

# The extended evolutionary synthesis: An integrated historical and philosophical examination

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## Abstract

Among biologists and philosophers, there is an ongoing debate over the Modern Synthesis and the Extended Evolutionary Synthesis. Some argue that our current evolutionary biology is in need of (at least) some substantial revision or nontrivial extension, while others maintain that the Modern Synthesis remains the foundational framework for evolutionary biology. It has been widely debated whether the Extended Evolutionary Synthesis provides a more promising framework than the Modern Synthesis. The nature and methodological implications of the Extended Evolutionary Synthesis were also examined. This paper offers an integrated historical and philosophical examination of the debate over the Extended Evolutionary Synthesis. It reviews the development of evolutionary biology of the twentieth century. It argues that there are substantial conceptual and theoretical differences between the Modern Synthesis and the Extended Evolutionary Synthesis, but they are not incommensurable paradigms in the Kuhnian sense. It also argues for a functional approach to the debate over these two frameworks of evolutionary theory.

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## 1 | INTRODUCTION

Among biologists and philosophers, there is an ongoing, hot debate over the Modern Synthesis and the Extended Evolutionary Synthesis. Some (e.g. Jablonka & Lamb, 2005; Koonin, 2012; Laubichler, 2010; Odling-Smee et al., 2003; Oyama, Griffiths, and Gray, 2001; West-Eberhard, 2003) argue that our current evolutionary biology is in need of (at least) some substantial revision or nontrivial extension, while others (e.g. Dickins, 2021; Dickins & Rahman, 2012; Futuyma, 2017; Lynch, 2007; Minelli, 2010; Noble, 2017; Wray et al., 2014) maintain that the Modern Synthesis remains the foundational framework for evolutionary biology. It has been widely debated whether the Extended Evolutionary Synthesis provides a more promising framework than the Modern Synthesis (e.g., Dickins, 2021; Futuyma, 2017; Laland et al., 2015; Müller, 2017). The nature and methodological implications of the Extended Evolutionary Synthesis were also examined (e.g., Gefaell & Saborido, 2022; Reis and Araújo, 2020). In this paper, I offer an integrated historical and philosophical analysis of the debate over the Extended Evolutionary Synthesis by examining both its historical development and philosophical implications. I begin with a historical introduction to the development of evolutionary biology of the twentieth century (Section 2). I then examine the nature of the Extended Evolutionary Synthesis and argue that the Extended Evolutionary Synthesis is basically an attempt for a new synthesis in the history of evolutionary biology (Section 3). Moreover, I assess the arguments concerning the methodological implications of the debate over the Modern Synthesis and the Extended Evolutionary Synthesis and argue for a pluralist stance (Section 4). Finally, I address a central issue of the debate (Section 5): will the emergence of the Extended Evolutionary Synthesis lead to a scientific revolution in evolutionary biology?

## 2 | A BRIEF HISTORY

Charles Darwin's *On the Origin of Species* (1859) made a profound impact on nineteenth century evolutionary studies. However, Darwin's theory of evolution by natural selection was not well received at the time and sparked controversy for decades. There were multiple, competing lines of enquiry in the study of evolution. Such a pre-paradigmatic period lasted until the 1940s when the Modern Synthesis took place (cf. Tanghe et al., 2021). The term Modern Synthesis was coined by Julian Huxley as the subtitle for his book, *Evolution: The Modern Synthesis*, published in 1942. Huxley (1942a) referred to the Modern Synthesis as a theoretical synthesis in which the Darwinian theory of evolution by natural selection and the Mendelian theory of genetics were incorporated into a new theory of evolution, especially thanks to the work of R. A. Fisher (1930), J. B. S. Haldane (1932), and Sewall Wright (1931).<sup>1</sup> The key idea of this new theory of evolution is summarised by Huxley with the words 'evolution is a joint product of mutation, recombination, and selection' (Huxley, 1942a, p. 29). Such a synthesis, argued Huxley, was of great importance to biology. On the one hand, it marked the end of the four-decade 'eclipse' of Darwinism and the rebirth of Darwinism as 'a modified Darwinism' (Huxley, 1942a, p. 27). On the other hand, the Modern Synthesis signalled the unification of biology. As Huxley (1942a, p. 26) puts it, 'Biology... has become a more unified science. It... no longer presents the spectacle of a number of semi-independent and largely contradictory sub-sciences, but is coming to rival the unity of older sciences like physics, in which advance in any one branch leads almost at once to advance in all other fields, and theory and experiment march hand-in-hand'.

In short, the Modern Synthesis was a movement that included a convincing refutation of the three major anti-Darwinian theories – the typological-saltationist, the teleological-orthogenetic and the transformationist-lamarckian and a synthesis of three major biological subdisciplines – genetics, systematics, and palaeontology (Mayr, 1993b; Smocovitis, 1992). Later the Modern Synthesis (MS), also called Evolutionary Synthesis (ES), was more often referred to a conceptual and theoretical framework that was shaped in this movement, especially in the 1940s.<sup>2</sup> One of the most influential founding documents of the MS is Theodosius Dobzhansky's *Genetics and the Origin of Species* (1937), whose central thesis is that '[e]volution is a change in the genetic composition of populations. The

study of mechanisms of evolution falls within the province of population genetics' (Dobzhansky, 1937, p. 16). The theses of Huxley's and Dobzhansky's books became two central tenets of the MS.

MST1. Evolution is a gradual process, resulting from genetic mutation, genetic recombination, and especially natural selection.

MST2. Evolution can be well explained in terms of population-level genetic changes. (cf. Lewin, 1980; Mayr, 1980, 1993a)

Based on these two central tenets, much important work (e.g. Lack, 1947; Mayr, 1942; Rensch, 1947; Simpson, 1944, 1949; Stebbins, 1950) was carried out in the 1940s.<sup>3</sup> Since then, the notion of MS as its 'foundation' has dominated the study of evolutionary biology (Buss, 1983; Lewin, 1980; Pigliucci, 2007).

Although the MS still remains a foundational framework for current evolutionary biology, both MST1 and MST2 have been contested since the 1970s. For example, Niles Eldredge and Stephen Jay Gould's theory of punctuated equilibria (1972) challenges MST1 by questioning that evolution is a gradual process, whereas the development of the biological sciences in the past five decades, especially in the fields of epigenetics, niche construction theory, evolutionary developmental biology (aka evo-devo), and genomics, seems to undermine MST2. As Massimo Pigliucci (2007) argues, there are some important evolutionary mechanisms or phenomena that are 'missing' from the MS. In other words, for many biologists and philosophers (e.g. Jablonka & Lamb, 2005; Laubichler, 2010; Odling-Smee et al., 2003), the significance of many important mechanisms or phenomena, including epigenetic inheritance, niche construction, and phenotypic plasticity, is incorrectly downplayed in the MS. In a nutshell, there are two main problems with the central tenets of the MS.<sup>4</sup>

Problem<sub>MST1</sub>. The MS overemphasises the significance and role of natural selection in evolutionary processes.

Problem<sub>MST2</sub>. The MS overemphasises the significance of genetic inheritance in hereditary processes.

As a result, there have been calls for the extension or revision of the MS since the 1970s (e.g., Eldredge, 1985; Gould, 1980; White, 1978). The Extended Evolutionary Synthesis (EES) is such a recent attempt. It was introduced and developed to provide an alternative framework to the MS for current and future evolutionary biology (e.g. Laland et al., 2015; Pigliucci and Müller, 2010).<sup>5</sup> The EES differs from the MS in some important respects. Laland et al., 2015 identify six main differences (see Table 1 for a summary). For example, the MS assumes that the major directing influence in evolution is natural selection, which alone explains why the properties of organisms match the properties of their environments (the pre-eminence of natural selection), while the EES assumes that developmental processes, operating through developmental bias and niche construction, as well as natural selection, contribute to the direction and rate of evolution and organism – environment complementarity (reciprocal

TABLE 1 Laland et al.'s analysis of the key differences between the MS and EES (Laland et al., 2015, p. 2).

The MS's core assumptions	The EES's core assumptions
Pre-eminence of natural selection	Reciprocal causation
Genetic inheritance	Inclusive inheritance
Random genetic variation	Non-random phenotypic variation
Gradualism	Variable rates of change
Gene-centred perspective	Organism-centred perspective
Macro-evolution based on micro-evolutionary processes	Macro-evolution based on various processes, including development bias and ecological inheritance

causation). In addition, the MS assumes that inheritance is fundamentally a process of the transmission of DNA information (genetic inheritance), while the EES assumes that inheritance extends beyond passing on DNA information to encompass epigenetic inheritance, physiological inheritance, ecological inheritance, behavioural transmission and cultural inheritance (inclusive inheritance) (Laland et al., 2015). Accordingly, acquired characters are not inherited according to the MS, while acquired characters can play important evolutionary roles by biasing phenotypic variants subject to selection, modifying environments, and contributing to heritability in the EES. Moreover, the MS assumes a gene-centred perspective: evolution requires and is often defined as change in gene frequencies. Populations evolve through changes in gene frequencies brought about through natural selection, drift, mutation, and gene flow. In contrast, the EES assumes an organism-centred perspective in the sense that developmental systems determine phenotypic variation and organisms modify selective environments. Evolution is redefined as a transgenerational change in the generation of heritable traits of a population. In other words, evolutionary process and inheritance are revised in a substantial way.<sup>6</sup> In a nutshell, the crucial difference between the MS and the EES is that the EES does not assume that ‘the burden of creativity in evolution (i.e. the generation of adaptation)’ rests on natural selection alone (Laland et al., 2015, p. 6).

### 3 | THE NATURE OF THE EES: A NONTRIVIAL EXTENSION OR AN INCOMMENSURABLE ALTERNATIVE?

A central issue in the recent debate concerns the nature of the EES. Is the EES a nontrivial extension of the MS, an incommensurable alternative to the MS, or something else? Some proponents of the EES (e.g. Laland et al., 2015) maintain that the EES is just a nontrivial extension of the MS. It is argued that the EES does call for a change of the foundational framework of evolutionary biology, a change that would not lead to a scientific revolution in a Kuhnian sense.<sup>7</sup> The key mechanisms of evolution identified by the MS, such as natural selection and genetic inheritance, remain important, but more need to be included. And these additional components (for example, epigenetic inheritance, niche construction, and phenotypic plasticity) are of equal importance to natural selection and genetic inheritance in the new framework. It is in this sense that the EES is an extension of the MS in the substantial way.

However, not all the proponents of the EES (e.g., Jablonka & Lamb, 2008; Noble, 2017) accept this modest account of the EES. It has been argued that the acceptance of the EES implies a radical transformation of the MS: ‘the EES proposes new ways to think about evolution, which involves substantial changes in concepts, processes, and notions of causality. The mechanisms highlighted by the proponents of the EES are not viewed by them as mere processes to be added to standard evolutionary theory, but as a different point of view that requires another interpretative framework’ (Reis and Araújo, 2020, p. 58). Juan Gefaell and Cristian Saborido (2022) even argue that the MS and the EES are incommensurable in three senses: semantic, methodological, and ontological. They argue that the concept of inheritance in the MS and the concept of inheritance in the EES are two distinct concepts; the MS and the EES differ radically in their research problems and explanatory foci; and the MS and the EES suggest distinct ontological accounts of organisms, the organism-environment relationship, and evolutionary causation. Thus, it seems to some that the EES is an incommensurable alternative to, rather than an extension of, the MS.

In contrast, many adherents of the MS are unconvinced by either of these two views. It is argued that, at best, the EES suggests some minor additions to the MS whose basic framework remains static. For example, Gregory Wray et al. (2014) agree with Laland and his colleagues on the point that niche construction, phenotypic plasticity, developmental bias, and epigenetic inheritance can alter evolutionary processes, but they doubt that they constitute the essential components of evolutionary biology. In their words, ‘[w]e invite Laland and colleagues to join us in a more expansive extension, rather than imagining divisions that do not exist. We appreciate their ideas as an important part of what evolutionary theory might become in the future. We, too, want an extended evolutionary synthesis, but for us, these words are lowercase’ (Wray et al., 2014, p. 164). Moreover, some advocates of the MS

hold a stronger position: the EES 'does not deliver theoretical change nor even an extension to the phenomena encompassed by the Modern Synthesis' (Dickins, 2021, p. 231).

In sum, there are four main views on the nature of the EES.<sup>8</sup>

**Strong EES:** the EES offers a completely new framework of evolutionary biology, which will eventually replace the MS.

**Moderate EES:** the EES introduces some new components to the core assumptions of the MS, though the old core assumptions are largely preserved.

**Moderate MS:** the EES introduces some new components, though the additions are not part of the core assumptions of the MS.

**Strong MS:** the EES can be fully accommodated within the MS.

It is clear that what is at issue is to what extent the EES differs from the MS. Proponents of the strong EES (e.g. Craig, 2010; Jablonka & Lamb, 2008; Müller, 2017; Noble, 2017; Reis and Araújo, 2020) argue that the EES is radically different from (or incommensurable with) the MS and the former will replace the latter eventually (see Figure 1), while supporters of the strong MS (Futuyma, 2017; e.g. Dickins, 2021) insist that the MS well accommodates everything introduced by the EES and the basic structure of the MS does not require any changes (see Figure 2). For proponents of the moderate EES (e.g. Laland et al., 2015), the EES extends the core assumptions of the MS (see Figure 3). For supporters of the moderate MS (e.g. Wray et al., 2014), the EES extends the MS but the core assumptions of the MS remain unchanged (see Figure 4).

From a philosophical point of view, there are substantial differences between basic concepts and core assumptions in the MS and the EES. For example, the EES's assumption of inclusive inheritance is not an extended version of the MS's assumption of genetic inheritance by simply adding new hereditary mechanisms such as epigenetic inheritance. In the assumption of inclusive inheritance, the significance of genetic inheritance is downplayed. That said, I argue that the substantial differences between basic concepts and core assumptions in the MS and the EES do not imply that the MS and the EES are two incommensurable paradigms in a Kuhnian sense, strictly speaking. For Thomas Kuhn (1970), a paradigm (as a disciplinary matrix) is a community-based consensus in a scientific field which dominates scientific practice. It is doubtful that the EES today counts as a Kuhnian paradigm. As a leading proponent of the EES indicates, there is a lot of work to do to demonstrate the full potential of the EES as a full-blown extended framework for evolutionary theory (Pigliucci, 2007, p. 2748). Therefore, I argue that the

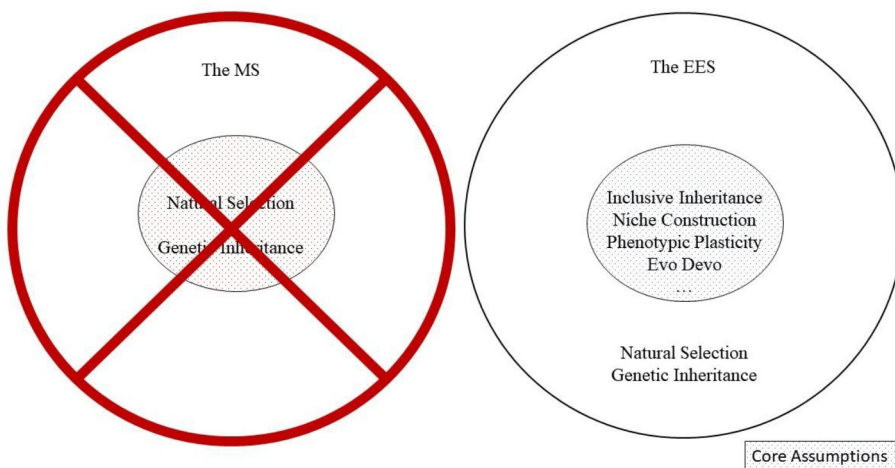


FIGURE 1 Strong EES.

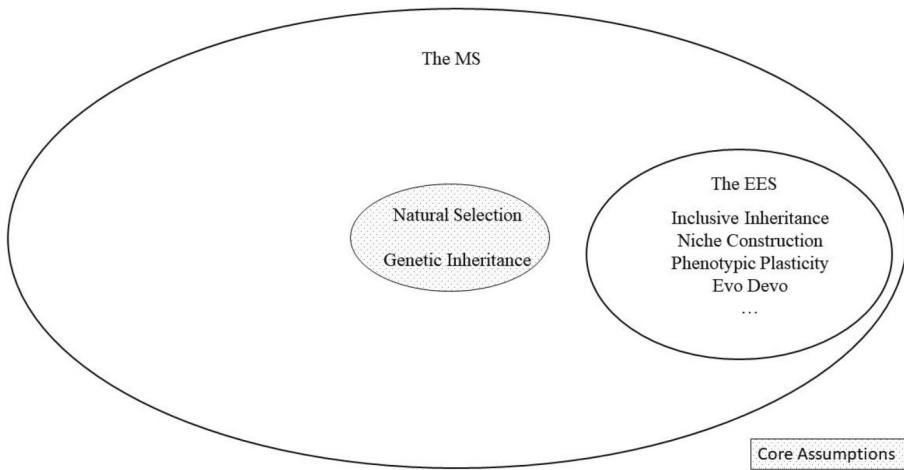


FIGURE 2 Strong MS.

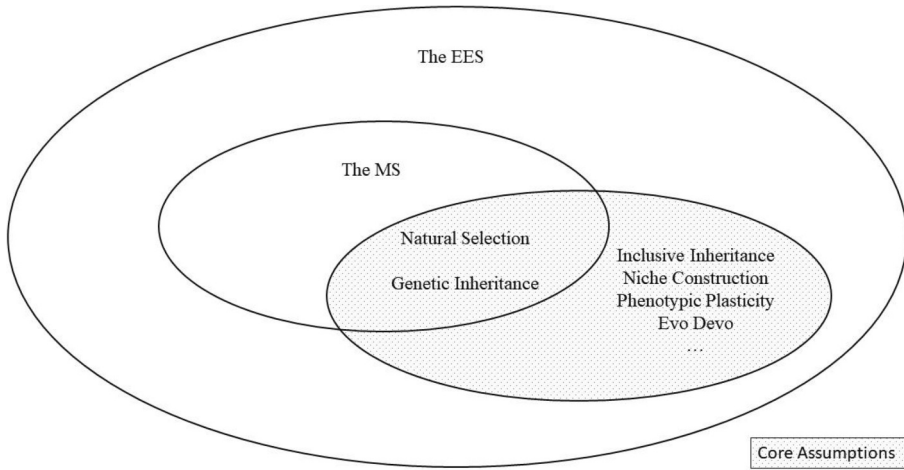


FIGURE 3 Moderate EES.

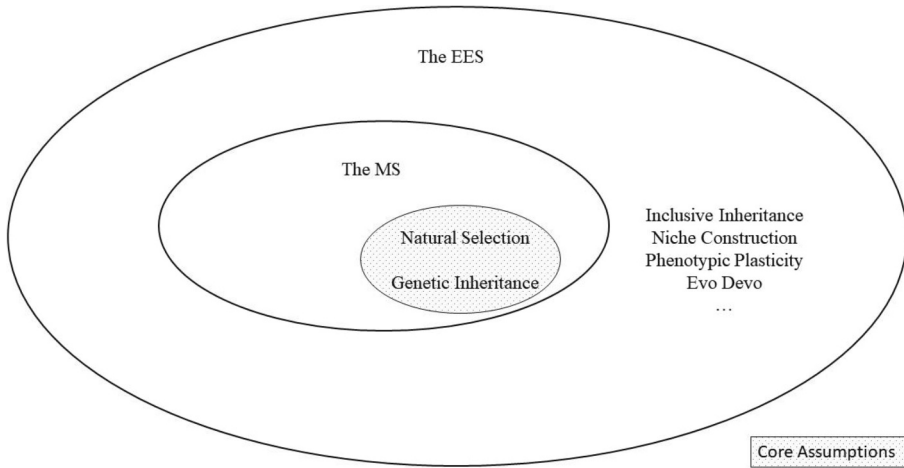


FIGURE 4 Moderate MS.

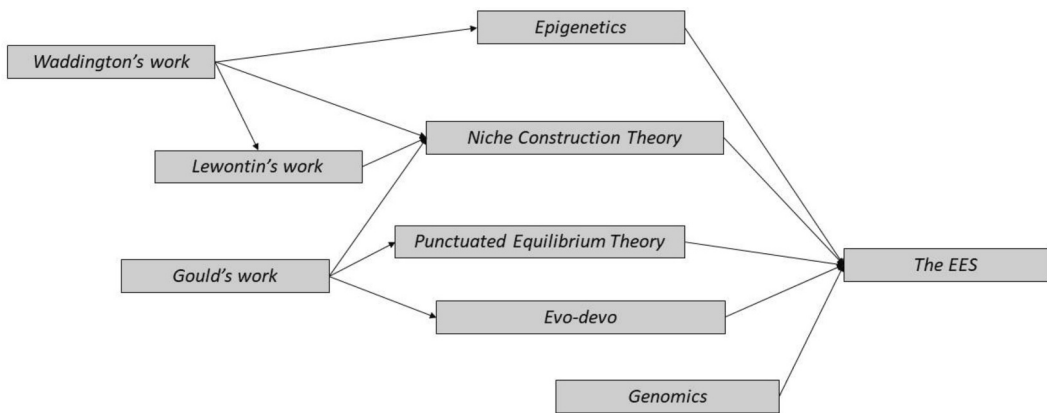


FIGURE 5 A partial account of the emergence of the EES.

EES aims for a framework which may become an incommensurable competitor with the MS if it successfully demonstrates its full potential after further development, but it is not yet a real rival of the MS, especially in terms of scope and fruitfulness.

From a historical point of view, the EES is just one of many attempts aimed at a new synthesis in the history of evolutionary biology. It tries to incorporate new findings from epigenetics, niche construction theory, evo-devo, and genomics into a new framework for evolutionary biology. The emergence of the EES well illustrates Yafeng Shan's web model of scientific development (2023). The development of epigenetics, niche construction theory, evo-devo, and other fields all contribute to the origins and development of the EES in the way of a synthesising web (see Figure 5).<sup>9</sup>

#### 4 | THE METHODOLOGICAL IMPLICATIONS: THE MS? OR THE EES?

Another central and urgent issue (especially for biologists) is whether we ought to replace the MS with the EES in practice. Whether advocating the strong EES or the moderate EES, proponents of the EES maintain that the EES should be favoured over the MS, as they argue that the EES provides a better or more promising framework of evolutionary biology than the MS. For example, Laland et al. (2015) put forward two arguments for a shift from the MS to the EES:

- A1. The EES makes novel predictions. Therefore, a shift from the MS to the EES is justified.
- A2. The EES raises new research problems and advances interdisciplinary studies across the biological sciences, social sciences, and medical sciences. Therefore, a shift from the MS to the EES is justified.

In contrast, adherents of the MS resist the call for a holistic shift from the MS to the EES. There are two main arguments in defence of the MS. First, it is argued that proponents of the EES mischaracterise the MS and in turn argue against a caricature of the MS. For example, Douglas Futuyma (2017, 8–9) explicitly rejects Laland et al.'s characterisation of the core assumptions of the MS, especially the assumptions of the pre-eminence of natural selection and genetic inheritance. Second, it is complained that the evidence for the core assumptions of the EES is still too weak. In particular, the significance of inclusive inheritance and developmental bias has been questioned due to lack of evidence (e.g. Dickins & Rahman, 2012; Futuyma, 2017; Wray et al., 2014). As Futuyma (2017, 10) argues, 'I have seen little evidential support for challenges to the basic tenets of the ES'.

It is clear that Laland et al.'s A1 is a Lakatosian argument by appealing to Imre Lakatos's notion of scientific progress. For Lakatos (1978a), a research programme is progressive if it generates novel and corroborated predictions. If the EES is a Lakatosian research programme as assumed by Laland et al., the EES is progressive. Nevertheless, A1 still fails to warrant a shift from the MS to the EES. Or, at least, A1 is incomplete for that purpose. For Lakatos (1978b, 6), a scientific revolution occurs typically when a research programme is progressive while its rival is degenerating. Laland et al. do not show that the MS is degenerating in a Lakatosian sense that the new auxiliary hypotheses of the MS are 'fabricated only in order to accommodate known facts' (Lakatos, 1978b, p. 5).

In comparison, A2 is more promising. It can be construed as an application of Shan's functional criterion of theory choice (2020): theory choice is a process of ranking theories in order to choose the most promising one in which promisingness is defined as potential usefulness.

[A] theory  $T_1$  is more promising than another  $T_2$  if  $T_1$  is more likely to provide some exemplary practices which are repeatable, and provide a reliable framework for further investigation to solve the unsolved problems and to generate more testable research problems across more different areas (or disciplines) than  $T_2$  after a further development of both. (Shan, 2020, 180–81)

Laland et al. (2015, 10–11) are very explicit on the point that the EES will 'contribute constructively to the future evolution of evolutionary theory' by '[stimulating] useful work' and 'strengthening ties to adjacent disciplines'. Therefore, it is legitimate for Laland and his colleagues to further develop the EES as a promising framework for evolutionary biology. In a similar vein, it is also reasonable for the advocates of the MS such as Dickens, Futuyama, and Wray to keep working on the MS as long as they can show the usefulness of the MS in practice and maintain that the MS is more promising than the EES. Such a functional interpretation of the debate over the MS and the EES allows us to adopt a pluralist stance on the methodology of evolutionary biology. As many (e.g. Chang, 2012; Kellert et al., 2006) have argued, taking a pluralist stance on scientific methodology is beneficial and healthy for scientific practice.<sup>10</sup>

## 5 | CONCLUSION: A SCIENTIFIC REVOLUTION (TO COME)?

Now let us move to the question of whether the emergence of the EES marks the beginning of a scientific revolution. Well, it depends on what we mean by a scientific revolution.<sup>11</sup> If you have a Kuhnian account in mind, it is clear that a scientific revolution in evolutionary biology is not yet coming. For Kuhn, a scientific revolution is a shift from one paradigm to another. It is fair to argue that most evolutionary biologists are still working with the MS. We are not in the mist of a chaotic period of the competition between multiple lines of enquiry. However, if you are thinking of a Laudanian account of scientific revolution, in which 'a scientific revolution occurs when a research tradition, hitherto unknown to, or ignored by, scientists in a given field, reaches a point of development where scientists in the field feel obliged to consider it seriously as a contender for the allegiance of themselves or their colleagues' (Laudan, 1977, p. 138), we are encountering a scientific revolution. Today, even adherents of the strong MS cannot ignore the existence of the EES. That said, as the contenders of the debate all admit, the proof of the pudding is in the eating.

Evolutionary biologists, whether they advocate the MS or the EES, have a lot of work to do to make sense of a rapidly growing amount of findings in molecular, developmental, and organismal biology. (Pigliucci, 2007, p. 2748).

Whether you agree with Gerd Müller on his view on the EES or not, I bet you must be sympathetic to his remark: 'This is an exciting period in evolutionary biology' (Müller, 2017, p. 9).



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## ENDNOTES

- <sup>1</sup> Huxley (1942b, 26) noted that the Modern Synthesis also benefitted from the contributions from Biometry, cytology, experimental embryology, developmental physiology, ecology, and systematics.
- <sup>2</sup> In order to avoid confusion, I will use the MS to refer to the conceptual and theoretical framework while the Modern Synthesis the historical episode or the movement in the 1930s and 1940s in the rest of this paper.
- <sup>3</sup> The period of 1941–1950 was regarded by Dobzhansky (1937, ix) as ‘the most fruitful decade in the history of evolutionary thought since the appearance of Darwin’s classic in 1859’.
- <sup>4</sup> Note that I am not claiming that there are only two main problems with the MS. As I will discuss, the MS also fails to address a number of evolutionary phenomena, mostly in the phenotypic realm. That said, the key point here is that both of the two central tenets of the MS are criticised.
- <sup>5</sup> The term ‘Extended Evolutionary Synthesis’ was coined by Pigliucci (2007) and Müller (2007). In the same year, Eva Jablonka and Marion Lamb (2007) coined a similar term ‘Expanded Evolutionary Synthesis’. Ulrich Kutschera and Karl J. Niklas (2004) also used the term ‘Expanded Synthesis’, though in a different sense.
- <sup>6</sup> For a detailed analysis, see Laland et al. (2015).
- <sup>7</sup> It is worth noting that Laland et al.’s argument (2015, 10) that a shift from the EES to the MS is not a Kuhnian scientific revolution is unsound. They incorrectly assume that a crisis is a prerequisite of a Kuhnian scientific revolution.
- <sup>8</sup> There are other views, though. For example, Tim Lewens (2019) adopts a pragmatic approach to the nature of the EES, while Alejandro Fábregas-Tejeda and Francisco Vergara-Silva (2018) argue for a dynamic account of the EES.
- <sup>9</sup> Gefaell and Saborido (2022) argue that the recent development of the MS and EES is more akin to scientific specialisation rather than a scientific revolution. It seems to me implausible. As shown in Figure 5, the development of the EES is a process of synthesising rather than a process of specialising.
- <sup>10</sup> It should be highlighted that taking the functional approach does not imply Hasok Chang’s normative active epistemic pluralism, whose basic idea is that that we should engage in actively cultivating multiple lines of enquiry. This is too liberal. The pluralistic stance implied by the functional approach is more restrictive or stronger: we ought to engage in actively cultivating multiple *useful* exemplary practices.
- <sup>11</sup> For a philosophical and historiographical analysis of scientific revolutions, see Shan (2023).

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