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# 2 The Extended Evolutionary Synthesis: a 3 metascientific view of evolutionary 4 biology, and some directions to transcend 5 its limits 6

## 7 Abstract

8 To approach the issue of the recent proposal of an Extended Evolutionary Synthesis (EES) put forth  
9 by Massimo Pigliucci and Gerd Müller, I suggest to consider the EES as a metascientific view: a  
10 description of what's new *in how evolutionary biology is carried out*, not only a description of  
11 recently learned aspects of evolution. Knowing 'what is it to do research' in evolutionary biology,  
12 today versus yesterday, can aid training, research and career choices, establishment of relationships  
13 and collaborations, decision of funding and research policies, in order to make the field advance for  
14 the better. After reviewing the concepts associated to the EES proposal (categorized for convenience  
15 as mechanisms, measures, fields, perspectives and applications), I show their transience, and sketch  
16 out ongoing disagreements about the EES. Then I examine the deep difficulties, i.e., the enormity and  
17 complexity of the covered field, affecting the achievement of trusted metascientific views; the  
18 insufficiency of conceptual analysis to capture the substance of scientific research; the entanglement  
19 between empirical and metascientific concepts, between multiple chronologies, and between  
20 descriptive and normative intentions; and the ineliminable stakeholding of any reviewer involved in

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the reviewed field. I propose that disciplines such as scientometrics, ethnography, sociology, economics and history, combined with conceptual analysis, inspire a more rigorous approach to the evolutionary biology scientific community, more grounded and shared, confirming or transforming claims for ‘synthesis’ while preserving their maintenance goals.

## Keywords

Biology; Evolution; Theory; Evolutionary Synthesis; Scientific Community; Modern; Extended

## Introduction

More than once, through its history, evolutionary biology has tried to get a meaningful snapshot of itself. A few of these crucial moments are defined ‘syntheses’. These include the Modern Synthesis some decades ago, and the Extended Evolutionary Synthesis today. In this paper I assume that a comprehensive and reliable picture of evolutionary biology is, in principle, very useful to evolutionary biology itself as a research enterprise. Fragmentation coming, for example, from compartmentalization and hyper-specialization, is often seen as hindering the advancement of the science of evolution in many ways (Sidlauskas et al. 2010). The lack of a general picture of evolution, or at least of a sense of communal endeavour, can prevent a researcher from grasping the potential evolutionary relevance of her study case, or from accessing precious resources. A sense of evolutionary biology as a moving whole can be crucial for many important issues such as biology training, or funding and rewarding policies. In this light, syntheses deserve careful consideration because of their potential ‘maintenance effects’, i.e., effects that ultimately aid evolutionary biology in pursuing its knowledge aims. This paper analyzes the Extended Evolutionary Synthesis and, indirectly, the Modern Synthesis. Both ‘syntheses’ are metascientific views, in that they consist in claims about ‘what it is to do research’ in evolutionary biology at different times. Only indirectly they

are scientific claims about evolutionary processes. As we shall see, metascientific views are intrinsically complex: they should require a great effort for domesticating a huge mass of scientific literature (the latter being, in turn, only one aspect of scientific work); they intertwine metascientific with scientific claims, descriptive with prescriptive aspects, and multiple historical chronologies; and they are often elaborated through conceptual analysis by one or few scientists who cannot but rely on their particular experience and hold stakes in the scientific debate.

In 1980 Ernst Mayr and William Provine (Mayr and Provine 1980) edited a reconstruction of the Modern Synthesis that was to become its official, although in fact multifarious, account. The account was paralleled and immediately followed by pleas for an extension of the Modern Synthesis. Some critics, like early Stephen Jay Gould (1980, 1982), were more radical, whereas others, like G. Ledyard Stebbins, adopted a more integrative approach (Stebbins and Ayala 1981; Stebbins 1983).<sup>2</sup> Calls for an extension of evolutionary theory and evolutionary biology were repeated over the years, invoking a transition from the Modern Synthesis (MS) to the Extended Evolutionary Synthesis (EES).

Here I focus on a recent initiative promoted by Massimo Pigliucci and Gerd Müller.<sup>3</sup> Pigliucci (2007) defined the MS as “the current paradigm in evolutionary biology [...] whose conceptual framework goes back to the 1940s” (p. 2743). For Müller (2007) the MS is “the prevailing theoretical framework of evolution that resulted from a combination of genetics, systematics, comparative morphology and palaeontology in the 1930s and 1940s” (p. 946). Both Müller and Pigliucci wanted to point out some missing elements of the MS that are being added by current evolutionary research. Initially, they both focused on ‘organic form’ as something overlooked by the ‘essentially’ genetic MS, then they

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<sup>2</sup> Stebbins is also considered among the architects of the MS (Pigliucci 2009, p. 220; Pigliucci and Müller 2010, p. 8; Stebbins 1950). Both Gould and Stebbins, although in different ways, moved towards macro-evolutionary extension of the MS (Serrelli and Gontier forthcoming). Pigliucci and Stebbins share, besides their interest in extending the MS, their specialization: both are botanists.

<sup>3</sup> It would be necessary to assess Pigliucci and Müller’s discontinuities and continuities with respect to previous works like Gould’s or Stebbins’s. This would be particularly important because the EES has the ambition of summoning the pleas that have been accumulating over the years. The analysis is however beyond the scope of the present review, but some disconnects will be mentioned.

63 consciously started a proliferation of reflections on the EES,<sup>4</sup> where, as we shall see, they assembled  
64 a broader extension beyond the issue of ‘form’.

65 The idea of an EES enjoyed some success. For example, several scientific journals reviewed the EES  
66 book (Pigliucci and Müller 2010) as a research proposal (Plutynski 2011; Reiss 2011; Travis 2011;  
67 Witteveen 2011; Handschuh and Mitteroecker 2012). Some scientists accepted the challenge of  
68 imagining how the EES will eventually be (Brooks and Agosta 2012), possibly pointing out neglected  
69 extensions (Boto 2010; Weber 2011). Some scholars used the EES perspective to look at evo-devo  
70 (Love 2009; Medina 2010), at population genetics (Akey and Shriver 2011), and at other fields (Noble  
71 2011; Danchin 2013; L.A.B. Wilson 2013), and many focused on epigenetics (Danchin et al. 2011;  
72 Schrey et al. 2012, Dickins and Rahman 2012). The socio-cultural sciences showed an interest in the  
73 extension of the MS as well (Mesoudi et al. 2013; Laland et al. 2009).<sup>5</sup>

74 The EES was described by Pigliucci and Müller as an addition of key concepts to evolutionary theory.  
75 After looking at their ideas in some detail, I am going to highlight the dynamism of concepts occurring  
76 in their view over a few years. The complexity of the EES as a metascientific view, and the challenges  
77 presented by its achievement, are addressed in the subsequent sections. The conclusion of the  
78 present paper is the following: if metascientific views are as important to scientific research as they  
79 seem, then, although their complexity cannot be eliminated, they should be specified and grounded  
80 by means of more adequate methodologies than the ones employed to date.

## 81 **1. Back to a theory of form?**

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<sup>4</sup> See, for example, Pigliucci (2008a,b,c, 2009), Pigliucci and Müller (2010), Müller and Pigliucci (2010), Craig (2010, 2011), Love (2012), Callebaut (2013), Mesoudi et al. (2013).

<sup>5</sup> An example in Europe was the project called “Implementing the Extended Synthesis in Evolutionary Biology into the Sociocultural Domain”, carried out in 2012-2013 by the Lisbon Applied Evolutionary Epistemology Lab (Serrelli and Gontier forthcoming). Detailed information on the project, which involved original research as well as interdisciplinary exchange through seminars and conferences, is available at <http://appeel.fc.ul.pt/>.

According to a review by Pigliucci (2007) entitled “Do we need an Extended Evolutionary Synthesis?”, the MS coincides with evolutionary genetics, as its foundations had consisted in a movement of “crystallization” of a “theory of genes” out of the original Darwinian “theory of form” (p. 2744). Pigliucci supported such a claim with a brief conceptual history of evolutionary biology, summarizing how 20th Century Darwinism overcame Lamarckism, and how Mendelism was made compatible with gradual change by means of statistical works by Fisher, Haldane and Wright (*Ivi*, p. 2744). He described the major theoretical contributions by Dobzhansky, Mayr, and Simpson in the 1940s, and then identified some missing elements in the MS, namely: development, studied separately by embryologists (p. 2745); ecology, secluded away as a background condition of evolution (*Ibidem*); implications of the ‘-omics revolution’, and its relationships to neutralism and complex genotype-phenotype interactions (pp. 2745-6); and phenomena such as plasticity, evolutionary capacitance, epigenetic inheritance (p. 2746). An EES would integrate a theory of form back into evolutionary biology (p. 2745). Some “bits and pieces” or “recurring ideas” (p. 2746) that will be part of the EES would be: *evolvability*, hinging on developmental systems’ modularity and robustness (p. 2746); *phenotypic plasticity* and the possibility of modes of evolution such as genetic accommodation (pp. 2746-7); *epigenetic and multiple inheritance* (p. 2747); *complexity theory*, revealing organizing principles different from natural selection (*Ibidem*); and *updated adaptive landscapes*, in light of work that reformulates their general shape (pp. 2747-8). Concluding the 2007 paper, Pigliucci anticipated a new, complex, constructive process analogous to the MS itself, a progressive “expansion of theoretical biology (in the broader sense of conceptual understanding of the discipline’s foundations)” (p. 2748).

Converging independently with Pigliucci, Müller (2007) identified a major deficiency of the standard MS in the missing explanation of organismal form (p. 943). Müller explained that evo-devo, defined as “a causal mechanistic approach towards the understanding of phenotypic change in evolution” (p. 945), has been focusing on the origin of phenotypic organization, going beyond genetics and gene

regulation to include “the dynamics of epigenetic interactions, the chemicophysical properties of growing cell and tissue masses, and the influences of environmental parameters” (p. 944). Evo-devo has, for Müller, three major theoretical themes – modularity, phenotypic plasticity, and evolutionary innovation – that cross-cut its different approaches. Like Pigliucci, Müller talked about “major departures” from the standard theory, that also constitute theoretical implications for extending the MS: *evolvability*, not simply equated with the amount of genetic variation; *emergence*, accounting for the appearance of phenotypic novelties that fuel natural selection; and *organization*, substantiating the characteristic organizational features of phenotypic evolution, such as modularity, homology, homoplasy, and body plans.

[FIGURE 1 HERE]

Soon after publishing their reviews, in July 2008 Müller and Pigliucci organized a meeting at the Konrad Lorenz Institute in Altenberg, Austria, gathering some biologists who had written about the extension of the MS, or were more or less willing to acknowledge such direction to their work (Whitfield 2008; Pennisi 2008). Proceedings of the meeting were published two years later as the book *Evolution: The Extended Synthesis* (Pigliucci and Müller 2010) echoing Julian Huxley’s classic (Huxley 1942, reprinted for the occasion). The introduction featured a summary diagram (Fig. 1.b) of the chapters’ themes,<sup>6</sup> arranged as elements that extend the MS. The diagram is a useful tool to analyze the EES proposal and its transformations through time (see below, Sect. 3). The 2010 diagram (Fig. 1.b) does not preserve Pigliucci’s nor Müller’s original lists. Pigliucci’s “complexity

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<sup>6</sup> Besides Pigliucci and Müller, the other fourteen scientists at Altenberg were John Beatty (“Reconsidering the importance of chance variation”), Sergey Gavrilets (“High-dimensional fitness landscapes and speciation”), David Sloan Wilson (“Multilevel selection and major transitions”), Gregory A. Wray (“Integrating genomics into evolutionary theory”), Michael Purugganan (“Complexities in genome structure and evolution”), Eva Jablonka (“Transgenerational epigenetic inheritance” with Marion J. Lamb), John Odling-Smee (“Niche inheritance”), Eörs Szathmáry (“Chemical, neuronal, and linguistic replicators” with Chrisantha Fernando), Marc W. Kirschner (“Facilitated variation” with John C. Gerhart), Stuart A. Newman (“Dynamical patterning modules”), David Jablonski (“Origination patterns and multilevel processes in macroevolution”), Günter P. Wagner (“Evolution of evolvability” with Jeremy Draghi), and philosophers Alan C. Love (“Rethinking the structure of evolutionary theory for an extended synthesis”) and Werner Callebaut (“The dialectics of dis/unity in the evolutionary synthesis and its extensions”). Müller contributed “Epigenetic innovation”, whereas Pigliucci “Phenotypic plasticity”.

theory” and “updated adaptive landscapes” and Müller’s “emergence” and “organization” are not shown. Indeed, the integrated theory of form hinging on the dynamic connection between genotype and phenotype that both Pigliucci and Müller had outlined in 2007 does not exactly correspond to the 2010 proposal. There, different problems are pointed to by several concepts, e.g., “genomic evolution”, “replicator theory”, “niche construction”. The EES will not be, eventually, (just) a theory of form. Let us examine the pillars of this EES in some detail.

## 2. Conceptual pillars of the EES

Setting aside facts – such as “common descent” – that are not questioned by the main EES advocates, I propose five categories in which the concepts represented in the diagrams of Fig. 1 would roughly fit: *mechanisms* such as epigenetic inheritance, genetic accommodation, or natural selection, *measures* such as plasticity, variation or robustness, *fields* such as evo-devo, *perspectives* such as niche construction, and *derived applications* of evolutionary models such as replicator theory. I invite the reader not to take my categories too seriously: later I will observe that not only categories, but also concepts are subject to arbitrary choices and modifications, and I will provide explanations for that. Accordingly, we cannot expect that my categorization of these concepts has any stability or value other than the sake of an ordered presentation. Then being said, let us navigate through the concepts by kind.

### 2.1. Mechanisms

Some conceptual pillars can be defined as mechanisms.<sup>7</sup> *Epigenetic inheritance* is perhaps the best-fitting example. In the 1950s, epigenetics meant a family of hypotheses about cell state being

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<sup>7</sup> Philosophers of science have recently turned ‘mechanism’ into a technical term, the focus of a view of science called ‘the New Mechanism’, and an object of conceptual enquiry (Machamer, Darden and Craver 2000, and later works). The New Mechanism has stimulated, for example, discussions on whether or not natural selection and drift are evolutionary mechanisms (Skipper and Millstein 2005, Millstein, Skipper and Dietrich 2009,

determined not only by genetic states, but also by “auxiliary” functional states of the nucleus and the cytoplasm, inherited from cell to cell through a non-genetic mechanism (Nanney 1958, 1959). Epigenetic inheritance was proposed as an explanation for organismal processes such as oncogenesis and aging of multicellulars (Lederberg 1958). Early radical claims were made that epigenetics overthrows the MS by adding different rules of transmission, such as maternal effect and theoretical reversibility (Løvtrup 1972; Ho and Saunders 1979). Epigenetics became really important later, with the elucidation of its molecular groundings ushered by Robin Holliday (1987; see Haig 2004). Today the molecular prototype of an epigenetic modification is DNA methylation inherited in cell proliferation (Holliday 1979), and epigenetic inheritance is also studied at the organismal, inter-generational level (Grossniklaus et al. 2013).

Another example of a pillar-mechanism, this time located in the Darwinian ‘core’, is *natural selection*. In the EES area we find *multilevel selection*, a mechanism that integrates different levels of selection, each of which works on units that aggregate units at the lower level. The origin of the idea of multilevel selection is traced back to Darwin trying to solve the puzzle of traits that are “good for the group” while being disadvantageous for the individual: in *Descent of Man* (1871), Darwin proposed selection among human tribes as a “straightforward solution” (Wilson 2010, p. 80-81) to the evolutionary puzzle of the persistence of “high standards of morality” that decrease individual fitness. All over the 20th Century, group selection underwent eclipses and rebuttals by mathematical means, while multilevel selection was evoked for the level of species, the level of genes, and others. More mathematical studies were made on the conditions of plausibility of multilevel selection (Okasha 2006), and on the evolutionary origins of levels of selection – the “Major Transitions” (Maynard Smith and Szathmáry 1995) – such as the origin of multicellularity, or colonial life, or the origin of life itself. For Pigliucci (2009, p. 221), “it is now clear that several levels of the biological

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Matthen 2010, Matthewson and Calcott 2011, Havstad 2011, Nicholson 2012). Here I use mechanism in a non-technical, vernacular scientific sense.



hierarchy are, at least theoretically, legitimate targets of selection, from genes to individuals, from groups of kin to populations to species” (see also Keller 1999).

## 2.2. Measures

Although *phenotypic plasticity* is sometimes referred to as a developmental process or a mechanism (Pigliucci et al. 2006), plasticity may be better seen as a measurable property of a genotype concerning the range of phenotypes that such genotype can produce in different environments (Pigliucci 2010). The concept is not new: it was coined by Woltereck (1909) along with the notion of reaction norm, i.e. the rule according to which the development of a phenotypic trait co-varies with specific features of the environment. Scientists such as J. M. Baldwin, C. H. Waddington and I. I. Schmalhausen anticipated that phenotypic plasticity of a trait would allow for phenotypic accommodation to environmental inputs during development, followed – if inputs are sustained for enough evolutionary time – by genetic accommodation, i.e. the intergenerational accumulation of genetic changes that eventually reduce plasticity of the trait (West-Eberhard 2003). According to Pigliucci (2010, p. 357) “Phenotypic plasticity is now the paradigmatic way of thinking about gene-environment interactions [...] and one of the best studied biological phenomena in the evolutionary literature”.

*Modularity* and *robustness* are other genetically determined properties that appear, along with plasticity, in the EES.

Modularity consists in the presence of modules, i.e. integrated structures that are repetitive, and that tend to persist and get reused in evolution. Modules can occur in different contexts such as the genome, individual morphogenesis, clades, broader phylogenies, at various scales. Modularity may not be properly a measure, but it comes in degrees,<sup>8</sup> and according to mathematical and simulations

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<sup>8</sup> Some people use Herbert Simon’s (1962) idea of near-decomposability as a model and a quantification of modularity.

studies it is expected to occur in huge superconnected networks such as the genome. Sometimes modularity is coherent across two levels, genetic and phenotypic, when genetic modules affect only a part of the phenotype with no deleterious pleiotropic effects on other parts (Müller 2007). But modularity at one scale is not necessarily aligned to other scales. Modular patterns in the phenotypes may also emerge at the phenotypic level, by the mechanics of cell differentiation in which cells induce each other to assuming states in the multistable landscape of cell states (Newman 2010). Müller (2007) explains that sometimes when a “unit of phenotypic construction” remains recognizable in anatomical architectures over evolutionary time, the molecular and developmental pathways that construct the unit change. According to Wagner and Altenberg (1996), in the phylogeny of animals modularity is most likely a derived state, the result of parcellation rather than integration, with the open question of whether modularity emerged by natural selection.

Robustness measures the reliability of outcomes in the face of perturbations, both environmental (e.g., temperature change) and internal (e.g., mutations). Genomes, biochemical networks, and developmental processes can be more or less robust to various kinds of perturbations with respect to some outcome (e.g., the phenotype, fitness). In development, robustness has long been known as canalization (Waddington 1940): most perturbations of the developmental process have a temporary effect that doesn’t affect the phenotypic outcome. Only some kinds of perturbations in restricted time frames can push the developing organism down a different developmental route. According to Félix and Wagner (2008), a system may be robust to stochastic noise, environmental change and genetic variation. Robustness to genetic variation includes robustness to mutational variation and robustness to the effect of recombination between alleles at different loci. “Robustness – Félix and Wagner write – is not an all-or-nothing property. It is a matter of *degree*” (p. 134).

*Evolvability* is understood in different ways (Pigliucci 2008a). On the one hand, evolvability has to do with standing variability and also with heritability (Houle 1992), the standing genetic variance in a population being a measure of the potential of that population to respond to natural selection, as

demonstrated by Fisher's fundamental theorem (1930). On the other hand, evolvability concerns genetic structure and its ability to produce evolutionary novelties (Wagner and Altenberg 1996). Another meaning of evolvability is related to 'key innovations' that make particular clades more speciose or adaptable. In all cases, evolvability is the capacity of a system for evolution, therefore it is the expected rate and amount of evolution correlated with certain characteristics. In some contexts, the meaning of evolvability is narrowed down to the rate of *adaptive* evolution (vs. any kind of evolution).

Plasticity, modularity, robustness, and evolvability are all measures that concern how natural selection works in populations. It is possible that patterns of gain and loss of these properties are due to natural selection (for adaptive plasticity, see Schlichting and Pigliucci 1998; Pigliucci et al. 2006; Wund 2012). On the other hand, more or less evolvable populations of plastic, or modular, or robust organisms will undergo different selective dynamics and trajectories. In any case, measures such as plasticity, modularity, robustness, and evolvability are thus seen as new concepts, absent in the MS, that explain how life evolves.

### 2.3. Fields

Some of the conceptual pillars are whole scientific fields. *Population genetics*, *paleontology*, and *natural history* are familiar 'actors' in many historical accounts of evolutionary biology (Mayr and Provine 1980; Gould 1980, 1982, 2002; Eldredge 1985, 1999), including Pigliucci's (2007, p. 2744; 2009, p. 220). Fields have their own history of change. For Pigliucci (2009), genomics started with the view that "once we 'decode' the genome of an organism we somehow gain a universal key to understanding its biology" (p. 223). This first phase was, for Pigliucci, "squarely within the conceptual framework of the rather gene-centric MS". Then genomics and other "-omics" fields renewed themselves by turning to system-level properties of entire networks of gene products. Fields have their own complex structure, subfields, and hybridizations. *Evo-devo*, as Müller (2007) says, is not

only a whole approach to evolution, rather it is itself composed by four approaches or “programmes”: comparative embryology and morphology, evolutionary developmental genetics, experimental epigenetics, and the theoretical and computational programme. *Complexity theory and network theory*, listed in the EES, are mathematical fields that are applied in many domains of biology and beyond. *Ecology* is called into question as a proper scientific field (2007, p. 2745; 2009, p. 221), not as a mere attention to environmental aspects. Pigliucci (2007, 2009) argues that the field of evolutionary ecology “barely scratches the surface of the field of ecology at large” (2009, p. 224), and wishes for some kind of future union between ecology and evolutionary biology.

#### 2.4. Perspectives

Some conceptual pillars are better seen as theoretical perspectives that can be adopted in the construction of evolutionary models. This is the case of *updated adaptive landscapes* and *niche construction*. Both perspectives are related to mathematical constructions. Landscapes are a geometrical representation of properties of a space of traits (Fusco et al., 2014). The geometrical representation and the conveyed properties become a perspective to set up evolutionary problems in empirical research and modeling. Niche construction is firstly a perspective pointing to biotic ecological impact and consequent natural selection feedbacks, and it inspires the construction of mathematical models or, more often, the modification of existing ones.

Gavrilets (1997) argued that Wright’s (1932) intuition of fitness peaks and valleys was way too simplified in light of the degree of connectedness of high-dimensional spaces. Gavrilets applied percolation analysis (originally developed in physics) to the space of possible genetic combinations of a population, showing that such space will surely be super-connected: any fitness value will certainly be the fitness value of a bundle of chains of combinations that are connected by means of single-allele substitutions. In other words, for each fitness value there will be a ‘giant component’ extending all the way throughout the space of possible combinations. The fitness function of a giant component

can be imagined as ‘holey’ because, although any pair of combinations in the giant component is connected by means of a series of single-allele neutral substitutions, there are pairs of combinations that are connected by very long chains. Gavrillets used these compelling mathematical considerations as a theoretical justification for his low-dimensional neutral models of speciation (2004). Pigliucci (e.g. Pigliucci and Kaplan 2006 chp. 7; Pigliucci 2007, 2008b; Pigliucci and Müller 2010) was more interested in possible direct implications for adaptation. He took holey landscapes as a perspective revealing the plausibility of neutral genetic exploration and fast switching from one giant component to another (called ‘extra-dimensional bypass’ by Gavrillets). In this respect, perhaps more appropriate than Gavrillets’s speciation works are Wagner’s studies on neutral networks, where a phenotypic trait, instead of fitness, is mapped on the multi-dimensional space of genetic combinations (e.g. Wagner et al. 1994; Wagner 2008, 2009).

Niche construction captures the basic observation that organisms impact and also actively construct their and others’ environment (Darwin 1881). Richard Lewontin (1978, 1983) and John Odling-Smee (1988) were among the authors who began to point out a ‘lack of modeling’ of the widespread phenomenon of niche construction in the mathematical core of evolutionary theory, i.e. population biology. Dawkins’s (1982) concept of ‘extended phenotype’ was an incomplete perspective (Odling-Smee et al. 1996, p. 295) in considering niche construction only as a product – not as a source – of natural selection. Since the 1990s the niche construction perspective has been a collector of examples brought to the attention of evolutionary theorists. Evolutionary niche construction models (Odling-Smee et al. 1996; Laland et al. 1996, 1999; Odling-Smee et al. 2003) were obtained by modifying consolidated two-locus multiplicative models in population genetics. The introduction of feedback from gene frequencies to selection pressures (influencing, in turn, gene frequencies) yields significant novelties in the dynamics. Therefore, niche construction models have been hailed as an important step forward in evolutionary modeling.

## 2.5. Derived applications

Finally, *replicator theory* – as presented by Fernando and Szathmáry in Pigliucci and Müller (2010) is a “lateral extension” of the MS, a further kind of concept.<sup>9</sup> It transfers a replicator-based view of natural selection (Campbell 1960; Dawkins 1976, 1982) to different, previously non-evolutionary disciplines such as chemistry, neuroscience, and linguistics. Fernando and Szathmáry explore, for instance, the conditions for the existence of chemical replicators able to undergo natural selection, in light of the emerging field of systems chemistry. They recognize several candidate types of replicators also in the human brain: synaptic replicators, topological neuronal replicators, and dynamical neuronal replicators. Building on the tradition of ‘neural Darwinism’ (Edelman 1987; Changeux 1985), Fernando and Szathmáry report several kinds of simulations and reflect on whether and how we can consider thought as a process of blind variation and selective retention (Campbell, cit.). They also introduce language in this framework, as a means of inter-brain neuronal replication. If, as we said, these works can be considered as tentative applications of the MS partly outside its domain, it is also true that they require conceptualizations and operationalizations that are considered eventually useful to biology. Attempts at extending the applicability of natural selection raise, for example, the common problems of defining heredity and fitness, of explaining how “unlimited heredity” arises from “limited heredity”, and of showing the evolution of evolvability. As Fernando and Szathmáry say, their studies can “contribute to the depth of the theory”, not only to its lateral extension, by shedding “new light on evolvability, exploration distributions in evolution, and the interplay of Lamarckian and Darwinian mechanisms, but strictly within the constraints of genetically based evolution...” (p. 242). “Exploration distributions” is a term from the theory of algorithms. Computer algorithms “explore” a space of possible combinations by realizing some of them through time. These simulations are used to study how evolution explores phenotype space, and to explain the emergence of correlations between different phenotypic traits (Toussaint 2003).

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<sup>9</sup> Other examples, reported by Callebaut (2010) as not sufficiently emphasized in Pigliucci and Müller (2010), are evolutionary economics, evolutionary medicine, and cultural evolution.

### 3. Restless concepts

As we shall see in the next section, the EES is first of all a “metascientific view” of such a broad field as evolutionary biology. Hard obstacles will be encountered by someone who, like EES advocates or the MS architects, wants to formulate a description of what is it to do research in evolutionary biology yesterday, today, and tomorrow. A strong dynamism in the set of EES concepts is thus to be expected. To look at how concepts wander throughout publications and diagrams, an apparently dull task, can be useful here.

Some concepts are stably there, e.g. evolvability (coupled, only in 2009, with modularity), epigenetic inheritance, and plasticity and accommodation (which also constitute one of Pigliucci’s specialties, e.g., Schlichting and Pigliucci 1998; Pigliucci 2001; cf. Scheiner 1999). Evo-devo, genomics, and multilevel selection are included since 2009 with small, essentially metatheoretical changes (evo-devo becomes qualified as “theory” in 2010, while multilevel selection loses such qualification; “genomics and network theory” switch to “genomic evolution”). Some elements are particularly labile. Complexity theory is dropped in 2010. Replicator theory only shows up in 2010. Ecology, listed as a missing element of the MS by Pigliucci (2007), participates to the EES only in the 2009 diagram. Contingency even jumps from being an element of the EES in 2009 to being a concept of the MS in 2010. Some concepts slip in in 2009 to be conserved in 2010, such as niche construction. The set of candidate concepts for an EES mutates through the different papers and works, even works by the same person – see Sect. 1 and Fig. 1. Of course, cartoon diagrams must be taken with a grain of salt: they are idealized and represent only some aspects of the EES discourse. That being said, in this search for the best arrangement of evolutionary concepts, many will recognize a persistent dose of arbitrariness.<sup>10</sup> For instance, evolutionary mechanisms (see 2.1) are arranged by EES proponents in

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<sup>10</sup> Since I am going to criticize an account of the EES based on lists of concepts, I don’t embark in the task of pointing out ‘elements’ (see classification in Sect. 2) that arguably extend the MS but are not considered in any EES work. There would be many examples, the most important being horizontal gene transfer (Boto 2010), symbiogenesis, and ‘horizontal evolution’ in general (Kutschera and Niklas 2004, Gontier 2007). In a previous

just *one of the many* possible alternative ways. Notice that the historical counterpart of epigenetic inheritance, which would be *genetic* or *germline inheritance*, is missing from EES diagrams. Instead we find *Mendelism* and *Mendelian inheritance*, but these are not alternative physiological mechanisms of inter-individual passage of traits: they rather describe a trans-generational traits distribution pattern<sup>11</sup>. Then, natural selection and multilevel selection are depicted as distinct pillars, but, granted that multilevel selection is accepted (Keller 1999), we may well argue that such acceptance implies the unity of selection, i.e. that multilevel selection *is* natural selection, and that natural selection *is* or *can be* multilevel. The split of natural selection and multilevel selection as two distinct pillars seems thus more of a way of marking certain theoretical studies than an addition of discrete new mechanisms as it is always presented. Indeed, the reflection on units and levels is inherent to evolutionary biology: it has never stopped since Darwin.<sup>12</sup> Interlevel dynamics are a pervasive issue, beginning with genetic selection vs. phenotypic selection which must be correlated over various time scales. Genotypes and phenotypes entertain non-linear relationships as shown for example by other mechanisms listed in the EES: *phenotypic accommodation* (i.e., adjustment, without genetic change, of variable aspects of the phenotype following a novel input during development) and genetic assimilation (loss of dependence on environmental cues, Pigliucci et al. 2006). *Accommodation* is depicted as stably associated with *plasticity*, whereas we might regard it as a further example of the multilevel complexity of the single mechanism of natural selection. We have seen that plasticity, modularity, robustness, and evolvability might not be evolutionary mechanisms

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footnote I already cited macro-evolutionary extensions of the MS that are poorly considered by EES advocates (Serrelli and Gontier forthcoming).

<sup>11</sup> To be fair, “Mendelian” applies also to the modern biological chromosomal theory of inheritance, not merely to the pattern inferred from crossing as Mendel reported in 1866. On the one hand, however, “Mendelian” is associated by EES advocates themselves to population genetics, and in that context “Mendelian” precisely points to the basic pattern of trait transmission. On the other hand, this is just one of the cases of polysemy that occur both in the EES and in this response of mine, polysemy that eventually comes out on the side of my more fundamental position about the serious paucity of conceptual analysis to account for evolutionary biology.

<sup>12</sup> Moreover, the reflection on units and levels is only one of the many lines of conceptual work on natural selection, with repercussions for empirical research. We would probably be able to capture crucial positions and passages from any line of reflection and consider them as pillars. For example, is natural selection alternative to drift? Is it a force? Is it distinguishable from sorting? I think we wouldn’t be able to crystallize ‘additional pillars’ out of these debates without a significant amount of arbitrariness.



but, rather, measures that improve understanding of natural selection. Their isolation as EES conceptual pillars seems justified by the fact that they are also attentions of an emerging way of conceiving variation in evolution. However, other conceptual arrangements could be possible in which these measures don't stand out as pillars. For example, we might suggest their subsumption into *multilevel selection* by understanding them as interlevel phenomena. As Müller (2007) notices, modularity "is pervasive at all levels of biological organization" (p. 944), and there can be various correlations among modules that occur at different scales in biochemical networks and physical processes of differentiation in development. Not by chance, modules have been proposed as units of selection (Wagner 1996). Robustness is even more constitutionally an interlevel property, concerning the stability of association between genotype and phenotype. Finally, the two most important meanings of evolvability both involve the genotype-to-phenotype map. Thus we might see the four measures as aspects of multilevel selection, but earlier we questioned the 'pillar' status of multilevel selection itself, so in the end everything might be collapsed back into natural selection.

If the set of concepts for an EES seems so dynamic over time, something even more radical happens to the Darwinian core and to its supposed extension by the MS. If we focus on the Darwinian core in Fig. 1, natural selection persists, but the other ingredients vary: in 2009 there is common descent (Fig. 1.a), whereas in 2010 variation and inheritance (Fig. 1.b). As for the MS, its additions to Darwinism change as well. According to Pigliucci (2009) the MS adds natural history, Mendelism, population-statistical genetics, and paleontology. Pigliucci and Müller (2010) only preserve Mendelian inheritance and population genetics, complementing them with gene mutation, contingency, and speciation and trends. I have been even too long in demonstrating that, hence, the arrangement of concepts proposed by the EES (including the arrangement proposed for the MS) is not only changeable, but also ostensibly arbitrary. The shaky identity of the MS may be a problem for the EES account that precisely depicts the MS as a stable set of constraining ideas, but this will be

addressed in section 5. In what follows I shall talk about discussions about the EES, and explore some of the intrinsic reasons that imply arbitrariness, disagreement, and sometimes confusion.

#### 4. The EES as a tricky metascientific description

We have reviewed most of the concepts listed by EES advocates. In Fig. 1 they are arranged in successive expansions. Notice that these expansions are meant to show not only cumulative growth of knowledge about evolution, but also the various transformations of evolutionary biology as a scientific field. The different circles aim at being representative of how working in evolutionary biology was, is, and will be at different times. The EES is thus, first of all, a metascientific claim (i.e., a claim about science), then a scientific claim (i.e., a claim about how life evolves). In fact, ongoing controversies on the EES mingle scientific and metascientific aspects. Single concepts of the EES have been questioned with respect to their scientific validity, relevance, or innovativeness (Reiss 2011). Coyne (e.g., 2009) questions, for example, the real evolutionary incidence of epigenetic inheritance due to the short life of epigenetic changes over generations. Some pillars create different factions concerning their compatibility with long-standing knowledge (e.g., for evo-devo, Minelli 2010 vs. Laubichler 2010). But many other issues are more exquisitely metascientific: they are about the science, not the world. Fields such as “population genetics” or “ecology” or “evo-devo” that are listed among EES conceptual pillars are metascientific concepts rather than scientific ones (more will be said on this below). Another purely metascientific debate is the one concerning *the age* of ‘pillars’: claims for additions to the MS are also claims for the long absence of some ingredient, for example ecology, from the field of evolutionary biology. Such absence is typically contested by groups of scientists who claim to have always taken ecology (or whatever pillar at hand) into consideration, or who point out forerunners. The timing of virtually each and every concept is a matter of metascientific quarrel between different members of the scientific community. There is also a more fundamental disagreement about the EES as such. Müller and Pigliucci (2010) observe

two opposite reactions to the EES: the “nothing-substantially-new” position and the “more-change-is-needed” position. The first position is seen as being represented by scientists such as Douglas Futuyma and Michael Lynch.<sup>13</sup> Futuyma (2011, 2014) thinks that evolutionary biology had absorbed and incorporated discoveries throughout its history, without the need for a formal reconsideration of evolutionary theory, and Lynch (2007) sees a multiplication of things to explain more than of explanations. The second position, expressed in papers such as Craig (2010, 2011), is against extending the MS because elements such as evo-devo would completely overthrow it: the MS would not be amendable. Although some of the cited workers actually have nuanced opinions, some of them did indeed express themselves in sharp contrast with the EES through various media (e.g., Coyne 2009). Proponents of the EES usually explain away such a diffuse dissent by the conservative inertia or active homeostasis of science, ‘paradigmatic’ almost in a Kuhnian sense. In any case, metascientific descriptions seem difficult to achieve and exposed to controversies.

#### *4.1 The scientist-field disproportion problem*

An obvious obstacle to the achievement of a metascientific consensus is what could be called the scientist-field disproportion. Evolutionary biology is vast in terms of involved people and labs all over the world, with their diversity and ever-changing boundaries. All sorts of science are being done in the world: do they fit the mind and the reach of one or few experts? How can we know what all those people are doing? Pigliucci (2009), to explain shifts in his list of concepts (Fig. 1), acknowledges the Altenberg meeting as an occasion for him to expand his thinking about evolutionary theory. Taking the cue from this, we ought to think that, in general and inevitably, concepts are included by the author partly as a function of contingent biographical and professional factors, such as the particular field of specialization, the network of professional contacts, the encounters that happen, or even some kind of personal taste. Factors like these are also subject to change over lifetime. All

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<sup>13</sup> Other protagonists are, e.g., Coyne (Hoekstra and Coyne 2007, Coyne in Pennisi 2008 and in Whitfield 2008), Hall (2000), Minelli (2010).

this speaks about the disproportion between any scientist's point of view and the necessary task of mapping the field, at any time in history.<sup>14</sup> Just think to how huge and fast-growing the scientific literature is today. A metascientific view aspires to describe the web of networks of researchers and labs that constitute evolutionary biology, i.e., people, along with their actions and knowledge, their instruments, the different media and various kinds of connections among them, and also, in part, the larger contexts in which they work and operate. When we are interested in an empirical concept such as phenotypic plasticity, then, we want to know for example where, when, how, and how much phenotypic plasticity was effectively studied in relation to evolution. And it is not even enough to know how frequently phenotypic plasticity is mentioned, or who are the most cited 'experts' of it. Before being able to demonstrate that plasticity is involved in the change of how evolutionary biology is practiced, we need to deal with how phenotypic plasticity is integrated in scientific practice, what is its incidence and role. How has the *understanding of* some concepts changed? And what is the *importance of* concepts in scientific work in different contexts and periods? In other words, how much research is theory-engaged and theory-driven (Scheiner 2013)? The fundamental problem of logical analyses of science is that scientists do not live inside theories, rather, at any particular moment in time, they have different versions or pieces of theory, with which they entertain diverse relationships. EES advocates have persisted in describing Darwinism, the MS, and the EES as nested sets of concepts and ideas, but evolutionary biology in 1980, in the 1930s, and in any moment in history is a working scientific community that has to be studied under more aspects. While rigorous methods such as meta-analysis are used to combine available scientific evidence, rigorous ways of knowing the scientific community seem scarcer.

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<sup>14</sup> To the scientist-field disproportion we will add, in Sect. 4, the 'flag effect': any scientist's claims are part of socio-epistemological and socio-economical dynamics where he or she has needs, aims, open accounts.

## 4.2 The scientific-metascientific mix problem

We have seen that elements as heterogeneous as, for example, natural selection, modularity, and paleontology constitute a mix of empirical and metascientific claims. Paleontology is actually one of the fields in which modularity can be studied (L.A.B. Wilson 2013), and paleontology provides and tests macroevolutionary models in which natural selection is more or less important. The logic of addition, in a sense so important in the “extension” approach of the EES, hardly works in an assemblage of scientific ideas (like natural selection) and metascientific ideas (like paleontology). It is true that some concepts seem one piece with fields, since they originate, at least in part, as generalized implications of particular fields. Evolvability, emergence, and organization are, for example, considered by Müller (2007) as general theoretical implications of evo-devo.<sup>15</sup> But fields are ways of doing science, not scientific concepts themselves. Indeed, any alleged implication (e.g., evolvability) of a particular field implication (e.g., evo-devo) is studied also by other fields, that in turn can share or borrow inspirations for their theoretical models. On the other hand, fields can cross-adopt ideas and concepts while remaining largely separated. Despite statements about niche construction being an example of “how ecology and evolutionary biology can be integrated” (Pigliucci 2009, p. 223), for example, existing niche construction models are in fact pure population genetics models.<sup>16</sup> Furthermore, long-standing fields can deal with concepts that are relatively recent. Take for example population genetics and evolvability. The diagram in Fig. 1 misleads about how much evolvability is integrated into (or even born out of) preexisting fields. Population genetics is often stereotypically associated with its initial scientific accomplishment of showing that “several discrete Mendelian genes can cumulatively produce the effect of a continuous, Gaussian distribution of phenotypes” (Pigliucci 2009, p. 220). *Mendelism* is thus the founding assumption of population genetics. But population genetics is an enduring empirical and theoretical field proceeding in the

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<sup>15</sup> We have seen with Pigliucci (2008a) that there are different kinds and sources of evolvability.

<sup>16</sup> Examples of integration between ecology and evolution are growing fast, but not where Pigliucci looks at (Loreau 2010).

development of more and more tools (Hartl and Clark 2007) that handle, or even uncover, many of the phenomena that are enlisted in the EES area, such as evolvability, multilevel selection, phenotype evolution. Pigliucci himself (2009) says that multilevel selection is essentially an “expansion of the mathematical theory underpinning evolutionary biology” (p. 221). Multilevel selection may thus be seen also as a part of population genetics, a fruit of the natural growth of a mathematical field.<sup>17</sup> On the other hand, some models can be insensitive to specific mechanisms, for example quantitative genetic models of phenotypic evolution stand largely invariant with respect to the particular development mechanisms (Pigliucci et al. 2006). Finally, hierarchical relationships among fields are another important aspect. For example, *complexity theory* and *network theory* can be *employed by* genomics, but also by evo-devo or ecology, or even by paleontology, because of their generality. It is true that complexity theory and network theory are autonomous fields, but their introduction into evolutionary biology looks more like an integration into the methods of existing fields than the addition of new fields. Many new measures and mechanisms happen to be introduced in this way. The EES is not always clear on the distinction between scientific and metascientific concepts. Pigliucci (2009, p. 222), for example, tried to attribute to each and every “component of the ES” a degree of “conceptual maturity” and a degree of “empirical support”. Relying on Gould’s (2002) triadic view of evolutionary theory, Pigliucci also tried to determine the impact of every EES component upon natural selection’s agency, efficacy and scope. These are interesting attempts, but EES components are logically heterogeneous, which makes them hardly comparable with respect to innovative load or degree of empirical support. Empirical support for measures like plasticity is a different issue than for fields like evo-devo, or perspectives like niche construction, or mechanisms like epigenetic inheritance, or transfers like applications of replicator theory. Measures are carried out. Old and new fields incorporate measures and perspectives and probe the evolutionary relevance of mechanisms by means of theories of other fields. When

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<sup>17</sup> Notice that past and present important population geneticists, like for example Timothy Prout, do not agree with multilevel selection being a part of population genetics. This is just a further example of multiple construability of a conceptual scheme of evolutionary biology.

responding to the claim that “ecology was never integrated in evolutionary biology” one can go metascientific and show off a field like evolutionary ecology, existing since the 1960s; another can go scientific and point out the widely known roles of ecological factors in speciation or macroevolution.

In this way, the mix of metascientific and scientific claims can create confuse discussions.

Metascientific claims are also claims about history. Consider Pigliucci’s claims quoted above: the MS is a paradigm and a conceptual framework that goes back to the 1940s, etc.; it was the crystallization of a theory of genes, and it is missing some important pieces that are being revealed today; indeed, we do need an EES. These are all metascientific claims, all historical, often oriented to the future.

This creates a double chronology that has to be taken into account when we deal, for example, with the EES. By EES we mean, on the one hand, the claims by EES advocates, and, on the other hand, one of the historical stages of evolutionary biology that the advocates describe. A further complication of metascientific claims is that they combine *description and prescription*: while they are meant to capture the present and past situation of the field, they also suggest future directions or point out certain ways of doing science that are more promising. The double chronology and the description-prescription duality are easily a source of ambiguities of metascientific claims. Is an EES already achieved? If so, since when? Or are we instead working on it? Or is the EES a future prospect still to come? And, in the latter case, is extension a normative or a descriptive claim (that is, does it concern what scientists *do* or what they *should* do)? Understandably, EES advocates seem to oscillate continually among these possibilities. Pigliucci (2007) argued for the *need for* an EES, and qualified it as forthcoming (p. 2646). For Müller (2007) evo-devo is an *already different* understanding of how development evolves, while its more general and deep implications are often overlooked. For Pigliucci and Müller (2010), new concepts are part of the current “practice” of evolutionary theory, but “Which of these will actually coalesce into a new kind of synthesis, augmenting the traditional framework, is a major challenge for the theorists of today” (p. vii). There is a “multifaceted research program” called the Extended Synthesis (p. 3); however, “an expanded theory of evolution [is] a

work-in-progress” (*Ibidem*), and the “current framework” has central tenets and assumptions yet to be relaxed (p. 4): “individual tenets of the Modern Synthesis can be modified, or even rejected, without generating a fundamental crisis in the structure of evolutionary theory” (p. 10). The prevalent position seems to emerge from these oscillations that the EES is something already here in practice and needing acknowledgement; at the same time, the EES is something whose existence requires a kind of conceptual, logical structure. The structure of the EES is still to come, and has to be worked out by theorists. Ambiguities like these are, I think, intrinsic of metascientific claims.

If EES theorists admit their uncertainties about what exactly the EES is or will be, they often seem secure about what the MS is or was. Perhaps the time distance between a metascientific claim and its target confers a sense of stability. Narratives of the MS are dry and standardized (see below, Sect. 4), but the underlying view on the matter is more shaky than it may seem. Metatheoretical terms are expected define what kind of theoretical ‘thing’ the MS is. For example, the MS is said to be a “conceptual framework” resulted from “the integration of several strands of evolutionary thought” (Pigliucci and Müller 2010, p. 3). It is also a set of claims (p. 5) or “tenets” that, however, “can be modified, or even rejected, without generating a fundamental crisis in the structure of evolutionary theory” (p. 10). The MS is also a theory (p. 3), a research program (p. 3), and a set of restrictions (pp. 13-14). The MS is defined as the “current paradigm” (Pigliucci 2007, p. 2743; Pigliucci and Müller 2010, pp. 3, 14) but, at the same time, Pigliucci states that the only paradigm shift had taken place with Darwin, at the origin of biology (Pigliucci 2007, p. 2748; see also Greene 1981). Metatheoretical terms for the MS are thus diverse and partly conflicting.<sup>18</sup>

Particular weight is given to terms such as “central tenets” (Pigliucci and Müller 2010, p. 4, 5) to convey the sense that the MS was a restrictive consensus on a structure made of conceptual pillars.

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<sup>18</sup> Other scholars employ still different terminologies. Scheiner (1992, 1999) for instance identifies two “central paradigms” in modern biology: the Modern Synthesis and the Molecular Synthesis. Syntheses are critical periods in which groups of relevant disciplines become focused on the same research program. For Scheiner, modern biology is undergoing a Final Synthesis between the two central paradigms, and this endeavour will be driven by the evolutionary side which has a larger perspective and is more theory-driven than the technique-driven Molecular Synthesis.



As we saw above, however, the set of concepts that are taken to represent the MS is not fixed. Besides, the evidence for such restriction doesn't seem systematic and fully convincing. Pigliucci and Müller, in their introduction to the EES book (2010), take one quotation from the beginning of a major textbook (Futuyma 1986, p. 12) as evidence for the narrowness and closure of the MS:

The major tenets of the evolutionary synthesis, then, were that populations contain genetic variation that arises by random (i.e., not adaptively directed) mutation and recombination; that populations evolve by changes in gene frequency brought about by random genetic drift, gene flow, and especially natural selection; that most adaptive genetic variants have individually slight phenotypic effects so that phenotypic changes are gradual (although some alleles with discrete effects may be advantageous, as in certain color polymorphisms); that diversification comes about by speciation, which normally entails the gradual evolution of reproductive isolation among populations; and that these processes, continued for sufficiently long, give rise to changes of such great magnitude as to warrant the designation of higher taxonomic levels (genera, families, and so forth) (Futuyma 1986, p. 12, cit. in Pigliucci and Müller 2010, p. 9).

Pigliucci and Müller seem to think that Futuyma's summary effectively represents the MS as a narrow 'tunnel vision' for evolutionary biology. But another quote, taken from an advanced point of the very same edition of Futuyma's textbook, is cited in Alan Love's chapter of Pigliucci and Müller's book as a "defense of the Modern Synthesis perspective" describing Neo-Darwinism as open and intrinsically integrative:

The power of neo-Darwinism lies in its generality of explanation. But like most general theories, it is highly abstract. It gains full explanatory power when concepts such as gene frequencies and selection are given empirical content by applying them to real features of real organisms: behavior, life histories, breeding systems, physiology and morphology. When this is done, however, new questions appropriate to those particular features emerge and

context-specific factors must be added to the theory (Futuyma 1986, p. 440, cit. in Love 2010, p. 416).

Notice that Love (2010) distinguishes between theory content and theory structure, with the possibility of different “presentations” to different aims. Futuyma’s paragraph reveals, for Love, “a commitment to a broad rather than narrow *representation of evolutionary theory*” (my emphasis, see also Love 2012).

The definition of the MS found in EES advocates is thus, at once, uncertain and self-confident. It is uncertain with respect to its metatheoretical status and the list of component concepts. It is confident in the conviction that the MS is well representable as a set of concepts, and also that the MS was a restriction of research questions by means of a narrow consensus on a few assumptions. But even in this respect we have different positions and anecdotal evidence. As we shall see (Sect. 5), the view of the MS resonates strongly with the account that was forcefully defended by Ernst Mayr especially during the 1970s (Mayr 1973). EES advocates seem to take Mayr’s version of the story at face value: the MS was a channeling of research questions and explanations, by means of a generalized agreement on a few key concepts and mechanisms. The history of biology, however, warns us against taking metascientific claims too literally. We saw important factors of complication in achieving a solid metascientific view. Now, traveling back in time to the MS, we will see that additional biases apply.

## 5. Useful flags: Syntheses in historical perspective

Ernst Mayr wrote:

The term “evolutionary synthesis” was introduced by Julian Huxley [...] to designate the general acceptance of two conclusions: gradual evolution can be explained in terms of small genetic changes (“mutations”) and recombination, and the ordering of this genetic variation

by natural selection; and the observed evolutionary phenomena, particularly macroevolutionary processes and speciation, can be explained in a manner that is consistent with the known genetic mechanisms (Mayr in Mayr and Provine 1980, p. 1).

We should contrast Mayr's account of the MS – taken at face value by EES advocates – with what historians of biology discover about the MS.<sup>19</sup> Cain (2009a), for example, focuses on the pragmatic and strategic utility of claiming, back in the 1930s, to be part of a modernizing team (see also Provine 1992, cit. in Delisle 2011, Smocovitis 1996). To the 'architects', the claim was a strategic move in many ongoing battles, and personally useful to their careers. 'Outsiders', as well, employed the MS in 'David and Goliath' narratives to muscle their way through. The idea that the MS is there as a certain object was born and cultivated for specific reasons in those years. Meanwhile – historians show – architects of the MS such as Huxley, Simpson, Dobzhansky, and Rensch held different research agendas or even "incommensurable epistemological frameworks" (Delisle 2011, p. 57; see also Cain 2003), and paradoxically the advertised narrow set of concepts ended up by being an obstacle to the advancement of these agendas. Cain (2009a)<sup>20</sup> argues that traditional historiography, following the lead of MS claims, has been affected by *historical realism* on the MS, and that many historical studies of the synthesis period create forced links between anything that was happening and that alleged overarching object, the MS. History can actually be told in very different ways – for example, Cain thinks that while an evolutionary synthesis at the theoretical level was proclaimed, a synthesis of taxonomy and systematics (old and new) was substantially more important. The 'constructed' nature of the MS was epitomized already by Burian (1988) when he defined the MS as a "moving target", with regards to both the list of its possible 'architects' and the boundaries of its research agenda.

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<sup>19</sup> Enlightening examples, beside cited Joe Cain, are Sahotra Sarkar, Betty Smocovitis, Michael Dietrich, William Provine, David Depew, Richard Delisle.

<sup>20</sup> Cain wrote many papers describing the overall situation in the MS period (2000, 2002a, 2009a, 2013). He also published equally interesting monographic studies focused on personalities such as Simpson (Cain 1989, 1990, 1992), Sewall Wright (Cain 2007), Julian Huxley (Cain 2010), Ernst Mayr (Cain 1994, 2009b), Theodosius Dobzhansky (Cain 2002b). Notice that, of course, Cain is just a telling example and that historians themselves are not monolithic at all in their consideration of the MS (cf., e.g., Sarkar 1992, 2004).

A step in the ‘objectivization’ of the MS was the 1980 Conference on the Evolutionary Synthesis whose proceedings are Mayr and Provine (1980). Ernst Mayr was a very influential figure throughout 20th Century evolutionary biology. He (1973) had battled to acknowledge “the naturalists” as he called them (e.g., zoologists, paleontologists) against an account of the MS that he saw as too imbalanced in favor of geneticists and mathematicians (targeting, e.g., Provine 1971). An important moment for the establishment of Mayr’s own view of the MS was the 1980 Conference. Mayr wanted to clarify “the sequence of events [1936-1947] leading to the synthesis, and to identify the factors responsible for the preceding disagreements” (*Ibidem*). But despite Mayr’s ‘general acceptance’ view of the MS, even a cursory reading of Mayr and Provine (1980) reveals a diversity of stories and visions of the MS across points of view, disciplinary backgrounds, geographical positions. As Provine noticed, the 1980 Conference and proceedings are not a great example of consensus and agreement on a small set of concepts, despite Mayr’s efforts. In the Epilogue, Provine wrote:

One note of unanimity at the conference may perhaps need to be revised. Although all participants seemed to agree that an evolutionary synthesis had occurred, they may have had different syntheses in mind. The evolutionary synthesis may therefore have appeared more cohesive during the conference than it actually was (Provine in Mayr and Provine, p. 408).

There is not much consensus on the proclaimed consensus, after all. 1980 was more the attempted construction of a consensus than it was the account of an already achieved agreement.

We must derive two lessons for our interpretation of the EES debate.

First, Ernst Mayr, along with others, produced, iterated, and defended for specific purposes the view of the MS that is now adopted in the EES. The Modern Synthesis was, first of all, a useful flag. The ‘conceptual pillars’ must not be understood as a faithful account of the scientific community at any time, but rather a manifesto flag for the ‘architects’ in their respective times. This awareness, along

with inconsistencies and shortages of the available descriptions of the MS, may make us more cautious in objectivizing the MS.

Second, EES claims may be analogized to MS claims: the EES can *itself* be seen as a useful flag, although obviously in a completely changed socio-political and scientific context. If the ‘flag effect’ is partly explanatory to the MS, there is no reason why we should not consider it when we think to the EES. A collection of conceptual pillars (Fig. 1) is not necessarily a good description of the status and transformations of evolutionary biology, whereas apparently it does make an effective flag, an aggregating flag reminiscent of Mayr’s ensign. The instabilities and disagreements we have described stand, in part, as symptoms for all these partiality aspects. On the other hand, the MS and the EES certainly represent more than partisan interests: they are pleas for the good of the field. With reference to the MS, Delisle (2011) talked about a “sociological synthesis” – made of transformations in the social configuration of science, exchange among disciplinary communities, institutional bridges – as something separate from conceptual unification that, for him and many others, was never quite achieved. The EES might represent a continuation of the struggle – already present in the MS – against disfunctional imbalance of prestige and resources granted to molecular methods vs. other methods, in an age of cheaper high-throughput sequencing that produces rivers of publications.<sup>21</sup> Other redistributions might be at stake, for example between botanists and microbiologists vs. zoologists, or concerning new means of knowledge such as simulations. The EES could be, today, a flag for many streams of study that have been suffering due to perceived scientific dominant tendencies or fashions, a flag recruited by an ongoing struggle for very basic needs of any scientist: funding, publication, consensus. Let us make some examples. Odling-Smee’s suggestion of niche construction (1988) waited some ten years to be taken up by a few mainstream modelers and population geneticists (Laland et al. 1996), who, in turn, offered their models to call for a global

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<sup>21</sup> One thing that becomes clear from a reading of the history of the MS is that it sought to present a unified front against the rise and usurpation of molecular biologists. This aspect of the story is quite relevant to understanding what’s going on with the EES as evolutionary biologists face up to the fact that many of their tools today are molecular.

rethinking of evolutionary biology (Laland et al. 2009), and still, it would appear, to date their effort have breached almost exclusively among philosophers and human scientists (e.g., Kendal et al. 2011). Jablonski's work on multilevel processes in macroevolution was part of the paleobiological revolution (Sepkoski and Ruse 2009; Sepkoski 2012) since the 1980s (Jablonski 1986). Macroevolution is today a big and consolidated field, but the most radical implications for evolutionary mechanisms are still unsettled (Serrelli and Gontier forthcoming). Jablonka has been a vocal and harsh critic of the MS for many years (Jablonka and Lamb 1989). On the other hand, the evolutionary importance of epigenetics has been considered negligible due, for example, to the lability of epigenetically transmitted modifications over evolutionary time, and proponents like Jablonka have long been accused from overusing a few experimental cases (e.g., Haig 2007). David S. Wilson (e.g., 2009) describes the scientific battle over group selection spanning 150 years, beginning with Darwin. Wilson himself started a strenuous defense of group selection since 1970s (Wilson 1975; Wilson and Dugatkin 1997; Sober and Wilson 1998). Notwithstanding peer-reviewed publications on the subject (Wilson and Wilson 2007; Eldakar and Wilson 2011), a multimedia battle still goes on with personalities such as Dawkins and Coyne that tirelessly deny any possibility of group selection in evolution. Kirschner and Gerhart started to defend evolvability in late 1990s (1998). Opponent, Lynch (e.g., 2007) keeps bringing back evolvability to its population genetics meaning (related to heritability) and defines other versions of evolvability as "speculation, which is almost entirely restricted to molecular and cell biologists and those who study digital organisms" (pp. 8602-3). These are some of the various fierce streams of research that have decided to become associated with the EES. Notwithstanding the various reasons of the involved actors, just like the MS had helped the advancement of science, the EES really contains very important questions: biology has indeed been changing, and is changing, around us in many senses; we do want to know how, how fast, how uniformly, what scientists can and should do to second positive movements and contrast negative ones. Answers could, for example, orient economic investment, policy, curriculum planning,

publication choices. But if the EES, like other pictures, is biased by ‘flag effects’, scientist-field disproportion, and all other complexity factors we have reviewed, where will we get those answers?

## **Conclusion: the need of pursuing the promises scientifically**

I have repeatedly remarked the potential benefit of knowing ‘what is it to do research’ to plan biology training, choose research lines in a lab, navigate career development, connect specific researches to broader contexts, and make policy decisions on research funding and reward, all in order to make the field advance for the better. These are the high stakes and the promises of encompassing metascientific views, such as the EES, that, at the same time, encounter remarkable difficulties on their way. The EES is a metascientific claim in its being a statement about what’s new *in how evolutionary biology is carried out*, not only a statement about what’s new in evolution as we know it. Massimo Pigliucci and Gerd Müller started off, in 2007, with their shared idea that evolutionary biology has been overlooking ‘form’ in favor of genes and genotypes too long. Thanks to some initiatives they organized, they then expanded and modified their ideas bringing about a list of many mechanisms, measures, fields, perspectives, and applications of evolutionary theory that were not present in the MS. The dynamism of the enlisted concepts might reflect the elusive vitality of current evolutionary research, although this would not apply to the equally dynamic portrait of the MS. At a deeper level lie the inherent, growing difficulties of any metascientific view: the vastness and complexity of any scientific field, the insufficiency of conceptual analysis to capture the thickness of scientific research, the entanglement between empirical and metascientific concepts, between multiple chronologies, and between descriptive and normative needs, as well as the inevitable stakeholding of any reviewer involved in the reviewed field. So how do we get insights about the shifting state of something so broad, fragmented, and lively like evolutionary biology? While databanks of specific research objects (a gene, a species) are flourishing, scientists don’t access

meaningful and rigorous data about the scientific community. Yet, let me suggest that helpful methods and notions exist in different disciplines, and perhaps would only need to be applied and integrated to construct a metascientific view of evolutionary biology.

What's the real trajectory of the consideration of phenotypes, or of ecology, in the community of evolutionary biologists? What is really happening to evolutionary biology in relation to what many people call 'evo-devo', or with what different groups call 'integration of evolution with ecology'? When and how, if ever, evo-devo changed the way evolutionary research is carried out in other parts of the field? Is epigenetic inheritance really related to new ways of doing science? Conceptual analysis of theories, beloved by philosophers and by some scientists, must be complemented to achieve accounts that are more grounded and useful to biologists. Real substance of metascientific views are the diffusion of those concepts, the changing role of those concepts in scientific research, and the congruent partitioning and repartitioning of the scientific community relating to various ways of being evolutionary biologists. Several studies already go in this direction. Scheiner (2013) performed some quick quantitative historical analyses of ecology to measure theory-engagement in that field. Something similar might be done to assess the integration between evolution and ecology. Love and colleagues (Love 2003, 2006, 2007; Love and Raff 2003; Raff and Love 2004) made interesting attempts to re-evaluate the received conviction that development was excluded by the MS. To this aim they mixed historical and conceptual methods: they dissected the different kinds of developmental studies that might have been excluded, looking for clues about possible exclusion of one or more of these 'embryologies'; they searched fields like morphology and paleontology that also were seemingly side-lined; they spelled out different kinds of exclusion. But even more can be done.

Information sciences have techniques for the automatic retrieval, analysis and representation in *corpora* of big data. Recent studies have focused on scientific/academic information, its search, recommendation and distribution (McCain et al. 2005, McCain 2008, 2009, Riviera 2013).



729 Scientometrics, i.e. the quantitative study of science, can reveal relations between units such as  
730 authors, disciplines, institutions, semantic elements. Study of patterns in citations, texts, and user  
731 behaviors (McCain 2013) through time can trace ‘lineages of ideas’ and reveal phenomena about the  
732 scientific community, such as fields emergence and decline. The ongoing explosion of online journals  
733 and digital archives matches perfectly these techniques, although it also demands corrections and  
734 creative solutions as the analysis goes back in time – as it will always do, since as we have seen  
735 metascientific claims are almost always historical claims. The domain of analysis can also be  
736 expanded multilingually to conference programmes and abstracts, research protocols, official  
737 documents, and to alternative media that are becoming more important in the economy of scientific  
738 work: online tools, institutional websites, science news and blogs.

739 Synthesis, if any, must have scientometric correlates, provided that, although textual search is very  
740 powerful, it must be guided by the right queries. At the same time, work in the social sciences  
741 demonstrates that understanding scientific communities is broader than bibliometrics. For example,  
742 quantities about scientific papers should be related to the (changing) social function of scientific  
743 papers (Riviera 2013). White and McCain (1998) affirm that techniques such as ‘authors co-citation  
744 analysis’ are “no substitute for extensive reading and fine-grained content analysis”: “they produce  
745 history of the cliometric sort, which leaves out almost all the good parts, [for example] what actually  
746 gave rise to the most significant work” (p. 327). The job of biologists has certainly changed, and we  
747 want to understand how: laboratory ethnography and biographical research have methods to  
748 answer (see Caduff 1999, Hess 2001), and also to bring about reliable indicators to obtain large scale  
749 descriptions of evolutionary biology. Some prior, qualitative study of research and writing practice in  
750 biology will be necessary in order to extract significant clues, indexes, proxies, and patterns that can  
751 feed quantitative research and yield meaningful answers. Ethnographic work must be in turn  
752 informed by sound theoretical knowledge and epistemological hypotheses, if it has to provide  
753 quantitative analyses with meaningful search keys. Then, if we really want to understand and

explain, it will be necessary to involve knowledge and methods from, e.g., the sociology (Gieryn 1983, Bourdieu 1993, Riviera 2013) and the economics (Stephan 1996, 2012, Sent 1999, 2013, Thicke 2013) of science, that hold important keys to the reasons for conformism and innovation, stability and change in science. Talking about the MS as a ‘constraining theoretical framework’ is interesting, but many quarrels on the plausibility of such a constraint arise, probably, from the lack of serious consideration of other really constraining factors: policies, politics, culture, economic investments, technology, reward structure of science, the social role of the evolutionists, the structure of the community, and the like. After all, scientific conformism that EES advocates attribute to the rigid theoretical framework they call the MS might well find appropriate pieces of explanation in the economic and social structure of science over the 20<sup>th</sup> Century. This is why we also need to ask economics and sociology to describe the social dynamics of evolutionary biology and the conditions and identities of evolutionary biologists over time and across geographical ranges. If these aspects are changing, considering them will be crucial in either the EES or other metatheoretical views we can build. The birth of a field is also the birth of a new way of doing science, as well as a statement of identity, and is described by the changing conditions of the scientific community, not only by the map of involved concepts. What can or cannot be done in a science is constrained and channeled by cultural, social, and economic aspects of science, for example technological advances and costs, or cultural obstacles regarding training, job market and evaluation, grant systems, publication, language barriers (Sidlauskas 2010). Sociology, ethnography, economics and history have tools and knowledge for all these explanatory aspects that, moreover, are essential to any description of a scientific community.

Scientific methods can let us observe metascientific change of evolutionary biology and, in face of their variety and heterogeneity, they should be themselves ‘synthesized’ in some way. The National Center for Evolutionary Synthesis (Sidlauskas et al. 2010) defines ‘synthetic science’ as an integration

of different kinds of data from multiple sources. Various kinds of synthetic science, achieved in diverse ways, exist.

My humble methodological suggestions are, at this stage, only meant to help the imagination of metascientific views built with a more scientific, interdisciplinary approach. Of course they will still be prone to complex chronologies and description-prescription oscillations, but they will certainly be more fecund of guidelines for choices and policies that will favor the growth of our knowledge of evolution more effectively than the familiar flaggish conceptual analyses. Closing the circle, a serious multi-disciplinary approach to the evolutionary scientific community could be able to *explain* the timely appearance of metascientific claims such as the MS and the EES, the useful flags. This would not prevent turning the contents of the MS and of the EES into quantifiable and testable hypotheses, and of course doesn't exclude that scientists like Pigliucci and Müller are interpreting correctly some global synthesis happening around us. What is certain, is that a complete answer to questions like Pigliucci's may only be sought by looking scientifically at the scientific community as such, relating the epistemological, social, and human aspects of what it is to do evolutionary biology over historical time. We will then be able to face Pigliucci's question "Do we need an Extended Evolutionary Synthesis?" on better grounds, whether to answer it or to reformulate it, in either case fulfilling the need for maintenance of evolutionary biology in a more shared and uncontroversial way.

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## Figures

### Figure 1

A comparison between the elements of an Extended Evolutionary Synthesis (EES) appearing in two different publications: (a) from Pigliucci (2009); (b) from the collective book *Evolution: The Extended Synthesis* (ed. by Pigliucci and Müller 2010). Each of the two diagrams describes the EES as inclusive of Darwinism (inner circle), the Modern Synthesis (middle circle), and additional concepts (outer circle). A comparison among publication (either with or without diagrams) uncovers dynamism and problematic factors of complexity in the development of Pigliucci and Müller's thought.

