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CHARLES DARWIN: REDUCTIONIST, HOLIST, OR BOTH?

We do on stage things that are supposed to happen off.
Which is a kind of integrity, if you look on every exit
as being an entrance somewhere else.

– Tom Stoppard, *Rosencrantz and Guildenstern Are Dead*

Abstract

Whether the work and thought of Charles Darwin can be more accurately described as reductionist or holist remains a strangely unresolved question to this day. Darwin is a legitimate heir to two distinct intellectual traditions: romantic natural philosophy of Von Humboldt and Goethe (with a significant inspiration drawn from Kant) and Victorian natural science of Herschel and Lyell. While Darwin's focus on uncovering evolutionary mechanisms (and, crucially, demonstration that a single type of mechanism – natural selection – explains much of the incredible diversity of living forms) induces many scholars to consider him an epitome of scientific reductionism, there appear to be equal grounds to regard this titan of science as thorougly holistic in his approach to life's history on our planet. Was Darwin, then, a reductionist or a holist? Perhaps there is another way to answer this question (or even better, another way to *ask* it): is it possible one can be reductionist *and* holist? Namely, contrary to eminently reductionist early and classical Modern Syntheses in evolutionary biology, both Darwin's original body of work and many today's developments in evolutionary biology, subsumed unter the label of Extended Synthesis – centered on shifting tempo and mode of evolution, punctuated equilibria, hierarchical multilevel selection, ecological-evolutionary-developmental (eco-evo-devo) feedback integration, phenotypic plasticity, and, last but not least, recent works by W. Ford Doolittle and others attempting to unify the Gaia hypothesis of James Lovelock and Lynn Margulis with evolution by natural selection and evolutionary worldview in general – seem to offer us a glimpse of complex multidimensional landscapes underlying biology as we know it (and, through continuing astrobiological reasearch, potentially also biology as we do *not* know it). All of this could be but a foretaste of a promising direction in our scientific and philosophical endeavor to understand life – one transcending the classical dichotomy of reductionism vs. holism, not without resonance with great philosophical traditions seeking the Union of Opposites.

Key Words: Charles Darwin · reductionism · holism · Extended Synthesis · Gaia hypothesis

Introduction

Issues related to reductionism in science – both old and new – are being incresingly raised, discussed and studied, as the general intellectual momentum appears to be increasingly shifting toward a more integrative and inclusive outlook on the natural world. In this context, classical legacy of titans of science is being re-examined and (re-)subjected to a philosophical critique informed by our evolving understanding. The foundations of modern biology laid down by Charles Darwin and Alfred Russel Wallace are certainly no exception in this regard. However, in spite of numerous thorough analyses accumulated over more than a century and a half, the question whether the general outlook of Charles Darwin can be more accurately described as reductionist or holist remains strangely unresolved.

The famous exchange between Robert J. Richards and Michael Ruse (Richards, 2002; Richards, 2004; Ruse, 2004; Richards & Ruse, 2016) is but one, though paradigmatic, example of two diametrally opposed readings of Darwin: as a champion of modern, in many ways reductionist, natural history or an adept of a more holistic description of Nature, with its countless aspects and moods. Evidence supporting either position is in no short supply, since Darwin is a legitimate heir to two distinct intellectual traditions: romantic natural philosophy of Von Humboldt and Goethe (with a significant inspiration drawn directly from Kant) and the Victorian natural science of Herschel and Lyell (Herschel, [1830] 1987; Liu, 2022). Opinions continue to differ as to which of these traditions had a more profound impact on Darwin's work. As aptly demonstrated by Greif (2015), it is questionable how far we can even trace these two influences as separate within Darwin's opus, since they appear to be, in some respects, intertwined. It is also notable that the scope (or, perhaps, the „flavor") of Darwin's original explanatory reductionism markedly differs from that of the Modern Synthesis; the latter, in turn, differs from many strands of thought comprising the ongoing Extended Synthesis in evolutionary biology. In an eponymous paper, Brooks (2011) poignantly likened this discrepancy to a "mastodon in the room" of evolutionary studies.

In this brief sortie into the philosophical no-man's land separating the two outlined positions on Darwin's historical standing with respect to reductionism vs. holism, we shall begin by reviewing some of the meanings the terms "reductionism" and "holism" have taken up as pertaining to science in general and biological sciences in particular. In a duly holistic (pun intended!) approach to our task, we will then try to show how these two seemingly irreconcilable views can seamlessly blend into a single perspective, revealing Darwin as a reductionist *and* a holist. We shall also proceed to some of the more "holistic" recent (on the historical timescale) developments in evolutionary thought and hopefully highlight some spearheading ideas that are prompting us to reconsider our understanding of the biological world, and attempt to see how much those ideas were prefigured (or at least anticipated) in Darwin's original opus. We will conclude our humble attempt by paying some homage to the ancient and sanctified philosophical concept of the Union of Opposites, as it potentially relates to philosophy of biology.

What Do We Mean by Reductionism?

As W. H. Thorpe (1974) insisted, not only is the term "reductionism" subject to a plurality of meanings and interpretations, but "a great many writers who in fact discuss this topic deeply do not use the word at all". The *Stanford Encyclopedia of Philosophy* (Brigandt and Love, 2023) distinguishes at least three types of reductionism: ontological, methodological, and epistemic. Ontological reductionism is the idea that everything, including biological systems, is constituted solely by elementary entities (such as atoms or molecules) and their interactions; according to methodological reductionism, complex systems are most fruitfully investigated by experimental studies directed at the deepest ontological level; while epistemic reductionism is limited to the claim that scientific knowledge pertaining to a high-level domain can be successfully reduced to another body of knowledge, focused on a lower (or more fundamental) level. Since the denial of ontological reductionism would, in biology, amount to vitalism or some of its reincarnations (Beckner, 1974), our discussion will mostly be centered at the other two. Perhaps the greatest percieved weakness (although undeniably also a stregth) of methodological reductionism is its tendency to isolate component entities and processes in order to study and understand them separately. This inevitably leads to simplification, and quite often oversimplification, of the complex explanandum. Works of philosophical critique directed at reductionism, particularly in biological sciences, are fairly abundant (for some recent examples, please see Soto & Sonnenschein, 2018 and Shyer & Rodrigues, 2025). Nevertheless, reductionist programs have been reasonably successful in a wide range of fields and provided us with answers to a wide array of research questions. Particularly relevant for this paper is genetic reductionism (the assumption that full explanations of biological phenomena and processes can be provided by genetic factors alone, coupled with the acceptance of genetic determinism), largely driven by contemporary rise of molecular genetics and very important in the context of both Modern and Extended Syntheses.

Peter Godfrey-Smith (2008) cautions that "there is a disconnect between what many philosophers [...] think of as the scientific practice of reductive or reductionist explanation, and what the most relevant scientific work is actually like". In brief, a higher-level framework is legitimately used to address questions pertaining to the dynamic of a complex system, even if there is a genuine reductionist understanding as to how this higher-level framework relates to lower-level processes or entities. This is widely accepted, and also authoritatively demonstrated by Dupré (1993), who captured well why most science dealing with complex systems tends to proceed with models based on established or putative mechanisms (Machamer *et al.*, 2002). For the purpose of our considerations, it is important to acknowledge that there is an extensive "middle ground" between extreme reductionist and anti-reductionist positions (*i. e.*, that explanations at the cellular or molecular level can *completely* account for *all* biological facts, and conversely, that higher-level explanations owe *nothing* to, nor have anything to gain from, knowledge of deeper levels of living entities or their communities). It is also important to bear in mind that ontological (and, to some extent, even methodological and epistemic) reductionism does not preclude – and may even require – an acceptance of general complexity, non-linearity, diverse dynamics, interactivity, multicomposition or multidirectionality. In a word, reductionism, in itself, does *not* imply ignorance of complexity, much less a tendency to over-invoke (or exculsively invoke) a single explanatory factor or principle.

What Do We Mean by Holism?

Charles T. Wolfe (2012) famously stated that "Holism is a term that always carries with it a residual dimension of mystery". David Sloan Wilson noted that "a lot of mischief can be created by [such] umbrella words, especially when the speaker has one concept in mind and the listener has another" (1988). In the perpective of history of biology, holism is importantly associated with the "organicism" of Ludwig von Bertalanffy and others (Drack, 2015; Baedke, 2019); even more importantly, it is inextricably linked with the concept of emergence (Broad, 1937; Johnson, 2010). The now thriving discipline of systems biology is generally considered holistic, and sometines even equated with holism itself (Gatherer, 2010; Kutschera, 2018), which is perhaps a logical inevitability, since its subject matter comprises the behavior of biological systems *as wholes*. The same can be said of ecology – the study of eco*systems* – although debates on the admissible or desirable (not to mention necessary) degree of reductionism in evolutionary ecology seem to be far from settled (Keller, 2019).

One must also remember that the term "holism" is very often (ab)used to support various mystifications, and/or offer a more "respectable" designation (a fig-leaf) to forms of (neo)vitalism. "Holism" is much too frequently used to designate purely phenomenological, "black box" approaches and associated circumvention of relevant knowledge of internal causal relationships. On the other side of the semantic spectrum, the term may – and not infrequently does – denote a simple preference for complex, multifactorial explanations, or merely an (uncontroversial) acknowledgement of non-linear processes and non-linearity in general. Since even the hardest reductionists tend to accept the old Aristothelian dictum that the whole is more (or different) than the sum of its parts, practical holism tends to be centered on emergent properties and processes that cannot be adequately analyzed or explained by appealing to lower organizational levels only (Ribatti, 2021).

After this capsule reminder of the philosophical content and connotations carried by the terms in question, we shall now proceed to try and see how these might (or might not) apply to the work of Darwin.

Charles Darwin: A Reductionist

In a text specifically treating the question of reductionism in Darwin's thinking (or evolutionary biology in general), Angelique Richardson (2013) points out that "Reductionism, as method or as ideology, and sometimes as both, seeks to explain the complex, the whole, or the interactive or dynamic according to the simple, the part, or the linear or unidirectional". Although in the previous section we have seen that this description may not necessarily fit all varieties of reductionism, the quote nevertheless captures some general reductionist aspects of scientific endeavors, including Darwin's. It is fair to say that, inspired by the *Weltanschauung* of his Victorian age, Darwin did, in principle, seek reductive explanations for the incredible opulence of natural phenomena and did espouse a primarily materialist (or physicalist), causal, mechanistic and individualistic explanatory mode, devoid of teleology and yet capable to accomodate the quasi-teleological corollaries of natural selection acting as a functional filter (Bouzat, 2014). The causal priority Darwin accords to natural selection can thus be considered reductive (Sober, 2009). A degree of reductive causal structure is also a prerequisite for Darwin's use of thought experiments to argue in favor of his theory (Lennox, 2005). Since heritable variation is indispensable in order to provide natural selection with the substrate to operate on, Darwin was compelled to assume a stable mechanism of heredity (which he not-too-happily sought in pangenesis) and has not been said in vain to have "desperately needed Mendel" (Berry & Browne, 2022); the true conjunction of Darwinian evolution and genetic determinism – reductive *par excellence* – had, however, to wait for the onset of the Modern Synthesis and the subsequent molecular genetic revolution (Bowler, 1989; Fairbanks, 2020). Another relevant aspect of Darwin's thought is his renowned gradualism, inherited from Charles Lyell – the important principle that the past is the key to the future, or that biological processes can, at least ideally, be extrapolated from the historical record just as geological ones. Gradualism is reductive inasmuch as it denies discontinuities (to be later called punctuations) in evolutionary history, *i. e.*, sudden changes brought about by catastrophic evens explainable only by contingency and thus irreducible (Gould, 1994; Raup, 1994; Marshall, 2023).

As a slightly nostalgic illustration, readers who grew up with Sir Clive Sinclair's legendary ZX Spectrum (as the author of these lines did) will immediately remember a little program called “Evolution” on side B of the enclosed *Horizons* demo tape. It actually represents a toy mathematical model of population dynamics engendered by a predator-prey relationship (foxes and rabbits) based on Lotka-Volterra equations – effectively the utmost simplification of the simplest example of the simplest class of working models in ecology. All this simplicity, however, does higlight a generic reductive aspect of standard investigations into biological (evolutionary) relationships. This reductive aspect – in the sense of isolating a single relationship out of a complex web – is present even in the most sophisticated models, their success in many fields of biomedical sciences notwithstanding, inasmuch as applying a principle, or a set of principles, to a given problem situation and abstracting from its countless other aspects perforce constitutes a reductive procedure (particularly since the chosen principles are generally those acting at a deeper structural/functional level of the process in question).

But was it indeed – in the above sense – all just “Foxes and Rabbits” for Darwin? Well, yes and no, as we shall discuss next.

Charles Darwin: A Holist

Darwin’s intellectual debt to german romanticism in general, and Kant and Goethe in particular, has already been noted in the nineteenth century (initially by Ernst Haeckel) and was recently summarized by Liu (2022). It is well known that Darwin, particularly in his younger days, was greatly influenced by romantic naturalism of Alexander von Humboldt (Darwin, 1905, Vol. I, p. 47; Lansley, 2016). Darwin’s descriptions of the natural world closely followed von Humboldt’s romantic ideals, although his explanations often did not. Gillian Beer (1983) noted that Darwin’s attitude toward scientific study of nature was romantic mainly in the sense that it was not intended to detract from its beauty or mystery, nor was Darwin ever inclined to forgo “the pleasures of observation”. While Darwin inevitably comes across as a stark reductionist in comparison to von Humboldt, in view of the latter’s strong and pervasive emphasis on all-encompassing interdependence (Stamenković, 2022), both great explorers appear to have been fully aware that no process in Nature unfolds in isolation and no natural phenomenon can be really understood on its own, without delving into the rich web of its interconnections with everything else.

Indeed, as a keen observer, Darwin knew that the actual evolutionary history of any given lifeform is unique, largely precluding precise deduction or prediction of observed properties from first principles. Such recognition that what we happen to see in the living world is highly contingent on countless historical circumstances was later reinforced by S. J. Gould in his famous “replaying the tape” thought experiment. In brief, the operation of natural selection is necessarily dependent on ecological context, and this cannot be simply reduced to its constituents. It is also true that it was Darwin who first proposed group selection as an evolutionary mechanism, notably in attempts to explain certain aspects of human evolution in *The Descent of Man* (Darwin, 1871). There Darwin specifically stated that all evolutionary innovation depends upon numerous "concurrent favorable developments". Many other passages in Darwin's writings attest that he never lost sight of the central fact that evolution is an open-ended process of adjusting to an ever-changing environment (protracted periods of stable equilibrium or near-stasis notwithstanding). Thus even the above mentioned (over) simplified dynamics of "foxes and rabbits" is generally the dynamic result of many ecological variables, whether they be explicated or subsumed under modelling mathematics. Furthermore, Darwin realized that there can also be significant feedback effects from species to the ecosystem (as evidenced by the time-honored example of beavers and their landscaping services, also mentioned in Darwin, 1871). In fact, what we now study under the topic "niche construction" and deem very important for understanding evolutionary-ecological dynamics (Odling-Smee *et al*., 1996) is amply referenced and discussed throughout Darwin's opus. These considerations are also in line with a key role of biogeography, exemplified by the peculiarities of Galapagos Islands and East Indies in the shaping of Darwin's and Wallace's theory, respectively (Brick, 2023).

Furthermore, natural selection itself (for Darwin as for us) is essentially an ecological filtering process, dependent on a complex environment – the *whole* of a complex environment, as it is. To take an iconic illustration, we may now know which exact genes have been altered in the process of differential evolution of Darwin's finches on different individual islands within the Galapagos archipelago (please see below), but environmental characteristics of these locales affecting the direction of change favored by natural selection none the less remain a necessary constituent of any evolutionary explanation. True, Darwin' uniformitarianism, inherited from Lyell, somewhat mitigated these consequences of historicity by postulating continuity of processes operating in deep time with those we see today (and doing away with those nasty discontinuities and sudden shifts in tempo certainly helps us be more reductive), but Darwin still retained a bird's eye view of what we would today call non-linear dynamics of the evolutionary process (for a thorough treatment of this aspect of evolutionary theory, please see Depew & Weber, 1995). Within the scope of this paper, suffice it to say that Darwin fully acknowledged the importance of both upward (bottom-up) and downward (top-down) causation (Campbell, 1974; Davies & Walker, 2016), as well as intricate functional integration of all organisms. In this vein, Ferdinando Boero (2015) listed many modern ecological concepts Darwin had clearly anticipated in the *Origin of Species* and his general ecologically-centered thinking (though the word ecology did not yet exist), making a considerable case for Darwin as a champion of scientific holism. Last but not least, it is not easy to miss the fact that Darwin's "entangled bank" – his magnificient closing metaphor of the *Origin of Species* (Darwin 1859, p. 489) – directly endorses an ecological holism.

Charles Darwin: A Reductionist *and* a Holist

Compared to the classic considerations of "genetic" vs. "organismic" level, the reductionism-holism debate in evolutionary biology has in the last few decades been greatly expanded in scope (Delisle, 2008). From this perspective, a new-old reading of Darwin's texts indeed demonstrates that (ontological) reductionism is not only compatible with, but actually complementary to (epistemic/explanatory) holism. It is not by chance that a very important role of analogy and metaphor is evident in Darwin's attempts at explaining the natural world. There are consequently good reasons to agree with Greif (2015) in his assertion that Darwin actually did much to transcend the gap between mechanicistic and romantic views of Nature. The same, *mutatis mutandis*, can probably be said of the perceived gap between reductionism and holism. Stripped to the essence, Darwin's idea that the incredible diversity of living creatures can be explained by an iterative combination of a stochastic process (random variation) and a non-stochastic, filtering step (natural selection) can, furthermore, be considered reductionist and holist in equal measure – on the one hand, it does, in a sense, offer a reductive explanation of living forms; on the other hand, it clearly entails complex *ensembles* (*i. e.*, wholes). After all, Jan Smuts, to whom we owe the very term "holism" (though its meaning has since somewhat evolved), in his seminal book *Holism and Evolution* (1926) already prefigures the above point by noting these twin reductionist-holist aspects of *The Origin of Species*: while natural selection, as a supreme explanatory principle, carries a reductionist tinge, the other main ingredient – non-directed variation – can only operate on species or traits (or more general selection units) embedded in a holistically construed wider environment. Indeed, Darwin's anti-essentialist conception of species (as mere categories for mentally organizing omnipresent variation) arguably removes the *Origin* a further step from strict reductionism, given that variation itself, whatever its causal explanations (largely inaccessible to Darwin and his contemporaries) *cannot*, in this context, *be reduced* to anything universally simplified.

To use another iconic example, Darwin's famous prediction that a moth with a very long proboscis will eventually be discovered in Madagascar (reviewed in Arditti, 2012), acclaimed by Alfed Russel Wallace by a comparison to no lesser feat than Le Verrier's discovery of Neptune (Wallace, 1867), may seem a rare example of biological science approaching the levels of reductionist prediction usually associated with physics or other "hard" sciences. However, if one looks a bit deeper, this prediction can be seen to be as much holist as reductionist – for it is, again, critically dependent on the wider (ecological) context, and the fact that we now know that evolution of this fascinating flower involved a pollinator shift (Wasserthal, 1997) only reinforces this point. Thus a complex (and philosophically overwrought) relationship between reductionist and holist aspects of science also applies to Darwin's work and adds to the already substantial list of teachable points offered by Darwin's biography and opus (Cohen, 2016). When we speak of Darwin's theory in this regard, though, it might be better, for the purpose of disambiguation from many common usages of the attribute "holistic", to choose another, more precise term, such as "synoptic" (in the sense of observing, considering, explaining or pertaining to all of the biosphere – or even all of the natural world – at the same time). If so, we might actually speak of Darwin's "synoptic holism" as a kind of *neti neti* – not quite reductionism and not quite anti-reductionism.

Reductionism and Holism: Dichotomy or No Dichotomy?

Having discussed Darwin's reductionist and holist tendences separately and concurrently, it is time to examine the possibility that this time-honored dichotomy may in fact be no real dichotomy at all and that it may have no substantive role in explaining Nature. This echoes the famous question posed by Leo Buss (1987): why can one not be reductionist and holist at the same time? Once again, not all versions of reductionism and holism are mutually exclusive – on the contrary, these can be, and often are, complementary approaches (Schuster, 2007). This insight is particularly important in the context of multilevel structural-functional, but also causal-processual map of organisms, ecosystems and the biosphere. Emergent properties seem to be everywhere. "Emergence arguably represents the major challenge for reductionist explanations of the world", we are reminded by Massimo Pigliucci (2014) in his take on reductionism and holism in evolutionary biology. And, as Johnson (2010) classicaly demonstrated, such emergence is fully compatible with ontological reductionism, since it may indeed primarily reflect the inaptitude of our brains – themselves a product of complex evolution – to (consciously) engage in massive parallel processing.

Conversely, even if we accept the strongest possible anti-reductionist stance, we can hardly expect to have successful explanations in biology without some considerations of *causal relevance* (in the sense of William Wimsatt [1982]) of component structures and processes within the biological whole, however construed. Although strict theoretical reduction of the complex overall evolutionary process to the principle of natural selection (*i. e.*, the deduction of countless lifeforms inhabiting this planet from this principle alone) is not possible – a reality much lamented by some biologists, as well as some philosophers of science – this principle nevertheless remains an indispensable part of any workable explanation, even the most non-reductive. After all, if explanatory holism is understood as an all-encompassing integration of knowledge at all levels, than knowledge of those more basic levels that are the subject of a reductionist's primary attention must still be necessary: we could hardly hope to integrate knowledge that we do not have in the first place.

This dependence of any and all emergent properties on hierarchical levels of complexity, *i. e*., internal structure within the emergent whole, in a way, reduces the reduction (pun intended!) to supervenience[1]. Full acknowledgement of universal evolutionary patterns at many – or all – supervenient levels of organization of the biological (and even non-biological) world in no way entails, much less constitutes reductionism *sensu stricto* (Князева, 2015). In other words, even if we justifiably say no to what one might dub "greedy" reductionism, we would probably – and for a good reason – strive to retain conceptual recognition of successive supervenient levels of structure, as illustrated by the concept of Haldane's ladder, superbly discussed in the astrobiological context by Ćirković (2012). (Whether below the lowest rung of that ladder, at the deepest level of reality, we can hope to find no more – or no less – than a Nāgārjuna-style emptiness (an emptiness empty even of emptiness itself), as recently suggested by Carlo Rovelli [2021] in his passionate exposition of the relational interpretation of quantum mechanics, remains a question for another day, or another paper.)

In this light, both reductionism and holism may be valid simultaneously as frameworks for different aspects (or different levels) of our explanatory pursuit. An important *caveat* is that not all levels of a biological system are causally relevant in all problem situations and contexts. Biological macromolecules do consist of atoms (*pace* Ernst Mach), each of them endowed with a baryonic nucleus composed of quarks, but deep understanding of quantum chromodynamics would hardly be of much assistance when we study, for instance, the intricacies of protein folding. The same applies to all other levels of structure. However, since deeper levels are still a *sine qua non* for the existence of higher ones (*i. e*., the latter are supervenient on the former), it follows that even the very epitomes of reductionism, such as Mendeleev's Periodic Table of the Elements or fundamental physical entities and forces, in a way, set the stage (or, indeed, *are* the stage) for a type of holism; the same, then, may be said of evolution as Darwin and Wallace envisaged it. Naturally, the holism we consider here is not of the variety that disregards the *verae causae* (to use Herschel's term) of percieved properties within the whole, for such an approach would surely be condemned to remain woefully superficial and explanatorily unsatisfactory. Therefore holism limited to a

1 For a formal definition of supervenience, we will once again resort to the *Stanford Encyclopedia of Philosophy* (McLauglin and Bennet, 2023): "A set of properties *A* supervenes upon another set *B* just in case no two things can differ with respect to *A*-properties without also differing with respect to their *B*-properties." For a representative meta-discussion of the concept of supervenience, please see Kim, 1990.

phenomenological overview cannot even be *truly* holistic: under the weakest of the weak assumptions of naturalism, the whole will necessarily (or at the very least plausibly) feature some causally relevant internal structure (subject to a degree of reductionism). Conversely, any fundamental underlying principle, if it is to explain our complex world, will necessarily (or at least plausibly) engender ever-increasing levels of complexity (subject to a degree of holism).

The Extended Synthesis and Gaia: A Holistic Revolution, or Re-Evolution?

As we know, apart from not being in the position to know exact mecanisms of heredity, Darwin was unaware of major discontinuities in the history of life on Earth. It may be just as well, for these would, *inter alia*, contradict Darwin's cherished gradualism. However, since more than half a century ago science has come to firmly recoginze the fact that tempo and mode of evolution are, at least in principle, not uniform (Gould, 1994), novel aspects now need to be considered. The (sub)theory of punctuated equilibrium of Stephen Jay Gould and Niles Eldredge strongly endorses the role of contingency in the evolutionary process, with multiple levels of selection, non-adaptive alterations and close ties between evolution and development (Gould & Eldredge, 1993). Gould's causal pluralism further precludes simple reductive predictions from insights into lower (or more general) organizational levels. Punctuated equilibrium is, thus, in a way, more holistic than early Modern Synthesis or strict adaptationism, but nevertheless retains "the fundamental feature of Darwin's vision – direction of evolution by selection at each level" (Gould, 1982). Furthermore, developmental processes happen to be much more (or, ironically, much less) than mere execution of a genetic "blueprint". Countless gene-gene and gene-environment interactions result in extreme complexity. The pathway(s) leading from genetic information to actual organism and its phenotypic traits is eminently non-linear and influenced by a myriad of factors. Evolutionary change generally occurs through modifications in the molecular machinery regulating this complex process, but the fixation of these modifications is brought about by interactions with the environment. For instance, we now know that Darwin's finches evolved their respective beak shapes by alterations in a few key regulator genetic loci (Enbody *et al.*, 2023), but we also know that fixating selection having acted on these alterations can be demonstrated as dependent on complex ecological settings (Podos & Schroeder, 2024). In addition to these eco-evo considerations, the advent of epigenetics has added new levels of complexity to the genotype-phenotype relationship, contributing to the recognition of multiple forms of phenotypic plasticity. While all these developments are undoubtedly also "holistic", the need to understand deeper structural levels can only become more acute.

From a bioinformatic and biosemiotic perspective, evolutionary process "explores" the overall (multidimensional) parameter space of possibilities. This parameter space is generally outlined by life's established information-coding concept and its associated evolvability (Janković & Ćirković, 2016; Barbieri, 2018). A fitness landscape (which, in this context, invariably pertains to inclusive fitness in a broad sense, as discussed by Frank [2025]) is another thoroughly holistic corollary of evolutionary theory. Although, by the very definition, never directed or predetermined, the evolutionary process traversing this landscape gets more or less channeled by various constraints. This channeling along "evolutionary alleys" cannot, however, be adequately described without comprehension of the landscape as a whole, and the holistic panorama this entails is, arguably, already implicitly present throughout the *Origin of Species*. The Extended Synthesis of evolutionary theory may thus be seen as no less than "Holistic Darwinism", and the term has already been tentatively introduced (Corning, 2008). In Holistic Darwinism, the study of natural selection is predominantly centered on functional relationships. These functional relationships may be thought of as "cooperation" in the broadest possible sense, that includes even antagonism and strife as long as the overall effect is beneficial to the larger whole (Janković *et al.*, 2022).

Another, related (and perhaps the ultimate) "holistic" development in biology is the rise and maturation of the Gaia hypothesis. Originally proposed by James Lovelock and Lynn Margulis (1974) in the nineteen seventies, Gaia now exists in many different versions, some of which remain less than scientific, while others are undergoing efforts to be made compatible with Darwinian evolution (Doolittle, 2019, 2025; Boyle, 2025). Key concepts of the latter are selection by persistence alone, multilevel selection including the biospheric level, and global homeostatic synergies as units of selection (what Doolittle [2017] calls "It's the song not the singer" approach to planetary evolution). Thus "Darwinized", Gaia becomes a valuable contribution to the study of life, both as it is known on Earth and as it potentially exists elsewhere in the Universe, viewed in the context of the ongoing astrobiological synthesis. Gaia is therefore increasingly becoming our true hope to transcend the tired divide between reductionism and holism in biological science. For in the context of Gaia, as Stoppard's immortal impresario from our introductory quote aptly reminds us, we truly need to "look on every exit as being an entrance somewhere else". Indeed, the Extended Synthesis is currently moving away from simplified reductionist explanations and edging toward an ever-greater recognition of a comprehensive, multilevel, non-linear, causally composite, ecologically embedded evolutionary process. While this is sometimes hailed as an abandonment of reductionism for holism, this extended view is actually reductionist *and* holist in the same sense as we tried to demonstrate for Darwin. To conclude somewhat poetically, Nature *is* evolution, and is neither an "ice castle" nor a "Pollock canvas"[2] – neither enthralled by a rigid predetermined form nor deprived of any form at all – but rather constantly re-constructed and repeatedly re-formed.

A Final Word: The (Ultimate) Union of Opposites

It is almost two decades since Giuseppe Damiani (2007) likened the dynamic relationship of epigenetics and genetics to that of Yin and Yang in Chinese philosophy. The union of opposites constitutes the ultimate endpoint of strong philosophical traditions in both East and West, notably Heraclitean, Taoist, and Nietzschean. According to the analytical psychology of Carl Gustav Jung, it is a key aspect of the process of individuation (the road to Selfhood). Ethical implications abound, particularly in the present era of Anthropocene: a dire need for an epistemological platform capable to support our collective individuation into an ecologically, economically and ethically sound planetary civilization – perhaps even a sort of Jungian mid-life enantiodromia of humankind (Fellows, 2022). As a union of opposites in her own right, a Darwinized Gaia might offer us just such a platform.

Conclusion

Whether perceived as reductionist, holist or both, the "dangerous idea" of Charles Darwin – an iterative combination of stochastic variation and non-stochastic selection – remains a cornerstone of our understanding of Nature, both in its classical (historic) form and as a living concept – the beating heart of the ongoing Grand Synthesis in life sciences.

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2 While the latter metaphor hardly requires explanation, the former – the ice castle – is borrowed from *Kingdom without Space*, a rather psychodelic interwar-era novel by Bruno Goetz (1919). For full implications of the metaphor, please see Von Franz (1970).

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