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3 **The structure of evolutionary theory: Beyond Neo-Darwinism,**
4 **Neo-Lamarckism and biased historical narratives about the**
5 **Modern Synthesis**

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20 **Abstract**

21 The last decades have seen frequent calls for a more extended evolutionary synthesis (EES) that
22 will supposedly overcome the limitations in the current evolutionary framework with its
23 intellectual roots in the Modern Synthesis (MS). Some radical critics even want to entirely
24 abandon the current evolutionary framework, claiming that the MS (often erroneously labelled
25 “Neo-Darwinism”) is outdated, and will soon be replaced by an entirely new framework, such
26 as the Third Way of Evolution (TWE). Such criticisms are not new, but have repeatedly re-
27 surfaced every decade since the formation of the MS, and they were particularly articulated by
28 developmental biologist Conrad Waddington and paleontologist Stephen Jay Gould.
29 Waddington, Gould and later critics argued that the MS was too narrowly focused on genes and
30 natural selection, and that it ignored developmental processes, epigenetics, paleontology and
31 macroevolutionary phenomena. More recent critics partly recycle these old arguments and
32 argue that non-genetic inheritance, niche construction, phenotypic plasticity and developmental
33 bias necessitate major revision of evolutionary theory. Here I discuss these supposed
34 challenges, taking a historical perspective and tracing the arguments by critics back to
35 Waddington and Gould. I dissect the old claims by Waddington, Gould and more recent critics
36 that the MS was excessively gene centric and became increasingly “hardened” over time and
37 narrowly focused on natural selection. Recent critics have consciously or unconsciously
38 exaggerated the long-lasting influence of the MS on contemporary evolutionary biology and
39 have underestimated many post-Synthesis developments, particularly Neutral Theory,
40 evolutionary quantitative genetics and the power and generality of the Price Equation. Critics
41 have also painted a biased picture of the MS as a more monolithic research tradition than it ever
42 was, and have downplayed the pluralistic nature of contemporary evolutionary biology,
43 particularly the long-lasting influence of Sewall Wright with his emphasis on gene interactions
44 and stochasticity. I argue that some of the criticisms of the MS and contemporary evolutionary

45 biology are primarily meta-scientific, revealing the underlying identity politics of critics when
46 pushing their alternative research agendas. It is still unclear what their proposed alternative
47 research frameworks would entail and why the existing theoretical framework is insufficient.
48 Finally, I outline and visualize the conceptually split landscape of contemporary evolutionary
49 biology, with four different stably coexisting analytical frameworks: adaptationism,
50 mutationism, neutralism and selectionism. I suggest that the field can accommodate the
51 challenges raised by critics, although structuralism (“Evo Devo”) and macroevolution remain
52 to be conceptually integrated within mainstream evolutionary theory.

53

54 **Keywords** Developmental bias · Extended Evolutionary Synthesis · Modern Synthesis ·
55 Macroevolution · Mutationism · Neo-Darwinism · Niche construction · Non-genetic
56 inheritance · Population Genetics · Phenotypic Plasticity · Quantitative Genetics · Third Way
57 of Evolution

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67 **5.1 Introduction**

68 The Modern Synthesis (MS) of evolutionary biology was one of the most important scientific
69 achievements in evolutionary biology during the twentieth century (Mayr 1993; Mayr and
70 Provine 1998; Cain 2009). The MS formed gradually, through a series of influential research
71 books and articles by Dobzhansky, Huxley, Mayr, Rensch, Simpson and several other biologists
72 (Mayr and Provine 1998; Reif et al. 2000). An important early achievement was the formation
73 of the *Society for the Study of Evolution* (SSE) in March 1946 and the establishment of its
74 scientific journal *Evolution*. Cain (2009) has described the MS as a shift away from *object-*
75 *based* (i. e. organisms) natural history to *process-based* (selection, gene flow, genetic drift)
76 natural history. Biologists and natural historians from the MS and onwards sought to explain
77 patterns within and among populations and species with current and past evolutionary
78 processes. The shift towards process-based natural history was stimulated by the developments
79 of mathematical population genetics in the decades before the MS, particularly contributions
80 by Fisher (Fisher 1930), Haldane (Haldane 1932) and Sewall Wright (Wright 1931, 1932).

81

82 It is important to emphasize that the architects of the MS aimed to be *synthetic*. Accordingly
83 the results of their efforts has sometimes been termed “*the synthetic theory of evolution*” (Reif
84 et al. 2000). Specifically, Mayr and others repeatedly emphasized that the MS incorporated
85 insights from several different fields, including genetics, systematics, paleontology and natural
86 history (Haffer 2007). This synthetic goal became evident in the famous debate between Mayr
87 and Haldane about the utility and limitations of so-called “bean bag genetics” (Mayr 1959;
88 Haldane 1964; Crow 2008; Dronamraju 2011). Mayr strongly criticized the mathematical
89 population geneticists Fisher, Wright and Haldane for ignoring gene interactions in their
90 theoretical models (Mayr 1959). Mayr instead emphasized what he felt was the more important
91 contributions by himself, Dobzhansky and other empiricists and naturalists in the formation of

92 the MS (Dronamraju 2011). In this famous debate with Haldane, Mayr clearly revealed that he
93 erroneously thought that the mathematical population geneticists were not aware of gene
94 interaction (epistasis), in spite of epistasis being central in Sewall Wright's Shifting Balance
95 Theory of evolution (Provine 1986; Wade and Goodnight 1998; Steffes 2007). In fact, Wright's
96 interest in genetic interactions, rather than simply additive effects of genes, is an example of
97 early system-level thinking that could be viewed as a predecessor to systems biology today.
98 Moreover, the fact that Wright, one of the founding fathers of modern population genetics, was
99 interested in such interactions and system-level phenomena of organisms establishes a forgotten
100 link between the organicist school (Peterson 2017) and early population genetics (Steffes 2007).
101 This forgotten historical link contradicts Mayr's claim and sweeping characterization of Wright
102 as a simple "bean bag geneticist" who was not aware of epistasis (Mayr 1959).

103

104 In retrospect, it is of course easy to point to many limitations of the MS, such that neither
105 developmental biology nor ecology had any central roles (Antonovics 1987; Endler and
106 McLellan 1988). This should not divert us from realizing that the aim of the MS architects was
107 – indeed – a synthetic one (Reif et al. 2000) and the MS has clearly served its purpose, at least
108 for sexually reproducing organisms (Novick and Doolittle 2019). Recent critics often describe
109 the MS as more simplistic and monolithic than it ever was, and have frequently exaggerated the
110 role of population genetics in the synthesis formation (Pigliucci 2007; Laland et al. 2014, 2015;
111 Noble 2015; Müller 2017). These biased narratives about the MS have plagued many
112 discussions about the state of contemporary evolutionary biology, which I discuss in this
113 chapter.

114

115 **5.2 What the Modern Synthesis was (and was not)**

116 A frequent claim made by critics of the MS is to equate it with “Neo-Darwinism” (Koonin
117 2009; Noble 2015, 2021). Ironically, this conflation is sometimes also made by defenders of
118 the MS (Charlesworth et al. 1982, 2017; Hancock et al. 2021). This conflation between the MS
119 and Neo-Darwinism is historically inaccurate (Reif et al. 2000; Chen et al. 2021) and can be
120 traced to the late developmental biologist Conrad Waddington (Waddington 1957; Wilkins
121 2008; Peterson 2017) and the late paleontologist Stephen Jay Gould (Gould 2002). Waddington
122 and Gould used the label Neo-Darwinism in a negative and condescending fashion when they
123 talked about the MS. However, Neo-Darwinism is a historical term that was coined several
124 decades before the MS by Romanes (Gould 2002) and was closely linked to August
125 Weissmann’s doctrine about separation of the germ line and the soma, i. e. the rejection of
126 Lamarckian inheritance of acquired characters (Jablonka and Lamb 2007; Pigliucci 2009). As
127 the name Neo-Darwinism implies, only one evolutionary force was recognized prior to
128 emergence of mathematical population genetics: Natural selection (sexual selection was still
129 not fully accepted). As emphasized by Lynch and other researchers, modern evolutionary
130 biology and its predecessor MS, clearly allows for multiple evolutionary processes in addition
131 to selection, specifically genetic drift, mutation and recombination (Charlesworth et al. 1982;
132 Lynch 2007; Svensson and Berger 2019), contrary to claims by some molecular biologists like
133 Eugene Koonin who incorrectly characterize the MS as just recognizing natural selection
134 (Koonin 2009). While Neo-Darwinism only recognized the single evolutionary force (natural
135 selection) that was discovered by Darwin and Wallace, the MS and evolutionary biology
136 developed in to a pluralistic field that incorporated multiple evolutionary processes that were
137 formalized by mathematical population genetics (Svensson and Berger 2019). Moreover, Mayr
138 himself explicitly clarified that the MS was distinct from Neo-Darwinism (Haffer 2007;
139 Pigliucci 2009) as did the paleontologist George Gaylord Simpson, another leading architect of
140 the MS (Simpson 1949).

141

142 Nevertheless, the conflation of the MS and Neo-Darwinism is still commonly made by some
143 critics of contemporary evolutionary biology. For instance, the physiologist Dennis Noble
144 (Noble 2013) claims that “*The ‘Modern Synthesis’ (Neo-Darwinism) is a mid-20th century*
145 *gene-centric view of evolution based on random mutations accumulating to produce gradual*
146 *change through natural selection*”. Noble further claims that “*all the central assumptions of*
147 *the Modern Synthesis (often also called Neo-Darwinism) have been disproved*” (Noble 2013).
148 Noble further argues that an extended “*Integrative Synthesis*” – an entirely “*new conceptual*
149 *framework*” - will “*replace*” the MS (Noble 2015). Similar confident claims have been put
150 forward by the molecular microbiologist James Shapiro (Shapiro 2011). Shapiro and Noble
151 launched “*The Third Way of Evolution*” (TWE) initiative a few years ago
152 (<https://www.thethirdwayofevolution.com/>) that claims to provide a middle path (“*Third*
153 *Way*”) between creationism and Neo-Darwinism. The enthusiasm for their project has – mildly
154 put – not been overwhelming among evolutionary biologists (Charlesworth et al. 2017). To
155 date, there are few leading evolutionary biologists who have openly embraced the TWE. TWE
156 has generated more enthusiasm among a vocal minority of philosophers, such as Dennis Walsh
157 and John Dupré, the latter who in 2012 characterized evolution as “*a theory in crisis*” (Dupre
158 2012). The sheer confidence by which some philosophers and critics of contemporary
159 evolutionary biology predict that contemporary evolutionary biology will soon be replaced by
160 an entirely new framework (details of which are very unclear) is remarkable, particularly as the
161 majority of evolutionary biologists are not even aware of the existence of TWE and carry on
162 their research as usual. Those who doubt this should join any of the regular evolutionary biology
163 congresses organized by the societies ESEB (*European Society for Evolution*) and SSE (*Society*
164 *for the Study of Evolution*) where little of this forthcoming paradigm shift announced by Noble,
165 Shapiro, Walsh and Dupré has been visible during the past decade. The impression one gets

166 from the efforts by these biologists and philosophers is that they are trying to launch a culture
167 war against contemporary evolutionary biology, by erroneously claiming that not much has
168 happened since the MS and by repeatedly equating the latter with Neo-Darwinism. The MS is
169 portrayed by these critics as a dogmatic monolith, and some of their criticisms are more meta-
170 scientific than scientific. The poor historical scholarship among some of these critics and their
171 inaccurate and biased characterizations of the MS suggests to me that the TWE is largely an
172 identity political project rather than presenting any serious challenge to the current theoretical
173 framework.

174

175 The main problem with Noble's and other similar criticisms of contemporary evolutionary
176 biology are the biased and historically misleading characterizations of the MS (see e. g. (Noble
177 2013, 2015, 2017, 2021)), where the MS is not only conflated with Neo-Darwinism but also
178 with the much later developments, such as Richard Dawkin's theory of the selfish gene
179 (Dawkins 1976). Any serious student of the history of evolutionary biology should know that
180 the MS emphasized evolving populations of organisms, or "population thinking" in Mayr's
181 terminology (Haffer 2007). The integrative nature of the MS with its emphasis on evolving
182 populations is therefore radically different from the more reductionistic perspective with
183 emphasis on individual genes, developed by Williams (Williams 1966) and Dawkins (Dawkins
184 1976). The more reductionistic genic perspective, in turn, is closely associated with
185 sociobiology and modern behavioural ecology that took place decades after the formation of
186 the MS (Ågren 2016). Lumping these later scientific and conceptual developments together
187 with the earlier MS neglects substantial differences between radically different research
188 traditions.

189

190 The conflation of the MS, Neo-Darwinism and later schools of thought is by no means restricted
191 to Noble and colleagues, but can sometimes also be seen in the writing of orthodox population
192 geneticists and theoretical evolutionary biologists, such as Brian Charlesworth and colleagues
193 (Charlesworth et al. 2017). One recent example is provided by Stoltzfus (2019), who in
194 discussing the pioneering statistical approach to studying selection that was developed by Lande
195 and Arnold (Lande and Arnold 1983) argues that “*quantitative genetics is the branch of*
196 *mathematical theory that most closely follows neo-Darwinian assumptions*” (Stoltzfus 2019; p.
197 57). This is a remarkable claim, considering that neither population nor quantitative genetics
198 existed as scientific fields more than 150 years ago when the term Neo-Darwinism was first
199 coined by Romanes. Today, the term Neo-Darwinism seems mainly to be used as a pejorative
200 label of the MS by those who would like to see radical conceptual change in evolutionary
201 biology (see e. g. (Koonin 2009; Noble 2015, 2021)), rather than as a descriptive term for a
202 specific historical school of thought.

203

204 Another common but misleading characterization of the MS is to label it “*the Modern Synthesis*
205 *theory*” (Müller 2017) or “*Standard Evolutionary Theory*” (SET) (Laland et al. 2015),
206 implying a closed and rigid system and a formal theory, against which challengers revolt. To
207 be fair, I have used the term SET myself when critically evaluating such claims (Svensson
208 2018). However, this was in response to the prior establishment of the term SET by Laland and
209 colleagues (Laland et al. 2015). Labelling the MS as a “theory” is, however, misleading, as it
210 was rather a loose conceptual framework of *how to do science* than a formal theory (Cain 2009).
211 Specifically, the establishment of the MS reflected a change in conceptual focus among
212 biologists towards evolutionary processes operating within populations, away from the previous
213 focus on object-based natural history and individual organisms (Cain 2009). It is quite telling
214 that there are very few mathematical equations produced by any the leading architects of the

215 MS or something that could be called theory in any meaningful or substantial way. To be sure,
216 the MS relied on mathematical population genetics theory as one of several underlying
217 frameworks (among other influences), however it was not equivalent to population genetics but
218 went far beyond it (*contra* Müller 2017). In fact, the main architects behind the MS were
219 organismal biologists and systematists like Dobzhansky, Mayr and Rensch and the
220 paleontologist Simpson (Mayr 1993; Mayr and Provine 1998). Since the MS is a research
221 framework of *how to do science* and a *perspective* rather than a formal theory, it follows that it
222 cannot be replaced by any new theory let alone a new paradigm, which has even been admitted
223 by one of the leading critics of contemporary evolutionary biology; Massimo Pigliucci
224 (Pigliucci and Finkelman 2014).

225

226 Another frequent characterization of the MS is that it is “gene centred” (Dupré 2021), implying
227 that it exclusively focusses on allele frequency changes in a shared gene pool, ignoring
228 organismal evolution (Laland et al. 2015). Although Mayr is sometimes claimed to have held
229 this narrow gene-centric view, in his later writings he clearly distanced himself from the narrow
230 view that evolution could solely be reduced to allele frequency changes (Haffer 2007). In fact,
231 one could probably argue the exact opposite: Mayr was sometimes not gene centric enough,
232 and frequently revealed his remarkable weak knowledge about population genetics theory, as
233 in the debate about bean bag genetics (Dronamraju 2011). The beanbag genetics debate showed
234 that Mayr did not seem to understand the finer details of mathematical population genetics
235 theory (Haldane 1964; Crow 2008) and revealed his lack of understanding that epistasis was
236 central to Sewall Wright’s thinking and his population genetic framework (Steffes 2007).
237 Provine noted that something similar could be said about Dobzhansky’s lack of understanding
238 of the details of mathematical population genetics in his collaboration with Sewall Wright
239 (Provine 1986).

240

241 Recently, Huneman (2019) reminded us that the MS was hardly as monolithic as critics like
242 Pigliucci, Laland, Noble and others have claimed it to be. One could even question the unity
243 and coherence between quite disparate research traditions within the MS (Svensson 2018;
244 Huneman 2019). The MS can be characterized as containing two rather distinct research
245 traditions: one adaptationist school focused on natural selection, primarily in the UK (Lewens
246 2019) exemplified by the collaboration between Ford and Fisher, and a more pluralistic school
247 in North America, exemplified by the collaboration between Sewall Wright and Dobzhansky
248 (Huneman 2019). In addition, we should not forget the German contribution to the MS with its
249 more structuralistic focus on development (Reif et al. 2000). The Israeli philosopher Ehud
250 Lamm notes in a critical book review that the MS was a complex evolutionary process that is
251 now well behind us (Lamm 2018), and similar views have been expressed by some science
252 historians (Reif et al. 2000; Cain 2009). Today, the MS mainly serves as a rhetorical figure and
253 an argument by those calling for radical conceptual change in evolutionary biology (Buskell
254 and Currie 2017; Lamm 2018). Clearly, much of the debate about the MS has less to do with
255 the synthesis *per se* and instead reveals that some reformers and critics are mainly engaged in
256 an identity political culture war, where the MS is portrayed as more rigid and dogmatic than it
257 ever was. The limitations of the MS are thus often used as an excuse to criticize contemporary
258 evolutionary biology, including (real or perceived) gene centrism or reductionism (Pigliucci
259 2007; Noble 2013, 2015, 2017; Laland et al. 2014, 2015; Müller 2017).

260

261 **5.3 Gould’s mixed legacy: strawman arguments and myths about the MS**

262 Here, I will focus on two common strawman arguments against the MS that were raised
263 repeatedly by Gould and – in spite of being refuted many times – continue to live on in ongoing
264 debates. These two arguments are, first the so-called “isotropy assumption” about variation

265 (Pigliucci 2019) and second, the claim that the synthesis “hardened” over time and became
266 narrowly focused on natural selection, ignoring other evolutionary processes such as genetic
267 drift (Gould 2002).

268

269 The isotropy assumption is the claim that the MS assumes that variation is equally likely in all
270 directions (Pigliucci 2019). Taken to its logical extreme, the isotropy assumption would say
271 that all variation is free, and that characters do not covary (Fig. 5.1A,B). In the more technical
272 language of evolutionary quantitative genetics, it would be equivalent to claim that all the off-
273 diagonal elements in the genetic variance-covariance matrix (\mathbf{G})(Steppan et al. 2002) are zero,
274 i. e. a very strong claim that traits are genetically uncorrelated with each other (Fig. 5.1B). One
275 could visualize this supposed isotropy assumption as the off-diagonal elements of \mathbf{G} being
276 spherical, rather than ellipses (cf. Fig. 5.1B vs. 1D). Such an extreme view is obviously a
277 caricature of both the MS and contemporary evolutionary biology. No leading evolutionary
278 biologist has such a naive view of unconstrained variation, to my knowledge. On the contrary,
279 it is clear that both Darwin and researchers working in the MS tradition were well aware of
280 genetic correlations, correlated growth and and correlated responses to selection (Charlesworth
281 et al. 1982; Svensson and Berger 2019; Svensson 2020), revealed, for instance, by the rich
282 literature on the evolution of allometric relationships (Bolstad et al. 2015; Tsuboi et al. 2018;
283 Svensson et al. 2021). Yet, Pigliucci (2019) claim that this isotropy assumption of
284 developmental processes and variation is a key feature of the MS, essentially re-iterating
285 previous older arguments by Gould (2002). One wonders how Pigliucci deals with the fact that
286 Julian Huxley – one of the architects of the MS – coined the term “allometry”, which is a prime
287 example of correlated variation and non-linear scaling relationships between traits (Huxley and
288 Teissier 1936)? Did Huxley really assume isotropic variation? Indeed, the evolution of
289 allometric relationships is a a popular theme in contemporary evolutionary biology research

290 (Bolstad et al. 2015; Tsuboi et al. 2018). If the isotropy assumption is so widespread as Pigliucci
291 (2019) claims: why have then genetic correlations, correlated responses to natural selection and
292 the evolution of genetic variance-covariance structures been the focus of so much evolutionary
293 biology research for decades (Lande 1979, 1980; Lande and Arnold 1983; Zeng 1988; Schluter
294 1996; Stepan et al. 2002)? The inevitable conclusion here is that the isotropy assumption is
295 neither an accurate characterization nor a strong argument against the MS or contemporary
296 evolutionary biology. See Salazar-Ciudad (2021) and Svensson and Berger (2019) for further
297 critique of the isotropy claim.

298

299 INSERT FIGURE 5.1 ABOUT HERE

300

301 Gould further claimed that the MS hardened, meaning that it became increasingly narrow and
302 exclusively focused on natural selection and that other evolutionary processes and stochasticity
303 thus were downplayed over time (Gould 1983, 2002). This so-called “hardening of the Modern
304 Synthesis”-argument is a popular and widespread myth that has frequently been re-iterated by
305 several later authors (Pigliucci and Müller 2010a; Huneman 2019). In fact, this so-called
306 hardening argument has seldom been questioned, but it appears to be accepted at face value
307 among some biologists and philosophers who otherwise seem to maintain a critical distance
308 from Gould (Huneman 2019). Here, I question Gould’s claim that the MS hardened, in line with
309 previous authors who have also critically dissected his highly biased historical narratives
310 (Orzack 1981; Sepkoski 2012; Svensson 2020). I argue that the hardening myth of the MS was
311 a deliberate exaggeration promoted by Gould to justify his own scientific project, aiming for
312 an expansion and radical revision of evolutionary theory (Gould 1980). To secure his place in
313 history, Gould pushed the hardening myth and other strawman arguments to paint a highly

314 biased view of the MS as excessively adaptationist and dogmatic, while brushing under the
315 carpet facts that ran counter to his views (Orzack 1981; Sepkoski 2012; Svensson 2020). An
316 uncomfortable fact that does not fit Gould's narrative include the tension between "Wrightian"
317 and "Fisherian" population genetics that was present from the beginning of the MS, and which
318 has shaped evolutionary biology ever since, contributing to its pluralism (Orzack 1981; Provine
319 1986; Coyne et al. 1997; Wade and Goodnight 1998; Goodnight and Wade 2000; Svensson
320 2018; Huneman 2019). Clearly, the Wrightian tradition with its emphasis on stochasticity,
321 genetic drift and gene flow has been a key part of the MS (Provine 1986), especially in North
322 America (Huneman 2019), where Gould spent his entire academic career. The existence of the
323 Wrightian tradition therefore partly refutes Gould's claim about the excessive adaptationism of
324 the MS (Orzack 1981). Moreover, the examples Gould used as evidence for his claim that the
325 MS hardened from its early formative years in the 1940s to later decades (Gould 2002) do not
326 hold up, upon critical inspection.

327

328 Gould re-read both original and updated versions of Dobzhansky's and Mayr's early synthesis-
329 books (Dobzhansky 1937; Mayr 1942). He argued that there was a much stronger emphasis on
330 selection in explaining patterns of genetic variation, polymorphisms and clines in nature in the
331 later editions (Gould 2002). This stronger emphasis on selection was interpreted by Gould as
332 an increasingly dogmatic attitude of these two major architects of the MS (Gould 1983, 2002).
333 An alternative, but more plausible interpretation is that both Dobzhansky and Mayr changed
334 their views in the face of new empirical evidence, rather than changing views for ideological
335 reasons or because they became more narrow minded. Dobzhansky, for instance, studied the
336 dynamics of chromosomal inversion polymorphisms in natural populations of *Drosophila*
337 (Dobzhansky 1970). The reason for studying these chromosomal inversion polymorphisms was
338 that Dobzhansky collaborated with Sewall Wright and was interested in studying genetic drift

339 and testing aspects of the Shifting Balance Theory (Provine 1986). Dobzhansky therefore
340 picked (putatively) neutral markers like chromosomal inversions with the aim to study genetic
341 drift. Dobzhansky and many others should be excused in that they could not see how this
342 seemingly arbitrary chromosomal character could be important to fitness or affect an
343 organism's phenotype in the pre-DNA era. Dobzhansky thus started with a neutral expectation,
344 but soon – to his surprise and disappointment (!) – he found out that these chromosomal
345 inversion polymorphisms fluctuated predictably with season and changing temperatures
346 (Dobzhansky 1970; Provine 1986). These fluctuations implied that these chromosomal
347 inversion polymorphisms were not entirely selectively neutral and did not change in frequencies
348 solely by genetic drift, as he had hoped (Provine 1986). Thus, Dobzhansky's empirical insight
349 that selection was operating on these chromosomal inversion polymorphisms can hardly be
350 characterized as a “hardening” or reflecting more dogmatic attitude where selection became
351 overemphasized. Instead it was rather the opposite: Dobzhansky clearly and at first
352 *underestimated* the importance of selection. To the extent Dobzhansky updated his view and
353 increasingly recognized the importance of natural selection, it was a hardwon empirical insight,
354 in striking contrast to Gould who never did any field work himself on extant organisms in
355 natural populations. Later work – on both *Drosophila* and many other organisms – has revealed
356 that chromosomal inversion polymorphisms are often targets of strong natural and sexual
357 selection with pronounced effects on organismal fitness (Noor et al. 2001; Kirkpatrick and
358 Barton 2006; Kupper et al. 2016; Hooper and Price 2017; Faria et al. 2019). Thus, the late
359 Dobzhansky was correct in upgrading the importance of selection, whereas the early
360 Dobzhansky clearly overestimated the importance of genetic drift.

361

362 Gould (2002) further argued that another sign of the hardening of the synthesis was how Mayr
363 changed his view of polymorphisms from being described as selectively neutral in his early

364 book *Systematics and the Origin of Species* (Mayr 1942) to being mainly interpreted in adaptive
365 terms in his later book *Animal Species and Evolution* (Mayr 1963). In Mayr's 1963-book such
366 polymorphisms (e. g. colour polymorphisms) were characterized in adaptive terms and as being
367 the target of selection. However, Mayr's changed opinion hardly represents any hardening
368 view, as claimed by Gould, but rather his increasing insights about the importance of selection
369 that the early Mayr clearly underestimated in 1942. Later empirical work on some of the
370 classical colour polymorphisms that were considered neutral characters by Wright and
371 contemporaries have revealed that they are more often than not targets of selection (Schemske
372 and Bierzychudek 2001; Turelli et al. 2001). More generally, recent research on colour
373 polymorphisms have revealed that such polymorphisms are often targets of natural or sexual
374 selection and upon closer inspection are seldom neutral (Wellenreuther et al. 2014; Svensson
375 2017). The fact that both Gould and the early Mayr in 1942 assumed *a priori* that seemingly
376 meaningless polymorphisms would be selectively neutral might reflect a lack of understanding
377 of population genetic theory by both of them. In all populations of limited size, genetic drift
378 will operate to a greater or lesser extent. The maintenance of polymorphisms and genetic
379 variation therefore requires the operation of some selective mechanism, like overdominant
380 selection or negative frequency-dependent selection (Svensson 2017). Thus, it is the
381 maintenance of variation (i. e. polymorphisms) that requires a selective explanation, not the
382 lack of variation (Svensson 2017). In contrast, lack of variation and the attainment of
383 monomorphism is the default expectation in all populations of limited size, an important aspect
384 of population genetic theory that neither Gould nor the early Mayr seemed to have fully
385 understood.

386

387 A third example of how Gould's claim about the hardening of the MS reflects increasing
388 empirical insights and not just a dogmatic change in mindset by the synthesis architects is the

389 study on Darwin's finches by the British ornithologist David Lack (Lack 1945, 1947). There
390 were two versions of Lack's book: one monograph published in the series *Occasional papers*
391 *of the California Academy of Sciences* in 1945 (Lack 1945) and another one only two years
392 later, published by Cambridge University Press (Lack 1947), but with very different messages.
393 In the 1945-version, Lack interpreted interspecific differences in bill size and bill shape mainly
394 in non-adaptive terms, such as bills being selectively neutral and primarily functioning as
395 species isolation mechanisms (Lack 1945). In contrast, in the 1947-version, Lack instead
396 interpreted the same bill differences in ecological terms, as reflecting interspecific niche
397 differentiation in terms of food resources (Lack 1947). The 1947-version was received and
398 reviewed enthusiastically by Mayr, who held Lack in high regard and who emphasized his
399 contribution to bring in ecology to the MS (Haffer 2007). Gould (1983) interpreted this shift in
400 interpretation by Lack as another example of the hardening of the MS, presumably caused by
401 Lack's strong personal connection with Mayr (Haffer 2007). However, it seems much more
402 likely that Lack's changed view reflected a genuine change of mindset, from a non-adaptive *a*
403 *priori* assumption that interspecific phenotypic differences are largely neutral and of little
404 significance, to a more realistic ecological view where they at least partly contribute to enhance
405 survival and reproduction in a species niche (Lack 1947). In retrospect, we know now, thanks
406 to the impressive later empirical field work by Peter and Rosemary Grant, that the interspecific
407 bill differences in Darwin's Finches are indeed targets of natural selection and affect inter- and
408 intraspecific competition (Grant and Grant 2014). Therefore, the later 1947-version of Lack
409 turned out to largely be correct (Lack 1947). In Lack's pioneering work we therefore rather see
410 a careful and thoughtful naturalist who changed his opinion and adopted a more realistic view
411 of phenotypic characters, away from an initially questionable assumption that these traits were
412 simply neutral and without any ecological importance to survival and reproduction. Gould –
413 unlike Lack - was a paleontologist and not a field biologist. Gould's lack of appreciation of

414 ecology could explain why he did not understand and appreciate the importance of subtle and
415 small phenotypic differences to organism's survival and reproduction.

416

417 Summing up this section: Gould's characterization of the hardening of the MS can be turned
418 entirely upside down: it was a healthy shift away from the unfounded assumption that most
419 characters were strictly neutral and without any importance to fitness to a more ecologically
420 realistic view that even small phenotypic differences could be important. The changing
421 perspectives of Dobzhansky, Mayr and Lack reflect a healthy updating of their views in the
422 face of new empirical evidence more so than any dogmatic stance. In fact, one can equally well
423 criticize the MS from the opposite perspective: the architects of the MS did not pay enough
424 attention to ecology and might have underestimated the importance of studying natural selection
425 directly in the field (Antonovics 1987; Endler and McLellan 1988). Antonovics (1987) pointed
426 out that the architects of the MS typically did not bother to even measure natural selection in
427 natural populations. Similarly, Endler and McLellan (1988) emphasized that few of the leading
428 figures behind the MS worked in natural populations of non-model organisms. It was not until
429 several decades after the MS that evolutionary biologists started to quantify natural and sexual
430 selection in the field to fill in this missing gap (Lande and Arnold 1983; Endler 1986).
431 Moreover, Mayr clearly underestimated the importance of natural selection and the importance
432 of different environments on islands and mainlands in his now largely discredited theory of
433 effect speciation through genetic revolutions (Barton and Charlesworth 1984; Haffer 2007).
434 The founder effect speciation model – which Mayr was very proud of – is a strictly neutral
435 model with little or no role for natural selection. The founder effect speciation model clearly
436 illustrates that Mayr often rather *underestimated* the power of natural selection, *contra* the
437 claims by Gould (1983) and others who in Mayr see a strong and dogmatic adaptationist. The
438 myth that the MS hardened and that it only recognized natural selection is a historically

439 questionable view that Gould promoted, but it continues to be re-iterated by some critics who
440 argue that we need radical conceptual change of contemporary evolutionary biology (Laland et
441 al. 2014, 2015; Müller 2017).

442

443 **5.4 Extrascientific criticisms of the MS: Adaptation without natural selection?**

444 Some past and recent criticism against the MS might not have only been scientifically
445 motivated, but extrascientific motives could also partly have played some role (Futuyma 2017).
446 Such extrascientific motives could be based on either ideology or religion, but they are often
447 dressed up as criticism of reductionism, or decrying the lack of any room for purpose in
448 evolution and in the MS, as exemplified by the writings by Noble (Noble 2013, 2015, 2017,
449 2021). Left-leaning biologists like Waddington and Gould were often critical of what they
450 perceived as genetic reductionism, and many times they had some good points in raising these
451 criticisms (York and Clark 2011; Peterson 2017). However, perhaps they went too far and were
452 also for some ideological reasons opposed to population genetics? Waddington and Gould
453 might for partly ideological reasons have exaggerated their critique of population genetics and
454 downplayed its huge importance for the development and progress of modern evolutionary
455 biology. Many public intellectuals and authors like Arthur Koestler openly flirted with
456 Lamarckism during the 20th century (Koestler 1971) because they felt that a Lamarckian world
457 with acquired inheritance would be more progressive and more hopeful than the cold Darwinian
458 world with no obvious room for any higher purpose (Futuyma 2017). The increased interest in
459 transgenerational epigenetic inheritance and the possibility that such epigenetic inheritance
460 might turn out to be adaptive can partly be explained by ideological leanings towards the
461 Lamarckian temptation (Haig 2007). This Lamarckian temptation still exist in the general
462 public and even in a small minority of some vocal biologists. For instance Eva Jablonka – a
463 leading critic of the MS and a strong proponent of the EES – insists in using the term

464 Lamarckian for phenomena like epigenetic inheritance (Jablonka and Lamb 2007). Jablonka
465 was criticized for this by the philosopher Peter Godfrey-Smith and the biologists Mary Jane
466 West-Eberhard and David Haig (Haig 2007; West-Eberhard 2007; Godfrey-Smith 2007). The
467 insistence that some variation – including mutations – are “directed” rather than random with
468 respect to the organism’s current needs (Godfrey-Smith 2007) is an old but discredited idea that
469 never seems to go away, in spite of being firmly refuted in many experimental studies (Lenski
470 and Mittler 1993; Futuyma 2017; Svensson and Berger 2019). Recent attempts to associate
471 transgenerational epigenetic inheritance to Lamarckism does not hold upon closer critical
472 scrutiny (Deichmann 2016; Loison 2018, 2021). Some of these molecular mechanisms are
473 likely to have evolved by a standard process of natural selection and are therefore evolutionary
474 outcomes, rather than evolutionary drivers (Loison 2018).

475

476 In light of the many failures during the 20th century to prove a central role for adaptive
477 Lamarckian inheritance in evolution, time now seems overdue to bury both Lamarckism and
478 Neo-Lamarckism (as well as Neo-Darwinism). Jablonka, Noble and others calling for an
479 extension or expansion of evolutionary biology have certainly not helped their own cause by
480 flirting with Lamarckism and directed variation. The (provocative) rhetoric by some critics of
481 contemporary evolutionary biology and their insistence on pushing the Lamarckian angle is
482 presumably the main reason why EES and TWE are still viewed with skepticism in large parts
483 of the evolutionary biology community (Welch 2016; Charlesworth et al. 2017; Futuyma 2017;
484 Svensson 2018). Noble’s claim that conscious processes and other clearly adaptive features in
485 organisms evolved because they serve a purpose (Noble 2021) deliberately avoids referring to
486 natural selection, the only scientifically known evolutionary process that can systematically
487 increase organismal adaptation across generations and which can explain adaptive organismal
488 design (Gardner 2013, 2017). Ironically, Noble’s obsession with purpose puts him conceptually

489 somewhat close to the ultra-adaptationists and Darwinists Grafen and Gardner in the so-called
490 “Formal Darwinism” project (Grafen 2014; Lewens 2019a). The main but crucial difference is
491 that Noble denies a central role of natural selection in explaining (apparent) design and purpose
492 of organisms. Noble seems to search for some other explanation than natural selection of
493 organismal adaptation and it is unclear if it is even a scientific one (Noble 2021). Similarly,
494 some critics of the MS and contemporary evolutionary more or less openly admit that they aim
495 to re-introduce metaphysical principles in biology by highlighting organismal “agency” (Walsh
496 2015; Buskell and Currie 2017; Dupré 2021), which the majority of evolutionary biologists,
497 including the present author, firmly reject, unless such perceived agency is described as an
498 outcome of natural selection. There are, however, many conceptual and philosophical problems
499 associated with introducing agency in to evolutionary thinking (Okasha 2018).

500

501 To the extent (apparent) purposeful organisms exist, evolutionary biologists explain their
502 currently adaptive traits by the standard process of natural selection that have operated on these
503 traits in the past and which still operate to maintain current function. This has implications for
504 the odd idea of “*adaptation without natural selection*” or “*adaptive evolution without natural*
505 *selection*” (Pigliucci and Kaplan 2000; Kull 2014), which is the claim that some adaptive traits
506 that increase organismal survival and/or success in a given environment are not products of, or
507 can not be explained by past or current natural selection. But adaptation without natural
508 selection is an oxymoron, at least if we measure adaptation in terms of fitness or organismal
509 performance. Any trait that enhances organismal fitness in a given environment relative to other
510 trait variants will (per definition) be target of selection, and once the trait has reached its
511 adaptive optimum, it will subsequently be maintained by stabilizing selection for its current
512 utility (Reeve and Sherman 1993; Hansen 1997). Such traits might (or might not) have evolved
513 for their current function, but current utility *implies* ongoing stabilizing selection (Hansen

514 1997). Hence, currently adaptive traits are (per definition) targets of selection, illustrating that
515 adaptation without natural selection is a meaningless phrase. In addition, such traits could also
516 have an evolutionary history of directional selection where they spread because of the
517 advantages they confer today, and only such traits would count as “true” adaptations, according
518 to Gould and Vrba (Gould and Vrba 1982). Traits for which current utility differ from the
519 selective benefits that drove their original spread were labelled “exaptations” by Gould and
520 Vrba (1982) and exaptations were claimed to be qualitatively different from “true” adaptations.
521 However, the term exaptation is problematic, as it sets up an arbitrary one-generation distinction
522 between the past and the present, as ultimately every trait must have evolved from another trait
523 in the first place. Moreover, exaptation is a one-generation term only, as a trait that is maintained
524 by selection for only one generation for its current function will (per definition) become an
525 adaptation (J. A. Endler, personal communication). Some authors insisting on using the term
526 adaptation without natural selection point to adaptive phenotypic plasticity as an example,
527 which can generate a fit between organism and environment within a single generation
528 (Pigliucci and Kaplan 2000) or they argue for plasticity-led evolution as an alternative to
529 adaptive evolution by natural selection (Kull 2014). The latter idea is often termed “plasticity
530 first” or described as “genes as followers, not leaders”, referring to Mary Jane West-Eberhard’s
531 original suggestions (West-Eberhard 2003).

532

533 Upon critical scrutiny, the superficial arguments above do not provide any evidence at all
534 against adaptive evolution being driven by natural selection. First, theory and empirical
535 evidence have clearly shown that adaptive phenotypic plasticity and phenomena such as genetic
536 assimilation can and are often targets of natural or sexual selection, show heritable variation
537 and can evolve by the standard process of selection (Lande 2009; Chevin et al. 2010; Svensson
538 et al. 2020). Second, the plasticity-first hypothesis and the idea of genetic assimilation of

539 originally plastic changes is (as indicated by the term “*genetic*” before assimilation) is not an
540 alternative to evolution by natural selection, but rather points to the possibility that *the initial*
541 *adaptive change can be achieved by a plastic adjustment of the organism followed by natural*
542 *selection on genetic variation that stabilizes the trait* (Price et al. 2003; Lande 2009). West-
543 Eberhard (2003) herself has been quite clear that her idea about plasticity-led evolution was not
544 mean to be an alternative to evolution by natural selection and genetic evolution, but rather an
545 *initiator* of subsequent evolutionary change, where phenotypes played a major role (“leaders”)
546 to the genetic change that followed (“genes as followers”). Specifically, she explicitly defines
547 evolution by stating (P. 32):

548

549 *“Strictly speaking, the units that replicate themselves most precisely, and therefore have cross-generational effects*
550 *that both reflect past differential reproduction and affect future reproduction, are genes. So genes are the most*
551 *appropriate units of evolution.”*

552

553 This quote by West-Eberhard is interesting insofar it reveals she adopts a fairly traditional view
554 on the definition of evolution, and she does clearly not see plasticity and genetic assimilation
555 as alternatives to adaptive evolution by natural selection. Following the definitions by leading
556 EES proponents (Laland et al. 2014, 2015), West-Eberhard, a leading proponent of plasticity’s
557 role in evolution, could thus be classified as “gene centric”. Interestingly, West-Eberhard
558 refused to co-author the papers by Laland et al. (2014; 2015) in their call for an EES. Her main
559 objection was that these authors did not explicitly define evolution in terms of genetic change
560 (Kevin Laland, personal communication). The quote above by West-Eberhard also reveals the
561 problems of using the term “gene centric” for those being critical of the EES, as it is obviously
562 possible to emphasize plasticity and phenotypes in evolution, but still be labelled as a gene
563 centrist.

564

565 The objections above against adaptive plasticity and associated phenomena such as genetic
566 assimilation exemplify adaptive evolution without natural selection also apply to other within-
567 generation phenomena that increase an organism's fitness in a given environment. Such within-
568 generation phenomena include thermoregulation and other regulatory behaviours, acclimation,
569 various physiological responses, dispersal, habitat selection etc. (Huey et al. 2003; Edelaar et
570 al. 2008; Edelaar and Bolnick 2019). Such adaptive within-generation modifications that
571 increase an individual organism's fitness or even mean population fitness are ecologically
572 important, but should be viewed as adaptive outcomes of evolution by natural selection (Fig.
573 5.2), rather than adaptations that formed without natural selection (cf. (Pigliucci and Kaplan
574 2000; Kull 2014)). Once again, there is an important distinction between evolutionary processes
575 leading to between-generation changes and evolutionary outcomes, as revealed in various
576 adaptation expressed during the life-time of individual organisms (Lynch 2007; Gardner 2013).

577

578 INSERT FIG. 5.2 ABOUT HERE

579

580 Finally, another class of extrascientific motives behind recent criticisms against the MS and
581 contemporary evolutionary biology could be boredom. All evolutionary biologists are (luckily)
582 not interested in the same things, and not everyone appreciates population and quantitative
583 genetics. It is most likely one of the motivations behind Pigliucci's push for the EES, as
584 exemplified in a critical dissection of Brian Charlesworth's views, who had expressed the
585 opinion that most of the problems in evolutionary genetics had been solved: "*Well, perhaps,*
586 *but some of us are not ready for retirement just yet*" (sic! P. 2744; (Pigliucci 2007)). The author
587 of the present chapter has, in some discussions with leading proponents of the EES,

588 encountered similar attitudes, for instance that “*reaction norms and population genetics are*
589 *boring*”. Similar views were expressed by the evolutionary developmental biologist Sean
590 Carroll in his book “*Endless Forms Most Beautiful: The New Science of Evo Devo*”, where he
591 declared that the development of form in butterflies and zebras was a more inspiring story to
592 tell about evolution than changes in gene frequencies (Carroll 2006). Population geneticist
593 Michael Lynch was, however, rather blunt in his dismissal of this criticism of population
594 genetics and stated: “*Evolutionary biology is not a story-telling exercise, and the goal of*
595 *population genetics is not to be inspiring, but to be explanatory.*” (Lynch 2007). He further
596 developed his criticism of Carroll and evolutionary developmental biology and the frequent
597 claim that this new field would supposedly overturn evolutionary biology by stating that “*No*
598 *principle of population genetics has been overturned by any observation in molecular, cellular,*
599 *or developmental biology, nor has any novel mechanism of evolution been revealed by such*
600 *fields.*” (Lynch 2007).

601

602 Although I am not a population geneticist, I strongly agree with Lynch that *the primary goal of*
603 *evolutionary biology is not to inspire but to explain.* For any theory that aims to be connected
604 to the real world, we should prioritize explanatory power over beauty. I strongly suspect that
605 my view is shared by most of my empirically oriented evolutionary biologist colleagues. The
606 fact that not everyone gets inspired by population and quantitative genetics theory is not a strong
607 or compelling argument that we need major conceptual change in our field.

608

609 **5.5 Scientific criticisms of the MS: from Waddington and Gould to the EES**

610 It did not take a long time after the formation of the MS for the developmental biologist Conrad
611 Waddington to express his discontent and bitterness against what he called *COWDUNG*, or

612 “*Conventional Wisdom of the Dominant Group*” (Peterson 2017). Waddington even negatively
613 labelled his former collaborator and co-author Haldane as a simple “Neo-Darwinist” (Peterson
614 2017). Waddington’s decision to distance himself from Mayr, Dobzhansky, Haldane and other
615 leading architects of the MS probably contributed to make his influence on modern evolutionary
616 biology much less than it could potentially have been (Peterson 2017). Waddington was
617 therefore not able to incorporate his views about epigenetics in to the mainstream of the MS
618 (Wilkins 2008). It is still an open question whether this was mainly the fault of Waddington
619 himself – deliberately distancing himself from the mainstream – or due to attitudes from Ernst
620 Mayr and the other synthesis architects (Peterson 2017).

621

622 In a similar vein, the late paleontologist Stephen Jay Gould rather decisively and aggressively
623 distanced himself from the MS and Neo-Darwinism (Sepkoski 2012). Interestingly, Gould
624 started his career as a fairly mainstream evolutionary biologist, building upon Ernst Mayr’s
625 rather orthodox theory of allopatric speciation (Mayr 1942). Gould and his collaborator Niles
626 Eldredge incorporated this allopatric theory in to their own theory of “punctuated
627 equilibrium” (Eldredge and Gould 1972; Sepkoski 2012). After successfully establishing
628 himself as a major player in the new and growing field of paleobiology and mathematical
629 models in macroevolution, Gould devoted a large part of his late career to popular science
630 columns in the journal *Natural History* (Sepkoski 2012). Gould also developed his criticisms
631 of the MS in many articles (Gould and Lewontin 1979; Gould 1980; Gould and Vrba 1982)
632 as well as in his late magnum opus *The Structure of Evolutionary Theory* (Gould 2002),
633 published in 2002, the same year as his death. In his critique of the MS and Neo-Darwinism,
634 Gould made several strong claims that received strong criticisms from other evolutionary
635 biologists (Orzack 1981). Some of Gould’s critics argued that he used extensive strawman
636 arguments against the MS (see section “5.3 Gould’s mixed legacy: strawman arguments and

637 *myths about the MS*” to justify his own scientific agenda aiming for a major paradigm shift in
638 evolutionary biology (Sepkoski 2012; Svensson 2020). While few would question Gould’s
639 scientific contributions to paleobiology, his popular outreach and his admirable fight against
640 creationism, a common (and still valid) criticism of his work is that he strongly exaggerated
641 the rigidity of the MS (Sepkoski 2012). For instance, Gould’s biased characterization of the
642 MS as excessively deterministic and adaptationist and his claim that it ignored random factors
643 and stochasticity (Gould 1980, 1981) received strong criticism by Orzack, Charlesworth,
644 Lande and Slatkin who also pointed to the influence of Sewall Wright on the development of
645 the MS (Orzack 1981; Charlesworth et al. 1982).

646

647 Some of the arguments used by Gould – despite being repeatedly countered and in many cases
648 refuted – have survived also after Gould’s death, and they regularly resurface in ongoing calls
649 about the necessity to extend the MS (Pigliucci 2007, 2009; Laland et al. 2015) as well as in
650 more radical calls for the entire replacement of MS (Noble 2013, 2015, 2017; Müller 2017).
651 Many critics re-iterate Waddington’s and Gould’s arguments in their calls for an entirely new
652 synthesis, and argue that insights from developmental biology and epigenetic mechanisms
653 (Table 5.1) in themselves necessitate a major revision, extension or replacement of the MS.
654 While it is quite clear that we now live in a post-Synthesis period, it is striking how the same
655 old tired arguments by Waddington and Gould resurface at regular intervals. In contrast, other
656 relevant criticisms against the limited scope of the MS, such as its relative neglect of ecology
657 (Antonovics 1987; Endler and McLellan 1988), are more seldom discussed.

658

659 **5.6 Recent challenges to the MS**

660 In the previous sections, I have shown how Gould systematically mis-characterized the MS for
661 several decades, making highly exaggerated claims about its strict focus on natural selection
662 and downplaying its pluralistic nature. However, discontent with the MS was present from its
663 early days, and a number of extensions, expansions and various “add-ons” have been suggested
664 (Table 5.1). Some molecular, developmental and theoretical biologists even argue that the MS
665 should be abandoned entirely or replaced, as it can no longer be fruitfully extended (Koonin
666 2009; Stoltzfus 2017; Müller 2017).

667

668 Closer inspection of Table 5.1 lead me to two conclusions. First, calling for a new synthesis by
669 pointing to limitations of the MS has been a popular and widely used tactic by critics for
670 decades to express strong discontent and push for new ideas, as already noted and discussed by
671 some philosophers and historians (Buskell and Currie 2017; Lamm 2018). In this context, the
672 MS has mainly served as a justification for other grand projects, often also labelled “syntheses”
673 of various kind. Second, the sheer number of phenomena that have been claimed to be missing
674 from the MS is rather bewildering, and it often difficult to see what these different factors have
675 in common (Table 5.1). For instance, in an early call for an Extended Evolutionary Synthesis
676 (EES), Pigliucci listed “*evolvability, phenotypic plasticity, epigenetic inheritance, complexity*
677 *theory and high-dimensional adaptive landscapes*” as phenomena largely unexplained by the
678 MS (Pigliucci 2007). The last of these phenomena – high-dimensional adaptive landscapes – is
679 odd, as this is a rather orthodox theoretical evolutionary genetic concept, developed by Sergey
680 Gavrilets (Gavrilets 2004), who has clearly distanced himself from the EES (Gavrilets 2010).
681 A few years later, Dennis Noble added “*replicator theory, genomic evolution and multi-level*
682 *selection*” to his version of the “*Integrated Synthesis*” (Noble 2015). About the same time as
683 Noble, Kevin Laland and colleagues restricted themselves to four phenomena in their version
684 of the EES: *Developmental bias, plasticity, non-genetic inheritance* and *niche construction*

685 (Laland et al. 2015). Before these recent initiatives, we saw Gould called for incorporation of
686 *species selection, hierarchical theory* and *macroevolution* in his proposed expanded version of
687 evolutionary theory (Gould 1982). Already in the 1950s Waddington highlighted *genetic*
688 *assimilation, epigenetics* and *gene interaction* that he felt were missing from the MS
689 (Waddington 1957; Wilkins 2008; Peterson 2017).

690

691 The sheer variety of disparate phenomena listed as challenges to the MS (Table 5.1) therefore
692 easily gives the impression that various critics have compiled their own “laundry lists” of
693 favourite topics that they feel have been duly neglected (Welch 2016). Or – to put it bluntly –
694 many of these phenomena have little to do with each other, and more reflect the personal
695 interests of critics and what they consider to be important. However, as material for a new
696 synthesis, it is obviously not enough to list a number of interesting phenomena, but there must
697 also be some common thread connecting them together in a convincing conceptual or
698 theoretical framework. Otherwise, biology risks becoming what the physicist Ernst Rutherford
699 dismissed as the mere “stamp collecting” of various facts, but with no theoretical coherence. It
700 is therefore not entirely unexpected that the novelty and theoretical coherence of the EES has
701 been questioned by some philosophers (Lewens 2019b; Buskell 2019, 2020; dos Reis and
702 Araújo 2020) and evolutionary biologists (Welch 2016; Charlesworth et al. 2017; Futuyma
703 2017; Svensson 2018). A rather blunt recent criticism of the EES is that it is neither an extension
704 nor a proper synthesis (dos Reis and Araújo 2020).

705

706 What should we make of all this? On the one hand, proponents of an EES have clearly
707 highlighted some interesting phenomena that deserve to be studied more in depth, such as
708 plasticity and non-genetic inheritance (Laland et al. 2015). On the other hand, skepticism

709 towards a new synthesis based on these and other phenomena prevail in the evolutionary
710 biology community and the EES is far from being embraced by the mainstream. One impression
711 one gets from Table 5.1 is that advocates of various extensions of the MS are conceptually split
712 among themselves and have difficulties in finding common ground. In particular, while some
713 EES-proponents strive for a simple extension (Pigliucci 2007, 2009; Laland et al. 2015) more
714 radical critics instead strive for “replacement”, or something we might consider a true paradigm
715 shift (Noble 2013, 2015, 2017). Whereas the former camp can be viewed as “reformers”, the
716 latter are better labelled as “revolutionaries”. A second impression from Table 5.1 is that it is
717 unclear why particular phenomena are highlighted as arguments for an extended synthesis (e.
718 g. plasticity, developmental bias, niche construction and non-genetic inheritance; (Laland et al.
719 2015)), whereas other interesting topics like the link between microevolutionary processes and
720 macroevolutionary patterns (Uyeda et al. 2011; Bell 2012; Hansen 2012; Svensson and
721 Calsbeek 2012a; Arnold 2014) are not included. The link between micro- and macroevolution
722 is even outrightly dismissed by some EES-proponents (Müller 2017):

723

724 *“A subtler version of the this-has-been-said-before argument used to deflect any challenges to the received view*
725 *is to pull the issue into the never ending micro-versus-macroevolution debate. Whereas ‘microevolution’ is*
726 *regarded as the continuous change of allele frequencies within a species or population ..., the ill-defined*
727 *macroevolution concept ..., amalgamates the issue of speciation and the origin of ‘higher taxa’ with so-called*
728 *‘major phenotypic change’ or new constructional types. Usually, a cursory acknowledgement of the problem of*
729 *the origin of phenotypic characters quickly becomes a discussion of population genetic arguments about*
730 *speciation, often linked to the maligned punctuated equilibria concept... , in order to finally dismiss any necessity*
731 *for theory change. The problem of phenotypic complexity thus becomes (in)elegantly bypassed. Inevitably, the*
732 *conclusion is reached that microevolutionary mechanisms are consistent with macroevolutionary phenomena ...,*
733 *even though this has very little to do with the structure and predictions of the EES. The real issue is that genetic*
734 *evolution alone has been found insufficient for an adequate causal explanation of all forms of phenotypic*
735 *complexity, not only of something vaguely termed ‘macroevolution’. Hence, the micro–macro distinction only*

736 *serves to obscure the important issues that emerge from the current challenges to the standard theory. It should*
737 *not be used in discussion of the EES, which rarely makes any allusions to macroevolution, although it is sometimes*
738 *forced to do so.”*

739

740 This rather blunt dismissal of macroevolution by Müller (2017) is certainly not a view shared
741 by many evolutionary biologists, including myself. Interestingly, this outright dismissal of
742 macroevolution by Müller above reveals a view and a lasting legacy that the EES seems to have
743 inherited from the MS, where macroevolution was sometimes simply viewed only as
744 “microevolution writ large” (Sepkoski 2012), although it is important to emphasize that at least
745 some representatives of the MS accepted macroevolution as an autonomous field of research,
746 distinct from microevolution (Stebbins and Ayala 1981) The comment is also interesting as it
747 reveals what Müller thinks is the challenging and interesting problem: the evolution of
748 organismal complexity. For Müller and other critics of the MS and contemporary evolutionary
749 biology, complexity is *the* big problem that we should focus on in explaining, rather than the
750 micro- and macroevolution link.

751

752 For several reasons, I think Müller’s viewpoint is mistaken and a dead end. First, complexity is
753 by no means easily defined, let alone explained. In fact, some complexity at the molecular level
754 might have little if anything to do with adaptive processes such as natural selection, but can
755 arise through neutral evolution alone. For instance, the theory of Constructive Neutral Evolution
756 (CNE) postulates that the accumulation of neutral mutation could build up considerable
757 complexity at the molecular level without any need for directional natural selection (Stoltzfus
758 1999; Muñoz-Gómez et al. 2021). There is some recent experimental evidence for CNE from a
759 study of long-term evolution of vertebrate steroid receptors that have increased in complexity
760 simply through neutral evolution (Hochberg et al. 2020). Such neutral evolution acted in a

761 ratchet-like fashion, leading to a state where current complexity is maintained by purifying
762 selection (Hochberg et al. 2020). I strongly suspect that Müller and other EES-proponents with
763 their strong focus on organismal phenomena are not very interested in such neutral evolution at
764 the molecular level and its consequences. Müller (2017) and others seem to implicitly assume
765 that complexity *per se* always needs some non-neutral explanation. That is not necessarily the
766 case. Null models of evolution can successfully explain the evolutionary increase in both
767 complexity and diversity (McShea and Brandon 2010). In contrast, natural selection is so far the
768 only known evolutionary force that can systematically increase fitness across generations and
769 that can convincingly explain the evolution of (apparent) purpose and adaptive features of
770 organisms (Gardner 2017). Null models like the Neutral Theory do not seem to be held in high
771 regard in the EES community and it is hardly mentioned in their writings (see e. g. (Pigliucci
772 2007, 2009; Laland et al. 2015)). This striking neglect in the EES community contrasts with
773 much of mainstream contemporary evolutionary biology and the population genetics
774 community where Neutral Theory holds a central position (Kern and Hahn 2018; Jensen et al.
775 2019).

776

777 **5.7 The re-emergence of mutation-driven evolution and directed variation?**

778 The architects of the MS correctly dismissed several alternative but now firmly discredited
779 evolutionary processes, such as the inheritance of acquired characters (i. e. Lamarckism),
780 orthogenesis (i. e. the innate tendency of organisms to evolve in certain directions towards a
781 “goal”), saltationism (evolution by large mutations) and the idea that mutations were the main
782 drivers of evolution rather than natural selection (“mutationism”)(Gould 2002). The idea that
783 mutations were the main drivers of evolution was championed by early Mendelians like Hugo
784 de Vries, Gregory Bateson and Thomas Hunt Morgan. These geneticists focused on mutations
785 of large visible effects, such as eye colour and wing mutants in *Drosophila*, often with abnormal

786 phenotypic effects (Gould 2002) but of questionable ecological importance for adaptive
787 evolution in natural populations. These laboratory-based geneticists did apparently not
788 understand or appreciate the importance of natural selection, as they studied organisms in strict
789 laboratory settings and they had little direct research experience from natural populations. It
790 was only when Dobzhansky entered the laboratory of Thomas Hunt Morgan that this
791 experimental genetic laboratory tradition in the US was merged with studies of natural
792 populations that he was trained in from his early educational years in Russia and the Soviet
793 Union (Gould 2002). As a result, Dobzhansky had a deep understanding of both genetics and
794 natural history and he realized that although mutations were an important part of the
795 evolutionary process, in themselves they could not achieve much without the aid of natural
796 selection (Dobzhansky 1970; Provine 1986). Both Dobzhansky and other contemporary
797 evolutionary biologists like Haldane understood that mutations were the ultimate source of
798 novel genetic variation and they both wrote about the mutational process in the years
799 immediately preceding the MS (Dobzhansky 1933; Haldane 1933). But these evolutionary
800 biologists concluded – correctly as it later turned out – that mutations alone were unlikely to
801 explain long-term directional evolution at the phenotypic level, in contrast to the claims of the
802 early mutationists.

803

804 Given the strong experimental and empirical evidence against directed mutations (Lenski and
805 Mittler 1993; Futuyma 2017; Svensson and Berger 2019) and the failure of the early
806 mutationists to appreciate the power of natural selection, it is astonishing that some
807 contemporary evolutionary biologists are pushing for a revival of mutationism or mutation-
808 driven evolution (Stoltzfus 2006; Nei 2013; Stoltzfus and Cable 2014). Mutationism was
809 closely connected to the theory of orthogenesis – the idea that internal factors were primarily
810 responsible for evolutionary change and that the external environmental factors (*aka* natural

811 selection) played only a minor role (Gould 2002; Stoltzfus 2006; Stoltzfus and Cable 2014).
812 According to the early Mendelians and mutationists, large-effect visible mutations were
813 important, and the role of natural selection was mainly to sort out the unfit variants. The
814 mutationists contrasted such a negative role of selection with the mutational process that they
815 felt was the real driver of evolutionary change. For good reasons, this view was firmly rejected
816 by the development of quantitative genetics theory and empirical insights from plant and animal
817 breeding (Fisher 1918). The early mutationists clearly overestimated the importance of
818 mutations and underappreciated standing genetic variation and the creative role of natural
819 selection, and mainly saw selection as a “sieve” that could only sort out the unfit (Beatty 2016,
820 2019). However, the sieve-analogy underestimates the importance of standing genetic variation
821 for adaptation (Barrett and Schluter 2008) and modern views of natural selection emphasize its
822 multivariate nature, and its more creative role in shaping the genetic and phenotypic correlation
823 structure of organisms (Sinervo and Svensson 2002; Svensson et al. 2021).

824

825 Those who try re-instate mutationism and mutation as the main driver of evolutionary change
826 are therefore likely to face strong resistance, for good historical and scientific reasons. No
827 serious evolutionary biologist today would question that mutations is the ultimate source of
828 novel genetic variation, and in neutral evolution (where selection is per definition is absent),
829 such neutral mutation pressure can lead to directional evolutionary trends (Sueoka 1988;
830 Svensson and Berger 2019). Moreover, mutation-driven neutral evolution can potentially result
831 in increased molecular complexity, as emphasized in Constructive Neutral Evolution (CNE), as
832 discussed in the previous section (Stoltzfus 1999; Hochberg et al. 2020; Muñoz-Gómez et al.
833 2021). There is clearly a potential role for CNE at the molecular level. However, it is important
834 to underscore that even if the initial buildup of such molecular complexity would be entirely
835 neutral and mutation-driven and with no role for natural selection, as soon as these molecular

836 complexes are affecting aspects of the organismal phenotype and thereby likely its fitness (e.
837 g. cell physiology and other aspects of cellular performance), they would immediately and (per
838 definition) become targets of purifying selection (Hochberg et al. 2020; Brunet et al. 2021).

839

840 Likewise, few evolutionary biologists deny that genetic effective population size (N_e)
841 determines the efficacy of natural selection, which becomes weaker and less powerful when N_e
842 is low, i. e. approaching neutrality (Lynch 2007, 2010; Jensen et al. 2019; Svensson and Berger
843 2019). It is uncontroversial to say that the likelihood of mutation bias leading to a fixation bias
844 increases with the inverse of N_e , as selection then becomes weaker relative to genetic drift
845 (Lynch 2007). These insights from standard population genetic theory are far away from the
846 original claims by the early mutationists. Mutation bias is, however, unlikely to play an
847 independent role in adaptive evolution, unless it is aided by genetic drift and/or selection (Lynch
848 2007; Svensson and Berger 2019). Recently, some researchers claimed, based on a
849 mathematical model, that mutation bias can play an important role in adaptive evolution even
850 in the absence of natural selection (Gomez et al. 2020). However, closer inspection of their
851 model assumptions reveals that for this to work, they have to assume unrealistically high
852 adaptive mutation rates (Gomez et al. 2020). It is therefore questionable how relevant this and
853 other models of mutation bias without selection are for evolution in natural populations.

854

855 Most evolutionary biologists today view mutations as a stochastic evolutionary process with no
856 directionality or purpose, with no foresight or any tendency for mutations to systematically
857 increase organismal fitness across generations (Svensson and Berger 2019). This view has
858 strong empirical support (Svensson and Berger 2019), although the representatives from the
859 fringe movement TWE (James Shapiro and Dennis Noble) question this and claim a role for

860 adaptive directionality, purpose and functionality of novel mutations (Shapiro 2011; Noble
861 2013, 2017). These authors claim that various aspects of genome organization and gene
862 expression in organisms are clearly functional and that these functional aspects of the genome
863 contradicts the traditional view of mutations as random (with respect to current utility and future
864 adaptation; (Svensson and Berger 2019)). For instance, Noble (2017) argues that the existence
865 of functionally significant targeted somatic hypermutations during the lifetime of individual
866 organisms contradict the standard assumption in evolutionary theory that mutations are random
867 with respect to fitness. Noble points to somatic mutations in the vertebrate immune system as
868 an example of such adaptive design, where mutations seem to have purpose, indicating adaptive
869 foresight (Noble 2017). However, both Noble and Shapiro conflate somatic mutations and
870 changes within the lifetimes of individual organisms with germline mutations and evolutionary
871 change across generations (Gardner 2013). Noble and Shapiro also overlook fundamental
872 differences between somatic mutations and germline mutations, such as that the former are
873 higher (Moore et al. 2021), and are also targets of selection due to their strong link to lifespan
874 and other life-history characteristics (Cagan et al. 2021). The existence of highly sophisticated
875 molecular repair mechanisms, patterns of adaptive gene expression, methylation and other
876 epigenetic mechanisms that Noble and Shapiro highlight is no evidence at all against natural
877 selection operating on random mutational input (Gardner 2013). Instead, and much more likely,
878 natural selection has operated on and shaped these molecular mechanisms and other aspects of
879 genomic architecture (Sinervo and Svensson 2002; Svensson et al. 2021), including both
880 somatic and germline mutation rates (Lynch 2010; Cagan et al. 2021; Moore et al. 2021).
881 Molecular features at the genomic level are therefore shaped by selection, drift, mutation and
882 recombination (Lynch 2007; Gardner 2013; Svensson et al. 2021), and should be viewed as
883 evolutionary outcomes rather than as evolutionary processes in their own right (Loison 2018).
884 Again, we are reminded that a common mistake made by some critics of contemporary

885 evolutionary biology – not only Noble and Shapiro – is to conflate evolutionary processes with
886 the products of evolution (Lynch 2007).

887

888 In contemporary evolutionary biology, the stochastic nature of mutations is often
889 conceptualized as historical contingency and the role of chance (Losos et al. 1998; Blount et al.
890 2018; Svensson and Berger 2019). Thus, adaptive evolution reflects the balance between the
891 deterministic role of natural selection that systematically increases organismal adaptation
892 across generations (“survival of the fittest”), and the nature and arrival order of novel mutations
893 that selection can act upon, the latter often called “arrival of the fittest” (Wagner 2015). All else
894 being equal, if selection operates on a character governed by multiple loci, those loci with the
895 highest mutation rates are more likely to produce novel adaptive mutations that can be “seen”
896 by selection and which subsequently will increase in frequency and become fixed through
897 successive selective sweeps (Xie et al. 2019). A case in point is the adaptive evolution of pelvic
898 reduction in stickleback fish (*Gasterosteus aculeatus*) after colonization and adaptation to
899 freshwater habitats in postglacial lakes (Xie et al. 2019). Molecular studies have revealed that
900 such pelvic reductions are achieved by recurrent deletions which are produced by *Pitx1*
901 enhancer sequences that increase double-strand breaks (Xie et al. 2019). As a result, elevated
902 mutation rates at this locus contribute to make genomic evolution highly parallel and more
903 predictable, through repeated and adaptive phenotypic changes. However, the spread and
904 fixation of these novel mutations are still driven by natural selection in the new freshwater
905 habitat (Xie et al. 2019). This example illustrates that elevated mutation rates alone are not
906 sufficient to drive adaptive and parallel evolution, but natural selection plays a crucial role in
907 the spread and fixation of novel variants. More generally, the role of mutational stochasticity,
908 including the arrival order of novel mutations has been recognized in contemporary
909 evolutionary biology, both theoretically and empirically, e. g. in mutation-order speciation

910 (Schluter 2009) and in research on historical contingencies (Blount et al. 2018). It therefore
911 appears that those arguing for mutation bias as an entirely novel evolutionary principle
912 (Yampolsky and Stoltzfus 2001; Stoltzfus and Yampolsky 2009; Gomez et al. 2020) might have
913 somewhat exaggerated their cause. It is currently difficult to see that mutation-driven evolution
914 or mutation bias (Nei 2013; Stoltzfus and Cable 2014) would require a major revision of the
915 current already quite pluralistic theoretical framework of evolutionary biology.

916

917 **5.8 Developmental bias, niche construction, non-genetic inheritance and plasticity**

918 The most recent challenge to contemporary evolutionary biology is the push for an EES (Table
919 5.1), as exemplified by the writings by Kevin Laland and colleagues (Laland et al. 2014, 2015).
920 The EES group argues that the current theoretical framework with only four main evolutionary
921 processes (selection, drift, recombination and mutation) based on population genetic theory
922 (Lynch 2007; Svensson and Berger 2019) is incomplete, and fails to fully explain phenotypic
923 evolution and organismal adaptation (Laland et al. 2014, 2015). Specifically, they argue that
924 evolutionary theory needs to take in to account four additional processes that they claim have
925 been neglected: *phenotypic plasticity*, *developmental bias*, *niche construction* and *nongenetic*
926 *inheritance* (Laland et al. 2015). Although many evolutionary biologists agree with Laland and
927 colleagues that these are important and interesting topics, it has been questioned if these
928 phenomena are really they game changers have been portrayed to be, and they do not
929 necessarily require a novel conceptual framework (Welch 2016; Charlesworth et al. 2017;
930 Gupta et al. 2017; Futuyma 2017; Svensson 2018). A major criticism is that these four factors
931 are all possible to incorporate in the current theoretical framework. I will not re-iterate these
932 criticisms in detail here, but briefly discuss why these four factors are not evolutionary
933 processes of the same kind as the evolutionary forces in population genetic theory (Lynch 2007;
934 Svensson and Berger 2019).

935

936 I suggest we can view these four factors as either *evolutionary outcomes* or *source laws*, and
937 sometimes both, when there exist feedbacks between evolutionary outcomes and selection (Fig.
938 5.2). However, I argue that these four factors are not *consequence laws* like the traditional
939 evolutionary processes of genetic drift, mutation, recombination and selection (Sober 1984;
940 Endler and McLellan 1988)(Fig. 5.2). Here, I define source laws, following the definitions by
941 Sober (1984), as the underlying causes of fitness differences, selection and mutation rates etc.
942 Examples of source laws are temperature, radiation, predation, climate and most aspects of the
943 external or internal abiotic or biotic environment organisms experience (Fig. 5.2). The source
944 laws influence the consequence laws, which directly change the heritable composition of
945 populations. Source laws, therefore, only indirectly influence the heritable composition of
946 populations, but they are important as they are the ultimate factors causing fitness differences
947 between phenotypes or genotypes (Sober 1984). Source laws therefore arise from ecological
948 and physical conditions, morphology and physiology of organisms, whereas consequence laws
949 are thus the evolutionary effects of these fitness differences (Sober 1984; Endler and McLellan
950 1988). Population genetic theory is a theoretical framework mainly focused on evolutionary
951 forces, such as the consequence laws of selection, drift, mutation and recombination and how
952 these consequence laws change the heritable compositions of populations (Sober 1984). In
953 contrast, the source laws deal with how variation in fitness arises and how fitness-trait
954 covariance relationships change due to changes in the biotic and abiotic environment (Endler
955 and McLellan 1988; Wade and Kalisz 1990). Source laws are typically studied within the
956 domain of ecology, rather than belonging to population genetics (Brandon 1990; Wade and
957 Kalisz 1990; Svensson and Sinervo 2000; Siepielski et al. 2017). Needless to say: a full
958 understanding of evolution will require a deep understanding of both source laws and
959 consequence laws, i. e. both of the ecological agents of selection and the evolutionary changes

960 that follow from how selection and the other evolutionary forces operate on populations (Endler
961 and McLellan 1988; Wade and Kalisz 1990).

962

963 The four factors highlighted by Laland and colleagues can therefore be viewed as source laws
964 that influence the strength, direction or mode of natural selection (Fig. 5.2). For instance,
965 phenotypic plasticity and various forms of habitat selection of organisms can counteract natural
966 selection, as exemplified by adaptive thermoregulatory behaviours in reptiles and the so-called
967 “Bogert effect” (Huey et al. 2003). In addition, but not mutually exclusive, these four factors
968 can also be viewed as evolutionary outcomes, or products of selection (Fig. 5.2). Under this
969 alternative perspective, these four factors are adaptive traits that are shaped by current and past
970 natural selection, but such traits can also shape future evolution on themselves. For instance,
971 there exists a well-developed quantitative genetic theory of the evolution of phenotypic
972 plasticity and reaction norms (Lande 2009; Chevin et al. 2010; Chevin and Lande 2011) that
973 has also inspired empirical research in natural populations (Svensson et al. 2020). Under this
974 view, phenotypic plastic traits are modelled and conceptualized as *function-valued traits*
975 (Kingsolver et al. 2001), where trait values are not fixed but change with the environment
976 (Stinchcombe and Kirkpatrick 2012). In this framework, reaction norms are viewed as
977 composite phenotypes, and their intercepts and slopes can be treated as traits that are targets of
978 selection (Lande 2009; Chevin et al. 2010; Svensson et al. 2020). The highly successful
979 quantitative genetic research program on phenotypic plasticity therefore partly contradicts the
980 claims by Laland and colleagues that phenotypic plasticity is neglected in contemporary
981 evolutionary biology. On the contrary, phenotypic plasticity has been a major research theme
982 for decades, starting already in the 1980s (Via and Lande 1985).

983

984 Similarly, the argument that contemporary evolutionary biology neglects developmental bias
985 and naively assumes isotropic variation, i. e. lack of correlations between traits (Gould 2002;
986 Pigliucci 2019) is obviously incorrect (Fig. 5.1; see also section “5.3 *Gould’s mixed legacy:*
987 *strawman arguments and myths about the MS*” for more detailed critique). As a counter
988 argument to this claim, one can point to an extensive body of population and quantitative
989 genetic research exploring mutational pleiotropy (Lande 1980), correlational selection and its
990 consequences for genetic correlations (Cheverud 1984; Phillips and Arnold 1989; Sinervo and
991 Svensson 2002; Svensson et al. 2021) and the evolution of genetic covariance structures in
992 general (Steppan et al. 2002). The term developmental bias does also have some inherent
993 problems as development will nearly always be non-isotropic (Salazar-Ciudad 2021). In a
994 quantitative genetic context, developmental bias may not even be meaningful or informative,
995 as it adds very little to our current understanding (Svensson and Berger 2019). Insightful
996 quantitative geneticists pointed out several decades ago that genetic variances and covariances
997 estimated at the population level do not only reflect genetics alone, but also epigenetic and
998 developmental effects as well as revealing the history of past ecology and selection (Cheverud
999 1984). Interest in developmental bias has its intellectual roots in structural explanations of
1000 animal form, based on physical principles, development, and ideas about self-organization, as
1001 exemplified in the work by the pioneering work by D’Arcy Thompson book “*On growth and*
1002 *form*” (Thompson 2014), in the anti-selectionist views expressed by Goodwin in “*How the*
1003 *leopard changed its spots*” (Goodwin 2001), Lima-De-Faria in “*Evolution without selection*”
1004 (Lima-De-Faria 1990) and in Rupert Sheldrake’s ideas about “morphogenetic fields”
1005 (Sheldrake 1995). The ideas in these and similar books are popular outside evolutionary biology
1006 circles, but are based on misunderstandings and are sometimes grounded in metaphysical
1007 arguments. It is a common misunderstanding by these and other anti-selectionists that the
1008 physical principles behind morphological development contradict or can replace adaptive

1009 explanations of traits based on natural selection. Indeed, structuralists and other critics have
1010 failed to understand the crucial distinction between proximate explanations of phenotype
1011 formation and ultimate explanations for the evolution of adaptive complexity, as originally
1012 explained by (Mayr 1961). Mayr's key insight was that proximate and ultimate causes were
1013 conceptually different but complementary questions, rather than being mutually exclusive.
1014 Mayr's distinction firmly established evolutionary biology as a legitimate research field,
1015 independent of functional biology, developmental biology and molecular biology (Dickins and
1016 Barton 2013; Conley 2019; Svensson 2020). Some advocates of the EES have questioned the
1017 proximate-ultimate distinction as a valid explanatory framework in evolutionary biology
1018 (Laland et al. 2011), but this has understandably encountered strong resistance from those who
1019 insist that this is still a useful conceptualization (Dickins and Barton 2013; Conley 2019). In
1020 contemporary evolutionary biology, internal factors like developmental bias (or developmental
1021 constraints) serve as a dispositional property of populations alongside with other dispositional
1022 factors like evolvability (Love 2003). Dispositional factors set the outer limits of the space
1023 within which selection operates (Maynard Smith et al. 1985). Viewed this way, developmental
1024 bias can also interact with selection to influence evolutionary trajectories (Schluter 1996). But
1025 developmental bias or developmental constraints, whether arising from principles of physics,
1026 genetics or development, is not an evolutionary force that can change the heritable composition
1027 of populations by itself (Maynard Smith et al. 1985), unlike the consequence laws of selection,
1028 drift, mutation and recombination (Sober 1984). Developmental bias is sometimes put on an
1029 equal footing and portrayed as an alternative to evolution by natural selection in explaining
1030 adaptive radiations (Brakefield 2006), but this is misleading. Developmental bias is not an
1031 evolutionary process that operates in isolation but rather this dispositional factor *interacts* with
1032 natural selection (Maynard Smith et al. 1985). For instance, genetic covariances can bias the
1033 evolutionary trajectory of a populations and delay the time until it reaches an adaptive peak

1034 (Schluter 1996)(Fig. 5.1A,C). However, in this scenario it is selection that drives the
1035 evolutionary change, not developmental bias or genetic covariances, which are not evolutionary
1036 forces, following Sober's definition (Sober 1984)(Fig. 5.2).

1037

1038 The third factor highlighted by Laland and colleagues is niche construction (Laland et al. 2015).
1039 This is the phenomenon by which organisms modify their local selective environments, such as
1040 earthworms modifying the surrounding soil structure or the classic example of the beaver
1041 building its dam (Odling-Smee et al. 2003). Odling-Smee et al. (2003) argued that such niche
1042 construction is a neglected evolutionary process and claimed that it deserved status as an
1043 alternative evolutionary route to organismal adaptation, on equal footing and as important as
1044 natural selection. While few evolutionary biologists would deny that organisms modify their
1045 local environments and many times in an adaptive fashion, only a minority view such niche
1046 construction as an evolutionary process of equal importance as natural selection. Accordingly,
1047 the claim that niche construction is neglected has been questioned, and it has been pointed out
1048 that niche construction is neither neglected nor is it an evolutionary process (Dawkins 2004;
1049 Brodie 2005; Scott-Phillips et al. 2014; Gupta et al. 2017; Svensson 2018). Another frequent
1050 criticism is that niche construction is too broad a term that encompasses too many phenomena,
1051 including both adaptive modifications by organisms such as the beaver dam, but also non-
1052 adaptive effects, such as the creation of toxic waste products under crowded conditions
1053 (Dawkins 2004; Gupta et al. 2017; Svensson 2020). That organisms modify their selective
1054 environments and that they therefore are active evolutionary agents and not solely passive
1055 objects of selection is interesting, but this has also been recognized by many other evolutionary
1056 biologists outside the core niche construction literature (Levins and Lewontin 1985; Huey et al.
1057 2003; Brodie 2005; Edelaar et al. 2008; Edelaar and Bolnick 2012, 2019; Svensson 2018).
1058 Niche construction is probably best viewed as a healthy reminder about the ecological context

1059 of evolution (Dickins 2020) and that organisms partly shape the adaptive landscape and the
1060 selection pressures they experience (Huey et al. 2003; Tanaka et al. 2020) . Niche construction
1061 also reminds us that both source laws such as the ecological causes of selection (Endler and
1062 McLellan 1988; Wade and Kalisz 1990) and the consequence laws of population genetics
1063 (Sober 1984) are equally important parts of evolutionary research.

1064

1065 From an empirical viewpoint, niche construction could be incorporated as phenotypic
1066 intermediate traits in causal graphs (Fig. 5.3). Traits can influence fitness both directly by being
1067 targets of selection, but also indirectly, by influencing other traits (i. e. niche construction
1068 activities)(Otsuka 2019)(Fig. 5.3). Niche construction can therefore readily be incorporated in
1069 the contemporary theoretical evolutionary framework (Otsuka 2019). Powerful tools in the
1070 form of causal graphs, path analysis and structural equation modelling have been available for
1071 a long time, whereby information about both traits and selective environments can be
1072 incorporated in the same analysis (Kingsolver and Schemske 1991; Svensson et al. 2002;
1073 Morrissey 2014; Otsuka 2019). I suspect, however, that advocates of niche construction theory
1074 will not be entirely satisfied with these pragmatic empirical solutions to incorporate niche
1075 construction into evolutionary research.

1076

1077 INSERT FIG. 5.3 ABOUT HERE

1078

1079 Finally, the fourth factor highlighted by Laland and colleagues is non-genetic inheritance,
1080 sometimes called extra-genetic inheritance or extended inheritance (Laland et al. 2015;
1081 Bonduriansky and Day 2018). This includes a broad range of inheritance channels outside
1082 DNA, such as various forms of transgenerational epigenetic inheritance (e. g. methylation and

1083 histone modifications), social learning, maternal effects etc. (Bonduriansky and Day 2018).
1084 This rapidly developing field cannot be covered in full detail here (see Bonduriansky and Day
1085 (2018) for an excellent overview). Opinions about non-genetic inheritance range from it being
1086 viewed a major game changer that will require a substantial revision of evolutionary theory and
1087 an abandonment of the MS (Jablonka and Lamb 2005, 2007; Jablonka 2017) to those who
1088 consider it as an “add-on” that can easily be incorporated in the existing evolutionary
1089 framework as a proximate mechanism (Dickins and Rahman 2012), or viewed as an
1090 evolutionary outcome of selection (Loison 2018). It is important to emphasize that the analytical
1091 framework of population genetics can be readily modified to model and analyze selection on
1092 other heritable units than genetic alleles, including epialleles (Lu and Bourrat 2018). The
1093 quantitative genetic approach in the Price Equation can statistically capture effects of
1094 nongenetic inheritance on the resemblance between relatives (Frank 1995, 1997; Rice 2004)
1095 and can also be generalized to other inheritance systems (Luque 2017; Luque and Baravalle
1096 2021). One strength of quantitative genetics is that is agnostic with respect to the heritable basis
1097 of traits (i. e. DNA vs. other mechanisms of inheritance) as it ignores genetic details (Steppan
1098 et al. 2002; Queller 2017). But it is worth emphasizing that also the theoretical machinery of
1099 population genetics originated well before our understanding of the structure of DNA
1100 (Charlesworth et al. 2017), meaning that the population genetic analytical framework can be
1101 applied to non-genetic inheritance through other heritable channels, including epialleles (Lu
1102 and Bourrat 2018).

1103

1104 Somewhat paradoxically, therefore, the deliberate neglect of mechanisms and details in the
1105 quantitative genetics also makes it extremely powerful and flexible (Steppan et al. 2002; Queller
1106 2017). However, this point does not seem to have been fully appreciated by all advocates of the
1107 EES. Proponents of the EES frequently portray contemporary evolutionary biology as being

1108 caught in a narrow tradition of one- or two-locus models of population genetics where the
1109 environment is deliberately excluded (Laland et al. 2015). This narrow portrayal of
1110 contemporary evolutionary biology ignores the many post-Synthesis developments and the
1111 central role quantitative genetics theory and empirical tools have played in evolutionary
1112 research. Work on phenotypic plasticity (Lande 2009; Chevin et al. 2010; Chevin and Lande
1113 2011; Svensson et al. 2020) and the evolutionary consequences of variation in social
1114 environments and Indirect Genetic Effects (IGE:s)(Bailey et al. 2018) exemplify such post-
1115 Synthesis quantitative genetic research. Quantitative genetics theory and tools are therefore
1116 extremely flexible and versatile and can be fruitfully adjusted to study many of the problems
1117 that EES advocates have highlighted. Other examples of such research is the relationship
1118 between non-genetic and genetic inheritance (Greenspoon and Spencer 2018; Rajon and Charlat
1119 2019), how trait interactions and intermediate traits such as niche construction can affect fitness
1120 (Morrissey 2014; Otsuka 2019) and how feedbacks from social or non-social environments
1121 jointly shape evolutionary dynamics (Hendry 2016; Bailey et al. 2018; Svensson 2018).

1122

1123 **5.9 Where are we?**

1124 Given the frequent calls for an expansion or extension of evolutionary theory (Table 5.1) and
1125 recent strong claims that the current evolutionary framework is incomplete, it might be
1126 worthwhile to step back a little and ask the same question as Ernst Mayr asked on Darwin
1127 Centennial Celebration in 1959 (Mayr 1959): “*Where are we?*”. In this chapter, I have critically
1128 reviewed the various attempts aiming to replace or extend the current evolutionary framework
1129 and the MS, which is claimed to still hold a strong influence on contemporary evolutionary
1130 biology (Table 5.1). My overview suggests that some of the more radical critics have failed to
1131 convince the majority of biologists that evolutionary theory is in crisis (Dupre 2012) and that
1132 the field is therefore in need for major reform, even replacement (Shapiro 2011; Noble 2013,

1133 2015, 2017; Müller 2017). As I have argued here, these claims paint a misleading picture of the
1134 current state of evolutionary biology and have grossly overstated the historical legacy and
1135 lasting influence of the MS. These critics have failed to appreciate the substantial changes to
1136 evolutionary biology that took place long after the MS was finished, such as the incorporation
1137 of the Neutral Theory of Molecular Evolution (Kimura 1983; Kern and Hahn 2018; Jensen et
1138 al. 2019) and the growth and development of evolutionary quantitative genetics as a tool to
1139 study phenotypic evolution over both micro- and macroevolutionary time scales (Arnold 2014).
1140 The TWE project, in particular, has produced very little constructive contributions to the
1141 development of current evolutionary biology research. I anticipate that the TWE will continue
1142 to be a fringe movement outside mainstream evolutionary biology, for good reasons. TWE
1143 proponents have promoted a highly biased and mischaracterized view of the MS that is far from
1144 historical reality and does not paint a fair view of the richness and synthetic ambition of this
1145 historically important attempt to unify biology (Reif et al. 2000; Cain 2009; Lamm 2018). I
1146 fully agree with Cain (2009) who argues that we should stop talking about the MS as if it is
1147 equivalent to contemporary evolutionary biology, and instead view it as a historical period that
1148 is now firmly behind us.

1149

1150 Other critics like the EES proponents are more modest in their ambitions to push for conceptual
1151 change in evolutionary biology (Table 5.1)(Laland et al. 2015). The phenomena the EES
1152 proponents highlight are clearly worthy of study, although not necessarily the game changers
1153 they are sometimes portrayed to be. These phenomena are fully compatible and possible to
1154 study within the current flexible and pluralistic evolutionary research framework. I anticipate
1155 that evolutionary quantitative genetics will grow in popularity and importance and will become
1156 increasingly and flexibly applied to phenomena like nongenetic inheritance, niche construction,

1157 phenotypic plasticity and developmental bias, often in combination with other tools like causal
1158 graphs and path analysis (Otsuka 2019).

1159

1160 The diverse and somewhat split conceptual landscape of contemporary evolutionary biology
1161 today can be described as a series of partly overlapping research frameworks that coexist stably,
1162 namely neutralism, mutationism, selectionism and adaptationism (Fig. 5.4). These research
1163 currents and traditions are mainly focused on microevolutionary processes within and between
1164 populations, but have not yet fully entered the macroevolutionary domain (Fig. 5.4). However,
1165 neutralist and selectionist perspectives are not restricted to population and quantitative
1166 genetics, but can be applied also to higher-level units as species, e. g. in evolutionary
1167 community ecology (Vellend 2016) and in ideas about species selection and random drift in
1168 macroevolution (Rabosky and Mccune 2010; Chevin 2016)(Fig. 5.4). Similarly to
1169 macroevolution, “Evo Devo” and other structuralist perspectives and research traditions, are
1170 still somewhat isolated from these four traditional research currents (Fig. 5.4). Evo Devo should
1171 probably be located close to mutationism, since this field is focused on questions about the
1172 origin of novel heritable variation (Fig. 5.4).

1173

1174 INSERT FIG. 5.4 ABOUT HERE

1175

1176 Researchers within each of these different traditional domains have partly different interests,
1177 and emphasize different evolutionary processes, namely genetic drift, mutation and selection
1178 (Fig. 5.4). The difference between selectionism and adaptationism might not be immediately
1179 obvious, but briefly, selectionists are mainly interested in *evolution as a process* and are
1180 following the tradition by Lande and Arnold (1983), whereas adaptationists are more interested

1181 *in adaptation as a state*, as exemplified by the work by Gardner, Grafen in the “Formal
1182 Darwinism Project” (Grafen 1988, 2014; Gardner 2017). Adaptationists like Grafen and
1183 Gardner are more interested in organismal adaptive design and the products of evolution than
1184 in the evolutionary process behind such adaptations. This adaptationist current has been labelled
1185 “Neo-Paleyan biology”, by the philosopher Tim Lewens and it is especially strong in the UK
1186 (Lewens 2019a). “Neo-Paleyan” refers to the Christian William Paley and other natural
1187 theologians in the UK prior to Darwin-era. Paley was made famous by Richard Dawkins in his
1188 popular science book “*The Blind Watchmaker*” (Dawkins 1986). The difference between
1189 adaptationism, selectionism, neutralism and mutationism illustrate the diversity of co-existing
1190 analytical perspectives in contemporary evolutionary biology. This diversity within
1191 contemporary evolutionary biology research contradicts sweeping characterizations of
1192 evolutionary biology as only allowing a single Neo-Darwinian perspective (Shapiro 2011;
1193 Noble 2013, 2015, 2017). The future will tell if and how the EES and the TWE will become
1194 integrated with one or several of these existing research currents. It seems to me that proponents
1195 of the EES and TWE are mainly focused on adaptationism but have less to say about
1196 evolutionary processes, and neither have they identified any convincing novel evolutionary
1197 process. These critics of contemporary evolutionary biology might therefore have more in
1198 common with the Formal Darwinists than they are willing to admit themselves (Fig. 5.4).

1199

1200 **5.10 Looking forward**

1201 Evolutionary biology is currently experiencing an exciting period with increasing amounts of
1202 large-scale genomic and phenotypic data and increased integration between neontological and
1203 paleontological approaches (Losos et al. 2013). Much of the current dramatic transformation of
1204 evolutionary biology is data-driven, whereas the basic theoretical and conceptual framework
1205 was established several decades ago, before, during and after the MS. For instance, adaptive

1206 landscape theory remains as a central organizing concept in contemporary evolutionary biology
1207 (Arnold et al. 2001; Gavrillets 2004; Svensson and Calsbeek 2012a), even though its theoretical
1208 foundations were laid out almost a century ago (Wright 1932). Similarly, quantitative genetics
1209 gave us tools like the genetic-variance covariance matrix (**G**) that still holds a central place in
1210 evolutionary theory and seems to grow in importance and popularity (Steppan et al. 2002;
1211 Queller 2017). Some philosophers and critics of the MS and contemporary evolutionary biology
1212 have rather bluntly dismissed both adaptive landscapes and **G**-matrices as inadequate or even
1213 misleading (Pigliucci 2006, 2008; Kaplan 2008). However, these critics failed to deliver any
1214 constructive alternative analytical approaches to study evolution. Their anticipated coming
1215 demise of the adaptive landscape and **G**-matrix evolution have accordingly not been fulfilled,
1216 and they clearly underestimated the explanatory power of these tools and approaches (Svensson
1217 and Calsbeek 2012b). In contrast to what these philosophers anticipated, adaptive landscape
1218 theory and **G**-matrix evolution are likely to remain for many years to come, largely because of
1219 the power and flexibility of these tools to link phenotypic patterns with underlying evolutionary
1220 processes (Arnold 2005). We see increasing efforts to extend quantitative genetic and
1221 population genetic theory and methodology to incorporate nongenetic inheritance, niche
1222 construction, phenotypic plasticity and other interesting phenomena that have been highlighted
1223 by EES proponents (Laland et al. 2015). These phenomena are increasingly being incorporated
1224 in the current research framework as various “add-ons” and refinements of existing theory (Day
1225 and Bonduriansky 2011; Bonduriansky et al. 2012; Greenspoon and Spencer 2018;
1226 Bonduriansky and Day 2018; Rajon and Charlat 2019). Thus, so far we have seen little of the
1227 radical conceptual change of evolutionary biology that some critics have claimed would be
1228 necessary (Pigliucci 2007, 2009; Noble 2013, 2015, 2017; Müller 2017). In short: gradual
1229 change has taken place and still happens to evolutionary biology, and there is no sign of major

1230 overhaul or any forthcoming paradigm shift at the horizon, contrary to the claims by some
1231 critics like Noble and Shapiro.

1232

1233 **5.11 Conclusions**

1234 In our largely data-driven era, it is important to step back, critically reflect on the historical
1235 roots of our field and think about the bigger conceptual picture. Many of the conceptual tools
1236 and theories we use in evolutionary biology have their intellectual roots in the MS-period from
1237 the last century. This does not mean that we still live in the MS era, despite frequent claims by
1238 critics of contemporary evolutionary biology (Noble 2015, 2021; Müller 2017). However, it is
1239 probably uncontroversial to state that theory development has not kept up the same pace as
1240 empirical developments during recent decades. The recent discussions and calls for various
1241 extensions to the current evolutionary research framework are therefore welcome, although my
1242 overview here suggest that critics have failed to convince the evolutionary biology research
1243 community at large that their proposed additions cannot be handled by the current framework.
1244 The challenge from the EES is a valuable reminder that it is not only is the spread of adaptive
1245 variants by selection that is interesting and important (as already emphasized in the traditional
1246 evolutionary framework), but so is also the origin of heritable variation through developmental
1247 mechanisms and plasticity, as well as source laws (Table 5.1; Fig. 5.2)(Endler and McLellan
1248 1988).

1249

1250 INSERT TABLE 5.1 ABOUT HERE

1251

1252 A positive development of the recent discussions about the MS, EES and TWE is that the
1253 relationship between philosophy and evolutionary biology might become strengthened and re-
1254 vitalized. Clearly, philosophy of science has an important role to play in the conceptual and
1255 theoretical development of evolutionary biology. Early and foundational work by Elliott Sober
1256 clarified the relationship between source laws and consequence laws, and formalized concepts
1257 about evolutionary forces (Sober 1984), as did Dan McShea and Robert Brandon in more recent
1258 work (McShea and Brandon 2010). Likewise, philosophers like Samir Okasha and Peter
1259 Godfrey-Smith clarified issues about origin and consequences of multi-level selection (Okasha
1260 2005; Godfrey-Smith 2009). These philosophers clearly knew both evolutionary biology and
1261 the history of the field, which presumably contributed to the success of their work.

1262

1263 Not all philosophy of biology has played that positive role, however, especially as some
1264 philosophers have uncritically re-iterated myths about the MS that were initially propagated by
1265 Gould and others, but which have already been refuted. I have critically scrutinized some of
1266 these myths in this chapter. The long-lasting legacy of Gould and some of his more
1267 controversial claims has not always been positive. These claims contributed to establish
1268 misunderstandings about the current state of evolutionary biology, one being that the field is in
1269 deep crisis (Dupre 2012). To avoid repeating such mistakes, philosophers should communicate
1270 and collaborate with both historians of science and evolutionary biologists (and *vice versa* of
1271 course). Otherwise, philosophers risk spending effort on small and insignificant problems that
1272 are of little interest except to other philosophers. Some such problems might even be purely
1273 semantic, such as the odd idea that natural selection is not really an evolutionary process but
1274 just a statistical outcome of lower-level phenomena (Walsh et al. 2002; Otsuka 2016). Most
1275 evolutionary biologists probably consider such questions as rather esoteric and of little interest
1276 or relevance to the field. Attempts to re-introduce metaphysics in evolutionary biology (Dupré

1277 2021), for instance, are unlikely to impress the evolutionary biology research community.
1278 Those arguing for organismal agency as an evolutionary process (Walsh 2015) but leave out
1279 natural selection as the most obvious explanation for apparent purpose or design (Noble 2021)
1280 are also unlikely to convince the majority of evolutionary biologists. It is worth re-iterating that
1281 the only known evolutionary process that can systematically increase organismal adaptation
1282 across generations and lead to (apparent) purpose is natural selection (Gardner 2013, 2017),
1283 although some critics of contemporary evolutionary biologist insist that adaptation can be
1284 decoupled from natural selection (Pigliucci and Kaplan 2000; Kull 2014; Noble 2021).
1285 Accepting that natural selection is the only known evolutionary process that can systematically
1286 increase organismal fitness and adaptation across generations does not mean that we could not
1287 appreciate within-generation phenomena such as phenotypic plasticity, habitat selection and
1288 adaptive niche construction (Edelaar and Bolnick 2019). Crucially, however, such within-
1289 generation phenomena are not evolutionary processes, but evolutionary outcomes (Gardner
1290 2013; Loison 2018, 2021). Furthermore, accepting natural selection as the only known
1291 evolutionary process that can systematically increase organismal adaptation across generations
1292 does not mean that we need to uncritically adopt a pan-adaptationist position where one would
1293 claim that most organismal features are adaptive, or that we need embrace the Neo-Paleyan
1294 adaptationist biology tradition (Lewens 2019a). There is still plenty of room for non-adaptative
1295 and maladaptive evolutionary processes like mutation, drift and recombination (Lynch 2007;
1296 Svensson and Berger 2019). The important point, however, is that these other evolutionary
1297 processes cannot systematically increase organismal fitness and adaptations across generations,
1298 like natural selection, although they can of course *decrease* fitness (Lynch et al. 1995; Svensson
1299 and Berger 2019). Increased understanding of evolution requires *both* bold new ideas and a
1300 deep and nuanced understanding of the rich history of the MS and how contemporary
1301 evolutionary biology has advanced over the past century.

1302

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1317 **Table 5.1.** A non-exhaustive list in chronological order, of different attempts and initiatives to extend, expand or replace the Modern Synthesis, pointing
 1318 to new phenomena, discoveries and various “add ons”.

1319

1320	Name (-s)	Term	Phenomena	References
1321	C.H. Waddington	Extended synthesis	Epigenetics	Waddington (1957) (Wilkins 2008)
1322			Genetic assimilation	
1323			Gene interactions	
1324				
1325	S.J. Gould	Expanded evolutionary theory	Hierarchical theory	(Gould 1980)
1326			Species selection	(Gould 1982)
1327			Nonadaptation	(Gould and Vrba 1982)
1328			Exaptation	(Gould 2002)
1329				
1330	J. A. Endler	A newer synthesis	Source laws	(Endler and McLellan 1988)
1331	T. McLellan		Ecology of natural selection	
1332			Origin of variation	
1333				
1334				
1335	M. Pigliucci	Extended Evolutionary Synthesis	Evolvability	(Pigliucci 2007)
1336	G. Muller		Phenotypic plasticity	(Pigliucci 2009)
1337			Epigenetic inheritance	(Pigliucci and Müller 2010b)
1338			Complexity theory	
1339			High-dimensional adaptive landscapes	
1340				
1341				
1342				
1343				

1344	E. Koonin	“A postmodern state, not so far a postmodern Synthesis”	Horizontal Gene Transfer (HGT)	(Koonin 2009)
1345			Gene duplications	
1346			Gene loss	
1347			Neutral molecular evolution	
1348				
1349				
1350	E. Danchin	Inclusive Evolutionary Synthesis <i>or</i> Expanded Evolutionary Synthesis	Nongenetic inheritance	(Jablonka and Lamb 2005)
1351	E. Jablonka		Cultural evolution	(Jablonka and Lamb 2007)
1352	M. Lamb		Information theory	(Danchin 2013)
1353				
1354	D. Noble	The Third Way of Evolution (TWE) <i>or</i> Integrated Synthesis	Evo-devo theory	(Noble 2013)
1355	J.A. Shapiro		Plasticity & Accomodation	(Noble 2015)
1356			Epigenetic inheritance	(Noble 2017)
1357			Multilevel selection	Shapiro (2011)
1358			Genomic evolution	
1359			Niche construction	
1360			Replicator theory	
1361		Evolvability		
1362				
1363	K.N. Laland	Extended Evolutionary Synthesis (EES)	Developmental bias	(Laland et al. 2014)
1364	T. Uller		Plasticity	(Laland et al. 2015)
1365	M.W. Feldman		Non-genetic inheritance	
1366	K. Sterelny		Niche construction	
1367	G.B. Muller			
1368	A. Moczek			
1369	E. Jablonka			
1370	J. Odling-Smee			
1371				
1372				
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1374				
1375				

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1899 **Legends to figures**

1900

1901 **Fig. 5.1. A.** When two phenotypic traits (here denoted Z_1 and Z_2) are uncorrelated with each
1902 other (as shown by circles) and are evolving on an adaptive landscape with one peak (denoted
1903 “optimum”) they will evolve in a straight direction towards the peak, and the evolutionary
1904 response to selection ($\Delta\mathbf{z}$) will be aligned with the selection gradient (β). **B.** A hypothetical genetic
1905 variance-covariance matrix (**G**: grey) and a mutational variance-covariance matrix (**M**: black)
1906 of four different traits ($Z_1 - Z_4$). Shown are the standing genetic and mutational variances of
1907 traits (diagonal elements) and the standing genetic and mutational covariances (off-diagonal
1908 elements). This hypothetical variance-covariance matrix is *isotropic*, meaning that traits vary
1909 independently of each other and genetic variation is equally abundant in all directions (hence
1910 all elements are circular, and traits are uncorrelated with each other). Some evolutionary
1911 biologists have argued that this isotropy assumption has been the default assumption in the MS
1912 and in evolutionary genetics (Gould 2002; Pigliucci 2019). **C, D.** In contrast to the isotropy
1913 assumption, phenotypic traits in natural populations are often genetically and phenotypically
1914 correlated with each other, shown here as variances and covariances as being elliptically
1915 shaped, rather than circular. In **C**, we see how such genetic covariance between the same two
1916 traits as in **A** (Z_1 and Z_2) result in a biased and curved evolutionary trajectory that delays the
1917 time needed to evolve to the fitness optimum. **D** shows a more realistic genetic variance-
1918 covariance matrix and a mutational matrix, where traits can be either positively (e. g. Z_1 and Z_2)
1919 , negatively (e. g. Z_1 and Z_4) or uncorrelated with each other (e. g. Z_2 and Z_3). Note that **G** and
1920 **M** are aligned in **D**, consistent with theory and empirical evidence suggesting that they are both
1921 shaped by the adaptive surface and correlational selection (Jones et al. 2014; Houle et al. 2017;
1922 Svensson and Berger 2019; Svensson et al. 2021).

1923

1924 **Fig. 5.2.** Source laws, consequence laws, evolutionary outcomes and feedbacks. Source laws
1925 refer to the factors (intrinsic or extrinsic) behind the consequence laws (e. g. natural selection).
1926 Consequence laws have been a major focus of population genetics and evolutionary biology
1927 (Sober 1984; Endler and McLellan 1988). Extrinsic source laws are the abiotic (e. g. climate)
1928 and biotic factors (e. g. predation or competition) that generate selection pressures and are thus
1929 agents or causes of selection (Wade and Kalisz 1990). Source laws could also be phenotypic
1930 traits themselves that have ecological consequences (i. e. intrinsic factors). For instance, body
1931 size has cascading ecological consequences in terms of population size, starvation endurance
1932 and thermoregulation, and could therefore lead to novel selection pressures. Evolutionary
1933 outcomes are the products of the consequence laws, and such outcomes are adaptations and
1934 various phenotypic traits that are shaped by selection, drift and the other consequence laws. A
1935 special class of evolutionary outcomes are the four factors highlighted by the EES:
1936 developmental bias, plasticity, niche construction and non-genetic inheritance (highlighted with
1937 “*” within another box with dashed line). These evolutionary outcomes (but also other
1938 phenotypic traits) can feed back and generate novel selection pressures on organisms. That is,
1939 an evolutionary outcome of selection can thus subsequently also become a source law, through
1940 feedbacks and reciprocal causation between selection and its products (Svensson 2018). For
1941 instance, the beaver dam is an evolutionary outcome or “extended phenotype” that changes the
1942 selective environment and influencing selection back on the beaver (Odling-Smee et al. 2003).
1943

1944 **Fig. 5.3.** Causal model and path diagram of the relationship between a standard phenotypic trait
1945 (Z_p : parental generation; Z_o : offspring generation), a niche construction phenotype (N_p : parent
1946 generation; N_o : offspring generation), fitness (W) and genetic inheritance (X : parental
1947 generation genotype; X' : offspring generation genotype). Direction of arrows denote causal
1948 relationships. The phenotypic trait influences parental fitness directly (β_Z : direct selection

1949 gradient), but also indirectly, through the niche construction trait that subsequently influences
1950 fitness (i. e. the pathway $\beta_{Z,N} * \beta_N$). In this example, the niche construction trait is not under
1951 direct genetic inheritance, although indirectly, through the genetic basis of Z_p . However, note
1952 that there is a pathway of non-genetic inheritance of the niche construction trait, since it
1953 influences the offspring environment in the next generation (“ecological inheritance”), e. g. the
1954 case of the beaver dam. Modified from Otsuka (2019).

1955

1956 **Fig. 5.4.** The split conceptual landscape of contemporary evolutionary biology.
1957 Microevolutionary research can be classified in to four different currents or analytical traditions
1958 shown in spheres: adaptationism, selectionism, neutralism and mutationism. These different
1959 currents are broad categorizations of different analytical frameworks and they are not
1960 completely separated, as indicated by the overlap between them. The three founders of
1961 mathematical population genetics (R. A. Fisher, J. B. S. Haldane and Sewall Wright) and their
1962 approximate positions are indicated. Fisher emphasized more strongly selection in large
1963 panmictic populations and adaptation of organisms, hence he overlap adaptationism and
1964 selectionism. Sewall Wright emphasized the interaction between neutral processes such as
1965 genetic drift and selection in subdivided population, hence he overlaps between selectionism
1966 and neutralism. Haldane was interested in the role of mutation in the evolutionary process and
1967 hence he can partly be put in the mutationist sphere. The “Formal Darwinism” school and “Neo-
1968 Paleyan” biologists like Grafen and Gardner is mainly a school found in the UK with a strong
1969 emphasis on adaptation as a state, rather than the evolution as a process. In contrast, the
1970 selectionist school is stronger in North America, and is more focused on the evolutionary
1971 process and is represented as the “Lande & Arnold”-school of measuring selection in natural
1972 populations. Neutralism is represented by Lynch and Kimura, whereas mutationism is
1973 represented by Nei. Finally, the two main challengers of the current evolutionary framework

1974 (the EES and TWE) are probably closer to the adaptationism current than any of the other
1975 schools. Macroevolution, paleontology and “Evo Devo” are still largely separated research
1976 domains from these microevolutionary currents, although their relative positions in the
1977 conceptual landscape are indicated.

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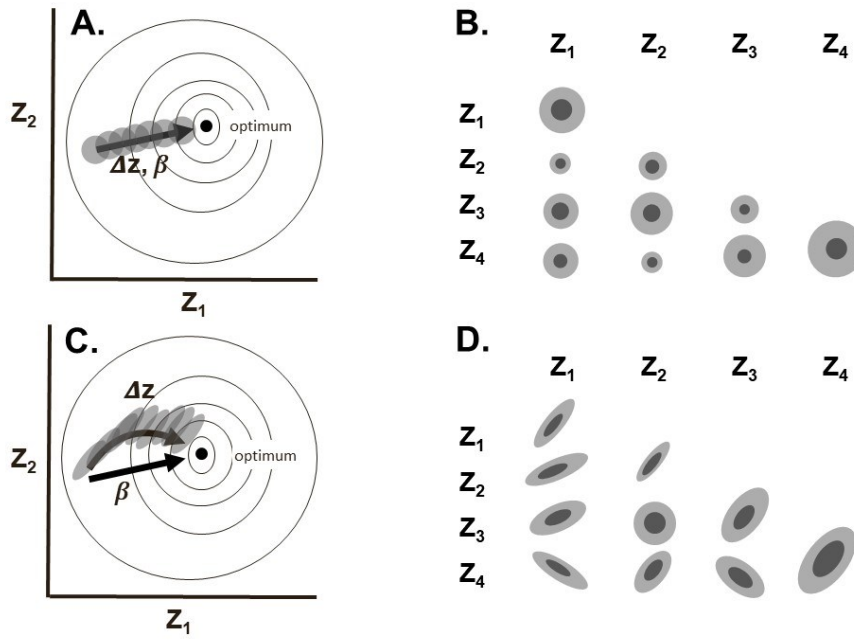
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Fig. 5.1



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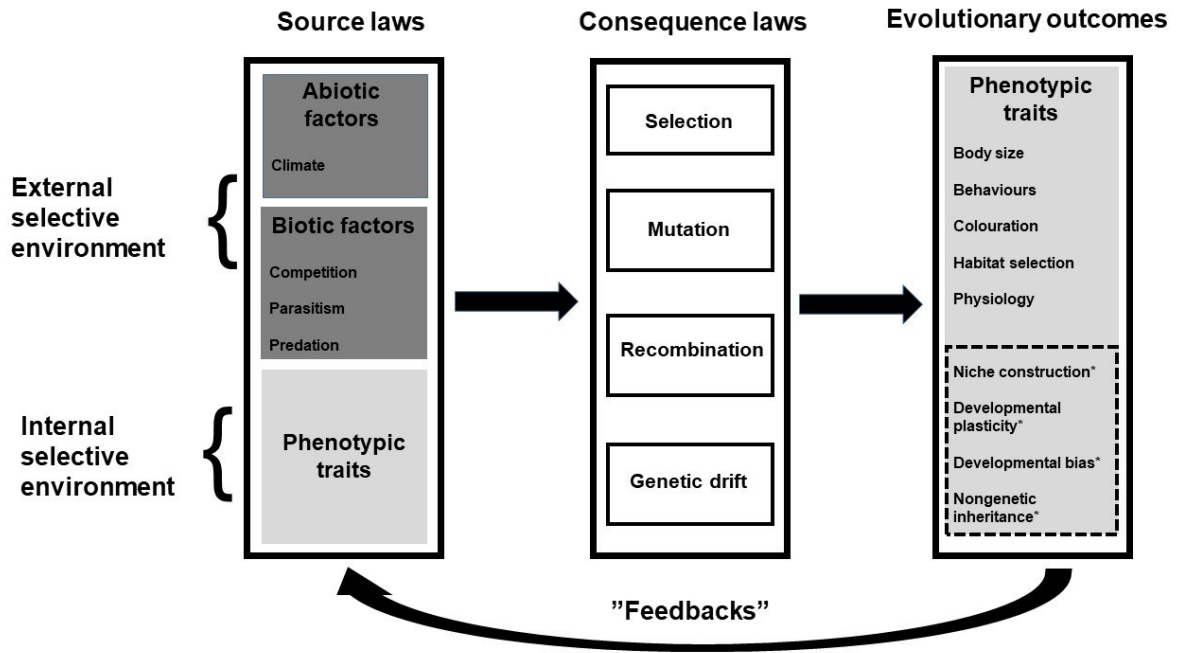
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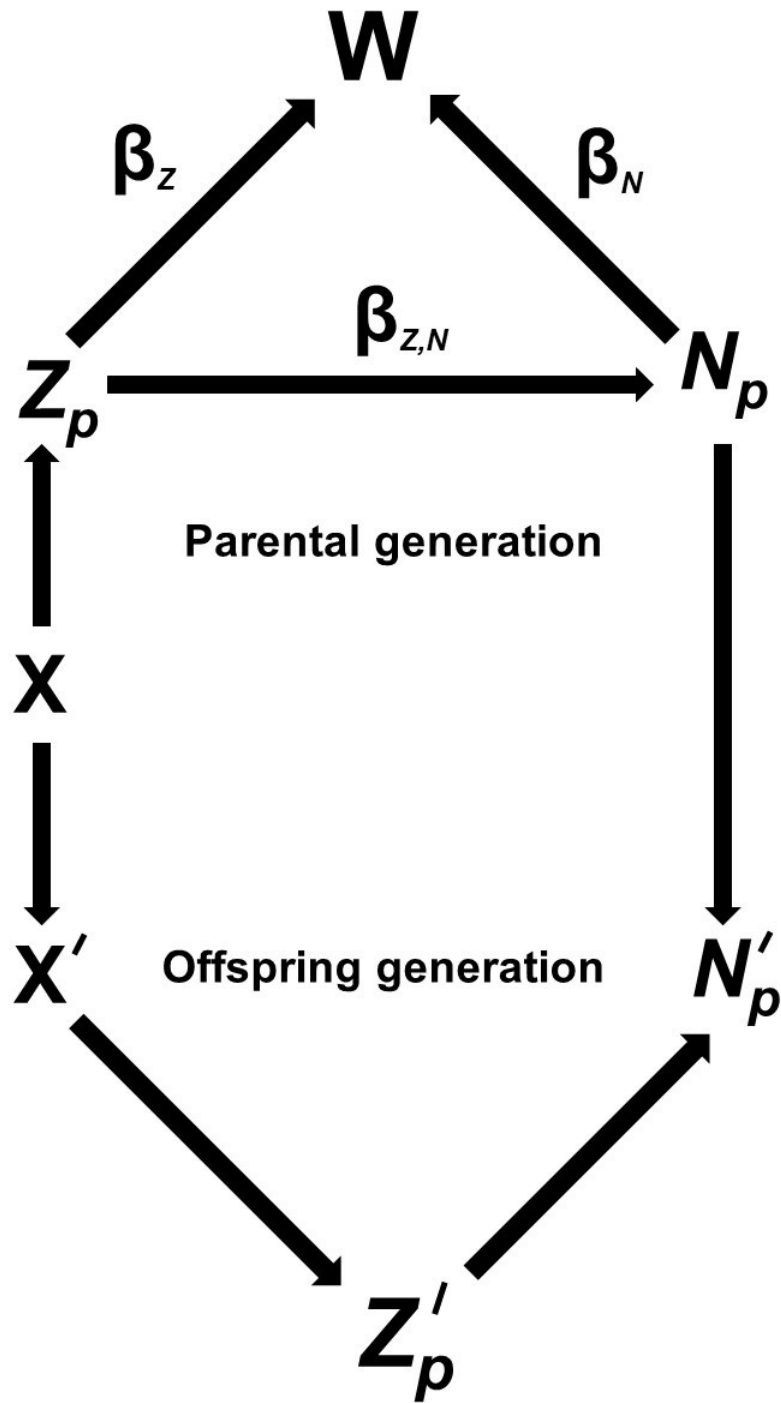
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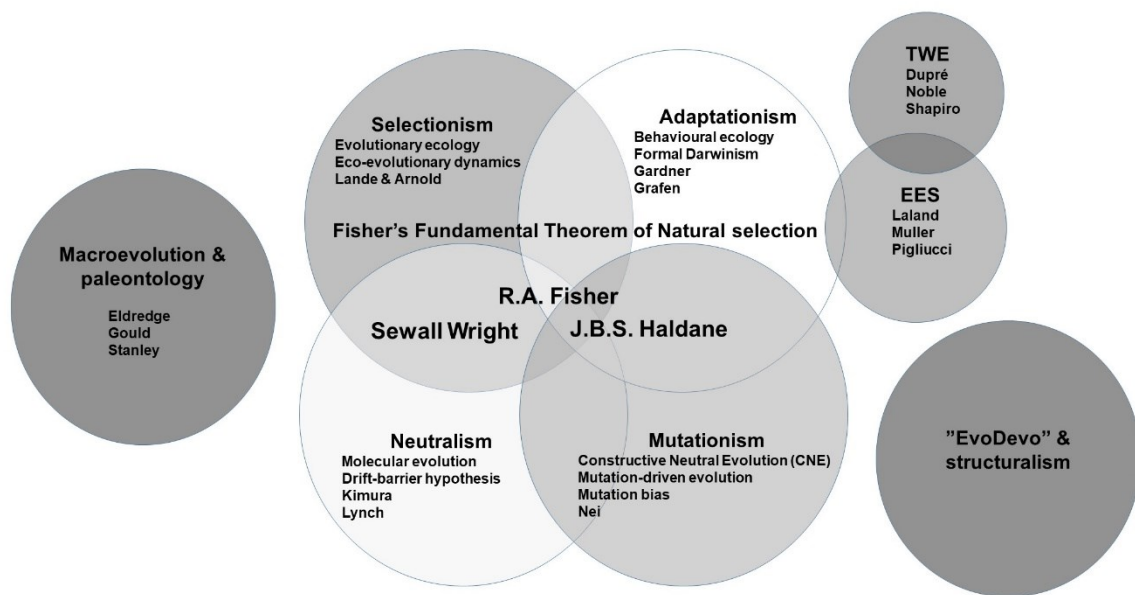
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