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

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Abstract

The last decades have seen frequent calls for a more extended evolutionary synthesis (EES) that will supposedly overcome the limitations in the current evolutionary framework with its intellectual roots in the Modern Synthesis (MS). Some radical critics even want to entirely abandon the current evolutionary framework, claiming that the MS (often erroneously labelled "Neo-Darwinism") is outdated, and will soon be replaced by an entirely new framework, such as the Third Way of Evolution (TWE). Such criticisms are not new, but have repeatedly re-surfaced every decade since the formation of the MS, and they were particularly articulated by developmental biologist Conrad Waddington and paleontologist Stephen Jay Gould. Waddington, Gould and later critics argued that the MS was too narrowly focused on genes and natural selection, and that it ignored developmental processes, epigenetics, paleontology and macroevolutionary phenomena. More recent critics partly recycle these old arguments and argue that non-genetic inheritance, niche construction, phenotypic plasticity and developmental bias necessitate major revision of evolutionary theory. Here I discuss these supposed challenges, taking a historical perspective and tracing the arguments by critics back to Waddington and Gould. I dissect the old claims by Waddington, Gould and more recent critics that the MS was excessively gene centric and became increasingly "hardened" over time and narrowly focused on natural selection. Recent critics have consciously or unconsciously exaggerated the long-lasting influence of the MS on contemporary evolutionary biology and have underestimated many post-Synthesis developments, particularly Neutral Theory, evolutionary quantitative genetics and the power and generality of the Price Equation. Critics have also painted a biased picture of the MS as a more monolithic research tradition than it ever was, and have downplayed the pluralistic nature of contemporary evolutionary biology, particularly the long-lasting influence of Sewall Wright with his emphasis on gene interactions and stochasticity. I argue that some of the criticisms of the MS and contemporary evolutionary biology are primarily meta-scientific, revealing the underlying identity politics of critics when pushing their alternative research agendas. It is still unclear what their proposed alternative research frameworks would entail and why the existing theoretical framework is insufficient. Finally, I outline and visualize the conceptually split landscape of contemporary evolutionary biology, with four different stably coexisting analytical frameworks: adaptationism, mutationism, neutralism and selectionism. I suggest that the field can accommodate the challenges raised by critics, although structuralism ("Evo Devo") and macroevolution remain to be conceptually integrated within mainstream evolutionary theory.

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

5.1 Introduction

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

It is important to emphasize that the architects of the MS aimed to be *synthetic*. Accordingly the results of their efforts has sometimes been termed *"the synthetic theory of evolution"* (Reif et al. 2000). Specifically, Mayr and others repeatedly emphasized that the MS incorporated insights from several different fields, including genetics, systematics, paleontology and natural history (Haffer 2007). This synthetic goal became evident in the famous debate between Mayr and Haldane about the utility and limitations of so-called "bean bag genetics" (Mayr 1959; Haldane 1964; Crow 2008; Dronamraju 2011). Mayr strongly criticized the mathematical population geneticists Fisher, Wright and Haldane for ignoring gene interactions in their theoretical models (Mayr 1959). Mayr instead emphasized what he felt was the more important contributions by himself, Dobzhansky and other empiricists and naturalists in the formation of the MS (Dronamraju 2011). In this famous debate with Haldane, Mayr clearly revealed that he erroneously thought that the mathematical population geneticists were not aware of gene interaction (epistasis), in spite of epistasis being central in Sewall Wright's Shifting Balance Theory of evolution (Provine 1986; Wade and Goodnight 1998; Steffes 2007). In fact, Wright's interest in genetic interactions, rather than simply additive effects of genes, is an example of early system-level thinking that could be viewed as a predecessor to systems biology today. Moreover, the fact that Wright, one of the founding fathers of modern population genetics, was interested in such interactions and system-level phenomena of organisms establishes a forgotten link between the organicist school (Peterson 2017) and early population genetics (Steffes 2007). This forgotten historical link contradicts Mayr's claim and sweeping characterization of Wright as a simple "bean bag geneticist" who was not aware of epistasis (Mayr 1959).

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

5.2 What the Modern Synthesis was (and was not)

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

Nevertheless, the conflation of the MS and Neo-Darwinism is still commonly made by some critics of contemporary evolutionary biology. For instance, the physiologist Dennis Noble (Noble 2013) claims that *"The 'Modern Synthesis' (Neo-Darwinism) is a mid-20th century gene-centric view of evolution based on random mutations accumulating to produce gradual change through natural selection"*. Noble further claims that *"all the central assumptions of the Modern Synthesis (often also called Neo-Darwinism) have been disproved"* (Noble 2013). Noble further argues that an extended *"Integrative Synthesis"* – an entirely *"new conceptual framework"* - will *"replace"* the MS (Noble 2015). Similar confident claims have been put forward by the molecular microbiologist James Shapiro (Shapiro 2011). Shapiro and Noble launched *"The Third Way of Evolution"* (TWE) initiative a few years ago (https://www.thethirdwayofevolution.com/) that claims to provide a middle path (*"Third Way"*) between creationism and Neo-Darwinism. The enthusiasm for their project has – mildly put – not been overwhelming among evolutionary biologists (Charlesworth et al. 2017). To date, there are few leading evolutionary biologists who have openly embraced the TWE. TWE has generated more enthusiasm among a vocal minority of philosophers, such as Dennis Walsh and John Dupré, the latter who in 2012 characterized evolution as *"a theory in crisis"* (Dupre 2012). The sheer confidence by which some philosophers and critics of contemporary evolutionary biology predict that contemporary evolutionary biology will soon be replaced by an entirely new framework (details of which are very unclear) is remarkable, particularly as the majority of evolutionary biologists are not even aware of the existence of TWE and carry on their research as usual. Those who doubt this should join any of the regular evolutionary biology congresses organized by the societies ESEB (*European Society for Evolution*) and SSE (*Society for the Study of Evolution*) where little of this forthcoming paradigm shift announced by Noble, Shapiro, Walsh and Dupré has been visible during the past decade. The impression one gets from the efforts by these biologists and philosophers is that they are trying to launch a culture war against contemporary evolutionary biology, by erroneously claiming that not much has happened since the MS and by repeatedly equating the latter with Neo-Darwinism. The MS is portrayed by these critics as a dogmatic monolith, and some of their criticisms are more meta-scientific than scientific. The poor historical scholarship among some of these critics and their inaccurate and biased characterizations of the MS suggests to me that the TWE is largely an identity political project rather than presenting any serious challenge to the current theoretical framework.

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

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

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

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

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

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

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

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

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

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

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

INSERT FIGURE 5.1 ABOUT HERE

Gould further claimed that the MS hardened, meaning that it became increasingly narrow and exclusively focused on natural selection and that other evolutionary processes and stochasticity thus were downplayed over time (Gould 1983, 2002). This so-called "hardening of the Modern Synthesis"-argument is a popular and widespread myth that has frequently been re-iterated by several later authors (Pigliucci and Müller 2010a; Huneman 2019). In fact, this so-called hardening argument has seldom been questioned, but it appears to be accepted at face value among some biologists and philosophers who otherwise seem to maintain a critical distance from Gould (Huneman 2019). Here, I question Gould's claim that the MS hardened, in line with previous authors who have also critically dissected his highly biased historical narratives (Orzack 1981; Sepkoski 2012; Svensson 2020). I argue that the hardening myth of the MS was a deliberate exaggeration promoted by Gould to justify his own scientific project, aiming for an expansion and radical revision of evolutionary theory (Gould 1980). To secure his place in history, Gould pushed the hardening myth and other strawman arguments to paint a highly biased view of the MS as excessively adaptationist and dogmatic, while brushing under the carpet facts that ran counter to his views (Orzack 1981; Sepkoski 2012; Svensson 2020). An uncomfortable fact that does not fit Gould's narrative include the tension between "Wrightian" and "Fisherian" population genetics that was present from the beginning of the MS, and which has shaped evolutionary biology ever since, contributing to its pluralism (Orzack 1981; Provine 1986; Coyne et al. 1997; Wade and Goodnight 1998; Goodnight and Wade 2000; Svensson 2018; Huneman 2019). Clearly, the Wrightian tradition with its emphasis on stochasticity, genetic drift and gene flow has been a key part of the MS (Provine 1986), especially in North America (Huneman 2019), where Gould spent his entire academic career. The existence of the Wrightian tradition therefore partly refutes Gould's claim about the excessive adaptationism of the MS (Orzack 1981). Moreover, the examples Gould used as evidence for his claim that the MS hardened from its early formative years in the 1940s to later decades (Gould 2002) do not hold up, upon critical inspection.

Gould re-read both original and updated versions of Dobzhansky's and Mayr's early synthesis-books (Dobzhansky 1937; Mayr 1942). He argued that there was a much stronger emphasis on selection in explaining patterns of genetic variation, polymorphisms and clines in nature in the later editions (Gould 2002). This stronger emphasis on selection was interpreted by Gould as an increasingly dogmatic attitude of these two major architects of the MS (Gould 1983, 2002). An alternative, but more plausible interpretation is that both Dobzhansky and Mayr changed their views in the face of new empirical evidence, rather than changing views for ideological reasons or because they became more narrow minded. Dobzhansky, for instance, studied the dynamics of chromosomal inversion polymorphisms in natural populations of *Drosophila* (Dobzhansky 1970). The reason for studying these chromosomal inversion polymorphisms was that Dobzhansky collaborated with Sewall Wright and was interested in studying genetic drift and testing aspects of the Shifting Balance Theory (Provine 1986). Dobzhansky therefore picked (putatively) neutral markers like chromosomal inversions with the aim to study genetic drift. Dobzhansky and many others should be excused in that they could not see how this seemingly arbitrary chromosomal character could be important to fitness or affect an organism's phenotype in the pre-DNA era. Dobzhansky thus started with a neutral expectation, but soon – to his surprise and disappointment (!) – he found out that these chromosomal inversion polymorphisms fluctuated predictably with season and changing temperatures (Dobzhansky 1970; Provine 1986). These fluctuations implied that these chromosomal inversion polymorphisms were not entirely selectively neutral and did not change in frequencies solely by genetic drift, as he had hoped (Provine 1986). Thus, Dobzhansky's empirical insight that selection was operating on these chromosomal inversion polymorphisms can hardly be characterized as a "hardening" or reflecting more dogmatic attitude where selection became overemphasized. Instead it was rather the opposite: Dobzhansky clearly and at first *underestimated* the importance of selection. To the extent Dobzhansky updated his view and increasingly recognized the importance of natural selection, it was a hardwon empirical insight, in striking contrast to Gould who never did any field work himself on extant organisms in natural populations. Later work – on both *Drosophila* and many other organisms – has revealed that chromosomal inversion polymorphisms are often targets of strong natural and sexual selection with pronounced effects on organismal fitness (Noor et al. 2001; Kirkpatrick and Barton 2006; Kupper et al. 2016; Hooper and Price 2017; Faria et al. 2019). Thus, the late Dobzhansky was correct in upgrading the importance of selection, whereas the early Dobzhansky clearly overestimated the importance of genetic drift.

Gould (2002) further argued that another sign of the hardening of the synthesis was how Mayr changed his view of polymorphisms from being described as selectively neutral in his early book *Systematics and the Origin of Species* (Mayr 1942) to being mainly interpreted in adaptive terms in his later book *Animal Species and Evolution* (Mayr 1963). In Mayr's 1963-book such polymorphisms (e. g. colour polymorphisms) were characterized in adaptive terms and as being the target of selection. However, Mayr's changed opinion hardly represents any hardening view, as claimed by Gould, but rather his increasing insights about the importance of selection that the early Mayr clearly underestimated in 1942. Later empirical work on some of the classical colour polymorphisms that were considered neutral characters by Wright and contemporaries have revealed that they are more often than not targets of selection (Schemske and Bierzychudek 2001; Turelli et al. 2001). More generally, recent research on colour polymorphisms have revealed that such polymorphisms are often targets of natural or sexual selection and upon closer inspection are seldom neutral (Wellenreuther et al. 2014; Svensson 2017). The fact that both Gould and the early Mayr in 1942 assumed *a priori* that seemingly meaningless polymorphisms would be selectively neutral might reflect a lack of understanding of population genetic theory by both of them. In all populations of limited size, genetic drift will operate to a greater or lesser extent. The maintenance of polymorphisms and genetic variation therefore requires the operation of some selective mechanism, like overdominant selection or negative frequency-dependent selection (Svensson 2017). Thus, it is the maintenance of variation (i. e. polymorphisms) that requires a selective explanation, not the lack of variation (Svensson 2017). In contrast, lack of variation and the attainment of monomorphism is the default expectation in all populations of limited size, an important aspect of population genetic theory that neither Gould nor the early Mayr seemed to have fully understood.

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

Summing up this section: Gould's characterization of the hardening of the MS can be turned entirely upside down: it was a healthy shift away from the unfounded assumption that most characters were strictly neutral and without any importance to fitness to a more ecologically realistic view that even small phenotypic differences could be important. The changing perspectives of Dobzhansky, Mayr and Lack reflect a healthy updating of their views in the face of new empirical evidence more so than any dogmatic stance. In fact, one can equally well criticize the MS from the opposite perspective: the architects of the MS did not pay enough attention to ecology and might have underestimated the importance of studying natural selection directly in the field (Antonovics 1987; Endler and McLellan 1988). Antonovics (1987) pointed out that the architects of the MS typically did not bother to even measure natural selection in natural populations. Similarly, Endler and McLellan (1988) emphasized that few of the leading figures behind the MS worked in natural populations of non-model organisms. It was not until several decades after the MS that evolutionary biologists started to quantify natural and sexual selection in the field to fill in this missing gap (Lande and Arnold 1983; Endler 1986). Moreover, Mayr clearly underestimated the importance of natural selection and the importance of different environments on islands and mainlands in his now largely discredited theory of effect speciation through genetic revolutions (Barton and Charlesworth 1984; Haffer 2007). The founder effect speciation model – which Mayr was very proud of – is a strictly neutral model with little or no role for natural selection. The founder effect speciaton model clearly illustrates that Mayr often rather *underestimated* the power of natural selection, *contra* the claims by Gould (1983) and others who in Mayr see a strong and dogmatic adaptationist. The myth that the MS hardened and that it only recognized natural selection is a historically questionable view that Gould promoted, but it continues to be re-iterated by some critics who argue that we need radical conceptual change of contemporary evolutionary biology (Laland et al. 2014, 2015; Müller 2017).

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

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

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

In light of the many failures during the 20th century to prove a central role for adaptive Lamarckian inheritance in evolution, time now seems overdue to bury both Lamarckism and Neo-Lamarckism (as well as Neo-Darwinism). Jablonka, Noble and others calling for an extension or expansion of evolutionary biology have certainly not helped their own cause by flirting with Lamarckism and directed variation. The (provocative) rhetoric by some critics of contemporary evolutionary biology and their insistence on pushing the Lamarckian angle is presumably the main reason why EES and TWE are still viewed with skepticism in large parts of the evolutionary biology community (Welch 2016; Charlesworth et al. 2017; Futuyma 2017; Svensson 2018). Noble's claim that conscious processes and other clearly adaptive features in organisms evolved because they serve a purpose (Noble 2021) deliberately avoids referring to natural selection, the only scientifically known evolutionary process that can systematically increase organismal adaptation across generations and which can explain adaptive organismal design (Gardner 2013, 2017). Ironically, Noble's obsession with purpose puts him conceptually somewhat close to the ultra-adaptationists and Darwinists Grafen and Gardner in the so-called “Formal Darwinism” project (Grafen 2014; Lewens 2019a). The main but crucial difference is that Noble denies a central role of natural selection in explaining (apparent) design and purpose of organisms. Noble seems to search for some other explanation than natural selection of organismal adaptation and it is unclear if it is even a scientific one (Noble 2021). Similarly, some critics of the MS and contemporary evolutionary more or less openly admit that they aim to re-introduce metaphysical principles in biology by highlighting organismal “agency” (Walsh 2015; Buskell and Currie 2017; Dupré 2021), which the majority of evolutionary biologists, including the present author, firmly reject, unless such perceived agency is described as an outcome of natural selection. There are, however, many conceptual and philosophical problems associated with introducing agency in to evolutionary thinking (Okasha 2018).

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

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

Upon critical scrutiny, the superficial arguments above do not provide any evidence at all against adaptive evolution being driven by natural selection. First, theory and empirical evidence have clearly shown that adaptive phenotypic plasticity and phenomena such as genetic assimilation can and are often targets of natural or sexual selection, show heritable variation and can evolve by the standard process of selection (Lande 2009; Chevin et al. 2010; Svensson et al. 2020). Second, the plasticity-first hypothesis and the idea of genetic assimilation of originally plastic changes is (as indicated by the term *"genetic"* before assimilation) is not an alternative to evolution by natural selection, but rather points to the possibility that *the initial adaptive change can be achieved by a plastic adjustment of the organism followed by natural selection on genetic variation that stabilizes the trait* (Price et al. 2003; Lande 2009). West-Eberhard (2003) herself has been quite clear that her idea about plasticity-led evolution was not mean to be an alternative to evolution by natural selection and genetic evolution, but rather an *initiator* of subsequent evolutionary change, where phenotypes played a major role ("leaders") to the genetic change that followed ("genes as followers"). Specifically, she explicitly defines evolution by stating (P. 32):

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

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

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

INSERT FIG. 5.2 ABOUT HERE

Finally, another class of extrascientific motives behind recent criticisms against the MS and contemporary evolutionary biology could be boredom. All evolutionary biologists are (luckily) not interested in the same things, and not everyone appreciates population and quantitative genetics. It is most likely one of the motivations behind Pigliucci's push for the EES, as exemplified in a critical dissection of Brian Charlesworth's views, who had expressed the opinion that most of the problems in evolutionary genetics had been solved: *"Well, perhaps, but some of us are not ready for retirement just yet"* (sic! P. 2744; (Pigliucci 2007). The author of the present chapter has, in some discussions with leading proponents of the EES, encountered similar attitudes, for instance that *"reaction norms and population genetics are boring"*. Similar views were expressed by the evolutionary developmental biologist Sean Carroll in his book "*Endless Forms Most Beautiful: The New Science of Evo Devo*", where he declared that the development of form in butterflies and zebras was a more inspiring story to tell about evolution than changes in gene frequencies (Carroll 2006). Population geneticist Michael Lynch was, however, rather blunt in his dismissal of this criticism of population genetics and stated: "*Evolutionary biology is not a story-telling exercise, and the goal of population genetics is not to be inspiring, but to be explanatory."* (Lynch 2007). He further developed his criticism of Carroll and evolutionary developmental biology and the frequent claim that this new field would supposedly overturn evolutionary biology by stating that *"No principle of population genetics has been overturned by any observation in molecular, cellular, or developmental biology, nor has any novel mechanism of evolution been revealed by such fields."* (Lynch 2007).

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

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

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

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

In a similar vein, the late paleontologist Stephen Jay Gould rather decisively and aggressively distanced himself from the MS and Neo-Darwinism (Sepkoski 2012). Interestingly, Gould started his career as a fairly mainstream evolutionary biologist, building upon Ernst Mayr's rather orthodox theory of allopatric speciation (Mayr 1942). Gould and his collaborator Niles Eldredge incorporated this allopatric theory in to their own theory of "punctuated equilibrium" (Eldredge and Gould 1972; Sepkoski 2012). After successfully establishing himself as a major player in the new and growing field of paleobiology and mathematical models in macroevolution, Gould devoted a large part of his late career to popular science columns in the journal *Natural History* (Sepkoski 2012). Gould also developed his criticisms of the MS in many articles (Gould and Lewontin 1979; Gould 1980; Gould and Vrba 1982) as well as in his late magnum opus *The Structure of Evolutionary Theory* (Gould 2002), published in 2002, the same year as his death. In his critique of the MS and Neo-Darwinism, Gould made several strong claims that received strong criticisms from other evolutionary biologists (Orzack 1981). Some of Gould's critics argued that he used extensive strawman arguments against the MS (see section *"5.3 Gould's mixed legacy: strawman arguments and* *myths about the MS"* to justify his own scientific agenda aiming for a major paradigm shift in evolutionary biology (Sepkoski 2012; Svensson 2020). While few would question Gould's scientific contributions to paleobiology, his popular outreach and his admirable fight against creationism, a common (and still valid) criticism of his work is that he strongly exaggerated the rigidity of the MS (Sepkoski 2012). For instance, Gould's biased characterization of the MS as excessively deterministic and adaptationist and his claim that it ignored random factors and stochasticity (Gould 1980, 1981) received strong criticism by Orzack, Charlesoworth, Lande and Slatkin who also pointed to the influence of Sewall Wright on the development of the MS (Orzack 1981; Charlesworth et al. 1982).

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

5.6 Recent challenges to the MS

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

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

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

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

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

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

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

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

For several reasons, I think Müller's viewpoint is mistaken and a dead end. First, complexity is by no means easily defined, let alone explained. In fact, some complexity at the molecular level might have little if anything to do with adaptive processes such as natural selection, but can arise through neutral evolution alone. For instance, the theory of Constructive Neutral Evolution (CNE) postulates that the accumulation of neutral mutation could build up considerable complexity at the molecular level without any need for directional natural selection (Stoltzfus 1999; Muñoz-Gómez et al. 2021). There is some recent experimental evidence for CNE from a study of long-term evolution of vertebrate steroid receptors that have increased in complexity simply through neutral evolution (Hochberg et al. 2020). Such neutral evolution acted in a ratchet-like fashion, leading to a state where current complexity is maintained by purifying selection (Hochberg et al. 2020). I strongly suspect that Müller and other EES-proponents with their strong focus on organismal phenomena are not very interested in such neutral evolution at the molecular level and its consequences. Müller (2017) and others seem to implicitly assume that complexity *per se* always needs some non-neutral explanation. That is not necessarily the case. Null models of evolution can successfully explain the evolutionary increase in both complexity and diversity (McShea and Brandon 2010). In contrast, natural selection is sofar the only known evolutionary force that can systematically increase fitness across generations and that can convincingly explain the evolution of (apparent) purpose and adaptive features of organisms (Gardner 2017). Null models like the Neutral Theory do not seem to be held in high regard in the EES community and it is hardly mentioned in their writings (see e. g. (Pigliucci 2007, 2009; Laland et al. 2015)). This striking neglect in the EES community contrasts with much of mainstream contemporary evolutionary biology and the population genetics community where Neutral Theory holds a central position (Kern and Hahn 2018; Jensen et al. 2019).

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

The architects of the MS correctly dismissed several alternative but now firmly discredited evolutionary processes, such as the inheritance of acquired characters (i. e. Lamarckism), orthogenesis (i. e. the innate tendency of organisms to evolve in certain directions towards a “goal”), saltationism (evolution by large mutations) and the idea that mutations were the main drivers of evolution rather than natural selection (“mutationism”)(Gould 2002). The idea that mutations were the main drivers of evolution was championed by early Mendelians like Hugo de Vries, Gregory Bateson and Thomas Hunt Morgan. These geneticists focused on mutations of large visible effects, such as eye colour and wing mutants in *Drosophila*, often with abnormal phenotypic effects (Gould 2002) but of questionable ecological importance for adaptive evolution in natural populations. These laboratory-based geneticists did apparently not understand or appreciate the importance of natural selection, as they studied organisms in strict laboratory settings and they had little direct research experience from natural populations. It was only when Dobzhansky entered the laboratory of Thomas Hunt Morgan that this experimental genetic laboratory tradition in the US was merged with studies of natural populations that he was trained in from his early educational years in Russia and the Soviet Union (Gould 2002). As a result, Dobzhansky had a deep understanding of both genetics and natural history and he realized that although mutations were an important part of the evolutionary process, in themselves they could not achieve much without the aid of natural selection (Dobzhansky 1970; Provine 1986). Both Dobzhansky and other contemporary evolutionary biologists like Haldane understood that mutations were the ultimate source of novel genetic variation and they both wrote about the mutational process in the years immediately preceeding the MS (Dobzhansky 1933; Haldane 1933). But these evolutionary biologists concluded – correctly as it later turned out – that mutations alone were unlikely to explain long-term directional evolution at the phenotypic level, in contrast to the claims of the early mutationists.

Given the strong experimental and empirical evidence against directed mutations (Lenski and Mittler 1993; Futuyma 2017; Svensson and Berger 2019) and the failure of the early mutationists to appreciate the power of natural selection, it is interesting that some contemporary evolutionary biologists insist in pushing for a revival of mutationism or mutation-driven evolution (Stoltzfus 2006; Nei 2013; Stoltzfus and Cable 2014). Mutationism was closely connected to the theory of orthogenesis – the idea that internal factors were primarily responsible for evolutionary change and that the external environmental factors (*aka* natural selection) played only a minor role (Gould 2002; Stoltzfus 2006; Stoltzfus and Cable 2014). According to the early Mendelians and mutationists, large-effect visible mutations were important, and the role of natural selection was mainly to sort out the unfit variants. The mutationists contrasted such a negative role of selection with the mutational process that they felt was the real driver of evolutionary change. For good reasons, this view was firmly rejected by the development of quantative genetics theory and empirical insights from plant and animal breeding (Fisher 1918). The early mutationists clearly overestimated the importance of mutations and underappreciated standing genetic variation and the creative role of natural selection, and mainly saw selection as a "sieve" that could only sort out the unfit (Beatty 2016, 2019). However, the sieve-analogy underestimates the importance of standing genetic variation for adaptation (Barrett and Schluter 2008) and modern views of natural selection emphasize its multivariate nature, and its more creative role in shaping the genetic and phenotypic correlation structure of organisms (Sinervo and Svensson 2002; Svensson et al. 2021).

Those who try re-instate mutationism and mutation as the main driver of evolutionary change are therefore likely to face strong resistance, for good historical and scientific reasons. No serious evolutionary biologist today would question that mutations is the ultimate source of novel genetic variation, and in neutral evolution (where selection is per definition is absent), such neutral mutation pressure can lead to directional evolutionary trends (Sueoka 1988; Svensson and Berger 2019). Moreover, mutation-driven neutral evolution can potentially result in increased molecular complexity, as emphasized in Constructive Neutral Evolution (CNE), as discussed in the previous section (Stoltzfus 1999; Hochberg et al. 2020; Muñoz-Gómez et al. 2021). There is clearly a potential role for CNE at the molecular level. However, it is important to underscore that even if the initial buildup of such molecular complexity would be entirely neutral and mutation-driven and with no role for natural selection, as soon as these molecular complexes are affecting aspects of the organismal phenotype and thereby likely its fitness (e. g. cell physiology and other aspects of cellular performance), they would immediately and (per definition) become targets of purifying selection (Hochberg et al. 2020; Brunet et al. 2021).

Likewise, few evolutionary biologists deny that genetic effective population size (N_e) determines the efficacy of natural selection, which becomes weaker and less powerful when N_e is low, i. e. approaching neutrality (Lynch 2007, 2010; Jensen et al. 2019; Svensson and Berger 2019). It is uncontroversial to say that the likelihood of mutation bias leading to a fixation bias increases with the inverse of N_e, as selection then becomes weaker relative to genetic drift (Lynch 2007). These insights from standard population genetic theory are far away from the original claims by the early mutationists. Mutation bias is, however, unlikely to play an independent role in adaptive evolution, unless it is aided by genetic drift and/or selection (Lynch 2007; Svensson and Berger 2019). Recently, Gomez et al. (2020) claimed, based on two-locus population genetic models, that mutation bias can play an important role in adaptive evolution provided that differences in mutation rates between loci are large relative to differences in selection coefficients and assuming that beneficial mutation rates were similar in magnitude to deleterious mutation rates. However, these asexual models in Gomez et al. (2020) assumed strong linkage disequilibrium and seem mainly suited to describe the evolutionary dynamics of microbes rather than outbred sexual organisms without such strong linkage disequilibrium. These and several other models of how mutation bias can result in mutation-biased adaptation are mainly one or two-locus population genetic models (Yampolsky and Stoltzfus 2001; Lynch 2007; Stoltzfus and Yampolsky 2009; Svensson and Berger 2019). To my knowledge there is not yet any quantitative genetic model of how mutation bias can influence adaptive evolution of continuous traits. These population genetic models with their underlying assumptions of relatively simple genetic architectures have shown that mutation bias can indeed result in mutation-biased adaptation under some rather strict conditions, such as in the presence of sign epistasis, fitness neutrality, small effective population size and/or when beneficial mutation rates are large relative to selection coefficients ((Yampolsky and Stoltzfus 2001; Lynch 2007; Stoltzfus and Yampolsky 2009; Svensson and Berger 2019). The assumptions of relatively high beneficial mutation rates relative to selection coefficients are entirely consistent with Haldane's and Fisher's early "opposing pressure" argument of why mutation rates need to be very high to overcome selection coefficients, i. e. mutation-selection balance (Fisher 1930; Haldane 1927; 1932; 1933). Thus, while mutation bias can theoretically indeed result in mutation-biased adaptation, it is mainly an empirical question how often and to what extent these rather stringent conditions for this to happen are fulfilled in natural populations, particularly for outbred sexual organisms and in populations with low mutation rates. When mutation-biased adaptation does occur, mutation bias does not operate in isolation from natural selection, although it leaves a molecular signature of unique mutational events that evolutionary biologists traditionally have conceptualized as historical contingencies, and which are easily accommodated within the contemporary evolutionary theoretical framework (Svensson and Berger 2019).

Most evolutionary biologists today view mutations as a stochastic evolutionary process with no directionality or purpose, with no foresight or any tendency for mutations to systematically increase organismal fitness across generations (Svensson and Berger 2019). This view has strong empirical support (Svensson and Berger 2019), although the representatives from the fringe movement TWE (James Shapiro and Dennis Noble) question this and claim a role for adaptive directionality, purpose and functionality of novel mutations (Shapiro 2011; Noble 2013, 2017). These authors claim that various aspects of genome organization and gene expression in organisms are clearly functional and that these functional aspects of the genome contradicts the traditional view of mutations as random (with respect to current utility and future adaptation; (Svensson and Berger 2019)). For instance, Noble (2017) argues that the existence of functionally significant targeted somatic hypermutations during the lifetime of individual organisms contradict the standard assumption in evolutionary theory that mutations are random with respect to fitness. Noble points to somatic mutations in the vertebrate immune system as an example of such adaptive design, where mutations seem to have purpose, indicating adaptive foresight (Noble 2017). However, both Noble and Shapiro conflate somatic mutations and changes within the lifetimes of individual organisms with germline mutations and evolutionary change across generations (Gardner 2013). Noble and Shapiro also overlook fundamental differences between somatic mutations and germline mutations, such as that the former are higher (Moore et al. 2021), and are also targets of selection due to their strong link to lifespan and other life-history characteristics (Cagan et al. 2021). The existence of highly sophisticated molecular repair mechanisms, patterns of adaptive gene expression, methylation and other epigenetic mechanisms that Noble and Shapiro highlight is no evidence at all against natural selection operating on random mutational input (Gardner 2013). Instead, and much more likely, natural selection has operated on and shaped these molecular mechanisms and other aspects of genomic architecture (Sinervo and Svensson 2002; Svensson et al. 2021), including both somatic and germline mutation rates (Lynch 2010; Cagan et al. 2021; Moore et al. 2021). Molecular features at the genomic level are therefore shaped by selection, drift, mutation and recombination (Lynch 2007; Gardner 2013; Svensson et al. 2021), and should be viewed as evolutionary outcomes rather than as evolutionary processes in their own right (Loison 2018). Again, we are reminded that a common mistake made by some critics of contemporary evolutionary biology – not only Noble and Shapiro – is to conflate evolutionary processes with the products of evolution (Lynch 2007).

In contemporary evolutionary biology, the stochastic nature of mutations is often conceptualized as historical contingency and the role of chance (Losos et al. 1998; Blount et al. 2018; Svensson and Berger 2019). Thus, adaptive evolution reflects the balance between the deterministic role of natural selection that systematically increases organismal adaptation across generations (“survival of the fittest”), and the nature and arrival order of novel mutations that selection can act upon, the latter often called “arrival of the fittest” (Wagner 2015). All else being equal, if selection operates on a character governed my multiple loci, those loci with the highest mutation rates are more likely to produce novel adaptive mutations that can be “seen” by selection and which subsequently will increase in frequency and become fixed through successive selective sweeps (Xie et al. 2019). A case in point is the adaptive evolution of pelvic reduction in stickleback fish (*Gasterosteus aculeatus*) after colonization and adaptation to freshwater habitats in postglacial lakes (Xie et al. 2019). Molecular studies have revealed that such pelvic reductions are achieved by recurrent deletions which are produced by *Pitx1* enhancer sequences that increase double-strand breaks (Xie et al. 2019). As a result, elevated mutation rates at this locus contribute to make genomic evolution highly parallel and more predictable, through repeated and adaptive phenotypic changes. However, the spread and fixation of these novel mutations are still driven by natural selection in the new freshwater habitat (Xie et al. 2019). This example illustrates that elevated mutation rates alone are not sufficient to drive adaptive and parallel evolution, but natural selection plays a crucial role in the spread and fixation of novel variants. More generally, the role of mutational stochasticity, including the arrival order of novel mutations has been recognized in contemporary evolutionary biology, both theoretically and empirically, e. g. in mutation-order speciation (Schluter 2009) and in research on historical contingencies (Blount et al. 2018). Those arguing for mutation bias as an entirely novel evolutionary principle (Yampolsky and Stoltzfus 2001; Stoltzfus and Yampolsky 2009; Gomez et al. 2020) might therefore have somewhat exaggerated their cause. It is currently difficult to see that mutation-driven evolution or mutation bias (Nei 2013; Stoltzfus and Cable 2014) would require a major revision of the current already quite pluralistic theoretical framework of evolutionary biology.

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

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

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

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

Similarly, the argument that contemporary evolutionary biology neglects developmental bias and naively assumes isotropic variation, i. e. lack of correlations between traits (Gould 2002; Pigliucci 2019) is obviously incorrect (Fig. 5.1; see also section *"5.3 Gould's mixed legacy: strawman arguments and myths about the MS"* for more detailed critique). As a counter argument to this claim, one can point to an extensive body of population and quantitative genetic research exploring mutational pleiotropy (Lande 1980), correlational selection and its consequences for genetic correlations (Cheverud 1984; Phillips and Arnold 1989; Sinervo and Svensson 2002; Svensson et al. 2021) and the evolution of genetic covariance structures in general (Steppan et al. 2002). The term developmental bias does also have some inherent problems as development will nearly always be non-isotropic (Salazar-Ciudad 2021). In a quantitative genetic context, developmental bias may not even be meaningful or informative, as it adds very little to our current understanding (Svensson and Berger 2019). Insightsful quantitative geneticists pointed out several decades ago that genetic variances and covariances estimated at the population level do not only reflect genetics alone, but also epigenetic and developmental effects as well as revealing the history of past ecology and selection (Cheverud 1984). Interest in developmental bias has its intellectual roots in structural explanations of animal form, based on physical principles, development, and ideas about self-organization, as exemplified in the work by the pioneering work by D'Arcy Thompson book *"On growth and form"* (Thompson 2014), in the anti-selectionist views expressed by Goodwin in *"How the leopard changed its spots"* (Goodwin 2001), Lima-De-Faria in *"Evolution without selection"* (Lima-De-Faria 1990) and in Rupert Sheldrake's ideas about "morphogenetic fields" (Sheldrake 1995). The ideas in these and similar books are popular outside evolutionary biology circles, but are based on misunderstandings and are sometimes grounded in metaphysical arguments. It is a common misunderstanding by these and other anti-selectionists that the physical principles behind morphological development contradict or can replace adaptive explanations of traits based on natural selection. Indeed, structuralists and other critics have failed to understand the crucial distinction between proximate explanations of phenotype formation and ultimate explanations for the evolution of adaptive complexity, as originally explained by (Mayr 1961). Mayr's key insight was that proximate and ultimate causes were conceptually different but complementary questions, rather than being mutually exclusive. Mayr's distinction firmly established evolutionary biology as a legitimate research field, independent of functional biology, developmental biology and molecular biology (Dickins and Barton 2013; Conley 2019; Svensson 2020). Some advocates of the EES have questioned the proximate-ultimate distinction as a valid explanatory framework in evolutionary biology (Laland et al. 2011), but this has understandably encountered strong resistance from those who insist that this is still a useful conceptualization (Dickins and Barton 2013; Conley 2019). In contemporary evolutionary biology, internal factors like developmental bias (or developmental constraints) serve as a dispositional property of populations alongside with other dispositional factors like evolvability (Love 2003). Dispositional factors set the outer limits of the space within which selection operates (Maynard Smith et al. 1985). Viewed this way, developmental bias can also interact with selection to influence evolutionary trajectories (Schluter 1996). But developmental bias or developmental constraints, whether arising from principles of physics, genetics or development, is not an evolutionary force that can change the heritable composition of populations by itself (Maynard Smith et al. 1985), unlike the consequence laws of selection, drift, mutation and recombination (Sober 1984). Developmental bias is sometimes put on an equal footing and portrayed as an alternative to evolution by natural selection in explaining adaptive radiations (Brakefield 2006), but this is misleading. Developmental bias is not an evolutionary process that operates in isolation but rather this dispositional factor *interacts* with natural selection (Maynard Smith et al. 1985). For instance, genetic covariances can bias the evolutionary trajectory of a populations and delay the time until it reaches an adaptive peak

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

The third factor highlighted by Laland and colleagues is niche construction (Laland et al. 2015). This is the phenomenon by which organisms modify their local selective environments, such as earthworms modifying the surrounding soil structure or the classic example of the beaver building its dam (Odling-Smee et al. 2003). Odling-Smee et al. (2003) argued that such niche construction is a neglected evolutionary process and claimed that it deserved status as an alternative evolutionary route to organismal adaptation, on equal footing and as important as natural selection. While few evolutionary biologists would deny that organisms modify their local environments and many times in an adaptive fashion, only a minority view such niche construction as an evolutionary process of equal importance as natural selection. Accordingly, the claim that niche construction is neglected has been questioned, and it has been pointed out that niche construction is neither neglected nor is it an evolutionary process (Dawkins 2004; Brodie 2005; Scott-Phillips et al. 2014; Gupta et al. 2017; Svensson 2018). Another frequent criticism is that niche construction is too broad a term that encompasses too many phenomena, including both adaptive modifications by organisms such as the beaver dam, but also non-adaptive effects, such as the creation of toxic waste products under crowded conditions (Dawkins 2004; Gupta et al. 2017; Svensson 2020). That organisms modify their selective environments and that they therefore are active evolutionary agents and not solely passive objects of selection is interesting, but this has also been recognized by many other evolutionary biologists outside the core niche construction literature (Levins and Lewontin 1985; Huey et al. 2003; Brodie 2005; Edelaar et al. 2008; Edelaar and Bolnick 2012, 2019; Svensson 2018). Niche construction is probably best viewed as a healthy reminder about the ecological context of evolution (Dickins 2020) and that organisms partly shape the adaptive landscape and the selection pressures they experience (Huey et al. 2003; Tanaka et al. 2020) . Niche construction also reminds us that both source laws such as the ecological causes of selection (Endler and McLellan 1988; Wade and Kalisz 1990) and the consequence laws of population genetics (Sober 1984) are equally important parts of evolutionary research.

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

INSERT FIG. 5.3 ABOUT HERE

Finally, the fourth factor highlighted by Laland and colleagues is non-genetic inheritance, sometimes called extra-genetic inheritance or extended inheritance (Laland et al. 2015; Bonduriansky and Day 2018). This includes a broad range of inheritance channels outside DNA, such as various forms of transgenerational epigenetic inheritance (e. g. methylation and histone modifications), social learning, maternal effects etc. (Bonduriansky and Day 2018). This rapidly developing field cannot be covered in full detail here (see Bonduriansky and Day (2018) for an excellent overview). Opinions about non-genetic inheritance range from it being viewed a major game changer that will require a substantial revision of evolutionary theory and an abandonment of the MS (Jablonka and Lamb 2005, 2007; Jablonka 2017) to those who consider it as an "add-on" that can easily be incorporated in the existing evolutionary framework as a proximate mechanism (Dickins and Rahman 2012), or viewed as an evolutionary outcome of selection (Loison 2018). It is important to emphasize that the analytical framework of population genetics can be readily modified to model and analyze selection on other heritable units than genetic alleles, including epialleles (Lu and Bourrat 2018). The quantitative genetic approach in the Price Equation can statistically capture effects of nongenetic inheritance on the resemblance between relatives (Frank 1995, 1997; Rice 2004) and can also be generalized to other inheritance systems (Luque 2017; Luque and Baravalle 2021). One strength of quantitative genetics is that is agnostic with respect to the heritable basis of traits (i. e. DNA vs. other mechanisms of inheritance) as it ignores genetic details (Steppan et al. 2002; Queller 2017). But it is worth emphasizing that also the theoretical machinery of population genetics originated well before our understanding of the structure of DNA (Charlesworth et al. 2017), meaning that the population genetic analytical framework can be applied to non-genetic inheritance through other heritable channels, including epialleles (Lu and Bourrat 2018).

Somewhat paradoxically, therefore, the deliberate neglect of mechanisms and details in the quantitative genetics also makes it extremely powerful and flexible (Steppan et al. 2002; Queller 2017). However, this point does not seem to have been fully appreciated by all advocates of the EES. Proponents of the EES frequently portray contemporary evolutionary biology as being caught in a narrow tradition of one- or two-locus models of population genetics where the environment is deliberately excluded (Laland et al. 2015). This narrow portrayal of contemporary evolutionary biology ignores the many post-Synthesis developments and the central role quantitative genetics theory and empirical tools have played in evolutionary research. Work on phenotypic plasticity (Lande 2009; Chevin et al. 2010; Chevin and Lande 2011; Svensson et al. 2020) and the evolutionary consequences of variation in social environments and Indirect Genetic Effects (IGE:s)(Bailey et al. 2018) exemplify such post-Synthesis quantitative genetic research. Quantitative genetics theory and tools are therefore extremely flexible and versatile and can be fruitfully adjusted to study many of the problems that EES advocates have highlighted. Other examples of such research is the relationship between non-genetic and genetic inheritance (Greenspoon and Spencer 2018; Rajon and Charlat 2019), how trait interactions and intermediate traits such as niche construction can affect fitness (Morrissey 2014; Otsuka 2019) and how feedbacks from social or non-social environments jointly shape evolutionary dynamics (Hendry 2016; Bailey et al. 2018; Svensson 2018).

5.9 Where are we?

Given the frequent calls for an expansion or extension of evolutionary theory (Table 5.1) and recent strong claims that the current evolutionary framework is incomplete, it might be worthwhile to step back a little and ask the same question as Ernst Mayr asked on Darwin Centenial Celebration in 1959 (Mayr 1959): *“Where are we?”*. In this chapter, I have critically reviewed the various attempts aiming to replace or extend the current evolutionary framework and the MS, which is claimed to still hold a strong influence on contemporary evolutionary biology (Table 5.1). My overview suggests that some of the more radical critics have failed to convince the majority of biologists that evolutionary theory is in crisis (Dupre 2012) and that the field is therefore is in need for major reform, even replacement (Shapiro 2011; Noble 2013, 2015, 2017; Müller 2017). As I have argued here, these claims paint a misleading picture of the current state of evolutionary biology and have grossly overstated the historical legacy and lasting influence of the MS. These critics have failed to appreciate the substantial changes to evolutionary biology that took place long after the MS was finished, such as the incorporation of the Neutral Theory of Molecular Evolution (Kimura 1983; Kern and Hahn 2018; Jensen et al. 2019) and the growth and development of evolutionary quantitative genetics as a tool to study phenotypic evolution over both micro- and macroevolutionary time scales (Arnold 2014). The TWE project, in particular, has produced very little constructive contributions to the development of current evolutionary biology research. I anticipate that the TWE will continue to be a fringe movement outside mainstream evolutionary biology, for good reasons. TWE proponents have promoted a highly biased and mischaracterized view of the MS that is far from historical reality and does not paint a fair view of the richness and synthetic ambition of this historically important attempt to unify biology (Reif et al. 2000; Cain 2009; Lamm 2018). I fully agree with Cain (2009) who argues that we should stop talking about the MS as if it is equivalent to contemporary evolutionary biology, and instead view it as a historical periodthat is now firmly behind us.

INSERT TABLE 5.1 ABOUT HERE

Other critics like the EES proponents are more modest in their ambitions to push for conceptual change in evolutionary biology (Table 5.1)(Laland et al. 2015). The phenomena the EES proponents highlight are clearly worthy of study, although not necessarily the game changers they are sometimes portrayed to be. These phenomena are fully compatible and possible to study within the current flexible and pluralistic evolutionary research framework. I anticipate that evolutionary quantitative genetics will grow in popularity and importance and will become increasingly and flexibly applied to phenomena like nongenetic inheritance, niche construction, phenotypic plasticity and developmental bias, often in combination with other tools like causal graphs and path analysis (Otsuka 2019).

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

INSERT FIG. 5.4 ABOUT HERE

Researchers within each of these different traditional domains have partly different interests, and emphasize different evolutionary processes, namely genetic drift, mutation and selection (Fig. 5.4). The difference between selectionism and adaptationism might not be immediately obvious, but briefly, selectionists are mainly interested in *evolution as a process* and are following the tradition by Lande and Arnold (1983), whereas adaptationists are more interested *in adaptation as a state*, as exemplified by the work by Gardner, Grafen in the "Formal Darwinism Project" (Grafen 1988, 2014; Gardner 2017). Adaptationists like Grafen and Gardner are more interested in organismal adaptive design and the products of evolution than in the evolutionary process behind such adaptations. This adaptationist current has been labelled "Neo-Paleyan biology", by the philosopher Tim Lewens and it is especially strong in the UK (Lewens 2019a). "Neo-Paleyan" refers to the Christian William Paley and other natural theologians in the UK prior to Darwin-era. Paley was made famous by Richard Dawkins in his popular science book *"The Blind Watchmaker"* (Dawkins 1986). The difference between adaptationism, selectionism, neutralism and mutationism illustrate the diversity of co-existing analytical perspectives in contemporary evolutionary biology. This diversity within contemporary evolutionary biology research contradicts sweeping characterizations of evolutionary biology as only allowing a single Neo-Darwinian perspective (Shapiro 2011; Noble 2013, 2015, 2017). The future will tell if and how the EES and the TWE will become integrated with one or several of these existing research currents. It seems to me that proponents of the EES and TWE are mainly focused on adaptationism but have less to say about evolutionary processes, and neither have they identified any convincing novel evolutionary process. These critics of contemporary evolutionary biology might therefore have more in common with the Formal Darwinists than they are willing to admit themselves (Fig. 5.4).

5.10 Looking forward

Evolutionary biology is currently experiencing an exciting period with increasing amounts of large-scale genomic and phenotypic data and increased integration between neontological and paleontological approaches (Losos et al. 2013). Much of the current dramatic transformation of evolutionary biology is data-driven, whereas the basic theoretical and conceptual framework was established several decades ago, before, during and after the MS. For instance, adaptive landscape theory remains as a central organizing concept in contemporary evolutionary biology (Arnold et al. 2001; Gavrilets 2004; Svensson and Calsbeek 2012a), even though its theoretical foundations were laid out almost a century ago (Wright 1932). Similarly, quantitative genetics gave us tools like the genetic-variance covariance matrix (**G**) that still holds a central place in evolutionary theory and seems to grow in importance and popularity (Steppan et al. 2002; Queller 2017). Some philosophers and critics of the MS and contemporary evolutionary biology have rather bluntly dismissed both adaptive landscapes and **G**-matrices as inadequate or even misleading (Pigliucci 2006, 2008; Kaplan 2008). However, these critics failed to deliver any constructive alternative analytical approaches to study evolution. Their anticipated coming demise of the adaptive landscape and **G**-matrix evolution have accordingly not been fulfilled, and they clearly underestimated the explanatory power of these tools and approaches (Svensson and Calsbeek 2012b). In contrast to what these philosophers anticipated, adaptive landscape theory and **G**-matrix evolution are likely to remain for many years to come, largely because of the power and flexibility of these tools to link phenotypic patterns with underlying evolutionary processes (Arnold 2005). We see increasing efforts to extend quantitative genetic and population genetic theory and methodology to incorporate nongenetic inheritance, niche construction, phenotypic plasticity and other interesting phenomena that have been highlighted by EES proponents (Laland et al. 2015). These phenomena are increasingly being incorporated in the current research framework as various “add-ons” and refinements of existing theory (Day and Bonduriansky 2011; Bonduriansky et al. 2012; Greenspoon and Spencer 2018; Bonduriansky and Day 2018; Rajon and Charlat 2019). Thus, sofar we have seen little of the radical conceptual change of evolutionary biology that some critics have claimed would be necessary (Pigliucci 2007, 2009; Noble 2013, 2015, 2017; Müller 2017). In short: gradual change has taken place and still happens to evolutionary biology, and there is no sign of major overhaul or any forthcoming paradigm shift at the horizon, contrary to the claims by some critics like Noble and Shapiro.

5.11 Conclusions

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

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

Not all philosophy of biology has played that positive role, however, especially as some philosophers have uncritically re-iterated myths about the MS that were initially propagated by Gould and others, but which have already been refuted. I have critically scrutinized some of these myths in this chapter. The long-lasting legacy of Gould and some of his more controversial claims has not always been positive. These claims contributed to establish misunderstandings about the current state of evolutionary biology, one being that the field is in deep crisis (Dupre 2012). To avoid repeating such mistakes, philosophers should communicate and collaborate with both historians of science and evolutionary biologists (and *vice versa* of course). Otherwise, philosophers risk spending effort on small and insignificant problems that are of little interest except to other philosophers. Some such problems might even be purely semantic, such as the odd idea that natural selection is not really an evolutionary process but just a statistical outcome of lower-level phenomena (Walsh et al. 2002; Otsuka 2016). Most evolutionary biologists probably consider such questions as rather esoteric and of little interest or relevance to the field. Attempts to re-introduce metaphysics in evolutionary biology (Dupré 2021), for instance, are unlikely to impress the evolutionary biology research community. Those arguing for organismal agency as an evolutionary process (Walsh 2015) but leave out natural selection as the most obvious explanation for apparent purpose or design (Noble 2021) are also unlikely to convince the majority of evolutionary biologists. It is worth re-iterating that the only known evolutionary process that can systematically increase organismal adaptation across generations and lead to (apparent) purpose is natural selection (Gardner 2013, 2017), although some critics of contemporary evolutionary biologist insist that adaptation can be decoupled from natural selection (Pigliucci and Kaplan 2000; Kull 2014; Noble 2021). Accepting that natural selection is the only known evolutionary process that can systematically increase organismal fitness and adaptation across generations does not mean that we could not appreciate within-generation phenomena such as phenotypic plasticity, habitat selection and adaptive niche construction (Edelaar and Bolnick 2019). Crucially, however, such within-generation phenomena are not evolutionary processes, but evolutionary outcomes (Gardner 2013; Loison 2018, 2021). Furthermore, accepting natural selection as the only known evolutionary process that can systematically increase organismal adaptation across generations does not mean that we need to uncritically adopt a pan-adaptationist position where one would claim that most organismal features are adaptive, or that we need embrace the Neo-Paleyan adaptationist biology tradition (Lewens 2019a). There is still plenty of room for non-adaptative and maladaptive evolutionary processes like mutation, drift and recombination (Lynch 2007; Svensson and Berger 2019). The important point, however, is that these other evolutionary processes cannot systematically increase organismal fitness and adaptations across generations, like natural selection, although they can of course *decrease* fitness (Lynch et al. 1995; Svensson and Berger 2019). Increased understanding of evolution requires *both* bold new ideas and a deep and nuanced understanding of the rich history of the MS and how contemporary evolutionary biology has advanced over the past century.

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

Name (-s)	Term	Phenomena	References
C.H. Waddington	Extended synthesis	Epigenetics Genetic assimilation Gene interactions	Waddington (1957) (Wilkins 2008)
S.J. Gould	Expanded evolutionary theory	Hierarchical theory Species selection Nonadaptation Exaptation	(Gould 1980) (Gould 1982) (Gould and Vrba 1982) (Gould 2002)
J. A. Endler T. McLellan	A newer synthesis	Source laws Ecology of natural selection Origin of variation	(Endler and McLellan 1988)
M. Pigliucci G. Muller	Extended Evolutionary Synthesis	Evolvability Phenotypic plasticity Epigenetic inheritance Complexity theory High-dimensional adaptive landscapes	(Pigliucci 2007) (Pigliucci 2009) (Pigliucci and Müller 2010b)

E. Koonin	"A postmodern state, not sofar a postmodern Synthesis"	Horizontal Gene Transfer (HGT) Gene duplications Gene loss Neutral molecular evolution	(Koonin 2009)
E. Danchin E. Jablonka M. Lamb	Inclusive Evolutionary Synthesis *or* Expanded Evolutionary Synthesis	Nongenetic inheritance Cultural evolution Information theory	(Jablonka and Lamb 2005) (Jablonka and Lamb 2007) (Danchin 2013)
D. Noble J.A. Shapiro	The Third Way of Evolution (TWE) *or* Integrated Synthesis	Evo-devo theory Plasticity & Accomodation Epigenetic inheritance Multilevel selection Genomic evolution Niche construction Replicator theory Evolvability	(Noble 2013) (Noble 2015) (Noble 2017) Shapiro (2011)
K.N. Laland T. Uller M.W. Feldman K. Sterelny G.B. Muller A. Moczek E. Jablonka J. Odling-Smee	Extended Evolutionary Synthesis (EES)	Developmental bias Plasticity Non-genetic inheritance Niche construction	(Laland et al. 2014) (Laland et al. 2015)

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Legends to figures

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

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

Fig. 5.3. Causal model and path diagram of the relationship between a standard phenotypic trait (Z_p: parental generation; Z_p: offspring generation), a niche construction phenotype (N_p: parent generation; $N_{p'}$: offspring generation), fitness (W) and genetic inheritance (X: parental generation genotype; X′: offspring generation genotype). Direction of arrows denote causal relationships. The phenotypic trait influences parental fitness directly (β_Z: direct selection

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

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

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

Fig. 5.1

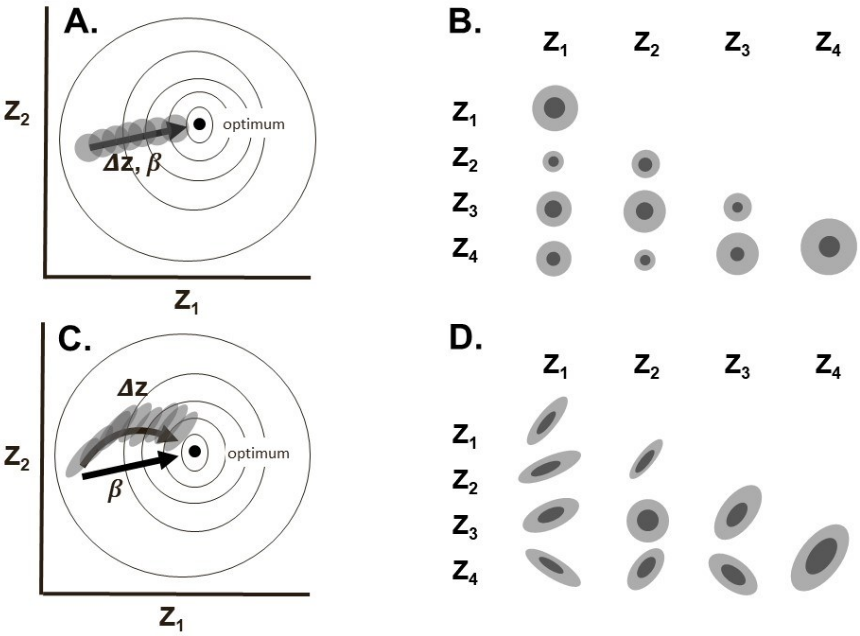

A.
Z_2
optimum
$\Delta z, \beta$
Z_1
B.
Z_1 Z_2 Z_3 Z_4
Z_1
Z_2
Z_3
Z_4
C.
Δz
Z_2
optimum
β
Z_1
D.
Z_1 Z_2 Z_3 Z_4
Z_1
Z_2
Z_3
Z_4

Fig. 5.2

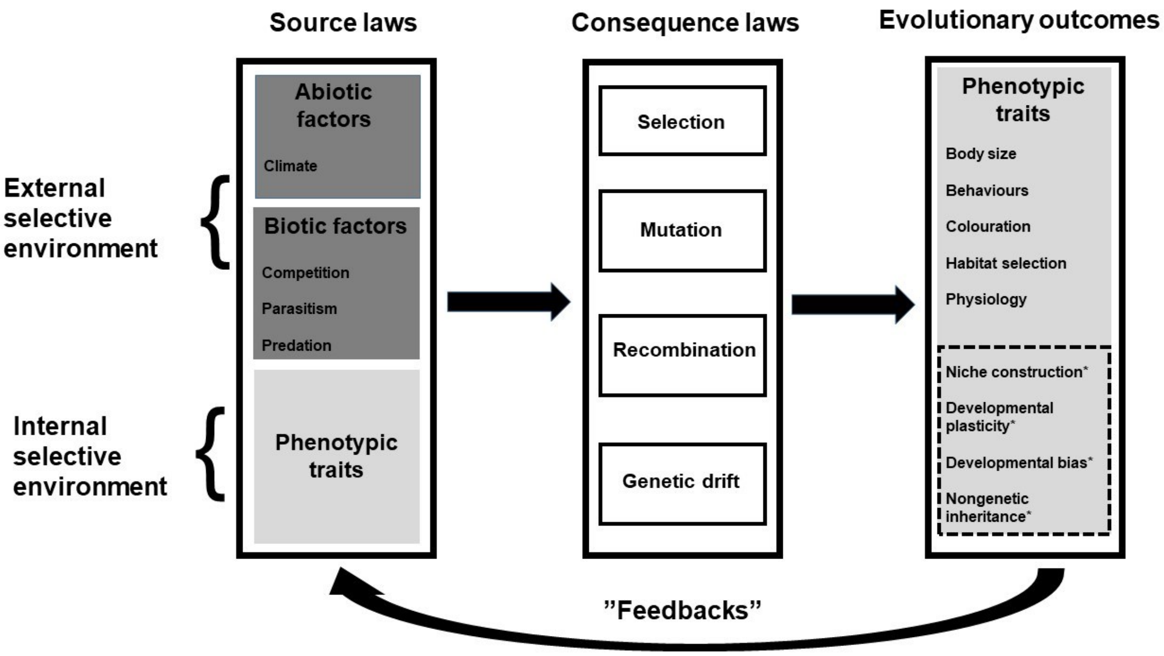

Source laws
Consequence laws
Evolutionary outcomes
External selective environment
Internal selective environment
Abiotic factors
Climate
Biotic factors
Competition
Parasitism
Predation
Phenotypic traits
Selection
Mutation
Recombination
Genetic drift
Phenotypic traits
Body size
Behaviours
Colouration
Habitat selection
Physiology
Niche construction*
Developmental plasticity*
Developmental bias*
Nongenetic inheritance*
”Feedbacks”

Fig. 5.3

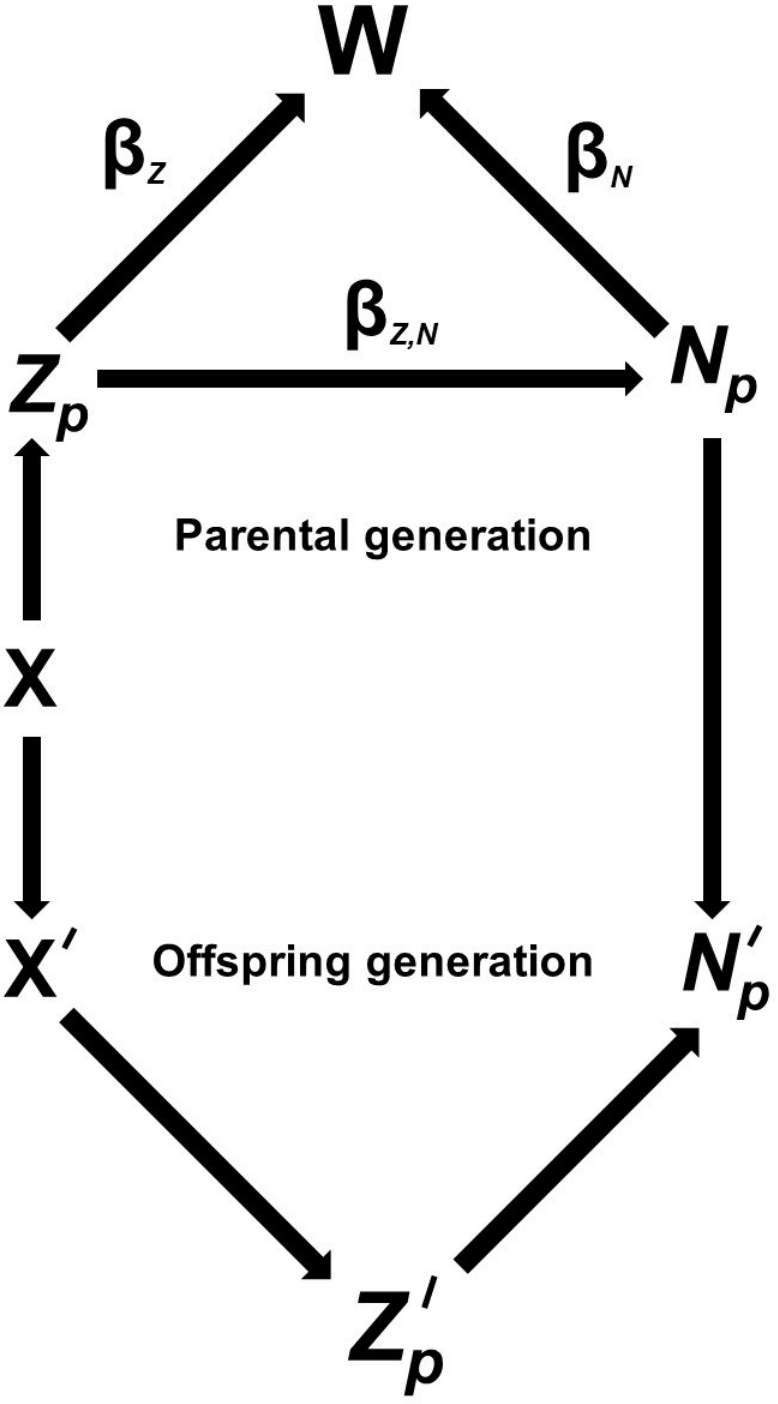
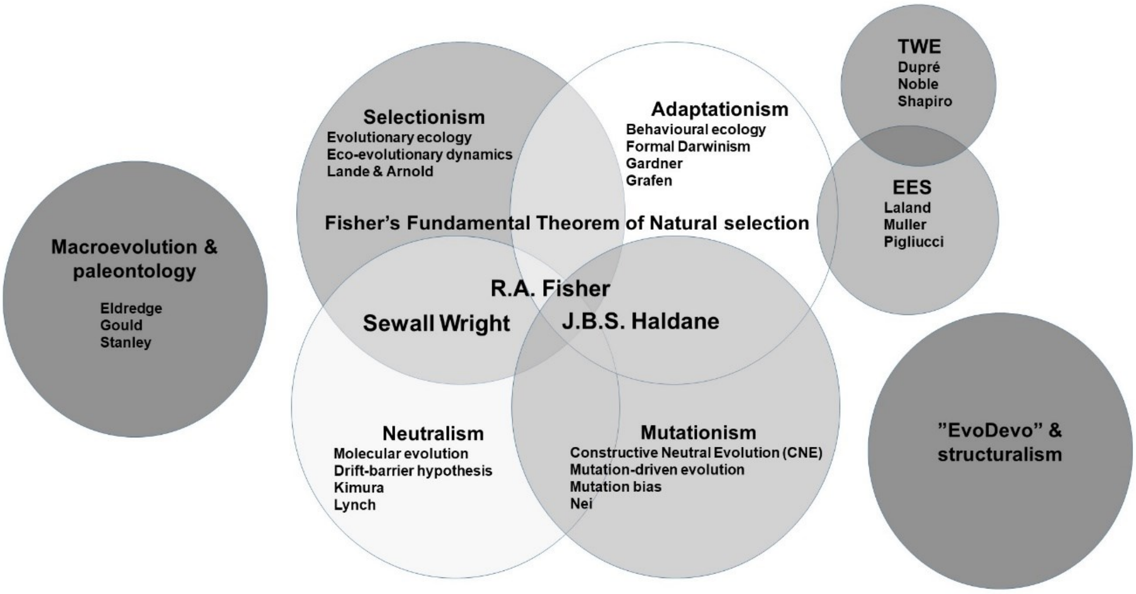

W
β_Z
β_N
$\beta_{Z,N}$
Z_p
N_p
Parental generation
X
X'
Offspring generation
N'_p
Z'_p

Fig. 5.4


Selectionism
Evolutionary ecology
Eco-evolutionary dynamics
Lande & Arnold
Adaptationism
Behavioural ecology
Formal Darwinism
Gardner
Grafen
TWE
Dupré
Noble
Shapiro
EES
Laland
Muller
Pigliucci
Macroevolution & paleontology
Eldredge
Gould
Stanley
Fisher's Fundamental Theorem of Natural selection
R.A. Fisher
Sewall Wright
J.B.S. Haldane
Neutralism
Molecular evolution
Drift-barrier hypothesis
Kimura
Lynch
Mutationism
Constructive Neutral Evolution (CNE)
Mutation-driven evolution
Mutation bias
Nei
"EvoDevo" & structuralism