

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

¹ "Riccardo Massa" Department of Human Sciences, University of Milano Bicocca

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

25 **Keywords**

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

27 **Introduction**

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

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

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

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

² 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.

³ 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,⁴ 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).⁵

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?**

⁴ 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).

⁵ 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/>.

82 According to a review by Pigliucci (2007) entitled “Do we need an Extended Evolutionary Synthesis?”,
83 the MS coincides with evolutionary genetics, as its foundations had consisted in a movement of
84 “crystallization” of a “theory of genes” out of the original Darwinian “theory of form” (p. 2744).
85 Pigliucci supported such a claim with a brief conceptual history of evolutionary biology, summarizing
86 how 20th Century Darwinism overcame Lamarckism, and how Mendelism was made compatible with
87 gradual change by means of statistical works by Fisher, Haldane and Wright (*Ivi*, p. 2744). He
88 described the major theoretical contributions by Dobzhansky, Mayr, and Simpson in the 1940s, and
89 then identified some missing elements in the MS, namely: development, studied separately by
90 embryologists (p. 2745); ecology, secluded away as a background condition of evolution (*Ibidem*);
91 implications of the ‘-omics revolution’, and its relationships to neutralism and complex genotype-
92 phenotype interactions (pp. 2745-6); and phenomena such as plasticity, evolutionary capacitance,
93 epigenetic inheritance (p. 2746). An EES would integrate a theory of form back into evolutionary
94 biology (p. 2745). Some “bits and pieces” or “recurring ideas” (p. 2746) that will be part of the EES
95 would be: *evolvability*, hinging on developmental systems’ modularity and robustness (p. 2746);
96 *phenotypic plasticity* and the possibility of modes of evolution such as genetic accommodation (pp.
97 2746-7); *epigenetic and multiple inheritance* (p. 2747); *complexity theory*, revealing organizing
98 principles different from natural selection (*Ibidem*); and *updated adaptive landscapes*, in light of
99 work that reformulates their general shape (pp. 2747-8). Concluding the 2007 paper, Pigliucci
100 anticipated a new, complex, constructive process analogous to the MS itself, a progressive
101 “expansion of theoretical biology (in the broader sense of conceptual understanding of the
102 discipline’s foundations)” (p. 2748).

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

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

116 [FIGURE 1 HERE]

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

⁶ 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”.

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

132 **2. Conceptual pillars of the EES**

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

143 **2.1. Mechanisms**

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

⁷ 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,

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

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

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

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

171 2.2. Measures

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

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

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

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

191 studies it is expected to occur in huge superconnected networks such as the genome. Sometimes
192 modularity is coherent across two levels, genetic and phenotypic, when genetic modules affect only
193 a part of the phenotype with no deleterious pleiotropic effects on other parts (Müller 2007). But
194 modularity at one scale is not necessarily aligned to other scales. Modular patterns in the
195 phenotypes may also emerge at the phenotypic level, by the mechanics of cell differentiation in
196 which cells induce each other to assuming states in the multistable landscape of cell states (Newman
197 2010). Müller (2007) explains that sometimes when a “unit of phenotypic construction” remains
198 recognizable in anatomical architectures over evolutionary time, the molecular and developmental
199 pathways that construct the unit change. According to Wagner and Altenberg (1996), in the
200 phylogeny of animals modularity is most likely a derived state, the result of parcellation rather than
201 integration, with the open question of whether modularity emerged by natural selection.

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

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

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

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

230 *2.3. Fields*

231 Some of the conceptual pillars are whole scientific fields. *Population genetics, paleontology, and*
232 *natural history* are familiar 'actors' in many historical accounts of evolutionary biology (Mayr and
233 Provine 1980; Gould 1980, 1982, 2002; Eldredge 1985, 1999), including Pigliucci's (2007, p. 2744;
234 2009, p. 220). Fields have their own history of change. For Pigliucci (2009), genomics started with the
235 view that "once we 'decode' the genome of an organism we somehow gain a universal key to
236 understanding its biology" (p. 223). This first phase was, for Pigliucci, "squarely within the conceptual
237 framework of the rather gene-centric MS". Then genomics and other "-omics" fields renewed
238 themselves by turning to system-level properties of entire networks of gene products. Fields have
239 their own complex structure, subfields, and hybridizations. *Evo-devo*, as Müller (2007) says, is not

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

248 *2.4. Perspectives*

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

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

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

275 Niche construction captures the basic observation that organisms impact and also actively construct
276 their and others’ environment (Darwin 1881). Richard Lewontin (1978, 1983) and John Odling-Smee
277 (1988) were among the authors who began to point out a ‘lack of modeling’ of the widespread
278 phenomenon of niche construction in the mathematical core of evolutionary theory, i.e. population
279 biology. Dawkins’s (1982) concept of ‘extended phenotype’ was an incomplete perspective (Odling-
280 Smee et al. 1996, p. 295) in considering niche construction only as a product – not as a source – of
281 natural selection. Since the the 1990s the niche construction perspective has been a collector of
282 examples brought to the attention of evolutionary theorists. Evolutionary niche construction models
283 (Odling-Smee et al. 1996; Laland et al. 1996, 1999; Odling-Smee et al. 2003) were obtained by
284 modifying consolidated two-locus multiplicative models in population genetics. The introduction of
285 feedback from gene frequencies to selection pressures (influencing, in turn, gene frequencies) yields
286 significant novelties in the dynamics. Therefore, niche construction models have been hailed as an
287 important step forward in evolutionary modeling.

288 *2.5. Derived applications*

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

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

312 **3. Restless concepts**

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

319 Some concepts are stably there, e.g. evolvability (coupled, only in 2009, with modularity), epigenetic
320 inheritance, and plasticity and accommodation (which also constitute one of Pigliucci’s specialties,
321 e.g., Schlichting and Pigliucci 1998; Pigliucci 2001; cf. Scheiner 1999). Evo-devo, genomics, and
322 multilevel selection are included since 2009 with small, essentially metatheoretical changes (evo-
323 devo becomes qualified as “theory” in 2010, while multilevel selection loses such qualification;
324 “genomics and network theory” switch to “genomic evolution”). Some elements are particularly
325 labile. Complexity theory is dropped in 2010. Replicator theory only shows up in 2010. Ecology, listed
326 as a missing element of the MS by Pigliucci (2007), participates to the EES only in the 2009 diagram.
327 Contingency even jumps from being an element of the EES in 2009 to being a concept of the MS in
328 2010. Some concepts slip in in 2009 to be conserved in 2010, such as niche construction. The set of
329 candidate concepts for an EES mutates through the different papers and works, even works by the
330 same person – see Sect. 1 and Fig. 1. Of course, cartoon diagrams must be taken with a grain of salt:
331 they are idealized and represent only some aspects of the EES discourse. That being said, in this
332 search for the best arrangement of evolutionary concepts, many will recognize a persistent dose of
333 arbitrariness.¹⁰ For instance, evolutionary mechanisms (see 2.1) are arranged by EES proponents in

¹⁰ 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

334 just *one of the many* possible alternative ways. Notice that the historical counterpart of epigenetic
335 inheritance, which would be *genetic* or *germline inheritance*, is missing from EES diagrams. Instead
336 we find *Mendelism* and *Mendelian inheritance*, but these are not alternative physiological
337 mechanisms of inter-individual passage of traits: they rather describe a trans-generational traits
338 distribution pattern¹¹. Then, natural selection and multilevel selection are depicted as distinct pillars,
339 but, granted that multilevel selection is accepted (Keller 1999), we may well argue that such
340 acceptance implies the unity of selection, i.e. that multilevel selection *is* natural selection, and that
341 natural selection *is* or *can be* multilevel. The split of natural selection and multilevel selection as two
342 distinct pillars seems thus more of a way of marking certain theoretical studies than an addition of
343 discrete new mechanisms as it is always presented. Indeed, the reflection on units and levels is
344 inherent to evolutionary biology: it has never stopped since Darwin.¹² Interlevel dynamics are a
345 pervasive issue, beginning with genetic selection vs. phenotypic selection which must be correlated
346 over various time scales. Genotypes and phenotypes entertain non-linear relationships as shown for
347 example by other mechanisms listed in the EES: *phenotypic accommodation* (i.e., adjustment,
348 without genetic change, of variable aspects of the phenotype following a novel input during
349 development) and genetic assimilation (loss of dependence on environmental cues, Pigliucci et al.
350 2006). *Accommodation* is depicted as stably associated with *plasticity*, whereas we might regard it as
351 a further example of the multilevel complexity of the single mechanism of natural selection. We have
352 seen that plasticity, modularity, robustness, and evolvability might not be evolutionary mechanisms

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

¹¹ 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.

¹² 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.

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

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

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

379 **4. The EES as a tricky metascientific description**

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

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

413 *4.1 The scientist-field disproportion problem*

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

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

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

¹⁴ 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.

445 4.2 *The scientific-metascientific mix problem*

446 We have seen that elements as heterogeneous as, for example, natural selection, modularity, and
447 paleontology constitute a mix of empirical and metascientific claims. Paleontology is actually one of
448 the fields in which modularity can be studied (L.A.B. Wilson 2013), and paleontology provides and
449 tests macroevolutionary models in which natural selection is more or less important. The logic of
450 addition, in a sense so important in the “extension” approach of the EES, hardly works in an
451 assemblage of scientific ideas (like natural selection) and metascientific ideas (like paleontology). It is
452 true that some concepts seem one piece with fields, since they originate, at least in part, as
453 generalized implications of particular fields. Evolvability, emergence, and organization are, for
454 example, considered by Müller (2007) as general theoretical implications of evo-devo.¹⁵ But fields are
455 ways of doing science, not scientific concepts themselves. Indeed, any alleged implication (e.g.,
456 evolvability) of a particular field implication (e.g., evo-devo) is studied also by other fields, that in
457 turn can share or borrow inspirations for their theoretical models. On the other hand, fields can
458 cross-adopt ideas and concepts while remaining largely separated. Despite statements about niche
459 construction being an example of “how ecology and evolutionary biology can be integrated” (Pigliucci
460 2009, p. 223), for example, existing niche construction models are in fact pure population genetics
461 models.¹⁶ Furthermore, long-standing fields can deal with concepts that are relatively recent. Take
462 for example population genetics and evolvability. The diagram in Fig. 1 misleads about how much
463 evolvability is integrated into (or even born out of) preexisting fields. Population genetics is often
464 stereotypically associated with its initial scientific accomplishment of showing that “several discrete
465 Mendelian genes can cumulatively produce the effect of a continuous, Gaussian distribution of
466 phenotypes” (Pigliucci 2009, p. 220). *Mendelism* is thus the founding assumption of population
467 genetics. But population genetics is an enduring empirical and theoretical field proceeding in the

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

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

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

¹⁷ 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.

492 responding to the claim that “ecology was never integrated in evolutionary biology” one can go
493 metascientific and show off a field like evolutionary ecology, existing since the 1960s; another can go
494 scientific and point out the widely known roles of ecological factors in speciation or macroevolution.
495 In this way, the mix of metascientific and scientific claims can create confuse discussions.

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

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

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

524 If EES theorists admit their uncertainties about what exactly the EES is or will be, they often seem
525 secure about what the MS is or was. Perhaps the time distance between a metascientific claim and
526 its target confers a sense of stability. Narratives of the MS are dry and standardized (see below, Sect.
527 4), but the underlying view on the matter is more shaky than it may seem. Metatheoretical terms are
528 expected define what kind of theoretical ‘thing’ the MS is. For example, the MS is said to be a
529 “conceptual framework” resulted from “the integration of several strands of evolutionary thought”
530 (Pigliucci and Müller 2010, p. 3). It is also a set of claims (p. 5) or “tenets” that, however, “can be
531 modified, or even rejected, without generating a fundamental crisis in the structure of evolutionary
532 theory” (p. 10). The MS is also a theory (p. 3), a research program (p. 3), and a set of restrictions (pp.
533 13-14). The MS is defined as the “current paradigm” (Pigliucci 2007, p. 2743; Pigliucci and Müller
534 2010, pp. 3, 14) but, at the same time, Pigliucci states that the only paradigm shift had taken place
535 with Darwin, at the origin of biology (Pigliucci 2007, p. 2748; see also Greene 1981). Metatheoretical
536 terms for the MS are thus diverse and partly conflicting.¹⁸

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

¹⁸ 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.

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

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

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

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

564 context-specific factors must be added to the theory (Futuyma 1986, p. 440, cit. in Love
565 2010, p. 416).

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

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

582 **5. Useful flags: Syntheses in historical perspective**

583 Ernst Mayr wrote:

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

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

590 We should contrast Mayr's account of the MS – taken at face value by EES advocates – with what
591 historians of biology discover about the MS.¹⁹ Cain (2009a), for example, focuses on the pragmatic
592 and strategic utility of claiming, back in the 1930s, to be part of a modernizing team (see also Provine
593 1992, cit. in Delisle 2011, Smocovitis 1996). To the 'architects', the claim was a strategic move in
594 many ongoing battles, and personally useful to their careers. 'Outsiders', as well, employed the MS in
595 'David and Goliath' narratives to muscle their way through. The idea that the MS is there as a certain
596 object was born and cultivated for specific reasons in those years. Meanwhile – historians show –
597 architects of the MS such as Huxley, Simpson, Dobzhansky, and Rensch held different research
598 agendas or even "incommensurable epistemological frameworks" (Delisle 2011, p. 57; see also Cain
599 2003), and paradoxically the advertised narrow set of concepts ended up by being an obstacle to the
600 advancement of these agendas. Cain (2009a)²⁰ argues that traditional historiography, following the
601 lead of MS claims, has been affected by *historical realism* on the MS, and that many historical studies
602 of the synthesis period create forced links between anything that was happening and that alleged
603 overarching object, the MS. History can actually be told in very different ways – for example, Cain
604 thinks that while an evolutionary synthesis at the theoretical level was proclaimed, a synthesis of
605 taxonomy and systematics (old and new) was substantially more important. The 'constructed' nature
606 of the MS was epitomized already by Burian (1988) when he defined the MS as a "moving target",
607 with regards to both the list of its possible 'architects' and the boundaries of its research agenda.

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

²⁰ 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).

608 A step in the ‘objectivization’ of the MS was the 1980 Conference on the Evolutionary Synthesis
609 whose proceedings are Mayr and Provine (1980). Ernst Mayr was a very influential figure throughout
610 20th Century evolutionary biology. He (1973) had battled to acknowledge “the naturalists” as he
611 called them (e.g., zoologists, paleontologists) against an account of the MS that he saw as too
612 imbalanced in favor of geneticists and mathematicians (targeting, e.g., Provine 1971). An important
613 moment for the establishment of Mayr’s own view of the MS was the 1980 Conference. Mayr
614 wanted to clarify “the sequence of events [1936-1947] leading to the synthesis, and to identify the
615 factors responsible for the preceding disagreements” (*Ibidem*). But despite Mayr’s ‘general
616 acceptance’ view of the MS, even a cursory reading of Mayr and Provine (1980) reveals a diversity of
617 stories and visions of the MS across points of view, disciplinary backgrounds, geographical positions.
618 As Provine noticed, the 1980 Conference and proceedings are not a great example of consensus and
619 agreement on a small set of concepts, despite Mayr’s efforts. In the Epilogue, Provine wrote:

620 One note of unanimity at the conference may perhaps need to be revised. Although all
621 participants seemed to agree that an evolutionary synthesis had occurred, they may have
622 had different syntheses in mind. The evolutionary synthesis may therefore have appeared
623 more cohesive during the conference than it actually was (Provine in Mayr and Provine, p.
624 408).

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

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

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

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

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

²¹ 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.

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

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

682 **Conclusion: the need of pursuing the promises** 683 **scientifically**

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

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

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

726 Information sciences have techniques for the automatic retrieval, analysis and representation in
727 *corpora* of big data. Recent studies have focused on scientific/academic information, its search,
728 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

754 explain, it will be necessary to involve knowledge and methods from, e.g., the sociology (Gieryn
755 1983, Bourdieu 1993, Riviera 2013) and the economics (Stephan 1996, 2012, Sent 1999, 2013, Thicke
756 2013) of science, that hold important keys to the reasons for conformism and innovation, stability
757 and change in science. Talking about the MS as a ‘constraining theoretical framework’ is interesting,
758 but many quarrels on the plausibility of such a constraint arise, probably, from the lack of serious
759 consideration of other really constraining factors: policies, politics, culture, economic investments,
760 technology, reward structure of science, the social role of the evolutionists, the structure of the
761 community, and the like. After all, scientific conformism that EES advocates attribute to the rigid
762 theoretical framework they call the MS might well find appropriate pieces of explanation in the
763 economic and social structure of science over the 20th Century. This is why we also need to ask
764 economics and sociology to describe the social dynamics of evolutionary biology and the conditions
765 and identities of evolutionary biologists over time and across geographical ranges. If these aspects
766 are changing, considering them will be crucial in either the EES or other metatheoretical views we
767 can build. The birth of a field is also the birth of a new way of doing science, as well as a statement of
768 identity, and is described by the changing conditions of the scientific community, not only by the
769 map of involved concepts. What can or cannot be done in a science is constrained and channeled by
770 cultural, social, and economic aspects of science, for example technological advances and costs, or
771 cultural obstacles regarding training, job market and evaluation, grant systems, publication, language
772 barriers (Sidlauskas 2010). Sociology, ethnography, economics and history have tools and knowledge
773 for all these explanatory aspects that, moreover, are essential to any description of a scientific
774 community.

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

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

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

795 **Acknowledgements**

796 The author thanks Samuel M. Scheiner and two anonymous referees for invaluable support and
797 useful suggestions on the text. Allen Rodrigo, Florence Debarre, Giuseppe Fusco, Alessandro Minelli
798 and Maria Berica Rasotto provided useful conference feedbacks. Research was carried out in a MIUR-
799 funded postdoc fellowship entitled "Philosophy of science and evolution: the 'extended synthesis'"
800 at the University of Milano Bicocca. Referring person was prof. Telmo Pievani, whom the author
801 warmly thanks.

802 **References**

- 803 Akey JM and Shriver MD (2011) A grand challenge in evolutionary and population genetics: new paradigms for
804 exploring the past and charting the future in the post-genomic era. *Front. Genet.* 2(July): 47.
- 805 Boto L (2010) Horizontal gene transfer in evolution: facts and challenges. *Proc. R. Soc. B* 277(1683): 819-27.
- 806 Bourdieu P (1993) *The Field Of Cultural Production*. Cambridge, UK: Polity Press.
- 807 Brooks DR and Agosta SJ (2012) Children of time: the extended synthesis and major metaphors of evolution.
808 *Zoologia (Curitiba)* 29(6): 497-514.
- 809 Burian R (1988) Challenges to the evolutionary synthesis. *Evol. Biol.* 23: 247–269.
- 810 Caduff C (1999) Ethnographies of science: conversation with the authors and commentary. *Cultural*
811 *Anthropology* 14(1).
- 812 Cain J (1989) *Moving Beyond Consistency: The Historical Significance of Simpson's Tempo and Mode in*
813 *Evolution*. PhD Thesis, Master of Arts, University of Maryland.
- 814 Cain J (1990) George Gaylord Simpson's 'History of the Section of Vertebrate Paleontology in the
815 Paleontological Society'. *J. Vert. Paleontol.* 10: 40-48.
- 816 Cain J (1992) Building a temporal biology: Simpson's program for paleontology during an American expansion
817 of biology. *Earth Sci. Hist.* 11: 30-36.
- 818 Cain J (1994) Ernst Mayr as community architect: launching the Society for the Study of Evolution and the
819 journal *Evolution*. *Biol. Philos.* 9: 387-427.
- 820 Cain J (2000) For the 'promotion' and 'integration' of various fields: first years of *Evolution*, 1947-1949. *Arch.*
821 *Nat. Hist.* 27: 231-259.
- 822 Cain J (2002a) Epistemic and community transition in American evolutionary studies: the 'Committee on
823 Common Problems of Genetics, Paleontology, and Systematics' (1942-1949). *Stud. Hist. Philos. Biol.*
824 *Biomed. Sci.* 33: 283-313.
- 825 Cain J (2002b) Co-opting colleagues: appropriating Dobzhansky's 1936 lectures at Columbia. *J. Hist. Biol.* 35:
826 207-219.
- 827 Cain J (2003) A matter of perspective: disparate voices in the evolutionary synthesis. *Arch. Nat. Hist.* 30: 28-39.
- 828 Cain J, Ed. (2007) *Sewall Wright Taught Me*. 3 volumes. London: Euston Grove Press.
- 829 Cain J (2009a) Rethinking the Synthesis period in evolutionary studies. *Studies in the History of Biology* 42: 621-
830 648.
- 831 Cain J (2009b) Ernst Mayr and the 'Biology of Birds'. In: Cain J and Ruse M (eds) *Descended from Darwin:*
832 *Insights into the History of Evolutionary Studies, 1900-1970*. *Trans. Amer. Philos. Soc.* 99, part 1,
833 Philadelphia: PA.
- 834 Cain J (2010) Julian Huxley, General Biology and the London Zoo, 1935–42. *Notes Rec. R. Soc.* 64: 359-378.
- 835 Cain J (2013) Synthesis Period in Evolutionary Studies. In Ruse M (ed) *The Cambridge Encyclopedia of Darwin*
836 *and Evolutionary Thought*. Cambridge: Cambridge University Press, pp. 282-292.
- 837 Callebaut W (2010) The dialectics of dis/unity in the evolutionary synthesis and its extensions. In: Pigliucci M
838 and Müller GB (eds) *Evolution: The Extended Synthesis*. Cambridge, Mass: MIT Press, pp. 443-481.
- 839 Callebaut W (2013) The tension between tradition and innovation. *Biol. Theor.* 7(3): 187-188.

- 840 Campbell DT (1960) Blind variation and selective retention in creative thought as in other knowledge
841 processes. *Psychological Review* 67: 380-400.
- 842 Changeux J-P (1985) *Neuronal Man: The Biology Of Mind*. Princeton: Princeton University Press.
- 843 Coyne J (2009) Are we ready for an extended evolutionary synthesis? In: Why evolution is true, 16 Feb 2009.
844 Available at: [http://whyevolutionistrue.wordpress.com/2009/02/16/are-we-ready-for-an-extended-](http://whyevolutionistrue.wordpress.com/2009/02/16/are-we-ready-for-an-extended-evolutionary-synthesis/)
845 [evolutionary-synthesis/](http://whyevolutionistrue.wordpress.com/2009/02/16/are-we-ready-for-an-extended-evolutionary-synthesis/)
- 846 Craig L (2010) The so-called Extended Synthesis and population genetics. *Biol. Theor.* 5 (2010): 117-123.
- 847 Craig L (2011) Criticism of the Extended Synthesis: a response to Müller and Pigliucci. *Biol. Theor.* 5: 395-396.
- 848 Danchin É (2013) Avatars of information: towards an inclusive evolutionary synthesis. *Trends Ecol. Evol.* 28(6):
849 351-8.
- 850 Danchin É, Charmantier A, Champagne FA, Mesoudi A, Pujol B and Blanchet S (2011) Beyond DNA: integrating
851 inclusive inheritance into an extended theory of evolution. *Nat. Rev. Genet.* 12(7): 475-86.
- 852 Darwin C (1871) *The Descent of Man and Selection in Relation to Sex*. 2 volumes. New York: Appleton.
- 853 Darwin C (1881) *The Formation of Vegetable Mold Through the Action of Worms, with Observations on Their*
854 *Habits*. London: John Murray.
- 855 Dawkins R (1976) *The Selfish Gene*. Oxford: Oxford University Press.
- 856 Dawkins R (1982) *The Extended Phenotype: The Gene As The Unit Of Selection*. Oxford: W.H. Freeman.
- 857 Delisle RG (2011) What was really synthesized during the evolutionary synthesis? A historiographic proposal.
858 *Stud Hist Philos Biol Biomed* 42(1): 50–9.
- 859 Dickins TE and Rahman Q (2012) The extended evolutionary synthesis and the role of soft inheritance in
860 evolution. *Proc. R. Soc. B* 279(1740): 2913-21.
- 861 Edelman GM (1987) *Neural Darwinism: The Theory Of Neuronal Group Selection*. New York: Basic Books.
- 862 Eldakar OT and Wilson DS (2011) Eight criticisms not to make about group selection. *Evolution* 65(6): 1523-6.
- 863 Eldredge N (1985) *Unfinished Synthesis. Biological Hierarchies and Modern Evolutionary Thought*. New York:
864 Columbia University Press.
- 865 Eldredge N (1999) *The Pattern of Evolution*. New York: Freeman & Co.
- 866 Félix M-A and Wagner A (2008) Robustness and evolution: concepts, insights and challenges from a
867 developmental model system. *Heredity* 100(2): 132–40.
- 868 Fernando C and Szathmáry E (2010) Chemical, neuronal, and linguistic replicators. In: Pigliucci M and Müller GB
869 (eds) *Evolution: The Extended Synthesis*. Cambridge, Mass: MIT Press, pp. 209-249.
- 870 Fisher RA (1930) *The Genetical Theory Of Natural Selection*. Oxford: Clarendon Press.
- 871 Fusco G, Carrer R and Serrelli E (2014) The landscape metaphor in development. In: Minelli A and Pradeu T
872 (eds) *Towards a Theory of Development*. Oxford: Oxford University Press.
- 873 Futuyma DJ (1986) *Evolutionary Biology*. Sunderland, MA: Sinauer.
- 874 Futuyma DJ (2011) Expand or revise? The evolutionary synthesis today. *Q. Rev. Biol.* 86(3): 203-208.
- 875 Futuyma DJ (2014) Can modern evolutionary theory explain macroevolution? In: Serrelli E and Gontier N (eds)
876 *Macroevolution: Interpretation, Explanation, Evidence*. Berlin: Springer, in press.

- 877 Gavrillets S (1997) Evolution and speciation on holey adaptive landscapes. *Trends Ecol. Evol.* 12: 307-312.
- 878 Gavrillets S (2004) *Fitness Landscapes and the Origin of Species*. Princeton: Princeton University Press.
- 879 Gieryn TF (1983) Boundary-work and the demarcation of science from non-science: strains and interests in
880 professional ideologies of scientists. *Am. Sociol. Rev.* 48(6): 781-795.
- 881 Gieryn TF (1999) *Cultural Boundaries Of Science: Credibility On The Line*. Chicago: University of Chicago Press.
- 882 Gontier N (2007) Universal symbiogenesis: an alternative to universal selectionist accounts of evolution.
883 *Symbiosis* 44: 167-181.
- 884 Gould SJ (1980) Is a new and general theory of evolution emerging? *Paleobiology* 6: 119-130.
- 885 Gould SJ (1982) Darwinism and the expansion of evolutionary theory. *Science* 216(4544): 380-7.
- 886 Gould S J (2002) *The Structure of Evolutionary Theory*. Cambridge, MA: Harvard University Press.
- 887 Greene JC (1981) *Science, Ideology, and World View: Essays in the History of Evolutionary Ideas*. Berkeley:
888 University of California Press.
- 889 Grossniklaus U, Kelly WG, Ferguson-Smith AC, Pembrey M, and Lindquist S (2013) Transgenerational epigenetic
890 inheritance: how important is it? *Nat. Rev. Genet.* 14(3): 228-35.
- 891 Haig D (2004) The (dual) origin of epigenetics. *Cold Spring Harb. Symp. Quant. Biol.* 69: 67-70.
- 892 Haig D (2007) Weissman Rules! OK? Epigenetics and the Lamarckian temptation. *Biol. Philos.* 22: 415-428.
- 893 Hall BK (2000) Evo-devo or devo-evo: does it matter? *Evol. Dev.* 2: 177-178.
- 894 Handschuh S and Mitteroecker P (2012) *Evolution - The Extended Synthesis*. A research proposal persuasive
895 enough for the majority of evolutionary biologists? *Human Ethology Bulletin* 27(1-2): 18-21.
- 896 Hartl DL and Clark AG (2007) *Principles of Population Genetics*, 4th edn. Sunderland, Mass: Sinauer Associates.
- 897 Havstad JC (2011) Problems for natural selection as a mechanism. *Philos Sci* 78(3): 512–523.
- 898 Hess DJ (2001) Ethnography and the development of science and technology studies. In: Atkinson P, Coffey A,
899 Delamont S, Lofland J and Lofland L (eds) *The Sage Handbook of Ethnography*. Thousand Oaks, Ca.: SAGE
900 Publications, pp. 234-245.
- 901 Hoekstra HE and Coyne JA (2007) The locus of evolution: evo-devo and the genetics of adaptation. *Evolution*
902 61: 995-1016
- 903 Holliday R (1979) A new theory of carcinogenesis. *Brit. J. Cancer* 40: 513.
- 904 Holliday R (1987) The inheritance of epigenetic defects. *Science* 238: 163.
- 905 Ho MW and Saunders PT (1979) Beyond neo-Darwinism—An epigenetic approach to evolution. *J. Theor. Biol.*
906 78: 573.
- 907 Houle D (1992) Comparing evolvability and variability of quantitative traits. *Genetics* 130: 195-204.
- 908 Huxley JS (1942) *Evolution, The Modern Synthesis*. London: Allen and Unwin.
- 909 Jablonka E and Lamb MJ (1989) The inheritance of acquired epigenetic variations. *J. Theor. Biol.* 139: 69-83.
- 910 Jablonski D (1986) Background and mass extinctions: the alternation of macroevolutionary regimes. *Science*
911 231: 129-133.

- 912 Keller L (ed) (1999) *Levels of Selection in Evolution*. Princeton, NJ: Princeton University Press.
- 913 Kendal J, Tehrani JJ and Odling-Smee J (2011) Human niche construction in interdisciplinary focus. *Philos. Trans.*
914 *R. Soc. B* 366(1566): 785-92.
- 915 Kirschner M and Gerhart J (1998) Evolvability. *Proc. Natl. Acad. Sci. U. S. A.* 95: 8420-8427.
- 916 Kutschera U and Niklas KJ (2004) The modern theory of biological evolution: an expanded synthesis.
917 *Naturwissenschaften* 91: 255-276.
- 918 Laland KN, Odling-Smee FJ and Feldman MW (1996) On the evolutionary consequences of niche construction. *J.*
919 *Evol. Biol.* 9: 293-316.
- 920 Laland KN, Odling-Smee FJ and Feldman MW (1999) The evolutionary consequences of niche construction and
921 its implications for ecology. *Proc. Natl. Acad. Sci. U. S. A.* 96: 10242-47.
- 922 Laland KN, Odling-Smee FJ, Feldman MW and Kendal J (2009) Conceptual barriers to progress within
923 evolutionary biology. *Found. Sci.* 14(3): 195-216.
- 924 Laubichler MD (2010) Evolutionary developmental biology offers a significant challenge to the neo-Darwinian
925 paradigm. In: Ayala FR and Arp R (eds) *Contemporary Debates in Philosophy of Biology*. Malden, MA:
926 Wiley-Blackwell, pp. 199-212.
- 927 Lederberg J (1958) Genetic approaches to somatic cell variation: summary comment. *J. Cell. Comp. Physiol.*
928 (suppl. 1) 52: 383.
- 929 Lewontin RC (1978) Adaptation. *Sci. Am.* 239: 156-169.
- 930 Lewontin RC (1983) Gene, organism, and environment. In: Bendall DS (ed) *Evolution From Molecules To Men*.
931 Cambridge, MA: Cambridge University Press, pp. 273-285.
- 932 Loreau M (2010) *From Populations To Ecosystems. Theoretical Foundations For A New Ecological Synthesis*.
933 Princeton, NJ: Princeton University Press.
- 934 Love AC (2003) Evolutionary morphology, innovation, and the synthesis of evolutionary and developmental
935 biology. *Biol. Philos.* 18: 309-345.
- 936 Love AC (2006) Evolutionary morphology and evo-devo. Hierarchy novelty. *Theor. Biosci.* 124: 317-333.
- 937 Love AC (2007) Morphological and paleontological perspectives for a history of evo-devo. In: Laubichler M and
938 Maienschein J (eds) *From Embryology To Evo-Devo: A History Of Developmental Evolution*. Cambridge,
939 Mass: MIT Press, pp. 267-307.
- 940 Love AC (2009) Marine invertebrates, model organisms, and the modern synthesis: epistemic values, evo-devo,
941 and exclusion. *Theor. Biosci.* 128(1): 19-42.
- 942 Love AC (2010) Rethinking the structure of evolutionary theory for an extended synthesis. In: Pigliucci M and
943 Müller GB (eds) *Evolution: The Extended Synthesis*. Cambridge, Mass: MIT Press, pp. 403-441.
- 944 Love AC (2012) Theory is as theory does: scientific practice and theory structure in biology. *Biol. Theor.* 7: 325-
945 337.
- 946 Love AC and Raff RA (2003) Knowing your ancestors: themes in the history of evo-devo. *Evol. Dev.* 5: 327-330.
- 947 Løvtrup S (1972) *Epigenetics. A Treatise On Theoretical Biology*. London: John Wiley & Sons.
- 948 Lynch M (2007) The frailty of adaptive hypotheses for the origins of organismal complexity. *Proc. Natl. Acad.*
949 *Sci. U. S. A.* 104: 8597-8604.
- 950 Machamer PK, Darden L and Craver CF (2000) Thinking about mechanisms. *Phil. Sci.* 67: 1-25.

- 951 Matthen M (2010) What is drift? A response to Millstein, Skipper, and Dietrich. *Philosophy and Theory in*
952 *Biology* 2: e102.
- 953 Matthewson J and Calcott B (2011) Mechanistic models of population-level phenomena. *Biol. Philos.* 26(5):
954 737–756.
- 955 Maynard Smith J and Szathmáry E (1995) *The Major Transitions in Evolution*. New York: Oxford University Press.
- 956 Mayr E (1973) The recent historiography of genetics. *J. Hist. Biol.* 6: 125-154.
- 957 Mayr E and Provine WB (eds) (1980) *The Evolutionary Synthesis: Perspectives on the Unification of Biology*.
958 Harvard University Press, Cambridge and London.
- 959 McCain KW (2008) Assessing an author's influence using time series historiographic mapping: the oeuvre of
960 Conrad Hal Waddington (1905–1975). *J. Assn. Inf. Sci. Technol.* 59(4): 510-525.
- 961 McCain KW (2009) Using tricitations to dissect the citation image: Conrad Hal Waddington and the rise of
962 evolutionary developmental biology. *J. Assn. Inf. Sci. Technol.* 60(7): 1301-1319.
- 963 McCain KW (2013) Game theory in the healthcare literature: a contextual co-descriptor analysis of MeSH term
964 assignments. In: *ASIST 2013*, November 1-6 2013, Montreal, Quebec, Canada. Available at:
965 www.asis.org/asist2013/proceedings/submissions/posters/12poster.pdf
- 966 McCain KW, Verner JM, Hislop GW, Evanco W and Cole V (2005) The use of bibliometric and knowledge
967 elicitation techniques to map a knowledge domain: Software Engineering in the 1990s. *Scientometrics*
968 65(1): 131-144.
- 969 Medina ML (2010) Two “EvoDevos”. *Biol. Theor.* 5(1): 7-11.
- 970 Mesoudi A, Blanchet S, Charmantier A, Danchin É, Fogarty L, Jablonka E, et al. (2013) Is non-genetic inheritance
971 just a proximate mechanism? A corroboration of the Extended Evolutionary Synthesis. *Biol. Theor.* 7(3):
972 189-195.
- 973 Millstein RL, Skipper RA and Dietrich MR (2009) (Mis) interpreting Mathematical Models: Drift As A Physical
974 Process. *Philosophy and Theory in Biology* 002(1): e002.
- 975 Minelli A (2010) Evolutionary developmental biology does not offer a significant challenge to the neo-
976 Darwinian paradigm. In Ayala FR and Arp R (eds) *Contemporary Debates in Philosophy of Biology*. Malden,
977 MA: Wiley-Blackwell, pp. 211-226.
- 978 Müller GB (2007) Evo-devo: extending the evolutionary synthesis. *Nat. Rev. Genet.* 8(12): 943-9.
- 979 Müller GB and Pigliucci M (2010) Extended Synthesis: theory expansion or alternative? A commentary on
980 Lindsay Craig. *Biol. Theor.* 5(4): 395-396.
- 981 Nanney DL (1958) Epigenetic control systems. *Proc. Natl. Acad. Sci. U. S. A.* 44(7): 712-717.
- 982 Nanney DL (1959) Epigenetic factors affecting mating type expression in certain ciliates. *Cold Spring Harb.*
983 *Symp. Quant. Biol.* 23: 327.
- 984 Newman SA (2010) Dynamical patterning modules. In: Pigliucci M and Müller GB (eds) *Evolution: The Extended*
985 *Synthesis*. Cambridge, Mass: MIT Press, pp. 281-306.
- 986 Nicholson DJ (2012) The concept of mechanism in biology. *Stud Hist Philos Biol Biomed Sci* 43(1): 152–63.
- 987 Noble D (2011) Neo-Darwinism, the Modern Synthesis and selfish genes: are they of use in physiology? *J.*
988 *Physiol.* 589(Pt 5): 1007-15.
- 989 Odling-Smee FJ (1988) Niche constructing phenotypes. In: Plotkin HC (ed) *The Role Of Behavior In Evolution*.
990 Cambridge, MA: MIT Press, pp. 73-132.

- 991 Odling-Smee FJ, Laland KN and Feldman MW (1996) Niche construction. *Am. Nat.* 147(4): 641-48.
- 992 Odling-Smee FJ, Laland KN and Feldman MW (2003) *Niche Construction: the Neglected Process in Evolution*.
993 Monogr. Popul. Biol. 37. Princeton, NJ: Princeton Univ. Press.
- 994 Okasha S (2006) *Evolution and the Levels of Selection*. Oxford: Oxford University Press.
- 995 Pennisi E (2008) Modernizing the Modern Synthesis. *Science* 321: 196-197.
- 996 Pigliucci M (2001) *Phenotypic Plasticity: Beyond Nature and Nurture*. Baltimore: Johns Hopkins University Press.
- 997 Pigliucci M (2007) Do we need an extended evolutionary synthesis? *Evolution* 61(12): 2743-9.
- 998 Pigliucci M (2008a) Is evolvability evolvable? *Nat. Rev. Genet.* 9(1): 75-82.
- 999 Pigliucci M (2008b) Sewall Wright's adaptive landscapes: 1932 vs. 1988. *Biol. Philos.* 23(5): 591-603.
- 1000 Pigliucci M (2008c) Down with natural selection? *Perspect. Biol. Med.* 52(1): 134-140.
- 1001 Pigliucci M (2009) An extended synthesis for evolutionary biology. *Ann. N. Y. Acad. Sci.* 1168: 218-28.
- 1002 Pigliucci M (2010) Phenotypic plasticity. In: Pigliucci M and Müller GB (eds) *Evolution: The Extended Synthesis*.
1003 Cambridge, Mass: MIT Press, pp. 355-378.
- 1004 Pigliucci M and Kaplan J (2006) *Making Sense of Evolution: The Conceptual Foundations of Evolutionary Biology*.
1005 Chicago: University of Chicago Press.
- 1006 Pigliucci M and Müller GB (eds) (2010) *Evolution: The Extended Synthesis*. Cambridge, MA: MIT Press.
- 1007 Pigliucci M, Murren CJ and Schlichting CD (2006) Phenotypic plasticity and evolution by genetic assimilation. *J.*
1008 *Exp. Biol.* 209: 2362-2367.
- 1009 Plutynski A (2011) *Evolution: The Extended Synthesis* edited by Massimo Pigliucci and Gerd Müller. *Reports of*
1010 *the National Center for Science Education* 31(3).
- 1011 Provine WB (1971) *Origins Of Theoretical Population Genetics*. Chicago: University of Chicago Press.
- 1012 Provine WB (1992) Progress in evolution and meaning in life. In Waters C and van Helden A (eds.) *Julian Huxley:*
1013 *Biologist and statesman of science*. Houston: Rice University Press, pp. 165-180.
- 1014 Raff RA and Love AC (2004) Kowalevsky, comparative evolutionary embryology, and the intellectual lineage of
1015 evo-devo. *J. Exp. Zool.* 302B: 19-34.
- 1016 Reiss JO (2011) Footnotes to the Synthesis? *Metascience* 21(1): 163-166.
- 1017 Riviera E (2013) *Mapping Scientific Literature. Structuring Scientific Communities Through Scientometrics*. PhD
1018 thesis in Applied Sociology and Methodology of Social Research, Università degli Studi di Milano-Bicocca.
1019 Available at: <http://hdl.handle.net/10281/40095>.
- 1020 Sarkar S (ed) (1992) *The Founders of Evolutionary Genetics: A Centenary Reappraisal*. Boston Studies in the
1021 Philosophy of Science, 142. Dordrecht: Kluwer Academic Publishers.
- 1022 Sarkar S (2004) Evolutionary theory in the 1920s: the nature of the "Synthesis". *Philos. Sci.* 71(5): 1215-1226.
- 1023 Scheiner SM (1992) Grand syntheses in the making: review of Stearns, S.C., *The Evolution of Life Histories*.
1024 *Science* 258: 1820-1822.
- 1025 Scheiner SM (1999) Towards a more synthetic view of evolution. *Am. J. Bot.* 86(1): 145-148.
- 1026 Scheiner SM (2013) The ecological literature, an idea-free distribution. *Ecol. Lett.* 16: 1421-1423.

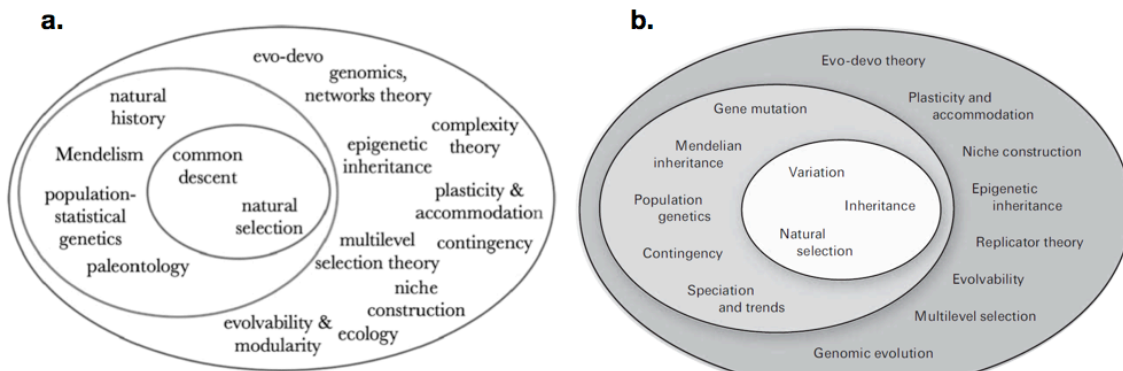
- 1027 Schlichting CD and Pigliucci M (1998) *Phenotypic Evolution: A Reaction Norm Perspective*. Sunderland, MA:
1028 Sinauer Associates.
- 1029 Schrey AW, Richards CL, Meller V, Sollars V and Ruden DM (2012) The role of epigenetics in evolution: the
1030 extended synthesis. *Genet. Res. Int.* DOI: 10.1155/2012/286164.
- 1031 Sent E-M (1999) Economics of science: survey and suggestions. *Journal of Economic Methodology* 6(1): 95-124.
- 1032 Sent E-M (2013) The economics of science in historical and disciplinary perspective. *Spontaneous Generations.*
1033 *A Journal for the History and Philosophy of Science* vol 7(1): 6-11.
- 1034 Sepkoski D (2012), *Rereading the Fossil Record: The Growth of Paleobiology as an Evolutionary Discipline*.
1035 Chicago: University Of Chicago Press.
- 1036 Sepkoski D and Ruse M (eds) (2009), *The Paleobiological Revolution: Essays on the Growth of Modern*
1037 *Paleontology*. Chicago: University Of Chicago Press.
- 1038 Serrelli E and Gontier N (forthcoming) Uniting micro- and macroevolution into an Extended Synthesis. In:
1039 Serrelli E and Gontier N (eds) *Macroevolution. Explanation, Interpretation, Evidence*. Berlin: Springer.
- 1040 Sidlauskas B, et al. (2009) Linking big: the continuing promise of evolutionary synthesis. *Evolution* 64(4): 871–
1041 880.
- 1042 Simon HA (1962) The architecture of complexity. *Proc. Am. Phil. Soc.* 106 (6): 467-482.
- 1043 Skipper RA and Millstein RL (2005) Thinking about evolutionary mechanisms: natural selection. *Stud Hist Philos*
1044 *Biol Biomed Sci* 36(2): 327-347.
- 1045 Smocovitis VB (1996) *Unifying Biology*. Princeton: Princeton University Press.
- 1046 Sober E and Wilson DS (1998) *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge,
1047 MA: Harvard University Press.
- 1048 Stebbins GL (1950) *Variation and Evolution in Plants*. New York: Columbia University Press.
- 1049 Stebbins GL (1983) Mosaic evolution: an integrating principle for the modern synthesis. *Experientia* 39: 823-
1050 834.
- 1051 Stebbins GL and Ayala FJ (1981) Is a new evolutionary synthesis necessary? *Science* 213(4511): 967-71.
- 1052 Stephan PE (1996) The economics of science. *Journal of Economic Literature* 34(3): 1199-1235.
- 1053 Stephan PE (2012) *How Economics Shapes Science*. Harvard University Press.
- 1054 Thicke M (ed) (2013) *Economic Aspects of Science. Spontaneous Generations. A Journal for the History and*
1055 *Philosophy of Science* 7(1).
- 1056 Toussaint M (2003) On the evolution of phenotypic exploration distributions. In: *Foundations of Genetic*
1057 *Algorithms 7 (FOGAVII)*, San Francisco: Morgan Kaufmann.
- 1058 Travis J (2011) The Modern Synthesis and its postmodern discontents. *Evolution* 65(5): 1517-1520.
- 1059 Waddington CH (1940) *Organisers and Genes*. Cambridge: Cambridge University Press.
- 1060 Wagner GP (1996) Homologues, natural kinds and the evolution of modularity. *Amer. Zool.* 36(1): 36-43.
- 1061 Wagner A (2008) Neutralism and selectionism: a network-based reconciliation. *Nat. Rev. Genet.* 9(12): 965–
1062 974.
- 1063 Wagner A (2009) Evolutionary constraints permeate large metabolic networks. *BMC Evol. Biol.* 9: 231.

- 1064 Wagner GP and Altenberg L (1996) Complex adaptations and the evolution of evolvability. *Evolution* 50: 967-
1065 976.
- 1066 Wagner A, Wagner GP and Similione P (1994) Epistasis can facilitate the evolution of reproductive isolation by
1067 peak shifts: a two-locus two-allele model. *Genetics* 138(2): 533-45.
- 1068 Weber BH (2011) Extending and expanding the Darwinian synthesis: the role of complex systems dynamics.
1069 *Stud. Hist. Phil. Biol. Biomed. Sci.* 42(1): 75-81.
- 1070 West-Eberhard MJ (2003) *Developmental Plasticity and Evolution*. Oxford, UK: Oxford University Press.
- 1071 White HD and McCain KW (1998) Visualizing a discipline: An author co-citation analysis of information science,
1072 1972–1995. *J. Assn. Inf. Sci. Technol.* 49(4): 327-355.
- 1073 Whitfield J (2008) Postmodern evolution? *Nature* 455(7211): 281-4.
- 1074 Wilson DS (1975) A theory of group selection. *Proc. Natl. Acad. Sci. U. S. A.* 72(1): 143-146.
- 1075 Wilson DS (2009) Truth and reconciliation for group selection. In: Scienceblogs. 19 posts from October 23 to
1076 November 17, 2009. Available at: [http://evolution.binghamton.edu/dswilson/wp-](http://evolution.binghamton.edu/dswilson/wp-content/uploads/2010/01/Truth-and-Reconciliation.pdf)
1077 [content/uploads/2010/01/Truth-and-Reconciliation.pdf](http://evolution.binghamton.edu/dswilson/wp-content/uploads/2010/01/Truth-and-Reconciliation.pdf)
- 1078 Wilson DS (2010) Multilevel selection and major transitions. In: Pigliucci M and Müller GB (eds) *Evolution: The*
1079 *Extended Synthesis*. Cambridge, Mass: MIT Press, pp. 81-93.
- 1080 Wilson DS and Dugatkin LA (1997) Group selection and assortative interactions. *Am. Nat.* 149: 336-351.
- 1081 Wilson DS and Wilson EO (2007) Rethinking the theoretical foundation of sociobiology. *Q. Rev. Biol.* 82(4): 327-
1082 348.
- 1083 Wilson LAB (2013) The contribution of developmental palaeontology to extensions of evolutionary theory. *Acta*
1084 *Zoologica* 94(3): 254-260.
- 1085 Witteveen J (2011) The softening of the Modern Synthesis. *Acta Biotheor.* 59(3-4): 333-345.
- 1086 Woltereck R (1909) Weiterer experimentelle Untersuchungen über Artveränderung, speziell über das Wesen
1087 quantitativer Artunterschiede bei Daphniden. *Verhandlungen der Deutsche Zoologische Gesellschaft* 19:
1088 110-172.
- 1089 Wright S (1932) The roles of mutation, inbreeding, crossbreeding and selection in evolution. In *Proceedings of*
1090 *the 6th International Congress of Genetics* 1: 356-366.
- 1091 Wund MA (2012) Assessing the impacts of phenotypic plasticity on evolution. *Integr. Comp. Biol.* 52(1): 5-15.

1092 **Figures**

1093 *Figure 1*

1094 A comparison between the elements of an Extended Evolutionary Synthesis (EES) appearing in two
 1095 different publications: (a) from Pigliucci (2009); (b) from the collective book *Evolution: The Extended*
 1096 *Synthesis* (ed. by Pigliucci and Müller 2010). Each of the two diagrams describes the EES as inclusive
 1097 of Darwinism (inner circle), the Modern Synthesis (middle circle), and additional concepts (outer
 1098 circle). A comparison among publication (either with or without diagrams) uncovers dynamism and
 1099 problematic factors of complexity in the development of Pigliucci and Müller’s thought.



1100