

# An introduction to the special issue: inferring macroevolutionary patterns and processes from microevolutionary mechanisms

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## Introduction

One of the major remaining challenges in evolutionary biology is to explain how evolution within and among populations (i.e., microevolution) gives rise to the patterns and processes of evolution across species and higher taxa (i.e., macroevolution). This special issue in *Journal of Evolutionary Biology* entitled “Inferring macroevolutionary patterns and processes from microevolutionary mechanisms” brings together a collection of contributions from diverse disciplines of biology to advance our understanding of the link between micro- and macroevolution. Since the Modern Synthesis (Huxley, 1942), the relationship between micro- and macroevolution has often been framed as a binary question: (a) Is macroevolution simply a linear extension of microevolutionary processes over longer time scales (Arnold, 2014; Charlesworth et al., 1982)? Or (b) does it involve processes that are qualitatively distinct from microevolution (Erwin, 2000; Gould & Eldredge, 1977; Stanley, 1982)? This dichotomy has, for decades, divided evolutionary biologists into those focussed on microevolution and those dedicated to macroevolution.

Past decades have seen several attempts to bridge the gap between micro- and macroevolutionary research (Arnold et al., 2001; Reznick and Ricklefs, 2009; Rolland et al., 2023). Their optimism has been supported by the wealth of molecular and phenotypic data and new statistical tools to study evolution across different evolutionary time scales. Consequently, the scope for updating the structural integrity of micro- and macroevolutionary research programmes is now greater than ever. Against this backdrop, this special issue is intended as a forum for researchers from different disciplines of evolutionary biology. Throughout the issue, readers will see theoretical and methodological frameworks established in one discipline being challenged by perspectives from other disciplines. We as guest editors have strived to illuminate the legitimacy of epistemic virtues in diverging opinions to share our perspective that the quest to bridge micro- and macroevolution provides

exciting opportunities for cross-disciplinary collaborations and new discoveries.

The idea for this special issue originated from a symposium held during the European Society for Evolutionary Biology Congress between August 14th and 19th, 2022, in Prague, Czech Republic. We extended invitations to symposium participants as well as other leading evolutionary biologists to contribute to this issue. The result is a diverse collection of theories, methodologies, synthetic reviews, perspectives, and empirical analyses drawn from natural systems, all aimed at deepening our understanding of the link between micro- and macroevolution. Despite the diversity of contributions, several converging themes have emerged: (a) the drivers of speciation dynamics, (b) the (in)consistencies in evolutionary rates across different time scales, (c) advancements in methods, and (d) the philosophical and epistemological issues about bridging micro- and macroevolution. Below, we will synthesize contributions around these four themes.

## The drivers of speciation dynamics

If we define micro- and macroevolution as evolution below and above the species level, the speciation process is literally the bridge between micro- and macroevolution. Although this definition has its own controversies (Kearney et al., 2024), it provides an operational point of departure. Consequently, the formation, maintenance, and reinforcement of divergence between reproducing populations have been extensively studied in the context of micro–macro debate (Mayr, 1982b; Reznick and Ricklefs, 2009). Thus, studying how the gradual adaptation of populations becomes the origin of new lineages and life forms, or the role of post-divergence processes such as character displacement (Grant, 1972; Losos & Schluter, 2000; Schluter, 2000) or hybridization (Mallet, 2007; Seehausen, 2004) on phenotypic change and diversification, have been the central subject of micro–macro discussion for decades (Coyne et al., 2004; Simpson, 1944, 1953).

These processes can give an intuition on how divergence can turn gradual changes into major evolutionary innovations such as aquatic/terrestrial transitions or the origin of complex organs (Mayr, 1982b). More recently, quantitative studies aimed at describing the speciation process in mathematical terms to estimate how individual-level variation can scale up to a greater level of organization for both phenotypic evolution (Aguilée et al., 2018; Duchen et al., 2020, 2021; Gaboriau et al., 2024) and species diversification (Alencar & Quental, 2021; Harvey et al., 2019; Li et al., 2018; Manceau et al., 2017). Additionally, our understanding of the process of speciation adds consistency to the debate around what constitutes a species, that in turn affects how macroevolutionary studies are defined, perceived, and executed (Irwin et al., 2001; Mallet, 2007; Wu, 2001). Contributions in this issue illustrate how spatially explicit models of divergence between individuals or populations build-up to generate patterns observable at the macroevolutionary scale.

To illustrate this trend, Couvert et al. (2024) explore general frameworks that employ models based on microevolutionary processes to predict patterns of lineage diversification. They present the historical developments and controversies surrounding three classes of models that can be used to achieve this goal. Building upon these existing models, they propose a new formalism for the speciation problem which has the potential to break the bonds of lineage-based diversification models. They argue that such developments can address how secondary contact, ratchet effects on the build-up of divergence, and the emergence of spatial barriers can affect diversification. Other contributions seem to endorse this claim, as each study about speciation dynamics presented in this special issue attempts at linking one of these three processes with macroevolutionary patterns. First, Freitas et al. (2024) formalize the speciation dynamics of populations inhabiting two islands that are either connected or isolated depending on the sea level. The study used historical sea-level oscillation over the past 800 thousand years, and kept track of each speciation and extinction event throughout the individual-based simulations. They argue that the balance of the complete phylogeny can be a sign of whether speciation is induced by migration or isolation, and noted that high isolation times accelerated speciation due to prolonged absence of secondary contact. Jamonneau et al. (2024) provide an empirical illustration of this phenomenon by testing the hypothesis that long-distance dispersal is a driver of speciation in freshwater fish subfamily Sicydiinae. By gathering phenotypic and genotypic data within and among species, the authors observed demographic expansions in multiple species and rapid phenotypic divergence. They envision that the high fecundity and high colonization ability of this subfamily lead to diversification through founder events and jump dispersal beyond the range distribution of the ancestral species, that are maintained by sea-level fluctuations. Zeng & Hembry (2024) examine the relationship between co-evolution of species and their rate of diversification, through individual-based simulations of co-evolving species. The authors argue that, for parasites or obligate mutualists, selection against phenotypic novelty impedes dispersal, thereby enhancing genetic differentiation across space, creating a ratchet effect that promotes species richness accumulation through speciation. Conversely, they argue that for host species, selection for novelty enhances dispersal, which impedes genetic differentiation across space and eventually, limiting species richness accumulation through

speciation. Finally, Ciccheto et al. (2024) studied how different modalities of landscape fragmentation influenced diversification by controlling the speciation process. The study uses an individual-based spatially explicit model on alternative spatial grids representing various landscape fragmentation scenarios. They use this approach to evaluate how spatial barriers affect measurements of macroevolutionary processes such as divergence rates or diversity imbalance. They demonstrate that over a fragmentation gradient, intermediate levels of fragmentation maximize diversification rates while high levels of fragmentation favour diversity imbalance.

## The (in)consistencies in evolutionary rates across time scales

Nowhere has the relationship between micro- and macroevolution been more rigorously debated than in studies of evolutionary rates. Starting from the seminal work of Gingerich (1983), the consistencies and inconsistencies in rates of molecular evolution, phenotypic evolution, and lineage diversification across different time scales have been widely documented and discussed (Estes & Arnold, 2007; Hansen & Houle, 2004; Harmon et al., 2021; Latrille et al., 2023; O'Meara & Beaulieu, 2024; Rolland et al., 2023; Uyeda et al., 2011). Three elements of this debate have key relevance to the current issue. First, rates of phenotypic evolution over long time scales are often too low compared with expectations under the drift model and empirical estimates of standing genetic and mutational variance (Hansen & Houle, 2004; Houle et al., 2017; Lynch, 1990). Second, standing genetic variance (e.g., evolvability; Hansen & Houle, 2008a; Houle, 1992) is typically high (Hansen & Pélabon, 2021) and selection is pervasive in nature (Endler, 1986; Hereford et al., 2004; Kingsolver et al., 2001). The outcome should be rapid evolution, but little evolution is observed in practice (Bradshaw et al., 1991; Kruuk et al., 2002; Pujol et al., 2018). These mismatches between expectations and observations in rates suggest a decoupling of micro- and macroevolution (Gould & Eldredge, 1977). However, third, mounting evidence shows that standing variation of contemporary populations are correlated positively with the rates and directions of phenotypic divergence among populations and taxa (Holstad et al., 2024; Houle et al., 2017; Hunt, 2007; McGlothlin et al., 2018; Rohner & Berger, 2023; Tsuboi et al., 2018; Voje et al., 2023). Four contributions of the issue address this problem.

First, Voje et al. (2024) used a comprehensive fossil record of diatom algae to question how the evolution of the adaptive landscape affects evolutionary rates and the direction of evolution. By fitting a set of models of phenotypic evolution (Hansen & Houle, 2008b; Voje, 2023) to two time-series sampled in different lakes, the authors test alternative scenarios of evolution in size. They found both time-series fit a model with a moving adaptive landscape and estimate rates of evolution that are congruent with observations in contemporary populations. They conclude that phenotypic evolution observed at the macroevolutionary scale may be a consequence of both gradual and sudden repositioning of adaptive peaks. From a theoretical perspective, Hansen (2024) envisions that the mode of evolution shifts as time expands from micro- to macroevolutionary scales. The study delineates three distinct stochastic processes which are giving rise to different rates of evolution, and formalizes the theoretical expectation under each of these processes. Although the mathematical

formulation presented allows a smooth transition from one process to the next, the author argues that they actually act to decouple the different scales by making macroevolutionary dynamics independent of microevolutionary parameters and vice versa. Focussing on the rising evidence for positive correlations between standing variation and divergence (Holstad et al., 2024; Voje et al., 2023), Tsuboi et al. (2024) claim that this pattern is non-trivial and represents a serious explanatory challenge for evolutionary biologists. The perspective offered by the authors is explicitly pluralistic, aiming to decentralize explanatory tactics and highlight complementary roles of quantitative genetics, comparative morphology, evo-devo, and palaeontology in resolving “the Paradox of Predictability.” Viewing issues surrounding rates of evolution from a methodological perspective, Latrille et al. (2024) formalize the expected relationship between standing variation and divergence under a neutral evolution to propose a neutrality index to test for different regimes of selection acting on a quantitative trait. The novelty lies in their dual-use of phenotypic and genomic data: the index they propose is a ratio of intra- and interspecies phenotypic variations normalized by nucleotide divergence and polymorphism obtained from a separate neutral set of markers. By applying this method to brain and body mass in mammals, the authors find evidence of diversifying selection, which contradicts some observations introduced in the preceding section. They argue that divergence (i.e., interspecies phenotypic variation) may be more comparable to phenotypic variance per substitution than to sequence-free estimators of variance. If so, the inconsistencies in rates of phenotypic evolution across time scales (Hansen & Houle, 2004; Houle et al., 2017; Lynch, 1990) may not be as severe as they initially appear.

### Microevolutionary processes as fuel for macroevolution: resurrecting the Felsenstein’s conjecture on phylogenetic comparative methods

It is unquestionable that much of our renewed interest to the micro–macro debate is fuelled by the development of statistical methods tailored to handle macroevolutionary data. The central role of phylogenetic comparative methods (PCMs) in our understanding of the relationship between micro- and macroevolution is widely appreciated (Cornwallis and Griffin, 2024; Harmon et al., 2021; Rolland et al., 2023). What is much less acknowledged is the fact that the most successful process-based models of phenotypic evolution in PCM—such as the Brownian motion and the Ornstein–Uhlenbeck models—were originally derived from a model of evolution in trait means in quantitative genetics (Felsenstein, 1988; Lande, 1976). Although motivations for improving statistical rigor in analyses of cross-species data have played a critical role in the development and dissemination of PCMs (Harvey & Pagel, 1991), the method-centric view of PCM often fell short in providing explanations for how these methods really help us addressing the link between micro- and macroevolution (Uyeda et al., 2018). It has even argued that PCMs are only addressing microevolutionary questions because causal contents of hypotheses tested by PCM often exclusively concern microevolutionary processes (Olson, 2021). Here, we highlight a perspective eloquently presented by Felsenstein (1988, p. 446) “My argument is that the methods used to

study the evolution of quantitative characters within populations can profitably be used on a phylogenetic scale to illumine the connection between pattern and process.” Viewing PCMs from this broad vantage point, four contributions in our special issue provide new insights into our approaches to address the link between micro- and macroevolution.

Revell et al. (2024) propose a new PCM that tests hypotheses about rates of evolution in discrete characters. This extends a class of PCM originally proposed by Pagel (1994) by allowing the transition rate matrix (i.e., the Q-matrix) of a continuous Markov model to differ among clades, lineages, or time periods. At a glance, this contribution exclusively concerns the domain of macroevolution. However, the authors point out several compelling cases where clear connections to microevolutionary processes have facilitated the development and implementation of PCMs, and motivate their work in light of the quantitative-genetic threshold model of Wright (1934). Focussing on the quantitative-genetic framework, Watanabe (2024) introduces a statistically and mathematically rigorous distribution theory for testing the (dis)similarity between variance and covariance matrices. This is a widely used approach to test the micro–macro link in evolutionary quantitative genetics (Arnold, 2023). The author proposes the squared cosine of the angle as a favourable metric for statistical tests and demonstrates its use through re-analyses of two published datasets. A more empirical approach, yet one that makes intriguing connections to PCMs, is taken by Tsuboi & Takahashi (2024). Focussing on cichlid fishes from Lake Tanganyika, the authors assess the role of sexually divergent selection and allometric constraints in shaping the pattern of sexual dimorphism among taxa. This assessment is performed at two levels of biological organizations: Interspecies level using PCMs where authors highlight the signature of rapid adaptations to changing sexual selection regimes; intraspecies level using allometry to show a restructuring of allometric constraints. Importantly, they showed tight allometry in the absence of sex-specific selection, enabling them to rule out the possibility that allometric constraints were weak to begin with. Leménager et al. (2024) take one step further. They envision that the congruence of intra- and interspecific variation is shaped by ecological circumstances, an idea they label “the niche variation hypothesis (NVH)”. Combining analyses of intraspecific variance with estimates of interspecific variation from PCM, the authors show partial support for NVH in floral traits of the flowering plant family Gesneriaceae. These studies illustrate how micro- and macroevolutionary data and methods can be conceptually unified to improve our mechanistic understanding of macroevolutionary processes and patterns.

### Philosophical considerations

The relationship between micro- and macroevolution has also been a popular theme in the philosophy of science (Ayala, 1982; Folguera & Lombardi, 2012; Huneman, 2017). Here, we do not review diverse philosophical accounts of this debate (e.g., Turner & Havstad, 2019), but introduction of some key roles of philosophical perspectives in addressing scientific controversy would be helpful. Love (2010) distinguished *content* and *structure* of a scientific theory. Content includes “empirical findings, dynamical models, and key concepts, among other items” (Love, 2010, p. 435) while structure concerns “how the contents are organized” (Love, 2010, p. 405).

According to Love (2010), evolutionary biologists often assess the value of theory by asking whether its content is sufficient. For example, proponents of the Modern Synthesis have long argued that established microevolutionary processes—mutation, selection, drift, and migration—are sufficient to describe macroevolutionary patterns (e.g., Charlesworth et al., 1982). However, sufficiency is not the only yardstick for evaluating a theory. An alternative approach is to evaluate evolutionary theory by comparing its structure to those of more established theories in physics, a perspective that is already making progress within the literature of systems biology and evo-devo (Kaneko & Furusawa, 2018). Recognizing the structural perspective allows viewing theory from an angle less frequently considered by biologists. As such, philosophical considerations offer biologists a moment to pause, step back, and analyse the network of causes, epistemic beliefs, practices, and scientific methods among conflicting opinions to navigate our thinking toward a resolution.

The perspective of Kearney et al. (2024) starts with a brief historical overview of how the distinctions between what we perceive as “microevolution” and “macroevolution” today have emerged. Through a review of the reticulated phylogeny and the halobiont concept, the authors underscore the challenges of compartmentalizing evolution into discrete units within the evolutionary hierarchy. A *dialectical* view of evolutionary processes and patterns is then proposed as a critical perspective to bridge micro- and macroevolution. Following Levins and Lewontin (1985), a dialectical view holds that parts and whole are interdependent, with no predefined directions of causality across levels of organization. In the context of micro–macro debate, dialecticians would argue against privileging any single level in our explanations of evolution—whether it be gene (Ågren, 2021; Dawkins, 1976), development (Lala et al., 2024), individual (Williams, 1996), population (Mayr, 2004), evolving metapopulation lineage (De Queiroz, 2007), or species (Mayr, 1982a). Instead, all levels are seen as interconnected parts of a dynamical system that are co-evolving through complex causal relationships (Buss, 1987; Sterelny, 1996). In a dialectical view of the world, therefore, evolutionary biologists are not well-positioned to say much about which levels and factors are more important than others. However, different kinds of causalities have different roles. The focus of the micro–macro debate, then, should be the identification of diverging and often complementary roles of different disciplines (Liow et al., 2023; Love et al., 2022; Rolland et al., 2023; Tsuboi et al., 2024), rather than an examination of what practices, methods, scholarly traditions, and cultures are superior in our explanation. In this way, Kearney et al. (2024) challenge the monolithic evolutionary theory championed by some architects of the Modern Synthesis.

## Future directions

This special issue demonstrates that the quest to link micro- and macroevolution continues to attract the interest of researchers across diverse disciplines of biology. Our special issue also suggests that the field is currently at a dynamic phase, with some areas of research proving unexpectedly successful while others face persistent challenges. Our assessment aligns with that of Schluter (2024), who recently remarked on the surprising success of quantitative-genetic variation to

predict aspects of macroevolution, contrasted by the struggle in linking descriptors of speciation processes to speciation–extinction dynamics. What deserves our attention is that the collection of articles in this special issue highlights multiple evolutionary processes and mechanisms operating at various levels and directions. We are witnessing a rising realization that a pluralistic view of evolution may be necessary to tighten the structural integrity of micro- and macroevolutionary research. Rather than seeking a single explanation, perspectives offered in this special issue invite readers to embrace multiple directions of causes and effects that play distinct and complementary roles in our understanding and explanation of the link between micro- and macroevolution.

Forty-four years ago, a colloquium entitled “Macroevolution: Patterns and Processes” was held at the Field Museum of Natural History in Chicago, Illinois, USA. Based on historical anecdotes (Levinton and Futuyma, 1982; Lewin, 1980), the schism between those who study microevolution and those who study macroevolution during this conference appears to have been so severe that “*many have declared the field to be in a sorry state*” (Futuyma, 1988, p. 217). The title of this special issue pays tribute to that pivotal moment in the history of evolutionary biology, which has profoundly influenced our perception of the micro–macro debate ever since. In closing, we shall ask ourselves: Is the field in a sorry state? The answer is a clear no. Our experience in bringing together this special issue has shown us uncharted possibilities of empirical and theoretical research and the growing excitement and promise of new collaborations. We hope that this special issue will facilitate the next round of research efforts to turn this promise into reality.

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## Author contributions

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