind of selection), which may open the way to develop a general 'Mathematical Theory of Selection'" (Price, 1995, 389).[9] If the *flexibility* of the Price Equation is fully recognized, no substantive modelling extension is required, and EES-phenomena could be considered already accommodated within Price's framework. In this sense, Price might be viewed as the principal "extended synthesist" in quantitative evolutionary biology—though, as Wray et al. (2014, 164) note, "these words are lowercase."

4.3 Mild Radicals: Beyond Standard Assumptions and Applications

Mild radicalism is not characterized by a fundamental rejection of standard quantitative evolutionary biology, nor does it deny that population models have always evolved. Rather, mild radicalism is defined by the view that the EES justifies *alternative uses* of population models, which require adopting *modelling assumptions* aligned with EES tenets. Consequently, the scope of population models must be broadened to encompass previously

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[9] It should be noted, however, that despite Price's aim, several authors have argued that the Price Equation is itself limited and warrants extension. Proposed extensions include treatments of migration (Kerr and Godfrey-Smith, 2009), categoric traits (Mann, 2025), or stochastic evolutionary processes (Rice, 2008a), among others (see Luque (2017)).

underexplored biological processes. The extension of population models must be taken as a constitutive and unavoidable element of the EES. This perspective acknowledges both the diversity of population models and their explanatory power in addressing phenomena beyond the standard analysis of genotypic frequency changes. Its emphasis, however, lies on the applicability of models and the assumptions underpinning each application, advocating an extension of modelling practices beyond their conventional uses.

Mild radicalism on the PM is thus entangled with the call for the EES and can be understood as part of it: unlike mild accretionists, mild radicals maintain that the models presented in the Appendix provide further support for the EES and, simultaneously, that the extension of models is itself a consequence of the EES. By contrast, mild accretionists see nothing particularly novel in the EES once its historical antecedents are taken into account.

A key point is that the *assumptions* and *applicability* of models (in the Appendix) are both motivated and justified by the EES. It is precisely the EES that spurs new applications of standard quantitative frameworks and advances new assumptions to be modelled. Mild radicals thus underscore the differing domains of applicability of existing models and maintain that these domains expand *because* of specific modelling assumptions justified by EES considerations. While richer analytical tools may not always be required, the assumptions concerning what aspects of reality the models should represent are themselves part of the modelling framework. Notably, much of the literature presented in the Appendix seems to fit in this position: new models are constructed by modification of existing ones in order to deal with EES-phenomena. Notably, in much of the literature reviewed, terms such as “unification” (e.g., Day and Bonduriansky, 2010), “integration” (e.g., Danchin et al., 2011), and “generalization” (e.g., Edelaar et al., 2023) appear as central to the stated goal of accounting for phenomena that remain unexplained. This, in turn, gave rise to new approaches that aim to fill explanatory gaps left by standard quantitative approaches. In this sense, quantitative evolutionary theory is indeed expanding.

Central to this discussion is our understanding of the role of mathematics in evolutionary biology (Morrison, 2014; Otsuka, 2019). There are multiple philosophical approaches to how models explain and represent reality. While some approaches may be more peripheral to the problem of models, such as a fictionalist account (Frigg, 2010), others are more directly relevant, notably, representationalist-perspectival accounts (Levin, 1966; van Fraassen, 2008; Godfrey-Smith, 2006; Massimi, 2020; Potochnik, 2017; for discussion, see Walsh and Rupik, 2023; Novelli and Rama, 2026). In these approaches, it is essential to recognize that models are epistemic tools designed to represent specific aspects of reality, and that their construction is guided by underlying assumptions about the systems they describe. These assumptions, in turn, become constitutive elements of the models themselves. For example, Fisher's Fundamental Theorem was used and interpreted by adopting assumptions characteristic of his historical and scientific context—such as a constant environment across generations[10]—whereas the niche construction models presented in the Appendix arise from a different set of assumptions, such as how organisms modify their environment across generations. Consequently, it is misleading to treat analytical tools as merely abstract mathematical structures, as if quantitative evolutionary biology were just mathematics. Rather, models function as devices crafted by biologists to achieve particular explanatory objectives, to which they attach specific interpretations, and which are embedded within broader research frameworks. An illuminating example is Morrisey (2015, 2050), who notes that "[m]ost quantitative genetic theory [...] is based on the linear components of relationships among traits and between traits and fitness." His model is, therefore, an *extension* of classical quantitative genetics under a different *modelling assumption:* non-linear development.

A central and systematized example is the Price Equation. As we saw, for some, the successful modelling of EES-phenomena using the Price Equation justifies a mild accretionist stance: a framework formulated nearly fifty years ago appears capable of accommodating contemporary empirical advances. Mild radicals, however, interpret the situation differently. Although Price formulated a "general theory of selection," any specific application of the Price Equation depends on particular modelling assumptions. In a recent analysis, Queller (2017) demonstrated that many of the central theorems in evolutionary biology are derived by reducing the second term on the right-hand side of the equation either to zero or to statistical noise (see also Luque (2017)). Crucially, this reduction is justified within a specific research program—one that foregrounds certain causal factors (such as selection on additive genetic variance) while occluding others (such as environmental change or non-genetic inheritance). Thus, the standard use and derivation of the Price Equation track the core commitments of the MS.

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[10] The Price Equation enables a different interpretation of Fisher's second term, showing that Fisher did not assume environmental constancy (Price, 1995; Okasha, 2006). However, this does not negate the fact that, in Fisher's time, the Fundamental Theorem was centered on the first term and on the analysis of genetic variance, without considering changing environments—i.e., that this is the way Fisher's Fundamental Theorem has been traditionally interpreted.

However, different uses are possible. A particularly illuminating example from EES proponents has been provided by Wade and Sultan (2023), which employs the Price Equation to uncover the evolutionary consequences of "niche-construction traits" for directional population change—with similar cases concerning non-genetic inheritance discussed by Day and Bonduriansky (2011), Helanterä and Uller (2010), and Otsuka (2015). To achieve this, they use the Price Equation in a *non-standard* manner: rather than treating the second term as negligible, they measure its evolutionary impact directly, while reducing the first term to zero. The applicability of this model thus shifts in accordance with a change in background assumptions—from interpreting the second term as noise to treating it as a source of directional evolutionary influence. Edelaar et al. (2023, 352) provided the most systematized, extended, and "generalized" use of Price Equation that "broaden our views on evolution" by modelling different EES-phenomena and going "[i]n contrast to a gene-centric view defining evolution only in terms of genetic change". Against the mantra "no adaptation without natural selection", they note that the Price Equation is a way of justifying the evolutionary importance of other factors causing adaptive traits: "Here we show that a *second driver* of adaptive evolution (the non-genetic inheritance of adaptively acquired traits) is numerically *independent* of natural selection" (Edellar et al., 2023, 369, emphasis added).

All in all, although all these models are formally derived from the Price Equation, the derivation relies on modelling assumptions that are themselves justified by distinct scientific research agendas: those of the MS on one hand, and the EES on the other (Rama, 2025). As a consequence, authors have argued that the primary epistemic role of the Price Equation is not to function as a model directly applied in evolutionary studies, but rather as a meta-model that underpins further derivations and thereby provides a suitable unifying framework for characterizing evolution (Gardner, 2008; Baravalle et al., 2025; Okasha, 2006, 2010; Okasha and Otsuka, 2020; Luque, 2017; Luque and Baravalle, 2021).

A similar scenario arises in the analysis of heritability within quantitative genetics (Slatkin, 2009; Danchin et al., 2011; Furrow et al., 2011; Wells and Stock, 2011; Fogarty and Wade, 2022). Many proposals seek to extend heritability analyses to incorporate factors beyond additive genetic variance—for example, through the concept of *inclusive heritability* to "*broaden* the concept of inheritance" (Danchin and Wagner, 2010, 216, emphasis added). In this process, quantitative genetics is neither abandoned nor fundamentally overhauled; rather, it is extended. Similarly, in the Appendix, there are different models of cultural evolution, a phenomenon that has long been appreciated (Fogarty et al., 2024), and indeed, it was one of the motivations behind Price's work. However, current models can approach cultural evolution by focusing on the limitations of existing models, as well as the need to integrate cultural evolution as part of the EES (Jablonka and Lamb, 2020). As a result, both the applicability of the models and the assumptions underpinning them become more closely aligned with the approach advocated by the EES.

4.4 Strong Radicals: Changing Models

Finally, the most radical position is represented by strong radicalism, which maintains that EES-phenomena cannot be adequately captured by existing quantitative models. According to this view, the formal methods themselves must be extended—or even replaced—to accommodate these phenomena. It is not "'business as usual' science", Laland et al. (2015, 10) argue, "it requires conceptual change". In short, new biological processes call for new mathematical tools. This position was already anticipated in one of the seminal EES papers by Pigliucci (2009, 221, emphasis added), who, in outlining future research directions, comments the "necessity for a *significant renovation* of the mathematical theory that accompanies the MS." He leaves the question open (although a parsimonious position is adopted in Pigluicci (2008)): "It remains to be seen whether this is an instance of population genetics theory reaching its limits in terms of the degree of biological complexity it can handle [...] or if a new but *substantial reformulation* of its methods and conceptual domain will move things forward again" (Pigliucci (2009, 221, emphasis added). Strong radicalism corresponds precisely to this call for a "substantial reformulation."

Limitations were adjudicated both to quantitative genetics and population genetics. One classical position here is represented by Lewontin's (1974) influential paper on the adequacy of quantitative genetics (see also Tabery (2014)). His main motivation is that standard analysis of qualitative genetics ignores certain biological phenomena that are relevant to understanding development, inheritance, and thus evolutionary causes. The complexity of developmental interactions imposes limitations on any quantitative methodology (Rama, 2026a), and "except under exceedingly restrictive, unrealistically simplified genetic and environmental conditions," quantitative genetics leaves us "lost in the [G×P] map" (Travisano and Shaw, 2013, 309). Pigliucci (2006), furthermore, has also pointed out the explanatory limits of advanced quantitative genetics, such as G-matrix models, which, even if they add a degree of complexity (and reality) by modelling genetic architectures, still face a deep foundational limitation "that undermines the whole G-based research program" (Pigliucci, 2006, 7).

Dupré (1993) represents a classic in organism-centered biology against the explanatory adequacy of population genetics, focusing primarily on the inadequacy of modelling evolution in terms of gene frequencies (see also Amundson (2005) and Laubichler (2010)). Craig (2010, 118), more recently, also held this position: "the population genetics foundation of the Modern Synthesis framework faces serious, potentially devastating challenges from the biological concepts emphasized by EvoDevo research", also stressing why we need to move beyond a gene-based approach in quantitative evolutionary biology: "Making the relevant changes to population genetics suggests at least that the central explanatory entity will no longer be the gene (as a Mendelian unit)" (Craig, 2010, 121).

Due to the rejection of a gene-centered approach to model evolution, strong radicals have offered conceptual critiques against the strategy used by strong accretionists: that, ultimately, developmental phenomena can be modelled using genetic approaches (Rama, 2024). Against this reductionism, strong radicals state that population models must account for the evolutionary role of development on its own. Sultan developed this argument in relation to norms of reaction (NoR) and the study of plasticity: "When the norm of reaction is viewed as a '*property of the genotype*,' the organism's developmental plasticity becomes simply an 'extended phenotype' emanating from the genes, and the evolution of these response patterns *can be understood in standard population-genetic terms*" (Sultan, 2019, 112, emphasis added). Against this interpretation, NoR and the plasticity of developmental means and products deserves a proper developmental account: plasticity is "an intrinsic property of organisms" (Sultan, 2021, p. 6). Modelling NoR with classical population genetics misrepresents the role of development in evolution and how this role must be conceptualized.

A similar scenario can be found in relation to non-genetic inheritance, in which the primary question informing models is conceptual: "Must we fundamentally revise our understanding of inheritance to incorporate these [non-genetic inheritance] new insights?" (Adrian-Kalchhauser et al., 2020, 1078). As we saw, strong accretionist treatment of non-genetic inheritance from the standard population genetic account is based on the idea that evolutionary questions are going to "be answered in terms of the natural selection of genes, with everything ontogenetic treated as solely a proximately causal process" (Mesoudi et al., 2013, p. 4). Opposing this view, strong radicals would respond that non-genetic inheritance deserves its own place in evolutionary models (see Appendix), and its effects in evolution cannot be downplayed to the genetic level. At the core of this position rely a view in which the transgenerational reconstruction of traits must be entangled with the developmental process behind trait ontogenesis (see Griesemer, 2014; Rama, 2026b): "[w]e need to return to an earlier, development- and organism-oriented view" (Jablonka & Lamb, 2020, 1) where "reproduction, inheritance, and development [were] all wrapped in one" (Gilbert, 2011, 121).

Beyond this conceptual criticism of strong accretionism, strong radicals are also motivated by the limitations of existing models. Many of the articles presented in the Appendix begin by outlining the assumptions and limitations of current models to justify their own proposals, which, directly or indirectly, explicitly or implicitly, are always related to EES-phenomena. In turn, we need a much more complex articulation of EES-phenomena in evolution to not misrepresent evolutionary processes and causes. This was the motivation for Gonzalez-Ferrero (2024) recent models in evo-devo dynamics, who, after analysing most detailed models in evolutionary quantitative genetics capable of addressing the role of development in evolution (such as Lande's multivariate approach), he concludes: "There is a lack of equations describing the long-term phenotypic evolutionary dynamics in gradient form while explicitly considering the developmental dynamics of phenotype construction and how development [quality] translates into genetic covariation [quantity]". Similarly, Fogarty and Wade's (2022, 9, emphasis added) analysis "draw out differences, *some substantial*, between models reliant solely on processes deemed core to the 'modern synthesis' and those that additionally incorporate a process emphasized by the extended evolutionary synthesis [which…] are *not already fully understood* through *conventional* quantitative genetics models."

Generalizing, new approaches, such as learning models of evolution (Watson et al., 2014, 2016), Rice's (2008b, 2012) dynamic quantitative approach, Morresey's (2014, 2015) nonlinear developmental dynamics, or Geoghegan and Spencer's (2012, 2013) population-epigenetic model, among others, depart from existing modelling limitations, a constrained explanatory scope, and the need to "expand our thinking" (Banta and Richards, 2018, 211) towards new territories. The modeling of EES-phenomena not only changes the applications (as mild radicals) but truly extends the explanatory power of quantitative evolutionary biology by advancing new modeling tools.[11]

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[11] Related to this position, Laubichler and Renn (2015) note that, while the Price equation is a suitable framework for modeling non-genetic inheritance in evolution, it entails a "quasi-independence" of system inheritance—proper to the partition of variants in the equation's structure—that precludes an adequate interactive view of systems of inheritance (but see Edelaar et al. 2023, 371).

5. Discussion: Towards a More Complex Image

In this article, I began by emphasizing that the extension proposed by the EES hinges on the establishment of a research agenda focused on the qualitative analysis of evolutionary processes and causal mechanisms, representing a framework distinct from the quantitative approach central to the MS. By providing a literature review, presented in the Appendix, a central conclusion of the article is that *a more complex understanding of the relationship between the EES and the MS is required*, as these frameworks cannot be neatly mapped onto the qualitative (EES) and quantitative (MS) domains. While such a distinction may have been more apparent in the early stages of the EES, the current state of research calls for a more intricate and integrated perspective. This, consequently, affects the motivations for the EES outlined in Section 2 (Baedke et al., 2020): a genuine *pluralism* in evolutionary biology requires the entanglement of diverse *research agendas*, which are not independent but intertwined, to integrate *experimental advances* with quantitative evolutionary modelling. Regardless of one's position in the PM, and particularly for proponents of the EES, the interplay between quantitative and qualitative approaches in evolutionary biology requires more sustained and in-depth analysis if it is to be representative of current modelling approaches. While pluralism in research agendas may still be a valid analysis, their neat mapping onto the EES and MS frameworks is less transparent than it was two decades ago.

Interpretations of population models may differ. For this reason, the present article has defined the *problem of models*, outlined its principal positions, and distinguished it from other issues identified by Lewens in the context of the EES debate. While I argued that the PM lies at the core of the EES discussion, it nonetheless retains a degree of independence from surrounding controversies. I end now by summarizing the central ideas advanced in this article to foster further discussion:

1. *The place of (evolutionary) quantitative genetics in the EES debate*. There is no possibility of reconciliation between strong radicals and strong accretionists. The former calls for rethinking quantitative approaches to evolution, stressing the limits of population genetics. The latter states that gene-frequency views of evolution still are the rule. However, mild positions are closer together, and here, quantitative genetics, and its phenotypic-oriented approximation, is definitely the key towards a less disruptive approach in the search for "transformations of the quality into the quantity" (Vidya et al., 2023; Svensson, 2018).

2. *What's in a model?* The PM debate would benefit from deeper engagement with the detailed analysis of mathematical models in science, including their idealization,

interpretation, and application in empirical contexts (Levins, 1966). This might be crucial to discern between, and possibly reconcile, mild positions. Key questions arise: What determines whether a model is genuinely new or merely a variant? Are modelling assumptions about reality truly constitutive of a scientific framework? Are alternative readings of the Price equation new models in their own right? Mathematical models are not accompanied by prescriptive instructions for use; it is the scientist's task to situate them within a biological (and historical) context, imbue them with meaning, and align them with specific epistemic aims from their scientific perspectives.

3. *A different call:* The relatively parsimonious extension proposed by the EES hinges on highlighting the need for a revised research agenda—one that focuses on the qualitative dimensions of evolutionary processes. Qualitative studies have long advocated for such an extension. However, a different call has been emerging, though not yet systematized, from within quantitative research. For both accretionist and radical perspectives, these calls are intertwined: the strength of MS's quantitative framework may be reinforced (for accretionists) or weakened (for radicals) by qualitative empirical inputs. Likewise, the evolutionary significance of EES-oriented qualitative analyses may be interpreted as substantial (radicals) or marginal (accretionists), depending on the evolutionary effects revealed through quantitative population models.

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Appendix: Literature review

Reference	Phenomena modelled	Modelling tools
Johannes et al. (2008)	Non-genetic inheritance	Quantitative genetics; epiQTL
Lehmann (2008)	Niche construction processes; Extended Phenotypes	Population genetics; Game theoretic models
Rice (2008b)	Evo-devo dynamics; Genetic architecture	Quantitative genetics
Kylafis and Loreau (2008)	Niche construction processes	Adaptive landscapes
Slatkin (2009)	Non-genetic inheritance; Heritable epialleles	Quantitative genetics
Post & Palkovacs (2009)	Eco-evolutionary feedbacks	Quantitative genetics
Helanterä and Uller (2010)	Non-genetic inheritance	Price Equation
Tal et al. (2010)	Non-genetic inheritance; Epigenetic variability	Quantitative genetics
Klingenberg (2010)*	Evo-devo dynamics	Quantitative genetics, G-matrices
Boyd and Richardson (2010)	Cultural group selection	Price Equation
Danchin and Wagner (2010)	Inclusive Heritability; Cultural Inheritance	Quantitative genetics
Gavrilets (2010)	Genetic architecture; epistasis	High-dimensional adaptive landscapes
Rice (2011)	The impact of development on evolution	Quantitative Genetics
Santure and Spencer (2011)	Genomic imprinting	Quantitative genetics
Danchin et al. (2011)*	Inclusive Heritability	Quantitative Genetics
Day and Boundaransky (2011)	Non-genetic inheritance	Price Equation
Shea et al. (2011)	Epigenetics Inheritance	Quantitative genetics; Selection- and detection-based model
Schoener (2011)*	Eco-evolutionary dynamics	Dynamic models; Eco-evolutionary feedback
Furrow et al. (2011)	Environment-Sensitive Epigenetics;	Quantitative genetics

	Epigenetic heritability	
Wells and Stock (2011)*	Epigenetic inheritance	Quantitative genetics; Heritability analysis
Wang et al. (2012)	Chromatin inheritance	Quantitative genetics
Hadfield (2012)*	Parental Effects	Quantitative genetics
Fox and Keer (2012)	Ecosystem functions	Price Equation
van Veelen et al. (2012)	Group Selection	Price Equation; Game theory
Conner (2012)	Evolutionary constraints	Quantitative genetics
Geoghegan and Spencer (2012)	Non-genetic inheritance; Epiallele transgenerational inheritance	Population-epigenetic models
Van Dyken and Wade (2012)	Reciprocal niche construction	Eco-evolutionary feedback; Adaptive dynamic model; Population genetics
Danchin et al. (2013)	Social inheritance; Gen-Culture inheritance	Quantitative genetics; Double pedigree
Schmitz et al (2013)	Epigenetic variance	Quantitative genetics
Geoghegan and Spencer (2013)	Heredity and stability of epiallelic variants	Population-epigenetic model
Salazar-Ciudad & Marín-Riera (2013)	Development-based GxP map	Adaptive Dynamics framework
Watson et al. (2013)	Developmental associative learning; Developmental memory; Non-linear developmental interactions	Learning models
Parvinen et al. (2013)	Ecological-adaptive dynamics; Plasticity	Function-valued adaptive dynamics
El Mouden et al. (2014)	Cultural inheritance; Behavioral evolution	Price Equation
Cortijo et al. (2014)	Epigenetic variants in complex traits	Quantitative genetics; QTLepi
Morrissey (2014)	Trait covariation; developmental constraints; Extended selection gradients	Quantitative genetics; Path analysis
Creanza and Feldman (2014)	Cultural niche construction	Population genetics

Travis et al. (2014)	Eco-evo feedbacks	Eco-evolutionary dynamics
Rivoire and Stanislas (2014)	Non-genetic inheritance; evolution of acquired characters	Quantitative genetics
Varona et al. (2015)	Epigenetic variance	Bayesian learning models; Quantitative genetics
Otsuka (2015)	Niche construction; Parental Effect; Developmental Interactions; Non-genetic inheritance	Price Equation; Causal Graphs
Morrissey (2015)	Non-linear developmental interactions	Evolutionary quantitative genetics
Watson and Szathmáry (2016)	Developmental associative learning; Evolvability; Eco-evo dynamics	Learning models
Watson et al. (2016)	Developmental associative learning; Evolvability	Algorithmic learning models
Nuño de la Rosa (2017)*	Evolvability	Quantitative genetics; G-matrices; Heritability analysis
Edelaar et al. (2017)	Plasticity; Habitat Choice	Individual-based simulation models
Baum (2017)	Behavioural evolution	Price Equation
Richards (2017)*	Plant epigenetics	Quantitative genetics
Uller and Helanterä (2017)	Non-genetic inheritance	Price Equation
Banta and Richards (2018)*	Epigenetics; non-genetic inheritance; epigenetic variability	Quantitative genetics
Boundariansky and Day (2018)	Non-genetic inheritance	Price Equation
Aguilar and Akçay (2018)	Gene-Culture Coinheritance; Trait behaviour evolution	Price Equation
Uller and Helantera (2019)*	Non-genetic inheritance	Price Equation
Edelaar and Bolnick (2019)	Phenotypic plasticity; Habitat choice (selection and adjustment of the environment)	Adaptive landscape
Gahlaut et al. (2020)*	Epigenetics; Epialles	Quantitative epigenetics
Bouchansky and Day (2020)	Non-genetic inheritance	Price Equation, Adaptive Landscapes

Henshaw et al. (2020)	Non-linear developmental interactions	Path analysis
Clark et al. (2020)	Niche Construction	Meta-analysis; Quantitative genetics
Tanaka et al. (2020)	Niche Construction	Dual adaptive landscapes
Anastasiadi et al. (2021)*	Non-genetics inheritance	Quantitative epigenetics
Baravalle and Luque (2022)	Cultural evolution; Dual-inheritance theory	Price Equation
Fogarty and Wade (2022)	Niche Construction: Ecological Inheritance	Quantitative Genetics
Wade and Sultan (2023)	Plasticity; Habitat Choice; Niche Construction	Price Equation
Gonzalez-Forero (2023)	Evo-devo dynamics; Non-genetic inheritance; Plasticity; Developmental bias; Social niche construction	Matrix Population Dynamics
Edelaar et al. (2023)	Niche construction; Parental Effect; Developmental Interactions; Non-genetic inheritance	Price Equation; Causal Graphs
Gonzalez-Forero (2023)	Evo-Devo Dynamics	Quantitative genetics; Matrix population models

*Table 1. Articles modelling related EES-phenomena from 2008 to the present. *Review article.* The literature review was conducted using a narrative approach. Relevant publications were identified primarily through searches in databases constrained by the particular period under analysis. An initial set of articles was selected based on their relevance to the research question and the explicit dialogue with the EES debate. Subsequently, a backward snowballing strategy was employed, whereby the reference lists of key articles—particularly review papers—were examined to identify additional relevant studies. This process was iterative, with search terms and inclusion criteria being refined as new themes and concepts emerged. Priority was given to peer-reviewed articles and influential reviews in the field of evolutionary biology.

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