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What's wrong with the modern evolutionary synthesis? A critical reply to Welch (2017)

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Abstract Welch (Biol Philos 32(2):263–279, 2017) has recently proposed two possible explanations for why the field of evolutionary biology is plagued by a steady stream of claims that it needs urgent reform. It is either seriously deficient and incapable of incorporating ideas that are new, relevant and plausible or it is not seriously deficient at all but is prone to attracting discontent and to the championing of ideas that are not very relevant, plausible and/or not really new. He argues for the second explanation. This paper presents a twofold critique of his analysis: firstly, the main calls for reform do not concern the field of evolutionary biology in general but rather, or more specifically, the modern evolutionary synthesis. Secondly, and most importantly, these calls are not only inspired by the factors, enumerated by Welch, but are also, and even primarily, motivated by four problematic characteristics of the modern synthesis. This point is illustrated through a short analysis of the latest reform challenge to the modern synthesis, the so-called extended evolutionary synthesis. We conclude with the suggestion that the modern synthesis should be amended, rather than replaced.

Keywords Modern evolutionary synthesis · Extended evolutionary synthesis · Genecentrism · Kuhn · Welch

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> The evolutionary synthesis has invited many challenges, and it has frequently been asserted that it is a failed paradigm.
>
> Douglas J. Futuyma (2010, p. 16)

A dispiriting urge to reform

Welch's (2017) explanation for why the field of evolutionary biology is plagued by a steady and "dispiriting" (p. 264) stream of claims that it needs urgent reform has received both positive (Coyne 2016) and negative (Pigliucci 2017) comments. Here, we take something of a middle ground: we focus on what seem to us to be valuable aspects or parts of his analysis but also argue that it is, in an important way, out of focus or off-target and incomplete.

It is difficult to quantify and compare the controversiality of scientific disciplines but the field of evolutionary biology seems indeed more characterised by calls for urgent and fundamental reform than sciences like nuclear physics, geology, organic chemistry, or linguistics. However, the main calls for fundamental changes do not target the field of evolutionary biology in general, as Welch claims, but rather, and more precisely, the modern evolutionary synthesis (MS). Ironically, this is borne out by the very examples of calls for reform that he cites (e.g., Ho and Saunders 1984; Gould 1980, 2002; Pigliucci and Müller 2010; Laland et al. 2014): they all concern criticisms of the MS.[1] In *Beyond Neo-Darwinism* (1984), for example, Ho and Saunders claim to offer the reader 'An Introduction to the New Evolutionary Paradigm'. Their book can be interpreted as an ambitious reply to a rhetorical question that Gould asked a few years earlier: 'Is a new and general theory of evolution emerging?' (1980). Likewise, Pigliucci and Müller (2010) do not target evolutionary biology in general but the MS more specifically.

Consequently, one of the primary ways in which the approach we take in this paper differs from that of Welch is in its focus on the MS instead of on the field of evolutionary biology in general. However, our point of departure is similar to Welch's. He believes that evolutionary biology is not fundamentally flawed but that the persistent calls for reform are rather inspired by a few distinct and inescapable properties of evolutionary biology and of living things, together with strong propensities of human beings to think in certain ways about life. Similarly, we believe that the fact that a steady stream of criticisms and challenges has not yet led to a profound modification, let alone a replacement of the 70-year-old MS, suggests—but certainly doesn't prove—that there is nothing fundamentally wrong with it.

If this is the case, then one should ask why it has been exposed to so much unrelenting and sometimes severe criticism in the course of the past six decades. Here, again, we differ from Welch: the properties and propensities that he mentions are

[1] It is no coincidence, in this respect, that Welch, as he himself points out, instead of engaging properly with specific arguments, largely draws an abstract picture of their content (for surveys of criticisms of the MS; see e.g., Ruse 1982; Burian 1988; Gayon 1990; Smocovitis 1996; Depew and Weber 2013; Futuyma 2010, 2015).

certainly contributing factors but the main cause of calls for reform in the field of evolutionary biology must be sought in the main subject of discontent, namely the MS itself. Buss (1987, p. 25) once wrote that "The synthetic theory cannot be incorrect; it can only be incomplete." It was a reiteration with a vengeance of Eldredge's (1985, p. 6) claim that "the synthesis is not so much incorrect as incomplete." We believe that it was, and indeed remains, not merely incomplete, however. It may not be fundamentally wrong but it was—and still is—more imperfect than the term 'incomplete' would have us believe.

In the next section of this article we will briefly discuss the explanatory factors, enumerated by Welch, and illustrate how they—or some of them—can help explain why the MS has been so often criticized. In the third section, we make use of Kuhn's (1962) historical development model of scientific disciplines to highlight the, from a comparative-historical perspective, atypical nature of the MS and, more specifically, to identify four peculiar and problematic properties of this paradigm. In a fourth section, we briefly investigate whether, and to what extent, the latest challenge to the MS, the so-called extended evolutionary synthesis (EES), was triggered by these four problematic characteristics. The last and concluding section presents the suggestion that we should amend the MS, rather than replace it. It is, in our opinion, not as flawless as its advocates uncritically assume but at the same time also not as fundamentally flawed as its most ambitious critics claim.

Welch's explanatory factors

Welch (2017) points out that his analysis of the general causes of the steady stream of calls to reform evolutionary biology is restricted in two ways.[2] Not only does he largely abstract from the specific content of the criticisms, he also ignores factors, common to the academic endeavour in general, that often provide a source of inspiration for criticisms, such as self-promotion and the quest for impact (see however, Welch 2017, footnote 2, pp. 264–265).[3] The factors that he does discuss can, as we

[2] In the second part of his paper, he examines how these causes coalesce in a special way for the study of adaptive function.

[3] Not every scholar is so reticent, however. Gould in particular has, more than once, been accused of being either confused or dishonest. Simpson (1984, p. xxvi), for example, reproached him for basing his attack against the MS on a straw man, i.e., a definition of gradualism that was not applicable to this theory (see also Charlesworth et al. 1982). Carroll (2004, p. 245) concludes a critical essay about his 'pseudo-revolutions' with the harsh observation that "it seems evident that Gould is not himself confused, though it is his purpose that his readers should be." Graur et al. (2013) made similar reproaches against the ENCODE project. Gupta et al. (2017a, p. 491) have, more recently, reproached EES advocates of niche construction theory as an important expansion of the MS, almost on par with the theory of natural selection, of engaging in "an exercise in academic niche construction" [see also Feldman et al. (2017), for a sharp reply, Gupta et al. (2017b) for a rebuttal of that reply and Futuyma (2017, p. 5) for an analysis of niche construction theory that is similar to that of Gupta et al. (2017a)]. The main part of their article concerns a detailed criticism of the allegedly exaggerated claims of the proponents of niche construction theory. It would be odd indeed if a quest for academic impact were not a source of inspiration for critics of the MS. It is very doubtful, however, that this quest has been a primary cause of serious criticisms of the MS.

have already indicated, be divided into three categories: evolutionary biology is a very rapidly evolving science with a very broad scope, evolving life is extremely heterogeneous, complex and variable, and 'something' about our attitude to the evolutionary past and to the natural world inspires us to make demands of evolutionary biology that we don't make of any other science. Some of these demands are morally inspired (i.e., biological facts have to underpin moral theories; see e.g., Rosenberg 1990; Wilson 2009), others have a more spiritual character (i.e., biological facts have to help us feel at home in the universe; see e.g., Kauffman 1995; Saunders 2003; Jacquet 2005). In short: a lot of writing about evolutionary biology "has its mind on higher things" (Welch 2017, p. 274).

Those 'higher things' certainly inspired a lot of writing about evolution before the inception of the MS. With its reliance on blind chance, Darwin's natural selection was—and remains—repugnant to people who looked for a guiding influence to life. As Jablonka and Lamb (2005, p. 21) put it: the idea that adaptation can occur through the inherited effects of use and disuse (Lamarckism) and the often-associated notion of goal-directed internal forces "fitted better with many peoples' deep-seated religious and moral beliefs" (see e.g., also Bowler 2009, p. 225). The architects of the MS were not entirely immune to moral or spiritual demands either (Ruse 2009), although it would go too far to claim that the MS was shaped by such concerns.[4] Much the same can probably be said of at least some of the alternatives that were proposed over the past decades for the MS, including the EES. Futuyma (2017, p. 9) certainly does not believe that "all advocates of an EES are impelled by emotional distaste for the utter lack of purpose and agency in evolution by natural selection." Although he adds: "but it may be useful to ask if our views of evolutionary theory are affected by extra-scientific values" (ibid.).[5]

As to the heterogeneity of life: both the fact that few generalizations in biology have no exceptions and that it is easy to identify phenomena which have been

[4] Delisle (2009, 2011) distinguishes several, quasi-incommensurable epistemological/metaphysical frameworks within which they "shoehorned" evolutionary mechanisms and speaks, in this respect, of an untenable pluralism in evolutionary biology. It is a science which, consequently, still is "in a pre-paradigmatic state of development even today" (Delisle 2009, p. 130). He points out that proponents of a progressive cosmos, like Huxley and Dobzhansky, could only avoid a rupture between man and the rest of nature by adopting an ethics which followed that progress or even contributed to it. Both scholars effectively placed humankind in the driver's seat of cosmic evolution.

[5] This interest in extra-scientific values or 'higher things' seems quite explicit in Denis Noble's so-called integrated synthesis (Noble 2006, 2017). The last chapter of his *Dance to the Tune of Life* (2017) is headed by a quote from Conrad Waddington's *The Strategy of the Genes* (1957): "Many humanist and religious authors (…) have drawn attention to [the MS's] damaging effects on man's spiritual life." That seems to be an important reason why Noble wants to replace the MS: he sees in systems biology and modern developments in, primarily, molecular genetics, an opportunity to develop an interpretation of evolving life that is more in tune with our spiritual needs. Although he is at the same time also very adamant that he does not want to let God back in. His alternative for what he calls "naïve theism" is creative purposiveness, "the human characteristic that is most often 'explained away' by reductionists" (Noble 2017, p. 251). It arises from "purposive processes in organisms" (p. 247) and is, in this sense, not mysterious at all: "Once we recognise that life and living organisms have purpose, the very possession of goal-directed behaviour is to express creativity, in its various social forms" (p. 255). See also Noble and Noble (2017).

relatively neglected in the literature but which have had a major influence on the evolution of some specific lineages, in Welch's view, makes it all too easy to collect and present 'revolutionary' biological data which, in reality, are not very revolutionary at all. The so-called tree of life offers a good example of a biological generalization that has turned out to be not so general after all. Modern data about the ubiquity of lateral or horizontal gene transfer (i.e., the non-genealogical transfer of genes between organisms) in bacteria are sometimes interpreted as a major and revolutionary challenge to the MS (e.g., Boto 2010; Koonin 2011) since they imply that the (entire) evolution of life cannot be presented as a tree anymore, whereas Koonin (2007), for example, believes the tree of life to be "a big part of the Modern Synthesis."[6,7]

A peculiar characteristic of evolving life that Welch does not mention, is that evolutionary processes proceed exceedingly slowly and that we only have faint and relatively scarce fossil traces of the unimaginably rich and long history of life on this planet. This helps explain why the field of evolution "attracts significantly more speculation than the average area of science" (Lynch 2007, p. 8603).

Lastly, the rapid development and broad scope of evolutionary biology also creates all kinds of problems. The resulting avalanche of new data, especially from molecular biology, easily creates the impression that these data must require new conceptual frameworks. The case of inherited epigenetic marks illustrates this point well. This kind of intergenerational transmission, which was not known at the time of the construction of the MS, smacks of Lamarckism since it implies the 'inheritance of acquired characteristics', a process which is supposedly anathema to the MS. It is one of the major reasons why many proponents of the EES argue that the MS has become outdated and should, at the very least, be extended in a non-trivial way (e.g., Jablonka and Lamb 2005, 2007, 2010; Noble 2015a).

Another reason why the broad scope of evolutionary biology is problematic is that it makes it almost inevitable that evolutionary key terms like 'gene', 'species' or 'fitness' will be used in different ways in various evolutionary disciplines. This, in turn, can lead to serious confusion and misunderstandings. Welch does not give this example, but even the term 'evolution' (and its cognates) is, of course, used multifariously. For example, Scott-Phillips et al. (2014) point out that their disagreements regarding the evolutionary significance of niche construction reflect different usages of key terms like 'evolutionary process'. However, as we shall argue in the next section, that is not the main problem, associated with the broad scope of evolutionary biology. The main reason why that broad scope and the associated multidisciplinary

[6] The related and, until fairly recently, also underestimated evolutionary phenomenon of hybridization has even been presented as the dominant factor or force in evolution. See: http://www.macroevolution.net/orientation.html (accessed 20 October 2017). McCarthy's revival of the theory of saltationism, i.e., his stabilization theory that claims that each species originates suddenly, when its recombinant karyotype becomes genetically stabilized, following a hybridization event between ancestral species, is presented as a possible Kuhnian revolution in evolutionary biology.

[7] Ironically, in their investigation of the legacy of *The Selfish Gene* (1976), Dawkins' (in)famous popularization of the MS, Yanai and Lercher (2016) present those same horizontally transmitted genes as good examples of 'selfish genes'.

status of evolutionary biology is so problematic is that it has seriously complicated the construction of the paradigm that guides research in this field (i.e., the MS).

Four problematic characteristics of the modern evolutionary synthesis

It is probably no coincidence that the question of how the MS emerged, remains "one of the most vexing problems in the history of biology" (Smocovitis 1996, p. xii; see e.g., also Amundson 2005, section 8.3), despite the existence of a veritable 'Synthesis Industry' (e.g., Mayr and Provine 1980; Mayr 1982; Smocovitis 1996; Gould 2002; Bowler 2009). So vexing in fact, that many scholars tend to avoid the subject of its historical origin altogether. This suggests that its true nature is still poorly understood, which, in turn, may help explain why it is a quite contentious paradigm. Here, we will look at this question through the prism of Kuhn's comparative model of how scientific disciplines develop historically.[8] It is an abstract historical analysis but, as we hope to show, is nevertheless clarifying. Kuhn's supposedly relativistic philosophy of science may be problematic (Lakatos and Musgrave 1970; Toulmin 1972; Laudan 1984) and his central and all-important analysis of the structure of scientific revolutions largely inapplicable to the history or present of evolutionary biology, but that does not mean that his development model—that encompasses more than scientific revolutions—cannot contribute to a better understanding of the MS.[9,10]

Kuhn claims that the history of a scientific discipline starts out with a confused and conflictual pre-paradigmatic phase. This first phase is characterized by philosophical discussions between various schools about the nature of the subject of the science in question. This is exactly what happened, not long after Darwin (1859) managed to put the once philosophical notion of 'evolution' on the scientific agenda: rather than being the first paradigm of evolutionary biology, Darwin's theory inspired the emergence of various evolutionary schools (Bowler 1983). These pre-paradigmatic evolutionary theories or approaches were certainly not alternative paradigms, as Mayr (2004, p. 165) claims, since they did not unify, but divide the

[8] In his foreword, Kuhn (1962) explained that his book was inspired by the study of a broad range of scientific disciplines, including biology. However, he only discusses examples from the history of the non-organic sciences.

[9] Steven Weinberg claims that Kuhn's theory took too much inspiration from the historical paradigm shift from Aristotelian to Newtonian physics that he discovered while preparing a series of lectures on the history of physics. He initially tried to interpret Aristotelian physics from a Newtonian perspective but discovered that it could only be understood from an Aristotelian perspective: "For Kuhn it seems to have been the paradigm of paradigm shifts, which set a pattern into which he tried to shoehorn every other scientific revolution" (Weinberg 2001, p. 204).

[10] Indeed, it may not even be very relevant to the study of the history of science in general. Historians have, in any case, tended not to make use of Kuhn's analysis of scientific revolutions in their actual work, even if they refer to it in principle (Reingold 1980). The application of his analysis to the history of biology has proven to be especially problematic (Greene 1971; Wilkins 1996; Mayr 1994, 2004; Marcum 2015, pp. 192–195). As Mayr (2004, p. 165) puts it: "Virtually every author who has attempted to apply Kuhn's thesis to theory change in biology has found that it is not applicable in this field".

community of evolutionary biologists and thus failed to fulfil the all-important sociological function of a paradigm (Kuhn 1970; Ruse 1978). The standard term for this pre-paradigmatic period, 'the eclipse of Darwinism' (Bowler 1983; Reif et al. 2000), is also misleading. Not only because, in reality, all pre-paradigmatic approaches of evolution were "equally criticized and rejected by one author or another" (Junker 2008, p. 496) but also because it is clearly whiggish since scholars at the time did not know that Darwinism would only temporarily be 'out of fashion'.

Our Kuhnian perspective suggests the same for the exclusion of population genetics from surveys of pre-paradigmatic evolutionary schools or for the portrayal of August Weismann's neo-Darwinism as the second stage in the development of evolutionary thought, after Darwinism and before the MS and the EES (Pigliucci and Finkelman 2014; Futuyma 2015; Müller 2017).[11] We know, from our post-paradigmatic perspective, that these two approaches of evolution were more advanced than other pre-paradigmatic theories: population genetics integrated Darwinian selection theory with the new science of genetics whereas Weismann championed so-called hard heredity (see however, Winther 2001) and natural selection. However, in the first decades of the twentieth century, they were, evidently, not seen as a kind of missing link between *On the Origin* and the later MS. It seems more accurate or appropriate to us to squarely include both interpretations or approaches of evolution among the various pre-paradigmatic evolutionary schools.

The pre-paradigmatic phase in the historical development of a science comes to an end when one pre-paradigmatic theory or approach manages to convince a majority of scientists because of its ability to solve important problems and because of the perspective it offers on all sorts of new problems for this group to resolve. This paradigm can be one of the pre-paradigmatic theories or a combination of various pre-paradigmatic theories. This corresponds with what Provine (1989, p. 61) called the "evolutionary constriction": one pre-paradigmatic approach of evolution, that of population genetics, came out victorious in the pre-paradigmatic struggle and non-Darwinian alternatives lost all credibility among a majority of biologists. However, in this respect, the history of evolutionary biology does not completely conform to Kuhn's model since the MS was, as we will explain in more detail below, evidently not only the result of a 'constriction' or only the product of a victory of one pre-paradigmatic theory or approach: population genetics was only the "formalized core of the MS theory" (Müller 2017, p. 2). For now it suffices to say that, as Smocovitis (1996, p. 171) puts it, it was not Darwin's *On the Origin* but the "modern synthesis" that would "function as the biological analogue of the 'Newtonian synthesis' in the grand narrative of the history of science" (see also Delisle 2011).[12] It was welcomed

[11] Jablonka and Lamb (2005, Ch 1) interpret the history of evolutionary biology in terms of four linear transformations of Darwin's Darwinism: Weismann's neo-Darwinism, modern synthesis neo-Darwinism, molecular neo-Darwinism and selfish gene neo-Darwinism. Doolittle Ford (2007) distinguishes five syntheses: Darwin's theory, the MS, the Molecular Synthesis, the Genomics Synthesis and the Metagenomics Revolution.

[12] Consequently, we do not agree with Dickins' and Rahman's (2012, p. 2914) claim that, from a Kuhnian perspective, "we can regard the MS as a period of scientific revolution (…)": the MS did not replace an existing paradigm.

as a breath of fresh air since "it was soon appreciated that a basis had now been laid on which future evolutionary studies could be safely built" (Young 1993, p. 218).

Inspired and guided by their paradigm, and freed from the endless pre-paradigmatic quarrels, scientists subsequently make swift progress. Their work becomes more esoteric and technical ('puzzle solving') and is increasingly communicated in specialized journals instead of books, directed at a general public. This is, again, a fairly good description of what happened once the MS was more or less generally accepted among evolutionary biologists as the right conceptual framework for the study of evolution. Dickins and Rahman (2012, p. 2914) speak in this respect of "many years of normal scientific activity exploring the hypothesis-space that it created."[13] However, at the same time, our Kuhnian perspective also reveals the MS to be, in this respect too, quite a peculiar theory for it 'underperformed' as a paradigm, in two ways: not only did it soon become the subject of calls for reform, the professionalization of evolutionary biology also proceeded surprisingly slowly (Antonovics 1987).[14]

This, in turn, brings us to four different but intertwined, problematic characteristics of the MS: it is not only the product of a lopsided constriction but also of an unfinished synthesis, it is burdened by an unresolved conflict and, lastly, it is also surprisingly fuzzy. It are these four characteristics of the MS—which, as we shall see, are all directly correlated with the extremely broad scope of evolutionary biology and the associated multidisciplinary nature of this science—that largely explain why the MS was less successful than other paradigmatic theories in putting an end to the kind of fundamental debates that are characteristic for the pre-paradigmatic phase in the historical development of a science: in evolutionary biology they continued, but now in the subdued form of a series of minor and major challenges to the MS. Or, as Bowler (2009, p. 347) puts it, the founders of the MS who had hoped that their paradigm would inspire a long period of what Thomas Kuhn called 'normal science' "were to be disappointed."

A lopsided constriction

In the first half of the twentieth century, each biological discipline that contributed to the construction of the MS defended a pre-paradigmatic approach to evolution that was inspired and influenced by the specific level, domain and/or aspect of evolving life that it studied. Eldredge (1985, pp. 11–12) speaks in this respect of a 'blind

[13] Burian (1988, p. 248) also speaks of a 40-year period of normal science but he adds that there are many ways of doing evolutionary biology and that this science is not dominated by one paradigm. It is maybe more accurate to say that the MS is an unusually heterogeneous or versatile paradigm.

[14] Antonovics (1987, p. 321) even believes that the MS "had little direct effect on the progress of evolutionary biology as a discipline (…)." After the foundation of the journal *Evolution: An International Journal of Organic Evolution* (1946), no other evolutionary journals appeared until the seventies; for a long time, textbooks were absent and evolutionary biology was, as late as 1987, rarely thought of as a discipline in its own right (i.e., there was a scarcity of international congresses, departments or university programs and institutional organizations, exclusively dedicated to evolution). This was nowhere more painfully transparent than in funding, or rather, the lack of it. See, in this respect, also Ruse (2009).

men and the elephant' routine. There was a no-holds-barred competition among disciplines, each vying for primacy in describing one part of the 'elephant' as though it somehow constituted a description of the entire 'elephant'. The problem was not so much that each discipline described only a part of the 'elephant', however, as that each interpretation of evolution was inspired and distorted by a specific field of study (Bowler 1983). Mendelists, for example, were drawn to de Vries' mutationism because they studied the intergenerational transmission of discrete and clearly defined characters (and the corresponding genes), field naturalists were attracted to Lamarckism because it seemed a good explanation for the diversity and the ubiquity of subtly adaptive patterns they observed in nature, whereas many paleontologists were adherents of orthogenesis, the idea that evolution unfolds with predictable directionality (Bowler 1983, 2009; Mayr 1982), because of the linear patterns they discerned in the fossil record.

Inevitably, the evolutionary approach of the discipline (population genetics) that won the no-holds-barred pre-paradigmatic competition—and, ipso facto, that of the MS itself—was also somewhat distorted, lopsided or skewed: it identified 'evolution' with its genetic dimension and, more particularly, with changes in allele frequencies. As Dobzhansky (1937, p. 11) put it: "Since evolution is a change in the genetic composition of populations, the mechanisms of evolution constitute problems of population genetics." This became the standard or default meaning of 'evolution' in the MS.[15]

An unfinished synthesis

Since the evolutionary theory or approach that came out victorious in the pre-paradigmatic struggle was that of one particular biological discipline, the construction of the MS, in contrast with that of a standard paradigm, had to include an additional

[15] It may help explain why the discovery (Kimura 1968, 1983) that the majority of evolutionary changes at the molecular level are caused, not by Darwinian selection but by random drift of selectively (nearly) neutral mutants, was portrayed or seen as a major, non-Darwinian challenge to the MS (King and Jukes 1969). Of course, Kimura (1983, p. xi) himself acknowledged that neutralism does not "deny the role of natural selection in determining the course of adaptive evolution (…)"—although legend has it that he was so reluctant to concede this that he asked his colleague James Crow to write this sentence for him (see Dawkins 2017, p. 121). Depew and Weber (1996, p. 363) therefore call it "a kind of Darwinism," although they also speak of "a substantial change in the Darwinian tradition" (ibid.). Likewise, Futuyma (2010, p. 20), one of the staunchest advocates of the MS, argues that neutralism constitutes "a radical change in perspective that I think has the best claim to being labeled a 'paradigm shift' in evolutionary biology in the last 50 years." Although, elsewhere, several defenders of the MS, including Futuyma himself, cite the idea that "many genetic changes have no fitness consequences" as an example of a mere extension of the MS (Wray et al. 2014, p. 163). It is indeed merely a modification of the way evolution at the genetic level is interpreted, albeit an important one: whereas the Hardy–Weinberg equilibrium baseline assumes that no change takes place, except if this equilibrium is disturbed by forces like mutation or forms of selection, neutralism claims that genetic evolution occurs at a regular rate (through drift), unless it is altered by forms of selection. However, if 'evolution' is semantically restricted to changes in the genetic composition of populations and if the general assumption is that these changes are predominantly adaptive, the discovery that, in reality, many or most molecular changes are neutral and ruled by chance can indeed easily be interpreted as a revolutionary paradigm shift.

synthesis of information from other biological disciplines. These data and concepts had somehow to be integrated within, or added to, the victorious population genetics approach of evolution, like planets to a sun. As Ruse (1999, p. 326) succinctly puts it: the MS came into being once "biological flesh was added" to the "formal skeletons" of the population geneticists. Or, conversely, the MS came into existence once the population genetics framework was applied to various biological disciplines (Huxley 1942), i.e., once a relatively small group of biologists (see e.g., Reif et al. 2000; Futuyma 2015), in a series of landmark publications, established the theoretical compatibility of a population genetics interpretation of evolution with the main findings of most of the sciences, dealing with evolution.[16] This synthetic process of integration or addition is sometimes distinguished from its result, the synthetic theory (Reif et al. 2000; Futuyma 2015), also known as a "supra-theoretical framework" (Burian 1988, p. 248) or a "*treaty*" (ibid.).[17]

With the benefit of hindsight, we can say that this atypical 'treaty' or synthesis aspect of the MS is a second reason why it was, in a manner of speaking, set up to be controversial from its inception, and especially once it 'hardened' (Gould 1983) and theoretical compatibility was turned into more stringent (and more pan-selectionist) explanations. Not only did not all life sciences (fully) participate in the synthesis operation—some of course did not yet exist—, practitioners of several biological disciplines also believed that their field of study should have contributed more to the MS than 'biological flesh'. Put differently, the MS was but "a Limited Consensus" (Gould 2002, Ch. 7) and an *Unfinished Synthesis* (Eldredge 1985).

The embryologist Waddington (1953, 1957), for example, soon took aim at the centrality of theoretical population genetics in the MS, to the exclusion of other biological sciences, like embryology. Indeed, all the major or most well-known challenges to the MS (neutralism, punctuated equilibrium, evo-devo, EES) are, or were, inspired by biological sciences that either did not (fully) participate in the synthesis—such as molecular genetics, microbiology, physiology, embryology and developmental biology—and/or that, according to at least some of their practitioners, were not taken sufficiently seriously by the architects of the synthetic theory. Gould and Eldredge (1977), for example, were not convinced that the MS could explain

[16] Gayon (1998) even believes that this was a conscious decision: during the Second World War, a group of American biologists decided to bring the skeleton of the population geneticists to life by adding flesh to it from several biological disciplines. The emergence of the MS was in any case, "very much a product of the way science was institutionalized in the English-speaking world, and we should be careful not to assume that it was typical of how genetics or evolution theory developed across the whole scientific community" (Bowler 2009, p. 273). In Germany and France, genetics had not become rigidly institutionalized and the study of heredity had, consequently, not become completely alienated from field studies, paleontology and their non-Darwinian approaches of evolution. However, the non-Anglo-Saxon world on the other hand also played a role in the construction of the MS (see e.g., Delisle 2011, p. 51; Reif et al. 2000).

[17] To make matters even more confusing, the term 'synthesis' is also sometimes used to refer to "the integration of the Darwinian selection theory and Mendelian genetics" (Bowler 2009, p. 326) and, as such, distinguished from the "unification of the various branches of biology" (ibid.).

the macroevolutionary patterns they observed in the fossil record.[18] Likewise, Noble (2011, 2013), a physiologist and one of the most ambitious modern critics of the MS, aims at a new synthesis between physiology and evolutionary biology (see also Noble et al. 2014).

An unresolved conflict

Even some of the architects of the MS were not completely comfortable with the idea that evolution can be reduced to genetic evolution in the way that Dobzhansky's definition seems to imply. Futuyma (2017, p. 2) points out that whereas Dobzhansky defined evolution in terms of changes of allele frequencies, other evolutionary biologists, like Rensch, Simpson and Mayr had a more "comprehensive conception" of evolution, one that included phenotypic evolution, speciation and differential proliferation of clades. He argues that these so-called organism-focused biologists nevertheless still recognized that phenotypic evolution and speciation occur by changes in allele frequencies.[19] This interpretation is not entirely indisputable, however. A small yet significant portion of the work of the paleontologist Simpson, for example, presented inconsistencies between the fields of paleontology and population genetics (Delisle 2011, p. 54).[20] Similarly, the paleontologist David Raup was first eager to apply population genetics to the fossil record but soon became convinced that this was not feasible (Ruse 2009). The zoologist Huxley (1942, p. 389) also stated that the processes driving macroevolution are not always identical to those instigating evolutionary changes within a species (Delisle 2011, p. 54).

Mayr, arguably one of the main architects of the MS, in particular, always remained a staunch critic of the reduction of evolution to changes in allele frequencies.[21] In the prologue to *The Evolutionary Synthesis* (1980, p. 12), he writes (contra

[18] At a certain point in time, Gould even (allegedly) began to toy with the idea of evolution through macromutations. In a third phase of their punctuated equilibrium endeavor (Ruse 1989, 2009), selection at the individual level was restored to a central place, but incorporated within a broader 'expanded' or 'hierarchical' theory of evolution. Evolutionary changes take place, not only at the molecular and the individual level—where conventional selection is important—, but also at the species level. The central theme of Eldredge's *Unfinished Synthesis* (1985) is that there are "additional entities and processes (…) germane to any complete conceptualization of evolution and beyond the conventional purview of evolutionary geneticists." See e.g., also Eldredge (1995).

[19] Rensch and Simpson, for example, may not have been talking about allele frequencies when they wrote, respectively, of 'evolution above the species level' and 'tempo and mode in evolution', but they both "recognized [allele frequencies] as the elementary, generation by generation process of change" (Futuyma 2017, p. 2). Put differently: they both accepted that changes in allele frequencies were the alpha and omega of evolution.

[20] Delisle (2011) claims that the MS was fairly successful sociologically (i.e., it unified evolutionary biologists) but not conceptually (i.e., the MS was surprisingly loose when it came to the interpretation of evolutionary mechanisms). He traces these internal cracks in the conceptual synthesis to the different epistemological, ethical and metaphysical commitments of its architects.

[21] Mayr (1959) also believed that population geneticists had erroneously credited themselves for being solely responsible for the populational—as opposed to essentialistic or typological—thinking that, in his opinion, facilitated the MS (see also Mayr 1973, 1982; Mayr and Provine 1980). Bowler (1996) and Waisbren (1988) argue that, respectively, paleontologists and morphologists also anticipated the revival of Darwinism.

Dobzhansky): "It is simply not true that evolution can be explained as a change in gene frequencies. (…) Changes in gene frequency are a by-product of adaptation and of the origin of evolutionary diversity (induced by natural selection) and not the other way around." His *Systematics and the Origin of Species* (1942) was inspired by the one-sidedness of the evolutionary literature at the time. The emphasis was almost exclusively on the change of gene frequencies in one single gene pool, as if speciation did not exist (Mayr 1992). Against this view, he argued that divergence was the key concept in evolution (Provine 1986, pp. 478–479). Not long after the MS had become established as a paradigm, he again charged that population geneticists had simplistically reduced evolution to a change in gene frequencies and ignored gene interactions, the organism and its environment. He concluded that, in spite of the almost universal acceptance of the MS, evolutionists were still far from fully understanding almost any of the more specific problems of evolution. There was "still a vast and wide open frontier" (Mayr 1959, p. 13). He also always defended the entire organism as the target of selection (Mayr 1963, 1982, 1988, 2001).

These two conflicting points of view or approaches correspond with the main dichotomy in biology (i.e., the genotype–phenotype distinction) and, not coincidentally, long predate the MS. One of the main pre-paradigmatic disputes had been between organism-focused naturalists (often Lamarckists) and gene-focused Mendelian experimentalists (saltationists). Mayr (1982, pp. 540–550) speaks in this respect of a "growing split among the evolutionists" in the decades before the inception of the MS: there was an ever-widening gap between the experimental biologists, who studied proximate causations, "with particular emphasis on the behavior of genetic factors and their origin" (Mayr 1982, p. 540) on the one hand, and naturalists who worked with whole organisms (mostly zoologists, botanists, and paleontologists) on the other hand.[22] This split began to emerge in the nineteenth century, once the evolutionists did not have to convince the world of the fact of evolution anymore. Other late nineteenth-century factors that contributed to this schism were the death of Darwin (1882), Weismann's rejection of any inheritance of acquired characters—it is of course also with his idea of the 'continuity of the germ-plasm' that the dichotomy between the soma and the germ-plasm or phenotype and genotype was introduced in biology—and the growing "disciplinary radiation" of biology.

The fact that both pre-paradigmatic approaches of evolving nature were not completely reconciled through the construction of the MS explains why, as Kutschera and Niklas (2004, pp. 261–262) point out, these two major camps of biologists "persist to the present day."[23] In his *Reinventing Darwin* (1995), Eldredge speaks, in this

[22] He claims that advances made in both pre-paradigmatic camps—more particularly in evolutionary genetics and evolutionary systematics—"eventually made a reconciliation of the two opposing camps possible and led to a synthesis of the valid components of the two research traditions" (Mayr 1982, p. 550). This claim seems to be contradicted by his own criticism of the MS: the reconciliation was not completely successful. The fact that Mayr disagreed with the population geneticists about the genesis of the MS (see note 21) also seems incompatible with this claim.

[23] They refer, on the one hand, to geneticists and mathematical modelers who study evolutionary processes with selected organisms in the laboratory and, on the other hand, to naturalists (taxonomists, paleontologists) who draw conclusions, based on studies of populations of organisms, observed (or pre-

respect, even of 'the great evolutionary debate'. He doubts whether naturalists or organismic biologists and genecentric 'ultra-Darwinians' will ever reach a general agreement. One thing is certain: the clash between proponents of the MS and the EES can, as will become clear below, to a certain extent, be interpreted as a new episode in that great debate.[24]

A fuzzy theory

Lastly, the convoluted construction of the MS, with its lopsided constriction, unfinished synthesis and imperfect reconciliation between organism-focused and gene-focused biologists, also explains why it has always remained a fuzzy or moving target. This confusion started "as soon as attempts were made to assess its status" (Smocovitis 1996, p. 22). As Burian (1988, p. 252) puts it: "far too often, the critics' general stance is seriously undermined by their misinterpretations of the synthesis." The "punctuationists" (i.e., Gould et al.), for example, mainly criticized "oversimplified versions of neo-Darwinism (…) rather than the original statements of this theory (…)" (Charlesworth et al. 1982, p. 493). Burian therefore characterizes the MS as a moving target. Similarly, Craig (2015, p. 255) speaks of a "fuzzy target that many different authors have described in many different ways," Amundson (2005, p. 162) of a historically and scientifically elusive entity, Delisle (2011, p. 50), as mentioned earlier, of a conceptually "surprisingly loose" theory, and so forth. The term 'misinterpretations' can be misleading, however: a patched-together theory, or, as Pigliucci (2017) puts it, "piecemeal work" that was elaborated in a wide array of loosely connected books, was bound to be 'misinterpreted'.

The MS does indeed mean different things to different people. Here too, the multidisciplinary nature of evolutionary biology plays an important role: biologists tend to interpret the MS from the perspective of their own specific discipline and field of study. It is, for example, probably no coincidence that Koonin (2007, 2011) believes that the tree of life is a central tenet of the MS and that, consequently, this theory has been falsified by the aforementioned discovery of the ubiquity of horizontal gene transfer in the prokaryote world that he studies. As a molecular biologist, he also believes that neutralism is a major part of the story of what he calls "the fall of the pan-adaptationist paradigm of the Modern Synthesis." Rose and Oakley (2007) even identify the MS with statements such as 'the genome is always a well-organized library of genes' and 'the durable units of evolution are species, and within them

Footnote 23 (continued)
served) under natural conditions. However, it seems to us that the main difference between both groups does not lie in their different methodology but in their differing focus, namely genes and organisms.

[24] Ho and Saunders (1984) illustrate how deep-seated the organismic revolt against the MS is. They believed that neutralism was "an important turning point in the history of ideas" (p. 4) as it helped to undermine the "validity of a theory of evolution that is essentially based solely on genes" (ibid.) and thus heralded "the fall from dominance of the genetic theory of natural selection—and the concomitant return of theories on organismic structure and form" (ibid.). Maynard Smith (1985, p. 39) called this "an astonishing remark." Firstly, Kimura is an orthodox neo-Darwinist and secondly, "in so far as he has departed from Darwinism, he has done so by abandoning the organism, not by espousing it" (ibid.).

the organisms, organs, cells, and molecules, which are characteristic of the species'. While these may have been implicit or explicit assumptions of mid-twentieth century biology, they were not really foundational to the MS. Mayr (1963, p. 586) defines the foundations of the MS as follows:

> The proponents of the synthetic theory maintain that all evolution is due to the accumulation of small genetic changes, guided by natural selection, and that transpecific evolution is nothing but an extrapolation and magnification of the events that take place within populations and species.

Futuyma's (2010, p. 3; see also Futuyma 2015, p. 31) summary of the 1959 version of the MS is much broader: randomness of mutations with respect to adaptive need, an abundance of genetic variation within populations, the centrality of population genetics and natural selection, gradualism (i.e., most phenotypic evolution occurs by an incremental succession of small changes), allopatry and founder effect (Mayr 1954), and the firm belief that microevolutionary processes can account for patterns of macroevolution, studied by morphologists and paleontologists. Tellingly, in a recent defense of the MS, he introduces his enumeration of six central tenets of the MS with the cautious words: "I think" (Futuyma 2017, p. 2).[25]

The latest challenge: the extended evolutionary synthesis

Let us now briefly examine whether, and to which extent, the latest challenge to the MS, the EES, has been inspired by the four problematic characteristics that were discussed in the previous section.[26] One of the arguments of the defenders of the MS—who thereby of course make use of their own disciplinary interpretation of this theory—is that the EES is based on the kind of misinterpretations of the MS that, as we just saw, are inspired by, or associated with, the fuzziness of this theory. Gupta et al. (2017a), for example, strongly disagree with the often-repeated claim of EES proponents that niche construction has been neglected by the MS. In a similar vein, Futuyma (2017) identifies various misinterpretations and misrepresentations of the MS by proponents of the EES. It is not correct that the MS prohibits any kind of 'large effect' mutation, as in paedomorphosis and polyploidy. He also gives various examples of niche construction and developmental constraints that prove that the MS is not as genecentric and negligent of developmental processes as proponents of the EES believe.

However, many of these alleged misinterpretations of the MS seem to us, in reality, to be caused or facilitated by ambitious estimations of the evolutionary importance of the biological phenomena or processes that inspire the EES. Proponents of the EES believe, for example, that developmental processes not only impose

[25] He writes: "The most important tenets of the ES, I think, are these (…)."

[26] Some of the factors, enumerated by Welch, can also help explain the emergence and/or the popularity of the EES, as previously indicated. However, we believe that it was mainly inspired or triggered by the four identified structural characteristics of, or structural flaws in, the MS.

constraints on evolution but also play positive and constructive roles in evolution as causes of novel, inheritable variants and adaptive fits (Laland et al. 2015; Müller 2017). If that were indeed the case, it would be correct that these processes have been relatively neglected by the MS. Likewise, if niche construction were, indeed, a fundamental evolutionary process, at par even with natural selection, as proponents of the EES claim, one would—contra Gupta et al.—have to conclude that it has indeed been neglected by the MS (Odling-Smee et al. 2003).[27]

The fuzziness of the MS may thus, at first sight (see, however, note 29), only be marginally involved in the emergence of the EES, the influence of the other three problematic characteristics of the former theory is more evident: the EES is not only mainly inspired by biological disciplines that were not (sufficiently) involved in the construction of the MS—such as molecular and developmental biology—it is also clearly a reaction to the genecentrism of the MS and a new emanation of the ancient schism between gene- and organism-focused disciplines and biologists. Müller (2017), one of the main and most ambitious proponents of the EES, implicitly refers to that schism when he points out that the new way of thinking about evolution of the EES is historically rooted in the not-so-new "organicist tradition" (p. 8). The EES is, in any case, very much inspired by an aversion for the genecentrism of the MS. Laland et al. (2014, p. 161), for example, argue that "important drivers of evolution, ones that cannot be reduced to genes, must be woven into the very fabric of evolutionary theory." Genes are not causally privileged as programs or blueprints, but are rather "parts of the systemic dynamics of interactions that mobilize self-organizing processes in the evolution of development and entire life cycles" (Müller 2017, p. 7). Consequently, in the context of the EES, organism-focused disciplines

[27] However, we do not think that this claim is warranted. Rather, we agree with Gupta et al. (2017a, p. 498) who argue that "the nonequivalence of NC and selection as evolutionary phenomena can clearly be seen in the fact that selection can mediate evolutionary change even in the absence of NC, whereas NC cannot mediate evolutionary change in the absence of selection." Something similar can be said about epigenetic as opposed to genetic intergenerational inheritance. Changes in germline DNA can have lasting evolutionary effects in the absence of the intergenerational transmission of epigenetic variants, whereas "epigenetic-inducing molecules" (Williams 2015, p. 2658)—such as miRNA's and modified histones—always require 'permissive' DNA sequences in order to have an effect. Indeed, Jablonka and Lamb (1995, p. xii) themselves admit that "epigenetic inheritance systems evolved through selection of DNA variations (…)." This is one reason why we believe that several proponents of the EES overestimate the evolutionary significance of epigenetic intergenerational inheritance. Noble (2015a), for example, claims that the discovery of the epigenetic inheritance of environmentally induced variations in the phenotype has falsified the MS. Since evolved and inherited 'permissive' DNA sequences are, in reality, still the ultimate source of this newly discovered form of inheritance, Williams (2015) believes, by contrast, that "neo-Darwinism is just fine." In a reply, Noble (2015b, p. 2659) claims that the MS prohibits the "inheritance of environmentally induced variation." He even portrays inheritable epigenetic changes as the modern equivalent of Darwin's gemmules (i.e., hereditary particles which were supposedly produced by all parts of the body). Darwin's pangenesis theory, he claims, has turned out "to be not so far removed from what we have now found" (Noble 2015b, p. 2659). In reality—and this is, in our opinion, a second reason why scholars like Noble overestimate the evolutionary significance of epigenetic intergenerational inheritance—the MS only prohibits the *genetic* inheritance of environmentally induced somatic variation, not the *epigenetic* inheritance of environmentally induced variation. We agree with Haig (2007, p. 424) that there is indeed a sense in which epigenetics allows the inheritance of acquired (adaptive) characters but that this sense does not contradict fundamental tenets of the MS.

like Laland's ethology, Müller's developmental biology or Noble's physiology, and the somatic and ecological phenomena that they study, are much more important or relevant than they are in the context of the MS.

Towards an amended modern synthesis?

Welch (2017) not only finds the steady stream of claims that the field of evolutionary biology needs urgent reform 'dispiriting', they even actively hinder progress because they misrepresent the field to a wider public, distract attention from the ways in which biologists can do genuinely new research and encourage 'neophilia' (i.e., the unwillingness to build on previous work, to integrate new findings and ideas with existing frameworks, etc.). Even critics of the MS should be able to sympathise with this complaint. Neophilia in particular can, as Futuyma (2015, p. 74) puts it, be "immensely counterproductive." Kutschera (2013, p. 544) even believes that, in the meantime, the MS has ceased to exist: "there is no longer a single, unifying 'Darwinian evolutionary theory'." Since the 1990s, evolutionary biology consists, instead, of many, not very well integrated theories that describe and explain different aspects of evolving life or its history. It is an analysis that is reminiscent of the evolutionary 'Dys-Synthesis' that Antonovics (1987) defended and the return to a "kind of pre-Synthesis" (p. 328) or pre-paradigmatic status that he envisaged, "with conflicts, controversies, and new discoveries" (ibid.). In a similar vein, Doolittle Ford (2007) believes that the so-called Postmodern Synthesis (see also Koonin 2011) is defined by explanatory pluralism. The final maturation or end-state of biology is, in his opinion, not some grand unifying theory but rather a heterogeneous explanatory toolkit. There cannot be such a unifying theory, any more than there can be one for human history.

We do not think that the future of biology will be characterised by the absence of a generally accepted, unifying evolutionary theory, any more than the future of cosmology will be characterised by the absence of a unifying cosmological theory. The MS has not been, and should not be, replaced with a heterogeneous and amorphous explanatory toolkit, nor with an EES, but rather with an improved version of itself. The topic exceeds the scope of the present, already protracted article and can here be only sketched in very broad, unsatisfying, preliminary and provisional outline, but the main idea behind such an amended MS is that it *should reflect the paradoxical nature of evolution, rather than the multidisciplinary nature of evolutionary biology*. What is now a somewhat 'pockmarked' and patchy reflection of that fragmented academic reality could thus become a paradigm that is more akin to that of a 'normal' or less pluralistic (i.e., multidisciplinary) science.

Biological evolution in the broadest—and non-MS—sense of the term (i.e., transgenerational changes in the sphere of life) is indeed somewhat paradoxical in that it is an extremely complex and multifaceted phenomenon that is nevertheless characterized by a simple logic. The complexity of evolving life in terms of levels (e.g., the genetic, epigenetic, protein and whole-organism level), domains (e.g., the evolution of birds, dinosaurs, whales and archaea), aspects (e.g., cladogenesis, non-adaptive evolution on the genetic or somatic level and extinction) and steering

events, phenomena, processes and mechanisms (the explanatory toolbox) is clear and incontestable. Yet, on the other hand, evolving life is also a quite elementary phenomenon as it revolves, to a significant *but often overestimated* extent, around genes and is, again to a significant extent, determined by natural forms of selection and by genetic drift.[28,29] This elegant, neo-Darwinian logic could become the hard core of an amended MS and other evolutionary factors—including phenomena like phenotypic plasticity, epigenetic inheritance and niche construction that can or may have an important impact on selective forces—its softer and pluralistic outer shell.[30] Lakatos (1978) proposed his distinction between a hard core of theoretical assumptions and a softer and fuzzier shell of auxiliary and more replaceable or dispensable hypotheses in a grandiose attempt to rescue science from Kuhn's (presumed) relativism. It might, in the case of the atypical, multidisciplinary science that is evolutionary biology, have a more practical use by helping to rescue it from that steady stream of dispiriting and confusing calls for minor and major reform that Welch and, undoubtedly, many other biologists so deplore.

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[28] We should indeed distinguish between, on the one hand, the, arguably, 'greedy' kind of genecentrism that is at the heart of the MS and, on the other hand, 'non-greedy' or 'sound' genecentrism. This distinction is certainly not entirely new. Jablonka and Lamb (2005, p. 5), for example, define the genetic dimension as the first dimension of heredity and evolution, as the fundamental system of information transfer in the biological world and as central to the evolution of life. That is a possible definition of 'sound' genecentrism. When they, on the other hand, point out that their book does not offer a challenge to "Darwin's theory of evolution through natural selection, but to the prevalent gene-based unidimensional version of it" (p. 4), they refer to the 'greedy' genecentrism of the MS. The idea that genes are often mere 'followers' instead of 'leaders' (West-Eberhard 2003; Jablonka 2006), for example, is incompatible with 'greedy' genecentrism but not necessarily with 'sound' genecentrism.

[29] To the extent that 'genecentrism' is a fuzzy notion, the fuzziness of the MS can be considered a major impetus behind the EES after all, since proponents of this alternative evolutionary framework consider genecentrism, as aforementioned, to be one of the most problematic characteristics of the MS. We certainly believe that the concept needs to be clarified (see also note 28). Evolving life may indeed be more organismcentred than adherents of the MS assume(d), that does not necessarily mean that it cannot be conceived as a genecentric phenomenon.

[30] This distinction, too, is not entirely new. Delisle (2011, p. 58) suggests that, faced with the broad spectrum of research agendas being conducted under the Darwinian umbrella, "perhaps the only alternative is a radical solution: to think of Darwinism as being confined to a minimal definition, that is, the support of natural selection in any shape or form (…)."

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