Macroevolutionary Issues and Approaches in Evolutionary Biology

Emanuele Serrelli and Nathalie Gontier

Abstract Many fields and approaches evidence, quantify, and analyze macroevolution. From biogeography to paleontology, from ecology to phylogenetics, and from biophysics to philosophy of biology, macroevolution elicits definitions and theoretical problems related to concepts such as species, lineage, ecology, niches, and extinction, which are relevant for general evolutionary biology. Macroevolutionary theories provide new epistemic frameworks to explain evolution in deep time, and macroevolution is also a phenomenon exemplified by myriads of real life-history case studies. This volume Macroevolution: Interpretation, Evidence and Explanation samples the rich reservoir of macroevolutionary knowledge, and evidences the macroevolutionary phenomenon in various episodes in time.

Keywords Macroevolution · Evolutionary biology · Speciation · Extinction · Deep time · Fossil record

Outlining the table of contents and writing an introduction to the various chapters of a book volume always comes with a reflection on the sequence in which we present the topics discussed by the authors, a sequence that in turn associates with the reasons we invited the scholars to contribute. Macroevolution on the one hand associates with theory formation and the methodological means by which we can interpret and explain evolution in deep time and above the species level. On the other hand, macroevolution is itself a phenomenon that can be evidenced by actual

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cases in life's history. For that reason, we have divided the book into two parts, one that focuses on theory formation, and one that evidences macroevolution.

1 Introduction to Part 1: Macroevolutionary Explanations and Interpretations

For the first part, Macroevolutionary Explanations and Interpretations, we invited our contributors to focus on the theoretical, methodological, and epistemological aspects of macroevolution, defined as a scientific area of research that endorses specific scientific practices. Evolutionary scholars today continue to disagree on the nature and scope of evolutionary theory. Is there such a single field as "evolutionary biology" or is evolution a phenomenon studied by a variety of scientific disciplines? How does the field of macroevolution relate to microevolutionary biological areas of research? Is the Modern Synthesis complete, and can it adequately explain macroevolutionary problems above the population level such as speciation and extinction, evolutionary trends, major transitions, biological hierarchies, or species sorting? Does macroevolution delineate one or multiple distinct area(s) of research, or does it merely complement microevolutionary theory and practice? Answers to these questions not only vary, but also they continue to raise significant debate between micro- as well as macroevolutionary scholars. We have sought out both the controversies and agreements, and we have invited our contributors to write on how they, from within their specific disciplines, understand and define macroevolutionary epistemology, and how they see their theoretical frameworks fit or dissociate from the standard evolutionary paradigm both in theory and practice. We have favored quality over quantity and invited a selected group of scholars to provide extensive review chapters instead of aiming for shorter, more concise position papers.

For **Douglas J. Futuyma**, a leader in evolutionary biology (Futuyma 2013), macroevolutionary theory primarily associates with on the one hand ideas on developmental constraints as introduced by adherents of punctuated equilibria, and on the other hand, with the role speciation plays in bringing forth biodiversity at an ecological and biogeographical level. He opens the first part by asking "**Can Modern Evolutionary Theory Explain Macroevolution**?" As one of the scholars who has long recognized the importance of the issues raised by macroevolutionary scholars, and who in his career has focused on reconciling aspects of punctuated equilibria theory with population genetics, he answers the question mostly in the affirmative. In his chapter, the author provides a rich contextualization of both the origin of the synthetic theory and how its architects tried to explain macroevolutionary above-population phenomena, as well as the challenges that evidence and hypotheses on developmental constraints and stasis, among others, pose to the synthetic theory. Futuyma provides historical insight into how post-synthetic evolutionary biologists have been reconciling these ideas into standard evolutionary theory, and he especially points toward the rising disciplines of evo-devo and evolutionary ecology as the means by which such reconciliation is possible. Eco-evo-devo presents a more evolved and richer synthetic evolutionary view, and the continuously evolving and expanding framework therefore remains valid.

That evolutionary theory is valid and is undisputed by macroevolutionary scholars (Ridley 2003). Nonetheless, many macroevolutionary scholars are less optimistic about how well microevolutionary theory can explain macroevolutionary problems or predict evolutionary outcomes. How do macroevolutionary scholars differentiate their research agenda from microevolutionary biology, and how do they define the microevolutionary fields they oppose? Macroevolutionary areas of research today associate with fields such as paleobiology, ecology, systematics, and biophysics, and scholars that form part of these fields in general think that microevolutionists place too much emphasis on genetic selection at the expense of other principles, such as physical and ecological ones, that equally contribute to our understanding of evolution.

Folmer Bokma tests some of the microevolutionary predictions on speciation, extinction as well as the mode and tempo of evolution in his chapter "**Evolution as a Largely Autonomous Process**." He gives a series of examples wherein he demonstrates the means by which microevolutionary scholars provide explanations and make predictions on the evolutionary fates of species as well as how they interact with other species (flowers and their pollinators, for example), and weighs them against the actual evolutionary history that those life forms undergo through time, which he in turn deduces from molecular phylogenetic analyses. His examples demonstrate an epistemic ambivalence and duality in the works of microevolutionists, which he characterizes as "ascribing change to natural selection when it occurs, but failing to account for the frequent cases where no evolution is observed" though it is predicted. To explain periods of stasis as well as rapid speciation, he turns to punctuated equilibria theory and agrees with many of the founders of macroevolutionary thought that in real-life history events, natural selection, in and of itself, cannot account for speciation, extinction, or stasis. Again, he firmly grounds these conclusions upon the incoming results of molecular phylogenetics, a rising field that today forms a bridge between fossils and genes, and where Bokma is a leading and pioneering expert. He furthermore turns to epigenetics and evo-devo to explain evolution as a largely autonomous process.

In his chapter "**Visualizing Macroevolution: From Adaptive Landscapes to Compositions of Multiple Spaces**," **Emanuele Serrelli** details how macroevolutionists have visualized life's evolution. By taking classic models of evolutionary change as depicted in adaptive landscapes as point of departure, Serrelli demonstrates that the original population geneticists understood evolutionary change mostly as the various distributions of genes within populations through time, while macroevolutionary schools of thought understand evolution as the outcomes of adaptations to environmental conditions, and thus favor a more spatial, ecological approach. He furthermore demonstrates how new visualizations of evolution conceived as occurring in multiple spaces, such as morphospaces, geographical, and ecological spaces, as well as diversity diagrams and distribution maps provide new methodological tools to deduce the major patterns and trends of life's evolution.

Stanley Salthe, one of the architects of the macroevolutionary discipline, understands biological evolution as part of a larger, cosmic evolutionary process that both transcends and influences the evolution of life. In his "**Toward a Natural Philosophy of Macroevolution**," he explains how on a cosmic scale a distinction can be made between the physical, chemical, biological, and social realm. Besides by biological principles such as natural selection, life evolves according to thermodynamic and overall physical principles that act within life, both in what regard its development as well as its survival, expansion, and extinction in ecological settings. Salthe emphasizes that taking on a macroevolutionary perspective implies a return to natural history research as well as natural philosophy. In such a framework, all the natural sciences, including physics and chemistry, are put to use in explaining just how it is that life originates, diversifies, and dies. He demonstrates how such a naturalistic, ecological approach to life necessitates hierarchical thinking and explains how especially biophysics is able to account for life at a grander scale.

Hierarchy theory is also the topic of **Ilya Tëmkin and Niles Eldredge**'s chapter, "**Networks and Hierarchies: Approaching Complexity in Evolutionary Theory**." One of the claims made by macroevolutionary scholars is that species and higher taxa are real entities or biological systems that evolve in an equally real biotic and abiotic environment, respectively, by proximal evolutionary processes and abiotic drivers. Such a stance, for Tëmkin and Eldredge, requires an ontological investigation into the multiple levels of the genealogical and economic (ecological) hierarchy. By understanding biological entities as hierarchically nested, complex emerging systems that occupy an equally hierarchical and multilayered economy, they demonstrate how hierarchy thinking provides new means to delineate and identify the underlying patterns and processes of evolution.

Ontological and epistemological hierarchy thinking also forms the topic of **Nathalie Gontier's** chapter "**Uniting Micro- with Macro- evolution into an Extended Synthesis: Reintegrating Life's Natural History into Evolution Studies**." She demonstrates how the modern synthesis defined evolution at a meso-level, and details how microevolutionary and macroevolutionary research schools necessitate a reconceptualization of older hierarchical levels such as the inorganic, organic, and superorganic. She furthermore details how both the micro- as well as macroschools have evolved different scientific practices and epistemic frameworks to understand life's evolution. Macroevolutionary scholars understand evolution as the outcome of natural history, while microevolutionary scholars understand evolution as the result of a causal mechanism (i.e., natural selection), and Gontier points out that the various epistemic stances underlie radically different concepts on matter, space, and most of all, time. Finally, she details how macroevolutionary thought currently extends the biological sciences and is successfully applied within the sociocultural domain.

2 Introduction to Part 2: Evidencing Macroevolution with Case Studies

Macroevolution does not merely define a specific scientific agenda; it also delineates a phenomenon. In the second part of this volume, Evidencing Macroevolution with Case Studies, we invited scholars to contribute with specific topics and examples that explain the specificity of macroevolution as a phenomenon. In our selection, we have of course had to make choices, because not all case studies and examples can fit one book volume. We have therefore focused on some of the most important macroevolutionary phenomena typical of eukaryotic evolution, namely the origin of eukaryotic sex, the evolution of distinct body plans, hominid evolution, speciation and extinction, and biodiversity.

Lutz Becks and Yasaman Alavi contribute with a chapter “**Using Microevolution to Explain the Macroevolutionary Observations for the Evolution of Sex**.” The origin and evolution of sex in eukaryotic organisms poses one of the biggest enigmas for evolutionary theory, and sex is rightfully characterized as one of the major transitions of life. Becks and Alavi understand the emergence of sex as a macroevolutionary phenomenon, which they define as an observation, and explain how traditional microevolutionary theories can explain its evolutionary emergence. More specifically, they understand sexual reproduction as an evolutionary pattern that associates with various geographic and phylogenetic distributions not found in asexual organisms and demonstrate how microevolutionary processes can explain the macroevolutionary observations.

Because species are considered real biological entities, macroevolutionary scholars also understand speciations as events resulting from processes often distinct from genetic selection. In the chapter titled “**Speciation: Expanding the Role of Biogeography and Niche Breath in Macroevolutionary Theory**,” **Alycia Stigall** discusses how a multiplicity of abiotic and biotic, external factors including, among others, climate change and plate tectonics as well as niche occupation and breath, and species invasions of ecological niches, underlies speciation events. She avers for understanding speciations as the outcome of multiple factors that often lead to speciation as combined factors that together bring forth evolutionary change. Stigall reviews some of the vicariant speciation events that occurred in bivalves and brachiopods (which are both shelled marine animals) that lived through the Late Devonian Biodiversity Crisis, a period that is designated as a crisis because the ecosystem underwent radical changes while the marine animals form an anomaly to these extinction events; as well as the Late Ordovician Richmondian Invasion, another crisis period characterized by fluctuating sea levels and associated invasions of foreign species that before did not occupy these niches, where the marine benthos fared less well in comparison with the period before they had to share their habitat. She ends with detailing the speciation events of North American horses of the Neogene (the second period of the Cenozoic), this time during a radiation period associated with favorable climate change and subsequent abundant food availability (grasslands).

Prokaryotes come in distinct shapes and sizes, and although they can form morphologically complex colonies, and most certainly contribute to the anatomical form of eukaryotic beings, they are mostly unicellular organisms that often contain organelle-like structures. The evolution and diversification of anatomically distinct body plans, organs, and organelles is typical of eukaryotic organisms. Macroevolutionary theory has played a significant role in reviving and reintegrating embryological and overall developmental biology into standard evolutionary theory.

In his chapter "**Morphological Misfits and the Architecture of Development**," **Alessandro Minelli** examines morphological "misfits," i.e., taxa whose morphology diverges from the conventional structural body plan of the major clade they belong to. A correct phylogenetic positioning of morphological misfits is therefore the first obligate step toward a tentative interpretation of their evolution. Some misfits are "systemic": homologies between them and their relatives are hard to find, while homologous structures are what enables morphological comparisons. Macroevolutionary research on body plan formation helps to make the degree of "evolutionary freedom" of a structure visible and enables insight into character evolvability. Divergent structures 'behave as evolutionarily independent modules,' because their independence is structural, and often results from the largely independent genetic control of their development, which is the case in arthropod segments for example. The neck of the giraffe, on the other hand, although very divergent in a phylogenetic context where necks are rather monotonous, is not a module, because it involves several body units. For Minelli, rapidly evolved misfits deserve detailed studies to estimate the time of their divergence from "normal" relatives.

Macroevolutionary phenomena also impact our own history. **Bernard Wood and Mark Grabowski** document "**Macroevolution In and Around the Hominin Clade**." The authors begin their work by delineating how paleontologists, informed by both micro- and macroevolutionary theory, classify fossil finds into species and genera to build taxonomies. They exemplify by listing the reasons why recent fossil finds such as *Sahelanthropus tchadensis*, *Orrorin tugenensis*, and the two *Ardipithecus* species (*Ardipithecus kadabba* and *Ardipithecus ramidus*) can, and for the authors cannot, be categorized as members of the hominin clade (which is a subclade of the hominids). Until more evidence is available, they suggest instead to designated them as "possible hominins." They go on to demonstrate how a variety of morphological and developmental features, including body growth, sexual maturation, and reduction in teeth size, so typical of the actual hominin clade, enable deductions on the tempo and mode of evolution. They exemplify how the evolution of *Australopithecus afarensis* and *Paranthropus boisei* is characterized by stasis, and they demonstrate how macroevolutionary morphological trends, such as increase in brain size and the overall morphological differences between *Homo neanderthalensis* and *Homo sapiens*, can be explained by drift. Finally, the authors end their chapter with an account of the difficulties posed by homoplasies, morphological traits present in sister taxa but not in their most recent common ancestor.

Finally, macroevolutionary theory not merely associates with the fossil record or the study of the dead, it also associates with the living and those who are threatened with extinction. The final case study, written by **Elena Casetta and Jorge Marques da Silva**, therefore focusses on bioconservation efforts in a chapter titled "**Facing the Big Sixth: From Prioritizing Species to Conserving Biodiversity**." Scholars in general distinguish between five large extinction events but Eldredge distinguishes a sixth that is imminent. Casetta and Marques da Silva first investigate the criteria by which species are declared extinct from an environmental ethics point of view, and subsequently focus on how species can be prioritized for conservation. They provide a rich overview and analysis of the distinct means by which the United States of America and the European Union delineate their conservation policies and give suggestions on how they can be improved.

3 Alternative Ways to Read the Volume

The division of the book into two parts is only one way in which scholars can read the book. Macroevolutionary research is also characterized by a set of specific research questions, and these questions present alternative ways in which we suggest the reader to digest the various chapters.

3.1 Macroevolutionary Fields and Approaches

Macroevolutionary research fields and approaches to macroevolutionary phenomena are remarkably many, and distinguishing between a research area or an approach is not always easy. Biogeography, for example, delineates a particular field of study, but in its approach it also demarcates a particular dimension that can be incorporated and put to use in other research fields. Consolidated areas of research that deal with macroevolutionary issues include paleontology, systematics, geology, ecology, phylogenetics, evolutionary developmental biology, population genetics, conservation biology, theoretical biology, biophysics, and philosophy of evolutionary sciences. Each field has developed a particular series of methodologies and theoretical frameworks, whereby macroevolution can be evidenced, quantified, and analyzed. This book samples and surveys a good deal of them.

Wood and Grabowski's chapter is very informative of how macroevolutionary inferences are made in *paleontology* (Benton 2004; Foote and Miller 2006) and in particular in *paleoanthropology* (Wood 2011; Begun 2013) which is a subbranch of both anthropology as well as paleontology. The hominin features they focus on, such as teeth and brain size, are much more durable than any systematic classification of our kind into genera and species which in many details remain unresolved due to the fragmentary nature of the fossil record. Because paleoanthropology sets out to reconstruct our own evolutionary past, the authors also note that our demand for conclusive resolution is disproportionate, and instead highlight why evolutionary inferences of the fossil record are by necessity only one means in which we can approach the problem of phylogenetic reconstructions.

As evidenced by **Bokma**, *molecular phylogenetics* provides a complementary means to find answers on macroevolutionary issues of deep time, and our increasing possibility to quantify, model, and simulate large-scale datasets, links fossils to genes (Prothero 2003). Bokma's work on the temporal patterns and rates of evolutionary change (the "tempo" of evolution) is based on pioneering work by Avise and Ayala (1975) where correlations between species richness and quantity of evolutionary change across clades evidence a central thesis of punctuated equilibria, i.e., evolutionary change is concentrated in speciation events.

Taxonomies that are developed within the field of *systematics* are often taken for granted, but the amount of theorizing and quantitative research that precedes any systematic reconstruction cannot be underestimated. As **Gontier** points out, systematics started out as a logical and philosophical discipline, but today, the classification of natural phenomena that are bounded in space and time into various taxa, and their division into subspecies, species, genera, kingdoms, and domains, necessarily precedes any evolutionary investigation into a specific group. Systematic classification impacts all the evolutionary sciences, and systematic classification is in turn subject to advances made in molecular genetics, evo-devo, biogeography, paleontology, and ecology, work that often necessitates taxonomic revisions (Minelli 1993; Wilkins and Ebach 2013).

Even the intuitively clear-cut distinction between sexually and asexually reproducing taxa turns out to be anything less than straightforward, as **Becks and Alavi** reveal. **Minelli** devotes some reflection on taxonomy in his exemplification of morphological misfits, case study anomalies that can lead to the introduction of novel taxonomical units. **Wood and Grabowski** understand fossil genera as different from "neontological" genera: they are "grades." A grade is an informal grouping united by a level of morphological or physiological complexity supposedly reflecting adaptation, without the strict phylogenetic requirements implied by "clades" (i.e., monophyletic groups) that fossil hominins cannot meet. Furthermore, inferences of function from morphology, such as the inference of bipedalism from a few skeletal characters, are, for Wood and Grabowski, particularly frail. Wood and Grabowski are "splitters" and think the "lumpers" underestimate the number of species there existed in the hominin clade, because morphological differences across the geographical range of a putative "species" may actually hide speciation events and many groups probably went extinct without fossilizing.

Biogeography is another fundamental macroevolutionary field. To understand the evolution of eukaryotic sex, **Becks and Alavi** compare the distributional range of asexuals and sexuals: asexuals tend to range to higher latitudes and altitudes, and they tend to colonize previously glaciated and devastated areas. Shallow waters can be coevolutionary "hot spots" for the evolution of sex.

In macroevolutionary time scales, biogeography inevitably flows into *geology*, *paleogeography*, and *paleoecology*. There is a very intimate relationship between *stratigraphy* and living beings, dating back to the seventeenth century, as shown for example by the principle of faunal succession: Fossilized flora and fauna succeed each other vertically in a specific, reliable order that can be identified over wide horizontal distances, and they are used as time markers for rocks. In macroevolutionary stratigraphy, geological layers are moreover tagged with the biotic evolutionary processes that are ongoing in the correspondent era at the appropriate time scale, normally spanning a few million years.

Stigall's approach to paleontology combines biogeographic methods with phylogenetics, bringing to light the speciation patterns of single genera. It also integrates *niche evolution analysis*, to study the macroevolutionary dynamics of generalists and specialists (Peterson et al. 2011). Niche evolution in a taxon can be measured by extrapolating from geographical distribution the niche parameters at one time slice, then by extrapolating from niche parameters the expected geographical distribution at a second time slice, and then by comparing the expectations with the actual distribution found in the fossil record. The concept of niche is also explained by **Serrelli** and used by **Salthe** in his comprehensive view of Earth's history.

Ecology is slowly but steadily entering the list of disciplines that are considered indispensable to understand macroevolution (Allmon and Bottjer 2001; Price 2003; Loreau 2010). Ecology is, as **Salthe** describes it, "the study of energy flow relations taking place on Earth between the influx of solar radiation and its reradiation into space," a unifying science that studies the world in terms of thermodynamics and hierarchical structures. **Becks and Alavi** show that community ecology may combine the available theoretical and experimental knowledge on the evolution of sex and accommodate pluralistic explanations combining the accumulation of deleterious mutations and Red Queen dynamics (Van Valen 1973). Some branches of ecology seem well prepared to face the increasing complexity revealed in macroevolution. For **Tëmkin and Eldredge**, ecology is not only a good half of the macroevolutionary story, but also the locus of the triggering causes of evolutionary change all the way through the biological hierarchies (Eldredge 1989, 1999).

Many essays in the book emphasize how *phylogenetic methods* are now able to process both morphological and molecular evidences and even take into account within-species diversity. The progress of phylogenetic techniques has greatly improved the inferential, predictive, and testing possibilities of evolutionary hypotheses (Wiley and Lieberman 2011).

Comparative disciplines such as morphology, physiology, cytology, and genetics remain fundamental; indeed, they are boosted thanks to the "skeleton" of relationships provided by phylogeny. *Evolutionary morphology*, in particular, studies the existence of clusters of species sharing similar anatomies. Morphological classifications are often a useful first organization of knowledge, as **Minelli** argues in his chapter. The categorization of morphological misfits in three morphological kinds—divergent by reduction, by building blocks, or by synorganization—guides the search for specific developmental pathways and steps along which their developmental schedules may have evolved.

"Steps" is correctly understood, like many other words in our book (e.g., "intermediate" or "transitional" form), in the context of macroevolutionary *trends*, an extremely important concept. Trends are recognizable long-term, large-scale changes that involve great numbers of species, genera, and even higher taxa (Turner 2011). **Wood and Grabowski** need the demonstration of trends in cranial, dental, and postcranial morphology. They cannot rely on single diagnostic traits, because traits come and go in phylogenies, and what is diagnostic for one period is not automatically for another one. Not all the differences between *H. sapiens* and Panini (chimpanzees and bonobo) may be used to distinguish ancestral Panini from ancestral *Homo*. If, on the one hand, *H. sapiens*' hypodontism came about as a reversion after million years of megadontism, on the other hand there are more reliable trends in the clade: An incipient *Homo*-like cranium will be diagnostic all the way back to stem hominins to tell basal hominins from basal Panini. Corroborated trends allow for back-tracing and provide criteria to distinguish taxa that lived close to their divergence time.

One of the most exciting fields approaching macroevolution today is *evolutionary developmental biology*, abbreviated EDB by **Futuyma**, and evo-devo by **Minelli** (Arthur 2002, 2011; Minelli and Fusco 2008), while others link evo-devo to ecology under the heading eco-evo-devo (see Gilbert 2012 and Ledón-Retting and Pfennig 2011 for an overview). For **Futuyma**, evo-devo inspires an improved theory of variation. **Minelli**, following a classification by Arthur (2000, 2002), emphasizes how most macroevolutionary differences seem to consist in modifications of the temporal, positional, and quantitative (metric or meristic) aspects of the ontogenetic production of individual body parts, and how important developmental trends are in macroevolution. Developmental modularity is evident in those misfits that are odd, not systemically, but only with respect to a few well-circumscribed body parts. Other misfits have uncommon life cycles, with oddly shaped stages or rearranged sequences of stages.

Knowledge and understanding of these macroevolutionary phenomena have exploded after the advent of developmental genetics. Molecular methods, for example, can now be used to determine that only some developmental modules are also structural modules, characterized by a more well-defined genetic control. Developmental genetics in macroevolutionary context is a fervent field, very rewarding but also very difficult for its struggle with "the intricacies of the genotype → phenotype map." **Bokma** refers to the evo-devo schools to explain developmental constraints, selection plateaus and stasis and demonstrates how, partly because of developmental mechanisms, evolution is a largely autonomous process. Stigall also turns to eco-evo-devo to explain phenomena such as phenotypic plasticity and niche construction as well as habitat tracking, migration, and niche invasion, because all present behavioral and thus anatomically underlain responses to ecological settings.

Futuyma gives his own reconciliation of *population genetics* with punctuated equilibria. The claim of punctuated equilibria (Eldredge and Gould 1972, based on Mayr 1942) that rapid evolutionary change is coupled with bottlenecks, is, for Futuyma, "surely wrong" in the light of available evidence. Instead, the claim that rapid evolutionary change is coupled with biological speciation is plausible. Futuyma's solution focuses on the niche heterogeneity that is expected in widespread species and highlights the role of reproductive isolation in protecting local adaptations from dissolution.

As **Serrelli** narrates in his chapter, population genetics is essentially a powerful mathematical theory of factors such as selection, mutation, drift, population size, and allele frequencies. The synthetic work of Sewall Wright in the 1930s already hinted to "the way in which both speciation and extinction can flow mechanically from the processes of modulation of variation," in the words of Lewontin (1980: 61). But today, macroevolution does not get forced into population genetics models. *Evolutionary quantitative genetics* addresses the complex dynamics of phenotypes and their genetic underpinnings under different regimes of selection and other conditions (Falconer and Mackay 1996; Roff 1997). Selection can be detected in the covariation of character complexes, instead of being assumed as an ad hoc explanation for postulated adaptive traits.

The same holds for developmental correlations that present another crucial role in explaining morphological evolution. **Wood and Grabowski** are confident that quantitative genetics can now be applied to detect the relative weight of natural selection and drift even in hominin fossils. **Becks and Alavi's** chapter illustrate how *population biology and genetics* (Hanski and Giaggiotti 2004; Hartl and Clark 2007) may be put to use to explain innovation or, at the opposite, persistence of macroevolutionary distributions. Why does sex evolve? And why are sexual populations or taxa not invaded and replaced by asexual taxa when sex seems to be a bad choice as it comes at high costs? The case of sex is particularly interesting because the evolving trait is also one that shapes variance and, consequently, microevolutionary mechanisms. The "short- and long-term effects of sexual reproduction" need to be studied mathematically: It is assumed that sex always increases variation, but mathematical models demonstrate that it is not always the case and identify boundary conditions. Other questions may be asked, such as could sex accelerate adaptation to new environments?

Gontier approaches research on sex, so typical of microevolutionary fields, from within *history and philosophy of science*, which are also fields that can contribute to macroevolutionary research. She details how epistemic approaches to the origin and evolution of eukaryotic sex as well as the asexual behavior characteristic of prokaryotes relate to sociocultural and political ideas on the common goods of society as well as the rise of liberal as social thought in the nineteenth century. Is sex a social behavior or is it an adaptive outcome that enables the fit to survive and reproduce successfully?

Also from within philosophy of science, **Serrelli** hones in on the different kinds of *modeling* that map macroevolution as the realization of actual life forms in the huge domain of possible virtual alternatives. Many modeling approaches use biologically unrealistic exploration mechanisms to study general properties of low-dimensional "spaces of possibilities" that imitate the biological possibilities. High-dimensional spaces, which require a holistic, probabilistic kind of mathematics with a strong role of statistics, are used to understand how whole genomes or sets of phenotypic traits should behave in macroevolution. Some models, such as sequence spaces of RNA and proteins for example, can even guide empirical work.

Although of course macroevolution is not liable to direct experimentation, *experimental evolution* is sometimes used in relation to macroevolution (Garland and Rose 2009). **Becks and Alavi** provide the example of the few experimental tests of mechanistic causes for the evolution of sex, limited by the use of model systems whose sexuals and asexuals do not actually coexist under natural conditions.

As **Casetta and Marques da Silva** demonstrate with their essay, *conservation biology* entered an age in which it needs to deal with macroevolutionary knowledge and tools (Louys et al. 2012). Importantly, however, empirical knowledge will never be enough to settle issues such as how species should be prioritized, which conservation targets deserve focus, and how biodiversity conservation should be ethically justified; rather, the authors note that "Conventions and procedures have to be agreed upon and established … facing the Big Sixth is not a matter for biologists only." Following Soulé the authors characterize conservation biology as a mission- or crisis-oriented discipline, and its relation to biology has been compared to that of surgery to physiology, or of war to political science. So, ethics—and *philosophy of science* more generally—joins the table of disciplines that deal with macroevolution.

Because macroevolutionary thought redefines the cosmic scale, hierarchy theory, an intrinsic topic of *philosophy*, plays a crucial role in theory formation. *Hierarchy theory* is discussed in the works of Salthe, Tëmkin and Eldredge, and Gontier. **Gontier** highlights how many macroevolutionary scholars define themselves as naturalists, because of the emphasis they put on historical narration of past events. Both Salthe and Gontier trace hierarchy theory and macroevolutionary thought back to natural philosophy as it developed in the nineteenth century, and as a naturalist, **Salthe** legitimizes the approach. For him, natural philosophy is "an attempt to construct a scientifically based 'Big Picture' understanding of the world" whose goal is to find the different realms of reality. His picture is ecological and Salthe criticizes 'idealistic' interpretations of ecology that are based on an attempt to unify energy and information. Instead, he chooses a "materialist" position that concentrates on energy connections and energy flows.

Hierarchy theory also presents scholars with a means to *unify* knowledge on macroevolution. Advised by Marjorie Grene, Eldredge (1985, 1986, 1989) first turned to *Hierarchy Theory* in the 1980s. **Tëmkin and Eldredge** present an up-to-date version of hierarchy theory tightly integrated with network theory. Biological systems are arranged hierarchically, with smaller units forming the components of larger systems: trees in a forest, cells in a body, organisms in a population, trophic groups in ecosystems, genes within chromosomes, within cells, within organs, within organisms, within populations, within species, within ecosystems. Hierarchy theory of evolution is a theory of how biological systems are hierarchically organized, how they function, and how evolution takes place through them over time. "Hierarchies" is a plural term in hierarchy theory, not only because every system (organism, local ecosystem) is an instance thereof (a hierarchical entity) but also because there are distinct kinds of hierarchies. The hierarchy theory the authors present in their work identifies two main kinds that they delineate as the only two that are really important in evolution. One is named "economic" or "ecological," and it is based on matter–energy transfers and ecological processes. The other is named "genealogical" or "evolutionary," and it is based on information and replication. The two hierarchies overlap at some point. For example, an organism is both an economic entity and a replicator, being part of ecological processes and also a fundamental element of a lineage. At other points, the two hierarchies are clearly distinct, for example a species is a genealogical entity that does not participate, as such, in any economic system. Even when the two hierarchies overlap, hierarchy theory sees them as ontologically distinct, they interact in complex ways, and it is their interaction that brings about the patterns of evolution at all scales.

Finally, **Salthe** and **Gontier** point out the important role the rising field of *biophysics* has in contributing to a richer understanding of macroevolutionary phenomena. **Salthe's** ecological perspective is very much inspired by thermodynamics. And **Gontier** reviews how abiogenesis, traditionally a field associated with physics, exo- and astrobiology, can shed light on the origin of life, a theme that remains understudied from within classic Neodarwinian theory. Complex adaptive systems theory is relevant for understanding the spontaneous generation of catalytic and autocatalytic biochemical systems. She also points out that naturalists adhere to a different notion of time that she associates with relativity theory and quantum physics which she distinguishes from Newtonian mechanical worldviews she sees as underlying research on cause and effect as well as the evolution of purposeful behavior in Neodarwinian frameworks.

3.2 Macroevolution Defined as Evolution at and Above the Species Level

Wood and Grabowski point out that macroevolution as a concept was first used in 1934, in the work of the Russian geneticist Filipčenko (see Sepkoski 2012). The authors further note that the most accepted technical definition of macroevolution is the one presented by Simpson (1944) and Hallam (1989) that define macroevolution as "evolution at and above the species level." Such a characterization of macroevolution is also adhered to by **Futuyma**, **Bokma**, **Casetta and Marques da Silva**, and **Gontier**. **Wood and Grabowski** note that "if the species is the rubicon that divides macroevolution from microevolution, then the type of taxonomic hypothesis that is adopted will have profound implications for what is included."

Defining macroevolution as evolution at and above the species level therefore first and foremost requires a good definition of species (Wilkins 2011), and such a definition impacts how scholars understand speciation and extinction events. **Wood and Grabowski**, following Smith (2009), consider five species concepts and divide them into two classes: process-related and pattern-related species concepts. Process-related species concepts include the biological species concept (BSC), the evolutionary species concept (ESC), and the species-mate recognition species concept (RSC). Pattern-related species concepts are the phenetic species concept (PeSC) and the phylogenetic species concept (PySC). Paleoanthropologists often uses the PySC and tries to identify the smallest clusters of populations that are recognizable from the available set of characters. But the taxonomical and, most of all, classificatory controversies surrounding the hominin clade lead the authors to adopt a dataset-relative definition of macroevolution as "what you can learn from the fossil record."

Gontier points out that Mayr's BSC defines species based upon "sexual exclusivity and geographical accessibility" and especially the former implies an annihilation of the sexual individual in favor of a higher-order classification: the group or the species. **Stigall**, who endorses the BSC, considers species as "groups of organisms that maintain genetic continuity by interbreeding among members of the group but that are distinct from other reproductive groups" and underlines that in the fossil record this condition by necessity has to be inferred from morphology. Stigall understands speciation as "the separation of a set of organisms into a newly isolated reproductive unit that is discrete from the ancestral species," typically happening in "less than ten thousand years." Stigall is interested in a geographical classification of speciation modes: most frequently speciation begins in allopatry, i.e., in geographical separation, although sympatric and parapatric speciation is considered possible, and, under an integrated view of macroevolution inclusive of the ecological environment; it is possible to say that modes of speciation themselves shift in prevalence over evolutionary time (Coyne and Orr 2004). As Stigall explains, allopatric speciation comes in two kinds: vicariance and dispersal. In vicariance, the geographic separation is due to the formation of barriers. In dispersal, it is due to active migration. While speciation by vicariance appears predominant in modern taxa and in the fossil record (for example in trilobites), in the Devonian Stigall finds an opposite prevalence of speciation by dispersal, in other words, an anomalously low proportion of vicariant speciation.

In **Tëmkin and Eldredge's** hierarchy theory, species are lineages demarcated by origin through lineage-splitting (or speciation) events and by eventual demise through extinction, although the temporal boundaries of species become less distinct at smaller time scales due to a gradual process of divergence that appears instantaneous at geological time scales. **Casetta and Marques da Silva** observe that when describing the Big Sixth, species concepts break down: several animals hybridize, either spontaneously or by human intervention, and hybridizing also becomes more likely as selective pressures increase. **Casetta and Marques da Silva** describe the ongoing mass extinction as partially caused by our own species and its activities (Wilson 2002). A symbol of the Big Sixth is the Amur leopard, which today, mainly due to habitat alterations caused by the exploitation of forests, only consists of about twenty individuals living in southwestern Russia. In the USA alone, the list of endangered species is huge, from the Grey Wolf to the Puget Sound Killer Whale. Casetta and Marques da Silva explain why a

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species-based approach to conservation will not work and point out the necessity of integrating macroevolutionary mechanisms and logics into conservation biology: “the aim is not just to save endangered species, but also to allow the continued production of novel diversity, i.e., to improve the conditions and mechanisms that help the diversity to be generated.”

If anthropogenic pressure depresses speciation rates, how can extinction be compensated? **Salthe’s** perspective embraces the recent socio-technological evolution of *H. sapiens*, seen as a fervent cooperator to universal energy dissipation. Salthe’s interpretation of macroevolution leads him to affirm that we should not be surprised at all if “disorder threatens everywhere, and we must work harder than seems reasonable to achieve anything.” Salthe holds a more conventionalist view of species: Species do not have a role in macroevolution since they are not ecological actors. The status of populations is not granted either, because although populations do play ecological roles, they actually do as aggregations of individuals. Yet, Salthe grants populations at least an indirect influence in regulating the abundance of individuals through their reproduction network. For Salthe, speciation is a by-product of natural selection that rewards the ability to switch to new energy sources as those being utilized become locally depleted.

Tëmkin and Eldredge, whose hierarchy theory sees species as genealogical entities, focus on the reproductive aspect: Species replication is the process of speciation, or cladogenesis, that results from the perturbation and partitioning of demic networks. In fact, the hierarchical framework proposed by the authors fixes the upper bound of evolution at the level of the species. Even though supra-specific entities (monophyletic taxa) do show patterns of differential survival, they lack the capacity to replicate: Evolution above the species level is an epiphenomenon that results from processes that occur at lower levels. Moreover, species are not interactors (Hull 1980, 1988). Interactors are those entities that interact with their environments in such a way as to make replication differential, and they belong in the economic hierarchy. The most extensive population-level interactor corresponds to a metapopulation, which is a geographic and ecological mosaic of contemporaneous avatars and, as such, a synchronous subset of a species lineage. Interactors are affected by physical perturbations. According to the sloshing bucket model (Eldredge 2003), the higher the level of perturbation, the higher the level in the economic hierarchy at which its effects will be expressed and, consequently, the higher the level of the genealogical hierarchy at which the evolutionary pattern of change in diversity and disparity will be recorded. Intermediate levels of environmental disturbance yield the maximum speciation rates, because they maintain a balance between population fragmentation and establishment of favorable conditions for isolate persistence.

Leaving aside the particular focus on levels and the species boundary, **Serrelli**, relying on current scientific practice, describes macroevolution as a simultaneous exploration of morphospaces, geographical spaces, ecological possibilities, and genealogical outgrowths. This exploration of multiple interrelated spaces may be represented by means of compositions of multiple graphical representations. Sometimes these visual representations take the form of landscapes: geographical landscapes (based on spatial distribution), genealogical landscapes (based on relatedness), morphological landscapes (based on shared combinations characters), and ecological landscapes (based on the combinations of environmental variables that are suitable for the considered organisms). The spaces of possibilities are connected in complex ways in macroevolution. For example, descent relationships may not go along with morphological resemblance, generating visualization conflicts. Knowledge of macroevolution must be creatively connected by means of composite pictures and, more importantly, composite and interdisciplinary studies.

Finally, several chapters approach macroevolution from the point of view of contemporary species. In particular, **Bokma** notices that with respect to fossil species, contemporary species are interesting because they allow biologists to observe more characters, at a molecular level, with their respective evolutionary rates. But the present also poses specific problems: declaring extinction, measuring biodiversity, quantifying and modifying our own impacts and effects for ethical reasons.

3.3 From Ediacara to the Grey Wolf: Embracing All of Life's History

Macroevolution is evolution on a large scale. It is therefore natural for macroevolution to span long periods of time and to embrace broad and diverse parts of the living world. In fact, not only the examples in this volume have such characteristic broad scope but they are also drawn from the actual history of life. Another way to read the volume is by following the geological age, the chronological order in which these phenomena first appeared.

In **Serrelli's** chapter, we get to know the earliest known complex of multicellular organisms: The worldwide Ediacaran biota, which existed from 575 to 541 Mya (million years ago), just preceding the more famous Cambrian explosion (Erwin and Valentine 2013). Most Ediacaran life forms left only indirect traces ("fossil traces"), but some of them had carbonate structures, and their fossils are found in Australia, Canada and Namibia (although, when they lived, their locations had completely different geographical coordinates than today, in a completely different configuration of continents).

Several chapters in our book refer to the Big Five, the five largest mass extinctions in the history of life on Earth: the Ordovician-Silurian, the Late Devonian, the Permian-Triassic, the End Triassic, and the Cretaceous-Tertiary (Raup 1991). But there is reason to believe that there are at least 7 major mass extinction events. The first major extinction event probably involves the mass extinction of prokaryotic anaerobe life forms that must have followed the great oxygenation event, the other, often dubbed the sixth extinction event is the one that faces us now and that is discussed by **Casetta and Marques da Silva**. The authors remind us that 99 % of the species that have ever lived on Earth are now extinct. Besides these Big Seven, extinction events occur constantly during life's evolution, on less grand scales, and the events are variable in intensity (Lawton and May 1995).

Stigall's chapter brings us back circa 450 Mya (Late Ordovician), in an area that today is near Cincinnati, Ohio. There, a cyclical pattern of sea level rise and fall determined periodical basin invasions by bivalves and other components of marine benthos. The author analyzes one of these invasions, the Richmondian, and studied how biodiversity and geographical differentiation fell down, speciation rate was depressed, and broad ranging species, during a moment in time, had prevailed on species with narrower ranges. Many millions of years later, precisely 375 Mya, the world went through the "Late Devonian biodiversity crisis." Again, the geographical context is characterized by sea level rises that, by connecting previously separated water basins, facilitated geographical invasion and limited the uprise of new physical barriers. The fossil record of brachiopods, bivalves, and other shallow sea organisms shows relatively high extinction rates as well as relatively low speciation rates. Of the two anomalous rates, the most determinant was the low speciation rate, because even clades with normal extinction rate had declined in number of species. There is a fundamental pattern connecting the Devonian biodiversity crisis with the Cincinnati invasions, granted some differences due to the global versus local scale: Physical events bring about invasions that destabilize ecological niches, generalists prevail, and speciation "by dispersal" overwhelms speciation by vicariance (see above).

Much more recently, between ca. 8 and ca. 5 Mya, in Africa, there lived the so far unidentified group that would become the common ancestor to both *H. sapiens* and chimpanzees/bonobos. **Wood and Grabowski** group this ancestor, along with all its descendants in a subfamily: Homininae. Later in the same continent, among Homininae, a tribe originated: the hominins (Hominini). This tribe would give birth to genera like *Australopithecus* and *Homo*. The current consensus, based mostly on molecular data, considers chimpanzees and bonobos as the "outgroup" for comparing hominins to each other, but within the hominin clade the phylogenetic context is all but clear: Fossils are rare and incomplete, taxa lack obvious ancestors, and there are many sources of error (Wood 2011). One of the reasons why these problems arise right here is that scientists and outsiders are uncommonly curious and demanding toward the hominin clade, looking for levels of detail that we would never ask to analog fossils of animals that are more distantly related to us.

While the ancestors of hominins lived in Africa, in North America, between the Miocene and the Early Pliocene (ca. 5.3 Mya), horse species (subfamily Equinae) went through an event traditionally referred to as an "adaptive radiation." **Stigall** demonstrates that in horses—which are vagile and migratory organisms—speciation by dispersal normally prevails on vicariant speciation. On land, as opposed to what happens in water, climate change may have led to geographical fragmentation, increase of vicariant speciation, and radiation, not necessarily adaptive to varying environmental conditions. From **Serrelli's** chapter, we learn that this phase of the evolution of horses was also well studied by one of the founders of the Modern Synthesis: George Gaylord Simpson. We see how Simpson (1944) described the phases by which a lineage of browser mammals, Hyracotheriinae, split into browsers and grazers under the effect of environmental change combined with correlation among some of their characters.

And **Gontier** demonstrates how macroevolutionary questions are today becoming the dominant mode by which we can approach sociocultural and linguistic evolution. She notes that on a grand cosmic scale, Julian Huxley already characterized evolution as going from the physical to the biological and psychosocial, and traces these ideas back to classic cosmic lineups that go from the inorganic to the organic and superorganic. Such classification has profoundly impacted our division of the sciences, that go from the physical and astronomical, to the natural and biological, and sociocultural sciences. Today, the sociocultural sciences and classic humanities are embracing an evolutionary approach to the study of human behavioral traits, languages, and cultures. And in these studies, a transition is taking place from studying isolated sociocultural and linguistic traits synchronically to understanding them diachronically, by tracing the genealogical origins of these traits across cultures in space and time. Such an approach by necessity takes on a macroevolutionary perspective, and she highlights how in particular the jargon associated with punctuated equilibria is finding its use in these new macrocultural fields.

3.4 A Rich Research Agenda

Many more fascinating topics are addressed in the dense chapters of this book. We end this introduction with listing some of the more open-ended research questions that are currently associated with macroevolutionary research fields.

What is the temporal pattern—the "tempo"—of macroevolution? **Tëmkin and Eldredge**, **Stigall**, and **Bokma**, all emphasize stability, and frame macroevolutionary change as coincident with the achievement of new equilibria after disturbance. The roots of contemporary approaches to the tempo of evolution have to be traced back to the idea of punctuated equilibria (Eldredge and Gould 1972) and to the lively methodological debate that followed, and still goes on today (Gould and Eldredge 1977, 1993; Lieberman and Eldredge 2014). **Wood and Grabowski** notice how the quest for detecting punctuated equilibria is translated, in paleontology, into four research questions on: (1) the relative importance of gradualist versus punctuated evolution, (2) the role of speciation events versus within-lineage evolution, (3) adaptive versus neutral processes, and (4) the operation and incidence of 'species selection.' But the authors point out that none of these questions can be answered definitely for the hominin clade. Significant improvements will be enabled by new technologies and methodologies, much more than by the accumulation of more and more fossils.

How is stasis explained? **Stigall** emphasizes geographical and ecological relationships; **Bokma** emphasizes the stability of development and the selection pressures exerted by traits on each other, while **Futuyma** concentrates on demic structure and interconnectedness. All these aspects, and many others, are integrated into **Tëmkin and Eldredge's** hierarchy theory of Evolution, for which "The overall stability of biological systems across levels of organization is not surprising given the general tendency of complex systems to acquire complex network architectures that ensure relative insensitivity to external perturbations."

What's the role of the environment in macroevolution? The biogeography of invasions and radiations demonstrates, for **Stigall**, environmental "control" over macroevolution, i.e., a direct causation of climatic and geologic events upon the periodic restructuring of biodiversity in the history of life. Mass extinctions, climate change, and continental drift all show the tremendous importance of physical factors in shaping the history of life. The environment has multiple causal roles also in hierarchy theory: "Environmental perturbations contribute to both generating variation at the molecular level and facilitate the expression of hidden phenotypic variance by compromising evolutionary capacitance. The spread and fixation of novel genotypes, ultimately responsible for producing taxic evolutionary patterns, are enabled by temporary removal of control over population dynamics brought about by environmentally triggered disruption or destabilization of ecological networks at the level of biocenosis." On the other hand, "the stochasticity and non-linear dynamics characterizing the processes of the biocenosis in flux" for Stigall, are another important contribution "to the evolutionary contingency of life's history."

But does such importance of the environment mean that macroevolution is adaptive? As **Serrelli** notices, macroevolution and adaptation are peacefully decoupled epistemologically, although, of course, still related in complex ways. Macroevolutionary phenomena such as speciation, diversity, and disparity, with their peculiar patterns, do not necessarily constitute adaptive "peak climbing," although, for instance, patterns of adaptation such as niche breadth are integral part of macroevolutionary explanations. Paleoenvironments were not a major factor controlling the extent of Ediacara morphospace. **Futuyma** addresses the issue of constraints: for him, constraints are demonstrated (e.g., by extinction) and relevant to evolution, although they do not explain stasis, nor do they jeopardize optimality and adaptation. **Minelli** considers the possibility that morphological uniqueness be a symptom of peculiar adaptations, which may in turn suggest adaptive dead ends. More radically, for **Bokma,** macroevolution is "a largely autonomous process." Bokma does not downplay the most representative and fascinating studies that historically convinced the scientific community of the agency and efficacy of natural selection, but Fisher's idea that complex traits have additive genetic basis is at best inaccurate, and its persistence is due to theoretical inertia in face of theoretical alternatives and empirical issues, such as missing heritability and the persistent abundant variation in ecology-related traits. The autonomy advocated by Bokma is not immediately in conflict with the environmental drive demonstrated by **Stigall**. In fact, **Bokma** focuses on the rate of adaptive change, which is autonomous from environmental change, whereas **Stigall** focuses on rates of speciation and extinction, which crucially depend on ecological events. Climatological influence does not necessarily mean *adaptive* drive, as shown in the case of horses, traditionally and hastily called an "adaptive radiation."

Is macroevolutionary change essentially concentrated during speciation events? All authors seem to agree upon a positive answer to this question. **Stigall** relies on the many studies in evolutionary biology—from Ernst Mayr, to Eldredge and Gould's (1972) punctuated equilibria, to contemporary followers and revisers—that have identified speciation as the fundamental locus of evolutionary change. In fact, in her framework, macroevolutionary "events" are *defined as* those critical periods *in which* evolution proceeded above the species level, with uncommon rates of speciation and/or extinction. For **Bokma,** there is little doubt that the number of speciation events is much more predictive of evolutionary divergence than the amount of environmental change. For **Futuyma**, according to the available evidence, biological speciation is indeed plausibly the typical context where rapid evolutionary change takes place. But, in the available evidence, Futuyma sees that speciation does not require bottlenecking, as reproductive isolation can arise in a widespread species that spans across heterogeneous niches (protecting, in turn, adaptations from dissolving into the species).

Are there any exquisitely macroevolutionary processes? **Stigall's** paleoenvironmental distribution data form the Late Devonian crisis demonstrate, for her, sorting in favor of broadly distributed, generalist, invasive species *versus* narrowly distributed, ecologically specialized species. Natural selection is a sorting process that happens among individual organisms in a population. Species sorting would be *another* sorting process, not completely analogous, of course, to natural selection. The peculiarly cosmopolitan Late Devonian fauna might be a result of species sorting, i.e., the preferential survival—in sustained large-scale environmental conditions—of invasive ecological generalists with low speciation rates. This hierarchical expansion of processes is one of the cores of hierarchy theory, presented orderly and carefully by **Tëmkin and Eldredge**. And if we think about the concept of *evolutionary potential* that for **Casetta and Marques da Silva** should inform conservation efforts, we may imagine conservation as a process of artificial deme or species selection, something that may or may not take place in nature, and that would yield trends of increasing evolutionary potential through time, visible at levels above the individual.

What is the relationship between micro- and macroevolution and how do both relate to evolutionary theory? Well, as **Bokma** tells us, the topic was considered an "old" question already by George Gaylord Simpson in 1944. **Gontier** confirms and explains how it relates to philosophical cosmologies, worldviews that delineate the cosmological hierarchy that have traditionally been brought to us in the form of Greek Chains of Beings, Medieval *Scala Naturae* and Far Eastern Wheels of Time. The question might be old, but the associated problems are all but resolved and all essays in this book demand for the composition of an articulate picture of micro- and macroevolution and how both define the field of evolutionary biology, as well as what the scope of evolutionary theory is in general.

What are the requirements on evolutionary theory with regard to prediction? **Gontier** discusses how especially Mayr, as one of the founders of the Modern Synthesis, was also involved in delineating a specific area of research for evolutionary biologists within academia. Classic physics is traditionally conceived as the queen science because it enables predictions on the future, while biologists cannot predict the future path of life. It remains impossible to predict speciation and extinction events. Nonetheless, the evolutionary sciences are on the rise and have successfully incorporated the sociocultural sciences that increasingly approach their subject areas from within an overall evolutionary framework. She also points toward different scientific practices among micro- and macro- evolutionary scholars. Microevolutionary scholars focus on the causal explanations of evolution and endorse uniformitarian epistemic stances that enable them to tackle questions on teleology and goal-directed behavior of living organisms, while macroevolutionary scholars take on more relativistic stances that she associates with epistemic pluralism that does not require evolutionary scholars to predict the future, but rather to narrate the past from within a series of referential frameworks that necessitate a comparative approach. **Futuyma** also writes interesting lines on prediction. With respect to macroevolutionary diversification, he compares evolutionary theory to meteorological theory that is able to provide explanation without large-scale prediction. On the other hand, Futuyma points out the innumerable successful predictions of DNA sequences and adaptive associations between phenotypic traits and environmental conditions. **Bokma** agrees that the existing evolutionary framework is not predictive over longer periods of time. In fact, he argues that the constant confirmation of the ubiquity of adaptation as a driver of evolution is largely an artifact of an epistemological bias. Other predictions, such as quantitative predictions about relationships between environmental change, genetic change, and speciation rates, can offer more sound evaluations and bring forward better evolutionary hypotheses.

How is human cultural evolution to be understood in macroevolutionary terms? **Salthe** mentions how cultural evolution—especially technological innovation—has been a crucial continuation of the tendency of evolution toward entropy. Evolution—cosmic, biological, and technological—has produced systems that depend upon, and produce, energy flows of greater and greater intensity through them. **Gontier** goes into the fine-grained epistemological nuances of studying cultures and languages as "beings" or biological individuals that blur the distinction between the "living" and the "dead" and shows the dance of ontological partitioning that has been going on for centuries in the definition of disciplines and their domains of study, a dynamic evolution that still goes on today with fascinating developments.

How does macroevolution relate to the Modern and Extended Synthesis? Macroevolution is the title of a collection in honor of Stephen Jay Gould (Vrba and Eldredge 2005). Gould, in his scientific testament, had written: "For some reasons still unclear to me, I always found the theory of how evolution works more fascinating than the realized pageant of its paleontological results, and my major interest therefore always focused upon principles of macroevolution" (Gould 2002, p. 38). Vrba, Stanley, Eldredge, and Gould were part of the paleobiological revolution that, in the seventies, brought forth theory and practice of macroevolutionary research. Decades have passed, and macroevolution not only remained a sustained and growing field of research but it also became entangled with more and more fields of biology, demanding for their specific empirical and theoretical contributions.

Several essays of the book address the relationship between macroevolution and the Modern Synthesis (MS). Although the MS, as a concept used to designate a shared theoretical framework, is itself a problematic object, Mayr and Provine (1980) describe the origin of the MS as an outcome of two distinct phases in time. The first phase, ranging from 1910–1920 to 1940 encompasses the reconciliation of Darwin's theory of natural selection with Mendel's theory of inheritance as well as with aspects of de Vries' and others' mutation theory. The 'second synthesis,' that took place from 1930 to 1940, was characterized by the incorporation of previously independent fields, such as systematics and taxonomy, zoology and botany, paleontology and morphology, and embryology. The 1980 account edited by Mayr and Provine was paralleled and immediately followed by pleas for an extension of the modern synthesis. One of those pleas came from within the field of paleobiology, where in the 1970s a 'revolution' took place (Sepkoski and Ruse 2009; Sepkoski 2012). Since Darwin, paleontology and its subject field, the fossil record, had been occupying a paradoxical position: Fossils were, on the one hand, necessary evidence, and, on the other hand, a place of embarrassing failures of prediction. Work by Simpson (1944), Eldredge and Gould (1972), and Stanley (1979) proved that the fossil record can indeed exhibit law-like patterns and regularities of its own. Subsequently, macroevolutionary scholars started to develop field-specific methods, but scholars on both micro- and macro- fields continue to disagree on whether macroevolution in and of itself requires a radical reconceptualization of Neodarwinism. **Gontier**, for example, points out that Eldredge repeatedly characterizes himself as a "knee-jerked Neodarwinian," while she attributes more revolutionary élan to Gould.

In his magisterial chapter, **Futuyma** provides an informative background on the foundation of the MS, which he designates as the Evolutionary Synthesis and focusses on the contributions made by scholars from a variety of countries who, although well-known in evolutionary circles, are not routinely listed as 'architects' of the discipline. Futuyma explains how founders of the evolutionary synthesis never really advocated that natural selection is the "sole cause" of evolution, and they merely provided evidence in favor of gradual evolution which they used to explain aspects of macroevolution. Scholars such as Bernhard Rensch, for example, provided macroevolutionary explanations for apparent orthogenetic trends. **Futuyma** exhorts critics to consider the particular challenges to which the Evolutionary Synthesis has responded successfully, and he downplays the idea of a 'hardening' of the late ES, emphasizing instead its flexibility. **Bokma**, on the other hand, in his focus on stasis and punctuations in macroevolution, points out that stasis was uncritically considered as fully compatible with basic evolutionary theory, and even denied as an observational fact. He agrees with Gould (1983, 2002) that the MS went through a "hardening" during the twentieth century, perhaps exacerbated by a defensive attitude.

Serrelli presents Ernst Mayr's description of the MS as a process engaging separate fields of research by virtue of communication, reciprocal awareness and familiarity, producing a shared vocabulary that is still largely used today in macroevolutionary studies. Serrelli explores how graphical representations may have worked as a major bridge between fields that were mutually independent, sometimes suspicious of each other, and locked.

4 Conclusion

In this introduction, we have given spots and keys to reading this rich volume on the interpretation, evidence, and explanation of macroevolution. The reader will be able to find more threads and much more knowledge running through the pages by our excellent contributors and will get the feeling of an exciting field of research that is going to grow even more and surprise us in the next years. While this book is being published, the debate on extending the Modern Synthesis is carried over on major scientific journals (e.g., Laland et al. 2014), as well as by other media. The interested reader will follow these developments to see how this debate will be settled, at least temporarily, in the next years, and the contributors of this book as well as we at the Applied Evolutionary Epistemology Laboratory are happy to have contributed to the overall debate.

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