Macroevolution

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Abstract

Macroevolution is the study of the patterns and processes associated with evolutionary change at and above the species level and includes investigations of both evolutionary tempo and mode. Tempo refers to the rate or pace of change, whereas mode refers to how that change occurs. Both the tempo and mode of macroevolution are difficult to predict based solely on the study of populations, organisms, and genes—the realm of microevolution. Important macroevolutionary discoveries include the observation that species rarely accrue net morphological change over their lifespan of millions of years, that episodes of mass extinction substantially modify the evolutionary trajectory of life on Earth, and that variation in rates of speciation, extinction and morphological change occurs over time, in different habitats, and across groups. The potential disconnect between microevolution and macroevolution suggests different processes may operate at different levels of biological organization, and at different spatial and temporal scales. Thus, macroevolution should be considered in concert with microevolution when determining the processes that have shaped the coevolution of Earth and life.

Keywords: Macroevolution, microevolution, tempo and mode of evolution, rate of speciation and extinction, mass extinctions

Introduction

Macroevolution is the study of *patterns* and *processes* associated with evolutionary change at and above the species level (i.e., species and clades). Two common examples of macroevolutionary change include the evolution of flowering plants or the transition of tetrapods onto land (see chapters “The Origin of Angiosperms” and “Evo-Devo of the Fin-to-Limb Transition”). Macroevolution is distinct from microevolution, which describes the patterns and processes associated with evolutionary change below the species level (e.g., among populations, individuals, and genes). An example of microevolutionary study would be genetic change between island populations of birds, or the appearance of genetic mutations. Although the definition by itself is not controversial amongst evolutionary biologists, the implications of macroevolution as “scaled up” from microevolution or, alternatively, “de-coupled” from microevolution has sparked heated debate for over 80 years (Futuyma 2015).

Evolutionary biology developed rapidly in the mid-20th century. For the first time, scientists provided mathematical models linking genes to morphologies and natural selection. This intellectual flowering resulted in the Modern Synthesis, a consensus amongst geneticists (such as Dobzhansky, Fisher, Haldane, and Wright), systematists (such as Mayr, Stebbins, and Rensch), and paleontologists (such as Simpson) that evolution was governed primarily by natural selection that caused changes in gene frequencies among populations. This process over geological timescales was assumed to explain sufficiently evolutionary patterns at all spatial and temporal scales – including those pertaining to higher taxa (Myers and Saupe 2013).

Breakthroughs in the 1970s, led by Eldredge and Gould (1972), Stanley (1979) and others, challenged this view of evolution. These researchers proposed that macroevolution was governed by different processes to those involved in microevolution, and that differences in spatial and temporal scales of evolution were real, significant, and worthy of study in their own right. Many proponents of this view consider microevolution as nested *within* macroevolution, with processes occurring at both scales having reverberating effects on the other, not unlike sloshing water wets higher and lower regions of a bucket (Gould 2002, Vrba 1980). While this debate continues (Futuyma 2015), several major advances in evolutionary theory have been uncovered using a macroevolutionary lens. These observations can be grouped broadly as pertaining to the *tempo* (or timeline) of evolution and the *mode* (or processes/mechanisms) of evolution.

Evolutionary *tempos* from a macroevolutionary perspective are long. For example, species are suspected of persisting an average of 1 – 5 million years (Myrs), and clades, composed of closely-related species that share a common ancestor, can persist for 20 Myrs or more. Consequently, macroevolution documents patterns of evolutionary change that occur on the timescale of thousands to millions of years (kyrs – Myrs). In a similar vein, macroevolutionary processes generating these patterns must also occur over extended time scales. For example, speciation in nature may occur over 5 – 40 kyrs or longer (Gould 2002). Investigations that have elucidated the *tempo* of evolution on macroevolutionary scales include: gradual versus punctuated evolutionary change, dynamic morphological stasis, community coordinated stasis, evolutionary radiations, and spatiotemporal patterns of biodiversity and disparity through time caused by variable rates of speciation, extinction and morphological change. These patterns are discussed in more depth in the “Tempo in Macroevolution” section below.

The *mode* of evolutionary change may also vary when viewed from a macroevolutionary versus microevolutionary lens. Natural selection characterizes well the morphological and genetic change observed within and between populations on a microevolutionary scale. However, it is unclear whether organismal-based natural selection is the dominant process that leads to species-level differentiation, or if selection occurs at multiple taxonomic levels (Stanley 1979, Gould 2002). Investigations that elucidate the *mode* of evolution on macroevolutionary scales include: selection at different hierarchical levels, the mechanisms of speciation, the effect of abiotic versus biotic factors in driving changes in diversity and disparity (see chapter “Morphological Disparity”), the causes of mass extinction events and their evolutionary and ecological effects, the factors responsible for evolutionary radiations, and the mechanisms driving the development of latitudinal diversity gradients (Saupe et al. 2019). These processes are discussed in more depth in the “Modes in Macroevolution” section below. In reality, the *tempo* and *mode* of evolution are linked, and it is often difficult to disentangle one from the other using current methodologies (Hunt 2012).

Tempo in Macroevolution

Researchers measure the *tempo* of evolution by characterizing rates of speciation, extinction and morphological change using both fossil and modern biological data.

Speciation and extinction rates

Global biodiversity is the result of both the production of new things (speciation) and the removal of existing things (extinction). These processes have been operating with varying rates since the origin of life and have been studied using fossil data covering life history over the last ~ 800 Myrs. Often, paleobiologists refer to the maxim that 99% of all species that have ever lived are now extinct. Thus, to gain an understanding of the patterns and processes governing *tempos* of speciation and extinction, a macroevolutionary perspective is required.

The rate of speciation is a measure of how many new species appear in an interval of time within a given taxon, habitat type, region or ecosystem. Although speciation may occur over years to kyrs, geologically speaking, speciation is observed as a discrete event in time, defined as the first occurrence of an organism from a given species (first appearance datum, FAD). However, the precise moment when a new species is produced is nebulous. There is no generally agreed upon definition for what constitutes 'sufficient' reproductive isolation in combination with genetic, morphological, ecological and behavioral differentiation to constitute two distinct species during the process of speciation. Speciation is also temporally challenging to define because it tends to occur over timescales for which empirical data are scarce. That is, if speciation occurs over 5 – 40 kyrs, this timeline is too long to be documented by modern empirical data but is often too short to be preserved in the fossil record; see Wiley and Lieberman (2011) for a review of species delimitation and speciation.

Extinction is no less muddled. The rate of extinction is a measure of how many species disappear in an interval of time within a given taxon, habitat type, region or ecosystem. Conceptually, extinction is the exact moment the very last individual of a species dies. However, extinction is also inescapable when, for example, the last male in a sexually reproducing population of females dies. There are also known population size limits that indicate destabilization and subsequent demise of a species, and thus extinction could also be counted when such a population size threshold is reached. The future extinction of species due to events in the past is commonly called "extinction debt" (Kuussaari et al. 2009). Like speciation, extinction occurs on a timeline that is difficult to directly study: biologists cannot search everywhere for the last remnant populations or individuals of declining species, just as the fossil record is unlikely to preserve those same few remaining individuals or populations. Thus, on geological timescales, extinction is operationally defined as the last occurrence of an organism from a given species (last appearance datum, LAD).

Speciation and extinction rates were traditionally calculated from paleobiological data and relied on FADs and LADs recorded in published compendia or online databases, such as the Paleobiology Database (www.paleodb.org/). Many equations have been proposed to quantify speciation and extinction rates from these count records. Most compute instantaneous rates and attempt to correct for incomplete knowledge of fossil occurrences (e.g., Alroy 2015). Time-calibrated molecular phylogenies are also used to provide information about speciation and extinction rates through time (e.g., Silvestro et al. 2018).

Estimating rates from phylogenetic information depends on a model of diversification; the simplest and most widely applied of these assumes a random speciation–extinction process. It should be noted, however, that it is difficult to disentangle diversification rates (speciation – extinction) from speciation and extinction rates individually. This can be particularly challenging using molecular phylogenies (see Pagel 2020). By quantifying how rates of speciation and extinction vary among taxa, across space, and through time, researchers formulate hypotheses of the processes and factors that initiate evolutionary change (see "Modes in Macroevolution" section).

The tempo of speciation

Investigations into speciation tempos have focused on whether rates have remained constant through time and space and whether they have varied within and among lineages. Fossil data provide evidence for periods of elevated speciation that have punctuated geological history. At the largest scales, there appear to be periods in the geological past when rates of evolution were particularly high; for example, during the Cambrian radiation when all phyla amenable to fossilization (except Bryozoa) first appeared within a 10 – 15 Myr interval (Erwin et al. 2011). Similar periods of rapid diversification have occurred since, such as after mass extinctions or after the origin of major evolutionary innovations (Jablonski 2017, Bambach 2006).

The causal factors (*modes*) behind these periods of elevated origination are debated. For example, traditional arguments for post-extinction radiations invoke ecological release and diversification spurred by the emptying of many niches at once—the classic supporting example being the radiation of mammals after the extinction of the non-avian dinosaurs. Based on this observation, palaeontologist and Modern Synthesis scientist G. G. Simpson popularized the term *adaptive radiation*, referring to rapid diversification accompanied by morphological and ecological change. A more agnostic term used to describe rapid diversification when the role of adaption is uncertain is *evolutionary radiation* (Lieberman 2012). Often, it can be difficult to determine whether a specific trait of an organism or group is produced by adaptive selection, or instead is a by-product of the evolution of some other characteristic. This would include both *exaptive* traits (those evolved for a different use than their current one) and traits produced by structural constraints (Myers and Saupe 2013; see also chapters "Developmental Exaptation" and "A Macroevolutionary Perspective on Developemental Constraints").

Elevated rates of speciation can also be associated with evolutionary innovation. In this case, innovation allows for occupation of new environments and the creation of new ecospace, particularly those involved in embryonic development, which can promote speciation (Jablonski 2017; see also chapter "Developmental Innovation and Phenotypic Novelty"). For example, Antarctic notothenioid fishes have evolved an antifreeze protein in their blood. The origination of this novel protein allowed the group to speciate into many of the open niches in the Antarctic region; hence, they are dominant members of these polar ecosystems. This innovation, however, was not tied to ecological opportunity, because it occurred *before* the onset of polar conditions in the Southern Ocean (Daane et al. 2019).

Of course, any discussion of elevated speciation rates assumes there exists some standard or average background rate from which to compare. While there is evidence for spikes in speciation during certain times in Earth history, debate exists as to whether speciation rates are relatively constant outside of these intervals or instead exhibit broad-scale secular trends over geological time (e.g., Alroy 2008). The constancy of speciation rates or lack thereof has implications for distinguishing among competing macroevolutionary hypotheses, including those supporting a role for biotic (intrinsic) mechanisms of evolutionary change versus abiotic (extrinsic) mechanisms (Myers and Saupe 2013). Global and/or within clade diversity dependence is one biotic hypothesis that supports competition and predation as significant controls on speciation and extinction rates—and therefore biodiversity levels. Diversity dependence describes the potential pattern of asymptotic diversity change through time. Diversity in this model is thought to reach a cap due to biotic pressures such as ecosystem filling. That is, once an ecosystem is "full" of species, competition for resources, predation pressure, and lack of open niche space prevent the addition of new species (e.g., Rabosky 2013). Alternatively, others ascribe a larger influence of abiotic mechanisms on diversification, such as temperature dependence or geography facilitating speciation and extinction rates, and do not think sufficient evidence exists for asymptotic diversity change (e.g., Condamine et al. 2019).

Variation in speciation rates over time may not be surprising given the diversity of life on the planet. However, speciation rates also vary within clades of closely related species, where one might predict they would be more generalizable. These variations seem to be dependent on time, geography, climate, and life-history strategies. Differential rates of speciation in groups living in tropical versus temperate regions has been invoked to explain the classic conundrum of *latitudinal diversity gradients*, in which the number of species increases from the poles to the tropics (Saupe et al. 2019).

One of the central goals of macroevolutionary studies is to quantify how speciation rates vary within and among lineages, and to understand the drivers responsible for rate variations at both levels. Do speciation rates decline throughout the history of a single clade? Are certain clades more apt to undergo evolutionary radiations than others? What is the contribution of intrinsic species characteristics (e.g., breeding behavior, developmental bias, dispersal ability) versus extrinsic factors (e.g., climate, geography)? These are all questions that may be tackled with data spanning long temporal intervals— the realm of macroevolutionary *tempo*.

The tempo of extinction

Quantifying extinction rates is equally important to macroevolutionary studies of *tempo* and discerning the dynamics of diversification. Like speciation, rates of extinction have not been constant throughout Earth history. One of the most important contributions of macroevolution is the identification and interrogation of two major scales of extinction: those that occur semi-continuously with mild-to-moderate intensity, described as *background extinction*, and those that occur periodically and with extreme intensity, known as *mass extinctions* (Table 1).

Distinctions between background and mass extinctions were first noted in the mid-1800s by John Phillips, but not quantified until the 1960s by Norman Newell and Otto Schindewolf. In the early 1980s, David Raup in collaboration with Jack Sepkoski identified patterns in both background and mass extinctions – including the observation of a secular decline in background extinction magnitude through time (Raup and Sepkoski 1982). This observation is an area of considerable interest in macroevolutionary science, with researchers debating what evolutionary processes (*mode*) may cause this phenomenon, and whether it is a real signal or artifact of fossil preservation and sampling biases (see Alroy 2008).

Patterns of background extinction were used to formulate one of the more contentious ideas in macroevolution – the *Red Queen Hypothesis*. Using an impressive compilation of diversity data, Van Valen (1973) examined taxon diversity compared to taxon duration across all major clades in the Phanerozoic. He found that paleo-survivorship curves were commonly linear, which indicates the probability of extinction is constant with respect to taxon age (duration) and that extinction probability may be decoupled from taxon duration. Van Valen interpreted this pattern to infer evolutionary *mode*, suggesting that species' extinction must be related to constantly changing biotic pressures, such that taxa must continually adapt to keep pace with ever better adapted competing organisms, just as the Red Queen in *Alice in Wonderland* told Alice she must always be running just to stay in place. In contrast, the Court Jester hypothesis (Barnosky 2001) suggests abiotic forcers, such as climate, are the major cause of species' extinction (more on this in "Modes of Extinction" below).

Sepkoski (1986) provided the first working definition of a mass extinction, which is still in use today: "any substantial increase in the amount of extinction (i.e., lineage termination) suffered by more than one geographically widespread higher taxon during a relatively short interval of geologic time, resulting in an at least temporary decline in their standing diversity". This definition is necessarily ambiguous in its description of intensity and rate (*tempo*), which largely reflects the difficulties in generalizing among conditions surrounding known mass extinction events. Operationally, mass extinctions are recognized by greater than ~ 75% extinction of species over an interval of ~ 2 Myrs or less. Mass extinction events also affect species globally, and the ecological and evolutionary recovery from them takes millions of years (Erwin 2001). These operational criteria reflect substantial research into the five largest mass extinction events recognized in the Phanerozoic, collectively termed the "Big 5": end-Ordovician, late Devonian, end-Permian, end-Triassic, and end-Cretaceous (Harnik et al. 2012, McGhee Jr et al. 2013) (Table 1).

Because their extinction rate is very high, mass extinctions substantially modified the evolutionary trajectories of life on Earth, often upsetting patterns and processes that had persisted for hundreds of millions of years. These sweeping evolutionary changes often cannot be predicted from the study of microevolutionary processes alone. Predicting which species survive or succumb to mass extinctions is difficult. In the famous example, the Cretaceous-Paleogene Mass Extinction ended the reign of non-avian dinosaurs—the prevailing large land animals for over 150 Myrs—and led to the rise of mammals that dominate today. Mass extinctions not only have large effects on the composition of species and clades present on Earth, but they also have enormous ecological influence, re-organizing communities and ecosystems (Table 1) (Erwin 2001, McGhee Jr et al. 2013). Although mass extinctions are both devastating and alluring, it is important to acknowledge that background extinction has been the predominant type of extinction observable in the 544 Myr history of life and occurs at a rate of about 5 – 15% of species per million years (Raup and Sepkoski 1982).

As with speciation, the study of macroevolution can compare and contrast the evolutionary effects of extinction events by delineating trends in extinction rates through time. This may include potential decline in the global background extinction rate, cycles in rates of extinction, and instances when speciation and extinction rates may be decoupled. Although speciation and extinction represent independent processes, study of their rates through time show they are often correlated positively (Alroy 2008). That is, periods of rapid speciation also tend to include high rates of extinction. The coupling of speciation and extinction has been invoked as evidence for the influence of biotic interactions in driving diversification dynamics: species need to die for new species to proliferate, implying a role for competition and the existence of ecosystem and global biosphere carrying capacities. However, the coupling of speciation and extinction rates could also reflect abiotic change as drivers of diversification: perturbations to the Earth system that cause widespread extinction may simultaneously create opportunities for population isolation, facilitating allopatric speciation (e.g., Vrba 1993, Myers and Saupe 2013 and references therein).

Morphological change

In addition to rates of speciation and extinction, the study of macroevolution can reveal the rate of morphological change both within and across lineages. Morphological evolution is usually studied by quantifying aspects of a species' phenotype, or what it looks like. Study of phenotypic traits usually occurs in one-dimensional (traditional morphometric descriptors) or multi-dimensional (geometric morphometric descriptors) continuous trait space (see chapter "Morphometrics in Evolutionary Developmental Biology"). Discrete character descriptors, however, such as the presence or absence of a trait, can also be studied. Such morphological traits can then be plotted against time or onto a phylogeny to measure rates of change and to test competing models of evolution (*mode*; see chapter "Morphological Disparity").

A significant ongoing debate in macroevolution is whether rates of morphological changes are predominately higher during speciation events compared to within the lifetime of a species. The theory of punctuated equilibrium by Eldredge and Gould (1972) demonstrated that species in the fossil record tended to exhibit long periods of morphological stasis *punctuated* by temporally-short bursts of substantial morphological change (Fig. 1). "Dynamic stasis," as this has since been dubbed, describes the hypothesis that natural selection continuously produces morphological change within populations of a species. However, the net sum of that change across the lifetime of the species is essentially zero (see Eldredge et al. (2005) for a detailed summary). For example, Rosemary and Peter Grant have spent decades studying morphological and ecological changes in Galapagos Finches (e.g., Grant and Grant 2011) – their work is an excellent example of a long-term, high resolution microevolutionary analysis. These birds show measurable morphological change in beak width through time that is linked to differences in food availability during wet and dry climate cycles. During wet periods, a larger variety of softer seeds are available and beak width tends to thin. In contrast, during dry periods, only hard, robust seeds are available to eat, and beak width tends to thicken. These data demonstrate a rollercoaster of morphological change: thin beaks → thick beaks → thin beaks → thick beaks, which summed across the lifetime of the study (40+ yrs) do not support net morphological change in a single direction (thin or thick).

The observation that species undergo no directional morphological change during their lifetime contrasts with the theory of *phyletic gradualism* (originally described, but not named, by Charles Darwin in *The Origin of Species*). Phyletic gradualism posits that morphological change is a slow, uniform, and gradual process occurring continuously during the lifetime of a species. Notably, examples of both punctuated equilibrium and phyletic gradualism have been identified. Thus, the important question is not whether rapid or gradual morphological change is true, but what is the relative frequency of each *tempo* throughout biological history. Compounding evidence from both fossil and genetic data over the past 50 years provides more support for the punctuational model (Fig. 1) (Gould 2002, Eldredge et al. 2005). These data lend directly to hypotheses of speciation *mode*, addressed below.

Morphological stasis observed across a suite of species in the same community is called *coordinated stasis*. Coordinated stasis is a pattern wherein groups of coexisting lineages display concurrent stability over extended intervals of geologic time separated by episodes of relatively abrupt *turnover* (the coordinated extinction or local extirpation of several species or clades that are then replaced by newly originating or immigrating groups) (Brett et al. 1996).

Rates of morphological change are likely tied intimately to rates of speciation and extinction. Just as with speciation and extinction, the rate at which morphological changes accrue is likely variable through time and across species, clades, and habitat. An important question in macroevolutionary studies of morphological change is the frequency of trait change to explain the diversity we observe in modern groups. For example, crown birds are an exceptionally diverse group that evolved < 75 million years ago. The clade includes species that are very large and small, herbivores and carnivores, polar and tropical, volant and nonvolant. Did birds evolve their range of traits early and rapidly in their evolutionary history, or did they accrue these traits slowly as they diversified in the Cenozoic? This question explores the link between the accumulation of morphological diversity, i.e., disparity, and taxonomic diversity, which are often decoupled (Fig. 2) (see chapter "Morphological Disparity").

Additional questions pertaining to the *tempo* of morphological change include whether traits evolve faster when a species or clade is younger or older? Do the same traits evolve at different rates within different evolutionary lineages? Some groups, for example, seem to be characterized by particularly slow rates of evolutionary change, sometimes referred to as 'living fossils.' Living fossils were first recognized by Darwin and can refer to clades with either low rates of morphological change and/or low rates of speciation for much of their evolutionary history (Stanley 1979): classic examples include the coelacanth, horseshoe crab, and ginkgo tree. Why some clades appear more or less *evolvable* – that is, capable of morphological and ecological change – is another important area of macroevolutionary study (see chapter "Evolvability"). Quantifying the *tempo* at which traits evolve within a lineage and throughout life history can inform on underlying evolutionary processes of mode.

The Modes of Macroevolution

The modes of macroevolution – that is, the mechanisms that spur speciation, extinction, and morphological and genetic change – are another important research arena that benefits from a macroevolutionary perspective. Researchers focus on the spatial and temporal scales across which these changes occur and try to disentangle biological or environmental factors that act to initiate, prohibit, or modify the magnitude and rate of these patterns.

Two overarching categories of factors responsible for driving evolutionary change have been proposed. *Extrinsic* factors include abiotic variables such as changes in temperature or precipitation, mountain building, tectonic plate movement, formation and migration of rivers, etc. *Intrinsic* factors pertain to biological phenomena such as the appearance of evolutionary novelties governed by changes in evolutionary development (see chapter “Developmental Innovation and Phenotypic Novelty”), response to predation or competitive pressures, and modification in food location, quantity or type, etc. Most often, intrinsic (or biotic) factors affect the genetic make-up of individuals, organisms, or populations. These processes tend to occur on geologically short timescales (yrs–kyrs), which places them in the realm of microevolutionary change (Myers and Saupe 2013). There are some important exceptions, for example, the evolution of predation in the Proterozoic fundamentally altered the evolution of eukaryotes, and the ecological dominance of predation in Cambrian ecosystems likely contributed to the radiation of shelly invertebrates (e.g., arthropods and mollusks; Erwin et al. (2011)). However, while these examples are notable, they are also infrequent; most intrinsic evolutionary change seems rooted in microevolutionary processes, such as natural selection, evo-devo factors, or possibly gene selection.

Extrinsic factors, on the other hand, have been demonstrated to substantially affect macroevolution. This may include more common, cyclical or continuous drivers, such as the movement of tectonic plates, climate changes, and sea level fluctuations. These types of drivers have often been related to background levels of speciation and extinction. They have also been shown to produce synchronous macroevolutionary change across lineages, for example in the climate-related turnover of fossil African bovids that formed the basis of Elizabeth Vrba’s Turnover Pulse Theory (1993). However, some extrinsic factors may result in major environmental perturbations that dramatically change the Earth system for thousands-to-millions of years. Factors such as large asteroid impacts or large igneous provinces (LIPs) tend to be infrequent and difficult to predict, but the macroevolutionary consequences of these types of events are profound (Table 1). Unanswered questions in macroevolutionary *mode* include: whether extinction triggers yield predictable kill mechanisms that can be extrapolated through time, what mechanisms act to couple or decouple speciation and extinction rates, what causes long periods of relative stability in Phanerozoic biodiversity, what factors initiated the explosion of diversity and disparity at the start of the Cambrian period, and what factors instigate large-scale morphological changes and/or evolutionary novelties.

Modes of Speciation

Historical thinking on *modes* of speciation can be traced back to pre-evolutionary scholars such as Carl Linneaus, Louis Agassiz, and William Paley’s Natural Theology. Secular views of speciation and the definition of evolution as *descent with modification* did not arise until Charles Darwin and Alfred Russel Wallace’s theories of evolution by natural selection. *Natural selection* is a microevolutionary process – or mode – that operates on individual organisms to remove unfavorable traits from a population (and thus species). Notably, neither Darwin nor Wallace were explicit regarding the mode of producing new species under their theory of evolution. Implicit in their theory was that gradual and continuous change in organism-level traits within populations by natural selection at some time reached a tipping point and produced a definable new species.

Speciation in this *mode* reflects a steady transformation of one species into a new one through a process called *anagenesis*. This is the process by which *phyletic gradualism* transpires. Anagenesis contrasts with the mode of speciation discussed above under the model of *punctuated equilibrium* (Eldredge and Gould 1972, Gould 2002). Under this model, speciation is discrete and rapid, and better described as the "splitting" of lineages vs. gradual transformation. This process is called *cladogenesis* (Fig. 1).

The difference between cladogenetic and anagenetic evolutionary change is linked in part to the processes (*modes*) hypothesized to produce new species. These were codified in the middle 20th century through the research of Modern Synthesis scientists. In particular, ornithologist Ernst Mayr defined two types of speciation: sympatry and allopatry. *Sympatric speciation* occurs when a lineage diverges within a single geographic area. That is, an ancestral species splits into one or more daughter species without the aid of significant geographic isolation. In contrast, *allopatric speciation* occurs when a population becomes geographically separated from the rest of its lineage, and divergence ensues in isolation (likely facilitated by different microevolutionary processes, including selection, micro evo-devo processes, and/or genetic drift). The differences between these two *modes* of speciation are important because each provides specific predictions regarding the factors that might contribute to lineage divergence. For example, in sympatric speciation, all populations within the species experience similar environmental conditions, and thus speciation is likely driven by intrinsic factors such as changes in feeding, mating, or other behaviors in response to competitive pressure, predator avoidance, or resource limitation.

In contrast, during allopatric speciation, the isolated population may experience very different extrinsic environmental conditions (e.g., if blown and isolated at a new location) in addition to potential pressures from intrinsic factors. Studying the process of speciation itself bridges microevolution and macroevolution, since populations (micro-scale) eventually form new species (macro-scale). However, as noted previously, the timescale over which speciation occurs (5 – 40 kyrs) makes studying the *modes* of speciation particularly difficult from either a micro- or macro-evolutionary perspective.

Whether speciation occurs in sympatry or allopatry is only one important piece of the macroevolution puzzle. Another important piece is how the "modification" in *descent with modification* is produced. The traditional microevolutionary view aligns with Darwin's hypothesis of natural selection. However, evolutionary change has been proposed to occur explicitly at the macroevolutionary level (implying the existence of unique macroevolutionary *modes*). Selection, for example, may not only work on organisms and their genes, but may also operate on species-level traits (Stanley 1979, Gould 2002, Jablonski 2008b). Under this contentious hypothesis, selection acts directly on species-level traits to produce new species or preferentially remove existing species. As with natural selection, this process would have reverberating effects on populations, individuals, and their genes. Similarly, selection at the species level would have an upward influence on the types of species comprising a clade. The effects of selection on one level will 'sort' the types of traits preserved at both higher and lower levels. Sorting differs from selection in that the *process* responsible for evolutionary change at the focal level transpired at a lower or higher level. An example of sorting at the genetic level would be observed changes in gene frequencies caused by the process of natural selection on organisms.

These ideas, termed the Effect Hypothesis by Elizabeth Vrba (1980), imbue a strict definition of how selection might operate. The Effect Hypothesis limits selection on species, or any other level, to "emergent" traits– that is, those traits that arise from the combined organization and structure of lower levels (i.e., populations, individuals and their genes). Traits that represent "aggregates" of these lower levels could not represent species selection, because any selection on these traits would reflect natural selection operating on individuals or populations, not selection at the species level (Gould 2002). An example of an aggregate trait would be plumage colour or number of digits on a limb. All Scarlet Macaws have red plumage, but one would not say that red plumage is caused by the organization of all populations and individuals defined as Scarlet Macaws. True emergent species level traits are difficult to define; some suggested examples include species mate recognition systems, geographic range size, population structure, or evolvability (e.g., Jablonski 2008b). For this reason, some researchers have argued that emergent traits are not necessary to delineate species selection, but effects on emergent fitness are, whereas others suggest selection does not occur at levels higher than the population and indeed that there are no unique *modes* of macroevolution distinct from those of microevolution (Futuyma 2015).

Modes of Extinction

Extinction has a dramatic effect on macroevolution via the process of sorting genetic, morphological, and behavioral traits in individuals, populations, species, and clades. Surprisingly, unlike the swirl of ideas surrounding evolutionary change, it was not until the research of Georges Cuvier, a French naturalist and the 'Father of Paleontology', that extinction was established as a legitimate concept in science. As mentioned above, extinction may transpire as *background extinction* or *mass extinction*, and these occur on different timescales with different intensities and causes (Table 1) (Bond and Grasby 2017, Jablonski 2008a, Harnik et al. 2012).

Extinction is rarely random across geological timescales, and certain traits may confer a higher or lower chance of survival. For example, species may be at higher risk for extinction during background times based on organismal traits such as poor dispersal ability or large body size, population level traits such as low population density, or potential species level traits such as small geographic range size or narrow environmental niche. These observations demonstrate *ecological* or *extinction selectivity,* but they are not (by themselves) indications of species- or clade-level selection (i.e., a macroevolutionary versus microevolutionary mode). Notably, studies comparing background and mass extinctions have demonstrated that patterns of ecological selectivity may differ in each regime (Jablonski 2008a).

Extinction *modes* associated with background and mass extinctions likely relate to both extrinsic environmental and intrinsic biological factors. Examples of extrinsic factors that have been linked to species' extinction include rapid climate modification, tectonic changes, volcanism and other natural disasters that affect habitat size, food supply and physiological functioning (Myers and Saupe 2013). Milankovitch cycles (changes in the Earth's tilt, wobble and orbit around the Sun) are one example of periodic (kyrs) climate change that is responsible for background extinction.

In addition to extrinsic factors, intrinsic, biotic factors may also contribute to background extinctions. Developmental constraints may limit species' evolvability and thus their chance of survival. Disease, predation, and competition may also affect habitat, food, and physiology, leading to the deaths of individuals, populations, and potentially species. A classic example is when macro-predation evolved in the Cambrian (541 Ma). During this period, large-bodied predators appeared in the fossil record coincident with macro-invertebrates developing hard shells (mollusks) and exoskeletons (arthropods). One hypothesis explaining these congruent patterns is that predators selectively extinguished prey that did not have predator-defense mechanisms in the form of hard body coverings (Erwin et al. 2011). This is observed again nearly 400 Myrs later, termed the Mesozoic Marine Revolution (Vermeij 1977), where marine predators developed enhanced morphological tools for crushing or dissolving shells. This was matched by prey developing thicker shells with deterring ornaments (e.g., large spikes), suggesting that prey without these traits were selectively eaten.

These examples are infrequent in the history of life but do demonstrate that predation pressure can be a significant biotic factor shaping patterns of extinction and evolutionary change. Other biotic factors that may influence background extinction are more nebulous in their macroevolutionary effect. These include factors such as competitive exclusion and disease. The former is still debated as a macroevolutionary (vs. microevolutionary) process (e.g., see Sepkoski Jr (1996) in the affirmative and Benton (1996) in the negative). Unfortunately, disease does not typically leave a fossil record and thus is mostly untenable for study across the large-scale history of life.

Mass extinction *modes* are debated, but the major hypotheses that match geological and fossil record observations relate exclusively to extrinsic environmental perturbations. In particular, mass extinctions seem to have substantial and irreversible effects on macroevolution when they are selective. For example, the mass extinction at the Triassic-Jurassic boundary (~ 201 Ma) wiped out reef dwellers in higher proportions than other marine species (Kiessling et al. 2007). This fundamentally altered shallow ocean ecosystems for 10s of Myrs of years, and survivors of this crisis determined the trajectory of reef evolution from that point forward.

The degree and specifics of mass extinction selectivity is determined by the events *triggering* the mass extinction, which set off a cascade of environmental and ecosystem changes – *kill mechanisms* – that directly impacted the survival of individual organisms, populations, species, and clades (Table 1). For example, the end-Permian mass extinction is thought be *triggered* by massive volcanic eruptions in Siberia. However, volcanism directly extinguished only those species that lived in Siberia. Global extinctions were instead caused by the *kill mechanisms* of climate change (warming), ocean acidification, and ocean anoxia caused by injection of volcanic gases (mainly carbon-based) into the atmosphere and oceans.

Thus, mass extinction *triggers* can be defined as things that initiate the conditions leading to elevated global extinction. Common triggers in the Phanerozoic are events such as large asteroid impacts or the emplacement of Large Igneous Provinces (LIPs; Bond and Grasby 2017). In contrast, *kill mechanisms* are defined as factors directly causing the deaths of organisms. Using the Phanerozoic fossil record as a case study, four major kill mechanisms have been identified: (1) climate change (especially warming), (2) ocean acidification, (3) ocean anoxia, (4) habitat change (including loss, fragmentation, and degradation of habitat at local and regional scales, and continental configuration at global scales). Importantly, different triggers may initiate the same or multiple kill mechanisms; for example, LIPs often cause climate change, ocean acidification, and ocean anoxia, as observed during the end-Permian mass extinction.

Modes of Morphological Change

Patterns of morphological change can be observed on macroevolutionary timescales and the *tempo* quantified. However, discerning the *mode* of morphological change is difficult for macroevolutionary studies. This is because morphological change ultimately derives from changes in the genetic makeup and developmental program of individuals, the purview of microevolution. That said, advances in evo-devo are elucidating the scales at which processes responsible for morphological change are observed in animals and plants. Moreover, macroevolutionary study of the fossil record may reveal large-scale drivers of morphological change and innovation and how morphology has been constrained (or not) over time.

Concluding Remarks

In this chapter, we defined macroevolution as the study of patterns and processes at and above the species level. Macroevolutionary investigations have revealed that microevolutionary processes do not sufficiently explain patterns observed at the species level (and higher) on long time spans and broad spatial scales. For example, the observation that dynamic morphological stasis is observed commonly in fossil species is incongruent with the many morphological changes observed among individuals in populations on microevolutionary timescales. The identification of dynamic stasis requires observations at the species level over long timescales and suggests that morphological change accrues at speciation events rapidly. This pattern of *punctuated equilibrium* was one of the first contributions of macroevolution to evolutionary theory.

This chapter focused on punctuated equilibrium and other unique macroevolutionary *patterns* that have been identified and contribute to a unified evolutionary theory. Some of these patterns include hierarchical structures of evolutionary change (e.g., multi-level selection theory and the process of sorting) and the identification of mass extinctions and their long-term ecological and evolutionary effects on life. This example also illustrates that the *tempo* of evolutionary change is non-constant. Macroevolutionary studies on long timescales show that rates of speciation, extinction, and morphological change vary across clades, among habitats, and through time. This observation is a fundamental contribution of macroevolution to our understanding of evolutionary theory.

In contrast to macroevolutionary patterns, many proposed macroevolutionary *processes* are still debated. This is a common phenomenon given that patterns are based on empirical observations, whereas processes are hypothesized explanations for what generated those patterns. Science is based on a method of rejecting hypotheses unsupported by data, thus identifying the “right” answer (vs. rejecting the “wrong” answer) is difficult and often contentious. However, by studying variations in evolutionary *tempo*, we can begin to slowly untangle evolutionary *mode* to glean the full picture of how life evolves on Earth.

There are many remaining puzzles in macroevolution, which makes the field an exciting one to study. Some of the most interesting questions are: the relative role of intrinsic versus extrinsic factors in directing evolutionary trajectories, including production of evolutionary novelties as linked to evo-devo; the degree to which speciation and extinction rates are coupled; if there are limits or carrying capacities to biodiversity and how they have changed through time; whether evolutionary and ecological rules have transformed throughout Earth history; and the degree to which disparity and diversity are coupled.

Cross-References:
A Macroevolutionary Perspective on Developmental Constraints in Animals
Developmental Innovation and Phenotypic Novelty
Developmental Exaptation
Evo-Devo of the Fin-to-Limb Transition
Evolvability
Levels of Organization in Evo-Devo
Stephen Jay Gould (1941-2002)
Evolution of Complexity
Coevolution and Macroevolution
Micro Evo-Devo
Morphological Disparity
Morphometrics in Evolutionary Developmental Biology
The Origin of Angiosperms

Figure and Table Captions

Figure 1. In phyletic gradualism, morphological change occurs continuously over time, leading to divergence among populations and eventually speciation. In punctuated equilibrium, species exhibit relative net stability in morphological traits during their lifetime, with morphological change occurring rapidly at splitting (speciation) events. Both branching diagrams illustrate hypothesized relationships among species and are referred to as *phylogenies*. Compounding evidence from fossil and genetic data over the past 50 years supports dynamic stasis within lineages, punctuated by rapid morphological change at speciation.

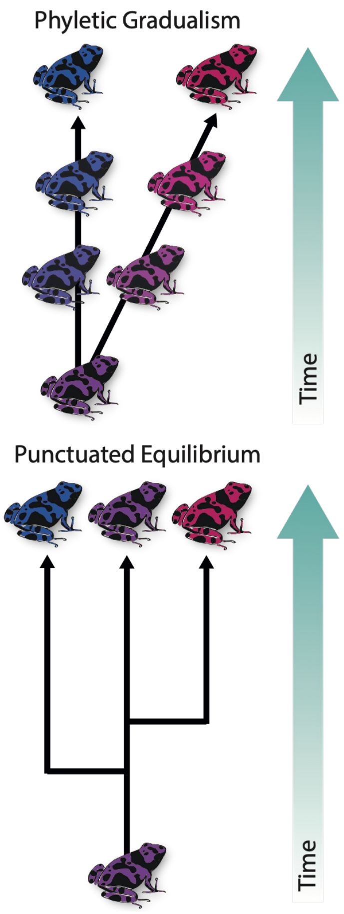
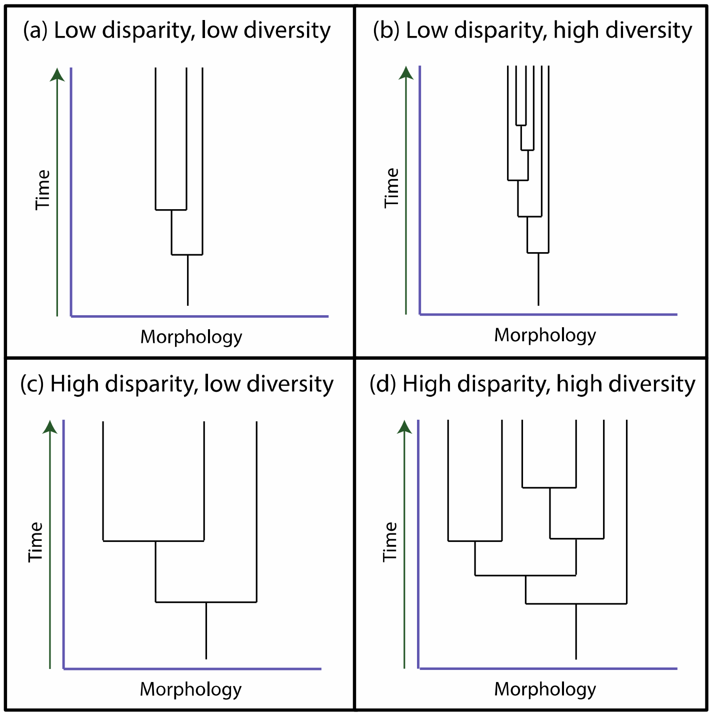


Figure 2. The relationship between disparity (morphological diversity) and taxonomic diversity described using phylogenetic trees showing hypothesized evolutionary history. These phylogenies show morphological change occurring at splitting (speciation) events. for morphological change occurring within lineages, see Figure 1. The concept of a living fossil is best represented in panel (a), whereas the concept of adaptive radiations is best represented in panel (d). In reality, many more tree shapes (topologies) exist that differ in number of splitting events and number of extinctions.



Tables

Major extinction events in Earth history ranked by their ecological and taxonomic severity. Triggers and kill mechanisms are ranked by confidence, with a large and small ‘x’ indicating high and low confidence in the mechanism, respectively. Data from (McGhee Jr et al. 2013, Harnik et al. 2012, Kaiser, Aretz, and Becker 2016, Bambach 2006, Balseiro and Powell 2020).

Time (Ma)	Extinction event	Taxonomic severity (rank)	Ecological severity (rank)	% spp lost	% genera lost	Example taxa lost	Mass Extinction Triggers			Mass Extinction Kill Mechanisms				
							Large Igneous Province	Asteroid Impact	Glaciation	Acidification	Anoxia	Warming	Cooling	Habitat Loss
66	end-Cretaceous	5	2	[redacted]	[redacted]	[redacted]	x	X		X		x	X	x
201	end-Triassic	2	3	[redacted]	[redacted]	[redacted]	X			X		X		
251	end-Permian	1	1	[redacted]	[redacted]	[redacted]	X			X	X	X	x	X
325	Serpukhovian	6	5	[redacted]	[redacted]	[redacted]			X				X	x
359	Famennian	4	7	[redacted]	[redacted]	[redacted]	X		x	x	X	x	x	
374	Late Devonian (end Frasnian)	5	4	[redacted]	[redacted]	[redacted]	x				X	x	X	X
445	end-Ordovician	3	6	[redacted]	[redacted]	[redacted]			X		x	x	X	X

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We were limited in the references we could cite and encourage the interested reader to follow citation trails in the contributions listed.

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