

Uniting Micro- with Macroevolution into an Extended Synthesis: Reintegrating Life's Natural History into Evolution Studies

Nathalie Gontier

Abstract The Modern Synthesis explains the evolution of life at a mesolevel by identifying phenotype–environmental interactions as the locus of evolution and by identifying natural selection as the means by which evolution occurs. Both micro- and macroevolutionary schools of thought are post-synthetic attempts to evolutionize phenomena above and below organisms that have traditionally been conceived as non-living. Microevolutionary thought associates with the study of how genetic selection explains higher-order phenomena such as speciation and extinction, while macroevolutionary research fields understand species and higher taxa as biological individuals and they attribute evolutionary causation to biotic and abiotic factors that transcend genetic selection. The microreductionist and macroholistic research schools are characterized as two distinct epistemic cultures where the former favor mechanical explanations, while the latter favor historical explanations of the evolutionary process by identifying recurring patterns and trends in the evolution of life. I demonstrate that both cultures endorse radically different notions on time and explain how both perspectives can be unified by endorsing epistemic pluralism.

Keywords Microevolution · Macroevolution · Origin of life · Evolutionary biology · Sociocultural evolution · Natural history · Organicism · Biorealities · Units, levels and mechanisms of evolution · Major transitions · Hierarchy theory

But how ... shall we describe a process which nobody has seen performed, and of which no written history gives any account? This is only to be investigated, first, in examining the nature of those solid bodies, the history of which we want to know; and 2dly, in examining the natural operations of the globe, in order to see if there now actually exist such operations, as, from the nature of the solid bodies, appear to have been necessary to their formation. (Hutton, cited in Teggart 1916: 249)

N. Gontier (✉)

Applied Evolutionary Epistemology Lab, Centre for Philosophy of Science,
Faculty of Science, University of Lisbon, Lisbon, Portugal
e-mail: nlgontier@fc.ul.pt

... We need a third gambit, one that admits history as a fair game to the scientific enterprise – but does so without exclusive attention to the individual facts of the matter. One that focusses on historical pattern. (Eldredge 1999: 10)

1 Introduction

When you look up micro or macro in a dictionary, the “micro” is defined as small or minute and “macro” as large or long. To exemplify the meaning of the words, many dictionaries will give you a lineup that goes from the micro to the meso to the macro. The terms stem from the ancient Greek *mīkrós*, *mésos*, and *makrós* and are loanwords borrowed from more ancient Indo-European (including Indo-Iranian) languages spoken by Vedic Indian and Mesopotamian peoples. Like their predecessors, Greek philosophers used the concepts as prefixes to form combinatorial words whereby the micro–meso–macro determined either the size or the temporal and chronological scale of the phenomenon denoted by the noun that followed in the combination.

Stated otherwise, the micro, meso, and macro refer to verbal, geometric, and arithmetic measurements of matter, space, and time. We still use the micro–meso–macro prefixes. Biochemists, for example, call DNA a macromolecule to indicate that it is a structure composed of smaller subunits; archaeologists divide the Paleolithic or Stone Age into a Lower Mesolithic and Upper Paleolithic period to give chronometric and spatial accounts of hominid tool technologies. Paleontologists use geological time to define visible eukaryotic multicellular life that evolved at the beginning of the Cambrian as transitioning from the Paleozoic or ancient life to the Mesozoic or middle life and the Cenozoic or more recent life.

The conceptualization of matter, space, and time brings us to the heart of cosmology, i.e., the study of the universe. Cosmologies are worldviews that function as epistemic systems that delineate the boundaries of the universe and everything in it. Over the ages, cosmologies have often been depicted in cosmographies such as ancient Greek Chains of Beings, Judeo-Christian *Scala Naturae*, or Far Eastern Wheels of Time that function as mappings of the world.

Aristotle, for example, distinguished between the realm of non-being (nothing), the physical realm of coming and becoming (the cosmos), and the metaphysical realm of being (roughly the aetiology or causes that underlie all order in the universe which he reified into an ultimate and final cause: the unmoved mover). The micro–meso–macro prefixes were exclusively used to measure the physical realm which these ancient peoples understood as a single cosmic whole that for the sake of analysis is dividable into embedded parts, i.e., the micro-, meso- and macrocosmos. Together, they form the great chain of being and becoming, and that chain of being and becoming, for Aristotle, follows metaphysical, causal laws that give teleological directionality to how change occurs.

Aristotle’s chain of being as well as his more ultimate distinction into 3 realms was synthesized into Judeo-Christian cosmologies where the micro–meso–macro come in the form of a lineup of distinct and hierarchically structured layers of

reality, respectively, made up of inanimate matter, animate (living) matter, and the celestial/divine. The latter ladder became reconceptualized in more scientific terms by Spencer (1862, 1876, 1915) who, following Hutton, distinguished a linear sequence that goes from the inorganic to the organic and superorganic. The micro or inorganic associates with chemistry and particle physics, the meso or organic with the life sciences which include the humanities as well as the earth sciences, and the macro or superorganic with astronomy and the planetary sciences. Early historical linguists, ethnologists, and sociologists adhered to a doctrine we now call organicism and understood languages, cultures, and societies as beings or living organisms, but Spencer reconceptualized these phenomena as extended organs of living beings that surpass the organic and thus also form part of the superorganic.

In all these hierarchical lineups, the living holds the middle between on the one hand the dead and on the other hand what transcends the living. In religious terms, that what transcends the living coincides with the supernatural and is therefore conceptualized as distinct in matter, space, and time. In scientific terms, what transcends the living can associate either with geology, physics, and astronomy, or, on a smaller scale, with sociocultural, linguistic, and political structures which equally surpass the individual or the collective. In the sciences, the organic has a more fluent connection with some aspects of the superorganic, because living beings can individually and collectively alter aspects of the superorganic, either ecologically speaking by altering the earth's surface and atmosphere, or in what regards the creation of new phenomena such as cultures and languages. However, the living cannot influence or alter star or planetary formations, or at least there is no evidence that proves we can, so eventually there is a rupture. In recent years, science has also made the divide between the inorganic and organic more fluent because we accept that living matter is made up of the same chemical compounds and physical particles. Life and inorganic matter both follow the same chemical and physical laws. Nonetheless, living matter evolves, and the evolution of life is considered to follow new rules which are formulated in the form of evolutionary mechanisms.

What is noteworthy is that none of these lineups converge with the actual history of the universe, which according to the current standard view goes from the Big Bang to star and planetary constellations, the evolution of life out of non-living matter on at least one of these planets, and the evolution of new phenomena out of life. It demonstrates that our ways to conceptualize the universe are outdated and biased toward more ancient cosmologies that no longer form part of our worldview. Huxley (1942, 1957), for example, when defining what he called "evolutionary humanism" tried to fix the problem and went from the cosmic to the biological to the psychosocial, but he was silenced by mainstream scientists, strangely so for being too fanatic.

Another observation drawn from investigating these scales is that life has always held the middle, but its exact position and beginning within a universal cosmic scale has been far from stable. Are populations, species, or higher taxa real? Are cultures, languages, and societal structures alive? These make up

fundamental questions of Western science. Biology is traditionally defined as the science of life and evolution as the change that life undergoes through time. But definitions of life are diverse. Darwin (1859) understood biological organisms as individual living beings. He evolutionized the study of the living by measuring how well organisms cope in the struggle for existence and how able they are in reproducing fertile offspring. By emphasizing struggle for existence and reproductive success, organisms are subjected to a two-way selection process, one natural and one sexual. Success is measured by how well organismal variation helps in survival and attracting mates. Both are tested within the environment. Organismal variation can be reduced to hereditary variation, but it is the organism that has to struggle. And selection can be explained by environmental parameters, but it is the organism that is selected, either by other organisms or by the abiotic environment. So there is a duality that takes the issues to a micro- and macrolevel, but only the organism–environment interface is considered real or relevant for study. Organisms collectively make up populations, but for Darwin, species are real in name only and in reality always “incipient” and prone to undergo further gradual change because of generational organismal–environmental interactions that eventually underlie descent with modification.

Evolutionary theory has therefore been mostly defined at a mesolevel. Following Darwin, the founders of the Modern Synthesis argued that the evolution of existing life occurs through the natural selection of adaptive organisms at the level of the environment as a consequence of the weeding out of maladaptive organisms that did not make it, either in the struggle for existence, or the battle between the sexes. Consequently, the unit of selection has traditionally been identified as the phenotype or living organism, and the level where selection occurs has been identified as the environment. In a very real sense, expanding evolutionary research toward a micro- and macrolevel implies an inclusion of the dead. It avers a recognition that the Modern Synthesis explains biogenesis but not abiogenesis and merely defines evolutionary research of existing life at a mesolevel, one that is inspired by older cosmologies.

Discussions on micro- and macroevolution reach their peak after the foundation of the Modern Synthesis and associate with advances made in fields such as on the one hand population and especially molecular genetics as well as organic biochemistry and, on the other, paleontology, ecology, systematics, and biophysics. These debates have been brought to us in the form of discussions on biological or genealogical and ecological hierarchies and what their epistemic entry points or levels of analysis are, major transitions, patterns, trends, evolutionary rates, and discussions on the mechanisms that cause variation, speciation, and (mass) extinction.

The debates invoke fundamental epistemological questions on spatiotemporal scales (material loci or units and levels as well as *tempos* of evolution), causation (mechanisms that underlie evolutionary change at these loci), and questions of reductionism and holism. Ultimately, they invoke an inquiry into how an evolutionary worldview necessitates a reconceptualization of matter, space, and time. Things can hardly become more fundamental, and herein lies the important

contribution to science that both micro- and macro-oriented evolutionary scholars have brought forth.

We currently find ourselves in the midst of this fascinating cosmological revolution. Although evolutionary theory was first formulated over 150 years ago, we are still delineating the consequences of an evolutionary worldview and the impact it has on our epistemic frameworks that are themselves formulated by an evolving species.

My background lies in evolutionary epistemology as well as comparative anthropological science of intellectual history, what Nietzsche called the genealogy of thought. As such, my contribution here involves an epistemic and historical contextualization of the evolutionary cosmological issues that the micro- and macroevolutionary debates bring forth, as well as an anthropological delineation of two distinct scientific cultures that, although they share a common cultural ancestor, have evolved distinct scientific practices and intellectual ideas to study evolution. In so doing, I build on the following three books written by Niles Eldredge, *Time Frames* (1985), *Reinventing Darwin*, *The Great Debate at the High Table of Evolutionary Theory* (1995), and *The Pattern of Evolution* (1999). The present work reads both as a comment and as an elaboration of these ideas.

2 Microevolution

In 1946, over fifty evolutionary scholars from various biological fields united in the first meeting of the Society for the Study of Evolution (Eldredge 1999: 138–40; Smocovitis 1996). The Society was an outgrowth of a North American National Research Committee, founded a couple of years earlier with the goal to investigate shared evolutionary problems of genetics and paleontology. The societal members elected George Gaylord Simpson as their president, and Ernst Mayr functioned as secretary. During their meetings, the scholars established a common epistemic framework for eukaryotic phylogeny: Multicellular organisms undergo descent with modification because they evolve by means of natural selection. The established theoretical framework served as the foundation of the Modern Synthesis (Huxley 1942; Provine and Mayr 1980) that, according to Mayr, designates:

... the general acceptance of two conclusions: gradual evolution can be explained in terms of small genetic changes (“mutations”) and recombination, and the ordering of this genetic variation by natural selection; and the observed evolutionary phenomena, particularly macro-evolutionary processes and speciation, can be explained in a manner that is consistent with the known genetic mechanisms. (cited in Gould 1982: 382)

Contrary to their intellectual ancestors, these founders did not address origin of life questions, and they stayed clear from ontogenetic and sociocultural sciences. At the time, there were good reasons that justified these decisions. History was no longer considered a science (Popper 1957). Weismann’s (1893) barrier caused for a rupture between ontogeny and phylogeny because scholars assumed that ontogenetically

acquired characteristics do not feed back into the gene pool. Consequently, embryological and overall epigenetic research (Waddington 1942) was not considered a relevant subject area of evolutionary biology. The founders also refrained from sociocultural behavioral research because the subject was simply not considered to define their area of research. At the time, behaviorist schools considered behavior an outgrowth of individual and societal learning, and learned behavior in turn was an acquired behavior that did not feed back into the gene pool. In so far as learning is underlain by neurocognitive conditions, the subject belonged to the neurological and psychological sciences; in so far as learning requires teachers, it is a sociocultural group behavior that needs to be studied by anthropologists and sociologists. These fields developed altogether different epistemic frameworks and scientific practices to understand behavioral phenomena. The adoption of early social Darwinian theories had caused havoc in colonial and war times (Eliav-Feldon et al. 2009; Fanon and Philcox 2004), and many of the founders of the Modern Synthesis spent a lifetime eliminating vitalist and historicist (unilineal, orthogenetic, straight line) evolutionary ideas. Rosalind Franklin's work had led to the discovery of the double helix (Watson and Crick 1953), which later became understood as a "frozen accident" (Crick 1968), and such conceptualization temporarily eliminated discussion with cytologists and cell biologists who investigated heredity beyond the nucleated genome (Margulis 1998: 25). Bacteriology was altogether considered a medical science. Bacteria, viruses, and fungi were known to genetically infect multicellular life during ontogeny (Avery et al. 1944; Griffith 1928; Lederberg and Tatum 1946; Morse et al. 1956), and such infections can alter fitness (Haldane 1949; Lederberg 1999), but it was assumed that most infections did not enter the germ line and were thus negligible from an evolutionary point of view.

For an evolutionary scholar that wanted to work within the epistemic boundaries delineated by the Modern Synthesis, little else remained but the study of genes. The microevolutionary tradition developed by trying to incorporate lower- and higher-order phenomena on the scale, but at the same time reducing these phenomena to a genetic level of analysis. Adaptation became synonymous with fitness (how many times genes are passed on), and natural selection became understood as genetic selection (Williams 1966), because ultimately, these dead structures are the only "survivors" and "beneficiaries" (Lloyd 1988, 2000) of evolution. By understanding living organisms as temporary "vehicles" that ride "selfish genes" (Dawkins 1976), the micromolecular genetic level is considered more lasting in time and therefore more real, just because genes are "replicators" that have "fecundity, longevity, and copying fidelity" (Dawkins 1976).

Such an approach is interesting, because it demonstrates an epistemic struggle with evolutionary time and a subsequent search for generational continuity and stability which the founders as well as Darwin proclaimed a necessary feature in order for natural selection to work. By taking the differential distributions of genes over populations as point of departure, it implies an annihilation of the individual living organism which had always been understood as the unit of selection. It is here that we therefore find a first attempt to "evolutionize" the dead, i.e., to apply evolutionary theory to non-living phenomena.

I give two examples, research on kinship and research on sex. In these debates on the targets and beneficiaries of selection, attention was first drawn to those who from a genetic point of view do not benefit. Statistically speaking, kinship and altruism do not enhance an individual's fitness though other members of a population can benefit from such cooperative actions. When asking what such traits are good for, Wynne-Edwards (1962, 1986) raised the possibility that such traits benefit the group. But such higher-order selection was fiercely denied by Williams (1971) and Maynard Smith (1964), Maynard Smith and Price (1973). Instead, calculations began that enable such seemingly altruistic behavioral traits to become reduced to individual fitness via reciprocity or tit for tat (Axelrod 1981, Hamilton 1964). In times of competition, it pays to cooperate. Nonetheless, questions of benefit are a natural outgrowth of questions on adaptation. If selection favors the fit, then traits can only evolve when they are somehow adaptive or they would not be selected in the first place. So if the individual living organism does not benefit, it must be either something above or below the organism that benefits, the group or the genes themselves.

Another conundrum, passionately studied in flower power times, was the benefit of prolonged sexual immaturity, menopause and andropause, homosexuality, and meiotic sex which constrains "selfish genes." Meiotic sex (Edwards 1998; Fisher 1930; Hamilton 1967; Maynard Smith 1978; Becks and Alavi this volume) involves the acceptance of half of the nucleated genes from total strangers in neglect of the individual's own genes. Why would evolution have taken such a route when organisms reproduced by division wherein they passed on their complete genome? The most common answer given was that genetic recombination is beneficial because it increases variation and it enables genetic repair or the masking of maladaptive traits (which the fruit fly experimenters already showed to be mostly recessive) in *future* progeny. In particular, the first argument implies a higher-order population level. By examining how well genes fare in a population's gene pool, mate choice and sexual fitness become understood as a form of group selection (Van Valen 1975). Given that it takes two, meiotic sex annihilates the sexual individual as an independent organism in favor of the study of genetic (re-)combinations at a population level. What matters more is the differential distribution of genes over populations *through time*.

Neo-Darwinian theory was very successful in reducing many seemingly social behaviors to a genetic level, but an equally valid question, from an epistemological and historical point of view, is why, from all behaviors, it was particularly social and cooperative behavior that received so much attention. One reason is the following. Evolutionary theory itself evolved in the nineteenth century as an outgrowth of discussions on sociopolitical debates on the common goods of society and moral debates on human nature. Without divine law, scholars sought naturalistic, secular principles that enable individuals to bond into societal political structures. Hobbes, for example, saw humans and the whole of nature as fierce and violent. Rousseau endorsed that all are good-natured but corrupted by society. Pierre Joseph Proudhon developed his political ideas on mutualism which gave way to socialism. The ideas developed, with on the one side, the liberal camp that understood nature as "red in tooth and claw" and, on the other side, the socialists.

Darwin was part of the liberals and the struggle he assumed, for Spencer was one of the “fittest” in a world filled with “parasites.” On the other side, you had the socialists and communitarians, one of them being Kropotkin who emphasized mutual aid (see Sapp 1994 for a discussion). These features were also found in nature, under the form of symbiosis, mutualism, and commensalism, but these ideas did not survive the synthesis, or better yet, they did, but in the form of parasitism and “master–slave” relationships that were studied as outcomes of behavioral features from within fields such as ecology. Because symbiotic behavior was understood as a type of socialism and studied from within ecology, the subject was not considered a hallmark of synthetic evolutionary studies. For Neo-Darwinians, who focused on the vertical transmission of nucleated genes, cooperation forms an anomaly. Another reason why especially sexual behavior received so much attention during the rise of microevolutionary studies is that eukaryotic sex forms a hallmark of natural and sexual selection theory (see Becks and Alavi this volume). If not for sex, traits cannot be passed on from one generation to the next. Finally, research on cooperation and social behavior in particular was also approved during the Darwin centennial, discussed in the next part.

2.1 Evolutionizing the Inorganic and Superorganic

Shortly after the Society for the Study of Evolution was founded back in 1946, the Darwin centennial was organized at the University of Chicago in 1959. Tax (1960) organized the event and invited the scholars whom Julian Huxley (1942) had called the founders of the Modern Synthesis (Theodosius Dobzhansky, E.B. Ford, Ernst Mayr, George G. Simpson, G. Ledyard Stebbins, Bernhard Rensch, and Sewall Wright), anthropologists, and behavioral scientists (including, among others, Daniel Axelrod, A. Irving Hallowell, Clyde Kluckhohn, Alfred Kroeber, Louis Leakey, Niko Tinbergen, Gordon Willey, and Leslie White), as well as religious leaders. The conference was organized around five panels: the origin of life, the evolution of life, man as an organism, the evolution of the mind, and social and cultural evolution, a lineup that Smocovitis (1999: 296–7) rightfully notes: “... follows both a logical sequence of the history of life on earth, and the logical ordering of knowledge: the physical sciences were followed by the biological sciences and the social sciences.”

It is easy to deduce from the program that the purpose of the meeting was to investigate the impact an evolutionary worldview had on all the sciences, from the micro- to the macrolevel. Following Huxley (1942, 1957) who in turn was highly inspired by his grandfather Thomas Henry Huxley as well as Herbert Spencer, it was both a plea for “universal evolution” and an attempt to undo the “eclipse of Darwinism” that had originated from the 1880s onward due to advances in symbiogenesis, neo-Lamarckianism, epigenetics, and embryology. Waddington was the only disturbance in that regard. The population geneticists had mechanized natural selection by mathematizing selection as gene distribution studies, and the founders

had put discontinuity and saltationist debates to rest, so it was now time to evolutionize the behavioral and sociocultural sciences.

In comparison, during the Chicago Darwin bicentennial that was chaired by the philosopher Robert Richards in 2009, the main themes were eco–evo–devo and History and Philosophy of Science, neither of which had been represented at the 1959 centennial. Back in 1959, the former schools were part of the eclipse that needed to be undone. The latter, philosophers of science, were altogether not engaged, with the exception of Nagel (1949, 1951) who, a couple of years earlier and from within logical positivism, had written on the use and abuse of teleology in biology, and Grace A. De Laguna, who wrote a positive review of the conference proceedings she characterized as having taken on a “fresh approach to the philosophical problem of ends in nature.” In her abstract and by following Pittendrigh (1958), she summarizes the problem as follows:

They accept ‘teleonomy’ only as descriptive, and neglect its significance for theory. The present thesis is that each of the three recognized phases of universal evolution: inorganic, organic, and post-organic initiated by the advent of man and his culture, is characterized and made possible by the emergence of a distinctive type of teleonomic organization. (De Laguna 1962: 117)

The centennial thus reinstated in a post-synthetic and post-war spirit the attempt to extend the principles of natural selection to phenomena studied within the behavioral, cognitive, and sociocultural sciences, in particular the “superorganic” goal-oriented behavior of the living (Axelrod 1981; Hamilton 1964; Tinbergen 1963; Trivers 1971; Williams 1966). Inspired by Pittendrigh and Williams’ notions on teleonomy, sociobiologists (Wilson 1975) took things altogether to another level. Early sociobiologists assumed that behavioral and cognitive traits were ultimately underlain by genes, and their scientific work initiated an era where specific genes were postulated for language, cognition, and cultural traits. In short, such investigations reinstated evolutionary research on ontogeny from within a Neo-Darwinian framework (Campbell 1960, 1974; Hahlweg and Hooker 1989; Tinbergen 1963).

What about the inorganic? Darwin’s *On the origin of species by means of natural selection* provides a theory of biogenesis, and it explains how existing life brings forth new life. He speculated that life evolved in a small little pond, a primordial soup, and that all living organisms are genealogically related through the blood line (Darwin 1859: 420–2) and thus brought forth from a single common ancestor (for a discussion, see Gontier 2011). But he did not go beyond this speculation to address the origin of life out of inorganic matter. This transition was mostly studied from within epigenetic circles (for a discussion, see Maienschein 2012), where scholars investigated abiogenesis by means of spontaneous generation instead of natural selection, to explain how the living evolved out of inanimate matter. The doctrine was called to halt by scholars such as Redi and Pasteur, who reintroduced more preformationist notions by defending that *Omne vivum ex vivo*, all life comes from pre-existing life. This credo also formed the basis for cell theory, which takes the cell as the basic unit of life and argues that all life comes from cells (Mazzarello 1999). The view strengthened Darwin’s evolutionary theory that all life shares a common origin wherefrom descent with modification follows (for a discussion, see Huxley 1870).

Thinking through the consequences of Darwinian evolution theory, and in the context of research on the origin of life, Haeckel (1866) and Huxley (1870), who coined the term abiogenesis and also denied it, were the first to universalize evolutionary theory toward the inorganic. Comparative research led Haeckel to theorize that “higher animals” had evolved from “protozoa” such as “monera” and subsequently diversified into kingdoms (“Protista,” Animalia, and Plantae). He depicted his monophyletic reconstructions in the first evolutionary trees of life that in turn gave credibility to his recapitulation theory alternatively known as his biogenetic law (literally, the law of the genesis or historical origin of life). During the First World War, he published a work on crystals which he characterized as “anorganic life” (Haeckel 1917) wherein he came very close to the work so typical of biophysics.

Returning to the Chicago 1959 centennial, what is interesting, and very reflective of the time, is the differentiation the organizers made between origin and evolution of life problems which they examined in two distinct panels. Back then, origin questions were frowned upon as speculative and unscientific because the initial conditions can neither be repeated nor observed, though today progress is indeed being made in that regard. But such scientific demands equally go out to the future, which we can neither observe nor induce, yet prediction is valued as one of the highest epistemic goods of any scientific theory. Equally, “what is life” questions are also often dismissed as unscientific, while on the contrary, mechanical questions on how life evolved, and thus, identifying the mechanisms of evolution is considered science. The 1959 panel on the origin of life was composed of physicists, biochemists, geneticists, and ecologists who focused on the ecological conditions favorable to evolve eukaryotic life on earth, the biochemical aspects of the double helix, and the evolution of physiology, especially nerve wirings.

The structure of genetic material had been discovered 6 years earlier through X-ray crystallography, and topics included how genes mutate and how they underlie general animal physiology. Analyzing the panel, it altogether remains a strange combination of scholars and topics. Participants included the astrobiologist Harlow Shapley, a participant of the great debate on the size of the universe and its nebulae (galaxies), who also introduced the “liquid water belt theory” that defines habitable zones for life; Sir Charles Galton Darwin, descendent of Darwin and physicist involved in X-ray crystallography; Hermann Joseph Muller, a Nobel laureate known for his work on the impact radiation has on genetic mutations; the geneticist Theodosius Dobzhansky and biochemist Earl A. Evans; Ralph W. Gerard, a neurophysiologist and behavioral scientist working on the chemicoelectric wirings of the central nervous system; Clifford Ladd Prosser, a comparative physiologist; Georgii F. Gause, a Russian biologist known for his ecological competitive exclusion principle that states that only one of two similar species competing over the same niche will survive (the other one will go extinct); and Hans Gaffron, a biochemist working on photosynthesis in plants.

One can only interpret such a selection for a panel on the origin of life from within the bias there existed among the founders of the Modern Synthesis and their predecessors to understand the evolution of multicellular life and to

understand that evolution exclusively by means of natural selection. Granted, great scientists such as Manfred Eigen (Eigen and Schuster 1977), Orgel (1973, 1992) and De Duve (1991) or the Schopf (1978) brothers and Fox and Dose (1972) were still coming of academic age (which on average takes a decade or two longer). But by then, Wallin (1927) had published his work on symbiogenesis, Pauling (1939) had already received the Nobel prize for his work on the nature of the chemical bond, Miller (1953) had performed his experiments on the primordial atmosphere of life that spontaneously generated amino acids, and Oparin's (1955) work had been translated and was well read within the Americas and Europe. Luria and Delbruck (1943), in discussions on Lamarckian versus Darwinian inheritance and the occurrence of mutations as random or directed toward environmental change, gave statistical evidence that bacteria mutate randomly and only subsequently become the target of selection. Avery et al. (1944), who pointed out that DNA and not proteins were the transforming factor during, what we now call, lateral gene transfer among strands of pneumococci were also not invited, and neither was Lederberg (1951, Zinder and Lederberg 1952), who discovered the mechanisms of transduction and bacterial conjugation and reintroduced the term abiogenesis before Carl Sagan did.

Perhaps funding ran out, but the composition of the 1959 Origin of Life panel does demonstrate a conscious selection of favoured topics as well as a lack of scholarly interaction between the founders of the Modern Synthesis and pioneers in areas such as abiogenesis, actual molecular genetics as opposed to theoretical population genetics, cytoplasmic heredity, and prokaryotic life. In their defense, it is true that such inclusion would not have involved a celebration of natural selection or Darwin per se. But in so far as they endorsed universal evolution and even accepted the possibility for selection to be directed as opposed to blind in what regards sociocultural evolution, much more so than later sociobiologists would, it remains strange why, besides selection, there appears to have been no room whatsoever for symbiogenesis or spontaneous generation (or self-organizing, autocatalytic complex adaptive systems as we call them today). Spontaneously generated, biochemical catalytic and autocatalytic systems show selectiveness, but much of this can be explained by electromagnetics, physics, and chemistry, rather than by struggle for existence and competition. This is one of the reasons why such views were not favoured at a time when biology was seeking its own field-specific and epistemic boundaries. Wright (1929, 1932) was there to defend drift, but he was part of the evolution panel, and drift, before Kimura (1968, 1983), was understood as a period of no selection rather than as a mechanism in and of itself.

Nonetheless, in relation to post-synthetic introductions of origin of life debates, and battles over which came first, genes (Eigen and Schuster 1977; Orgel 1973, 1992), proteins (Miller 1953; Miller and Urey 1959; Kauffman and Levin 1987; Kauffman 1995), or cells (De Duve 1991; Fox and Dose 1972; Oparin 1955), the inorganic eventually became evolutionized. Today, all known evolutionary theories (natural selection, symbiogenesis, spontaneous generation or self-organized complex adaptive systems theory, lateral gene transfer, drift, punctuated equilibria) are, to some extent, put to use to understand abiogenesis.

It was especially Eigen (1996: 547), who selectionized the inorganic or “prebiotic” by asking whether “‘being alive’ really [is] a necessary prerequisite of selective and evolutionary behavior.” His theory on the autocatalytic hypercycle explains, from a selectionist point of view, the origin of autocatalytic RNA molecules and DNA compartmentalization into larger genomes. His background in physics and his adherence to Shannon’s rising information theory even enabled him to turn natural selection into a physical law of functional optimization toward increasing complexity:

That is how a physical interpretation of the Darwinian principle might sound. According to Darwin’s principle, whatever is better adapted spreads out and displaces its less well adapted predecessor. Thus, complexity, built upon simplicity, has accumulated throughout biological evolution from the first single-celled organisms to human beings. Evolution as a whole is the steady generation of information - information that is written down in the genes of living organisms. ... Today we can apply our knowledge to molecular systems such as genes and the products of their translation. We can also investigate in a much more objective way the physical nature of the Darwinian principle: theoretically, by defining accurately the prerequisites and constraints, and experimentally, by exact control of experimental conditions. We find that the selection principle is neither a mystical axiom immanent in living matter nor a general tendency observable primarily in living processes. On the contrary, it is - like many of the known physical laws - a clear ‘if-then’ principle, that is, a principle according to which defined initial situations lead to deducible behavior patterns. It is thus analogous to the law of mass action, which regulates the attainment of the quantities of the components in a chemical equilibrium. (Eigen 1997: 17–8)

It is a complex theory, but the short version is that within genetic landscapes—to be read quite literally, in the context of (pre-)RNA worlds (Cech 1986; Gilbert 1986), not the wild type, but the most optimal variations of the wild type (the quasi-species) together *as a group* are the target of selection. In order for the quasi-species to overthrow the wild type (and thus to evolve by splitting), it needs to be more optimal. It is a bit like the “hill-climbing” metaphor Dawkins (1996) uses to describe what he calls “accumulative selection.” Eigen (1996: 19):

Selection contains an element of exact ‘if-then’ behavior. It has nothing to do with the tautological interpretation ‘best adapted = selected’. ‘Selection’ could in principle just refer to any kind of preference. But here it means a particular kind of preference, which adheres unerringly to a single scale of values. Selection is based upon self-replication. It distinguishes sharply between competitors, it constructs a broad mutant spectrum on the basis of value, and in this way it organizes and steers the entire, complex system.

Selection becomes understood as replication of preferential information. Eigen and Dawkins’ ideas find their roots in the works of Fisher (1930) and Wright (1929), with that very important difference that Eigen saw his ideas on natural selection as a physical law restricted to the early “life” of replicators (RNA and DNA molecules and viruses). Eigen therefore pointed out the limit of natural selection. As soon as there is a distinction between a genotype and a phenotype (and thus an established translation machinery), he argued that selection occurs at the level of the cell, which is different from how selection occurs at the level of replicators.

The chief criticism of Darwin's idea was directed against its supposed claim to explain all of evolution. However, the development of life, from molecular systems to human beings, has passed through many stages of organisation, and, while some of these were Darwinian in nature, many were fundamentally different. Since the preservation of all living systems is based upon reproduction, selection plays a role at all levels. But selection is expressed in many different ways, sometimes as coexistence or even cooperation, and sometimes as competition and the often irreversible weeding-out of some forms of life. (Eigen 1996: 29–30)

Eigen's introduction of information theory and focus on increasing levels of complexity and optimization also inspired scholars such as Szathmáry (2002, 2006), and other researchers interested in the major transitions of life, as well as scholars that form part of the field of biosemiotics. For Eigen, for example, the origin of autocatalytic replicators, and their compartmentalization into a genome, was a transition that marked a "peculiar 'once-forever'—selection mechanism [...] a consequence of hypercyclic organization" (Eigen and Schuster 1977: 542). Oparin, for example, once asked why life does not originate *de novo* on a daily basis. The most popular answer in his time was that existing life takes up all resources, which is an ecological argument. The answer scholars like Eigen, Jacob (1977), or Monod (1971) gave is that it is so unlikely an event, that if it were to happen once, it will most definitely not happen twice due to the complexity involved. Life genealogically builds upon what exists, and what exists is the outcome of once-forever events, likely at the time, but often not repeatable thereafter. This tinkering argument is based upon an understanding of genes as carrying an increasingly complex informational code, and just because of its emphasis on information and increasing complexity, it is so popular with creationists (Hoyle 1981), whom assume that such tinkering requires an intelligent designer.

Nonetheless, if the origin of the genetic code was a "once-forever" event, another way of stating the latter is as follows: However the genome evolved, it is unique to that period. In so far as the situation of viruses resembles that realm, probably because they too are remnants of that particular phase (see, e.g., Villarreal 2004; Villarreal and Defillips 2000), they too can be studied as examples of hypercyclic organization. But beyond that, the law of selection stops and selection takes on different forms, sometimes as co-evolution, sometimes it is completely overthrown by other mechanisms and thus, itself, as a mechanism, not selected simply because the if-then conditions are not met. If correct, then such a view would imply a higher-order sorting or selection of evolutionary mechanisms. One of the challenges we are faced with is understanding how various and distinct evolutionary mechanisms work together to bring forth the phenomenon that evolution is.

Finally, ecology, for the founders as well as the organizers of the centennial, was by and large reduced to the study of genetic landscapes (Serrelli this volume), as well as the conditions for habitable life on earth. Research on both ontogeny and ecology (Odling-Smee 1988; Van Valen 1973, 1976), which are both areas of research that were first defined by Haeckel, became reintroduced in standard Neo-Darwinian theories from the 1960s and 1970s onward, partly because of advances

in symbiosis and symbiogenesis (Margulis 1970, 1981) and partly due to advances in macroevolutionary fields, including biophysics. Eldredge (1985b, 1989, 1992), Gould (1977), Lewontin (1983, 2000), Gould and Lewontin (1979), and Stanley (1979; Eldredge and Stanley 1984), for example, were quite active in reinstating ecology, ontogeny, and biophysics as valid sub-branches of the Neo-Darwinian framework. I return to this later in the text.

Today, the movements evolved into, on the one hand, the new sociocultural evolutionary sciences, including evolutionary psychology, evolutionary linguistics, and evolutionary anthropology (for a review, see Gontier 2012a) and, on the other hand, the schools that associate with eco–evo–devo research. Eco–evo–devo today reinstates a mesolevel analysis between the biomolecular (micro) and ecological and systematic (macro) sciences. Within the sociocultural sciences, especially the work of Jablonka and Lamb (1989) and Oyama (1985) was foundational. Typical of the eco–evo–devo approach is that scholars try to define and map actual life history, by, e.g., correlating genes with organismal phenotypes and sociocultural, biotic, and abiotic environments. On the other hand, work on symbiosis and symbiogenesis and reticulate evolution in general remains poorly integrated in Neo-Darwinian theory.

2.2 *Universalizing Selection*

One of the reasons why the microevolutionary tradition has been so successful is that it has been able to “universalize” (Cziko 1995; Dawkins 1982a; Dennett 1995) natural selection theory into a common scientific language, not by searching for the law that natural selection can be (as Eigen had demonstrated), but the pattern that natural selection produces as well as the parameters that need to be present for natural selection to work. These parameters and patterns have been mostly formulated in the form of heuristics. Starting with the units and levels of selection debate (Brandon and Burian 1984), evolutionary epistemologists (Bradie 1986) and evolutionary biologists have identified “universal” units of selection such as the replicator (Dawkins 1982a), the interactor (Hull 1981), and the reproducer (Griesemer 2000), and they have been engaged in identifying the levels where selection occurs (Brandon 1982; Godfrey-Smith 2009; Okasha 2005). Such research relates to hierarchy theory and the quest for the major transitions, or patterns and trends of life that especially natural selection, understood as the selection of information, has brought forth in all domains of life (Maynard Smith and Szathmáry 1995; see Brandon and McShea 2010 for a critique).

Overall, the universalization of selection is characterized by abstracting a general template from natural selection that provides information on how the mechanism works (Gontier 2006a, b). This template can then be used as a heuristic to study the evolution of genes, organisms, culture, cognition, and language. In biology, Lewontin (1970: 1) has defined such a template or “logical skeleton” of natural selection as “phenotypic variation, differential fitness, and heritability of

that fitness.” And ten years earlier, Campbell (1960), the founder of evolutionary epistemology, argued that such a general formula of natural selection is “blind variation and selective retention.” This means that as soon as one can identify something that varies blindly and is selectively retained, that something evolves by means of natural selection. In sum, the work by scholars engaged in universal selectionism has led to finding (1) more units and levels of selection and (2) the conditions under which natural selection operates, conditions they formulate in the form of a heuristic, logical skeleton, or formula.

Both approaches are today somewhat being synthesized into the new and rising field of Biosemiotics (Barbieri 2008a, b; Favereau 2005; Hoffmeyer 2008), where, as the name implies, the evolution of informational codes serves as a new means to delineate the major transitions of life from within a more historical perspective.

3 Macroevolution

In his *Structure of Scientific Revolutions*, Kuhn (1962) characterized scientific practice as a paradigm, defined in his preface as “scientific achievements that for a time provide model problems and solutions to a community of practitioners.” Scientific development goes through distinct phases from preparadigm and paradigm formation phases, to phases of paradigm execution, and paradigm reform or scientific revolutions. The latter result from how well scientific frameworks deal with anomalies that challenge the tenets of an accepted paradigm. Anomalies cause paradigm instability and scientific crisis. Either scientists are able to solve the anomalies from within the standard epistemic framework, or they develop another paradigm that either solves the issues or gives hope that it eventually will.

The historical developments of Darwinian and Neo-Darwinian evolutionary theories follow Kuhn’s description of scientific revolutions quite accurately. Darwin (1859) did not find evidence for the fixity of species, which was a tenet in the standard paradigm of his time. Instead, his voyages had made him come to believe that species evolve. He knew that if true, his ideas would cause for a scientific revolution. Calling his *Origin of Species* “one long argument,” Darwin (1859: 495) recognized that he had merely provided a hypothesis based upon generalizations of observable artificial selection in animal and plant breeding. For such a generalization to become a theory, rigorous scientific testing and proof was needed. In Chaps. 6 and 9, Darwin also pointed out anomalies or objections to his arguments. One of them was the lack of evidence for intermediate forms (“insensibly graded series,” Eldredge 1995: 95) in the fossil record. Darwin countered the objection by arguing that not his hypothesis, but the fossil record was incomplete.

During the “eclipse of Darwinism,” other anomalies were found (see Bowler 2003 for an overview). The rediscovery of Mendelian genetics and the introduction of mutation theory questioned Darwin’s gemmules theory and his ideas on genetic blending. More discontinuous and saltational views emerged as a

consequence (see Gould 1977, 2002 for an overview). These anomalies were solved from within the evolutionary paradigm by the theoretical population geneticists who synthesized natural selection theory with Mendelian heredity laws and who advanced a more gradual and continuous interpretation of genetic mutations (see Schwartz 1999 for an overview). The scholars provided mathematical and experimental proof for the theory of evolution and turned the hypothesis into a scientific theory, Neo-Darwinism, that formed the basis for paradigm selection by the founders of the Modern Synthesis.

Neo-Darwinist population geneticists are best regarded as executors of the program. They have been solving anomalies that phenomena such as altruistic and sociocultural behavior and eukaryotic sex pose to the Neo-Darwinian framework. By incorporating below and above organismal phenomena, they have had to make compromises to both Darwin's original theory of natural selection and the synthetic framework, but at the same time, they have been able to expand its scope and application range.

The macroevolutionary perspective as we know it today has been introduced from within the field of paleontology by Niles Eldredge and Stephen J. Gould in the early 1970s when the Modern Synthesis was well formed and on the expanding. Eldredge and Gould started out as executors of that particular program, but in so doing, they found anomalies that lead to crisis. Scholars in this tradition accept the lack of intermediates in the fossil record as a fact, they find evidence for periods of stasis, and they demonstrate that speciation and extinction are events that often occur rapidly. Scholars on both sides of the scale are currently investigating whether the Neo-Darwinian framework can overcome this crisis that research on stasis, speciation/extinction, and the lack of intermediates introduces, or whether the findings necessitate a scientific revolution.

When studying the evolution of trilobites, *Phacops rana* and *Phacops iowensis* which Eldredge (1971: 162) called "true biospecies," he did not find intermediate species. Instead, he encountered long periods of morphological stasis within the trilobites, and when variation in eye lenses did come along, older forms were rapidly replaced. Speciation was a rare event rather than a natural outcome of incessant and continuous anagenetic evolving which would imply intermediates (for a detailed description, see Eldredge 1985a). The speciation events that occurred appeared to have been driven by the spatiotemporal distributions of the species; geography, group size, and how ecological regions are populated by real individuals as opposed to how genes map onto genetic landscapes. New traits become fixed in marginal groups isolated from their parental species, and they split and rapidly replace the older population. In other words, Eldredge explained morphological change of trilobites by making use of Mayr's model of allopatric speciation by peripheral isolates and saw it as an anomaly to "phyletic gradualism" that endorsed speciation to occur through anagenesis where species "gradually and systematically evolve themselves out of existence" (Eldredge 1995: 69). For Eldredge, Mayr's model explained the gaps he found in successive strata. But he went further, by arguing that such a model annihilates the necessity to postulate intermediates, and furthermore encourages the idea that most species evolve through cladogenesis.

The majority of species preserved in epeiric sediments show no change in species-specific characters throughout the interval of their stratigraphic occurrence, and the phyletic model is inapplicable to most of these elements of the fossil record. Instead, change in, or development of, species-specific characters are envisioned as occurring relatively rapidly in peripheral isolates. Morphological stability of epeiric species is attributed to stabilizing selection. (Eldredge 1971: 166)

At first, Eldredge explained morphological stasis as a form of stabilizing selection, and later and inspired by Vrba (1980, 1985a, b), Lieberman (2000; Lieberman et al. 1993, 1995, 2005, 2007), Lieberman and Dudgeon (1996), Lieberman et al. (1995, 2007), Eldredge et al. (2005) would understand it as an outcome of drift and habitat tracking. A parallel with Sewall Wright's shifting balance theory was first made by Thomas Schopf in the introduction to the first punctuated equilibria paper (Eldredge and Gould 1972). By denying that genetic selection plays sufficient role, drift and habitat tracking are recognized as independent mechanisms, not merely the result of a genetic level in evolution; rather, they add an ecological level, very much in the same way as Hubbel (2001) applies ecological drift to describe biodiversity and biogeography (Rosindell et al. 2011).

Returning to the 1970s, around the American Museum of Natural History and Columbia University, a group had been developing where Eldredge would become part of. Together with Stephen J. Gould, who found the same results in land snails, Eldredge published the consequences of their findings a year later (Eldredge and Gould 1972). Their conclusions can be summarized as follows:

1. Gaps in the fossil record are real, and when no intermediates are found, then there is no "insensibly graded fossil sequence" (Eldredge and Gould 1972: 87);
2. Inspired by Hennigian cladistics of genealogical or ancestral-descent relationships (Eldredge 1971: 157); in anticipation of Ghiselin's (1974) notion of species as biological individuals, they claimed that "biospecies" are real because they have stratigraphic and thus historical existence (a beginning, life span, and ending in time p. 92), and species demonstrate a type of stasis or "homeostasis" that surpasses "genetic revolution" (a term coined by Mayr, p. 114)—they never denied the occurrence of genetic mutations or the importance of genetic selection, what they claimed was that neither suffice to cause speciation;
3. Speciation is rare, but when it occurs, it occurs rapidly and species evolve by splitting because of allopatric speciation by peripheral isolates (p. 96);
4. The history of life is characterized by punctuated equilibria rather than by phyletic gradualism, and the former is a consequence of "the theory of allopatric speciation" and "implies that a lineage's history includes long periods of morphological stability, punctuated here and there by rapid events of speciation in isolated subpopulations" (pp. 108–10);
5. Trends are real (p. 110);
6. The Modern Synthesis is biased toward phyletic gradualism, but macroevolution (understood as the evolution of species or speciation) and also stasis of species cannot be fully explained by microevolutionary theory by which they meant genetic selection theory—the critique goes out to microevolutionary schools of thought much more than it goes out to Darwinism or general evolutionary theory as some creationists have falsely claimed.

In a Popperian sense, one anomaly rightfully disproves all, but it would only be the beginning of a long series of publications where scholars would confirm both their results and the pattern of stasis and rapid speciation in numerous lineages (reviewed in Gould and Eldredge 1977, 1993), including our own (Eldredge and Tattersall 1982; Gabrowski and Wood this volume). In a way, it was neither the trilobites or the snails, nor their theory of punctuated equilibria that made the difference. The major conclusion was that an exclusive focus on genetic distributions and population levels so typical of the microevolutionary perspective did not fully explain speciation and large-scale trends. Their work marked a beginning of a fresh breath of air for paleontologists who, ever since Darwin, were treated like the stepchildren of evolution. Eldredge and Gould's work justified other scholars to speak up against the claims of the Synthesis, in favor of what the data and the fossil record actually said. It marked a beginning of macroevolutionary thought as distinct from microevolution and a celebration of the work performed by paleontologists, systematists, and ecologists which had been eclipsed.

3.1 *“Evolutionizing the Dead” by Means of Organicism*

Like microevolutionary scholars, macroevolutionary scholars have also introduced an inclusion of “the dead” by emphasizing the evolutionary impact that phenomena traditionally not conceived as living have. Macroevolutionary scholars recognize species and higher taxa such as genera and phyla as historically real entities that occupy space and time. The species–genera distinction was introduced by Aristotle. In Judeo-Christian tradition, which was more influenced by Plato, it was believed that species were created by God according to fixed prototypes. Taxonomic classification, including Linnaean systematics, was nonetheless understood as a theoretical and logical discipline, where universals and particulars were distinguished based upon logical dichotomies. As theoretical frameworks, they showed the order of the universe, but like any universalia (theoretical concepts), their independent existence was questioned by nominalists and accepted by realists (for a discussion, see Gontier 2011). Darwin adhered to a nominalistic species concept, thereby claiming that species are not real, but Mayr (1942) introduced his biological species concept that defines species based upon sexual exclusion. He did so out of necessity because the gene population point of view annihilates the living sexual individual. And his theory of allopatric speciation due to peripheral isolates equally demarcated species in ecological terms. With Mayr, species become understood as bounded in space and time, due to sexual compatibility and geographical accessibility requirements. Eldredge and Gould took the reasoning further by “evolutionizing” and “geneologizing” not only species but also higher taxa. I give two examples, one from Eldredge's work and one from Gould's.

For Eldredge (1999: 22–3), species are “real entities, ‘individuals’ with births, histories, and deaths.” They are real genealogical entities that occupy an equally real ecological space in the history of life. When Ghiselin (1974) introduced his

ideas of species as biological individuals, an approach Eldredge adopted, Ghiselin quite literally, revitalized the organic notion of beings that was so typical of pre-synthetic evolutionary and historical thinkers of the nineteenth century. Back then, languages and cultures were considered real organic and organismic beings or natural kinds as philosophers call it. All have a birth, life history, and ending in time from which linguistic, cultural, and sociopolitical genealogies could be inferred. Because they were beings, they even reproduced, though not by replication, but by splitting (diffusion) or merging (cultural blending or acculturation, Gontier 2006c; Kressing et al. 2014). Inspired by linguistics and language genealogies, Darwin argued that all biological organisms are also genealogically related through what we call genetics and what he called the blood line (discussed in Gontier 2011). The discovery of genetic material and Weismann's barrier blocked such continuity, and anthropological fields would introduce notions of historical particularism instead, claiming that no genealogy of sociocultural knowledge can be drawn because every culture has its unique and particular history. The unique and particular history of biological species, in turn, was genealogized by Hennig who revitalized the idea of natural kinds, and this work was foundational for Ghiselin when he argued that species are biological individuals.

By building on both Hennig's cladistics that are a "truly 'scientific' way of deriving evolutionary histories and taxonomies" (Eldredge 1999: 8) and Ghiselin's work, Eldredge understands species as real historical entities, beings or individuals that occupy space and time. Species genealogies are more stable in time than the individual organisms that make them up. His research studies on stasis (Eldredge et al. 2005), living fossils (Eldredge and Stanley 1984), extinctions (Eldredge 1991a, b), and biodiversity (1992, 1997; Casetta and Marques da Silva this volume) are investigations into the geological life span, the actual natural history of species, both in what regards their origin, genealogy and ending, as well as in what regards their relation to the natural environment. As an ardent environmentalist, much of Eldredge's career has also focused on "biologizing" and "evolutionizing" the abiotic environment. The abiotic environment is relevant for understanding biological evolution, not as a level where genetic selection occurs, but as an evolutionary and causal factor that impacts the evolution of life.

Echoing some of Darwin's strongest themes and denials, modern evolutionary biology emphasizes genes and biotic interactions at the expense of explicit links to the physical world. Ecology plays a muted role in evolutionary theory. And patterns in the history of life – patterns strongly linked with the physical history of the earth – still await full integration with evolutionary theory. (Eldredge 1999: 95)

That ecology is real becomes most clear in his distinction between an ecological/economic and genealogical hierarchy (a distinction he first made in 1985, but for an overview, see Eldredge 2008). That surely was not part of the Modern Synthesis, but it can be incorporated into a reworked version, in so far as Darwin himself attributed more causality to the environment than his predecessors did.

We also find this idea with Gould (1989: 228) who argued that "Evolutionary change (as opposed to mere variation) is produced by forces of natural selection arising from the external environment (both physical conditions and interactions with

other organisms).” Nonetheless, Gould (1977) was more inspired by developmental and genetic studies. Contrary to Eldredge, who explained stasis as the outcome of stabilizing selection and later drift, Gould investigated the “homeostatic” life span of species as a possible consequence of ontogenetic constraints (Gould 1977) and genetic aging (Gould et al. 1987). By understanding eukaryotic genera and clades as real historical individuals, that have a beginning, life span, and ending in time, he studied that life span or genealogy by looking for trends in eukaryotic multicellular evolution that indicate a “new arrow of time to specify the direction of evolution” (Gould et al. 1987: 1437). In association with the MBL group (for overviews, see Sepkoski and Ruse 2009), Gould investigated clade typology and concluded that the evolution of marine invertebrates and terrestrial mammals, among others, portrays a maximal disparity (rather than adaptive radiation which he rejected as a notion, Gould et al. 1987: 1438) or “bottom-heaviness” at the beginning of the clade. This bottom-heaviness is followed by rapid decimation and subsequent species diversification within a few remaining lineages. Gould (1989: 304) interpreted this bottom-heaviness as:

early experimentation and later standardization. Major lineages seem able to generate remarkable disparity of anatomical design at the outset of their history – early experimentation. Few of these designs survive an initial decimation, and later diversification occurs only within the restricted anatomical boundaries of these survivors – later standardization.

Dawkins had launched the notion that genes are the ultimate survivors of selection. Inspired by Lerner and Valentine, Gould asked whether genetic systems do age. By believing that “organisms as well as environments were different in Cambrian times, [...] the explosion and later quiescence owes as much to a change in organic potential as to an altered ecological status” (Gould 1989: 230). He assumed that early multicellular life, though morphologically different, had a “shared genetic heritage, now dissipated” (Ibid.: 231–2). Since the Middle Cambrian, a period in life that is well preserved in the Burgess Shale Formation currently in the Canadian Rockies of British Columbia, no new phyla or “body plans,” as he called them, have evolved, for which he raised the possibility that the genetic systems had aged. Gould was a true visionary of the evo–devo schools that emerged with the discovery of the homeobox gene complex (Gehring 1992) and regulatory, homeotic genes in general (Davidson and Erwin 2009), when he wrote:

I have no profound suggestions about the potential nature of this genetic ‘aging’, but simply ask that we consider such an alternative. Our exploding knowledge of development and the mechanisms of genetic action should provide, within a decade, the facts and ideas to flesh out this conception. [...] We cannot, for now, go beyond such crude and preliminary suggestions. (Gould 1989: 231)

Gould found the anomalies less commensurable with Neo-Darwinian theory, though he too emphasized repeatedly that he himself was a Darwinist, because Darwin himself was a pluralist. For Gould (1982: 383):

The non-Darwinian implications of punctuated equilibrium lie in its suggestions for the explanation of evolutionary trends [...] not in the tempo of individual speciation events. Although punctuated equilibrium is a theory for a higher level of evolutionary change, and must therefore be agonistic with respect to the role of natural selection in speciation,

the world that it proposes is quite different from that traditionally viewed by palaeontologists (and by Darwin himself) as the proper geological extension of Darwinism. The “gradualist-punctuationalist debate”, the general label often applied to this disparate series of claims, may not be directed at the heart of natural selection, but it remains an important critique of the Darwinian tradition.

Because both Eldredge and Gould understand higher taxa as real, (mass) extinction and origination/speciation are equally real phenomena, and their history in time and space can become documented. Another logical outcome is research on both biological/genealogical and ecological hierarchies (Tëmkin and Eldredge this volume). In that regard, and as a part-time historian of science, Gould (1981) was more interested in debunking cultural biases of the scale, while Eldredge has been actively engaged in developing new hierarchical frameworks.

Finally, if species are real, it raises questions on species sorting. In fact, if all higher taxa, such as kingdoms or phyla, are real because they demarcate actual historical groups in space and time that can be delineated based upon ecological niches, geological strata, morphological layout, and mechanisms according to which they evolve, one could in principle ask whether there exists some type of sorting from Woese and Fox (1977) three domains downward. Eldredge and Gould kept it to questions of species sorting and developed the ideas further in collaboration with Vrba (1989), Vrba and Eldredge (1984), Vrba and Gould (1986). The rationale is that in so far as natural selection in combination with drift and abiotic factors causally influences speciation, it becomes natural to ask whether any or all somehow influence speciation to be differential and thus to show trends or arrows in time. Eldredge (1999: 23):

If species are construed as real historical entities – with the aforementioned births, histories, and deaths – that in itself suggests the very real possibility that there are factors that bias those births and deaths. And that means that there very probably is a higher-level analogue to natural selection – species selection, or, as I have come to prefer, species sorting. The apparent directionality of trends, we suggested, might be the result of, say, differential species survival ...

Species, as biological beings, reproduce, not by replication, but by splitting or cladogenesis, and as such also introduce a pattern of descent with modification that is in turn characterized by punctuated equilibria rather than phyletic gradualism. For Gould, the importance of punctuated equilibria had been that it lent insight into such trends:

At the macroevolutionary level of trends, the theory of punctuated equilibrium proposes that established species generally do not change substantially in phenotype over a lifetime that may encompass many million years (stasis), and that most evolutionary change is concentrated in geologically instantaneous events of branching speciation. [...] (Gould 1982: 383)

Returning to Kuhn, does macroevolutionary research call for a revolution? Gould was more revolutionary than Eldredge. For Eldredge (1985b), the Synthesis is merely “unfinished,” and he takes: “... being called anti-Darwinian very personally. ... I have always thought of myself as more or less a knee-jerk Neo-Darwinian” who has “felt that, with one or two major exceptions, my version of how the evolutionary process works lines up very well with Darwin’s” (Eldredge 2006: 36).

He accepts, as Thomas Huxley did, that the theory of natural selection does not necessitate gradualness, and he understands his ideas as a geological extension of Darwinian theory, which is why he has tried to time speciation based upon geological strata. But the fact of the matter is that by understanding speciation as an outcome of ecological and geographical factors, much more so than as a consequence of genetic selection, he attributes causation to the abiotic environment rather than understanding it as the mere scene or level where genetic selection occurs.

Migration was one of the four elements of the Modern Synthesis, but if habitat tracking or niche construction have causal influence on the future course of evolution, then, as Lewontin (2000) pointed out, such selective behavior goes out from active organisms rather than selective environments that weed out passive individuals (also see Stigall this volume). The field of ecology was not part of the Modern Synthesis and became introduced post-synthetically, in both the micro- and macroevolutionary schools. Ecologically oriented scholars have done excellent work in finding causal factors that explain stasis, evolution, and extinction (Futuyma this volume; Bokma this volume) that go beyond genetic selection. These include drift, habitat-tracking, abiotic environmental changes, developmental constraints, and biophysical constraints as well as affordances. Such research has created a scientific necessity to integrate environmentalist and ecological approaches into the evolutionary discipline. Quite often, the environment provides causal non-genetic factors that influence how species originate, evolve, and die. Climate change, meteor impacts, soil, and atmosphere composition all can influence the evolutionary faith of species and higher taxa. Thermodynamic and other physical laws (Bohm 1980; Kauffman 1995; Prigogine 1980; Stanley 1979; Stanley this volume; Thompson 1917; von Bertalanffy 1928, 1940, 1950) also play crucial roles, as enablers as well as constrainers in both the formation of biochemical and anatomical form and its development and extinction. Ecology, systematics, and biophysics today are on the rise, and macroevolutionary scholars have most certainly contributed to their recognition by averring for a wider recognition of the importance of development, biophysics, and ecology in providing a fuller view on the evolution of life.

These ideas find their origin in the period designated as the eclipse of Darwinism and associate with presynthetic ideas, and these ideas also form part of the credo of scholars who call out for an extended evolutionary synthesis (Gontier 2010b; Pigliucci 2009; Pigliucci and Müller 2010). It is probably also the main reason why topics such as stasis and eco–evo–devo ranged so high at the 2009 Chicago bicentennial. As an audience participant, I found it nothing less than amazing how ideas associated with the “eclipse of Darwin,” characterized as heretic by the founders of the Synthesis, and first reintroduced from within macroevolutionary streams of thought were presented as basic subject areas of Neo-Darwinism and approached from within universal Darwinian (Dawkins 1983; Dennett 1995) and universal selectionist (Czicko 1995) accounts.

3.2 *Universalizing Punctuated Equilibria*

The study of actual scientific practice teaches us that hypotheses and theories are tested for their use, not merely for their truth or corroboration to the truth, as Popper (1957) or logical empiricists assumed. Universal Darwinism and Universal Selection theory have proven to be useful to understand certain aspects of behavior. Punctuated equilibria theory has equally proven its use by designating a shared theoretical framework by which we can understand the history and evolution of natural kinds such as species and higher taxa. It is safe to say that many of its claims, including that species, extinctions, speciation, stasis, and gaps are real, are not only accepted as part of scientific language, but they are intensely studied as phenomena in need of explanation by scholars on both micro- and macrosides.

Punctuated equilibria theory and macroevolutionary research in general, and cladistic analysis in particular, have furthermore provided a universal methodological toolkit that is used to comprehend non-gradual vertical descent.

Just as the tenets of natural selection theory have been universalized across disciplinary boundaries and across the cosmic scale, so too the basic tenets of macroevolutionary outlooks in general and punctuated equilibria in particular have been universalized. Punctuated equilibria theory describes a pattern of evolution: Long periods of stasis are intermitted by short periods of rapid change (Eldredge and Gould 1972). Eldredge and Gould were among the first scholars within the field of paleontology to adopt cladistics which is an intrinsic genealogical method, and as such, they have been exemplar for macroevolutionary research of the living as well as the dead, both sub- and superorganically. Darwin argued that species share common genealogical descent, and as Eldredge rightfully notes, Hennig's cladistics method is the best scientific method available today to infer such genealogy or actual life history, because it is through such cladistic analysis that one can infer the patterns of evolution.

Cladistics, in keeping with the original search for natural kinds, but imbued with an evolutionary perspective, boils down to a search for the actual distribution of the features, or 'characters', of organisms. It turns out that such characters are complexly, hierarchically nested just as are the taxa they define. (Eldredge 1999: 70)

The major breakthrough cladistics has brought forth is that it enables to infer genealogies of the actual life history of populations and species. But one can just as well use them to study the actual genealogy or "half-life" of chemical substances such as proteins or genes, as well as particular morphological and behavioral traits. These genealogies of natural kinds enable the building of phylogenetic taxonomies and hierarchies of the evolution of these specific phenomena. In short, traits can be morphological, but also genetic, behavioral, or cultural, and their origin, history, and ending can be mapped across time and space.

With the rise of whole-genome-sequencing techniques and our growing possibility to compute and study large data sets across time and space, fields such as meta- and comparative genomics are introducing macroevolutionary

reconstructions of various aspects of life's history. The application of phylogenetic reconstruction methods that map the spread and distribution of genes has confirmed the pattern of punctuated equilibria in both extinct and extant taxa (Bokma 2002; Bokma and Monroe 2010; Pagel et al. 2006; Venditti and Pagel 2008, 2010).

Historical linguists have from the nineteenth century onward and in close parallel with evolutionary biologists attempted to reconstruct the natural genealogies of languages (Gontier 2011; Kressing et al. 2014). When Lorenz (1958) and Tinbergen (1963) first defined ethology, they wanted nothing less than to build a taxonomy of behavior and thus give the natural history or the genealogy of different behavioral traits by mapping when they first arose in time and how they evolved, spread, went extinct, or transitioned into something new. Equally, Nietzsche (1874) wanted nothing less than to launch the study of the genealogy of intellectual thought in our species, and when Campbell (1960, 1974) introduced the field of evolutionary epistemology, he wanted to map the evolution of knowledge from bacteria to humans. These ideas are now finally entering the sociocultural sciences. Today, anthropologists and archeologists are increasingly mapping the evolution of material culture by making use of phylogenetic and cladistics analyses. From within sub-branches of anthropology that are increasingly designated as macroarcheology and macroanthropology, scholars are reconstructing the beginning, evolution, and ending of "superorganic" traits across space and time.

Any and all such mappings by necessity take on a macroevolutionary approach, because we have to go beyond individual organisms, groups, and species, and focus on the genealogy or life history of the specific traits, i.e., genes, languages, or cultural artifacts themselves, beyond and across the beings that house them. And such research necessitates an investigation into their biogeography or how they populate the evolutionary landscape. Beyond gene pools, scholars are just beginning to map morphological, proteomic, viromic, genetic, linguistic, and material culture pools. It are eventually such tree and network analyses that enable us to infer patterns of evolution, patterns that include stasis, branching, and merging. These patterns in turn give clues to the pace of evolution as well as the mechanisms that underlie the natural history or evolution of these phenomena.

Today, phylogenetic methodologies are applied to model macroevolutionary, ancestral–descent relationships of our kind (Eldredge and Tattersall 1982; Schwartz and Tattersall 2001; Wood this volume) as well as the cultural historical dispersal of material artifacts (Currie et al. 2010; Borgerhoff Mulder et al. 2006; Eldredge 2011; Eldredge and Tëmkin 2007; Lipo et al. 2006; O'Brien et al. 2002; Pagel and Meade 2006; Steele and Kandler 2010) and languages (Atkinson et al. 2008; Mace and Jordan 2011; Pagel et al. 2007). These phylogenetic models provide rigorous evidence for the pattern of punctuated equilibria in strands of linguistic and cultural evolution, as well as patterns of merging. Such research also necessitates new hierarchical thinking on cultural traits and behavioral phenomena, how they relate to their inventors, and how they transcend them. In sum:

The macroevolutionary approach in archeology represents the most recent example in a long tradition of applying principles of biological evolution to the study of cultural change. Archeologists working within this paradigm see macroevolutionary theory as an effective

response to the shortcomings of Neo-Darwinian biological evolution for studying cultural evolution. Rather than operating at the level of individual traits, macroevolutionary archeologists emphasize the role of hierarchical processes in cultural change. ... Major cultural change, when it happens, is likely to be rapid, even revolutionary, with periods of rapid change separated by periods of relative stasis of actively maintained stability. (Zeder 2008: 1)

Concepts such as stasis, rapid turnovers, and constraints, or exaptations (Gould 1991; Gould and Vrba 1982) that form part of the technical language introduced by macroevolutionary scholars are also applied on a metaphorical level in the socio-cultural sciences to describe certain aspects of linguistic and cultural evolution that cannot be accounted for by universal selectionism (d’Errico 2003; d’Errico and Stringer 2011; Tattersall 2014).

Universalizing punctuated equilibria, and thus developing a universal heuristic of the pattern, implies that we identify the mechanisms that underlie both the long periods of stasis and the short periods of rapid change. Several mechanisms can lead to stasis, including overall developmental, genetic, or epigenetic constraints (Carroll 2005; Davidson and Erwin 2006; Futuyma 2005, 2010 this volume; Gehring 1999; Gould 1977, 1989; Jablonka and Lamb 1995), stabilizing selection (Lieberman et al. 2005; Lieberman and Dudgeon 1996; Schmalhausen 1949) or drift (Bentley and O’Brien 2011; Bentley et al. 2004; Eldredge et al. 2005; Hubbel 2001; Kimura 1968, 1983; Masel et al. 2007). Numerous mechanisms can explain rapid change or speciation, such as symbiogenesis (Margulis 1970, 1999; Gontier 2007, 2012b), hybridization (Arnold 2006, 2008), lateral gene transfer (Gogarten et al. 2009), and virulation (Ryan 2006, 2009), the Baldwin effect (Baldwin 1896), or the Ratchet effect.

4 A Clash of Scientific Cultures

Natural selection is not the beginning, as a physical force that stands above and beyond time, it is the fallout, the record of history. (Eldredge 1998: 96)

In the 1980s, Maynard Smith (1983, 1984) invited paleontologists to join the high table of evolutionary theory. The invitation was followed by polemic debates in various articles and books. One of those responses came from Niles Eldredge in his book *Reinventing Darwin: The Great Debate at the High Table of Evolutionary Theory*. In it, he characterized John Maynard Smith, Richard Dawkins, and George Williams as ultra-Darwinists sitting at one side of the table, and on the opposite side, he positioned Stephen Jay Gould, Elisabeth Vrba, Stanley Salthe, and himself, whom he characterized as naturalists.

Ultra-Darwinists were those scholars who adhered to a microevolutionary perspective by reducing the theory of evolution by means of natural selection to the *mechanical study* of how genes underlie evolutionary change at a population level. In other words, they had taken genetic change at a population level as normative and causal for evolutionary change at all ranks of life. Naturalists, on the other hand, studied evolutionary history from within a macroevolutionary perspective and endorsed more holistic epistemic stances that included paleontological, biogeographical, ecological, physical, and systematic areas of research. Their research

had been descriptive and had focused on finding recurring patterns and trends in various ranks of life that surpass the population level.

The problem for the naturalists was that the *actual history* of how life changes does not converge with the normative framework of how life *should* change. At the heart of the debate lie radically opposing views on how evolutionary research has to be conducted, and whose epistemic stance, the microreductionist or macroholistic perspective was more scientific. While the ultra-Darwinists were concerned with detailing the underlying mechanism of evolution (which they associated exclusively with genetic selection), paleontologists were concerned with describing life's history. In other words, it was a clash of scientific cultures where different epistemic practices had evolved. Eldredge (1995: 2):

What is really at stake is diametrically opposed suppositions of how evolutionary biology should be conducted. Maynard Smith put the geneticist's position succinctly: paleontology is about history. It is the paleontologist's job to elucidate what the evolutionary process has wrought over the last 3.5 billion years. But evolutionary theory is about how the evolutionary process works. And that, to a geneticist, means how genetic information, underlying the production of the physical appearance (and physiologies and behaviors) or organisms, comes to be modified over the course of time. What can a paleontologist, trapped under the dead hand of history, possibly have to say about the mechanics of genetic change? After all, science is supposed to concern itself with how things work.

Eldredge (1995: 5) blamed ultra-Darwinists a form of "physics envy," because "they seek to transform natural selection from a simple form of record-keeping, a filter that biases the distribution of genes between generations, to a more dynamic, active force that molds and shapes organic form as time goes by." By wanting to turn natural selection into a constant physical force, they endorsed a form of "extrapolationism" because they assumed that evolution by means of natural selection was a steady-state, lawlike phenomenon where gradual changes in gene frequencies suffice to explain evolution at all time and in all ranks of life. For the naturalists, the steady-state, lawlike theory of evolution by means of natural selection that had been developing did not converge with the actual history of life, and the geneticists' point of view could not simply be extrapolated to large-scale systems defined as populations, species, and ecosystems.

But on the other side of the table (Dawkins 1982b, 1983; Maynard Smith 1983), it was argued that natural history is merely descriptive and that an evolutionary theory should aspire to transcend narration of singular, non-repetitive, and unobservable events, by finding the laws or mechanisms, the underlying causes that bring forth evolution. For ultra-Darwinists, natural history research or the narration of actual historical origination and extinction events, in and of itself, cannot explain the causes and effects of evolution.

4.1 Delineating the Scientific

These debates are not unique to evolutionary biology. All sciences at one point or another have developed debates about whether their science should be primarily

“descriptive” or “normative,” for example, as philosophers of science, in turn inspired by moral philosophers, call it. Inspired by de Saussure, linguists, anthropologists, and sociologists, for example, know the debates as diachronic (historical and descriptive) over synchronic (structural and functional) research, and in physics, we find debates on Newtonian mechanics versus the new theoretical (bio) physics associated with relativity theory, quantum mechanics, chaos theory, and thermodynamics. The reason these debates are similar is they share common intellectual roots to which I turn in this section.

Should evolutionary science describe history or find its causes? And can science tackle origin questions (or extinction questions for that matter) in a scientific manner, or should science reduce itself to the study of repeatable and observable events? These questions associate with five basic and inter-related problems.

1. The problem of causality: Should science be historical and observational and perform a kind of record-keeping, or instead be aetiological, and focus on finding the underlying causes, the reasons why things are the way they are? The ultimate question here is: Can we go beyond record-keeping and find constancy in underlying mechanisms?
2. The problem of predictability: Should science explain what *is* (either mechanically or historically), or should it be able to explain what *ought* to be? In other words, can science make predictions on the future and inferences from the past?
3. The problem of uniformity or constancy over time: Does observation enable prediction and inferences on causality? Does what happens in the present immediately set the norm for the past as well as the future?
4. The problem of determinism or relativity: Is the universe determined by fixed laws, or is evolutionary change relative and dependable upon changing variables?
5. The problem of knowing: Can we, human observers and theoreticians, come to everlasting and objective truths, or merely develop temporary, local knowledge perspectives, from within a variety of epistemic stances?

The problems are indeed interrelated, because mechanisms can only be invoked when change, and that what causes it, is constant through time, or, in other words, determined by everlasting and unchanging laws. Predictability also depends upon the constancy of the mechanism over time. Favoring a normative view therefore implies a uniformitarian epistemic stance.

So a connection has to be forged between uniformitarianism, gradualism, and reductionism: extrapolationism, the projection of commonly observed rates and processes as a prediction of what history *ought* to look like. (Eldredge 1999: 40)

In 1965, Gould wrote a paper titled *Is uniformitarianism necessary?* wherein he distinguished between two types of uniformitarianism: substantive uniformitarianism that endorses “uniformity of rates of geological change” and methodological uniformitarianism that assumes “time and space invariance of natural laws.” The pattern of punctuated equilibria proves that substantive uniformitarianism is false, and according to Gould (1965), methodological uniformitarianism, which assumes

constancy of natural laws, is obsolete, most of all because laws are interspersed by other, often random events that function as disturbances to these laws. In other words, catastrophism, or the acceptance that abiotic random events such as meteor impacts can influence extinction and the future course of evolution of remaining life (e.g., Alvarez et al. 1980), is valid.

Both Eldredge (1985b) and Gould (1987) spent a significant amount of their career fleshing out the origin of uniformitarian views and the notions on time that it brings forth. Uniformitarianism was introduced by Hutton, popularized by Lyell (1830, 1832, 1833), and endorsed by Whewell (1833). Uniformitarianists assume that adequate observational knowledge of the present should suffice to inductively infer the past and predict the future. But, these early scholars did so because they endorsed a lawlike physical view of nature in line with Newtonian mechanics that was inspired by Cartesian philosophy, where space, matter, and therefore also time are absolute and thus a priori determined, linear, constant, and irreversible. Such a stance enables uniformity and predictability toward the past as well as the future because laws are real, steady, and constant. These scholars started from the assumption that the universe, its laws, and our knowledge of them were the result of a benign God. As such, scientists became objective viewers that transcend nature and take on a God's-eye view (Pinxten 1997). This brings us right back to cosmology or better yet, the transition from studies on *cosmogony* (the origin of the cosmos) to *cosmology* (the scientific study of its underlying causes, or *aitia*).

Newtonian physics is best known among philosophers and physicists for validating only Aristotle's *causa efficiens* which associates with the how question: how does matter move and how do phenomena function? It calls out for a mechanical approach, but it nonetheless assumes perfect, eternal, and harmonious functionality in the best of all possible worlds. In short, all these scholars, as firm believers of Judeo-Christian genesis so beautifully depicted in the *scala naturae* of their time, assumed that the cosmos followed perfect and constant, clocklike mechanical laws because they were, in deistic worldviews, the "hand of God" so to say. God did not have to intervene, like was the case in theistic worldviews, because nature follows predictable and teleological perfection.

Such views no longer form part of our worldview. As Eldredge put it:

Most laws are descriptions of what happens given the existence of a set of conditions. Thus, while we might tend to think of gravity as some sort of process (gravity is one of the four basic 'forces' physicists investigate), Newton's and all subsequent 'laws' of gravity are simply generalizations about just what will happen given the existence of two hunks of matter of specified mass and distance apart. (Eldredge 1985b: 174)

With the rise of relativity theory, quantum mechanics, and chaos theory, we are necessitated to acknowledge that our cosmologies or epistemic frameworks are bounded by observational stances and probabilistic analyses, as well as colored by our cultural and theoretical frameworks. In our cosmologies, there is no God's-eye view, and there are no reifiable constant physical forces, or if there are, we do not know them. The best we can do is define the conditions of change of current and past events, generalize from there, and compare the generalizations, which brings forth a statistical analysis.

Philosophers and scientists alike are fond of the idea that an evolutionary theory pertaining to any sort of system is unlikely to be established without a convincing mechanism, a well-articulated and corroborated process of change. ... Darwin is still commonly supposed to have succeeded where all others before him had failed in establishing the credibility of evolution because he supplied a process that could plausibly account for the history of life: natural selection. ... the contention involves whether pattern is preeminent over process in establishing credibility of an evolutionary theory.' (Eldredge 1998: 98)

The naturalists, mostly because of the importance they give to biophysics (Bohm 1980; Kauffman 1995; Prigogine 1980; Stanley this volume), have made the cosmological transition from a teleological to a relativist worldview and have allowed it to enter evolutionary science, while microevolutionary scholars endorse a more ambivalent view that tries to fit the old cosmologies into the new. I give two examples to explain this transition: the rise of natural history research and the clock metaphor.

Evolutionary science is an outgrowth of eighteenth- and nineteenth-century research on the natural history of the cosmos. Advances in physics had caused for a transition from a geocentric to a heliocentric worldview, which in turn had raised doubts about the divine order of the world which scholars had for centuries been depicting in *scala naturae* where the earth was traditionally placed in the center of the universe. From the Renaissance onward and culminating in the Enlightenment, scholars sought out the natural history of the universe (for an overview, see Duhem 1969, 1985).

Natural history research started in an age when travel stories of colonizers, gentleman scientists, and missionaries reported on foreign cultures, languages, political systems, and fauna and flora; when historical linguists were mapping the natural genealogies of the world's languages; when anthropologists *avant la lettre* were providing the first narrations of foreign cultures; and when moral philosophers such as Hobbes, Rousseau, Hume, Smith, and Mill debated the natural as opposed to divine condition of man as well as the status of "common goods," in "primordial" (which they associated with non-Western) as well as sociopolitical societies. In short, natural history research was characterized by encompassing attempts to narrate the natural history of the world and everything in it by referring to its natural "generation" or "development" in opposition to its divine origin.

The term evolution comes from the Latin noun *ēvolūtiō* (the act of reading, or unrolling a script, or narrating a history) and the verb *ēvolvō* (ex—out of and *vōlvō*—roll) and denotes development or unfolding. In this context, it was used in teleological, preformationist circles where especially medics and to some extent natural history students studied the growth of organismal form by trying to narrate its historical development through time. But it was equally used in this context, by cultural and linguistic scientists such as Auguste Schleicher or Max Müller; sociopolitical scientists such as Auguste Comte and Herbert Spencer, Karl Marx, or Kropotkin; philosophers of history such as Hegel, Herder, and Nietzsche; or geologists such as Hutton, Lyell, or Bronn. In these circles, the study of the development of natural beings (languages, cultures, societies, political structures, or biological species) was therefore, more than anything, the study of natural, chronological sequences of change that beings go through, or stated differently, it is the study of historical change through

time. From within the major languages used to develop the scientific worldview, i.e., ancient Greek, neo-Latin, English, German, and French, scholars first used terms such as “development,” “entwicklung,” and “développement,” to refer to processes of historical change of sociopolitical, biological, or earthly form through time, and this development eventually became denoted as evolution.

These investigations into the natural history of the earth and its inhabitants raised doubts on the age of the globe, the fixity of natural kinds (languages, cultures, societies, and species), and whether or not we live in the best of all possible worlds. In sum, it questioned the traditional assumptions there existed on matter, space, and time. In particular, the latter gave way to two types of “conservation ethics”: *musealisierung*, the nineteenth century is typified by the rise of the great natural history museums of France, London, Vienna, Brussels, and New York (see, e.g., Lübke 1990); and patriotism and nationalism, the encounter of “the other” made especially European scholars emphasize and favor their own natural history. In particular in Prussia, works by Kant, Hegel, Fichte, Herder, and eventually Marx, Nietzsche, and Heidegger would take on the question of time in relation to history.

Before, the act of conducting historical research involved a narration of past events, and such narration was often biased toward Western history and cosmology. But the natural history students went further and wanted to find the patterns and deeper lying meaning of historical change as well as the ultimate nature of time. In short, they wanted to “scientificize” history, which they did by postulating equally biased developmental and vitalist laws of generation and decay so typical of the nineteenth century. They understood time as directional. More specifically, time was directed toward a given end state, and development was understood as progression toward that end state. Such a view entails a continuation of teleological thinking.

Comte and Spencer, for example, assumed a steady progress from nomad to shepherd to industrialized and civilized man. Their analyses of time were inspired by religious and philosophical ideas on the world’s beginning, duration, and eschatological ending. By adhering to a non-cyclical, linear, and teleological worldview, they assumed that form necessarily develops according to a given and fixed plan, if not of divine origin then through natural cause by means of natural (physical and developmental) laws. Social Darwinists eventually understood natural selection, interpreted as the survival of the fittest, as one such law. Natural history research induced a first attempt to find a deeper and higher pattern or order in history which brought forth the stadial, unilineal, orthogenic, and racial theories that eventually became used and abused to justify racism, imperialism, and hegemony, as well as the two world wars.

This type of historical research is today called historicism (Popper 1957), and after the havoc it had caused in the wars, and for good reason, such research became condemned. Instead of “morphologically” comparing cultures and placing them on a developmental scale, sociocultural and linguistic scientists averred for historical particularism and the incommensurability of cultures and languages, which brought forth synchronic instead of diachronic investigations. This means that comparative research became redefined, not as a historical discipline, but as a

functionalist/structuralist discipline where cultural and linguistic “universals” are examined in their particular form in the variety of cultures, languages, and societal structures that exist. de Saussure (2006) in linguistics, Malinowski (1944) in anthropology, and Durkheim (1895) or Talcott Parsons (1975) in sociology averred for a synchronization of the sociocultural sciences where the organic and developing natural kinds of before became reinterpreted as closed systems underlain by functional operationalist, universal and determining dead structures that, in their operations, work similar to natural clocks and in accordance with steady laws. In philosophy, science was equally argued to progress and advance toward the truth, which is why they assumed that older theoretical frameworks could be reformulated in “more advanced,” later-developed scientific frameworks through “bridge laws” that enable a harmonious synchronization of human thought toward knowledge. Such “synchronization” also entered the biological sciences, where mechanical, functionalist, and structuralist explanations of underlying causes became favored over historical narrations.

When the early natural history and evolutionary scholars were developing their ideas, they neither foresaw nor planned the havoc it would bring forth. It would be foolish to think that the terrors of colonialism and the world wars were brought forth by such research instead of economic, political, and religious reasons. Nonetheless, it would be equally foolish to deny that it contributed to the general *Zeitgeist* of the time and served as a justification for the crimes against humanity. We, who know the consequences of the early attempts to scientify the study of natural history, therefore have an obligation to investigate and try to understand what could have caused this early historical research to have gone so wrong. One of the reasons why historical research in the nineteenth century was typified by orthogenic views is that they lacked an evolutionary concept of time and instead continued to adhere to a teleological notion of time. Time is absolute, irreversible, lineal, progressive, and directed toward a final goal. And the reason matter attained its goal was because it was subjected to natural laws that gave directionality toward the end state. Eternal forces actualize inherent potential. That is why the missionaries, for example, did what they did. They assumed a favored position by claiming to have insight into the eschatological end state of the universe, and the “civilization” of “barbaric men,” for them, was an act of charity wherein they helped actualize the potential of “underdeveloped” cultures.

To make this point more explicit, let us look into the second example, the metaphor of a clock. Hume (1739) really did hit the sore spot by treating matters of morality and matters of causality in the same way because both go from what *is* to what *ought* to be. We have seen the sun come up today, yesterday, and all the days of our lives as far as we can remember. Our ancestors who lived before us also saw the sun coming up on a daily basis, and we have scientific evidence that she did so from the moment earth was formed and started its orbit around it. We have good scientific theories today that explain why we perceive the sun as coming up and going down, and these theories predict that the orbits of the earth and sun will undergo no significant change for many ages to come. But in the end, the prediction that the sun will come up tomorrow is not 100 % guaranteed, and

however probable the prediction is today, based upon the parameters available to us, it is *our expectation* that she will. And that expectation in the end is based upon uniformitarian, teleological, and clockwork notions of the universe. Hume on the other hand explained all predictions as well as moral prescriptions as human expectations and considered them the dominion of what we today call psychology.

Throughout the years, the problem has only intensified. The logical positivists held firm beliefs that our languages, be they expressed in logic, mathematics, or natural language, somehow relate to the world and that theories can be bridged because they are commensurable just because science progresses toward the truth. Wittgenstein provided proof based upon logic that we cannot demonstrate that language, mathematics included, refers to the world. Moreover, even if we did possess the perfect language to explain the state of affairs of the world, the mere fact of endorsing an evolutionary worldview necessitates that whatever we are able to predict today will only happen if the world does not change and if the parameters we define in our scientific language as valid and foundational remain so and thus do not alter at a different moment in time.

Western science had grown from assumptions that humans lived in a perfect world, that filled an absolute space, with an absolute and irreversible time, and humans were considered to have insight into the perfect mechanisms of the world, which they described in a perfect language that they had received from a perfect God. The age of the Renaissance and the age of Enlightenment were a celebration of this human capacity, a capacity that enabled to take on a “God’s-eye view,” and to become humanistic gods themselves, that know right from wrong, truth from falsehood, and future from the past.

Descartes, a firm believer, introduced mechanical thinking within the field of epistemology, and he was the first to introduce the idea that the natural world functions as a clock. He inspired Newton who inspired Paley, who inspired Dawkins, in thinking that we live in the best of all possible worlds because mechanical laws lead to an optimal and balanced cosmos. The clock metaphor is an argument for design that is based upon teleological arguments. In line with his mind–body distinction, Descartes fought animism by arguing that anatomically, organisms function perfectly according to physiological mechanisms that make their organs function as parts of a harmonious clock of which the sum of the parts defines the whole. The mechanical laws according to which they function so adequately for Descartes proved the existence of God. Paley, as an ardent adherent of intelligent design *avant la lettre*, would build upon these ideas, and this argument for optimization is exactly what we find in Dawkins’ (1995) work, who characterizes natural selection as a “blind watchmaker.” Inspired by Fisher and the “hill-climbing metaphor” used to describe Sewall Wright’s landscapes, and by introducing the idea of “accumulative selection,” he has always had an ambiguity in what regards the predictive powers of selection:

The theory of natural selection provides a mechanistic, causal account of how living things came to look as if they had been designed for a purpose. So overwhelming is the appearance of purposeful design that, [...] we still find it difficult indeed boringly pedantic, to refrain from teleological language when discussing adaptation. Bird’s wings are obviously ‘for’ flying, [...]. (Dawkins 1982a: 161)

For Newton, time and space were absolute and irreversible, and truth was conceived to be singular. William Whewell, another firm believer, attacked the standard historical thinking of his time that was characterized by narration and instead reinstated aetiology, the Greek study of causes. Whewell endorsed that inductive research enables generalizations on these causes. But he could only do so by accepting Hutton's and Lyell's principle of uniformity which is a direct consequence of living in a Newtonian steady-state universe where it finds its justification. In such a world, you have steady cause and steady effect, under all circumstances according to the same final or unchanging teleological forces. Empiricism might be observation based, it no less assumes, just like rationalist deductionism, that laws are constant. In fact, that was the main contribution scholars like Lyell and Whewell advanced: Insight into eternal laws comes from observation, not inborn categories of the mind. As Gould (2002: 102) put it:

History presents two special problems: (1) frequent absence of evidence, given imperfections of preservation; and (2) uniqueness of sequences, unrepeatability in theory contingent complexity, and thereby distancing the data of history from such standard concepts as prediction, and experimentalization. We may epitomize the dilemma in the following way: many people define science as the study of causal processes. Past processes are, in principle, unobservable. We must therefore work by inference from results preserved in the historical record. We must study modern results produced by processes that can be directly observed and even manipulated by experiment – and we must then infer the causes of past results by their “sufficient similarity” ... which presents results. This procedure requires, as Mill ... and other philosophers recognized long ago, a methodological assumption of temporal invariance for laws of nature.

When Mayr (1961) was creating a discipline for evolutionary biology, he found himself troubled by cause and effect in biology. Ever since Newton, only the how question, the question about mechanism, was considered science. Aristotle's what and what for questions were abandoned because they introduce teleology, and that is exactly what the organizers of the Darwin centennial and microevolutionary biologists were reintroducing. Ernest Nagel, a logical positivist (one of those who believed we possess the perfect logical scientific language) and philosopher of physics, was a firm believer in reductionism and singular truth. Mayr was hesitant in adopting a genetic reductionist stance and argued instead for the unity of the genotype and phenotype. He distinguished between functional/operational (synchronic) and evolutionary (diachronic) biologists. The first study operational clocks (the physiology of organisms or “programs guaranteeing behavior that increases fitness”), and the latter, instead of asking “what for,” ask “how come” which is a question directed toward the past that requires *historical analysis* (for a more elaborate discussion, see Gontier 2012a).

As such, Mayr revived the study of natural history and found a scientific way to get rid of the teleology. He validated the fact that biologists cannot and in fact need not make predictions about the future, in the same way physicists do. Because biology is a study of evolutionary history, it is directed toward the past, because it explains the present in a historical, sequential manner. Evolutionary biology is not a science that needs to predict the future, because the future of biological life is itself unpredictable. Mayr did excellent work in delineating

biology as a scientific field in and of itself, a discipline that stands on its own two feet where physical laws cannot simply be bridged into evolutionary ones. Natural selection is a mechanism, not because it explains the future, but because it explains the past. Mayr never endorsed either teleology or teleonomy. Similar discussions were also held between biophysicists and classic physicists, in what regards the second law of thermodynamics, but these go beyond the scope of the present paper. For a good analysis, I refer the reader to the 1995 special issue in *Physicalia Magazine*, where Bricmont (1995) and Prigogine debated the problems of predictability in relation to matters of indeterminacy as brought forth by chaos theory (also in relation to the Sokal–Bricmont affair).

Returning to Eldredge's naturalists, these scholars conceive the clock to be more crooked. Lewontin (2000: 81), for example, in responding to Dawkins, said:

In biology, this “what for” question is not the same as it is in the analysis of the parts of a motorcar or a clock. [...] In the case of the organism there are, of course, general functions such as motion, respiration and reproduction that are common, but there are many particular functions, peculiar to different life forms, that cannot be known in advance. In addition it is by no means true that every part serves a function. Many features of organisms are the epiphenomenal consequences of developmental changes or the functionless leftovers from remote ancestors.

We can easily see that it is a clash of epistemic cultures, one inspired by the old and one by the new. In particular, Lewontin's latter argument also makes implicit reference to Gould and Vrba's (1982) notion of exaptations, which is another means by which uniformitarianism can be fought. Naturalists take on a more relativistic view. In both science and philosophy, relativism carries bad connotations because “anything goes,” but that need not be the case. What a relativist stance does most is mark a transition from epistemic monism toward epistemic pluralism. Stated differently, it rejects the notion of a single universe and a single truth, in favor of multiple explanations, and in the most fascinating scenario, it accepts ontological pluralism. What does that mean?

Fill a glass up to its exact middle. That glass is either half-full or half-empty. If you call it half-full, you might be an optimist, and if you call it half-empty, that might indicate you are a pessimist. Reality is that the glass is both half-full and half-empty, and whatever stance you prefer, it eventually lies in the eye of the beholder. Quantum mechanics has taught us the exact same thing in what regards waves and particles. And the micro–macroevolutionary debate has done the same for the study of the evolution of life; one can explain life by its genes, or by its natural history. It demonstrates first and foremost that a particular frame of reference underlies any and all scientific observation as well as theory formation, and that frame of reference is brought forth by either instruments or human observers and therefore also partially bounded by both. Science is human, and in reality, truth need not be singular for the glass is both half-full and half-empty.

We no longer live in a Newtonian world where space is absolute, time is irreversible, everything works in the form of a mechanical clock, and observers take on a God's-eye view to deduce the everlasting truths about the universe. All we have are our frames of reference, and these immediately call out for epistemic

pluralism. We can scientifically justify a microstance as well as a macrostance, there is scientific proof for both, and we can compare both to one another and incorporate them into yet another framework. But we cannot transcend these frameworks. All we can do is develop as many frames of reference as possible. The latter entails a reconstruction of biorealities, work that was first taken on by the early natural history scholars and that today is well on its way to define actual scientific practices. I return to this latter point in the following section.

Simpson (1944), for example, when introducing the macroperspective in paleontology, was most of all thinking through the consequences that thermodynamics, relativity theory, and quantum physics have on our notions of evolution. Such branches of physics necessitate more pragmatic and operational, instrumental definitions of causality as well as science, which becomes understood as a practical and instrumental attempt to infer the conditions of change. Pragmatism and instrumentalism (other words used to denote relativism) were first introduced by scholars such as James (1907, 1909) and Duhem (1954). Teggart (1916, 1925), who inspired Eldredge in both his definition of punctuated equilibria and the epistemic stance it necessitates, was very much inspired by these scholars when he wrote that:

‘As the sciences have developed,’ William James says, ‘the notion has gained ground that most, perhaps all, of our laws are only approximations.’ ‘Investigators have become accustomed to the notion that no theory is absolutely a transcript of reality, but that any of them may from some point of view be useful. Their great use is to summarize facts and to lead to new ones.’ Obviously, then, it is not the function of science to gratify the desire of men to certainty. No scientific ‘law’ is to be regarded otherwise than as a ‘working hypothesis’ which has proved of value in organizing some phase of experience. ‘The conception,’ Bertrand Russell says, ‘of the ‘working hypothesis’, provisional, approximate, and merely useful, has more and more pushed aside the comfortable eighteenth century conception of ‘law of nature’. (Teggart 1925: 163)

Take something as simple as the syllogism, if A then B, so if you have A, then it is B, at all times and everywhere. It forms the core of cause and effect in Aristotle as well as Newton’s world, but it is not part of ours. If the evolutionary sciences have taught us anything, it is that if A, that A sometimes evolves by means of natural selection, sometimes by drift, sometimes by symbiogenesis, sometimes by lateral gene transfer, sometimes due to external events in the abiotic world, sometimes just not at all, and most of the time through a combination of all the previous at different levels of an all but perfect agglomeration we humans call “organism.” The point is that how evolution occurs is conditional upon the parameters, and these are not stable. Another way of saying this is that it is a logical necessity, within an evolutionary worldview, to assume that the means by which change occurs themselves are variable through time, and what caused evolution in the past might neither set the conditions for the present, nor for the future. The directionality we sometimes find in life is there because of historical reasons and might change in the future. It all depends upon the stability of the initial conditions, which themselves change in an evolving world.

Such a view does not at all call out for the end of science because “anything goes,” and it merely marks the beginning of a new epistemic stance, one that is characterized by epistemic plurality and the reconstruction of biorealities:

epistemic referential frameworks of life that describes the genealogy of natural kinds, biological individuals. And these genealogies lend insight into the underlying mechanisms or heuristics, i.e., the specific conditions through which phenomena originate, change, and end.

Both the micro- and macroperspectives have, from within their own set of references, created new and inspiring referential frameworks, evolution according to genes, evolution according to environmental conditions. Others have developed evolutionary views according to lateral gene transfer, symbiogenesis, drift, physics, etc. The frameworks enable us to compare and as such approximate or corroborate not one but multiple biological realities and provide a fuller understanding of just how it is that evolution comes about. And such work, most of all, is brought about through reconstructions of natural history.

It is no coincidence that both the micro- and macroperspectives reintroduce a notion of organicism, by revitalizing the dead and investigating their natural history, according to genetic shifts in populations over time, or according to external factors that define the conditions of change. It is a return to the natural history scholars' epistemic framework, something which can only be celebrated.

5 Conclusion: Reintegrating History by Reconstructing Biorealities of the Dead

Patterns in the history of life have been suggesting for at least a half century that there are regularly occurring sets of conditions that seem to control evolutionary activity – dampening it, often for longer periods, and triggering often rapid evolution at other times. Like ecological succession, evolution produces, not isolated events, but repeated pattern which hold clues to how the process works – specifically, how the physical world of matter-in-motion impacts the biological realm. (Eldredge 1998: 5)

What was the eclipse of Darwinism, really? Why it was one of the most illuminating periods in the reconstruction of the natural history of life. It marks a time that coincides with the introduction of the genies: morphogenesis, ontogenesis, phylogenesis, monogenesis, polygenesis, heterogenesis, embryogenesis, epigenesis, spermatogenesis, somitogenesis, symbiogenesis, psychogenesis, anthropogenesis, biogenesis, abiogenesis, and so on. Any and all terms defined new fields that set out to narrate the natural history of various aspects of life, by giving the natural genealogy of the parts that make up the wholes and by reconstructing their generation and decay through space and time. But, alas, without cladistics at their disposal, and still too much inspired by their teleological worldviews, most of the researchers, with a fair exception of the symbiologists, endorsed a form of orthogenesis, a straight-line evolution toward a predefined end state. There is no scientific proof for any of the orthogenic claims that were ever made, and with the foundation of the Modern Synthesis, the genies turned into logies where natural selection was the underlying mechanism that was assumed to explain all. Subsequently, synchronization followed.

Nonetheless, studies on the natural history of life remained an activity performed either in the margins or outside the Modern Synthesis. Scholars who studied symbiosis were one of the first to accept life's multilinearity and multidimensionality. The theory of symbiogenesis, a term first coined by Merzhkowsky (1905, 1910), from its onset, has explained how multicellular life historically evolved through symbiotic mergings and has rejected a single common origin from its very beginning. Such symbiotic mergings, in a very real sense, entail a form of time travel, where the old can merge into the new, but the new can equally merge with the old. Reticulate evolution brings forth multidirectionality and multidimensionality, concepts that also formed the hallmark of neo-Lamarckianism, and it defines studies on cytology, where scholars investigate the actual processes that occur in cellular life; ecology, which studies the natural and actual organism–organism and organism–environmental interactions; embryology, which studies the actual developments of organisms; and paleontology, which studies the actual natural history of species and higher taxa. All these fields are first and foremost historically and data driven rather than theory-driven sciences. Their scholars aim to explain real-life events and at present that implies a narration of past events much more so than it provides explanatory frameworks that point out their constant underlying conditions of change. Nonetheless, the patterns such researchers found can be applied and generalized outside their context of discovery. Symbiogenesis, for example, is not a unique event in the history of eukaryotic cells, it is a repeated mechanism whereby multiple life forms speciate (Brucker and Bordenstein 2013; Carrapiço and Rodrigues 2005; Carrapiço forthcoming; Gontier 2015). Scholars that associate with these fields are therefore increasingly calling out for a revision of the Modern Synthesis because their facts do not add up with the theorized claims of how life *should* evolve, while they can explain many real-life evolutionary events.

In contrast, the Modern Synthesis developed because of mathematical generalizations of theoretical rather than actual population genetics and how they behave in imaginary adaptive landscapes. Mathematics is also what enabled Neo-Darwinians to generalize and “universalize” natural selection theory to all domains of life, where prisoner dilemmas and other mathematical models enable theoretical scholars to model the evolution of life without so much as looking at its actual history. We must not forget that the Modern Synthesis itself was formulated before the genetic code was deciphered and before scholars could actually “see” or cladistically map the chemical structures and compounds that make up cells, organisms, and populations.

Either fields such as exobiology, cytology, epigenetics, paleontology, ecology, and embryology were excluded from the general framework of the Modern Synthesis, or their theoretical frameworks and empirical evidence only accumulated after the Modern Synthesis was formed. What unites all these diverse fields is that they have developed diverse techniques to enable better insight into the actual natural history that life has undergone and the various paths it has chosen. Large genome-sequencing techniques, proteomics, the virome, the microbiome, metabolic pathways, behavior, and material culture, today, are studied phylogenetically, by mapping their actual historical and geographical dispersals across space

and time. Equally, in fields such as biophysics, scholars are just beginning to map the natural history of the earth, by documenting the genealogy, the beginning, “life span,” and ending of chemical cycles such as the nitrogen and water cycle (Volk 1995, 1998). Doolittle (1999, 2010) together with Dawkins one of the most fierce opponents of the Gaia hypothesis—that views our planet as a living organism with a beginning, life span, and ending in time—is now actively engaged in reconstructing actual cell histories by understanding them as biological individuals. The work indeed is noble, but it nonetheless makes use of the same kind of reasoning that scholars such as Margulis and Lovelock (1974) used when they understood earth as a natural being.

We currently find ourselves in the midst of a return to natural history, and we have finally found the instrumental tools that enable to reconstruct the evolutionary lineages of the dead. These reconstructions together shed new light on the evolution of the living. By decomposing the living into various sub- and superunits, and investigating the individual history of each and every one of them independently, we have reached an age of epistemic plurality (Gontier 2010a). We can describe organisms based upon the evolution of their genes, their microbiome, their virome, their morpho- or embryogenesis, etc. And together, that brings forth a better understanding of various and distinct biorealities.

Scholars associated with the extended synthesis are today proving that besides natural selection, the conditions of change that define other evolutionary mechanisms can also be generalized toward other domains of life and applied beyond their original context of discovery. It is hard to think about evolutionary patterns without the mechanisms, the conditions of change, by which they are brought forth. Natural selection was mainly defined through the study of eukaryotic animal lineages and first focused on extant species in their natural habitat as well as extinct species as they present themselves in the fossil record. Today, when possible, comparative genetic research (as opposed to morphometric comparisons) lends insight into the exact ancestral–descendant relationships of animals in deep time, and as described above, natural selection has been “universalized” to non-biological domains of life. Drift was first defined based upon research on the existence of neutral organismal traits (Darwin 1959). Later, it became defined in theoretical terms as a statistical property of theoretical population models, first at a molecular genetic level (Kimura 1968, 1976, 1983) and then at a species and above species as well as environmental level (Hubbel 2001). The mechanisms of hybridization (Arnold 2006) (divergence with gene flow or introgression) were mostly obtained from the study of plants and, albeit to a lesser extent, animals. Symbiogenesis (Wallin 1927; Kozo-Polyanski 1924; Margulis 1970, 1981) became defined based upon the study of organismal, symbiotic interactions as well as investigations into the evolutionary origins of the various organelles present in the eukaryotic cell. The mechanisms that underlie lateral gene transfer (transformation, transduction, conjugation) were first obtained from studies into how prokaryotes, viruses, protozoa, and fungi underlie infection and disease in organisms (Avery et al. 1944; Lederberg and Tatum 1946; Morse et al. 1956). Today, genealogical research enables generalizations of the underlying mechanisms to

all domains of life, because whole-genome analyses enable scholars to calculate the exact amounts of species-specific and alien (acquired) genes (Doolittle 1999, 2010; Woese 1998). Both epigenetics and evo–devo investigate how evolution can be informed by specific post-genetic (e.g., post-translational changes in protein structures) and more general ontogenetically acquired characteristics (Jablonka and Lamb 1989).

The history of life is characterized by repeating patterns and trends. Evolutionary patterns are hard to describe without making reference to evolutionary theories that identify the pattern and seek out to explain the likelihoods or necessities by which it occurs. We are still very much in the dark about those conditions, but scholars have made good progress in what regards recurring patterns.

Evolution appears to move across a horizontal, a vertical, and a reticulate axis. Not all life forms remain extant, and whole types and all individuals go extinct. Not all life forms remain constant. That is as basic as it gets. To give more patterns, we need to refer to evolutionary theories such as natural selection, symbiogenesis, and lateral gene transfer.

Conditions of change are by and large defined in terms of internal and external, biotic and abiotic, and organismal and environmental parameters. The principles of conditional change are defined in terms of evolutionary mechanisms. Evolutionary mechanisms in turn are theoretical generalizations, working hypothesis on the natural history of various life strands through time. In other words, they are generalizations of how conditional change appears to have occurred in the past, and they can be tested for how well they are generalizable toward other phenomena beyond their context of discovery.

Evolution by drift, for example, gives a random or non-directional pattern. The outcome of natural selection is vertical descent with modification, and the emerging pattern can be either unilineal or bifurcating. Symbiogenesis or LGT gives reticulate, multidirectional patterns of horizontal mergings.

Based upon how widespread and persistent the evolutionary mechanism is across lineages, the emerging pattern can be argued to be stable if not permanent in time. Selection will always lead to diversification, drift will always be random, and symbiogenesis or reticulate evolution in general will always involve mergings. If either pattern ceases to emerge in time, the mechanism ceases to be active, or better yet, the conditions for that particular kind of change are not met. Patterns are thus causally explained by referring to postulated parameters that define conditional change. And that is eventually what an evolutionary mechanism is, it is not a constant force.

Moreover, these reconstructions again necessitate us to acknowledge that truth need not be singular. At one point in time, eukaryotes evolved according to symbiogenesis, at another point in time, they did so by means of natural selection, and at yet another period in time, they evolved by drift. Most of the time, they do not evolve at all, and when they do, they evolve by a combination of these means, simply because the organisms themselves are compositional structures. As such, we also need to investigate whether there is some higher-order sorting of mechanisms, and what would define the parameters of such sorting.

Evolutionary mechanisms are theoretical frameworks that define the parameters and conditions of change under well-defined circumstances. Genes evolve by

means of natural selection if certain conditions are met, and symbiogenesis and drift equally occurs when certain well-defined conditions are met. When these conditions are not met, life does not evolve according to that pattern. What we need to do is find the conditions of change.

Evolution is spontaneous, random, and selective, and species come into being through splitting and merging, which can occur slow or fast. We can use a lot of fancy words to say things differently, but that is basically it. These are the heuristics or working hypotheses scholars have been working with, and the fancy words used to describe them imply a scientification of the problems. All have proven their use, in so far as all have been put into scientific theories and mathematical models that explain the data they aim to describe.

If time is relative because it is a measurement of movement of matter through space, and if how matter “moves” is variable, then it is more relative to repetition of initial conditions and thus more uncertain. Most of all, these theories are awaiting an epistemic framework that enables us to deal with the multiple dimensions of the evolutionary biorealities they have opened, not in the least by an evolutionary reconceptualization of our notion of time. Never has a generation of natural history scholars been studying actual historical material phenomena in time and space without a solid concept of either. Time is a hallmark of evolutionary science. Without time, there would be no origin or evolution of life, where through time living organisms change. Nonetheless, as natural and real as time appears to us, much of how we conceptualize time is the result of sociocultural constructs.

For the ancient Greeks and the Vedic Indians, time was cyclical and repetitive. Earth, fire, water, wind, and void/aether, the periodic table *avant la lettre*, made up the micro-, meso-, and macrocosmos, which were considered embedded structures. Much like Russian dolls, they made up inanimate, animate, and divine matter (a fire hearth, language, and the God Prometheus, for example). These beings underwent generation and decay, but eventually, time was cyclical, because without a second law of thermodynamics, the elements themselves did not undergo decay, but rather they kept their integrity which is why the world could cyclically start over and reincarnate. For the Vedic Indian as well as ancient Greek philosophers, time is not real. Aristotle, for example, defined time in terms of the motion of matter, and this concept was also foundational for Newton and the whole of Western science. Although time is absolute, because space and matter are, time itself is a derivative of matter in motion, which is why we use different “calendars” and time scales, such as geological time, sidereal or tropical zodiac time, or heat. Our switch from a geocentric to a heliocentric worldview did not affect our watches in any way. Nonetheless, if we or any other living species travel a couple of thousand miles, we most certainly experience a change in time, and biological individuals have evolved circadian rhythms that enable them to deal with them. Time, whatever it is, is most certainly real for the living.

Equally, an organismal body is made up of different moving elements, which each follows their own pace. The cells of our body form complex and differentiated structures such as bones, vascular systems, organs, neurons, and a brain.

These structures as well as the cells and the genes they are composed of differ in how they occupy space and time. Your skin cells rejuvenate at a monthly basis. The cells undergo mitosis, and the older ones die. Every 6 weeks, your lung cells do the same. Your organelles and the genetic material they contain replicate and regenerate at different time intervals than the cell's nucleus. All have a different life span, a different beginning, and ending in time. In so far as the structures that compose you have come into existence before, in previously existing generations, they are more constant in time than you. The compositional structure that is "you" only exists once in so far as your specific compositions never come into existence twice. You have a clear beginning, life span, and ending in time. But it takes numerous generations of living cells to repeat the structures that form your existence over a longer period in time. Equally, it takes a couple of days before all cells that make up your body die, and the microbial communities that inhabit you live on for quite some time.

Current research is evolutionizing all. We are evolving toward a recognition of the existence of multiple units, levels, mechanisms, and kinds of evolution, and it is the challenge of our and future generations to investigate how they together make up the multilinear and multidimensional biological realities that have evolved (Gontier 2010a).

Acknowledgments The work was written with the support of the John Templeton Foundation (grant ID 36288) and the Portuguese Fund for Scientific Research (grant ID SFRH/BPD/89195/2012). The author is grateful to Diederik Aerts, Luís Borda de Agua, Francis Heylighen, Octávio Mateus, and Emanuele Serrelli for useful comments to the text.

References

- Alvarez LW, Alvarez W, Asaro F, Michel HV (1980) Extraterrestrial cause for the cretaceous-tertiary extinction. *Science* 208(4448):1095–1108. doi:[10.1126/science.208.4448.1095](https://doi.org/10.1126/science.208.4448.1095)
- Arnold ML (2006) *Evolution through genetic exchange*. Oxford University Press, New York
- Arnold ML (2008) *Reticulate evolution and humans: origins and ecology*. Oxford University Press, Oxford
- Atkinson QD et al (2008) Languages evolve in punctuational bursts. *Science* 319(5863):588
- Avery OT, Macleod CM, McCarty M (1944) Studies on the chemical nature of the substance inducing transformation of pneumococcal types. Induction of transformation by a deoxy-ribonucleic acid fraction isolated from pneumococcus type III. *J Exp Med* 79:137–157
- Axelrod R (1981) The evolution of cooperation. *Science* 211:1390–1396
- Baldwin JM (1896) A new factor in evolution. *Am Nat* 30(354):441–451
- Barbieri M (2008) Biosemiotics: a new understanding of life. *Naturwissenschaften* 95(7):577–599
- Barbieri M (ed) (2008) *The codes of life: the rules of macroevolution*. Springer, Berlin
- Bentley RA, O'Brien MJ (2011) The selectivity of social learning and the tempo of cultural evolution. *J Evol Psychol* 9:125–141
- Bentley RA, Hahn MW, Shennan SJ (2004) Random drift and culture change. *Philos Trans R Soc B* 2711547:1443–1450
- Bohm D (1980) *Wholeness and the implicate order*. Routledge, London
- Bokma F (2002) Detection of punctuated equilibrium from molecular phylogenies. *J Evol Biol* 15:1048–1056

- Bokma F, Monroe MJ (2010) Punctuated equilibrium in a neontological context. *Theory Biosci* 129(2–3):103–111
- Borgerhoff Mulder M, Nunn CL, Towner M (2006) Macroevolutionary studies of cultural trait variation: the importance of transmission mode. *Evol Anthropol* 15:52–64
- Bowler PJ (2003) *Evolution: the history of an idea*, 3rd revised and expanded edition. University of California Press, Berkeley
- Bradie M (1986) Assessing evolutionary epistemology. *Biol Philos* 1(4):401–459
- Brandon RN (1982) The levels of selection. In: Brandon RN, Burian RM (eds) *Genes, organisms, populations: controversies over the units of selection 1984*. MIT Press, Cambridge, pp 133–139
- Brandon R, Burian Richard M (eds) (1984) *Genes, organisms, population: controversies over the units of selection*. MIT Press, Cambridge
- Brandon RN, McShea D (2010) *Biology's first law: the tendency for diversity and complexity to increase in evolutionary systems*. University of Chicago Press, Chicago
- Bricmont J (1995) Science of chaos or chaos in science? *Physica Mag* 17(3–4):159–208
- Brucker RM, Bordenstein SR (2013) The capacious hologenome. *Zoology* 116(5):260–261
- Campbell DT (1960) Blind variation and selective retention in creative thought as in other knowledge processes. *Psychol Rev* 67(6):380–400
- Campbell DT (1974) Evolutionary epistemology. In: Schlipp PA (ed) *The philosophy of Karl Popper*, vol I. LaSalle, New York, pp 413–459
- Carrapico F (forthcoming) In: Gontier N (ed) *Reticulate evolution*. Springer, Dordrecht
- Carrapico F, Rodrigues T (2005) Symbiogenesis and the early evolution of life. *Proc SPIE* 5906:59060R-1–59060R-4
- Carroll SB (2005) *Endless forms most beautiful: the new science of evo-devo*. WW Norton, New York
- Cech TR (1986) RNA as an enzyme. *Sci Am* 255(5):76–84
- Crick FHC (1968) The origin of the genetic code. *J Mol Biol* 38:367–379
- Currie TE, Greenhill SJ, Mace R (2010) Is horizontal transmission really a problem for phylogenetic comparative methods? A simulation study using continuous cultural traits. *Philos Trans R Soc B* 365(1559):3903–3912. doi:[10.1098/rstb.2010.0014](https://doi.org/10.1098/rstb.2010.0014)
- Cziko G (1995) *Without miracles: universal selection theory and the second Darwinian revolution*. MIT Press, Cambridge
- d'Errico F (2003) The invisible frontier: a multiple species model of the origin of behavioral modernity. *Evol Anthropol* 12:188–202
- d'Errico F, Stringer CB (2011) Evolution, revolution or saltation scenario for the emergence of modern cultures? *Phil Trans R Soc B* 366:1060–1069
- Darwin C (1859) *On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life*. John Murray, London
- Davidson EH, Erwin DH (2006) Gene regulatory networks and the evolution of animal body plans. *Science* 311:796–800
- Davidson EH, Erwin DH (2009) Evolutionary innovation and stability in animal gene networks. Part B: molecular and developmental evolution. *J Exp Zool* 314B(3):182–186
- Dawkins R (1976) *The selfish gene*. Oxford University Press, New York
- Dawkins R (1982a) *The extended phenotype*. Oxford University Press, New York
- Dawkins R (1982b) Replicators and vehicles. In: Brandon NR, Burian RM (eds) *Genes, organisms, populations 1984*. MIT Press, Cambridge, pp 161–179
- Dawkins R (1983) Universal Darwinism. In: Hull DL, Ruse M (eds) *The philosophy of biology*. Oxford University Press, New York, pp 15–35
- Dawkins R (1995) *River out of Eden*. Basic books
- Dawkins R (1996) *Climbing mount improbable*. W. W. Norton and Company, New York
- De Duve C (1991) *Blueprint for a cell: the nature and origin of life*. Neil Patterson Publishers, Burlington
- De Laguna GA (1962) The role of teleonomy in evolution. *Philos Sci* 29(2):117–131
- de Saussure F (2006) *Writings in general linguistics*. Oxford University Press, New York
- Dennett D (1995) *Darwin's dangerous idea*. Simons and Schuster, New York
- Doolittle FW (1999) Phylogenetic classification and the universal tree. *Science* 284:2124–2129. doi:[10.1126/science.284.5423.2124](https://doi.org/10.1126/science.284.5423.2124)

- Doolittle FW (2010) The attempt on the tree of life: science, philosophy and politics. *Biol Philos* 25:455–473
- Duhem P (1954) The aim and structure of physical theory, 2nd edn (1991). Princeton University Press, Princeton
- Duhem P (1969) To save the phenomena, an essay on the idea of physical theory from Plato to Galileo. University of Chicago Press, Chicago
- Duhem P (1985) Medieval cosmology: theories of infinity, place, time, void, and the plurality of worlds. University of Chicago Press, Chicago
- Durkheim E (1895) The rules of sociological method, preface to the second edition (trans: Halls WD, 1982). The Free Press, New York
- Edwards AWF (1998) Natural selection and the sex ratio: fisher's sources. *Am Nat* 151(6):564–569. doi:[10.1086/286141](https://doi.org/10.1086/286141)
- Eigen M (1996) Steps towards life: a perspective on evolution. Oxford University Press, New York
- Eigen M, Schuster P (1977) The Hypercycle: a principle of natural self-organisation. Part A: emergence of the hypercycle. *Naturwissenschaften* 64:541–565
- Eldredge N (1971) The allopatric model and phylogeny in Paleozoic invertebrates. *Evolution* 25(1):156–167
- Eldredge N (1985a) Unfinished synthesis: biological hierarchies and modern evolutionary thought. Oxford University Press, New York
- Eldredge N (1985b) Time frames. Simon and Schuster, New York
- Eldredge N (1989) Macroevolutionary dynamics: species, niches and adaptive peaks. McGraw Hill, New York
- Eldredge N (1991a) The miner's canary: extinctions past and present. Prentice Hall Books, New York
- Eldredge N (1991b) Fossils: the evolution and extinction of species. Abrams, New York
- Eldredge N (ed) (1992) Systematics, ecology and the biodiversity crisis. Columbia University Press, New York
- Eldredge N (1995) Reinventing Darwin: the great debate at the high table of evolutionary theory. Wiley, New York
- Eldredge N (1997) Dominion. University of California Press, Oakland
- Eldredge N (1998) Life in the balance: humanity and the biodiversity crisis. Princeton University Press, Princeton
- Eldredge N (1999) The pattern of evolution. W. H. Freeman and Co., New York
- Eldredge N (2006) Confessions of a Darwinist. *V Q Rev Spring* 82(2):33–53
- Eldredge N (2008) Hierarchies and the sloshing bucket: toward the unification of evolutionary biology. *Evol Educ Outreach* 11:10–15
- Eldredge N (2011) Paleontology and cornets: thoughts on material culture. *Evol Educ Outreach* 4:264–373
- Eldredge N, Gould SJ (1972) Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf TJM (ed) Models in paleobiology, Freeman, Cooper and Co., New York, pp 82–115
- Eldredge N, Salthe SN (1984) Hierarchy and evolution. *Oxf Surv Evol Biol* 1:184–208
- Eldredge N, Stanley SM (eds) (1984) Living fossils. Springer, New York
- Eldredge N, Tattersall I (1982) The myths of human evolution. Columbia University Press, New York
- Eldredge N, Tëmkin I (2007) Phylogenetics and material cultural evolution. *Curr Anthropol* 48:146–153
- Eldredge N, Thompson JN, Brakefield PM, Gavrillets S, Jablonski D, Jackson J, Lenski R, Lieberman B, McPeck M, Miller W (2005) The dynamics of evolutionary stasis. *Paleobiology* 31:133–145
- Eliav-Feldon M, Isaac B, Ziegler J (2009) The origins of racism in the west. Cambridge University Press, Cambridge
- Fanon F, Philcox R (2004) The wretched of the earth/Frantz Fanon; translated from the French by Richard Philcox; introductions by Jean-Paul Sartre and Homi K. Bhabha. Grove Press, New York

- Favareau D (2005) Founding a world biosemiotics institution: the international society for biosemiotic studies. *Sign Syst Stud* 33(2):481–485
- Fisher RA (1930) *The genetical theory of natural selection*. Clarendon Press, Oxford
- Fox S, Dose K (1972) *Molecular evolution and the origin of life*. W.H. Freeman and Co, San Francisco
- Futuyma D (2005) *Evolution*. Sinauer Associates, Sunderland
- Futuyma D (2010) Evolutionary constraint and ecological consequences. *Evolution* 64(7):1865–1884. doi:[10.1111/j.1558-5646.2010.00960.x](https://doi.org/10.1111/j.1558-5646.2010.00960.x)
- Gehring WJ (1992) The homeobox in perspective. *Trends Biochem Sci* 17(8):277–280. doi:[10.1016/0968-00049290434-B](https://doi.org/10.1016/0968-00049290434-B)
- Gehring WJ (1999) Lifting the lid on the homeobox discovery. *Nature* 399:521–522
- Ghiselin M (1974) A radical solution to the species problem. *Syst Zool* 23(4):536–544
- Gilbert W (1986) Origin of life: the RNA world. *Nature* 319:618. doi:[10.1038/319618a0](https://doi.org/10.1038/319618a0)
- Godfrey-Smith P (2009) *Darwinian populations and natural selection*. Oxford University Press, New York
- Gogarten M, Gogarten JP, Olenzinski L (eds) (2009) *Horizontal gene transfer: genomes in flux*. Humana Press, Springer
- Gontier N (2006a) Evolutionary epistemology. In: Fieser J, Dowden B, Beebe J (eds) *The internet encyclopedia of philosophy*. <http://www.iep.utm.edu/e/evo-epis.htm>
- Gontier N (2006b) Introduction to evolutionary epistemology, language and culture. In: Gontier N, Van Bendegem JP, Aerts D (eds) *Evolutionary epistemology, language and culture: a non-adaptationist systems theoretical approach*. Springer, Dordrecht, pp 1–26
- Gontier N (2006c) Evolutionary epistemology and the origin and evolution of language: taking symbiogenesis seriously. In: Gontier N, Van Bendegem JP, Aerts D (eds) *Evolutionary epistemology, language and culture: a non-adaptationist systems theoretical approach*. Springer, Dordrecht, pp 195–226
- Gontier N (2007) Universal symbiogenesis: a genuine alternative to universal selectionist accounts. *Symbiosis* 44:167–181
- Gontier N (2010a) Evolutionary epistemology as a scientific method: a new look upon the units and levels of evolution debate. *Theor Biosci* 129(2–3):167–182
- Gontier N (2010b) Darwin's legacy. *Theor Biosci* 129(2–3):77–87
- Gontier N (2011) Depicting the tree of life: the philosophical and historical roots of evolutionary tree diagrams. *Evol, Educ Outreach* 4(3):515–538
- Gontier N (2012a) Applied evolutionary epistemology: a new methodology to enhance interdisciplinary research between the human and natural sciences. *Kairos* 4:7–49
- Gontier N (2012b) Introducing universal symbiogenesis. In: Pombro O et al. (eds) *Special sciences and the unity of science*. Springer, Dordrecht, pp 89–111 (Logic, Epistemology, and the Unity of Science 24). doi: [10.1007/978-94-007-2030-5](https://doi.org/10.1007/978-94-007-2030-5)
- Gontier N (ed) (2015) *Reticulate evolution*. Springer, Dordrecht
- Gould SJ (1965) Is uniformitarianism necessary? *Am J Sci* 263:223–228
- Gould SJ (1977) *Ontogeny and phylogeny*. Belknap, Harvard University Press, New York
- Gould SJ (1981) *The mismeasure of man*. W. W. Norton, New York
- Gould SJ (1982) Punctuated equilibrium—a different way of seeing. *New Sci* 94(Apr. 15): 137–139
- Gould SJ (1986/1989) *Wonderful life*. Penguin books, London
- Gould SJ (1987) *Time's arrow, time's cycle*. Harvard University Press, Cambridge. ISBN 0-674-89198-8 online preview
- Gould SJ (1991) Exaptation: a crucial tool for an evolutionary psychology. *J Soc Issues* 47(3):43
- Gould SJ (2002) *The structure of evolutionary theory*. Harvard University Press, Cambridge
- Gould SJ, Eldredge N (1977) Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* 3(2):115–151
- Gould SJ, Eldredge N (1993) Punctuated equilibrium comes of age. *Nature* 366(6452):223–227. doi:[10.1038/366223a0](https://doi.org/10.1038/366223a0)

- Gould SJ, Lewontin RC (1979) The spandrels of san marco and the panglossian paradigm: a critique of the adaptationist programme. *Proc Royal Soc Lond B* 205:581–589
- Gould SJ, Vrba ES (1982) Exaptation: a missing term in the science of form. *Paleobiology* 8:4–15
- Gould SJ, Gilinsky NL, German RZ (1987) Asymmetry of lineages and the direction of evolutionary time. *Science* 236(4807):1437–1441
- Griesemer J (2000) Development, culture and the units of inheritance. *Philos Sci* 67:S348–S368
- Griffith F (1928) The significance of pneumococcal types. *J Hyg* 27(2):113–159. doi:[10.1017/S0022172400031879](https://doi.org/10.1017/S0022172400031879)
- Haeckel E (1866) *Generelle morphologie der organismen: allgemeine grundzüge der organischen formen-wissenschaft, mechanisch begründet durch die von c. Darwin reformirte decendenz-theorie*. Georg Reimer, Berlin
- Haeckel E (1917) *Kristallseelen, studien über das Anorganische Leben*. Alfred Kroner Verlag, Leipzig
- Hahlweg K, Hooker CA (eds) (1989) *Issues in evolutionary epistemology*. State University of New York Press, Albany
- Haldane JBS (1949) Disease and evolution. *Ric Sci Suppl A* 19:68–76
- Hamilton WD (1964a) The evolution of social behavior. *J Theor Biol* 1:295–311
- Hamilton WD (1964b) The genetic evolution of social behavior, I and II. *J Theor Biol* 7:1–52
- Hamilton WD (1967) Extraordinary sex ratios. *Science* 156(3774):477–488. doi:[10.1126/science.156.3774.477](https://doi.org/10.1126/science.156.3774.477)
- Hoffmeyer J (2008) *Biosemiotics: an examination into the signs of life and the life of signs*. University of Scranton Press, Scranton
- Hoyle F (1981) Hoyle on evolution. *Nature* 294(5837):105
- Hubbell S (2001) *The unified neutral theory of biodiversity*. Princeton University Press, Princeton
- Hull DL (1981) Units of evolution. In: Brandon NR, Burian RM (eds) *Genes, organisms, populations*, 1984. MIT Press, Cambridge, pp 142–159
- Hume D (1739/2000) *A treatise of human nature*. Oxford University Press, Oxford
- Huxley TH (1870) Biogenesis and abiogenesis. In: Huxley TH (2011) *Collected essays*, vol 8. Cambridge University Press, Cambridge, pp 229–271. doi: <http://dx.doi.org/10.1017/CBO9781139149273.009>
- Huxley J (1942) *Evolution: the modern synthesis*. Allen and Unwin, London
- Huxley J (1957) The three types of evolutionary process. *Nature* 180:454–455
- Jablonka E, Lamb MJ (1989) The inheritance of acquired epigenetic variations. *J Theor Biol* 139(1):69–83
- Jablonka E, Lamb MJ (1995) *Epigenetic inheritance and evolution*. Oxford University Press, Oxford
- Jacob F (1977) Evolution and tinkering. *Science* 196:1161–1166
- James W (1907) Pluralism, pragmatism, and instrumental truth. In: *A pluralistic universe*. Harvard University Press, New York, pp 321–324
- James W (1909) Pragmatism: a new name for some old ways of thinking. Longmans Publishing Group, New York, pp 52–61
- Kauffman SA (1995) *At home in the universe*. Penguin Books, London
- Kauffman SA, Levin S (1987) Towards a general theory of adaptive walks on rugged landscapes. *J Theor Biol* 128:11–45
- Kimura M (1968) Evolutionary rate at the molecular level. *Nature* 217(5129):624–626
- Kimura M (1976) How genes evolve: a population geneticist's view. *Ann Génét* 19(3):153–168
- Kimura M (1983) *The neutral theory of molecular evolution*. Cambridge University Press, Cambridge
- Kozo-Polyansky B (1924) *Symbiogenesis: a new principle of evolution*, edited and translated by Fet V, Margulis L 2010. Introduction by Peter H Raven. Harvard University Press, Cambridge
- Kressing F, Fangerau H, Krischel M (2014) The global phylogeny and its historical legacy—a critical review of a unified theory of human biological and linguistic co-evolution. *Med Stud Int J Hist Philos Ethics Med Allied Sci* 4:15–27. doi:[10.1007/s12376_013_0081-8](https://doi.org/10.1007/s12376_013_0081-8)

- Kuhn TS (1962) *The structure of scientific revolutions*. University of Chicago Press, Chicago
- Lederberg J (1951) *Papers in microbial genetics: bacteria and bacterial viruses*. University of Wisconsin Press, Madison
- Lederberg J (1999) Haldane JBS (1949) on infectious disease and evolution. *Genetics* 153:1–3
- Lederberg J, Tatum EL (1946) Gene recombination in *E. coli*. *Nature* 158(4016):558
- Lévi-Strauss C (1952) *Race and history* (UNESCO)
- Lewontin R (1970) The units of selection. *Annu Rev Ecol Syst* 1:1–18
- Lewontin R (1983) Gene, organism, and environment. In: Bendall DS (ed) *Evolution from molecules to men*. Cambridge University Press, Cambridge, pp 273–285
- Lewontin R (2000) *The triple helix: gene, organisms and environment*. Harvard University Press, New York
- Lieberman BS (2000) *Paleobiogeography: using fossils to study global change, plate tectonics, and evolution*. Kluwer Academic Publishers, New York
- Lieberman BS, Dudgeon S (1996) An evaluation of stabilizing selection as a mechanism for stasis. *Palaeogeogr Palaeoclimatol Palaeoecol* 127:229–238
- Lieberman BS, Vrba ES (2005) Stephen Jay Gould on species selection: 30 years of insight. *Paleobiology* 31:113–121
- Lieberman BS, Allmon WD, Eldredge N (1993) Levels of selection and macroevolutionary patterns in the turrillid gastropods. *Paleobiology* 19:205–215
- Lieberman BS, Brett CE, Eldredge N (1995) A study of stasis and change in two species lineages from the middle devonian of New York state. *Paleobiology* 21:15–27
- Lieberman BS, Miller W III, Eldredge N (2007) Paleontological patterns, macroecological dynamics and the evolutionary process. *Evol Biol* 34:28–48
- Lipo CP, O'Brien MJ, Collard M, Shennan SJ (eds) (2006) *Mapping our ancestors: phylogenetic methods in anthropology and prehistory*. Aldine Transaction, Hawthorne
- Lloyd E (1988) *The structure and confirmation of evolutionary theory*. Greenwood Press, Westport
- Lloyd E (2000) Units and levels of selection: an anatomy of the units of selection debates. In: Singh et al. (eds) *Thinking about evolution: historical, philosophical, and political perspectives*. Cambridge University Press, Cambridge, pp 267–291
- Lorenz K (1958) The evolution of behavior. *SCIAM* 199(6):67–78
- Luria SE, Delbrück M (1943) Mutations of bacteria from virus sensitivity to virus resistance. *Genetics* 28(6):491–511
- Lübbe H (1990) Zeit-Verhältnisse. Über die veränderte Gegenwart von Zukunft und Vergangenheit. In: *Zeitphänomen Musealisierung*, S 40–45
- Lyell C (1830) *Principles of geology, being an attempt to explain the former changes of the Earth's surface, by reference to causes now in operation*, vol 1. John Murray, London
- Lyell C (1832) *Principles of geology, being an attempt to explain the former changes of the Earth's surface, by reference to causes now in operation*, vol 2. John Murray, London
- Lyell C (1833) *Principles of geology, being an attempt to explain the former changes of the Earth's surface, by reference to causes now in operation*. vol 3. John Murray, London
- Mace R, Jordan F (2011) Macro-evolutionary studies of cultural diversity: a review of empirical studies of cultural transmission and cultural adaptation. *Philos Trans R Soc Lond B Biol Sci* 366:402–411
- Maienschein J (2012) Epigenesis and preformationism. The stanford encyclopedia of philosophy. In: Zalta EN (ed). <http://plato.stanford.edu/archives/spr2012/entries/epigenesis/>. Retrieved 20 Feb 2013
- Malinowski B (1944) *A scientific theory of culture and others essays*. The University of North Carolina Press, Chapel Hill
- Margulis L (1970) *Origin of eukaryotic cells*. Yale University Press, New Haven
- Margulis L (1981) *Symbiosis in cell evolution*. Freeman, New York
- Margulis L (1998) *The symbiotic planet: a new look at evolution*. Orion Books, London, Phoenix
- Margulis L, Lovelock JE (1974) Biological modulation of the Earth's atmosphere. *Icarus* 21:471–489

- Masel J, King OD, Maughan H (2007) The loss of adaptive plasticity during long periods of environmental stasis. *Am Nat* 169(1):38–46. doi:[10.1086/510212](https://doi.org/10.1086/510212)
- Maynard Smith J (1964) Group selection and kin selection. *Nature* 201(4924):1145–1147
- Maynard Smith J (1978) The evolution of sex. Cambridge University Press, Cambridge
- Maynard Smith J (1983) The genetics of stasis and punctuations. *Annu Rev Genet* 17:12
- Maynard Smith J (1984) Paleontology at the high table. *Nature* 309(5967):401–402. doi:[10.1038/309401a0](https://doi.org/10.1038/309401a0)
- Maynard Smith J, Price GR (1973) The logic of animal conflict. *Nature* 246(5427):15–18. doi:[10.1038/246015a0](https://doi.org/10.1038/246015a0)
- Maynard Smith J, Szathmáry E (1995) The major transitions in evolution. Oxford University Press, New York
- Mayr E (1942) Systematics and the origin of species. Columbia University Press, New York
- Mayr E (1961) Cause and effect in biology. *Science* 134(3489):1501–1506
- Mazzarello P (1999) A unifying concept: the history of cell theory. *Nat Cell Biol* 1(1):E13–E15. doi:[10.1038/8964](https://doi.org/10.1038/8964)
- Merezhkowsky C (1905) Ueber natur und ursprung der chromatophoren im pflanzenreiche. *Biologisches Zentralbl* 25:595–596
- Merezhkowsky C (1910) Theorie der zwei plasmaarten als grundlage der symbiogenesis, einer neuen lehre von der entstehung der organismen. *Biol Zentralbl* 30:278–288, 289–303, 321–347, 353–367
- Miller SL (1953) A production of amino acids under possible primitive Earth conditions. *Science* 117:528–529
- Miller S, Urey H (1959) Organic compound synthesis on the primitive Earth. *Science* 130(3370):245. doi:[10.1126/science.130.3370.245](https://doi.org/10.1126/science.130.3370.245)
- Monod J (1971) Chance and necessity. Alfred A. Knopf, New York
- Morse ML, Lederberg EM, Lederberg J (1956) Transduction in *Escherichia Coli* K-12. *Genetics* 41(1):142–156
- Nagel E (1949) The meaning of reduction in the natural sciences. In: Stauffer RC (ed) *Science and civilization*. University of Wisconsin Press, Madison, pp 99–135
- Nagel E (1951) Mechanistic explanation and organismic biology. *Philos Phenomenological Res* 11:327–338
- Nietzsche F (1874) *Vom Nutzen und Nachteil der Historie für das Leben*. Leipzig
- O'Brien MJ et al (2002) Two issues in archaeological phylogenetics: taxon construction and out-group selection. *J Theor Biol* 215(2):133–150
- Odling-Smee FJ (1988) Niche constructing phenotypes. In: Plotkin HC (ed) *The role of behavior in evolution*. MIT Press, Cambridge, pp 73–132
- Okasha S (2005) Multilevel selection and the major transitions in evolution. *Phil Bio* 72:1013–1025
- Oparin A (1955) *L'origine de la vie*. Editions en langues étrangères, Moscow
- Orgel LE (1973) The origins of life: molecules and natural selection. Wiley, New York
- Orgel LE (1992) Molecular replication. *Nature* 358(6383):203–209
- Oyama S (1985) The ontogeny of information: developmental systems and evolution. Cambridge University Press, Cambridge
- Pagel M, Meade A (2006) Estimating rates of lexical replacement on phylogenetic trees of languages. In: Forster P, Renfrew C (eds) *Phylogenetic methods and the prehistory of languages*. McDonald institute Monographs, Cambridge, pp 173–182
- Pagel M, Venditti C, Meade A (2006) Large punctuational contribution of speciation to evolutionary divergence at the molecular level. *Science* 314:119–121
- Pagel M, Atkinson Q, Meade A (2007) Frequency of word-use predicts rates of lexical evolution throughout Indo-European history. *Nature* 449:717–720
- Parsons T (1975) The present status of structural-functional theory in sociology. In: Parsons T (ed) *Social systems and the evolution of action theory*. The Free Press, New York

- Pauling L (1939) *The nature of the chemical bond and the structure of molecules and crystals*. Cornell University Press, Ithaca
- Pigliucci M (2009) An extended synthesis for evolutionary biology. *the year in evolutionary biology*. *Ann NY Acad Sci* 1168:218–228
- Pigliucci M, Müller G (eds) (2010) *Evolution: the extended synthesis*. MIT Press, Cambridge
- Pinxten R (1997) *When the day breaks: essays in anthropology and philosophy*. Lang Frankfurt am Main, Switzerland
- Pittendrigh CS (1958) Behavior and evolution. In: Roe A, Simpson GG (eds) *Behavior and evolution*. Yale University Press, New Haven, pp 390–416
- Popper K (1957) *The poverty of historicism*. Routledge, London
- Prigogine I (1980) *From being to becoming*. Freeman, New York
- Provine WB, Mayr E (eds) (1980) *The Evolutionary synthesis: perspectives on the unification of biology*. Harvard University Press, Cambridge
- Rosindell J, Hubbell SP, Etienne RS (2011) The unified neutral theory of biodiversity and biogeography at age ten. *Trends Ecol Evol* 26(7):340–348
- Ryan F (2006) Genomic creativity and natural selection. *Biol J Linn Soc* 88:655–672
- Ryan F (2009) *Volution*. Harper Collins, London
- Sapp J (1994) *Evolution by association: a history of symbiosis*. Oxford University Press, New York
- Schmalhausen II (1949) *Factors of evolution: the theory of stabilizing selection*. Blakiston, Oxford
- Schopf W (1978) The evolution of the earliest cells. *SCIAM* 239:85–103
- Schwartz J (1999) *Sudden origins: fossils, genes, and the emergence of species*. Wiley, New York
- Schwartz JH, Tattersall I (2001) *Extinct humans*. Westview Press, USA
- Sepkoski D, Ruse M (eds) (2009) *The paleobiological revolution*. University of Chicago Press, Chicago
- Simpson GG (1944) *Tempo and mode in evolution*. Columbia University Press, New York
- Smocovitis VB (1996) *Unifying biology: the evolutionary synthesis and evolutionary biology*. Princeton University Press, New York
- Smocovitis VB (1999) The 1959 Darwin centennial celebration in America. In: Elliot C, Abir-Am P (eds) *Commemorations of scientific grandeur, Osiris vol 14(1999)*, pp 274–323
- Spencer H (1862/1958) *First Principles*. DeWitt Revolving Fund, New York
- Spencer H (1876) *The principles of sociology*, vol 1 and 2. Appleton, New York
- Spencer H (1915) *Essays: scientific, political, and speculative*. Appleton, New York
- Stanley SM (1979) *Macroevolution*. W. H. Freeman, San Francisco
- Steele J, Kandler A (2010) Language trees \neq gene trees. *Theory Biosci* 129:223–233
- Szathmáry E (2002) Units of evolution and units of life. In: Pályi G, Zucchi L, Caglioti L (eds) *Fundamentals of life*. Elsevier, Paris, pp 181–195
- Szathmáry E (2006) The origin of replicators and reproducers. *Phil Trans R Soc Lond B Biol Sci* 361:1761–1776
- Tattersall I (2014) Communication and human uniqueness. In: Gontier N, Pino M (eds) *The evolution of socialcommunication in primates*, Springer, Dordrecht, pp 219–229
- Tax S (ed) (1960) *Evolution after Darwin: the university of Chicago centennial*, 3 volumes. University of Chicago Press, Chicago
- Teggart FJ (1916) Prolegomena to history. *Univ Calif Publ Hist* 4(3):155–291
- Teggart FJ (1925) *Theory of history*. Yale University Press, London
- Thompson DW (1917) *On growth and form*. Cambridge University Press, Cambridge
- Tinbergen N (1963) On aims and methods of ethology. *Z Tierpsychologie* 20:410–433
- Trivers RL (1971) The evolution of reciprocal altruism. *Q Rev Biol* 46(1):35–57
- Van Valen LA (1973) A new evolutionary law. *Evol Theor* 1:1–30
- Van Valen LA (1975) Group selection, sex, and fossils. *Evolution* 29:87–94
- Van Valen LA (1976) Ecological species, multispecies, and oaks. *Taxon* 25:233–239
- Venditti C, Pagel M (2008) Speciation and bursts evolution. *Evol Educ Outreach* 13:274–280

- Venditti C, Pagel M (2010) Speciation as an active force in evolution. *Trends Ecol Evol* 25:14–20
- Villarreal LP (2004) Are viruses alive? *SciAm* 291(6):97–102
- Villarreal LP, Defilippis V (2000) A hypothesis for DNA viruses as the origin of eukaryotic replication proteins. *J Virol* 74(15):7079–7084
- Volk T (1995) *Metapatterns across space, time, and mind*. Columbia University Press, New York
- Volk T (1998) *Gaia's body: toward a physiology of the Earth*. Copernicus Books. Springer, Berlin
- Von Bertalanffy KW (1928) Kritische theorie der formbildung, borntraeger
- Von Bertalanffy KW (1940) *Vom molekül zur organismenwelt*. Akademische Verlagsgesellschaft Athenaion, Potsdam
- Von Bertalanffy L (1950) An outline of general systems theory. *Br J Hist Sci* 1(2):134–162
- Vrba ES (1980) Evolution, species and fossils: how does life evolve? *S Afr J Sci* 76:61–84
- Vrba ES (1985a) Ecological and adaptive changes associated with early hominid evolution. In: Delson E (ed) *Ancestors: the hard evidence*. A.R. Liss, New York, pp 63–71
- Vrba ES (1985b) Environment and evolution: alternative causes of the temporal distribution of evolutionary events. *S Afr J Sci* 815:229–236
- Vrba ES (1989) Levels of selection and sorting, with special reference to the species level. *Oxf Surv Evol Biol* 6:111–168
- Vrba ES, Eldredge N (1984) Individuals, hierarchies and processes: towards a more complete evolutionary theory. *Paleobiology* 10:146–171
- Vrba ES, Gould SJ (1986) The hierarchical expansion of sorting and selection: sorting and selection cannot be equated. *Paleobiology* 122:217–228
- Waddington CH (1942) The epigenotype. *Endeavour* 1:18–20
- Wallin IE (1927) *Symbiogenesis and the origin of species*. Williams and Wilkins Company, Baltimore
- Watson JD, Crick FHC (1953) A structure for deoxyribose nucleic acid. *Nature* 171(4356):737–738
- Weismann A (1893) *The germ-plasm: a theory of heredity*. Charles Scribner's Sons, New York
- Whewell W (1833) *Astronomy and general physics considered with reference to natural theology*. W. Pickering, London
- Williams GC (1966) *Adaptation and natural selection*. Princeton University Press, Princeton
- Williams GC (ed) (1971) *Group selection*. Aldine Atherton, Chicago
- Wilson EO (1975) *Sociobiology: the new synthesis*. Harvard University Press, Cambridge
- Woese CR (1998) The universal ancestor. *PNAS* 95(12):6854–6859
- Woese CR, Fox GE (1977) Phylogenetic structure of the prokaryotic domain: the primary kingdoms. *PNAS* 74(11):5088–5090
- Wright S (1929) The evolution of dominance. *Am Nat* 63(689):556–561. doi:[10.1086/280290](https://doi.org/10.1086/280290)
- Wright S (1932) The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proc 6th Int Conf Genet* 1:356–366
- Wynne-Edwards VC (1962) *Animal dispersion in relation to social behavior*. Oliver and Boyd, London
- Wynne-Edwards VC (1986) *Evolution through group selection*. Blackwell Scientific, Oxford. ISBN 0-632-01541-1
- Zeder MA (2008) The Neolithic macro-evolution: macroevolutionary theory and the study of cultural change. *J Archeol Res* 17:1–63. doi:[10.1007/s10814-008-9025-3](https://doi.org/10.1007/s10814-008-9025-3)
- Zinder ND, Lederberg J (1952) Genetic exchange in Salmonella. *J Bacteriol* 64(5):679–699