



## CHAPTER 1

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# THE EVOLUTION OF THE BIOLOGICAL SCIENCES

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## EPISTEMIC PLURALISM IN BIOLOGICAL EVOLUTION

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EVOLUTION is a phenomenon that is originally studied from within the biological sciences. The latter have evolved numerous disciplines and research areas that can be grouped into seven main schools (Figure 1.1). Several of these schools can be clustered further into megastructures called *paradigms* (Kuhn, 1962). **Darwinism** marks the onset of modern evolutionary thinking and it lies at the foundation of the **Modern Synthesis**. Darwinism and the teachings of the Modern Synthesis together are referred to as the *Neo-Darwinian paradigm*. **Micro-, Meso-, and Macroevolutionary schools** are expansions of the Neo-Darwinian paradigm, and together with the school of **Ecology**, they constitute the paradigm called *Ecological Evolutionary Developmental Biology (Eco-Evo-Devo)*. The **Reticulate Evolution** school evolves somewhat independently of these Darwinian-based research schools.

In what follows, the major theses of these schools and paradigms are discussed. Afterwards, the chapter provides a universal definition of evolution and looks into how distinct units, levels, and mechanisms underlie theorizing on evolutionary hierarchies and evolutionary causation. The following chapter examines how the diverse evolution schools are applied and implemented into the symbolic sciences.





**FIGURE 1.1:** Evolutionary theories develop along seven main research schools: Darwinism, the Modern Synthesis, Microevolution, Meso-evolution, Macroevolution, Ecology, and Reticulate Evolution. The schools in blue represent the Eco-Evo-Devo paradigm. The concepts are explained in the body of the text where they are marked in bold.

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## DARWINISM

**Darwinism** refers to the nineteenth century school of evolutionary thought that commences with the publication of Darwin's (1859) volume *On the Origin of Species by Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life*. In this work, in part inspired by Malthusian economics, Darwin hypothesizes that population growth inevitably leads to a **scarcity of resources** (life necessities) that in turn brings forth a **struggle for existence** between '... either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions



of life' (Darwin, 1859, p. 63). This struggle for existence, according to Darwin (1859, p. 62), has an impact on both the survival chances and the reproductive success (or fitness) of the organism. Individuals demonstrate **variation** in organismal traits that either help or disable them in the struggle for existence over scarce resources, and in the battle between the sexes over reproductive mates. Some traits are beneficial or *adaptive*, others are deleterious or *maladaptive*, and still others are *neutral*. Accordingly, organisms with adaptive traits are more likely to be preserved long enough to pass on their traits to future generations than are organisms with maladaptive traits, and it is this process that Darwin calls **natural selection**. **Sexual selection** refers to the additional influence that mate choice has on organismal fitness. Here too, organisms with traits deemed attractive to the opposite sex are thought to have more chance to reproduce and thereby to pass on their traits to future generations.

Darwin thus already recognizes that organismal traits are the subject of **inheritance**. He furthermore conjectures that both forms of selection, natural and sexual, influence what kind of organismal variation is transmitted to future generations, with adaptive traits standing a better chance than maladaptive ones. Over time, the natural and sexual selection of organisms with adaptive traits leads to a **gradual** shift in populations resulting in a pattern whereby organisms demonstrate **adaptation** to their surroundings and the species they belong to demonstrate **descent with modification**.

## THE MODERN SYNTHESIS

It is an empirical observation that children resemble their parents, but for Darwin (1859, p. 13), 'The laws governing inheritance are quite unknown'. **Hereditary laws** first become described by Gregor Mendel, six years after Darwin wrote the *Origin of Species*. Largely ignored at that time, Mendel's work is rediscovered at the turn of the twentieth century, and for a while, together with theories of **genetic mutation** (de Vries, 1901–1903), the laws are recruited to counter Darwinian thinking (Bowler, 1983). But by the 1940s, scholars active in the field of **Theoretical Population Genetics** are able to reconcile mutation theories and hereditary laws with selection theory. This marks the founding of the **Modern Synthesis** (Huxley, 1942; Provine & Mayr, 1980; Smocovitis, 1992). Also known as the Neo-Darwinian Synthesis, it gives new meaning to Darwin's old ideas.

Theoretical Population Geneticists construct important, mathematically founded theories on how genes can be dissociated from organisms and conceptualized as forming populations of genes or *gene pools* that can in turn be visualized as spreading out or flowing over what are called *fitness landscapes*. In these models, adaptation becomes understood as a form of hill climbing in a rugged landscape. Such research furthermore gives way to the mathematical conceptualization of **genetic drift** (Wright, 1932; Kimura, 1983) that is understood as a random walk in this landscape by a subpopulation that eventually leads to a shifting balance (Dietrich & Millstein, 2008; Plutynski, 2007).



In association with these statistical models, the founders of the Modern Synthesis also introduce theoretical **species concepts and speciation models** (Mayr, 1963), as well as discussions of large-scale **evolutionary trends** (Simpson, 1944). Also counted among the founders of the Modern Synthesis are **Experimental Evolutionists** (Morgan, 1932) known for their many artificial breeding experiments and x-ray-induced mutation studies conducted with fruit flies and other animals in order to better understand variation at individual and population levels.

## EXPANSIONS OF NEO-DARWINISM

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The founders of the Modern Synthesis are known for examining hereditary traits on a theoretical and an experimental level. Today, empirically driven scientific advances have expanded the Neo-Darwinian paradigm further into what are now three distinguishable sub-schools that study evolution, respectively, at a micro (genetic), meso (organismal), and macro (species) level.

### Microevolution

**Microevolutionary schools** associate with the discovery, based upon Rosalind Franklin's work, of the double helix structure of DNA and the subsequent deciphering of the genetic 'code' (Watson & Crick, 1953; Morange, 1998; Sarkar, 2005). The fields of **Biochemistry and Molecular Genetics** have been reinterpreting Darwin's conceptualization of heredity as well as the Theoretical Population Geneticists' concepts of genetic traits and mutations, **gene flow and migration**.

During *mitosis* (cell division) or *meiosis* (the formation of the reproductive cells), for example, genes demonstrate high copying fidelity, and this founded the idea that genes are **replicators** that have more longevity than the organisms they belong to (Dawkins, 1976). The ideas that genetic mutations are rare and accidental copying errors of a fixed code, coupled with the assumption that genes mutate at a steady rate, has helped to substantiate **molecular clock theories** (Zuckerandl & Pauling, 1965). By building on results from DNA, RNA, and amino acids **sequencing**, these theories try to capture the *pace* of evolution. In fields such as cladistics and systematics, molecular clock theories help to estimate the *time of divergence* of evolutionary lineages. Originally able to unravel only small segments of biomolecular sequences, these fields are now evolving into the **(multi)-omics** (Narad & Kirthanashri, 2018; Huang, 2018) such as genomics, proteomics, and metabolomics that enable *big data mining* (Krassowski et al., 2020). Successful examples of such mining studies include the Human Genome Project (Venter et al., 2001), the Chimpanzee Genome Project (Chimpanzee Sequencing and Analysis Consortium, 2005), the Cancer Genome Atlas (Cancer Genome Atlas Research Network, et al., 2013), the Neanderthal Genome Project (Green et al., 2008, 2010), the





Human Protein Atlas (Uhlén et al., 2015), and the Expression Atlas (Papatheodorou et al., 2020).

## Mesoevolution

Traditional molecular genetic studies originally focused on the passive replicative aspects of genetic material. However, such passive views on genes today are moderated by our more advanced understanding of development and the role played therein by genetic and environmental factors. These are studied from within **Mesoevolutionary schools**.

Mesoevolutionary schools originate by continuing Darwin's focus on the *organism*, and they originally do so mainly as a way to counter the *gene-reductionism* brought about by the Modern Synthesis and the Microevolutionary-oriented evolution school. *Strictu sensu*, these latter schools investigate genes, what they encode for, how they mutate, and how they are passed on to future generations. How traits evolve across generations in time marks the study of *phylogeny* (evolution), which is traditionally opposed to *ontogeny* (development). Such a rigid distinction, however, ignores an organism's *life history*, and it ignores the *cyclic developmental patterns* that return each generation anew. Consequently, development has, traditionally, wrongly been assumed not to impact evolution.

One of the first scholars to point out this problem is Gould (1977), who in his book on ontogeny and phylogeny reexamines the important contributions made by early embryologists and developmental scientists to our understanding of how *morphology* (bodily form) develops and how it runs through similar stages across the animal kingdom (Figure 1.2, top). The book helped to lay the foundation of the evolutionary developmental (**evo-devo**) movement that studies these developmental patterns, from conception until death (Arthur, 2011; Carroll, 2005; Hall, 2012; Oyama et al., 2001).

Embryologists investigate the crucial role that **modularity** (Altenberg, 1995; Wagner, 1996) as well as *timing* plays in the development of body plans. Vertebrate embryonic development, for example, is typified by a *gastrulation phase* where the *blastula* (the multicellular complex that forms from the *zygote*, the fertilized egg) arranges into a multilayered structure: the *ectoderm* (outer layer), *mesoderm* (middle layer), and *endoderm* (inner layer). From these germ layers, *organs* such as the stomach, liver, pancreas, lungs, heart, and kidneys, and *systems* such as the respiratory system, the digestive system, the vascular, lymph, and the nervous systems evolve. These systems (von Bertalanffy, 1950) are studied for their *functions* from within the field of **physiology** (Noble, 2011, 2013).

The developmental, mesoevolutionary school today also integrates knowledge from Microevolutionary, genetic, and biochemical research. Scholars now know that the different segments that underlie vertebrate embryogenesis, organogenesis, and overall morphogenesis are governed by the same *homeotic* or regulatory genes.



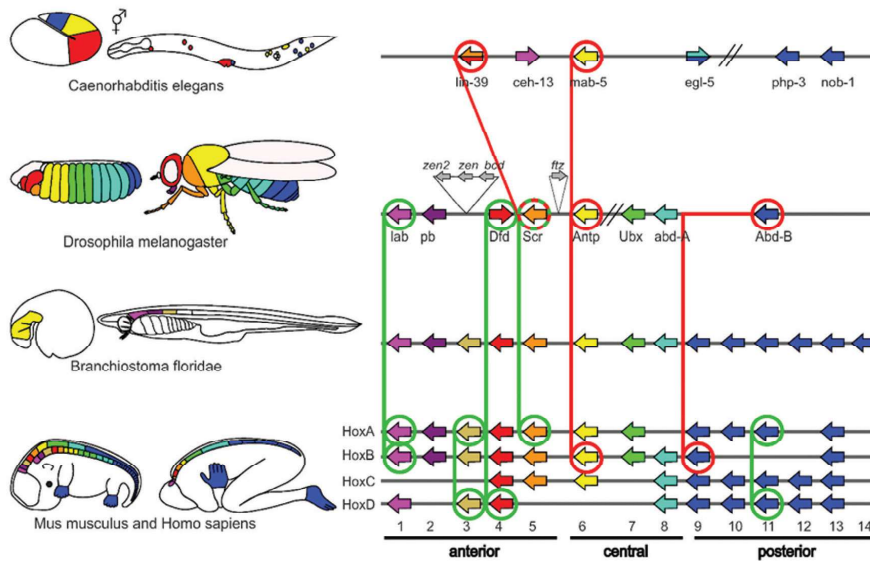
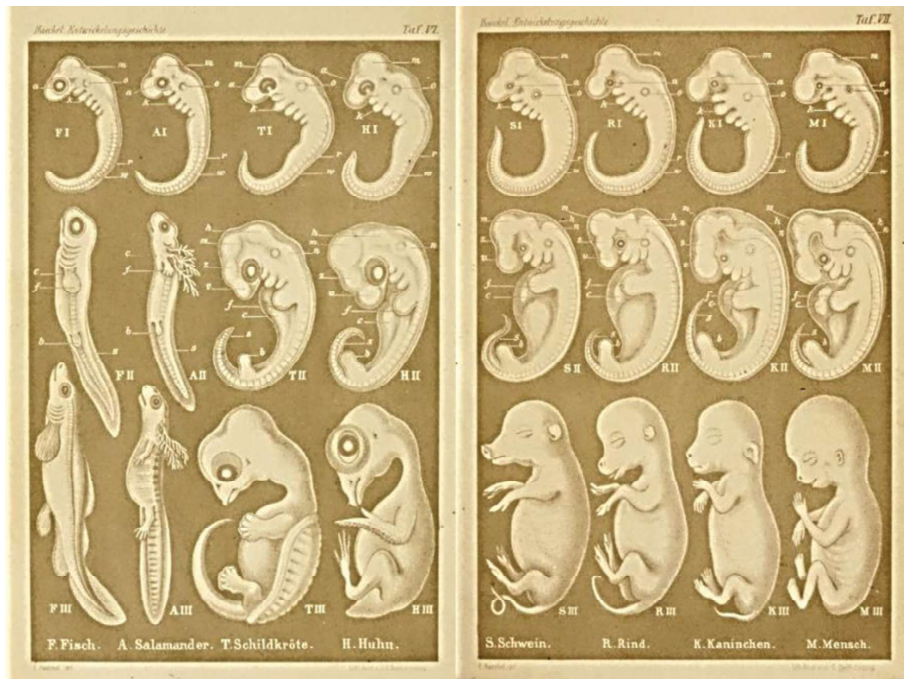


FIGURE 1.2: Embryology and hox genes.

Top:

Haeckel's (1874) controversial comparative drawings of embryos at three different stages of embryogenesis that follow the gastrulation phase. Depicted from left to right are the embryos of a fish, salamander, turtle, chicken, swine, cow, rabbit, and human.

Bottom:

Homeotic genes are a group of genes that regulate the cell differentiation and morphogenesis of vertebrates. The picture depicts a schematic of the homeotic genes and their corresponding body segments for a species of fruit fly (*Drosophila melanogaster*) and their homologous counterparts in a roundworm (*Caenorhabditis elegans*), Florida lancelet (*Branchiostoma floridae*), mouse embryo (*Mus musculus*), and adult human (*Homo sapiens*)

Sources: (A) Reproduced from Haeckel, E. (1874). *Antropogenie*. Leipzig: Engelmann. (B) Reproduced with permission from Hueber, S. D., Weiller, G. F., Djordjevic, M. A., & Frickey, T. (2010). Improving Hox protein classification across the major model organisms. *PLOS ONE* 5(5), e10820 under a CC-BY-3.0 license.

These structures are thus *homologous* across species which means that they have a shared ancestry. Homeotic genes shared by all vertebrates and some invertebrates, for example, include the *homeobox gene complex* (Figure 1.2, bottom; De Robertis et al., 1990, p. 47; Hueber et al., 2010; McGinnis et al., 1984; Gehring, 1996, Davidson & Erwin, 2006).

The onset, location, and duration of activation of homeotic genes brings forth differential structures at a species level, lending new meaning to the understanding of genetic mutations. Minor genetic alterations in regulatory genes can lead to rapid and drastic evolutionary changes in body plans, while changes in *structural* genes instead bring forth individual variation.

Evo-devo thus investigates *gene-regulatory networks* which are the signaling pathways from genotype to phenotype that underlie the formation of protein structures and tissues. **Epigenetics** (Pardee et al., 1959; Jacob & Monod, 1961; Løvtrup, 1972; Ho & Saunders, 1979; Hallgrímsson & Hall, 2011; Jablonka & Lamb, 1995; Waddington, 1953) goes one step further by additionally examining how extra-genetic factors enable and constrain gene expression and development thereby setting limits to *evolvability* (Wagner & Altenberg, 1996). All epigenetic processes involve a form of *learning* and this occurs at a molecular, cellular, or organismal level. The knowledge acquired through learning can become transmitted phylogenetically and this can impact evolution long term.

Epigenetic changes at the *molecular* and *cellular* level (Felsenfeld, 2014) can occur in chromatin regulation or epigenetic change can be induced by mobile genetic elements. Changes in **chromatin regulation** result in changes in gene expression which becomes enhanced, inhibited, or otherwise modified; and this can be understood as a form of ‘developmental programming’ (Straussman et al., 2009). Examples are changes induced by histone modification or DNA methylation. Chromosomes consist of chromatin fibers made up of proteins called histones that bind the DNA together into a tight coil. *Histone modification* (Stedman & Stedman, 1950) involves a loosening or tightening of the wrap of DNA around histons, thereby enabling or disabling gene transcription and translation. *DNA methylation* (Riggs, 1975; Mohn et al., 2008) is another mechanism that plays a significant role in gene regulation. Gene regulatory mechanisms enable the attribution of cell function during embryogenesis where *stem cells* (cells that are pluripotent because they have the ability to become any kind of cell in the body) differentiate into their destination cells (e.g. heart or lung cells, or neurons). Environmental influences such as diet, exercise, and chemicals can induce epigenetic changes in both histone binding and methylation, and this molecular learning can impact overall health and disease as well as aging.

**Mobile genetic elements** (McClintock, 1950; Shapiro, 2011) are DNA segments such as transposons, retrotransposons, or bacterial plasmids. These segments can switch location by cutting or copying and pasting their sequence to other regions within the genome they belong to, or they can transfer DNA sequences to viruses or other genomes or cells belonging to different species or bacterial types. Their movement can insert, delete, or otherwise alter existing DNA sequence structure in a way that has been compared to ‘natural genetic engineering’ (Shapiro, 2011). The dynamicity displayed by mobile genetic elements therefore challenges the replicator notion of genes.

Examples of epigenetic change at the *organismal* and *behavioral* level are the alterations induced by the Baldwin effect or by phenotypic plasticity. The **Baldwin effect** (Baldwin, 1896) emphasizes phenotypic flexibility *expressed by organismal learning* (Badyaev, 2009; Sznajder et al., 2012). When faced with a new or changing environment, an organism's ability to learn new behavior helps to overcome genetic constraints. The Baldwin effect is often opposed to **phenotypic plasticity** (West-Eberhard, 1986, 2003; Sultan, 2017). Also known as developmental or epigenetic plasticity, or as gene-switching, this refers to the phenotypic flexibility *expressed by the genome*. The same genome brings forth alternative phenotypes when environmental circumstances vary. A switch from one phenotype to another can happen rapidly, and the alternative phenotype can become fixed for the population, without the genome actually undergoing genetic mutations. Phenotypic plasticity can lead to punctuated and epigenetic evolutionary innovation, and this in turn can enhance divergence and speciation. Jablonka and Lamb (1995) furthermore understand *symbolic inheritance* or the transmission of information (Shannon & Weaver, 1949) through language and other communicative systems as an epigenetic system.

In summary, Evo-devo schools and Epigenetics are demonstrating that neither organisms nor genes are simply selected passively, either by the environment or by sexual mates (Lewontin, 1983). The Modern Synthesis, that understood organisms as programmed by fixed genes, is also flawed. Rather than viewing the gene/organism-environment relationship as dyadic in kind, a more dialectical approach is needed (Gould & Lewontin, 1979; Gontier, 2018b).

The study of how natural selection operates not only on organisms but also on internal structures (Lewontin, 1983) such as genes or gene segments, organs, and physiological systems has brought forth new research on the *units* (Lewontin, 1970; Hull, 1981) and *levels* (Brandon, 1982) of selection. This has led to theorizing on **multilevel selection** (Okasha, 2006; Sober & Wilson, 1999), the nature of **complexity** (Simon, 1962), and the **major transitions of evolution** (Table 1.1, Maynard Smith & Szathmáry, 1995; Szathmáry, 2015).

It is primarily within this Mesoevolutionary school that scholars are advocating for an *Extended Evolutionary Synthesis* (Pigliucci & Müller, 2010; Laland et al., 2015) or *Third Way of Evolution* (Shapiro & Noble, 2021). However, the criticism that the Modern Synthesis is unfinished (Eldredge, 1985) is also put forward by Ecological and Macroevolutionary schools. The former study the *place* where evolution occurs, yielding research on the *economy* or resource management of evolution (Haeckel, 1866), and the latter study the *time* of evolution. Time here is understood as both the *pace* at which evolution occurs, and how evolution occurs over *deep time* in the geological record (*the geological time scale*). The following sections turn toward these schools.



**Table 1.1: The major transitions in evolution**

Maynard Smith & Szathmáry's (1995) original version		Szathmáry's (2015) '2.0' version
Criterion used to mark transitions is 'increasing complexity,' which is defined differentially by the 'reaching of a Darwinian threshold', the 'introduction of new types of information and information transfer', the 'division of labor', and the 'overcoming of free-riders to facilitate cooperation'.		Criterion used to mark transitions is the origin of a new 'biological individual'.
From	To	Origin of
1 <i>Naked replicating molecules</i>	<i>Molecular populations arranged within compartments (protocells)</i>	<b>Protocells</b> (catalysts-replicators-chromosomes-cells)
2 <i>Independently replicating genes (selfish replicators)</i>	<i>Cooperating chromosomes</i>	
3 <i>RNA (ribozymes that function as genetic information and as enzymes)</i>	<i>*DNA, differentiation between genes and enzymes (proteins) that mark a division of labor</i>	<b>Prokaryotes</b> (molecular networks-ribosomes-genetic code)
4 <i>Prokaryotes (cells without nucleus; i.e. bacteria and archaea)</i>	* Eukaryotes (cells with nucleus) and the origin of organelles (more division of labor)	<b>Unicellular eukaryotes</b> (nucleus-mitochondria-mitosis-meiosis/sex)
5 Asexual individual clones	* Sexual populations	<b>Plastids</b> (recursive endosymbiosis and lateral gene transfer between organelles and nucleus)
6 Single-celled eukaryotic organisms (protists)	Multicellular eukaryotic organisms (fungi, animals, plants) with cellular differentiation (more division of labor)	<b>Multicellular eukaryotes</b> (genetic and epigenetic inheritance)
7 Solitary individuals	Colonies (with non-reproductive castes, e.g. bees, termites, and ants) (more division of labor and origin of eusociality)	<b>Eusocial animal societies</b> (organisms and superorganisms)
8 Pre-linguistic primate societies	* Human societies with syntactic language	<b>Societies with language</b> (cultural groups)
* Transitions considered as 'difficult;' <i>Italics refer to the Pre-RNA world and prokaryotic cells;</i> Regular text refers to eukaryotes; <b>Bold refers to a new biological individual.</b>		

## Macroevolution

In the **Macroevolutionary school**, debates on evolutionary trends, the major transitions of evolution, and the search for the units and levels of evolution pose questions about the nature of *above-organismal phenomena* such as *populations and species* and how natural selection operates within and upon them (Jablonski, 2008; Sepkoski & Ruse, 2009); as well as how we need to conceptualize **evolutionary hierarchies** (Eldredge, 2008;





Gontier, 2021; Pattee, 1973; Salthe, 1985; Tëmkin & Eldredge, 2015). Even natural selection is now recognized to occur at different **tempos and rates**. Scholars distinguish between different **evolutionary patterns** (Eldredge, 1985). Natural selection, for example, is described by Darwin (1859) to bring forth a pattern of *descent with modification*. But contrary to what he thought, such descent need not always be *gradual*. Rather, Eldredge and Gould (1972) have demonstrated that evolution is often characterized by a pattern of *punctuated equilibria*, where long periods of *stasis* (Eldredge et al., 2005) are intermitted by episodes of rapid evolutionary change. Punctuated equilibria help to explain phenomena such as phenotypic plasticity as well as **adaptive radiations** where one or a few species rapidly evolve into a variety of new species. Adaptive radiations and drift in turn help to account for life's **biodiversity** (Wilson, 1984; MacArthur & Wilson, 1967; Hubbell, 2001; Seddon et al., 2016). Biodiversity is characterized not only by the abundance of life form but also by both gradual and punctuated (**mass**) **extinctions** (Benton & Harper, 2009), where the *evolutionary lineages* that are studied in the fields of **cladistics and phylogenetics** die out. This research links to *conservation ethics*.

## ECOLOGY

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Micro-, Meso-, and Macroevolutionary schools are nowadays often grouped together with the school of Ecology. Together, they form the superstructure currently designated as the *Eco-Evo-Devo program* (Hall, 2003; Gilbert & Epel, 2008). The school of **Ecology** studies the place of evolution, and traditionally, the locus of evolution is identified as the environment. It is in the environment that Darwin suggested that a struggle for existence occurs due to a scarcity of natural resources, leading Van Valen (1973) in particular to emphasize that the environment is not merely physical or *abiotic*. Rather, the environment is mostly *biotic*, which means that it is made up of other living organisms. The scarcity of resources is thus induced by *competition* that occurs amongst living organisms that engage, for example, in *consumer–producer* or *predator–prey relationships*, and that in turn make up the typical **food chains, cycles, and webs** studied by ecologists (Egerton, 2007). Ecological relationships can lead to *co-evolutionary arms races* between species, where one species has to evolve to keep up with the other, which is a phenomenon studied by the **Red Queen Hypothesis** (Van Valen, 1973). Ecology here sides with hierarchy and multilevel selection theory, and Ecology in particular studies the relation that exists between different organisms belonging to the same and to different species in the context of the *communities, ecosystems, and biomes* that they form, the *energy fluxes or dynamics* that exist between them, and how these impact **energetics** (Lotka, 1922, 1925; Van Valen, 1976; Saks et al., 2009) or **bio(geo)chemical cycles** (Lovelock & Margulis, 1974; Jacobson et al., 2000; Volk, 2003; Egerton, 2017). This further translates into economic studies on how resources are produced, managed, optimized, or wasted.

**Table 1.2: Niche construction according to Lewontin\***

Niche construction refers to the organismal capacity to construct/build a niche/environment.

**1. Organisms partly determine their niche.**

There is never an exact fit or complete adaptation of an organism to the environment.

E.g. A bush can be part of the habitat of a butterfly, while a tree is not.

**2. Organisms literally construct the environment that surrounds them.**

Organisms actively modify their surroundings.

E.g. Beavers build dams.

**3. Every act of consumption is an act of production.**

Organismal behavior has an ecological impact on the biotic and abiotic environment.

E.g. The first photosynthetic organisms changed earth from an oxygen-low to an oxygen-rich planet.

**4. Organisms learn to anticipate the external conditions that the environment provides.**

This distinguishes the problem of adaptation (fitting to an environment) from that of adaptability (the ability to evolve new traits, possibly by learning).

E.g. Many organisms harvest food for the winter.

**5. Organisms modify external signals according to their constitution.**

The interaction between an organism and its environment is mediated by the organismal body.

E.g. If the external temperature rises, an internal signal will lead to the release of certain hormones that cool down the body and prevent it from overheating.

\* Lewontin, R. C. (2000). *The triple helix*. Cambridge, MA: Harvard University Press; Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society B: Biological Sciences* 205(1161), 581–598.

Of great importance here is the study of **niche construction** (von Uexküll, 1921, 1937; Lewontin, 2000; Sinha, this volume) and **ecological inheritance** (Odling-Smee, 1988). In line with the more active role attributed to organisms, organisms are recognized to significantly alter and even to altogether construct their environment. Niche construction (Table 1.2) leaves an *ecological footprint* that spans generations. All of us, for example, live in the oxygen-rich environment created by the first photosynthetic life; human children inherit the created sociocultural environment from older generations; and future generations will unfortunately inherit the problems caused by the pollution induced by human activity.

## RETICULATE EVOLUTION

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The **Reticulate Evolution School** identifies symbiosis, symbiogenesis, lateral gene transfer, infective heredity, and hybridization as important evolutionary mechanisms and processes (Carrapiço, 2015; Gontier, 2015; Sapp, 1994; Shapiro & Noble, 2021). These mechanisms and processes require a rethink of the evolutionary importance that *co-operation* plays in species *interactions* and how they complement competition-focused



**Table 1.3: The spectrum of symbiotic associations**

Neutralism (0, 0)	Indifferent for all symbionts
Commensalism (+, 0)	Beneficial for one, indifferent for the other/s
Amensalism (–, 0)	Harmful for one, indifferent for the other/s
Mutualism (+, +)	Beneficial for all
Parasitism (+, –)	Beneficial for one, harmful for the other/s
Synnecrosis (–, –)	Harmful for all

selection theory. The different mechanisms and processes that underlie reticulate evolution can be united into a single research school because *pattern-wise*, during reticulation, evolutionary lineages cross *horizontally*. Lineages sometimes also *merge* into new ones. Scholars active in the Reticulate Evolution school therefore propose to replace *tree* of life images and metaphors, that focus on the vertical ramification of evolutionary lineages, with a more accurate *web of life* metaphor and with *network* models (Doolittle, 1999; Baptiste & Papale, 2021). In this section, the mechanisms and processes of reticulate evolution are briefly discussed.

**Symbiosis** (Margulis, 1991; Gontier, 2016) is an ecological phenomenon that refers to the multiple interactions that exist during ontogeny between organisms belonging to different species. Symbiosis is a neutral term, and the ontogenetically occurring symbiotic interactions can be beneficial or harmful for the *symbionts* (the interacting organisms), or they can remain indifferent from the symbiosis (Table 1.3).

**Symbiogenesis** (Margulis, 1998) is an evolutionary mechanism that occurs when symbiosis becomes *hereditary*. Symbiogenesis has played an important role in the evolution of eukaryotic cells. The cells of *multicellular* organisms such as *fungi*, *plants*, and *animals* are *eukaryotic*. Besides a nucleus, the cytoplasm of eukaryotic cells also harbors small bodies called *organelles*, and some of these organelles have a *prokaryotic* origin. That means that once free-living bacteria have long ago entered some of the first eukaryotic cells and commenced an intracellular symbiosis or *endosymbiosis*. Over time, this resulted in a loss of organismal identity for the symbiotic bacteria that permanently transformed and evolved into the organellar structures. Organelles that have such a symbiotic origin include mitochondria and chloroplasts. *Mitochondria* evolved from alfa proteobacteria and are found in fungi, animal, and plant cells where they supply the cell with energy; and *chloroplasts* evolved from cyanobacteria and are found mostly in algal and plant cells where they underlie photosynthesis (Figure 1.3). Note that besides mitochondria and chloroplasts, eukaryotic cells carry more organellar structures and their evolutionary origin remains unknown.

Symbiosis and symbiogenesis play an additional and important role in evolution by underlying **holobiont** formation (Margulis, 1991; Guerrero et al., 2013). This is the process whereby different living beings interact in such a way that they function as a new spatiotemporal entity. Humans, for example, maintain symbiotic associations with

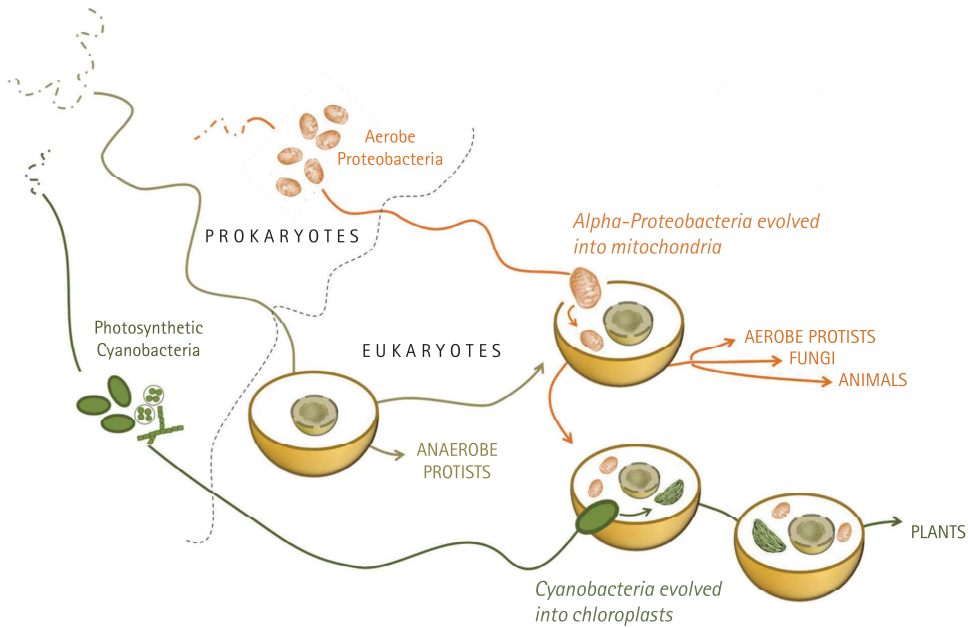


FIGURE 1.3: The evolution of mitochondria and chloroplasts by symbiogenesis.

Source: © Nathalie Gontier

their *microbiome* (Berg et al., 2020) and *virome* (Anderson et al., 2003) and together they form one heterogenous and functional entity (Figure 1.4). The genomes of these interacting symbionts, together with the host genome, have been conceptualized as forming a *hologenome* (Rosenberg & Zilber-Rosenberg, 2011).

Another important mechanism of reticulate evolution is **lateral gene transfer** (Keeling & Palmer, 2008); the phenomenon whereby gene-carrying entities such as organisms but also viruses exchange genes horizontally. When a cell is infected with a virus, for example, that virus copies its DNA into the host genome and it makes the host genome ignore its own genes to the benefit of the viral genes (Ryan, 2009). Research on symbiosis and lateral gene transfer therefore also links to **infective heredity** (Lederberg, 2003) or the impact *health and disease* has on evolution; and it links to hierarchy theories and multilevel evolution theories.

A final mechanism whereby reticulate evolution occurs is by way of **hybridization**. This happens when members of different species belonging to opposite sexes mate and produce offspring (Arnold, 2009). This too enables the introgression of genes from one species into another, and we know that such mixing has occurred frequently enough within the hominin lineage to leave genetic traces thereof (Ackermann et al., 2019; Chen et al., 2020; Green et al., 2010; Prüfer et al., 2014; Vernot & Akey, 2014).

Note that all forms of reticulate evolution can induce rapid and abrupt evolutionary change and that symbiotic relations can lead both to coevolution as well as to stasis. Mitochondria and chloroplasts, for example, have gone through an initial phase of gene





**FIGURE 1.4:** Humans maintain numerous symbiotic associations with their microbiome and virome.

loss, and some of the genes have relocated to the nucleus of the host, but overall, they are highly conserved and semi-stable structures that evolve at a lower evolutionary rate than the organisms they belong to. This is because they are inherited directly from the mother, and thus no genetic recombination takes place. For this reason, they are also excellent biochemical markers that help in the tracing of evolutionary ancestry (Cavalli-Sforza, 1997; Pääbo, 2014).

## A UNIVERSAL DEFINITION OF EVOLUTION

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The concept of evolution today is no longer synonymous with that which evolves as a result of natural selection, or that which is studied from within the Modern or Neo-Darwinian Synthesis. We therefore need a more universal definition of evolution that applies equally to the phenomena studied by Micro-, Meso-, and Macroevolutionary, Ecological, or Reticulately-oriented schools.

As diverse as the fields are, all the petals of the flower of evolution have identified means or *mechanisms* whereby *units* or objects of evolution evolve at distinct loci or *levels*. Within a field called Applied Evolutionary Epistemology (Gontier, 2010, 2017, 2018a, 2018b, 2021), I have therefore redefined evolution as that which occurs when units evolve (change) at levels of an ontological hierarchy by mechanisms and processes



**Table 1.4: Applied evolutionary epistemology**

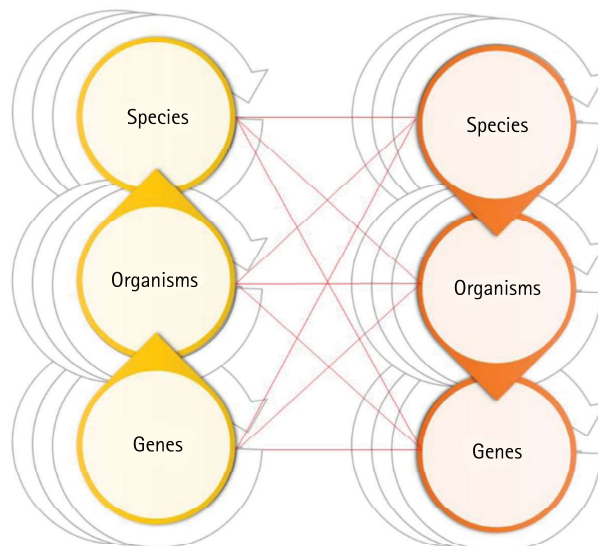
1. Universal **definition** of evolution  
Evolution occurs when units evolve (change) at levels of an ontological hierarchy by mechanisms and processes.
2. A derived universal evolutionary **methodology**  
Studying evolution involves a search for units, levels, and mechanisms, and allocating them into ontological hierarchies.

(Table 1.4). This definition also provides a methodology whereby we can study evolution, namely, studying evolution involves a search for units, levels, and mechanisms, and situating them into an ontological hierarchy.

Examples of hierarchies are the classic evolutionary hierarchy that goes from genes and organisms to species, or the ecological hierarchy that goes from organisms to populations, to species and communities (Simon, 1962; Pattee, 1973; Mayr, 1982; Eldredge & Salthe, 1984; Salthe, 1985; Grene, 1987). Hierarchies such as these are a methodological means to get a grip of the different ontological layers of reality that are relevant for the study of evolution.

Hierarchies also help to define evolutionary causation (Gontier, 2018b, 2021). Causation can be understood as an upward, downward, reticulate, or circular movement along the strands of a hierarchy (Figure 1.5).

The traditional Neo-Darwinian paradigm, for example, understands genes, organisms, and species as real entities (Hull, 1980, 1981; Mayr, 1982; Ghiselin, 1974) that together form a genealogical hierarchy (Eldredge, 1985). Within this tradition, causation



**FIGURE 1.5:** Upward (yellow), downward (orange), reticulate (red), and self-causation (gray).

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is understood as an *upward* movement (Bechtel, 2011; Bechtel & Richardson, 1993) whereby genes bring forth organisms, and organisms bring forth species.

Within Evo-Devo schools and Epigenetics (Pardee et al., 1959; Ho & Saunders, 1979; Jablonka & Lamb, 1995; Emmeche et al., 2000; Hallgrímsson & Hall, 2011; Shapiro, 2011; Noble, 2013), scholars instead investigate how the life history of organisms can alter genetic material, and such is a form of *downward* causation (Campbell, 1974) where the higher level of the genealogical hierarchy affects the evolution of a lower level of that hierarchy.

The genealogical hierarchy is based upon the genealogical descent line where genetic material or information is transmitted. Eldredge (1985) has argued that the genealogical hierarchy can be complemented by an ecological hierarchy, where much more than an informational code is transferred. Genes, for example, are part of cells that group into organisms and populations, and these exchange all sort of matter and energy within the economy of nature. This brings forth a dual hierarchy that is characterized by horizontal interactions between both hierarchies (Tëmkin & Eldredge, 2015).

Interactional hierarchies are also studied within reticulate evolution schools, and this requires an understanding of *reticulate* causation (Gontier, 2021). When genes of one organism are exchanged horizontally with the genome of another organism, or when distinct organisms hybridize, such implies reticulate interactions between distinct ontological hierarchies.

A final form of causation is *self-causation*. Self-causation is often studied in the behavioral and cognitive sciences where scholars investigate how organisms can demonstrate *autopoiesis* (Maturana & Varela, 1980). Autopoiesis refers to the capacity to self-maintain and self-regulate, and this underlies *teleonomic* (Pittendrigh, 1958) or goal-oriented behavior (Corning, 1983, 2014; Vane-Wright, 2014). That self-causation exists has often been denied because it requires causation to occur at the *focal* level rather than at a level above or below the entity under study. If that focal level is an organism, then autopoiesis requires the recognition that, beyond being regulated by its genes, the organism itself makes goal-directed choices. Even though there is a causal chain of events from genes to organisms, once in existence, and thus at a *later* point in time, humans learn to self-regulate and self-maintain. This enables them to demonstrate free will that by far surpasses the initial influence of their genes. Self-causation occurring at the same ontological level of a hierarchy can be explained by taking into account that over time, the focal level can start to self-maintain.

## CONCLUSION

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As we come to the end of our glance at the distinct petals of the flower whereby I have characterized evolutionary biological research, we can conclude that evolution is a heterogenous phenomenon that can occur according to a number of mechanisms and processes researched by distinct evolutionary schools, some of which can be grouped into larger paradigms, some of which cannot. There thus does not exist a single

all-encompassing research framework or evolutionary paradigm; and this is due, on the one hand, to the division of the evolutionary sciences, and on the other, to the pluralistic nature of evolution. Current focus therefore lies, not on how distinct sciences and schools can be unified, but on how we can account for this evolutionary pluralism. Of major importance in this is how we define units, levels, mechanisms, and evolutionary hierarchies, and how these can account for evolutionary causation. The following chapter examines how these diverse schools are differentially implemented into the symbolic sciences.

## ACKNOWLEDGMENTS

Written with the financial support of *Fundação para a Ciência e a Tecnologia* (FCT), the Portuguese Foundation for Science and Technology, Grant IDs SFRH/BPD/89195/2012 and DL57/2016/CP1479/CT0066.

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