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Macro and Micro Evolution

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Synonyms

Large-scale evolution; Megaevolution; Phyletic evolution; Population genetics; Small-scale evolution

Definition

Microevolution is the result of processes that lead to small changes in the phenotype at the population or species level, typically occurring over shorter time scales. These changes most commonly arise from alterations in the genetic composition of the population and are thus consequences of mutations or changes in allele frequencies within the population. Through the action of natural selection, these changes can accumulate and potentially give rise to adaptations. Typical microevolutionary processes include *mutations*, *natural selection*, *stability-based sorting*, *evolutionary drives*, *genetic drift* and *draft*, *gene flow*, and *speciation*.

Macroevolution arises from processes that influence evolution above the species level, typically occurring over longer time scales. These processes lead to the emergence and diversification of higher taxa that significantly differ from existing clades. The criterion for macroevolutionary success is achieving the highest possible ratio between speciation and extinction frequencies. Typical macro-evolutionary processes include *adaptive radiations*, *species selection*, *extinctions*, *evolutionary trends*, and *symbioses*.

Introduction

Biological evolution is a long-term process during which the characteristics of organisms change over generations. These changes are typically expected to lead to better adaptation of organisms, or their populations, to the environment, and, through the emergence of evolutionary novelties or entirely new species, to the diversification of evolutionary lineages. A fundamental question that has accompanied the study of evolution from its beginnings is what processes influence its course and their relative importance. There is no doubt that certain evolutionary changes occur even over short time scales, from one generation to the next. These so-called microevolutionary processes include *mutations* and *epimutations*, *natural selection*, *stability-based sorting*, *evolutionary drives*, *drift*, *draft*, and *gene flow*. However, can these processes fully explain evolution, or do additional macroevolutionary mechanisms come into play over longer time scales?

The history of responses to this question is intriguing and speaks to the development of the field of evolutionary biology itself. In the nineteenth and early twentieth centuries, researchers often tended to view microevolution and macroevolution as two separate domains within the realm of evolution. Both of these terms were coined by Yuri Filipchenko, a Russian entomologist and mentor to the renowned geneticist and evolutionary biologist Theodosius Dobzhansky. According to Filipchenko (1927), Charles Darwin explained with his gradualistic theory of natural selection only evolutionary processes at the species level. (This theory is stating that organisms adapt through the differential survival of offspring differing only in minor variations of inherited traits, Darwin, 1859.) According to this approach, microevolutionary processes, for instance, could account for the induction of dark morphs of the peppered moth (*Biston betularia*) in areas with significant industrial pollution. This change in coloration allows for effective camouflage on the lichen-free soot-covered trunks of birch trees in these industrial areas. However, it was not expected, according to this viewpoint, that a completely new species would eventually emerge from this moth, for example, one that could metabolize and utilize the emissions released by humans. The emergence of new species and higher taxa associated with the evolution of significant evolutionary innovations was considered as the domain of macroevolution. A domain that is characterized by different processes and governed by distinct rules. For example, prior to the advent of Mendelian genetics, the concept of *saltations* was popular, suggesting that new traits and, consequently, taxonomic groups arise through large, abrupt mutations with a significant impact (Goldschmidt, 1933).

With the advent of Mendelian genetics and, more importantly, the subsequent formulation and hardening of the *modern evolutionary synthesis*, a completely different perspective gained prominence. A notable proponent of this view was, e.g., Theodosius Dobzhansky (1937), as mentioned earlier. Since his time, most neo-Darwinists tend to perceive macroevolution as merely an extension of microevolution on a grand scale, encompassing long spans of time, broad spatial dimensions, and a broader taxonomic scope (see “Dawkins, Richard” chapter). Microevolution and macroevolution thus differ only in degree; evolutionary novelties and new species do not arise through specific macroevolutionary processes but rather through the prolonged influence of microevolutionary mechanisms. In the same way that gradual erosion can level mountain ranges like the Himalayas over time, proponents of this perspective argue that the pressure of natural selection acting on slight differences among individuals within a population could lead to the transition of tetrapods to a terrestrial lifestyle, the evolution of new forms of learning, mating rituals, and dozens of other adaptations. When adherents of this view speak of macroevolution, they typically refer to the long-term outcomes of microevolutionary, or simply put, evolutionary processes.

Nonetheless, it is evident that there are processes that influence evolution exclusively above the species level. For example, the existence of *species selection* (see “Evolution by Non-individual Selection Pressures” the dedicated chapter) is considered relatively undisputed today. According to Michael Hautmann (2020), macroevolution simply selects not intraspecific but interspecific variability. Mutations are not the source of innovations for macroevolution; instead, it is *speciation*, and the criterion for success is the maximal difference between the frequency of speciation and *extinction*. Further phenomena that cannot be solely explained from the perspective of microevolutionary processes include the emergence of new species, the issue of *adaptive radiations*, *evolutionary trends*, *extinctions*, and *symbioses*.

In the contemporary understanding, macroevolution has become a sort of catch-all category for various evolutionary phenomena on large time scales. A significant difference from the Filipchenko's era at the turn of the nineteenth and twentieth centuries is the shared belief that microevolutionary processes profoundly influence evolution even at the level of species and higher levels. There is no such thing as two separate evolutionary domains. However, in contrast to the time of strict *neo-Darwinism*, there is a prevailing view that specific macroevolutionary processes find application here, which do not apply at the microevolutionary level and can have far-reaching consequences for evolution.

Microevolution

The term *microevolution* in its standard understanding was first used by Yuri Filipchenko (1927) to refer to evolution within a species (or population) based on Darwinian principles. Reductively, we can describe microevolutionary processes as those that change the allele frequencies of different genes within a population. However, due to the existence of non-genetic forms of heredity, we can also include other processes that lead to heritable changes in the phenotype. The most important microevolutionary processes are:

Mutations and Epimutations

Mutations can be described as changes in the structure of genetic material, altering the content (semantics) while still adhering to the rules of genetic information encoding (syntax). Mutations may or may not manifest in an organism's phenotype, and their consequences can be neutral, harmful, or rarely beneficial to organisms. In a broad sense, we can classify any changes to the DNA chain (or RNA in the case of RNA viruses such as the influenza virus) as mutations. However, many of these changes, such as double-strand breaks, will, in all circumstances, have a damaging character. It is during the repair of such damage that (other) mutations often arise. Mutations are a crucial source of variability at the species level, which natural selection can work with. For more information on the types, characteristics, causes, and consequences of mutations, please refer to "Mutations" chapter.

Epimutation is a heritable change in gene regulation triggered by one of the epigenetic mechanisms. Unlike mutations, epimutations do not alter the nucleic acid chain itself or the genetic information it contains; instead, they affect how this information is interpreted. Like mutations, epimutations can be neutral, harmful, or beneficial to organisms. However, since they often result from specialized mechanisms, they generally lead to increased fitness in their carriers under the conditions that induced them. Another important feature that distinguishes epimutations from mutations is their duration. Epimutations can be transmitted transgenerationally, but typically only for a few (occasionally a few dozen) generations. For more information on epigenetics, its physiological mechanisms, the transmission of epigenetic signals, and their consequences for evolution, please refer to "Mutations" chapter.

Natural Selection

Natural selection was independently described by three British naturalists around the mid-nineteenth century: Patrick Matthew (Matthew, 1831), Charles Darwin, and Alfred Russel Wallace (Darwin & Wallace, 1858). However, the most extensive research on this process, its evidence, evolutionary significance, correlations, and consequences, was undertaken by the pioneer of evolutionary biology, Charles Darwin (Darwin, 1859). A more detailed discussion of selection can be found in "Algorithms, Natural Selection" chapter.

At this point, let us summarize that for a system to be subject to natural selection, its constituent entities must originate through replication or reproduction from one another and exhibit sufficient *heritability* of traits (see "Heritability" or "Trait Heritability" chapter). Furthermore, descendant entities need to vary in their characteristics (e.g., due to mutations), and the environment in which this entire process unfolds must be sufficiently complex. While a certain simple form of selection can occur even in a uniform environment (favoring the speed and accuracy of reproduction), the diversification and emergence of the evolutionary innovations usually associated with biological evolution depend on the heterogeneity and variability of conditions.

Selection can occur at various levels, including morphological, physiological, developmental, and behavioral. However, when discussing micro- and macroevolution, the last two merit special emphasis because they can retroactively influence the action of selection across different species. The evolutionary role of changes in individual development was somewhat overshadowed throughout most of the twentieth century. Still, their significance is now emphasized by the field of *evolutionary and developmental biology* (*evo-devo*, see "Evo-Devo (Evolutionary-Developmental) Approach" chapter). There are compelling reasons for the prominent role of developmental changes in the process of evolution. Firstly, almost all organismal traits develop during ontogeny, consistently relying on more fundamental features. Even a minor change in embryonic development, such as sensitivity to sex hormones, can have far-reaching consequences. For instance, it can impact behavior, including sexual preferences or sexually dimorphic behaviors (Berenbaum & Beltz, 2011).

From an evolutionary perspective, it is even more crucial to recognize that development itself, the map of relationships between genotype and phenotype (of which development is a fundamental component), represents the outcome of meta-evolution. This meta-evolution, known as *evolution of evolvability*, which we could readily consider a macroevolutionary phenomenon, determines how future (quasi)random mutations and environmental factors will influence the phenotype (Pavlicev & Wagner, 2012; Toman & Flegr, 2018b). This results in phenomena such as *phenotypic plasticity* (see "Phenotypic Plasticity" chapter), often with two or more distinct morphs, which is called *polyphenism*. Other related phenomena include developmental *robustness* to environmental and genetic changes, or *parallelism*, where related lineages seemingly inexplicably exhibit homologous traits by altering the regulatory elements of the same developmental modules.

Another equally vital yet often overlooked level of selection involves behavioral changes. Behavior itself is a phenotypic trait subject to evolution, just like body shape or intensity of metabolism. Crucially, behavioral patterns reversely affect how selective pressures act on a particular species. This phenomenon is known as the *Baldwin effect*, named after the American psychologist James Baldwin (see the dedicated chapters – "Baldwin Effect", "Adaptation: Preadaptations"). It is evident that organs (or traits in

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general, including behavioral patterns) actively used by an organism are more likely to undergo positive selection, based on how they are utilized. In simpler terms, the limbs of quadrupeds would have never evolved from the fins of lobe-finned fish if they were not actively used by these animals for walking. Especially among cognitively and behaviorally rich organisms capable of learning, such as animals, every organism has the ability to use its organs (traits) differently. Learning and behavior therefore have a direct impact on evolution, both within species and across larger temporal and taxonomic scales. For example, in the evolution of epigamic behavior, intricate loops form between the traits (e.g., bird songs or dances) subjected to sexual selection, their elaboration, and development, and the preferences for these traits, only to be abandoned later, in favor of different traits, e.g., during the emergence of a new species (see "Runaway Sexual Selection Model"). However, the Baldwin effect also plays a crucial role in the evolution of more mundane traits, like foraging methods.

Stability-Based Sorting

Stability-based sorting (SBS) is a general principle that, in biological evolution, emphasizes the stability of particular lineages, traits, and characteristics of organisms (see the chapter "Adaptation: Stability-Based Sorting"). In contrast to the widely recognized mechanism of natural selection, which is based on the differential survival and reproduction of entities exhibiting inheritance (organisms), SBS does not require entities to reproduce or show heredity. Instead, it champions the principle of persistence, advocating for the accumulation of traits and entities that are stable and can endure over time. Simply put, stable entities persist, whereas unstable ones either vanish or transform. This process is universally applicable to both material and immaterial entities, ensuring that any system with memory will ultimately accumulate entities that persist the longest.

Owing to their historical character, SBS operates within every biological system and across all timescales. Though selection can swiftly accumulate beneficial traits in the short term, it is SBS that determines the fate of traits, species, and clades in the long term. For instance, while the human brain, an "evolutionary marvel," has granted us major advantage in natural selection and unparalleled dominion over Earth, it has also driven us to create potentially self-destructive tools like weapons of mass destruction. Therefore, simpler and more persistent biological entities without any tendency to evolve more complex brains, such as tardigrades, might endure longer due to their intrinsic stability and ultimately "win" in the process of SBS.

The notion that stability is a determinant of survival dates back at least to Empedocles of Acragas, an ancient Greek philosopher. In his *Zoogony*, he theorized that Earth spontaneously generated various creatures through the random amalgamation of disembodied organs, but only those that were inherently stable – viable – managed to persist. This concept reemerged in the twentieth century (see Toman & Flegr, 2017b), while the idea of inequality between sorting and selection was revitalized in modern evolutionary theory by Elisabeth Vrba and Stephen J. Gould (1986). They posited that certain organismal characteristics might evolve not solely due to selection but through sorting. This perspective shift suggested that not every trait in an organism must offer a selective advantage; some may persist purely due to their stability.

SBS is instrumental in both macroevolution and microevolution. In the realm of microevolution, its potential primary importance lies in maintaining genetic polymorphism within populations. This is achieved by accumulating alleles with negative frequency-dependent fitness effects. These alleles are favored by selection when rare within the population but penalized when common, in a similar manner to, e.g., the beaks of red crossbills (*Loxia curvirostra*). These birds have two morphs with beak tips curving either to the left or right. These morphs differ in their ability to extract seeds from conifer cones, with the less common morph having more food available at any given time. Being the rarer morph thus provides a selective advantage, which helps maintain an equal frequency of both morphs over time. While alleles with frequency-dependent fitness effects might arise less frequently than those with constant fitness effects, they tend to accumulate over time in a population's gene pool. This dynamic has significant evolutionary consequences, as it enables sexual species in complex and fluctuating environments to adapt quickly and flexibly to transient conditions by simply shifting frequencies of various alleles already present in the gene pool. However, it also makes their irreversible changes more challenging, a notion encapsulated by the *theory of frozen plasticity* (see chapter "Adaptation: Postadaptations").

Selection has recently been suggested as a specific instance of SBS. In classical SBS, entities compete based on their static stability, i.e., slowest rates of expiration. In contrast, entities that originate from one another and express heredity undergo sorting based on dynamic stability, which can be described as the competition for the largest difference between producing copies of themselves and their expiration – natural selection (Toman & Flegr, 2017b).

Evolutionary Drives

Under the heading of evolutionary drives, we can summarize several semi-deterministic processes occurring at the level of genetic information carrier, namely, DNA or RNA, resulting from their physical and chemical properties (Alphey et al., 2020). The first example is a *mutational drive*. Mutations are random in terms of their impact on the phenotype, but not in terms of their location, molecular nature, or frequency of occurrence. The type of mutation and its position within the chain strongly depend on the specific nucleotide and the nucleotides that surround it. Various factors, such as whether it is located on the leading strand or the lagging strand during DNA replication, the frequency at which it is transcribed, its position within the nucleosome, epigenetic modifications, temperature, and other factors, also have a significant impact.

Considering that a significant portion of mutations arises during the repair of DNA, a separate *reparation drive* is typically distinguished. It differs from simple mutational pressure in the sense that reparatory mechanisms have evolved and fine-tuned through previous evolution. The frequency and types of mutations caused by DNA repair are thus partially subject to selection. Mutational and reparatory drives are responsible for certain large patterns within the genome. For example, methylated GC nucleotide pairs often mutate to GT because the deamination of methylated cytosine results in thymine. The subsequent step in such substitution is changing G to A. Therefore, in regions where a GT pair replaces GC, certain reparatory mechanisms preferentially substitute nucleotide T for nucleotide C, leading to a correct repair if the mutation was indeed a result of cytosine deamination. However, if the mutation occurred in the opposite strand with the incorrectly inserted

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nucleotide being G, the repair mechanism conserves the mutation. In regions where both substitutions occur with similar frequency, the reparatory drive enriches the strand with GC. The entire process likely reinforces itself, as GC-rich regions "breathe" less, meaning they are less likely to spontaneously transition to a single-stranded state, reducing the frequency of deaminations and increasing the frequency of "incorrect" repairs on GC. In contrast, regions with fewer GC pairs breathe more frequently, leading to more frequent substitutions of C for T and subsequently G for A. This positive feedback between lower GC representation and higher pair breathing frequency results in the creation of AT-enriched isochoric regions (Fryxell & Zuckerkandl, 2000).

Mutational and reparatory drives can also account for significant differences in the genome composition among different, often closely related, species. Another type of evolutionary drive is the *molecular drive*, through which repetitive, so-called selfish DNA spreads within a population. Typical examples of such genetic elements are alleles capable of overwriting their counterparts on the homologous chromosome during gene conversion, segments that propagate during the slippage of a nucleotide chain during replication, or through unequal crossing over. Particularly interesting category of these elements are *transposons*, which can "cut" themselves from the DNA strand in various ways and insert themselves elsewhere. This allows them to spread horizontally across different regions of the genome and even among different members of a species' gene pool. The importance of these elements in evolution is underscored by the fact that more than half of the human genome has its origins in them (Burns & Boeke, 2012). Extensive changes in the repetitive component of the genome can be highly dynamic and occur within just a few generations. The presence of elements spreading through molecular drives may not affect an individual's phenotype or can even reduce the fitness of their carriers, for example, by placing an excessive burden on the replication machinery. These elements essentially parasitize on the processes of replication and transcription. However, it would be a mistake to underestimate their evolutionary significance, whether in the creation of new genes, mechanisms of reproductive isolation, and thus origination of new species, or origination and evolution of bona fide genomic parasites like viruses.

A special category of evolutionary drives, encountered only in sexually reproducing species, is the *meiotic drive*. Through this process, elements spread that can bias the likelihood of ending up in the egg rather than the polar body to their advantage. In more extreme cases, alleles that spread through meiotic move can even harm cells carrying an alternative allele, reducing the fertility of their carriers. Entire sex chromosomes can also become the subject of meiotic drive, ultimately leading to chromosomal rearrangements and speciation.

Genetic Drift

Genetic drift is a term used to describe random shifts in allele frequencies within a population's gene pool (Masel, 2011). Unlike selection, where the probability of allele fixation is determined by its contribution to fitness, or drives in which the physical and chemical properties of a motif jointly determine the likelihood of spread or even the fixation of a given motif, drift represents a purely stochastic process. Given that only a small subset of the vast number of potential allele combinations is realized in each successive generation, allele frequencies will inevitably change due to the influence of pure chance. It is essential to keep in mind that allele frequencies in the next generation always depend on the frequencies of alleles in the current generation. The effect of chance therefore gradually amplifies. As a result, drift leads to the fixation and elimination of alleles even when they have minimal or no impact on the fitness of organisms.

The concept of genetic drift has become indispensable in explaining the fate of neutral and nearly neutral alleles. In a sufficiently large population – which includes virtually all populations we encounter in reality – neutral alleles will ultimately either become fixed or eliminated. The key parameters that determine the probability and duration of the fixation of a particular allele are its frequency in the population and the population size. Through the action of drift, there is an equal likelihood of increasing or decreasing the frequency of a given allele. An allele that occurs only once in the population, such as a new mutation, has only a 50% chance of being passed on to sexually produced offspring. Therefore, the genetic variants that occur at higher frequencies in the population have an advantage. In fact, the probability of fixing a neutral allele is equal to its representation in the population – a neutral allele A, present in a ratio of 9:1 compared to a similar allele B, fixes with a 90% probability. Population size then determines how long each neutral allele will remain in the population with a nonzero frequency. In larger populations, both the fixation and elimination of alleles take longer, which typically results in greater genetic polymorphism, meaning a greater diversity of alleles present.

However, the population size also influences which alleles with weak effects on fitness will still behave as neutral and which will be subject to natural selection. As the population size decreases, the relative effectiveness of selection diminishes, and the significance of chance, and thus the efficiency of drift, increases. Most new alleles are weakly deleterious, and in large populations, they are promptly removed by selection. Not that drift has no effect on the fate of selectionally significant alleles, but the influence of selection is relatively stronger. In small populations, the frequencies of such alleles are governed solely by chance, and they can even become fixed. As noted in *Muller's ratchet theory* (Muller, 1964), small populations are, for this reason, under constant pressure to accumulate slightly deleterious mutations, which can lead to the non-viability of individuals within a given species. A way out of this dead end can be a significant increase in population size (prokaryotes) or sexual reproduction, which renews variability in the number of harmful mutations among individuals in each generation. As a result, selection can eliminate individuals carrying a large number of mildly harmful mutations, thus reducing the average number of these mutations in the population (eukaryotes).

Genetic Draft

The concept of genetic draft emphasizes that each allele of every gene represents a physical segment on the DNA molecule of a given chromosome. Therefore, whether a specific allele becomes fixed or, conversely, is eliminated from the population is to some extent influenced by the alleles found in its immediate vicinity (Smith & Haigh, 1974). The elimination of most allelic variants in a specific genomic region, and in extreme cases, the fixation of a single allele, due to the presence of an allele – for example, a new mutation – with significantly positive fitness effects in this region, is referred to as a *selective sweep*. The continual removal of alleles due to the emergence of significantly harmful alleles in their vicinity is known as *background selection*. In both cases, the outcome of genetic draft is the disappearance of genetic polymorphism. It is generally assumed that the more significant influence on the loss of polymorphism, and thus the fixation of certain alleles, has the slower but universally acting background selection, rather than the faster process of selective sweep, which requires the occurrence of rare, highly advantageous mutations. However, selective sweep is more readily detectable.

In its extreme form, these phenomena are encountered in asexual prokaryotic organisms, where the genome, aside from the possibility of horizontal gene transfer, behaves as a single integrated unit. In the presence of antibiotics, lineages of resistant bacteria can outcompete all their rivals, even though their genome carries a range of suboptimal mutations. This is purely because antibiotic resistance represents the ultimate evolutionary trump card. In sexually reproducing organisms, the impact of draft is limited by the fact that during the formation of gametes by meiosis, crossing-over occurs, which recombines the genetic information acquired from both parents. However, the closer two DNA segments are, the less likely it is for crossing-over to occur between them. Therefore, draft also plays a significant role in sexual organisms, but it remains confined to the immediate vicinity of a significantly advantageous or disadvantageous allele. On top of that, genetic draft is of fundamental importance in sexual organisms wherever crossing-over does not occur, especially in organelle DNA and in non-recombining regions of sex chromosomes.

Gene Flow and Speciation

The last microevolutionary process we will mention is gene flow. We can describe it as the constant transfer of alleles between populations of the same or related species due to the movement of migrants or dispersal stages in otherwise sessile organisms. Although it is an ecological phenomenon, gene flow has a significant impact on evolution in both the short and long term – under certain circumstances, it can either accelerate or decelerate it. Theoretical analyses show that surprisingly small numbers of migrants over long distances are enough to make the behavior of a system with relatively isolated subpopulations resemble that of a connected system (Scott Mills & Allendorf, 1996).

The formation of migrants can be advantageous, even from a natural selection perspective. Offspring spread further away from their parents and relatives, reducing the likelihood of competition. However, the frequency at which different populations send out migrants depends even on other factors. A remarkable case of gene flow is the creation of persistent stages that can remain dormant for up to thousands of years, thus ensuring a kind of gene flow over time. This has several evolutionary consequences. Firstly, such adaptation increases the *effective population size* and, consequently, the efficiency of selection. From our perspective, the possibility of the repeated emergence of pathogenic infections, whether in livestock and crops or in humans, is of more concern. On top of that, the formation of persistent stages significantly modulates the selection regime of the species as a whole, allowing it to avoid unfavorable conditions ("sleep through it"), which makes its environment subjectively less variable and often leads to evolutionary stasis (Toman & Flegr, 2017a).

Gene flow in space also has significant evolutionary consequences. First and foremost, it is the main source of new alleles and, consequently, evolutionary innovations within individual populations. In this regard, it often far surpasses the possibilities of mutations. Due to the constant flow of alleles among subpopulations experiencing drift, living in different conditions, and imposing varying demands on their members, a greater genetic polymorphism can be maintained in the species' gene pool. These same processes also maintain species cohesion and, to some extent, prevent the species from evolving in many different, mutually contradictory directions. The cessation of gene flow, leading to genetic uniformity through drift and the isolation of a subpopulation from alleles in subpopulations living in different conditions, can, on the other hand, lead to its unidirectional differentiation and, consequently, the emergence of a new species (Flegr, 2013).

The emergence of a new species, known as *speciation*, is generally considered by most authors as the hypothetical boundary between microevolution and macroevolution. According to this concept, processes occurring below this level are referred to as microevolutionary, while those occurring at higher levels are labeled as macroevolutionary. Speciation has historically received significant attention and is therefore discussed in "Speciation" chapter. In this context, it is worth mentioning that the formation of a new species can be an abrupt event (such as through the erroneous doubling of chromosome numbers during the origin of gametes) or a very gradual process (resulting from the progressive strengthening of reproductive isolation barriers between populations from different regions). Similarly, the formation of a new species can occur in direct contact with members of the parental species or after various forms of geographic isolation. The variability of different aspects of speciation leads to the often blurry and protracted nature of the process. Potential new species in the early stages of speciation frequently interbreed with members of the parental species or other related lineages, forming species complexes that may also include secondarily asexual lineages. Human evolution is no exception; increasing evidence suggests that various representatives of the *Homo* genus (e.g., *Homo sapiens*, *Homo neanderthalensis*, and Denisovans) not only could interbreed but indeed did interbreed (Sankararaman et al., 2012). In many groups, the delineation of distinct species is, therefore, rather a matter of interpretation than simple issue.

Macroevolution

The term *macroevolution* was first used by Yuri Filipchenko (*1927*) to denote evolution beyond the species level, governed by distinct, non-Darwinian mechanisms. While the modern definition aligns with the first part of this definition, debates persist regarding its relationship with microevolution. Nonetheless, it is clear that microevolutionary mechanisms are not excluded by macroevolutionary ones and play a role even in larger temporal and taxonomic scales. The most significant macroevolutionary processes include the following.

Adaptive Radiations

Adaptive radiations represent a typical macroevolutionary phenomenon. They can be described as a sudden burst of speciations, potentially giving rise to new, fundamentally distinct, evolutionary lineages. From the study of paleontological records and DNA comparisons of living organisms, we know that such events have occurred throughout history and have sometimes significantly transformed life on Earth. The best-known example is probably the *Cambrian explosion*, during which bilaterally symmetrical marine animals rapidly achieved modern diversity in

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form, function, and species richness over a few million years, or even temporarily surpassed it. A comparable event has not recurred in the evolution of multicellular animals (Marshall, 2006).

Uneven rates of speciation can be attributed to several non-mutually exclusive factors. One factor involves changes in external conditions and the associated selective pressures. Another factor occurs when a species enters an entirely vacant *ecological niche*. This can happen due to expansion into previously unoccupied environments (e.g., newly formed islands or land during the Paleozoic era) or as a result of significant evolutionary innovations that greatly increase an organism's *ecological valence* (e.g., active predation of macroscopic organisms also during the Paleozoic era). Last but not least, ethological factors can contribute to a fast diversification. An excellent example of a species explosion is the repeated diversification of cichlid fishes in the East African rift lakes. Cichlids, upon invading these habitats, diversified into hundreds of different species due to the colonization of new environments, ecological specialization, and, notably, ethological mechanisms – specifically, mutual recognition of members of the same species based on their coloring and patterns on their body surfaces. The explosive radiation of species driven by ethological mechanisms, however, comes with certain drawbacks. In the case of cichlids, when lake water clarity significantly deteriorated due to eutrophication, many previously described and originally distinct cichlid species merged into one (Seehausen et al., 1997). As species and evolutionary lineages derived from them diversify and gradually occupy new niches, the potential for further diversification diminishes, eventually concluding an adaptive radiation. However, certain exceptional places, such as dynamically changing archipelagos, may continue to serve as ongoing speciation hotspots.

In addition to the *ecospace model of adaptive radiation* mentioned above, *genetic* or develop*mental explanations* are also considered. These hypotheses suggest that lineages gradually alter their *genetic architecture*, reducing the likelihood of producing major evolutionary innovations. At first glance, this concept may seem incompatible with the fact that all evolutionary lineages on Earth are of the same age. However, as described by the framework of the so-called evolution of evolvability, genetic architecture evolves toward optimal developmental robustness and the efficient reflection of the environment with its selective pressures. While this process may not necessarily reduce the potential for speciation, it likely ensures that increasingly robust phenotypic solutions which have been successfully tested under similar conditions in the past will be preferentially generated, decreasing the probability of major evolutionary novelties that could give rise to significant adaptive radiations. The "reset" of this process, characterized by relaxing genetic architecture interdependencies and reinstating variability in seemingly "frozen" traits, can only occur under specific circumstances. Such circumstances may lead to significant evolutionary innovations, radiations, and ultimately the origin of new genera and higher taxa as described by the *theory of frozen evolution* (see Toman & Flegr, 2018a, b).

Lastly, adaptive radiations can also be driven by adaptations that increase the probability of speciations or decrease the probability of extinctions. For example, the loss of wings in insects resulting in numerous isolated populations within a species often leads to a significant increase in speciation rates. Conversely, sexual reproduction reduces the risk of a species going extinct in variable conditions. Both of these adaptations may, in hindsight, appear to trigger radiations. However, from a global perspective, it seems that the majority of adaptations that enhance speciation rates also increase extinction rates and vice versa.

Species Selection

Species selection can be described as the competition for the greatest difference between speciation and extinction rates. This process is probably the most widely accepted macroevolutionary mechanism, and many authors even reduce macroevolution to this concept (Hautmann, 2020). A dedicated chapter in this encyclopedia is devoted to this subject "Evolution by Non-individual Selection Pressures".

At this point, let us emphasize that species selection is NOT a competition among species for ecological success, but solely the above-mentioned competition for the most frequent speciation and the rarest extinction events. Empirical research indicates that species selection is likely a significant phenomenon that can profoundly influence evolutionary processes on a large scale. As an example, consider the remarkable success of birds associated with their high species diversity, seemingly defying the limited isolation of bird populations. The key advantage for this group has been the combination of the ability to fly with high-level cognitive and behavioral capabilities. While the first adaptation significantly reduces the risk of extinctions, the second, involving learning, behavioral plasticity, and species discrimination based on subtle differences in appearance, song, or behavior, increases the rates of speciations. Flying pterosaurs with smaller and simpler brains, for instance, probably never achieved comparable diversity (Butler et al., 2009).

A higher rate of daughter species formation can also lead to a form of positive feedback further amplifying its advantages. It is more likely that a suddenly vacant niche (e.g., following the extinction of a specialized predator) will be opportunistically occupied by a lineage that frequently produces new species, rather than an even better-predisposed lineage that speciates only rarely. It is likely due to this effect that after the connection of the two Americas by the land bridge, the placental mammals from North America prevailed in South America, while only fragments of the South American marsupial fauna remained. Similar number of species of both faunas migrated in both directions. However, North American placentals speciated – and occupied temporarily vacant niches – at a high pace, whereas South American marsupials were much slower in this regard.

Extinctions

Very important but often overlooked are the large-scale evolutionary phenomena associated with extinctions (Raup, 1991). More than 99% of all species that have ever lived on Earth have gone extinct, and the same fate awaits all the species living today. While the success in natural selection can be described as "survival of the fittest," the perspective on extinction is rather "survival of the luckiest." Considering that environmental changes include conditions beyond the adaptability limits of a given species, the survival or extinction of individual species is ultimately determined by chance. It depends on the preadaptations (see the dedicated chapter "Adaptation: Preadaptations") generated under entirely different selection pressures and in different contexts that a species carries. For example, the mass extinction at the end of the Cretaceous period, around 65 million years ago, caused by the

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impact of an asteroid in the region of the modern Gulf of Mexico and supported by other catastrophic environmental changes, favored the survival of small opportunistic animals capable of seeking refuge in burrows or nests. Hence, mammals, modern birds, and lizards prevailed among terrestrial representatives, while large non-avian dinosaurs did not.

Extinctions can vary in intensity. Although a clear line cannot be drawn between different cases, it is still useful to distinguish *background extinctions* from *mass extinctions*. Background extinctions occur continuously, with their probability positively correlating with the specialization of a species and negatively with its population and range sizes. Hence, today's most endangered species are typically those on islands. Mass extinctions, on the other hand, are caused by catastrophic external or, more rarely, endogenous factors affecting the ecosystem. The most common causes of mass extinctions include the impacts of large cosmic bodies, large-scale effusive volcanism, significant changes in ocean and atmospheric chemistry, fluctuations in sea levels, and drastic temperature variations. It is worth noting that these factors are often interconnected and mutually reinforcing during critical periods. The ecological or, less commonly, taxonomic specificity may also be related to the causes of mass extinctions. The most prominent well-documented mass extinction event was the one at the Permian-Triassic boundary around 252 million years ago. This extinction event stands out both in severity and impact compared to other mass extinctions of the *big five*, which also encompass the end-Cretaceous mass extinction mentioned earlier.

Mass extinctions have significant consequences for macroevolution. Following these events, there are approximately 10 million years of recovery periods during which biodiversity gradually returns to its original levels. Faunas during these periods can sometimes be clearly distinguished from the normal state. Initially, these periods are dominated by widely distributed, generally smaller, and more generalist species (Button et al., 2018). Occasionally, *Lazarus species* of seemingly extinct taxa may appear in the fossil record, although they usually do not diversify to the restoration of the previous diversity and disparity of their respective taxa. This is likely due to only a small portion of each taxonomic group, the part that presumably went extinct, predominantly gives rise to new lineages.

Furthermore, mass extinctions lead to the *turnover of dynasties*, replacing one ecologically dominant group with another. Despite opportunistic filling of ecological niches mentioned above in the context of species selection, this allows organisms preadapted to their effective utilization to take over the respective positions. It appears that similar factors can also influence the composition of entire communities. Those that persist tend to be more stable and efficient, reflecting a decrease in extinction rates and increasing biodiversity over the last 550 million years (Newman & Sibani, 1999).

Mass extinctions can even reverse some evolutionary trends. Certain ecological indicators suggest that in the extinctions of species with large interconnected unstructured populations, parasites, especially multi-host viruses or pathogens with durable resting stages, may have played a crucial role. Adaptations that lead to such a state, such as sociality, advanced cognitive systems, and others, may prove disadvantageous in the long run. Therefore, lineages progressively evolving such traits may be removed in the process of stability-based sorting (see the dedicated chapter "Adaptation: Stability-Based Sorting").

Evolutionary Trends

We can generally define macroevolutionary trends as long-lasting, unidirectional changes in character traits or their groups, resulting in significant changes in these traits over time, and exceeding the lifespan of one species (McNamara, Despite some discussions about the definition of macroevolutionary trends, their actual existence, and classification, we can assert that many such trends have indeed manifested or are still manifesting in evolution.

Trends that are not mere statistical artifacts can essentially have two different sources, although they intricately overlap in real situations. The first possibility is the *wall effect*. If there is an impassable boundary, such as a minimum body size, random evolutionary changes will continuously shift the maximum away from this boundary. The result is a trend in the maximum. The second possibility is that a real force underlies the trend. For instance, a certain form of selection, an evolutionary drive, or the non-random generation of new variability imposed by *evolutionary constraints*, i.e., the genetic architecture of an evolutionary lineage (McShea, 1994). This can lead to trends in the mean value of traits.

Long-term directed selection pressures are described, for example, by the Dawkins-Krebs *concept of the arms races*, in which competitors, parasites and hosts, or predators with prey respond to each other's adaptations (Dawkins & Krebs, 1979). It remains an open question whether the runaway evolution of universally advantageous cognitive abilities throughout the history of life on Earth, akin to the concept of the *Dennettian Tower* (Dennett, 1995), might be a result of similar competition but on a more generalized level. On top of that, it is possible that certain evolutionary trends have been driven by species selection. For instance, if species characterized by larger body sizes speciate more frequently, the body size of members within the respective clade will increase over time.

Trends can also be divided based on their scope, into *local* and *global trends*. Local trends encompass a variety of well-supported and highly disputed taxonomically limited patterns. One well-supported example is the trend of repeated suture complexification in Paleozoic nautiloids. Another example, albeit somewhat disputed, is the increase in body size and brain size during the evolution of the *Homo* genus. Global trends that manifest in the evolution of life repeatedly among unrelated groups or are characteristic of life on Earth as a whole are even more intriguing. These global trends traditionally include rather vague notions of increasing fitness, body size, energy efficiency, diversity, or *disparity* (morphological and functional richness). Yet, we can also find more specific patterns such as the reduction in the number of body segments and their specialization or the increase in the performance of the central nervous system.

One of the significant global trends is undoubtedly the increase in *hierarchical complexity* of organisms, meaning the number of nested levels that make up their bodies. Reaching new levels repeatedly characterizes the evolution of eukaryotic organisms, especially. It has even been suggested that this is a trend driven on a large scale (Toman & Flegr, 2018a). This is because it could be a by-product of the evolution of evolvability, specifically the genetic architecture mentioned earlier, which enhances the efficiency of evolutionary responses to past challenges even at the expense of reducing the probability of significant innovations. However, excessive reduction of this *macroevolutionary potential* may lead to stagnation. Which leads us to the beginning – the best way to restore macroevolutionary potential could be the transition to a higher level of hierarchical organization, either through self-replication and coordinated regulation of the resulting conglomerate (as in the emergence of multicellularity) or through collaboration with unrelated partners (as in symbiotic relationships).

The question then arises, in the context of human evolution, whether evolutionary trends can lead to the development of excessive traits, i.e., traits that may reduce the fitness of their bearers. Many aspects of human behavior, such as extreme *altruism* toward unrelated individuals that goes as far as self-sacrifice or sacrificing one's own reproduction, can exhibit this characteristic. The persistence of such adaptations is problematic, if not impossible, in biological systems. Selfish individuals would quickly outcompete their more altruistic peers simply because they produce a much larger number of offspring. However, at least in the case of humans, a significant portion of evolutionary competition has shifted to the realm of *cultural evolution*. This cultural evolution can help populations overcome the individual selfish advantages mentioned earlier, and through complex social structures, achieve larger population sizes and ecological dominance.

Symbioses

While individualistic concepts emphasizing the role of individual or even *gene-level selection*, following the *theory of the selfish gene* (see the dedicated chapters "Selfish Alleles" and "Dawkins, Richard"), dominated the evolutionary explanations in the 1970s and 1980s, in recent decades, models of mutual, and often interspecific, cooperation have gained importance. Such symbiotic relationships ranging from *parasitism* on one end, through close interactions with unclear benefits, to mutually beneficial *mutualism*, permeate the evolution of life from its origins. It turns out that without understanding these essentially historical events, we have no chance of comprehending the history of life on Earth.

The pivotal figure associated with the resurgence of interest in symbiotic interactions was Lynn Margulis, who proposed the hypothesis about the origin of more complex, eukaryotic, cells by the fusion of simpler prokaryotic cells (Margulis, 1970). (We now know it involved the merger of an archaeal cell from the Asgard group with an alpha- proteobacterium, which gave origin to the *mitochondria*, see e.g., Donoghue et al., 2023.) Such *symbiogenetic events* also played a role in the emergence of green plants (with cyanobacteria as the ancestor of chloroplasts) and various eukaryotic algae. However, the current form of the biosphere was significantly influenced also by looser mycorrhizal collaborations between higher plants and fungi, reproductive symbiosis between flowering plants and insects, trophic symbioses of termites, hematophagous and sap-sucking insects, ruminants, and other mammals with single-celled eukaryotes and bacteria, and many other symbiotic interactions.

Even humans are more of a *holobiont* than solitary individuals, composed of a host and a long list of microbial symbionts. As demonstrated by the continually growing number of studies, gut symbionts facilitate digestion, support the production of essential nutrients, and communicate with the brain directly via secreted neurotransmitters, neural plexuses, and the nervus vagus (Cryan et al., 2019).

Another form of symbiosis is the phenomenon of *domestication* of livestock and crops by humans and certain insects. While domesticated species lose the ability to survive independently in the wild, the original independence is also weakened in the domesticator. The whole symbiotic complex becomes a new evolutionary unit.

The Relationship Between Microevolution and Macroevolution

In the introduction, we mentioned the complicated history of the terms microevolution and macroevolution, as well as the lack of consensus among different researchers in their understanding. Within the framework of the modern evolutionary synthesis, one often encounters the view that macroevolutionary events are exclusively the result of microevolutionary processes. According to this perspective, microevolutionary processes not only have an impact on long-term evolution but are also the only processes at play in macroevolution. Macroevolution becomes merely a label for the study of longer-term evolutionary phenomena (Dawkins, 1982). Other researchers believe that while interesting macroevolutionary phenomena exist, the mechanisms underlying them are largely identical to those in microevolution. This perspective leads to an ongoing debate about *emergence* and the nature of *emergent phenomena*, i.e., the question of whether we can fully reduce macroevolutionary phenomena to microevolutionary ones (Dietrich, 2010; Grantham, 2007).

The persistent adherence to this approach is probably also motivated by the fact that the division between microevolution and macroevolution is often exploited by creationists in their arguments. While microevolutionary processes can be observed, for example, in bacterial cultures, long-term evolutionary changes can only be inferred indirectly from species distributions, phylogenetic relationships among organisms, or paleontological findings. Creationist authors attempting evidence-based debates frequently argue that biological evolution is limited to small (and hardly deniable) microevolutionary changes within species (or *kinds*), while variation at and above the level of kinds – the subject of macroevolution – was created by some divine entity (Wood et al., 2003).

In contrast to the mainstream of evolutionary biology, certain authors have historically argued for the real existence of evolutionary processes operating above the level of the species, complementing microevolutionary processes. For example, Stephen J. Gould highlighted the existence of an entire hierarchy of evolutionary processes, some of which act over shorter, while others over longer time scales (Gould, 1980). George G. Simpson also discussed microevolution, macroevolution, and even megaevolution in a similar vein (Simpson, 1944). Beyond this, he considered *quantum evolution*, the idea that evolution does not always progress gradually, and that significantly different taxa can arise more rapidly. The processes accompanying such events do not contradict microevolutionary processes but require specific ecological, population, or genetic conditions. Unlike scientists from the turn of the nineteenth and twentieth centuries, he did not set microevolution against macroevolution but viewed them as complementary. Along the same line of thought, we can include the idea that macroevolution, as a process worthy of specific delineation, is synonymous with species selection (Hautmann, 2020).

Lastly, we can adopt a perspective that emphasizes the historical nature of evolutionary processes (Erwin, 2010).

From this viewpoint, microevolutionary processes are those that follow specific "rules of the game." In other words, they involve changes and their phenotypic expressions that adhere to established evolutionary constraints and do not alter the relationships within the *genotype-phenotype map*. In specific groups, they often manifest as somewhat canalized parallel emergence of similar variants – for example, cooperative breeding in marmosets and humans, if we stick to examples involving behavior. In contrast, macroevolutionary processes can be understood as those that directly or indirectly disrupt the existing order. They usually lead to the emergence of singular, *contingent* traits, such as linear chromosomes, chloroplasts, or clonal multicellularity, and result in a significant modification of the rules guiding the evolution of respective groups and, indirectly, often the rest of the biosphere. They can bring about substantial changes in the genetic architecture and, in extreme cases, give rise to entirely new *Darwinian systems*. In other words, they encompass *major evolutionary transitions*, such as the origin of eukaryotes, sex, individual development in multicellular organisms, and cultural evolution (Szathmáry, 2015).

Cross-References

- Adaptation: Postadaptations
- Adaptation: Preadaptations
- Adaptation: Stability-Based Sorting
- Algorithms, Natural Selection
- Alleles: Selfish
- Baldwin Effect
- Broad Sense Heritability
- Epigenetics
- Evo-Devo (Evolutionary-Developmental) Approach
- Mutations
- Phenotypic Plasticity
- Richard Dawkins
- Speciation
- Trait Heritability

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