# The Darwinian Core of Evolutionary Theory and the Extended Evolutionary Synthesis: Similarities and Differences

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## Abstract

In this paper, we evaluate debates surrounding calls for an Extended Evolutionary Synthesis in light of the Darwinian core of evolutionary theory, which was somewhat broader than the Modern Synthesis. We suggest that Darwin's nuanced operationalization of natural selection rested upon two innovations: the atomization of individuals into trait-variants, and a reconceptualization of heredity in terms of transmission of trait-variants. Darwin also implicitly differentiated between the causes and consequences of selection, noting that while selection acts on individuals, it is actually trait-variants that are consequently differentially transmitted, and the species that is eventually modified. This is important because the individual, with inherencies and agency, is largely relevant only when examining the causes of selection, with trait-variants being the more appropriate unit for studying its consequences. Consequently, we emphasize the importance of restricting the use of 'fitness' to one-step change in trait-variant frequency, instead of also using it for lifetime reproductive success of individuals, or even trait-variants. Fitness, thus defined, is always inclusive, circumventing much unnecessary debate. We also present a schematization of explananda in evolutionary biology, and suggest a framework for the comparative evaluation of factors affecting evolutionary change. We further suggest that the controversial 'gene's eye view of evolution' is best seen as not one, but two distinct views, one Fisherian and the other Dawkinsian, and that conflating them has led to considerable unnecessary debate. In conclusion, we suggest that it is helpful to view received evolutionary thought as an evolving set of explanations, intertwined with one another to varying degrees, rather than a distinct, static Modern Synthesis. This leads to our viewing various processes and factors affecting the origin, dynamics and patterns of prevalence of variants at various levels of biological organization, as representing differing but complementary parts of a complex, nuanced, multifarious and evolving standard evolutionary theory.


**Word-count:** 300


**Key-words:** Modern Synthesis; natural selection; trait-variants; Darwinian fitness; reproductive output; transmission fidelity; transmission efficiency; gene's eye view of evolution.

## Introduction

In this paper, we discuss some issues that often come up in the context of debates between the supporters of Modern Synthesis (henceforth, MS) and the Extended Evolutionary Synthesis (henceforth, EES). These issues primarily pertain to the (i) role of the individual in evolutionary explanations, (ii) nature(s) of Darwinian fitness (henceforth, fitness), (iii) often neglected non-genetic interpretations of quantitative genetic theory, (iv) relationships between different evolutionarily important factors, and (v) role of development in evolutionary explanations. When discussing contentious issues, it is helpful to be clear about one's potential biases, points of view and focus at the outset. Our backgrounds are in various areas of biology, and all four of us are empirical evolutionary biologists also interested in, and engaged with, theory. Between us, we work primarily on the evolution of life-histories, dispersal, social organization, adaptations to crowding, population stability, and sexual conflict. One of us works primarily in the wild, on large mammals and birds, while the other three work with laboratory systems of microbes or dipterans. We also share an interest in many issues in the history and philosophy of evolutionary biology. More to the point, all of us would self-identify as having been trained, and presently working, within the broad framework of the MS. Nevertheless, we are appreciative of, and sympathetic to, many aspects of the calls for an ESS, although we find some aspects of the ESS discourse – both on history and mechanisms – to be somewhat muddled and often overhyped. Here, we discuss some aspects of the EES-MS debate in the historical context of the changes in evolutionary thinking from Darwin's times to the present. We also try to place this ongoing debate within the broader context of what evolutionary biology needs to explain. In this attempt, we have tried, as far as possible, to set our biases aside and follow the sentiment expressed in this Urdu couplet by Nabraas Akbarabadi:

کھیل ہے یہ سب نظریے کا، اے بیخُد، چھوڑ دے
ہر نظریے کا تقاضہ توڑ کر بن جا نظر

*khel hai ye sab nazariye ka, ai Bekhud, chhor de*
*har nazariye ka taqaaza tor kar ban ja nazar*

(Leave aside illusions born of many different points of view:
Break the shackles of perspective, be vision personified!)

Although discomfort with the perceived restrictive nature of some of the views that were eventually codified in the MS of the mid-twentieth century was intermittently articulated, both before (*e.g.*,

Bateson, 1894; de Vries 1905; and the work of Woltereck, Nilsson-Ehle, Johannsen, Romashoff and Timoféeff-Ressowsky, discussed in Sarkar, 1999, 2006) and after the synthesis (*e.g.*, Goldschmidt 1940; Waddington, 1953; Eldredge & Gould, 1972; Gould & Lewontin, 1979; Stanley, 1979; Dey & Joshi, 2004), the present form of calls for an EES took clearly discernible shape only in the early twenty-first century, roughly coinciding with the publication of 'Evolution: the Extended Synthesis' by Pigliucci & Müller (2010). The EES, which is claimed to be a significant extension to the mid-twentieth century MS, is an umbrella term used to cover at least four somewhat distinct, though overlapping, aspects of evolutionary thinking: (1) an additional focus on non-genic inheritance, including epigenetic, cultural and ecological inheritance; (2) supposedly novel conceptualizations of evolutionary forces, such as niche construction and developmental or mutational bias; (3) a rethinking of the logical status of various evolutionarily important factors, including natural selection, niche construction and developmental or mutational bias; and (4) a renewed emphasis on keeping the individual organism, with inherency and agency, at the centre of evolutionary thinking (Laland et al., 2015; Newman 2022a,b). Over the past decade or more, there has been considerable debate about many of the claims made by EES proponents (*e.g.*, Laland et al., 2014; Gupta et al., 2017a,b; Feldman et al., 2017; Charlesworth et al., 2017; Svensson, 2018; Dickins & Dickins, 2018; Buskell, 2019; Lewens, 2019; Dickins, 2021). In general, these arguments juxtapose EES with MS, and there is as yet no general consensus on whether EES marks a seriously consequential extension to the MS, or whether the phenomena highlighted by EES are readily accommodated within the MS.

In this paper, we examine various aspects of the EES-MS debate by focussing on what we label the Darwinian Core of evolutionary theory (DC), encompassing the views of Darwin on evolution as contained in his books and other writings. In our delineation of the DC, we emphasize not only aspects that are very well recognized, such as the assertion that natural selection is the major driver of adaptive evolution, but also important aspects that have often not received much attention, such as why development was relegated to the periphery of evolutionary explanation by Galton (1872), long before the marginalization of development from heredity by Morgan (1926) and others (the latter discussed by Sarkar, 2006), and how the atomization of the individual (*sensu* Gould & Lewontin, 1979) was actually a largely unrecognized but nevertheless fundamental component of what Mayr (1955, 1959, 2004) regarded as one of Darwin's greatest contributions, and somewhat controversially termed 'the shift from typological to populational thinking' (for detailed critiques of this interpretation by Mayr, see Greene, 1992; Amundson, 1998, 2005; Winsor, 2006a,b; Hey, 2011). The point we wish to make is that there are not just many similarities but also quite a few

differences between DC and MS, with the latter representing a slightly narrower conceptualization of the evolutionary process. We use the term MS, adopted from the title of Huxley's (1942) book, to refer to the consensus view of the key elements of the evolutionary process – putting together insights from Mendelian genetics, cytogenetics, population and quantitative genetics, studies of genetic and chromosomal variations in nature, natural history, systematics and palaeontology – that crystallized during the period between 1918 and 1950 (Rao & Nanjundaiah, 2017; Sarkar, 2017). The MS, it should be noted, was slightly broader than Neo-Darwinism, a view of evolution heavily influenced by the views of Weismann (1889, 18893a,b, 1902) on the primacy of natural selection and the impossibility of the inheritance of acquired characters, that developed in the few decades after Darwin (Reif et al., 2000). Unfortunately, the term Neo-Darwinian Synthesis was also often used later as a synonym for MS, potentially creating confusion for one first encountering this literature (Reif et al., 2000).

At this point, we would also like to take a step back and take a broader view of the domain of evolutionary biology, and locate the issues discussed in this paper in the context of that bigger picture. Evolutionary biology attempts to provide explanations for the hitherto puzzling observations of the "relatedness of species, diversity of species, and adaptedness of species" (Rose, 1998). Darwin (1859, 1868, 1871), to varying degrees, provided explanations for all three of these ubiquitous observables of the living world: for relatedness and diversity through descent with modification, with selection playing a role in promoting diversification of new species, and for adaptedness through selection. Darwin, however, focussed disproportionately on explaining adaptedness, possibly because that was the aspect often stressed when arguing for the role of a creator in the origin of life-forms (*e.g.*, Paley 1802). Adaptedness was, in fact, a principal concern of the uniquely British natural theology tradition, and this might explain why subsequent British evolutionists have given far more attention to explaining adaptation compared to, say, the origins of form (Ågren, 2021).

We elaborate upon the tripartite explanandum above, to list out some overarching categories of issues that evolutionary biology must address, and to locate the DC, MS and EES within this schema to better examine their inter-relationships. Mirroring the dichotomous categories of microevolution and macroevolution, potentially bridged by speciation, we examine how evolutionary biology needs to explain issues of origin, increase and persistence of phenotypic variations that give rise to observed spatio-temporal patterns of variations at different levels of biological organization. For our purposes, we find it helpful to think of six such categories of issues

that any science calling itself evolutionary biology needs to address, three each for macro-evolutionary and micro-evolutionary phenotypic variations, respectively (Table 1).

| | **ATTRIBUTES AND CONSEQUENCES OF PHENOTYPIC VARIATIONS** | | |
|---|---|---|---|
| **NATURE OF PHENOTYPIC VARIATIONS** | **1. Origins** | **2. Dynamics of relative abundance** | **3. Resultant patterns in time and space** |
| **A. Macro-evolutionary** | **1A) *"macro-origins"***<br><br>How do macro-evolutionary variants (forms) arise? Are certain variants more/less likely to occur in different contexts? | **2A) *"macro-dynamics"***<br><br>What are the factors/mechanisms affecting the dynamics of relative abundance of different macro-evolutionary variants (forms) over a given time span? | **3A) *"macro-patterns"***<br><br>How do 1A and 2A result in different spatio-temporal patterns in the diversity of macro-evolutionary variants (forms)? |
| **B. Micro-evolutionary** | **1B) *"micro-origins"***<br><br>How do micro-evolutionary trait-variants arise? Are certain variants more/less likely to occur in different contexts? | **2B) *"micro-dynamics"***<br><br>What are the factors/mechanisms affecting the dynamics of relative abundance of different micro-evolutionary trait-variants over a given time span? | **3B) *"micro-patterns"***<br><br>How do 1B and 2B result in different spatio-temporal patterns in the diversity of micro-evolutionary trait-variants within species? |

**Table 1.** One way of categorizing the major explananda that need to be addressed by a science terming itself evolutionary biology (see text for details). We will henceforth refer to these six categories by their combinatorial labels, "*micro*/*macro*-*origins*/*dynamics*/*patterns*".

Like most schemata in biology, this is a fuzzy rather than a clearly and unambiguously delineated organization of explananda. We believe, nevertheless, that this is a useful schema, and one to which we will return repeatedly. Here, we explain the sense in which we are using some of these terms and make a few general points about how different types of evolutionary explanation map onto this schema.

We use the term macro-evolutionary phenotypic variations to refer to the appearance of either new traits altogether, *e.g.*, horns in a hitherto hornless species, or new variants of existing traits that are

well beyond the known range of distribution of trait-variants of that trait, *e.g.*, a phytophagous insect that can utilize a novel food plant species belonging to a different angiosperm family than the plants normally used by that insect species. This is also sometimes termed the appearance of novel forms (*e.g.*, Carroll, 2005). By trait-variants, we mean alternative versions of a traits; our usage mirrors the sense in which Darwin (1859, 1868) used the terms 'characters' and, more frequently, 'variations'. By micro-evolutionary phenotypic variations we mean the appearance of new trait-variants of an existing trait close to, or within the range of known variation in that trait. Since speciation, according to the biological species concept for obligate sexually reproducing species, involves reproductive isolation as a definitional criterion (*e.g.*, Howard & Berlocher, 1998), we note that species defined thus can originate through, and be separated by, either micro- or macro-evolutionary variations.

All the six categories above encompass elements of both process and pattern, albeit to considerably varying degrees. The categories "*macro-origins*" and "*micro-origins*" include considerations of how new variations arise at different levels, yielding novel forms or trait-variants, as also those of patterns in how various variations differ in the likelihood of their arising at a given time and population. In recent times, diverse investigations spanning both these categories are often integrated into discussions of the origins of evolutionary innovation (*e.g.*, Erwin, 2021). The categories "*macro-dynamics*" and "*micro-dynamics*" include considerations of the time-dynamics, across varying time-scales, of absolute or relative numbers, biomass, or other relevant measurables, of alternative macro- or micro-evolutionary variations within an ensemble, including persistence or extinction. The categories "*macro-patterns*" and "*micro-patterns*" focus on the patterns in the distributions of macro- and micro-evolutionary variations across space and time that result from processes under "*macro-origins*" and "*macro-dynamics*", and under "*micro-origins*" and "*micro-dynamics*", respectively. It should be noted that chance plays a role in practically all the processes across these six categories. We speculate that the separation between changes happening at these two levels of variation – micro- versus macro-evolutionary – was perhaps even more blurred during the early stages of the evolution of life on earth, and perhaps still is today in protists and monerans that exhibit a level of organismal complexity that is similar to what was probably the case in early evolution. In simple, often unicellular, species, it is likely that far more mechanisms are shared between "*macro-origins*" and "*micro-origins*", and under "*macro-dynamics*" and "*micro-dynamics*", respectively, than is the case in more complex metazoans.

We further note that evolutionary biology since Darwin has addressed these six categories in an uneven manner. The category "*macro-origins*" is presently largely the domain of evo-devo and was relatively neglected for several decades in the twentieth century (Amundson, 2005). Although we now better understand how developmental genetic networks (*e.g.*, Salazar-Ciudad et al., 2001; Salazar-Ciudad, 2009) and also non-genetic, often physical, properties of cells and organisms (*e.g.*, Salazar-Ciudad et al., 2003; Newman & Bhat, 2009; Bhat et al., 2016; Tickle & Urrutia, 2016; Newman, 2021, 2022a,b) can shape the origins of new forms, the level of detail and generality with which we understand issues in this category of explaining origins of variation is somewhat less than that in the category "*micro-origins*". Discussions of developmental bias, developmental constraints and the role of development in shaping the morpho-space anisotropically (*e.g.*, Salazar-Ciudad, 2021) also fall largely within "*macro-origins*", although they are also conceived of as affecting processes and outcomes here categorized as "*macro-dynamics*" and "*macro-patterns*", as part of a perspective primarily informed by palaeontology, systematics and biogeography in the past, and supplemented today by molecular phylogenetics, phylogenomics and phylogeography. It is also worth stressing here that selection is an important, though by no means only, process particularly in "*micro-dynamics*" phenomena and, therefore, helps shape patterns mostly in the category "*micro-patterns*". It is not clear how significant a role selection plays as a "*macro-dynamics*" process, although it is likely to be far less pervasive than it role as a "*micro-dynamics*" process (Newman, 2022a).

Our understanding of the origin of novel trait-variants ("*micro-origins*") has progressed quite a bit since Darwin's unsuccessful attempts to grapple with this vexed issue through his theory of pangenesis (Geison, 1969; McComas 2012). A large proportion of the explanations for "*micro-origins*" phenomena derives from genetics, involving both mutations in the broadest sense, including chromosomal changes and changes in gene expression (*e.g.*, Dobzhansky, 1937; Graves et al., 2017; Seabra et al., 2018; Fitzgerald & Rosenberg, 2019; Barter et al., 2020; Dowle et al., 2020), as well as the recombinational shuffling of standing genetic variation, especially for quantitative traits (Teotónio et al., 2009; Mueller et al., 2013; Matuszewski et al., 2015; Philips et al., 2018; Hickey & Golding, 2021; Kawecki et al., 2021). The now fairly well accepted role of phenotypic plasticity in preceding and facilitating adaptive evolutionary change (discussed in detail in Pfennig, 2021) also has a bearing on issues in the category "*micro-origins*". There is also, more recently, input from evo-devo towards understanding the origins of the kind of variation relevant to micro-evolutionary change, variously termed devo-evo (Prasad & Joshi 2003; Joshi, 2005) or micro-evo-devo (Nunes et al., 2013). Issues in the category "*micro-dynamics*" – the domain of

classic micro-evolutionary dynamics as affected principally by mutation, migration, selection, and drift – are by far the most studied and well understood, compared to those in the other five categories of our schema in Table 1. The category "*micro-dynamics*" is also largely the only category that Darwin's (1859, 1868, 1871) work successfully addressed in any detail, through his enunciation of the principle of natural selection; his attempt to illuminate "*micro-origins*" processes via pangenesis did not persist very long. The bulk of the work done on "*micro-dynamics*" issues today lies within the domain of population genetics and genomics, quantitative genetics, and ecology, in particular evolutionary ecology. The category "*micro-dynamics*" was also the primary focus of the MS, although it also attempted to incorporate issues of speciation into its purview. Issues in the category "*micro-patterns*" have also been covered in a lot of MS work, in conjunction with "*micro-dynamics*" issues. One unfortunate consequence of the preponderance over time of "*micro-dynamics*" and "*micro-patterns*" explanations, compared to most other categories in this schema, has been the tendency of text-books of evolution to often convey the impression that the issues dealt with under these two categories essentially cover a very large part of the domain of evolutionary explanation.

The origin of species, despite the eponymous title of his book, was not really addressed by Darwin (1859) at all, save to express the hopeful view (his 'principle of divergence') that, consonant with his uniformitarian beliefs, "*micro-dynamics*" processes would, over long spans of time, aided by geographical separation, result in the origin of new species and, thus, eventually result in variations of the category "*macro-origins*". Not surprisingly, given the conceptual centrality of species as a category in many areas of biology, speciation – a term coined by Cook (1906) – has attracted the interest of researchers from evo-devo, systematics, palaeontology, phylogeography, ecology, population genetics, and quantitative genetics, largely during the second half of the twentieth century (*e.g.*, Mayr, 1982; Koeslag, 1995; Howard & Berlocher, 1998; Gavrilets, 2003; Baker, 2005; Via, 2009). Patterns in species diversity can result from a complex interplay of "*micro-patterns*" and "*macro-patterns*" processes, but work on these issues has not been as extensive as that on speciation (*e.g.*, Cracraft, 1982; Vrba, 1984; Jablonski 2008), perhaps because processes in the categories "*macro-origins*" and "*macro-dynamics*" are not as well characterized as those in the categories "*micro-origins*" and "*micro-dynamics*". We have preferred to ignore the category of species in our categorization of phenotypic variation (Table 1) because phenotypic variation both within- and among-species can span from micro-evolutionary to macro-evolutionary. Therefore, for example, a possible categorization of variation within species, across species and higher taxa would tend to obfuscate an appreciation of processes acting on substantially different types of variation.

We next briefly explain our priorities in, and motivation for, writing this piece, harking back to the poetic sentiment expressed in the first paragraph of this section. In terms of the schema in Table 1, three of us (SD, AJ & NGP) work almost entirely within the domain of "*micro-dynamics*", whereas TNCV works primarily within the "*micro-dynamics*" and "*micro-patterns*" categories. We have chosen not to comment on every aspect of the EES-MS debate in detail, especially those already extensively and clearly discussed in the literature, preferring to focus on a sub-set of issues that we believe are neglected, or at least under-appreciated, in this debate. We agree that inheritance, especially cultural and ecological inheritance, can often be non-genetic (*e.g.*, Jablonka & Lamb, 2005; Helanterä & Uller, 2010; Danchin et al., 2011, 2019; El-Mouden et al., 2014; Prasad et al., 2015; Bonduriansky & Day, 2018; Jablonka & Noble, 2019; Adrian-Kalchhauser et al., 2020), and that both these forms of inheritance have a major role to play in the evolutionary process. Although there is now some evidence for trans-generational epigenetic inheritance (*e.g.*, Jablonka & Raz, 2009; Klosin & Lehner, 2016), as well as for its underlying mechanisms (Fitz-James & Cavalli, 2022), in a few systems, we think that it would be premature to attempt an assessment of how common or rare it is in nature. Moreover, there is relatively little evidence as yet for persistent trans-generational epigenetic inheritance over large numbers of generations. We agree that extended phenotypes and niche construction are important phenomena in evolution, but we disagree with many of the claims made by niche construction proponents. This last issue has been already discussed in detail, and we refer the interested reader to a triptych of critique, response, and counter-response (Gupta et al., 2017a; Feldman et al., 2017; Gupta et al., 2017b). Over the past two decades, we have been, almost in equal measure, excited, enlightened, frustrated and disappointed by various facets of the EES literature. We believe that at least some of the issues under debate lack the level of clarity one would have hoped for, while others have not been discussed in sufficient detail, or at all. Our approach in this paper, consequently, is that of a metaperspective (*sensu* Hester & Adams, 2014) rather than a review, although we have also tried to provide a reasonable and eclectic, though by no means exhaustive, entry into the relevant literature. We hope that our efforts will contribute to some enhancement of the clarity with which we, as a community, describe, discuss, and debate the structure of evolutionary thought.

## The Darwinian Core (DC) of evolutionary theory

We have been guided in writing this paper by a belief that a deeper and more nuanced appreciation of the past often facilitates an improved understanding of the future, eloquently expressed by Allama Iqbal thus:

سامنے رکھتا ہوُں اِس دورِ نِشاط افزا کو میں
دیکھتا ہوُں دوش کے آئینے میں فردا کو میں

*saamne rakhta hoon is daur-e-nishaat-afzaa ko main*
*dekhta hoon dosh ke aaine mein fardaa ko main*

(The golden age that has gone by, is always in my heart and mind;
And in that mirror of the past, I see the future times outlined)

In this spirit, we now outline some aspects of the DC that we think have not received as much attention as they should have. Darwin (1859) is universally acclaimed for two major contributions that comprehensively changed biological thinking: (i) marshalling a compelling body of evidence for the occurrence of evolutionary change, which has never been seriously doubted since, thereby explaining why species and higher taxa appear to be connected by genealogical relationships, and (ii) providing a potent mechanism – natural selection – for adaptive evolutionary change. These two contributions went a long way towards explaining the diversity, relatedness and adaptedness of species, even though Darwin's 'hypothesis of natural selection', unlike his 'hypothesis of descent', gained widespread acceptance only several decades after it was first put forward (Gayon, 1998). Another important contribution of Darwin's, according to Mayr (1955, 1959), was to usher in a shift from typological or essentialist thinking to populational thinking among biologists. This assertion of Mayr's was strongly critiqued, and it was pointed out that most influential biologists pre-Darwin were largely not essentialist in their thinking (Greene, 1992; Amundson, 1998, 2005; Winsor, 2006a,b; Hey, 2011). Mayr (2004), however stuck to his claim, and this assertion of a shift in thinking, after Darwin, from typological to populational mode is still commonly encountered in text books, and in books on evolution aimed at a general audience (*e.g.*, Rose, 1998). We suggest that the relevant shift in Darwin's thinking was actually one from typological/essentialist to variational mode in the very limited context of how hereditary transmission mediates selection. We return to this issue after mentioning what we think are some very major and unappreciated contributions of Darwin to evolutionary thought, because this shift from a typological to variational understanding of heredity is intertwined with both contributions.

In our opinion, neither the notion of descent with modification, nor that of selection, by itself qualifies as a profoundly novel intellectual contribution by Darwin, though both were undoubtedly important and consequential. The general idea of descent with modification had been expressed frequently in Europe, in both biological and general circles, over the century preceding Darwin (Freeman & Herron, 2013). Similarly, notions approximating the idea of natural selection to varying degrees can been seen, over a span of about 2300 years, in the writings of Empedocles (Gottlieb, 2000), Lucretius (Campbell, 2003), Nasir al-Din Tusi (Alakbarli, 2001), and, closer to Darwin and Wallace's time, of W. C. Wells and Patrick Matthew (Freeman & Herron, 2013), and of H. G. Bronn, unfortunately known to much of the Anglophone world only as the translator of Darwin's (1859) book into German (Gliboff, 2008). Indeed, in a footnote on the first page of 'An historical sketch of the progress of opinion on the origin of species previously to the publication of the first edition of this work', added as a preface to most editions (after the second) of *The Origin of Species*, Darwin quotes Aristotle, who himself is paraphrasing Empedocles only to disagree with him, and notes that, "We see here the principle of natural selection shadowed forth".

We believe that, more than the idea of natural selection, it was its operationalization by Darwin in a particularly useful manner that constituted a very significant and novel intellectual contribution. This operationalization, in turn, rested upon two major conceptual innovations: the atomization of the individual into traits, and the reconceptualization of heredity as needing to explain not only the perpetuation of holistic types, but also the generation and transmission of trait-variants. These innovations of Darwin's are often erroneously ascribed to either genetics as it emerged in T. H. Morgan's lab, or the MS (*e.g.*, Gould & Lewontin, 1979; Allen, 1985; Amundson, 2005). We note that these same two conceptual innovations also informed the work of Mendel around the same time. Not surprisingly, therefore, these innovations eventually led to development being excluded from explanation of both transmission genetics and micro-evolutionary change. This novel conceptualization of heredity, influenced by the experience of breeders, was one of Darwin's most unappreciated contributions to the discipline that later became known as genetics. We will discuss the consequences of Darwin's atomization of individuals and reconceptualization of heredity for how we conceive of and use the notion of fitness in a later section. Here, we focus on Darwin's reconceptualization of heredity and then delineate what we believe to be the constituents of the DC.

Darwin's thinking on heredity and evolution was influenced by natural history, biogeography, systematics, medicine, and breeding. The first three influences were reflected in his setting up of the problem of evolution by recognizing that species and higher taxa appeared to be connected by

genealogical relationships and, moreover, appeared to be well adapted to their respective ecological contexts and lifestyles. His solution to the problem – the mechanism of natural selection – was almost entirely inspired by analogy to breeding (in sharp contrast to Wallace, who did not believe domesticated animals to be relevant to understanding natural selection: Gayon, 1998), whereas his views on heredity were influenced by developments in both medicine and breeding, especially in the late eighteenth and early nineteenth centuries (a detailed account of thinking about heredity in this period can be found in the papers in Rheinberger & Müller-Wille (2003), and Müller-Wille & Rheinberger (2007)). Prior to the late eighteenth century, ideas pertaining to heredity were vague and diffused, with no specific focus on transmission of variations, and heredity was considered inseparable from reproduction, thus falling within the domain of embryology. A corollary to this was that heredity was viewed primarily as ensuring the stability of the type via the transmission of similarities that unified all individuals of a species or variety. Elements of this view lingered on into the late nineteenth century alongside more specific conceptualizations that viewed heredity, in the sense of transmission, as a phenomenon distinct from embryology and physiology (Churchill, 1987), and both approaches to the vexed problem of heredity can be seen in Darwin's writings.

The key conceptual developments in the study of heredity before Darwin, which culminated in the early- to mid-nineteenth century writings of Prosper Lucas (Kendler, 2021) and Imre Festetics (Szabó & Poczai, 2019), were a focus on the transmission of variations to offspring, as well as a conceptualization of heredity as a distinct phenomenon, with its own 'laws', requiring to be explained in its own terms, rather than as a subsidiary component of reproduction, physiology, or embryology (Churchill, 1987; López-Beltrán, 1992, 2003; Wood, 2003; Szabó & Poczai, 2019; Kendler, 2021). The significance of these developments for the subsequent study of both genetics and evolution is reflected in the fact that both Darwin and Mendel independently realized the importance of atomizing individuals into trait-variants, and treating the transmission of trait-variants as distinct and independent of their expression. It is now known that Mendel was aware of Darwin's work in considerable depth (Fairbanks, 2020), but not vice versa (Sclater, 2006), and there is no evidence that they were influenced by each other on the related issues of atomization and distinguishing the transmission of trait-variants from their phenotypic manifestation.

Darwin (1859, 1868; and essays printed in Darwin, 1909) was interested in both the origin and transmission of trait-variants, and considered a spectrum of types of possible variation within a species, ranging from the continuous, effectively rendering each individual unique, through small discontinuous but widespread variations, implying that many individuals in a population could

share very similar trait-variants that might be advantageous under some environments, to discontinuous ‘sports’ of larger effect, arising in one or a few individuals (Bowler, 1974). In the absence of any clear knowledge of the mechanism by which variations arose, he believed axiomatically that variations were ubiquitous, generated almost continuously, and typically heritable (Bowler, 1974; Gayon, 1998). Moreover, Darwin (1859, 1868) believed variations to arise from the interaction between an organism and its environment, with a subsequent inheritance of the acquired characters. Darwin’s writings on heredity are often somewhat vague and muddled, even self-contradictory at times, especially when he explores the relationship between the origin, expression, and transmission of trait-variants, and, therefore, between development and heredity, in his theory of pangenesis (Geison, 1969; Gayon, 1998; McComas, 2012). This is undoubtedly because he was grappling with fundamental issues and concepts for which there was little empirical support, and which were imbued by much confusion at the time. Unfortunately, this ambiguity means that one can usually find specific quotes from Darwin’s writings that can be deployed to support whichever side of the development-heredity argument one wishes to bolster.

It has often been suggested that Darwin treated development and hereditary transmission as a unified whole (*e.g.*, Winther, 2000; Amundson, 2005), but we suggest that this is a misrepresentation, especially if we examine Darwin (1868), and not just Darwin (1859), as also argued persuasively by Gayon (1998). Basically, Darwin (1868) rested his case for treating development separately from the transmission of trait-variants to offspring (heredity, in his words) on the phenomenon of reversion, or atavism, which refers to a character in a pedigree often skipping one or more generations before ‘reappearing’. Darwin interpreted this not so much as evidence for reversion to a varietal type, as was common at the time, but rather as a strong indication that individuals were mosaics of characters (trait-variants), some expressed during development, and others latent. Latent characters, though not expressed were, nevertheless, transmissible to offspring, suggesting that development and heredity could be delinked. Summing up, Darwin (1868) wrote that, therefore, reversion “... proves to us that the transmission of a character and its development, which ordinarily go together and thus escape discrimination, are distinct powers...”. This argument for the separation of development and hereditary transmission of trait-variants was later reinforced even more explicitly and graphically by Galton (1872). The notion of individuals being a mosaic of trait-variants, of course, also arises naturally from the experience of breeders. This view was developed clearly by Darwin (1859, 1868; also see his 1844 essay in Darwin, 1909, and some of his writings collected in Barrett, 1977), emphasizing that the breeders’ adage of ‘like begets like’ was not an expression of the conservative perpetuation of an overall varietal ‘type’ during reproduction

(*e.g.*, a crow gives rise to a crow), but rather a statement of the heritable nature of preferred trait-variants among individuals within a variety that could be independently selected for (*e.g.*, one can successfully select for larger beak size in a given variety of crows). The separation of development from heredity should not, however, be taken to imply that Darwin considered development to be unimportant to evolution, as opposed to its being irrelevant to understanding the transmission of trait-variants from parents to offspring, and its evolutionary consequences. When considering large scale variations among related taxa within lineages, Darwin (1859) focused on changes in ontogeny, drawing on the tradition of comparative morphology and embryology, and even tried to interpret the principle of recapitulation in terms of differing selection pressures acting on different stages of the ontogeny. Moreover, Darwin also noted that growth correlations – his term for correlations among traits resulting from developmental processes operating during ontogeny – could cause micro-evolutionary change without selection, as well as constrain the ability of selection to effect micro-evolutionary change.

When discussing selection and the gradual modification of species or varieties by the accumulation of variations, however, Darwin retained his primary focus on specific, largely independent, and small scale trait-variants (Howard, 2009; Deichmann, 2010), and also emphasized that bearing favourable trait-variants essentially improved the chance that an individual would survive better and reproduce more than others who did not bear those trait-variants (Darwin 1859, 1868; also see his 1844 essay in Darwin, 1909, and some of his writings collected in Barrett, 1977). As pointed out by Gayon (1998), Darwin seems to have clearly seen that while selection acts on individuals within a species or variety, it is actually trait-variants that are consequently differentially transmitted to the offspring generation, and the species or variety that is eventually modified by the differential accumulation of subsets of trait-variants over generations. This is a view that has successfully withstood the test of time, and also highlights the substantial difference between Darwin's conception of selection and those of Alfred Russel Wallace (Darwin & Wallace, 1858), who thought that selection acted primarily between varieties rather than individuals, or Herbert Spencer (1893), who conceived of selection as acting on individuals considered as a whole rather than on atomized trait-variants. There are some further aspects of Darwin's very nuanced conception of selection that are worth mentioning. Darwin (1859, 1868, 1871) clearly realized that selection acted on individuals that differed in their reproductive success, and that reproductive success could be achieved through better survival or greater reproduction, or both. Linking the relative reproductive success of individuals bearing different subsets of trait-variants to whether those trait-variants would tend to increase or decrease in the offspring generation was the intervening process of

hereditary transmission. As Darwin put it in his essay of 1844 (reproduced in Darwin, 1909), “Can it be doubted, from the struggle each individual has to obtain sustenance, that any minute variation in structure, habits, or instincts, adapting that individual better to the new conditions, would tell upon its vigour and health? In the struggle, it would have a better chance of surviving; and those of its offspring which inherited the variation, be it ever so slight, would also have a better chance. Yearly more are bred than can survive; the smallest grain in the balance, in the long run, must tell on which death shall fall, and which shall survive. Let this work of selection on the one hand, and death on the other, go on for a thousand generations, who will pretend to affirm that it would produce no effect, when we remember what, in a few years, Bakewell effected in cattle, and Western in sheep, by this identical principle of selection”. Thus, the hereditary transmission of trait-variants was a crucial component of selection, together with the twin struggle for survival and mates. Not having any knowledge of the mechanisms of heredity, Darwin was essentially agnostic regarding the origin of trait-variants, but assumed that the transmission fidelity (Box 1) of trait-variants was sufficiently high that it ensured that greater reproductive success, on an average, of individuals bearing a particular trait-variant in one generation would translate into an increased representation of that trait-variant in the offspring generation. Darwin, moreover, also appreciated that selection could operate through the enhanced reproductive success of close relatives, rather than that of the individual under consideration, and offered this insight as a possible explanation for the seeming paradox of altruistic sterility in honey bee workers (Darwin, 1859).

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**Box 1. Transmission fidelity and change in frequency of trait-variants**

Darwin’s conception of natural selection can be viewed as an algorithm that maps the ecological success of trait-variants in the struggle for existence, as reflected in their reproductive output, on to the evolutionary success of those trait-variants, as measured by a one-generation change in relative abundance, through the intervention of heredity. Thus, it is heredity, gene-based or otherwise, that drives the degree of concordance between relative reproductive output of a trait-variant and the one-generation change in its relative frequency. A reasonably strong concordance between ecological and evolutionary success is required for selection to result in adaptive evolutionary change. Key to this role of heredity is the degree to which offspring resemble their parent(s) with regard to the trait under scrutiny. In this context, we define transmission fidelity using a simple example of discrete generation uniparental inheritance, with no difference in survival to reproduction and total offspring production among individuals exhibiting different variants of that trait.

Let there be $m$ possible variants of a trait among individuals in a population, with frequencies $0 \leq f_i \leq 1$ ($i = 1..m$). Upon reproduction, assume that individuals exhibiting the $i^{th}$ trait-variant produce, on an average, a fraction $x_{ii}$ of their offspring exhibiting the same trait-variant, with the remainder ($1-x_{ii}$) exhibiting one of the other trait-variants, potentially including those with zero frequency in the parental generation. Then, $0 \leq x_{ii}\ 0 \leq 1$ is the transmission fidelity of the $i^{th}$ trait-variant.

Next, consider the frequency of the $i^{th}$ trait-variant in the next generation. This will depend upon not just the transmission fidelity of individuals exhibiting the $i^{th}$ trait-variant, but also the frequency of the $i^{th}$ trait-variant among the offspring of individuals exhibiting all other trait-variants. Let $x_{ij}$ be the probability that an individual exhibiting trait-variant $i$ in the parental generation produces an offspring exhibiting trait-variant $j$ ($j = 1..m$, but $\neq i$); clearly $\sum_{j \neq i}\ x_{ij} = 1-x_{ii}$. The, the frequency of the $i^{th}$ trait-variant in the next generation will be given by $f'_i = f_i x_{ii} + \sum_{j \neq i}\ f_j x_{ji}$. The point to be noted is that, even in this simple example with constant $x_{ii}$ and $x_{ij}$ over generations, and equal survival to reproduction and total offspring production by all individuals, regardless of which trait-variant they exhibit, the frequency of a trait-variant in the next generation will depend not just on its frequency in the previous generation and its transmission fidelity, but on the frequency of all other trait-variants in the previous generation and their respective probabilities of producing offspring exhibiting the focal trait-variant, which partly depend on their respective transmission fidelities.

In more realistic scenarios, changes in the frequency of trait-variants will be driven by differences among trait-variants in survival to reproduction, as well as in reproductive output. Moreover, for many inheritance systems, including the familiar gene-based Mendelian one, both $x_{ii}$ and $x_{ij}$ will often be frequency-dependent and, thus, liable to change over generations as frequencies of trait-variants change. Transmission fidelities may also change based on the mating system, *i.e.*, random mating, assortative mating, inbreeding etc. In general, high transmission fidelities will result in positive correlations between ecological and evolutionary success of trait-variants. Conversely, for many sets of $x_{ii}$ and $x_{ij}$ values, ecological and evolutionary success of trait-variants can be uncorrelated or even negatively correlated, thus generating the possibility that transmission fidelity patterns in some cases might even negate the effects of higher reproductive output on frequency increase. These points are elaborated further in Box 2.

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While he believed that selection acted on individuals most of the time, Darwin (1859) did not rule out the possibility, especially in social animals, of selection tending to increase the representation in

a species of trait-variants that enhanced the survival and persistence of social groups. One can view Darwin's conception of natural selection as providing a sort of algorithm which can accommodate multiple component mechanisms in varying contexts, rather than a specific mechanism. This algorithm, independently of the underlying mechanisms, serves to map the ecological success of trait-variants in the struggle for existence, as reflected in their reproductive output, on to the evolutionary success of those trait-variants, as measured by a one-generation change in relative abundance, through the intervention of heredity, as long as heredity ensures reasonably high transmission fidelity of the trait-variant in question. This crucial role of heredity in mediating adaptive evolutionary change can also be thought of as linking the causes of selection to their consequences for the composition of a population (*sensu* Joshi, 2005). Essentially, Darwin's conception of selection has not really been improved upon in the next one and half centuries except to apply its logic to phenomena unknown in Darwin's time, such as meiotic drive or transposable genetic elements, or to add mathematical detail to our appreciation of its consequences. It is in this sense that we think that, more than just the idea of natural selection, it was Darwin's nuanced elucidation of the myriad ways in which it could operate that constituted a major intellectual innovation.

In light of the above discussion, we now list what we believe to be the important constituents of what we refer to as the DC, in language more in consonance with our times than Darwin's.

1. Species arise from pre-existing species (descent with modification) and can diverge from one another over time (principle of divergence), thus explaining the diversity and relatedness of species.

2. Heredity must explain not just the transmission of similarities common to all members of a species, but also the transmission of individual trait-variants.

3. Individuals can be usefully thought of as a mosaic of reasonably independent trait-variants. Trait-variants are ubiquitous, arise almost continuously, in ways affected by the environment, and tend to be transmissible to offspring with fairly high and similar fidelity.

4. Organisms are typically involved in a struggle for existence, involving competition for resources, refuge from enemies, and mates. Certain trait-variants can confer advantages in this struggle to the individuals bearing them, or to relatives of those individuals.

5. Ecological success in the struggle for existence is ultimately measured by offspring production (also termed reproductive success). Though it is individuals that reproduce, one can meaningfully consider the average reproductive success of all individuals bearing a particular trait-variant as the reproductive success of that variant in comparison to that of other alternative variants of the same trait.

6. If the reproductive success of a trait-variant is higher than those of alternative variants of the same trait, the trait-variant will increase in representation in the next generation (this follows from 3, above). If the conditions that facilitated its higher reproductive success prevail over a long time, it may even entirely replace alternative variants of the same trait in a population.

7. Points 4, 5, and 6, above, constitute the typical process of selection, as commonly understood, as it operates among individuals. Selection can, however, also operate among groups in some situations. Selection provides an explanation for the adaptedness of species and is the major, but by no means the only, factor playing a role in micro-evolution and speciation.

8. Selection among individuals includes both differential reproductive success and, possibly differential transmission fidelity of the alternative trait-variants. Darwin's (1868) views on the latter are not very clear, but he, nevertheless, implicitly considered heredity to be an integral component of the selection process (for a very different and, in our opinion, erroneous view on this issue, see Bourat, 2015).

9. Considerations of development are not relevant to understanding hereditary transmission of trait-variants. They can, however, be important for understanding the origin of large scale variations among species or higher taxa, as well as some instances of micro-evolutionary change via growth correlations that can act independently of, or antagonistically to, selection.

10. Processes like selection, that can result in differentiation among populations, can also drive speciation over long periods of time (uniformitarianism). Change within a species via selection is typically slow (gradualism) (for a nuanced discussion of this issue, see Sober & Orzack, 2003).

Of the ten points making up the DC, only Darwin's gradualism and uniformitarianism have largely failed the test of time. In all other respects, the DC has not been seriously challenged, though many of its tenets have been considerably elaborated and added to in the past one and half centuries.

## The crystallization of the Modern Synthesis (MS)

از حُسنی ملیحی خود، شوری بہ جهان کردی
هر زخمی و بِسمِل را، مصروفی فُغان کردی
*az husn-e-maleeh-e-khud, shorey ba-jahaan kardi*
*har zakhmi-o-bismil ra, masroof-e-fughaan kardi*
(With piquant beauty, you did raise, a tumult spanning wordly space
Thus shrinking anguished, injured souls, to lamentation's forlorn face
– Maulana Jami)

We now turn to the relationship of the MS to the DC. The scientific history of the MS, and its foundations, consequences, and shortcomings, have already been extensively discussed over the past few decades (*e.g.*, Mayr & Provine, 1980; Antonovics, 1987; Gould, 2002; Sarkar, 2004; Amundson, 2005; Rose & Oakley, 2007; Plutynski, 2009; Pigliucci & Müller, 2010; Stoltzfus, 2017; Charlesworth et al., 2017; Dickins & Dickins, 2018; Hunemann, 2019; Dickins, 2021), and we will, therefore, restrict ourselves to highlighting certain aspects of the MS-DC relationship that we believe warrant greater attention than they have hitherto received. Darwin and the MS are separated by about 60-80 years and, during this time, there were several consequential developments in the attempt, inspired by Darwin, to understand evolution in terms of an interplay between ecology and heredity. On the one hand, there was a new focus on interpreting findings in natural history, biogeography, palaeontology and systematics in terms of evolutionary principles and, on the other, attempts to interpret the principles of heredity and selection statistically, rapidly yielding ground in the early 1900s to Mendelian genetics. Advances in development did not play a very major role in this phase of the growth of evolutionary thought. Ironically, August Weismann's attempt to provide an explanation for differentiation of cell types in the course of embryonic development led to a further separation of development and heredity, and also seemed to rule out the possibility of the inheritance of acquired characters due to the sequestration of the germplasm early in development (Weismann 1889, 1893a; but see also Winther, 2001), thus leading to a narrowing of the DC that was only partly ameliorated in the MS. Weismann (1893b, 1902) also insisted on the primacy of selection over heredity in evolution, in the context of critiques of the efficacy of selection in bringing about evolutionary change (Galton, 1877, 1889, 1894; Spencer

1893). A good account of this phase in evolutionary thought, termed Neo-Darwinism by George Romanes and others, is given by Forsdyke (2001).

The most consequential development between Darwin and the MS that substantially determined the form the MS took was undoubtedly the rediscovery of Mendel's work in 1900, followed by the linking of Mendel's hypothetical factors (genes) to chromosomal locations, largely through work in T. H. Morgan's laboratory in the early decades of the twentieth century (Schwarz, 2008). Darwin had placed heredity centre-stage in the study of evolution, even though his theory of pangenesis did not last, being discredited experimentally by Galton (1871) shortly after its full exposition by Darwin (1868). The early decades of twentieth century genetics not only cemented heredity in this central position in evolutionary explanation, but also completed the already substantial exclusion of developmental considerations from our understanding of heredity, a process ironically led by T. H. Morgan, an embryologist who was initially opposed to the ideas of both Mendel and Darwin (Allen, 1985; Amundson, 2005; Sarkar, 2006, 2017). Once the principles of transmission genetics had been verified, and extended from families to populations, it became crucial – in light of the tension between heredity and selection in preceding decades – to ascertain whether the Darwinian conception of selection was in fact compatible with the now known mechanism of heredity (Sarkar, 2004; Joshi, 2017b).

In many respects, the MS represented a conceptual narrowing of the scope of evolutionary thinking embodied in the DC, even though it was factually more expansive, incorporating new findings from heredity, evolutionary ecology, palaeontology and systematics. This narrowing is also reflected in the view that large parts of the MS that incorporated genetics into the view of adaptive evolutionary change through selection, especially the work of Ronald Fisher and Sewall Wright, are better described as constituting a reduction rather than a synthesis (Sarkar, 2004), although that distinction is not very relevant to our purposes in writing this paper. We now examine some of the ways in which the MS differed from the preceding DC, and emphasize certain aspects of the conceptual shifts involved, which we believe are important to understanding several sources of confusion in the evolutionary discourse over the past many decades, especially those surrounding the so-called gene's eye view of evolution (Ågren, 2021). We do this by listing once again the ten major constituents of the DC, along with a brief explanation of how the MS changed or did not change each of them, and then offering some thoughts on how to resolve some of these confusions.

1. Species arise from pre-existing species (descent with modification) and can diverge from one another over time (principle of divergence), thus explaining the diversity and relatedness of species.

*Essentially unchanged in the MS.*

2. Heredity must explain not just the transmission of similarities common to all members of a species, but also the transmission of individual trait-variants.

*Accepted implicitly, in a much narrower form, in the MS through the incorporation of Mendelian transmission genetics in families and populations. MS, unlike DC, incorporated a specific mechanism – genes and principles of their transmission – of heredity. Thus a more generalized view of heredity was narrowed down to a specifically Mendelian one.*

3. Individuals can be usefully thought of as a mosaic of reasonably independent trait-variants. Trait-variants are ubiquitous, arise almost continuously, in ways affected by the environment, and tend to be transmissible to offspring with fairly high and similar fidelity.

*In the MS, trait-variants are often characterized at the level of the genotype or karyotype, rather than phenotypically. Genotypic/karyotypic trait-variants are ubiquitous, arise almost continuously by mutation and changes in the structure and number of chromosomes during meiosis/gametogenesis. The MS differs from the DC in ruling out the inheritance of acquired characters in the Lamarckian sense, though some aspects of the environment are thought to play some role in generating mutational variation. By basing inheritance solely on Mendelian genetics, the MS implicitly takes a more nuanced stance on transmission fidelities than the DC: in Mendelian genetics, transmission fidelities can vary among genotypic variants and are typically frequency-dependent (Box 2). Thus, in the MS, it is implicit that the positive relationship between reproductive success and increase in frequency of a variant can break down as a result of frequency-dependence and mating system (see also point 8 in this list). In the DC, Darwin's characterization of the 'powerful principle of heredity' implicitly assumed that transmission fidelities of all trait-variants are > 0.5. It is not clear whether Darwin thought that transmission fidelities could vary among trait-variants. A good discussion of some issues pertaining to transmission fidelity can be found in Frank (2012).*

4. Organisms are typically involved in a struggle for existence, involving competition for resources, refuge from enemies, and mates. Certain trait-variants can confer advantages in this struggle to the individuals bearing them, or to relatives of those individuals.

*Essentially retained in the MS, albeit with a slightly more abstract view of 'competition', including that between allelic or genotypic trait-variants, as opposed to competition between individuals.*

5. Ecological success in the struggle for existence is ultimately measured by offspring production (reproductive success). Though it is the individual that reproduces, one can meaningfully consider the average reproductive success of all individuals bearing a particular trait-variant as the reproductive success of that variant in comparison to that of other alternative variants of the same trait.

*Essentially retained in the MS, with trait-variant often being construed more specifically as a genotypic variant.*

6. If the reproductive success of a trait-variant is higher than those of alternative variants of the same trait, the trait-variant will increase in representation in the next generation (this follows from point 3 in this list). If the conditions that facilitated its higher reproductive success prevail over a long time, it may even entirely replace alternative variants of the same trait in a population.

*Essentially retained in the MS, with trait-variant often being construed more specifically as a genotypic variant, but with the caveat that the relationship between reproductive success and increase/decrease of a trait-variant can be complex (see also Box 2, and point 3 in this list). Since genic heredity follows Mendelian rules, transmission fidelities of genotypic trait-variants are frequency dependent, permitting the maintenance of stable polymorphisms, the existence of unstable polymorphisms and sensitivity to initial conditions, and complex and often counter-intuitive behaviour of genotypic frequencies under selection and different mating systems*.

7. Points 4, 5, and 6, in this list, constitute the typical process of selection as it operates among individuals. Selection can, however, also operate among groups or at levels below the individual in some situations (Lewontin, 1970). Selection provides an explanation for the adaptedness of species and is the major, but by no means the only, factor playing a role in micro-evolution and speciation.

*Essentially unchanged in the MS, but with a somewhat greater emphasis on the primacy of selection, and of selection acting among individuals rather than groups, than in the DC*.

8. Selection among individuals includes both differential reproductive success and possibly differential transmission fidelity of the alternative trait-variants. Darwin's (1868) views on the latter

are not very clear, but he, nevertheless, implicitly considered. heredity to be an integral component of the selection process.

*Essentially retained in the MS, in a stronger form than in the DC, but very well disguised, and not reflected explicitly in how selection is discussed. Because of its commitment to exclusively genic heredity, the MS depicts micro-evolutionary dynamics in a manner that makes it hard to see the implicit effects of transmission fidelity on change in genotypic or allele frequencies (see also Box 2, and points 3 and 6 in this list). This problem is exacerbated by the large-scale deployment in population genetics of models that track micro-evolutionary change through allelic rather than genotypic frequencies, at least when random mating can be assumed. The benefit of tracking alleles rather than genotypes is that the number of state variables is reduced. The drawback is that, because allelic variants have a transmission fidelity of 1, unless mutation is invoked, the role of transmission fidelity as an integral part of the selection process, and the effects of mating system on transmission fidelity, are rendered implicit and invisible. Moreover, the discourse in much population genetics-based MS writing, though not in behavioural ecology, tends to consider selection as operating on viability by default, treating sexual selection or fecundity/fertility selection almost as afterthoughts. This further obfuscates the roles of heredity and mating system, because differential reproductive success of genotypes in viability selection models arises entirely through genotypic differences in viability, and the effect of transmission fidelity is subsumed into the non-linear, frequency-dependent marginal allelic fitness terms.*

9. Considerations of development are not relevant to understanding hereditary transmission of trait-variants. They can, however, be important for understanding the origin of macro-evolutionary variations among species or higher taxa, as well as some instances of micro-evolutionary change via growth correlations that can act independently of, or antagonistically to, selection.

*Essentially unchanged in the MS, but with a greater tendency to see development as irrelevant to the origin of macro-evolutionary variations among species or to micro-evolutionary change.*

10. Processes like selection that can result in differentiation among populations can also drive speciation over long periods of time (uniformitarianism). Change within a species via selection is typically slow (gradualism).

*Essentially unchanged in the MS.*

**Box 2. Transmission fidelity in population and quantitative genetic models**

In this Box, we use the formalism from Box 1 to illustrate how the gene-based Mendelian mechanism of heredity for trait-variants coded for by genotypes at one locus results in a frequency-dependent, type-variant-specific pattern of transmission fidelities. Moreover, the pattern of transmission fidelities is potentially affected in a type-variant-specific manner by the mating system. We also discuss, for polygenic trait-variants, the relationship between transmission fidelity of a trait-variant and its breeding value.

Consider three trait-variants (1,2,3), coded for by genotypes $A_1A_1$, $A_1A_2$, and $A_2A_2$, respectively. Let their frequencies in a given generation be $f_1$, $f_2$, and $f_3$, respectively. We assume no differences among trait-variants in survival to reproduction, or reproductive output. If the mating system is that of complete selfing, the transmission fidelities, and proportion of offspring exhibiting each of the other possible trait-variants, are given by:

$x_{11} = 1$; $x_{12} = 0$, $x_{13} = 0$

$x_{22} = 0.5$; $x_{21} = 0.25$, $x_{23} = 0.25$

$x_{33} = 1$; $x_{31} = 0$, $x_{32} = 0$.

Note that, in this case, transmission fidelities differ between trait-variants 2 and 1,3, but are constant across generations for all three trait-variants. Moreover, even in the absence of differences in expected reproductive output, $f_1$ and $f_3$ will increase over generations, relative to $f_2$, because

$f'_1 = f_1 + 0.25f_2$

$f'_2 = 0.5f_2$

$f'_3 = f_3 + 0.25f_2$.

This change in the phenotypic composition of the population is driven entirely by the differences in transmission fidelity across trait-variants, and is non-adaptive in that it does not result in any increase in the average expected offspring production of the population.

Now, consider another non-adaptive example involving the same trait-variants, but under a random mating system. Now, the transmission fidelities, and proportion of offspring exhibiting each of the other possible trait-variants, are frequency-dependent, and given by:

$x_{11} = f_1 + 0.5f_2$; $x_{12} = f_3 + 0.5f_2$, $x_{13} = 0$

$x_{22} = 0.5$; $x_{21} = 0.5(f_1 + 0.5f_2)$, $x_{23} = 0.5(f_3 + 0.5f_2)$

$x_{33} = f_3 + 0.5f_2$; $x_{32} = f_1 + 0.5f_2$, $x_{31} = 0$.

Therefore, the trait-variant frequencies in the next generation are given by

$$f'_1 = f_1(f_1 + 0.5f_2) + 0.5f_2(f_1 + 0.5f_2)$$

$$f'_2 = 0.5f_2 + f_1(f_3 + 0.5f_2) + f_3(f_1 + 0.5f_2)$$

$$f'_3 = f_3(f_3 + 0.5f_2) + 0.5f_2(f_3 + 0.5f_2)$$

These equations for change in trait-variant frequency will result in Hardy-Weinberg equilibrium in one generation when the following are satisfied:

$$f_1 = (f_1 + 0.5f_2)^2$$

$$f_2 = 2(f_1 + 0.5f_2)(f_3 + 0.5f_2)$$

$$f_3 = (f_3 + 0.5f_2)^2.$$

These two simple examples of an alternative mathematization of basic one-locus population genetics models serve to demonstrate several points about transmission fidelities under Mendelian heredity. First, differences in transmission fidelity across trait-variants can lead to changes in the phenotypic composition of a population even in the absence of differences in relative reproductive output (fitness) across trait-variants. Second, transmission fidelities can change if the mating system changes. Third, equilibria in trait-variant frequency ($f'_i = f_i$ for all $i$) can arise because losses of similar phenotype offspring of one's own ($f_i(1\text{-}x_{ii})$) can be exactly offset by gain of similar phenotype offspring through the reproduction of other type-variants ($\sum_{j \neq i} f_j x_{ji}$), for all $i,j$. Finally, if we consider typical one-locus selection models, which assume differences in relative reproductive output (fitness) across trait-variants, inequalities between the various $f_i(1\text{-}x_{ii})$ and $\sum_{j \neq i} f_j x_{ji}$ can similarly result in equilibria in trait-variant frequency by exactly cancelling out the fitness differences among trait-variants; this is what happens in the canonical case of overdominance for fitness in a one-locus model. More generally, in selection models, inequalities between the various $f_i(1\text{-}x_{ii})$ and $\sum_{j \neq i} f_j x_{ji}$, which change over generations due to frequency-dependence of the $x_{ii}$ and $x_{ji}$ terms, interact with among-trait-variant fitness differences in shaping the dynamics of trait-variant frequencies, thereby underscoring the role of transmission fidelity as an integral part of the selective process.

The above examples assume discrete trait-variants arising from different genotypes at a locus, and the broad implications generalize to traits governed by a small number of loci. If we consider quantitative (polygenic) traits, then trait-variants are continuous rather than discrete, with each phenotypic value constituting a distinct trait variant. In such cases, the transmission fidelity of a trait-variant is closely associated with its breeding value, the deviation of the mean phenotypic value of its offspring from the overall population mean. Transmission fidelity of a trait-variant

would then be reflected by the deviation of the mean phenotypic value of the offspring of all individuals exhibiting that trait-variant (these individuals may have different underlying multi-locus genotypes) from the phenotypic value for that trait associated with the common trait-variant of the parental individuals.

Two main points we wish to stress here, when considering Mendelian heredity, are that (i) transmission fidelity affects how differences in reproductive output among trait-variants translate into changes in their frequencies in complex frequency- and mating system-dependent ways, resulting in diverse patterns of dynamics that will not necessarily culminate in the fixation of the trait-variant with the greatest reproductive output, and (ii) this important role of transmission fidelity in the selective process is implicit and largely hidden in the standard mathematization of population and quantitative genetics models, especially when they use allele rather than genotypic frequencies as state variables because, in the absence of mutation or migration, an allelic variant has a transmission fidelity of 1, even though genotypic variants do not.

We note, in conclusion, that the Price (1970) equation also explicitly incorporates the notion of transmission fidelity in its apportioning phenotypic change to a sum of terms representing selection (differential reproduction) and transmission fidelity, respectively. A similar exercise to the one above, that interprets population genetics models from the perspective of the Price equation, can be found in Box 2 of Joshi (2020).

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As we can see, the differences between the MS and the preceding DC are neither very large nor substantive in a conceptual sense, although some statisticalist philosophers of evolution have a somewhat different view (see Walsh et al., 2017). The MS retained Darwin's (1859, 1868, 1871) crucial atomization of individuals into traits, his realization that development was largely irrelevant to understanding either heredity or micro-evolutionary change, and his central insight that differential reproductive success of trait-variants would, thanks to heredity, translate into altered representation in subsequent generations. Elements of the DC that were not included in the MS were the Lamarckian inheritance of acquired characters, the recognition of group selection in the classic sense as potentially important in some evolutionary scenarios, the possibility of a variety of mechanisms of inheritance, and the appreciation that development may have a major explanatory role in issues surrounding the origin of macro-evolutionary variations, the divergence among species, and some instances of micro-evolutionary change. Surprisingly, the MS strengthened the

claim of both gradualism and uniformitarianism, especially in its genetic expressions (*e.g.*, Dobzhansky, 1937), even though these were not conceptually crucial to the Darwinian *weltanschaung*.

The MS differed from the DC in having an explicit mechanism of heredity in the form of Mendelian genetics. While this helped show that the mechanism of natural selection was indeed compatible with heredity (Fisher, 1930; Wright, 1931, 1932; Haldane, 1932), it also had some, perhaps unintended, consequences that have resulted in considerable ongoing confusion about the units and levels of selection, in addition to ruling out non-genic forms of inheritance. The MS, especially in its population genetics *avatar*, substituted the more specifically construed genotypic trait-variants for phenotypic trait-variants and, moreover, when a random mating assumption could be deployed, typically modelled the dynamics of genotypic trait-variants at the allelic rather than the genotypic level. It also introduced the concept(s) of fitness, which was heuristically useful but also led to a lot of confusion (*e.g.*, Kimbrough, 1980; Matthen & Ariew, 2001; Sober, 2001; Ariew & Lewontin, 2004; Roff, 2008; Orr, 2009) of the kind that Wittgenstein (1921/fresh Eng. transl. 1994) had warned about. The use of allelic level trait-variants and fitness as reproductive success diverted attention from the essential nature of selection acting among individuals, including transmission fidelity as an integral component, and also from the effects of frequency and mating system on transmission fidelity (see Box 2). In addition, this focus on allelic variants also gave rise to an entirely avoidable and long-lived debate about whether the individual or the gene (allele) is the most appropriate unit of selection (*e.g.*, Okasha, 2006; Ågren, 2021), by facilitating what is often termed the gene's eye view of evolution. To our mind, this is a misleading contrast: the crucial difference is between individuals and trait-variants, and this was introduced as early as in the DC. We suggest that, in this DC perspective, there is no dispute about the biological units relevant to the causes and consequences of selection, respectively. For understanding the causes of selection, the relevant unit is the individual, whereas for studying the consequences of selection, it is the trait-variant, and not the individual. The contradistinction of the individual to the gene, that happens very commonly in the units of selection debates, merely, and unhelpfully, mapped the original individual versus trait-variant contrast onto a broader and extremely contentious debate about genetic determinism versus free will, or agency. We discuss this issue, and its consequences for the conceptualization of fitness, in greater detail in a later section. The levels of selection debate about whether selection acts primarily on individuals or groups was eventually, after a few decades of extreme antipathy to group selection, resolved, especially with the development of multi-level

selection theory (Frank, 2013 and references therein; Okasha, 2006; detailed accounts in Lewontin, 1970; Sober & Wilson, 1998).

Interestingly, and in a striking reminder that the episodes in the history of ideas are often as inexplicable as those in the history of states, the MS involved two very different treatments of the earlier biometric work on selection and heredity by Rafael Weldon and Karl Pearson by the same individual – Ronald Fisher. The work of Weldon and Pearson was itself a development of earlier statistical insights from Galton, but differing from it in significant ways, especially regarding his doubts about the efficacy of selection in the face of heredity (discussed in Joshi, 2017a,b), On the one hand, Fisher's (1918) treatment of traits affected by a large number of genetic loci with small individual effects on a phenotype effected a reduction of biometry to Mendelian genetics (Sarkar, 2004), whereas on the other (Fisher 1930, 1941), it gave rise to what was, although couched in explicitly genetic terms, essentially a phenotypic theory of Darwinian micro-evolutionary change (*i.e.*, quantitative genetics *e.g.*, Mather, 1943), in stark contrast to the overall highly genetic bias of the MS. We discuss this in the next section.

## Quantitative genetics as a phenotypic theory

ہوئی مِنّتکشِ تابِ شُنیدن داستاں میری

خموشی میں ہوئی مدفُون ہر آہ و فُغاں میری

*hui minnatkash-e-taab-e-shuneedan dastaan meri*

*khamoshi mein hui madfoon har aah-o-fughaan meri*

(My story begs a listening crowd, that hears with comprehending skill

Till then, my sighs and forlorn cries, lie buried in this silence, still

– Nabraas Akbarabadi)

Several years ago, we had expressed our surprise that quantitative genetics does not appear in any comprehensive or meaningful way in the EES-MS debate, despite its essentially constituting a phenotypic theory of micro-evolutionary change that does not necessarily assume genic inheritance, and being far more inclusive and flexible than population genetics in this role (Joshi, 2005; Prasad et al., 2015). With the notable exception of work by Etienne Danchin and colleagues (*e.g.*, Danchin et al., 2011, 2013, 2019), and some specific attempts to integrate epigenetic inheritance and

946 quantitative genetic analyses (*e.g.*, Spencer, 2003, 2009; Santure & Spencer, 2011; Banta &
947 Richards, 2018), the situation is unchanged. We think this is odd because quantitative genetics
948 actually incorporates or addresses some of the issues that EES proponents often accuse evolutionary
949 genetics of overlooking. We reiterate some of these aspects here and also discuss how, like
950 population genetics, quantitative genetics also tends to obscure some facets of the role of
951 transmission fidelity in micro-evolutionary change.
952
953 To describe quantitative genetics as dealing with the inheritance of polygenic or continuous traits,
954 as text-books tend to do, is about as fair as describing the phenomenal Brazilian footballer Ronaldo
955 as someone who ran about a field kicking a ball. It is an accurate, but ultimately trivial, description
956 that fails to capture the essence of the achievement involved. Quantitative genetics grew out of
957 Fisher's (1918) demonstration that the statistical results of Karl Pearson and the biometricians on
958 the phenotypic correlations between relatives were consistent with Mendelian genetics, on the
959 assumption that continuous phenotypes could result from the effects of many genes with
960 individually small phenotypic effects. The validation of previous work on heredity and evolution,
961 by showing it to be consistent with Mendelian principles, was an urgent and significant concern in
962 the years following the rediscovery of Mendel's work. However, although it was couched in
963 specifically genetic terms, quantitative genetics essentially provided a phenotypic theory of micro-
964 evolutionary change (Joshi, 2005; Prasad et al., 2015; Queller, 2017). The concept of the breeding
965 value (additive genetic value) of an individual with a given phenotypic value in a certain population
966 and environment was effectively a way of operationalizing transmission fidelity in the absence of
967 any knowledge of the details of the genotype to phenotype mapping, thus distilling out the
968 consequential essence of the complex polygenic mechanism of heredity (see also Box 2).
969 Transmission fidelity could thus be combined with reproductive success of individuals with
970 differing phenotypic values, to yield evolutionary change in the location of the mean of the
971 phenotypic distribution of that trait in that population and environment, due to selection. Even in the
972 specific context of an underlying Mendelian genetic model, the additive genetic value of an
973 individual accounts for the statistical effects of dominance and epistasis within its genome on
974 offspring phenotype, something that is often not appreciated. Essentially, the Breeders' equation in
975 quantitative genetics describes the one-step shift under selection in the mean of a phenotypic
976 distribution for a continuous trait as $R = h^2.S$, where $R$ is the response, reflecting the one-step
977 change in mean phenotypic value, $h^2$ is the ratio of additive genetic variance (the variance in
978 breeding values among individuals) to the phenotypic variance, and $S$ is a measure of the strength of
979 selection. In this formulation, $h^2$ and $S$ effectively reflect transmission fidelity of trait-variants with

different phenotypic values (Box 2), and their reproductive success, respectively. The original formulation of breeding value (or additive genetic value) by Fisher was for a case of random mating (Falconer, 1985), but the logic can be extended to non-random Mendelian mating systems (Muralidharan & Jain, 1992a,b), or even to systems with arbitrary non-genic mechanisms of heredity, by re-defining breeding value as a transmission fidelity metric for trait-variants and quantifying it appropriately. Thus, the quantitative genetics framework has the flexibility to explain micro-evolutionary change under non-genic inheritance through its inclusion of a transmission fidelity perspective (Danchin et al., 2011, 2013, 2019), and could be fruitfully used very generally across diverse systems, even though this flexibility is often hidden behind its explicitly genetic presentation. A systematic elucidation of when a generalized quantitative genetic framework will or will not suffice to capture micro-evolutionary dynamics under non-genic inheritance could be a fruitful avenue of further research.

Another point worth noting about the quantitative genetics formulation is that it explicitly includes the phenomenon of phenotypic plasticity, something the MS is often accused of ignoring. The partitioning of phenotypic value of an individual into a genotypic and an environmental value, and a stochastic error term ($P = G + E + e$) incorporates the notion that the same genome can give rise to different phenotypic values for a trait in different environments, the text-book definition of phenotypic plasticity. A genotypic value by environmental value interaction ($G$ x $E$ interaction) implies genetic variation for phenotypic plasticity, and a $G$ x $E$ covariance of the beneficial sort can constitute adaptive phenotypic plasticity.

Finally, we stress that continuous traits affected by many multi-allelic loci of individually small phenotypic effect have a tremendous ability to generate multiple trait-variants (individuals with different phenotypic values for that trait) through the shuffling of standing within- and among-locus genetic variation alone (Teotónio et al., 2009; Mueller et al., 2013; Matuszewski et al., 2015; Philips et al., 2018; Hickey & Golding, 2021; Kawecki et al., 2021). One outcome of this is that even a sample of relatively few genomes from a population can rapidly regenerate the full pre-sampling phenotypic distribution. Therefore, the criticism that available phenotypic variation in a population may not be isotropic (*e.g.*, Salazar-Ciudad, 2021) might often not hold true for continuous traits within populations, at least in the sense of availability of variants, even if not in the sense of a uniform distribution of the probabilities of their occurrence.

## The nature(s) of fitness, and a micro-evolutionary red-herring

هر لهذه به شکلی بُتان عیّار بر آمد، دِل بُرد و راون شُد

هردم به لباسی دیگران یار بر آمد، گه پیِر و جوان شُد

*har lehzeh ba-shakl-e-butaan ayyaar bar aamad, dil burd o nihaan shud*

*hardam ba libaas-e-digaraan yaar bar aamad, geh peer-o-jawaan shud*

(The Beloved, in artful varied forms, does steal my heart and then depart

One moment young, another old, in myriad garbs; this is his art

– Maulana Rumi)

Although the exact origins of the term ‘fitness’ are hard to pinpoint, both the term and the concept featured repeatedly in the work of Karl Pearson and, by the time the MS was being announced (Huxley, 1942), were an important part of the micro-evolutionary lexicon and conceptual tool-kit (Gayon, 1998). However, fitness has been used in multiple senses in the MS and later, resulting in manifold confusions that reflect its ultimate origins in Spencer’s (1864) misplaced rejection of trait-variants as the units of selection in favour of whole individuals, implicit in his coining of the most unfortunate phrase ‘the survival of the fittest’. The crux of the problem is that fitness, even in its correct and restricted micro-evolutionary context, is variously defined on both individuals and trait-variants (phenotypic, genotypic or allelic), and can be used to mean the reproductive success of an individual, the average reproductive success of individuals exhibiting a specific trait-variant, the one-step change in frequency of a trait-variant, or the long-term expected evolutionary success of a trait-variant or lineage. Thus, fitness is used both as a causal predictor of subsequent changes in relative representation of different types in a population, as well as a descriptor of those changes (Ariew & Lewontin, 2004). Indeed, fitness, like Rumi’s ‘artful Beloved’ seems to appear before us in varied forms and disguises at different times and places. Text-books exacerbate this confused state of affairs by often defining fitness, towards the earlier part of the book, as the reproductive success of individuals, without mentioning that it is but one of the senses in which the term is used, and then, ironically, proceeding to use fitness in one or more of its other senses later on. Such a use of fitness for different sorts of attributes of entities at various levels of biological organization is clearly undesirable, as has been repeatedly pointed out (Kimbrough, 1980; Matthen & Ariew, 2001; Sober, 2001; Ariew & Lewontin, 2004). Yet, with the notable exception of the work of Earnshaw-Whyte (2012), no resolution has been offered beyond a cogent argument that fitness cannot possibly

do justice to the myriad roles we expect it to play (Ariew & Lewontin, 2004). Here, we outline the contours of what we believe is a long overdue and useful resolution.

The following discussion pertains only to micro-evolutionary change in frequencies of trait-variants due to selection, falling under the category of '*micro-dynamics*' issues in the schema presented in Table 1. Indeed, strictly speaking, it is best to restrict consideration of selection to situations where entities at or below the level of a species are being considered. The concept of selection implicitly includes a notion of competition, albeit often in a broadly metaphorical sense, and it is not clear whether entities at the level of higher taxa can be meaningfully thought of as being in competition. We will mostly restrict ourselves to discussing selection at the level of an individual, as contrasted to a trait-variant, as that is the comparison about which much confusion has arisen in the past. The two most crucial questions that need to be addressed to clarify the confusions about fitness are: (i) whether fitness is better conceived of as an attribute of an individual, or is it more useful to think of fitness as ascribable, on an average, to a trait-variant as an abstract entity (collection of all individuals in a population exhibiting that trait-variant)? and (ii) whether fitness is better conceived of as a measure of reproductive success (*e.g.*, lifetime offspring production) or as reflecting a one-step change in frequency (the time-step will typically, but not always, be a generation) of the relevant entity type? Our answer to these questions is that it is best to think of fitness as reflecting the change in relative representation of a trait-variant in the population. Indeed, we believe that the individual is not much more than a red-herring in the context of trying to understand and depict micro-evolutionary change (*i.e.*, the consequences of selection), and one that has led to tremendous confusion in evolutionary discourse, as we discuss below.

The popularity of defining fitness as an attribute of an individual, reflecting its reproductive success in a given ecological context, seems to arise from the intersection of a comfort with agential thinking and a failure to differentiate between the relevance of agency in different biological contexts and at different levels of biological organization, for example cells versus individual organisms (Okasha, 2018). It appears that the tendency to ascribe agency to humans, animals, plants and even inanimate objects has deep roots in the human mind (*e.g.*, Dennett, 2006; Lindstrøm 2015), and it could perhaps have arisen through what Rose (1998) termed 'immanent Darwinism'. However, it needs to be recognized that the agency of a living individual, or of its constituent cells, is largely only relevant in the contexts of ecology (including successful reproduction) and development, but not in the domain of explaining the dynamics of micro-evolutionary change. This is because individuals, considered holistically, are effectively a unique constellation of variants of

many different traits and, as such, have no continuity across generations, unlike the trait-variants themselves. The agency of an individual can, therefore, affect its reproductive success, but not any meaningful measure of micro-evolutionary dynamics, because the transmission fidelity of any of a unique set of trait-variants is zero, by definition. A unique individual may produce many offspring, but none of them will be the same as the parent, except in the case of asexual reproduction. This might be termed the 'infinite individuals problem' for sexually reproducing species: if individuals are phenotypically unique, then any explanation of micro-evolutionary dynamics at the level of the individual will be restricted to a description of how one set of unique individuals was replaced by another set of different, equally unique, individuals in the next generation. For this reason, we believe, as did Darwin, drawing upon the experience and practices of breeding, that it is best to focus on trait-variants, not individuals, if our analyses are to have any chance of explaining patterns in micro-evolutionary change arising as a consequence of selection.

Having settled upon the trait-variant as the appropriate focus of an analysis of micro-evolutionary dynamics, we now consider whether reproductive success or a one-step change in the frequency of trait-variants constitutes a better way of thinking about fitness. The reproductive success of a trait-variant can be equated to the average reproductive success of all individuals in the population who exhibit that variant, while the one-step change in frequency quantifies the difference, across a generation, in the representation of that trait-variant in the population, relative to other variants of the same trait. Defining fitness as reproductive success may at first sight appear to satisfy the scientist's inherent *ceteris paribus* privileging of *a priori* prediction over *post facto* description, because fitness differences among trait-variants can then be thought of as predicting changes in their frequency over generation. However, in this context, all else is rather emphatically not equal. Differential reproductive success of trait-variants is positively correlated with relative representation in the next generation only under the implicit DC assumptions that transmission fidelities of trait-variants are typically high, and similar in magnitude (see also Box 2). Thus, the ability of fitness defined as reproductive success to serve as a predictor of change in frequency is not inherent in the measure. The only other benefit of defining fitness as the reproductive success of a trait-variant is that it preserves the notion that fitness is an intrinsic attribute of a type, or to be more precise, of the interaction between the biological characteristics of a type and its ecological context. Thus, we can treat fitness, as text-books typically do, as a type attribute, and consider frequency-, density-, or sex-dependent fitnesses to be special cases. While this usage confers the comfort of familiarity, we do not believe this is helpful, any more than the tendency of genetics text-books to treat epistasis as a 'deviation' or 'exception' to Mendel's laws is. If, on the other hand,

we define fitness as the one-step change in the frequency of a trait-variant, there are several conceptual benefits.

First, fitness of the trait-variant now incorporates not just reproductive success but also transmission fidelity, which renders explicit the connection between fitness and the process, as opposed to the act, of selection. When a breeder trying to develop a variety with large body size chooses the biggest individuals in a population to breed from, that is an act of selection, which may or may not yield a response depending upon the level of additive genetic variance for body size in that population. At the same time, the entire process of generating the variety with larger average body size than its ancestors, encompassing both the act of selection, and the response to it, is also referred to as selection: this is what we are terming the process of selection. Our point is that the act of selection involves only differential reproductive success, whereas the process of selection requires differential *heritable* reproductive success, thereby encompassing the act of selection, transmission fidelity, and the response to selection. We suggest that a concept and definition of fitness that reflects the process of selection is preferable to one that merely reflects the act of selection, even though the difference is only one of perspective.

Second, because the one-step increase in the frequency of a trait-variant depends on the interaction between bearers of alternative variants of that trait for survival, refuge and reproduction, fitness defined thus is always frequency-dependent. Because this measure of fitness includes transmission fidelity, it follows that fitness defined thus is also always dependent upon the mechanism of inheritance (genic or otherwise) as well as on the patterns of interaction among individuals that can alter the trait-variants they bear. These interactions, in situations of genic inheritance, constitute the mating system *i.e.*, the set of probabilities of individuals with trait-variant $i$ mating with individuals bearing trait-variant $j$ ($i,j, = 1..n$, if there are $n$ variants of that trait in the population); in cases involving cultural inheritance, interactions would be reflected in the likelihood of an individual bearing cultural trait-variant $i$ passing on $i$ to an individual that earlier exhibited cultural trait-variant $j$, via learning, in its broad sense. In all such interactions, not just means but also variances will have consequences for the resulting micro-evolutionary dynamics. This manner of defining fitness, therefore, also opens up the possibility of a more general unified theory of selection that is agnostic to the mode of inheritance, something which a definition of fitness as reproductive success does not easily support, though quantitative genetics successfully took some steps in that direction. In essence, this is what the Breeders' Equation in quantitative genetics achieves, by combining fitness as reproductive success (in the $S$-term) with transmission fidelity pattern (in the $h^2$-term for

univariate selection, or the **G**-matrix for multivariate selection), although this is not immediately obvious from the form of the equation because the $h^2$-term and the **G**-matrix are formulated in explicitly genetic terms, though they need not necessarily be so. This approach becomes more clearly apparent in the Price (1970) equation, with its ascribing of phenotypic change to the sum of terms representing selection (differential reproduction) and transmission fidelity, respectively. Similar approaches for understanding dynamics in diverse non-biological systems as generalized Darwinian processes are also now being explored (*e.g.*, Reydon & Scholz, 2015), potentially justifying Haeckel's expectation that Darwinian thinking would become important even in disciplines beyond biology (Richards, 2008) and Price's (1995) desire to do for selection what Claude Shannon achieved for information.

Third, and perhaps most importantly, once fitness is defined as a one-step change in trait-variant frequency, fitness is always inclusive, unless transmission fidelities of all trait-variants equal 1. This is because the fitness of a trait-variant accrues either through the reproduction of individuals bearing that trait-variant (direct fitness), or through the reproduction of individuals bearing another trait-variant, but with transmission fidelity less than 1 (indirect fitness). This is a more satisfying property for fitness, compared to the situation at the individual level in which fitness can be either direct or inclusive, depending on social context, and will likely reduce the confusion that surrounds the debates around kin-selection and inclusive fitness (reviewed by Frank, 2013; Birch & Okasha, 2015; Kramer & Muenier, 2016).

In contrast to these benefits of treating fitness as one-step frequency change, any advantage of defining fitness as reproductive success accrues only if we define fitness on individuals. However, as we have seen, that definition cannot properly capture the essence of the process of selection due to the infinite individuals problem. Consequently, we believe that there is a strong case for restricting the use of fitness to one-step frequency change in alternative variants of the same trait, and not using fitness to also refer to reproductive success, or to individuals. We stress that we are not suggesting that measuring and thinking about the lifetime reproductive success of individuals is not important to understanding microevolutionary change: its importance is entirely retained in our perspective. All we are suggesting is that we not label the lifetime reproductive success of an individual as its 'fitness', restricting the use of that term to the one-step change in the frequency of a trait-variant. We next touch upon some of the various confusions that would be dispelled by doing this.

One of the most contentious issues in micro-evolution in the past half century has been the gene's eye view of evolution (recent book-length review by Ågren, 2021), initially popularized by Dawkins (1976), though its antecedents go back to Williams (1966) and, some argue, to Fisher (1930) and Hamilton (1964a,b). We discuss whether or not Fisher's (1918, 1930, 1941) conceptualization of the role of genes in micro-evolutionary dynamics can be justifiably considered a key part of the Dawkinsian gene's eye view of evolution in the next section, restricting ourselves here to the implications of our perspective on fitness for certain aspects of the gene's eye view debates. In addition to the debates around the gene's eye view of evolution, there has been a slightly more narrowly focussed debate around kin-selection and inclusive fitness (of individuals) in the context of the evolution of altruism, a debate that began just a few years after Hamilton (1964a,b) first published his detailed treatment of the problem (reviewed by Frank 1998, 2013). We believe that these long-standing debates are less substantial than the papers addressing them might lead one to believe, and that they arise partly from confusions resulting from the idiosyncrasies of classical population genetics modelling, and some of the confusions about fitness and the role of individuals in micro-evolutionary dynamics discussed above, in addition to the fact that there are often multiple approaches to formulating a problem, with the choice of formulation often being driven by familiarity and convenience. Long-standing debates in ecology and evolution often have their roots in such conceptual confusions and imprecise use of terms; debates on more straightforward issues tend to get resolved relatively quickly (Kitcher, 1987; Joshi, 2022).

One unfortunate consequence of the greater visibility of population genetics (over quantitative genetics) in explanations of micro-evolutionary dynamics under selection is that, because population genetics models typically treat trait-variants at the allelic rather than phenotypic level, the contrast between individual and trait-variant has been translated into a contrast between individuals and genes. Thus, discussion of how to best model micro-evolutionary change has become conflated with the debate between genetic determinism and agency or free will in humans, reflected onto non-human species (*e.g.*, Walsh, 2015; Sultan et al., 2022). Because of this conflation, the genes versus individuals debate inflames passions to a degree that the more accurately focussed debate about trait-variants versus individuals would probably not. While it is true that a gene's eye view narrative of micro-evolutionary dynamics is often accurate as long as there are no significant gene-by-gene interaction effects on phenotypes, it breaks down in the face of such interactions due to the complex behaviour of marginal allelic fitnesses (Sober & Lewontin, 1982). When a gene's eye view is applied to situations of micro-evolutionary dynamics that do not involve phenotypes with a simple genotype to phenotype mapping, as is the case in most

evolutionary ecology studies, it tends to collapse into a vague belief that the transmission fidelity of the trait-variants is high because they are gene-based. This is actually untrue, because transmission fidelities of genetically encoded (genotypic) trait-variants can differ among variants, are typically frequency-dependent, and are therefore also dependent on the mating system, causing them to change in complex ways as the frequencies of the trait-variants change (see Box 2). This has historically been one factor contributing to the discomfort of many evolutionary geneticists with a lot of optimization-based explanations in evolutionary ecology (*e.g.*, Rose et al., 1987), although this discomfort also partly derives from the tension between static and dynamic approaches to modelling (Frank, 1998, paper 12). Despite its limitations, however, the gene's eye view has undoubtedly been successful in illuminating several aspects of the micro-evolutionary process. We suggest that the success of the gene's eye view, in terms of both book-keeping and heuristic value, is not so much from its focus on genes *per se*, but on genes *qua* trait-variants, albeit defined at the allelic level, as opposed to individuals, bringing with it the added benefit of often being able to assume a transmission fidelity of 1, a point that appears not to have been widely appreciated (*e.g.*, by Okasha, 2006; Ågren, 2021).

The evolution of altruistic behaviours is another area where failure to clearly distinguish between the roles played by individuals and trait-variants in micro-evolutionary change has led to considerable confusion. When Hamilton (1964a,b) first worked out his genetical theory of social evolution, he did all his analysis at the level of trait-variants defined at the level of genotype or allele, deploying population genetics models under some simple assumptions about the genetic underpinnings of the relevant trait-variants. Yet, he sandwiched all his analysis of change in frequency of genetic trait-variants between an introduction and a discussion section that treated the entire issue in terms of individuals and their reproductive success, making the connection through the fact that a genetic trait-variant could increase in frequency if the altruist's behaviour increased the reproductive success of other individuals with whom it shared alleles identical by descent (*e.g.*, genetic relatives or kin), even at the cost of its own. This renders these extremely important papers somewhat disconcerting and difficult to read. This tendency of Hamilton's to analyze problems in social evolution at the level of trait-variants, but then present the ideas at the level of individuals, is attested to from personal experience by Frank (2013), and has led to much debate over the meaning of kin-selection and inclusive fitness, often tending to obscure the fact that kin-selection is a testable hypothesis whereas inclusive fitness is an aid to doing genetic book-keeping at the level of individuals, rather than alleles. Frank (1998, 2013) has discussed many aspects of these debates at length, especially highlighting how this emphasis on an, in our view entirely avoidable,

individual's-eye view led to a misleading focus on kinship, or overall genetic similarity between individuals, as opposed to more narrowly focussed genetic or phenotypic similarity with respect to specific relevant traits, which in turn led to much debate about the relative merits of kin-selection versus multi-level selection book-keeping when studying social evolution. Such confusion between genome wide-similarity and genetic similarity at specific relevant loci is also found in interpretations of the cost of sex as being that of genome dilution (Williams, 1975; Shields, 1988), based on the misplaced belief of the relevance to the evolution of reproductive mode of the genome dilution occurring because asexual mothers share the whole genome with offspring, as compared to sexual mothers who share only half their genomes (Joshi & Moody, 1998). This common but unfortunate urge to explain microevolutionary dynamics at both the level of the individual (or multi-locus genome) and the trait-variant (or one-locus genotype) permeates much of the discourse in evolutionary biology, particularly in behavioural ecology, even on topics not involving altruism, and creates confusion, especially for beginning students.

To sum up, we believe that we gain nothing but comfort, and lose considerable clarity, when we try to explain micro-evolutionary dynamics by 'thinking of an individual as acting so as to enhance its fitness', direct or inclusive. We suggest that it would be better if we stuck to explaining micro-evolutionary dynamics at the level of trait-variants. The debates about direct versus inclusive fitness, kin- versus individual-selection, and individuals versus genes, are all, to our mind, partly a consequence of failing to appreciate the underlying conceptual structure of genetic models of micro-evolutionary dynamics, especially the fact that all fitness in the sense of one-step change in trait-variant frequency is inclusive, except when modelled at the allelic level of trait-variants in the absence of mutation (which is what happens in most simple models of population genetics). The distinctions between direct and inclusive fitness, or kin- and individual selection, for example, seem to us to largely be artefacts of trying to tell the story at the level of individuals rather than trait-variants, whereas all underlying analysis is actually at the latter level. We also suggest that an inclusion of transmission fidelity into the definition of fitness better reflects the process of selection, and helps focus attention on the role of mating system and mechanisms of heredity in mediating the micro-evolutionary outcomes of differences in reproductive success among trait-variants. One advantage that population genetics brought to the MS, as compared to the DC, was a better implicit appreciation that transmission fidelity of trait-variants had a complex dependence on trait-variant frequency, mating system and the details of the hereditary system, and that, therefore, the trait-variant with the highest reproductive success would not necessarily rise to very high frequency, an insight often not appreciated fully in evolutionary ecology (Rose et al., 1987), especially when

deploying optimization models to explain the evolution of alternate trait-variants (strategies). Yet, because population genetics models are often framed and, more importantly, analyzed at the level of allelic rather than genotypic trait-variants, in systems with random mating and no mutation, the crucial role of transmission fidelity in mediating micro-evolutionary outcomes of differences in reproductive success among variants is often obscured and difficult to immediately discern (see Box 2). That is why we recommend a focus on fitness defined as one-step frequency change, at the level of trait-variants rather than individuals, as a prescription for enhanced clarity in our engagement with issues of micro-evolutionary dynamics. We note, however, that fitness defined as one-step change in frequency must still be calculated in diverse ways for different evolutionary problems, depending on context (*e.g.*, Roff, 2008). Our prescription has much in common with the statisticalist perspective of some philosophers of evolution (see esp. Matthen & Ariew, 2002; Walsh, 2007; Earnshaw-Whyte, 2012; Walsh et al., 2017), although their work is often not that familiar to many researchers in evolutionary biology: the terminology they use can sometimes differ from that of evolutionary biologists, and their work is typically published in the literature on philosophy rather than evolutionary biology.

## One gene's eye view of evolution, or two?

آفاقها گردیده ام مهری  بُتان ورزیده ام
بِسیار خُوبان دیده ام لیکِن تُو چیزی دیگری
*aafaaq-ha gar deede-am, mihr-e-butaan warzeede-am*
*bisyaar khoobaan deede-am, lekin too cheez-e-deegari*
(I wandered till the ends of worlds, endured the love of idols, too
Of all the beauties I did see, I never found one quite like you
– Amir Khusro)

Since the rediscovery of Mendel's laws in 1900, there have been many, and varied, attempts to integrate Mendelian genetics into our understanding of the evolutionary process, some more helpful and pervasive than others. However, to our mind, the manner in which Fisher (1918, 1930 and esp. 1941) conceptualized and analyzed the role of Mendelian genes in mediating adaptive micro-evolutionary dynamics under selection remains uniquely elegant, insightful, and consequential for our understanding of this aspect of the Darwinian conception of the evolutionary process. In particular, we believe that it is neither helpful nor accurate to conflate the Fisherian

conceptualization of the role of genes in evolution with the later gene's eye view of evolution, deriving largely from the work of Williams (1966) and Dawkins (1976); here, we briefly explain the reasoning behind this assertion.

Over the past few decades, the so-called gene's eye view of evolution (for a recent book-length review, see Ågren 2021) has been at the centre of many criticisms of the MS made by proponents of the EES. For example, EES proponents often raise concerns that the MS ignores the importance of organismal agency and inherency in evolutionary explanation, that genes rather than individuals have been considered as the appropriate units of selection and micro-evolutionary dynamics, that genes have been imbued with an almost causal role in mediating micro-evolutionary change, and that, in general, genes seem to have more or less displaced the organism as the central focus of micro-evolutionary explanation. Typically, this canonical account of the gene's eye view of evolution is depicted as constituting an integral part of the MS. In this section, we argue that the typical depiction of the gene's eye view of evolution as arising from the merging together of population genetics and the Darwinian principle of natural selection, especially in the work of Fisher (1918, 1930, 1941), is a somewhat misleading and overly simplistic rendering of what should be, in fact, a far more nuanced account. We suggest that it is more appropriate to think in terms of two distinct gene's eye views of evolution, one primarily Fisherian and the other primarily due to Dawkins (1976) and, to a considerable degree, G. C. Williams (1966). In our opinion, the substantial differences between these two gene's eye views of evolution are often glossed over and, consequently, the two are conflated. This conflation often makes it appear as though critics of the gene's eye view of evolution are rejecting not just the Dawkinsian perspective, but also much of the population or quantitative genetics perspective deriving from the work of Fisher and others. This, not surprisingly, results in strongly-worded responses from those who identify with the MS and find the Fisherian gene's eye view to be very useful in understanding many aspects of the evolutionary process. We note that many of these people, including us, do not find the Dawkinsian gene's eye view particularly helpful and, indeed, believe that it can often be misleading. It is worth observing in this context that one of the earliest and most cogent critiques of the Dawkinsian perspective came from the viewpoint of classical population genetics (Sober & Lewontin, 1982). Moreover, among evolutionary biologists, it is typically the developmental biologists and population geneticists that are the least favourable to the Dawkinsian gene's eye view of evolution, while behavioral ecologists are largely supportive, a strange combination if the Dawkinsian and Fisherian gene's eye views were indeed substantially similar in conception and nuance.

We find it useful to compare the Fisherian and Dawkinsian gene's eye views along the twin axes of the distinction between the causes and consequences of selection, on the one hand, and what exactly they seem to have been trying to achieve through their work, on the other. The first statement in the preface of *The Genetical Theory of Natural Selection* (Fisher, 1930) provides an instructive contrast. Fisher (1930) begins his book with the declaration, "Natural selection is not Evolution"; Dawkins' (1976) arguments in *The Selfish Gene*, can reasonably accurately be summarized as proclaiming that natural selection is, in fact, more or less equivalent to evolution. This contrast is not surprising, given the differences in their training and in the general state of evolutionary thought in their respective times, and the fact that, consequently, their principal aims were quite different. Fisher, trained as a mathematician and, working at a time when it was critical to show that the Darwinian principle of natural selection was entirely compatible with the recently understood principles of Mendelian heredity, primarily focused on the consequences of selection, no doubt because a lot of the controversy over selection in the preceding decades had been about whether selection could actually be efficacious in promoting adaptive evolutionary change in the face of heredity, the latter often being thought of as a conservative mechanism opposed to change in the phenotypic composition of the population (discussed in detail by Gayon, 1998). Dawkins, trained as an ethologist and working in the period just after the heated group versus individual selection debates sparked off by Wynne-Edwards (1962), understandably had interests spanning both the causes and the consequences of selection, and seems to have been primarily interested in convincing behavioural ecologists to stop thinking in terms of group selection and focus, instead on individuals, especially through the lens of asking what was good for their genes. The similarities between the approaches of Fisher and Dawkins, unlike their differences, are fairly inconsequential, being limited to a shared focus on adaptive evolutionary change and on genes as mediating the consequences of selection. They both also seemed to believe that the roles of mutational or developmental bias in micro-evolutionary dynamics were typically small enough to be safely ignored, which may not necessarily be appropriate. While undertaking this comparison of the two gene's eye views, we note also that Fisher's (1918, 1941) quantitative genetics perspective does not seem to have influenced Dawkins' (1976) thinking to any appreciable degree. This is significant because the 'average-effect' conceptualization of the response to selection by Fisher (1941) effectively allowed an approximate black-boxing of the complex and diverse ways in which gene-by-environment covariances and interactions arise when individual organisms have to make a living in the complex natural world with which they reciprocally interact. As a result, the complexity of the causes of selection could be meaningfully set aside, while he focused on how formulations reflecting transmission fidelities (*i.e.*, breeding values and their variance, $V_A$, and the notion of

heritability, $h^2$) could be used to understand the consequences of selection, using trait-variants as a focus. Dawkins (1976), on the other hand, appears to have implicitly dealt with situations of traits affected by one or a few genes, wherein the genotpye-to-phenotype map was simple. This is why the Dawkinsian gene's eye view breaks down in the presence of gene-by-gene interactions, as pointed out by Sober & Lewontin (1982). This difference of perspective between the Fisherian and Dawkinsian gene's eye views is non-trivial: Fisher (1918, 1941) grappled with, and suggested means for approximately resolving, the complex effects of polygenic control of traits, and the multi-facted interactions between organisms and their environments, on patterns in the transmission fidelity of trait-variants, whereas Dawkins (1976) did not. Instead, Dawkins appears to have assumed, much like Darwin, that transmission fidelities would typically be sufficiently high and similar across trait-variants so as to ensure good correspondence between reproductive and evolutionary success.

We now examine these two versions of the gene's eye view of evolution in the context of the four common concerns raised by those uncomfortable with the reductionism seemingly implied in them. The critique that the gene's eye view ignores the importance of organismal agency and inherency in evolutionary explanation applies primarily to the Dawkinsian gene's eye view. The Fisherian gene's eye view focuses on genes (as trait-variants) in the specific context of modeling the consequences of selection. Fisher's (1918, 1941) conceptualizations do also implicitly take into account complex and environment-dependent genotype-to-phenotype maps that arise due to interactions between organism and environment, and this is of course where the inherency and agency of individual organisms plays a role. This point is often missed, in our opinion, because Fisher's statistical resolution of this complexity into a measure of the resulting transmission fidelity under Mendelian inheritance rendered his treatment of the consequences of complex organism-environment interactions implicit and, therefore, not immediately apparent.

The next common critique that genes rather than individuals have been considered as the appropriate units of selection and micro-evolutionary dynamics is also largely pertinent only to the Dawkinsian gene's eye view. In Fisher's work, the gene is an appropriate unit of understanding and tracking micro-evolutionary dynamics within the domain of understanding the consequences of selection. It is only in Dawkins' work, perhaps more in rhetoric than his thinking, that it often appears that genes are being promoted as an appropriate unit of selection in the contexts of trying to understand both the causes and the consequences of selection. We reiterate that, in our opinion, the appropriateness and utility of genes (strictly, mostly alternative alleles, sometimes alternative one-

or a few-locus genotypes) as units on which we can base our understanding of the consequences of selection derives from their being trait-variants, as opposed to individuals, and not from their being genes *per se*. For understanding the causes of selection, the appropriate and useful unit of selection is the individual organism (or in some cases the entire multi-locus genome), and not the trait-variant, whether phenotypic, genotypic or allelic in nature.

Similarly, the critiques that genes have been assigned an almost causal role in mediating micro-evolutionary change, and that they sometimes seem to have displaced the organism as the central focus of micro-evolutionary explanation, are also germane only to the Dawkinsian gene's eye view. Again, Dawkins' (1976) rhetoric, if not necessarily his underlying thinking, does often appear to imply that genes are somehow integral even to considerations of the causes of selection. Even if this was not, perhaps, his intent, this is often the impression left on students when they first read *The Selfish Gene*. This appearance of the gene having supplanted the organism as the central focus of micro-evolutionary explanation, not surprisingly, elicits an impassioned response from at least a plurality, if not an absolute majority, of evolutionary biologists who are exquisitely cognizant of the role of individuals, and their reciprocal interactions with their environments, in shaping the causes of selection. We think it unfortunate that many evolutionary biologists, nevertheless, do not seem to appreciate the irrelevance of individual organisms to considerations of the consequences of selection.

For the reasons articulated above, it is our view that the conflation of the Dawkinsian and Fisherian gene's eye views of evolution is not just inaccurate, misplaced and misleading, but has also contributed substantially to both the content and harsh tenor of some aspects of the EES-MS debates. Unfortunately, the Dawkinsian gene's eye view, because of its conflation with its Fisherian counterpart, is often wrongly taken to represent a central tenet of the MS. While the Fisherian gene's eye view was indeed central to the MS conception of the micro-evolutionary process, the Dawkinsian view is not. Indeed, the Dawkinsian gene's eye view is far more extreme and simplistic than its Fisherian counterpart, and often clearly inapplicable to "*micro-dynamics*" processes, which is why most population geneticists fail to ascribe to it any great significance in the context of micro-evolutionary explanation. An appreciation of this point would, we think, dissolve one aspect of the EES-MS debates altogether, and, in a lighter vein, developmental biologists and population geneticists would find themselves on the same side of a debate, with the narrow viewpoint of *The Selfish Gene* on the other. Finally, we would like to, nevertheless, stress that there is one domain of evolutionary explanation in which the Dawkinsian gene's eye view is valid and holds entirely, as

also highlighted by Ågren (2021). This is, entirely unsurprisingly, the domain of understanding the evolutionary dynamics of selfish genetic elements within-individuals, and the patterns of their prevalence within- and among-individuals. We find it very fitting that a gene's eye view identified with *The Selfish Gene* (Dawkins, 1976) should actually be appropriate and useful for understanding evolutionary changes in patterns of prevalence of selfish genetic elements. In our opinion, however, an evolutionary understanding of the dynamics of selfish genetic elements is more a vindication of the appreciation that any replicator can act as a unit of selection in the appropriate context, than a vindication specifically of the Dawkinsian gene's eye view of evolution in its entirety. This is not to say that the Dawkinsian view is not helpful in understanding evolution; however, its usefulness seems to derive from, and is restricted to, certain features it has in common with the Fisherian gene's eye view, such as the focus on trait-variants rather than individuals for understanding the consequences of selection, and an appreciation that selection as a process is more generally applicable than specifically to organismal evolution.

## The evolutionary shaping of the distribution of phenotypes

پھِرا کرتے نہیں مجرُوحِ اُلفت فِکرِ درماں میں
یہ زخمی آپ کر لیتے ہیں پیدا اپنے مرہم کو
*phira karte nahin majrooh-e-ulfat fikr-e-darmaan mein*
*ye zakhmi aap kar lete hain paida apne marham ko*
(They wander not in search of cure, Love's injured souls are firm and calm
To all the myriad wounds they nurse, they are themselves a soothing balm
– Allama Iqbal)

Before we begin to sum up by taking a comparative look at the DC, MS and EES in the next section, we would like to briefly share some thoughts on a certain perspective on the six-fold schema we introduced at the beginning of this paper (Table 1); we think this perspective may permit the development of a framework within which we can examine claims about the logical relationships of different evolutionarily relevant phenomena such as selection, mutation, transmission fidelity, hybridization, developmental bias, or niche construction, as well as discuss issues about proximal versus distal causes of variation. We develop these ideas here primarily in the context of micro-evolutionary change, but we hope that this framework will be fully extendable in detail to macro-evolutionary change at higher levels of biological variation, too.

We suggest that the frequency distribution of phenotypic trait-variants in a population at present can be viewed as having arisen from a sequence of past alterations to distributions ancestral to the focal one. If we ignore for a moment the critical analysis of treatments of developmental bias by Salazar-Ciudad (2021), using our focus on within-population trait-variants of the scale typical of micro-evolutionary change as our excuse, we can say that a multitude of processes, culminating in one, some, or all of selection, mutation, migration and drift in the immediate preceding generation affect the present distribution. Selection here includes both selection bias, resulting from differential reproductive success, and transmission bias, via the pattern of transmission fidelities, across trait-variants. The penultimate distribution that these processes act on is, of course, generated by the cumulative effects of these processes over multiple preceding generations in this populational lineage, underscoring the fact that these processes affect both the input and output distributions at any generational time-step. Factors like mutational bias (Stoltzfus & McCandlish, 2017; Cano & Payne, 2020), and developmental inherencies and biases at the level of micro-evolutionary variants (Nunes et al., 2013; Salazar-Ciudad, 2021; Newman, 2022a,b) will also play a role in shaping these distributions of phenotypic trait-variants, but the magnitude of this role with respect to micro-evolutionary variations seems at present difficult to estimate empirically.

If we now consider earlier ancestral distributions in this populational lineage, they too would have been shaped by phylogenetic effects of even more ancestral lineage(s) which, in turn are likely to have had their own phenotypic distributions shaped in part by these same processes of selection, mutation, migration and drift, as well as the inherencies and biases intrinsic to biological systems at various levels of organization. In some cases, if a lineage splits, for whatever reason, the initial differences between daughter lineages could be of the "*micro-origins*" type, with subsequent adaptive evolution in different ecological contexts sometimes inducing further divergence in their respective phenotypic distributions that would qualify as being of the "*macro-origins*" type. In other cases, the daughter lineages could remain separated only by "*micro-origins*" level variations, even after the passage of considerable evolutionary time, especially if the split did not involve the daughter lineages thereafter living in very different ecological contexts. However, in the case of lineage splits occurring early in the evolutionary history of life-forms, often these splits could result from "*macro-origins*" level differences to begin with. Thus, the newly established daughter lineages could often differ not just in their distributions of a very similar set of trait-variants, but often by having two distributions encompassing a fairly different set of trait-variants, resulting in the saltational origin of new species or higher taxa. In such macro-evolutionary lineage splitting events,

the alteration of the distribution, both in terms of the domain of variants represented as well as their associated frequencies, would likely be achieved through processes other than selection, involving primarily developmental mechanisms falling within the "*macro-origins*" category of our schema in Table 1. Similarly, inter-specific hybridization events could effect sudden large changes to phenotypic distributions with respect to both the domain of variants represented as well as their associated frequencies and, once again, developmental processes would be important in determining the nature of successful hybridization events and their effects on the distribution of trait-variants in the initial population of the resulting hybrid species. A good discussion of the kinds of developmental and other phenomena that would fall within our "*macro-origins*" category (Table 1) can be found in Newman (2022a,b).

In classical population genetics models within the MS, both mutation and migration effectively reduce the transmission fidelities of allelic variants, the former explicitly and the latter implicitly. Therefore, selection, construed as encompassing differences in transmission fidelity among trait-variants, in addition to differences in their reproductive success, can also be conceptualized to include the effects of mutation and migration by subsuming their effects into transmission fidelity, constituting one locus of fuzziness in the boundary between processes in the "*micro-origins*" and "*micro-dynamics*" categories (Table 1). Selection in the broad sense just described is, of course, also tempered by drift, reflecting not just sampling errors but all kinds of stochasticity in the transmission of trait-variants to the next generation (strictly speaking, migration can be subsumed into selection when it is trait-variant-dependent, and into drift when it is trait-variant-independent, but that distinction is not crucial for the present discussion), We note that the cumulative effects of this broad-sense selection are largely restricted to ancestor-descendant lineages within species, pertinent to the "*micro-origins*", "*micro-dynamics*", and "*micro-patterns*" categories (Table 1). Development, on the other hand primarily acts to create entirely new ancestor-descendant lineages, effects pertinent to the "*macro-origins*" and perhaps "*macro-dynamics*" categories (Table 1), even though it may also have some, relatively smaller, role to play in generating trait-variants of the micro-evolutionary, within-lineage, kind through the kinds of mechanism considered in devo-evo or micro-evo-devo (*sensu* Prasad & Joshi 2003; Nunes et al., 2013, respectively). On the whole, though, it seems to us that key developmental processes tend to be relatively more conserved within- than between-lineages. Consequently, the interventions of development and broad-sense selection in the evolutionary process appear to be largely distinct, although constituent processes of both may well interact within our category of "*micro-dynamics*". We do not have much feel for processes under the "*macro-dynamics*", and "*macro-patterns*" categories (Table 1), but our feeling

is that these are not particularly well understood, especially the latter, and we hope that future investigations will both refine and extend our understanding in this regard.

If we look at the two other major phenomena invoked in the calls for an EES in the context of this framework, it is clear that they play somewhat subsidiary roles in the evolutionary process, relative to both broad-sense selection and development, in the sense discussed above. Both non-genic inheritance and niche construction would appear to get assimilated into selection in this broad sense. Non-genic inheritance essentially affects the pattern of transmission fidelity of trait-variants, an integral component of broad-sense selection. Of course, non-genic inheritance also opens up the possibility of inheritance of characters acquired via environmental effects through epigenetic or ecological inheritance, or through cultural inheritance by learning. Cultural inheritance also enables horizontal (among members of the same cohort within a generation), oblique (from parental generation individuals to non-offspring), and reverse (from offspring generation individuals to parental generation individuals) inheritance, in addition to vertical (parent to offspring) inheritance which is the only form available under genic inheritance, especially in metazoa, if we discount the low frequency of horizontal gene transfer in such taxa. Cultural inheritance of the symbolic kind also permits inheritance over time-steps much larger than one generation: aspects of our behavioural phenotype can be altered by reading Aristotle or Rumi. However, in terms of the logical structure of the framework described above, these myriad corollaries of non-genic inheritance do not disturb the conception of selection in the broadest sense, being assimilable into the pattern of transmission fidelities. They can, however, affect rates of change of frequency of trait-variants very substantially, especially in the case of cultural inheritance. Nevertheless, we should add the caveat that our speculations in this regard are those of outsiders; none of us is technically a student of cultural inheritance or learning. It also seems to us that a detailed survey of the implications of each of these corollaries for how processes in the "*micro-origins*", "*micro-dynamics*", and "*micro-patterns*" categories (Table 1) play out in evolution is not as yet available, although this could also be an expression of our ignorance of the relevant literature. In comparison to non-genic inheritance, niche construction seems to play an even more supporting role, in that its effects on broad-sense selection are quantitative rather than qualitative, unlike the effects of non-genic inheritance. In the absence of accompanying non-genic inheritance of the niche constructing phenotype, niche construction by itself does not affect the pattern of transmission fidelities of trait-variants. Its primary effect is merely to increase the reproductive success of its bearers, by modifying the environment to be more suitable for their survival or reproduction.

Examining the various evolutionarily relevant phenomena in this framework thus reveals that development, non-genic inheritance and niche construction have very different logical relationships with selection in terms of how and in which specific context they exert their effects on the distribution of trait-variants within- and among-lineages. Development acts largely orthogonally to broad-sense selection and, in this sense, may well be considered a phenomenon belonging to the same logical category as selection, broadly conceptualized. In terms of its effect on within-lineage trait-variant distributions, it is also more distal than broad-sense selection, which is far more proximate. Non-genic inheritance can be subsumed into broad-sense selection but can have major, qualitative-grade effects on the outcomes of broad-sense selection. Niche construction can also be subsumed into broad-sense selection but, by itself, is likely to have smaller, quantitative-grade, effects on the outcomes of broad-sense selection, compared to non-genic inheritance. It is, thus, clear that the three major elements that make up the calls for an EES are actually very different in the manner in which they affect important aspects of evolutionary explanations.

## The Extended Evolutionary Synthesis (EES) in the context of the Darwinian Core (DC) and the Modern Synthesis (MS)

اُڑائے کُچھ ورق لالہ نے، کُچھ نرگِس نے، کُچھ گُل نے
چمن میں ہر طرف بِکھری ہوئی ہے داستاں میری
*udaaye kuchh waraq lale ne, kuchh nargis ne, kuchh gul ne*
*chaman mein har taraf bikhri hui hai daastaan meri*
(Tulip, Narcissus, and Rose, all took some pages from my book
And garden-wide did spread them: thus, my tale immortal did become)
– Allama Iqbal)

We have already compared the MS and the DC in a previous section in order to assess how much they differed, and in what specific manner. We now examine the major issues raised in the calls for an EES and try to fit them into the framework established in earlier sections. The main issues that proponents of the EES feel were neglected in the MS are the role of development, non-genic inheritance, and niche construction, respectively, in evolutionary explanation (summarised in Laland et al., 2015). There is also a discomfort with the perceived emphasis of the MS on gradualism and uniformitarianism (*e.g.*, Eldredge & Gould, 1972; Gould, 2002; Salazar-Ciudad & Jernvall, 2005; Newman & Bhat, 2009; Beatty, 2022). We are also uncomfortable with the gradualism and unformitarianism, and with the lack of consideration of non-genic inheritance and

developmental (as opposed to merely developmental genetic) mechanisms in mediating micro-evolutionary change. On the other hand, we believe that many of the claims of both the neglect and conceptual importance of niche construction in evolutionary thinking are exaggerated and often misplaced (Gupta et al., 2017a).

We are also somewhat uncomfortable with the use of the term ‘synthesis’, in the context of both the MS and, even more so, the EES. At least in the sense of Hegelian dialectics (Maybee, 2020), ‘synthesis’ implies a dialectical combination of antithetical elements into a coherent whole (see also Sarkar, 2004). As we see it, the development of evolutionary thinking after Darwin has been more of a steady accretion of new facts and insights around a relatively unchanged essence embodied in the DC, rather than a sequence of syntheses. Before the calls for an EES took on the largely self-assigned accoutrements of a heresy, about 10-12 years ago, an alternative term ‘Standard Evolutionary Theory’ (SET) was also used for the MS, emphasizing the fact that it was an evolving set of explanations, some closely, and others more loosely, intertwined with one another (Kutschera & Niklas, 2004; Pigliucci & Kaplan, 2006). In the minds of many of us who broadly identify our research as falling within the MS paradigm, the MS actually represents something more like an evolving SET constituting a sort of ‘framework theory’, rather than the often narrow and dogmatically gene-centric way in which it is represented in many text-books; Antonovics (1987) actually referred to the evolutionary milieu in the 1970-80s as a dys-synthesis! We suspect that the well-known ‘phylogenetic inertia’ seen in text-books has played a role here, because some of the early text-books of evolution were written by researchers closely associated with Dobzhansky, who espoused a fairly narrow, gene-based, gradualist and uniformitarian view of evolution, even equating evolution with a gradual change in allele frequencies in a population (*e.g.*, Dobzhansky, 1937). In fact, the received text-book view of the MS was inordinately influenced by Th. Dobzhanky and E. Mayr (also largely committed to gradualism: Meyer, 2005), whereas the somewhat more nuanced and differing perspectives of people like J. B. S. Haldane, G. G. Simpson, and G. L. Stebbins did not receive that extensive a representation. In contrast to the impression left by text-books, we have scarcely ever encountered the gradualist and uniformitarian positions among practising evolutionary biologists who self-identify with the MS paradigm in a broad sense, as opposed to the narrow text-book sense.

We look forward to a more meaningful incorporation of developmental perspectives, both evo-devo and devo-evo (or micro-evo-devo), as well as non-genic inheritance (especially cultural and ecological), into evolutionary thinking about problems pertaining to both the origin and prevalence

of micro- and macro-evolutionary variations. In particular, we think that a developmental perspective is likely to yield better explanations in the future not just of the "*macro-origins*" and "*micro-origins*", but also the "*macro-dynamics*", and "*macro-patterns*" categories (Table 1), by enhancing our understanding of developmental effects on parameters associated with lineage splitting and within-lineage phyletic change. Developmental considerations can also play a role in explanations within the "*micro-dynamics*" and, therefore, "*micro-patterns*" categories (Table 1), as Darwin had recognized with his emphasis on growth correlations, and we hope that future work in micro-evo-devo will prove fruitful in this regard. Non-genic inheritance directly impacts our understanding of phenomena under the "*micro-dynamics*" category, with the effects of oblique, horizontal and reverse inheritance on micro-evolutionary dynamics likely to be a rich field of inquiry. We further believe that such an enhancement to evolutionary thinking will very much be in the spirit of the DC which was fairly agnostic about mechanisms underlying heredity and variation, albeit out of a necessity born of ignorance. In the spirit of Joseph Felsenstein's assesment of the contributions of R. A. Fisher to population genetics, we suspect that evolutionary biology for quite a long time to come might justifiably be described as 'an exercise in writing footnotes to Darwin'. We also prefer not to think of the steadily expanding domain and detail of evolutionary explanation as constituting an evolutionary theory. It is more like an intertwined mass of multiple growing theories, but also with diverse interstices. In this sense, we agree with the sentiment that we need an enlargement of evolutionary explanation, not another 'synthesis' (Antonovics, 1987; Stoltzfus, 2017). Given this view, we think it is unfortunate that EES, especially in the writings of certain people, has been projected as being somehow antithetical to the Darwinian view of evolution. This is accomplished by treating the MS as synonymous with Darwinian thought, ignoring some of their differences with regard to factors other than selection and heredity, and then depicting the MS in an extremely narrow manner, effectively setting up a straw-man. The fact that text-books often also depict the MS quite narrowly unfortunately contributes to the acceptability of this rhetorical tactic. This has sadly, but not surprisingly, often provoked somewhat dogmatic and intransigent responses from many who broadly identify with an evolving SET rooted in Darwin's crucial insights.

Unfortunately, scientific disciplines with an elaborate and well-articulated set of views on their principal questions can often react like religious orthodoxies bolstered by venerated canonical texts, turning inwards and protecting their borders from incursion (Kitcher, 1987; Joshi, 2005, 2014). The other side of this coin is the continuing attraction of what we term the 'Galileo syndrome' – we scientists often like to see ourselves as champions of heretic interpretations of the natural world, struggling against the oppressive obduracy of the orthodoxy. Together, these two phenomena tend to

result in discussion giving way to debate, and often dispute, thereby constraining rather than facilitating intellectual progress.

## Summary and conclusions

کھول کر آنکھیں میرے آئینۂ گُفتار میں
آنے والے دور کی دھُندلی سی اِک تصویر دیکھ
*khol kar aankhein mere aaina-e-guftaar mein*
*aane waale daur ki dhundli si ik tasveer dekh*
(Behold in the mirror of my words and rhymes:
A shadowy picture of the coming times
– Allama Iqbal)

In some ways, the EES-MS debates are reminiscent of the old Indian parable of the blind men and the elephant, with each arguing for a different identification of the animal based on which part of it they happened to touch (first recorded from Buddhist sutras, English translation on pgs. 93-96 of Strong, 1902). Evolutionary biology covers a vast domain and the evolutionary process essentially encompasses the whole of biology, trifurcated, in one perspective, among the three major interacting phenomena of development, ecology and heredity (Joshi, 2005). There is more than a little element of people talking past each other in the EES-MS debate, with both sides often tending to conflate their set of insights and understanding with the entirety of evolutionary explanation. Even the very notion of an ‘extended’ evolutionary synthesis seems to implicitly assume that a single, comprehensive and unified ‘theory of evolution’ is not just desirable, but possible. We think that it is unlikely that we can have such a unified theory, which would be nothing less than a ‘unified theory of everything’ in biology. The effects of evolution, as argued persuasively by Rose et al. (2005), appear to be local rather than global, suggesting that perhaps the only grand generalization possible about evolution is that it occurs, although this realization obviously does not preclude useful theorizing about sub-phenomena within evolution.

As a consequence of the above, we believe that it is worthwhile to compare different sub-phenomena within evolution based on whether, and how, they impinge upon the origin, dynamics or patterns of prevalence of micro- or macro-evolutionary variations (see Table 1). We suggest that selection is relevant, and very important, to understanding the dynamics of, and patterns in, the

prevalence of alternative trait-variants ("*micro-dynamics*" and "*micro-patterns*" in Table 1). Development or mutation, which exercises its phenotypic effects through development, on the other hand, are relatively more relevant than selection when addressing questions about the origin and, to a lesser degree, the dynamics, of micro- and macro-evolutionary phenotypic variations. Niche construction, contrary to many claims, primarily plays a role, along with many other ecological processes, in modulating the action of selection. Moreover, the relevance and centrality of selection in evolutionary explanation are largely restricted to explanations of adaptive micro-evolutionary dynamics; it may not even make sense to think of selection among alternative life-forms as an analogous process to selection among trait-variants (what would one make of the question whether an annelid bauplan had higher fitness than an arthropod one, given that they would normally occupy very different ecological niches?). Thus, selection does have a fairly important position, relative to several other phenomena, but only in a subset of evolutionary explanation, in the context of explaining the prevalence of trait-variants subject to processes affecting micro-evolutionary dynamics. Species selection may be similar to selection among trait-variants, but it is not yet very clear as to how widespread it is, or indeed the degree to which its mechanisms can be considered analogous to those through which selection operates on trait-variants within species. Critically evaluating the possibility of selection among species, or among life-forms, is difficult in the present state of our knowledge of the relevant phenomena. Some kind of generalized process, in the sense of altering the available phenotypic space, however, does seem to occur at multiple levels of biological organization, although it is not clear that one can equate this phenomenon with selection in its classical micro-evolutionary sense. It is also important to appreciate that the simplistically sweeping and all-encompassing manner in which the MS is unfortunately often described in text-books of evolution is actually far removed from the much more nuanced views of most of us who work within the domain of, and identify our research programmes with, the MS.

We also think that it is high time we revisited some of the ways in which we have conceptualized fitness and selection because focussing on transmission fidelities as an integral part of fitness, and restricting the use of the term fitness to the one-step rate of increase of trait-variants, actually clears up quite a few existing confusions in the field, by illuminating their underlying cause. Similarly, we believe that discussions of the role of the individual in evolutionary explanation would benefit from a consideration of which specific phenomenon in evolution one is trying to explain. Individuals are important foci for considerations of development, and of the effects of ecological context on survival and reproduction, *i.e.*, for questions pertaining to the causes of selection. However, in trying to explain the prevalence of alternative trait-variants (*i.e.*, the consequences of selection),

focussing on individuals is a distraction that has already led to considerable confusion within the field over the last many decades, especially in evolutionary ecology. We believe that debates between those who think that individuals are important to evolutionary explanation, and those who do not, have largely been unproductive, as have the debates about the units of selection, precisely because there has been insufficient attention paid to what exactly it is about the evolutionary process that one is trying to explain through a consideration of an individual or a trait-variant, respectively.

We should also point out that, given our focus on the EES-MS debates, we have entirely ignored, including in our categorization in Table 1, one very important perspective on the evolutionary process: that of coevolution. Species interactions, anatogonistic and mutualistic alike, not only shape the evolution of individual species but, in many ways, are integral to most instances of selection and, indeed, life itself (Thompson, 2005, 2013). It is perhaps not entirely a coincidence that some of the earliest tests of Darwinian explanations of evolution in nature, as opposed to the laboratory (Dallinger, 1878), were in the context of species interactions: mimicry (Bates, 1861; Müller, 1879), and pollination (Müller, 1873). With this caveat out of the way, we now adumbrate what we feel are the eleven major take-home messages from what has been discussed in this paper. We will then conclude with some thoughts about the way ahead for the resolution, or rather the dissolution, of the EES-MS debate.

The main points that we would like readers to take from this paper, starting from the most general and proceeding to the more specific, are the following:

1. One can meaningfully think of diverse areas and aspects of evolutionary explanation as mapping onto a schema organized into six categories of questions pertaining to the origins, dynamics and patterns of prevalence of micro- and macro-evolutionary phenotypic variations (Table 1). Most concerns of the DC and MS are seen to be about explaining the dynamics and prevalence of trait-variants ("*micro-dynamics*" and "*micro-patterns*" in Table 1), whereas the more cogent aspects of the calls for an EES mostly focus on explanations of the origin (and secondarily, to a lesser degree the dynamics) of variations, primarily, but no longer exclusively, at the level of macro-evolutionary phenotypic variations.

2. In addition to marshalling a compelling body of evidence for evolution in the sense of species being related through ancestor-descendant relationships, and describing natural selection as a potent

mechanism for adaptive evolutionary change, Darwin also made three other very significant, and somewhat under-appreciated, contributions that shaped subsequent evolutionary thinking: the five together constitute the conceptual crux of the DC. One was to reconceptualize heredity by shifting its focus from the preservation of types across generations to the transmission of variation among individuals, even siblings. The others were to focus on trait-variants rather than individuals (the atomization of the individual), and on mechanisms for changes in their prevalence. It was these three latter contributions that permitted the development of a theory of micro-evolutionary dynamics, and also initiated the consequential emancipation of heredity, in the sense of transmission, from the confining embrace of both development and the individual, a process eventually completed almost sixty-five years later by T. H. Morgan and others.

3. Overall, the MS represented a narrowing of the DC, though not as greatly as Neo-Darwinism (see discussion in Forsdyke, 2001), largely because of the need to show that evolutionary explanations of the mechanisms for change in the prevalence of trait-variants were consistent with the newly re-discovered principles of Mendelian genetics. The DC was more open to varied mechanisms for both the generation of trait-variants and their transmission to offspring. However, some elements of the MS, like quantitative genetics, were actually broader and more nuanced than is often thought to be the case. The phenomena considered under the aegis of the EES calls are best seen as complementary to those emphasized in the MS, in some cases, harking back to the broader, more eclectic, DC.

4. Since quantitative genetics is typically encountered only cursorily, as a small part of a population genetics course, it has been largely unrepresented or misrepresented in the EES-MS debate. Many critiques of the MS (for perceived errors of omission) are actually seen to be misplaced in the light of a clearer understanding of the essential nature of quantitative genetics. Despite its name, quantitative genetics constitutes, *inter alia*, a phenotypic theory of micro-evolutionary dynamics that permits the many complexities of the genotype to phenotype map, including phenotypic plasticity, and gene-by-gene and gene-by-environment interactions, to be distilled into the genetic variance-covariance matrix which, in turn, is what mediates, via transmission fidelities, between selection acting on individuals and the consequent evolutionary change.

5. Quantitative genetics is consistent with Mendelian genetics, but can also be deployed to explain micro-evolutionary dynamics in systems with arbitrary systems of inheritance, so long as the analogues of heritability or the genetic variance-covariance matrix can be delineated. In this sense,

quantitative genetics constitutes a far more general theory of micro-evolutionary dynamics than population genetics, which is limited by the twin assumptions of Mendelian inheritance and simple control of the relevant phenotypes by one or a few genetic loci. A better appreciation of the nature of quantitative genetics would render some EES-MS discussions more meaningful and useful.

6. At present, the term fitness is variously used to quantify the reproductive success of an individual, the average reproductive success of individuals exhibiting a specific trait-variant, the one-step rate of increase of a trait-variant, and the long-term evolutionary success of a trait-variant or lineage. We strongly suggest that the use of the term fitness should be restricted to the one-step rate of increase of a trait-variant. This usage explicitly reflects the important role of transmission fidelity as a fundamental part of the process of selection, linking variation in reproduction of individuals exhibiting different trait-variants to differences in prevalence of those trait-variants. As a corollary, we believe it is not helpful to talk about the fitness of individuals as a synonym of their reproductive success, since this only results in confusion, particularly noticeable in the literature on kin-selection (see 8, below).

7. Individuals, with their inherencies and agency, are important to explanations pertaining to ontogeny and ecology, since it is the individual that reproduces and interacts with its abiotic and biotic surroundings (*i.e*., the *causes* of selection). Yet, a theory of micro-evolutionary change in the prevalence of different trait-variants (*i.e*., the *consequences* of selection) cannot be built at the level of the individual, since every individual, considered holistically as a complex multi-trait phenome, is essentially unique. This implies that, at the level of individuals, it will be possible to only describe the replacement over time of one set of unique individuals by another set of completely different unique individuals.

8. Focusing on trait-variants as the meaningful units on which micro-evolutionary change can actually be described and quantified also highlights the misconceived nature of the units of selection arguments focussed on individuals versus genes/genotypes. A phenotypically unique individual cannot exhibit a change in frequency over multiple generations: it can only exhibit a one-time change from being alive to being dead. The consequential issue, therefore, is whether to consider phenotypic or genotypic trait-variants as the units of micro-evolutionary change in any given scenario, and the choice will depend on context. As a result, ascribing fitness to individuals is not helpful (see 6, above), except to assuage a deeply ingrained discomfiture that we experience when unable to ascribe agency to objects that play a role in our explanations of the world and cosmos.

Focussing on trait-variants as the units of micro-evolutionary change, together with limiting the use of the term fitness to the one-step rate of increase of a type-variant, also entails the desirable consequence of rendering all fitness inclusive, thereby eliminating a major source of confusion and debate – the unnecessary distinction between direct and inclusive fitness.

9. Development is important, indeed crucial, to a large subset of evolutionary explanations, especially those dealing with issues pertaining to the origin of phenotypic variations. Nevertheless, a detailed understanding of development, or of the complex genotype to phenotype map, is largely unnecessary for constructing and deploying a meaningful and useful theory that can approximate patterns in the dynamics and prevalence of trait-variants. Unfortunately, since work on the prevalence of trait-variants has historically constituted a very large proportion of research on evolution, a misleading impression that development is unimportant to explaining evolution has sometimes been created, especially in text-books.

10. It is useful to think of not one, but two gene's eye views of evolution, that should not be conflated. The Dawkinsian (Dawkins, 1976) and the Fisherian (Fisher, 1918, 1930, 1941) gene's eye views of evolution differ substantially, and it is only the latter that is integral to the MS.

11. Heredity, in the broad sense of a mechanism(s) inducing positive correlations between parent and offspring phenotypes, or even phenotypes of interacting individuals not related to one another (as in cultural inheritance), is important in evolution because it connects the behavioural or reproductive success associated with a trait-variant to its consequent prevalence. As a mediator of transmission fidelity, heredity is, in fact, inseparable from both fitness and selection. It is important, however, to break out of our twentieth century epistemological straitjacket that conflated heredity with the strictly parent-offspring transmission of genes. Epigenetic, ecological and cultural inheritance all have potentially important roles to play in evolution, and can serve to link not just parents and offspring, but also unrelated individuals within and across generations. More importantly, differences in the kinds of transmission fidelity patterns of trait-variants that are primarily passed on by one or the other alternative mechanism of inheritance can greatly impact observed patterns of micro-evolutionary dynamics, even if the ecological factors associating some benefit with those trait-variants remain unchanged.

To sum up, our view on the EES-MS debate is that there is actually relatively little to debate about, barring rhetoric, if we get past our parochial sub-disciplinary viewpoints and take a much broader

view of the domain of evolution. For example, the complaint that the MS does not address the origins of form, often made in the evo-devo literature, is akin to reprimanding evo-devo for not shedding light on the dynamics of allele frequencies under the joint effects of mutation, drift and selection. Existing theories of micro-evolutionary dynamics do not even try to address the origins of form (contra Newman, 2021). It should be possible to appreciate that while development is very relevant to questions about the origin of macro- and even micro-evolutionary variations, it can nevertheless be safely ignored when addressing most questions about the prevalence of alternative micro-evolutionary variants, at least to a good level of approximation. We need to appreciate that phenomena highlighted in the MS, and in the calls for an EES, respectively, have their primary focus on different categories of questions outlined in the schema in Table 1, and that approaches focused on different phenomena are, thus, complementary rather than conflicting, and that none of these approaches has a claim to represent either the whole of evolutionary biology, or its most important components. We believe that the EES-MS debate has been exacerbated by the changing cultural milieu of science, in which 'marketing' has become increasingly crucial to how impactful any piece of work will be assessed to be (Joshi, 2014; Gupta et al., 2017a). This leads inexorably to exaggerated claims to novelty and generality, as well as to rhetorical flourishes that serve to obfuscate rather than emphasize similarities or complementarities across approaches. Dialogue, unfortunately, becomes difficult when the participants are largely talking down to, or past, one another. Yet, evolution is far bigger than all of us and, indeed, than all of our sub-disciplinary biases and viewpoints, and meaningful dialogue across the diverse sub-disciplines that make up evolutionary biology is what is really needed at this time. It might, therefore, be advantageous now to abandon the EES-MS dichotomy altogether, and discuss various processes and factors affecting the origin, dynamics and patterns of prevalence of variants, at various levels of biological organization, as differing but complementary parts of a complex, nuanced, multifarious and evolving SET, in the spirit of Bob Dylan (2014), when he wrote in the song 'Caribbean Wind': "*...there ain't a thing you can do about it, so let us just agree to agree*".

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