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Opinion

Cross-disciplinary information for understanding macroevolution

Lee Hsiang Liow, [1,4,*,@] Josef Uyeda, [2,4,@] and Gene Hunt [3,4,@]

Many different macroevolutionary models can produce the same observations. Despite efforts in building more complex and realistic models, it may still be difficult to distinguish the processes that have generated the biodiversity we observe. In this opinion we argue that we can make new progress by reaching out across disciplines, relying on independent data and theory to constrain macroevolutionary inference. Using mainly paleontological insights and data, we illustrate how we can eliminate less plausible or implausible models, and/or parts of parameter space, while applying comparative phylogenetic approaches. We emphasize that such cross-disciplinary insights and data can be drawn between many other disciplines relevant to macroevolution. We urge cross-disciplinary training, and collaboration using common-use databases as a platform for increasing our understanding.

Macroevolution needs both model development and cross-disciplinary insights

The age of using **timetrees** (see Glossary) to infer genealogical relationships and evolutionary history was ushered in by the advent of cheaper sequencing, increasing computational power, and mounting sophistication of phylogenetic models [1–3]. Timetrees are common starting points for inferring evolutionary history, **diversification rates**, trait evolution, and the factors that shape them. The fossil record, with its direct temporal information, has also long been used to infer macroevolutionary history. However, paleontological approaches are challenged by spotty data with many temporal, spatial, and taxonomic gaps. Similarly, whereas extant timetrees often sample extant clades quite thoroughly, they contain little direct information about past lineages and events [4].

In the absence of direct past information, **phylogenetic comparative methods (PCMs)** use statistical models to reconstruct history, often using extant timetrees. The development and elaboration of PCMs for studying diversification (using **birth–death models**), trait evolution, and their interrelationships have triggered incredible growth in our understanding of evolutionary history and processes over deep time, and their use constitutes standard practice when studying comparative data across extant and sometimes fossil species [5]. In these models, historical reconstructions are often the direct target of inference, such as the estimation of ancestral states or past evolutionary rates. Other times, such reconstructions are used to gain understanding of a specific relationship: for instance, the evolutionary correlation between two traits. However, reconstructed histories are usually based on a single model or a limited set of models. This means that while some types of uncertainties (e.g., topological or branch-length uncertainties) may be incorporated, the uncertainty associated with unexamined but plausible models is usually not taken into account. The existence of such a blind spot raises profound concerns over the dependence of inference on the finite set of models a researcher chooses for reconstructing the past [6,7] and applies to model-based macroevolutionary reconstructions in general.

Highlights

The rapid accumulation of information from diverse sources – such as cheap sequencing and growing community databases, together with improvements in computational speed – has fueled a growth in increasingly complex models in many fields, including macroevolutionary biology.

Despite the rate of increase in data accumulation, temporal, taxonomic, and other data gaps will always exist.

It has become apparent that macroevolutionary models are often impossible to distinguish, even with huge volumes of data.

A way out of this quandary is to use independent information across disciplines to limit plausible models and to constrain parameters.

[1]Natural History Museum, University of Oslo, Oslo 0562, Norway
[2]Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA, 24061, USA
[3]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA
[4]These authors contributed equally to this work.

*Correspondence:
l.h.liow@nhm.uio.no (L.H. Liow).
[@]Twitter: @lhiow (L.H. Liow), @pseudacris (J. Uyeda), and @GeneHunt_NMNH (G. Hunt).

In an important recent paper on this topic, Louca and Pennell [6] showed that extant timetrees cannot distinguish among different diversification scenarios, regardless of the amount of data available. Thus, an infinite number of different speciation and extinction histories will form a **congruence class** of explanations that are all equally compatible with any given extant timetree. In other words, any particular phylogenetic outcome is consistent with a myriad of models and histories that are not statistically **identifiable**. As solutions, authors have variously suggested focusing on *a priori* hypotheses [8], different parameterizations of diversification rates [9,10], or potentially returning to classical comparative questions that involve comparing sister groups [11]. One particularly fruitful new avenue for alleviating the congruence class problem could be to broadly sample model spaces to recognize their common features for identifying robust macroevolutionary inferences [12].

These suggestions are promising, but broadly illustrate the heavy reliance on models for interpolation where empirical information is missing. It may appear that PCMs are currently mired in uncertainty, stuck between increasingly complex models that may not be distinguishable or estimable and simpler versions that are incapable of capturing realistic evolutionary dynamics. Here, we reject such pessimism, and view PCMs as essential to further progress in macroevolutionary research. We argue that the data and insights needed to illuminate the path forward are largely already in hand. However, improving understanding and future model development needs cross-disciplinarity to connect, constrain, and inform models with disparate data sources and knowledge. While our focus is on illustrating how the 'blind spots' of PCMs can be illuminated by such community efforts, we likewise expect reciprocal benefits of increasing integration of (phylogenetic) methods and data in other macroevolutionary disciplines. We emphasize that phylogenies will remain key to understanding clade diversification and its causes, as these provide (via topology and branch lengths) information on the timing of events and processes [5], despite difficulties related to model identifiability [6].

Cross-disciplinary integration to constrain models and parameters

This parable from ancient India is a well-known one: never having seen an elephant, some blind men each touched a small part of the animal and were adamant that their own limited experience describes the whole animal. While standing from the vantage points of our own specific disciplines, we can be subject to the same lack of appreciation for a holistic view of evolution.

Progress may be made by reaching for independent information and evidence that can impose constraints and hence inform evolutionary history [8,13], to avoid the pitfalls of a fragmented or '1D' view of macroevolution. Because we are most familiar with insights and data from the fossil record, we will largely use paleontological examples to illustrate how independent constraints have been or can be applied to alleviate the diminishing returns in using increasingly complex PCMs. Other approaches could supply independent information in macroevolutionary questions – including ecological theory [14], paleoclimate and biogeographic processes [15], developmental biology [16,17], quantitative genetics [18], and others (Figure 1) – but we develop these avenues less in this opinion. One seemingly obvious way to use the fossil record in PCMs is to incorporate species sampled in the past in phylogenies [6,19]. Alas, simply adding fossil taxa in timetrees, though it may have other benefits, will not resolve the impasse of congruent diversification models [13].

Constraining diversification models

Many simulation studies have noted the greater difficulty in estimating extinction compared to speciation when using extant timetrees [20,21]. Empirical estimates of extinction from extant timetrees are often unrealistically low, or even zero [4] (Box 1). Different explanations have been proposed for very low estimates of extinction [22,23] but what is pertinent here is that this result

Glossary

Adaptive zones: a concept introduced by paleontologist G.G. Simpson that describes the range of phenotypic values that lineages can hold when adapted to a specific set of environmental conditions, or a specific ecological niche.

Birth–death models: a family of stochastic process models used to study how the number of species changes through time via speciation and extinction.

Congruence classes: models that are equally likely to have given rise to any given timetree. Models in the same congruence class are not identifiable (see identifiability) from one another.

Diversification rates: rates of speciation (or genus origination) and extinction usually estimated using phylogenetic tree topologies with branch lengths or using observations of fossils with temporal information.

Identifiability: the theoretical possibility of inferring the true values of a given model's underlying parameters, if a large number of observations are made for the purpose.

Likelihood surface: when statistical models are fitted to empirical data, the joint probability of observing the data for a given set of parameters is called the likelihood. Over a set of parameter values, the likelihood forms a surface with peaks and valleys, the peaks and ridges representing regions of parameter space that are more likely to generate the observed data.

Macroevolutionary parameters: variables in a macroevolutionary model that may be estimated from data. These parameters may be more or less interpretable/accurate biological measurements of features of the evolutionary processes, depending on the model and the data used.

Ornstein–Uhlenbeck (OU) models: a family of models of continuous trait evolution that combines a Brownian motion diffusion process with a deterministic pull toward an optimal trait value. At the macroevolutionary scale, these models are often used to describe adaptation to an optimal state. They can also have a microevolutionary interpretation, capturing the action of stabilizing selection and genetic drift near an adaptive peak.

Pagel's λ: a commonly used scaling of internal branches of a phylogeny, related to Brownian motion evolution of traits. $\lambda = 0$ indicates no phylogenetic influence is inconsistent with a very large body of paleontological evidence which suggests that speciation and extinction should roughly balance [4,24], a balance that is also observed in shallower extant timetrees [25]. As Raup remarked: 'for an evolutionary biologist to ignore extinction is probably as foolhardy as for a demographer to ignore mortality' [24], and yet many extant timetree studies accept low or zero extinction rates in their inferences.

The independent information about extinction from the paleontological record can be used in multiple ways. If multiple macroevolutionary models are considered, there is good justification to simply exclude models that suggest trivial levels of extinction as inconsistent with paleontological knowledge [26]. Alternatively, one can use distributions of extinction parameters from fossil studies (e.g., Box 1) as the basis for parameter priors in a Bayesian analysis. More general paleontological findings can also inform the kinds of models that are developed and considered. For example, paleontological studies commonly reveal differences in origination and extinction rates among taxa [27], which provides independent support for modern phylogenetic approaches that allow such rates to shift on tree branches [20,28]. Additionally, paleontological rates tend to vary over time with low temporal autocorrelation, and with occasional time intervals with exceptionally high rates [29]. These observations support phylogenetic approaches that allow pulses or rates that shift at multiple points in time [21,30]. Less supported by the aggregate paleontological literature are phylogenetic approaches that model temporal change in rates as smooth curves or jumps to new persistent states [31]. Such general paleontological principles should be a consistent part of phylogenetic model development, and future efforts could more directly link measurements from the fossil record as priors and parameters used in phylogenetic modeling. Similarly, models of extinction and speciation in paleontology should be, and in fact are, increasingly formulated so that their parameters are equivalent to those in birth–death models to allow direct comparisons to tree-based rates [32].

One area that has seen recent and notable success in integrating cross-disciplinary information is the spatial dynamics of diversification. This field has long debated the roles of macroevolutionary history versus present-day environmental conditions and processes in explaining geographic patterns of diversity [33]. Historical processes have sometimes been incorporated indirectly in these studies, for example, by predicting diversity from biome area that is integrated over geological time, rather than just being computed from present-day maps [33,34]. It has also recently become feasible to more directly model speciation, extinction, dispersal, and niche evolution through time, with climate dynamics taken from the output of earth system models [15,35,36]. Such diversification models are run over realistic spatial configurations based on modern geography, sometimes additionally accounting for changing continental arrangements. Recent studies taking this approach have demonstrated that realistic spatial configurations and climatic drivers can recreate well-established patterns, such as latitudinal, longitudinal, or elevational diversity gradients, even when ecological and evolutionary processes are simulated as operating uniformly on the globe. The power of this approach will only grow as increasingly sophisticated climate models become better able to replicate climate dynamics over longer timescales [37].

Constraining trait evolution models

As with diversification, models of trait evolution have rapidly increased in number and complexity, and have likewise encountered statistical challenges in the form of congruence classes and weakly identifiable or unidentifiable parameters. In navigating these challenges, we argue for using macroevolutionary models that have the potential to be biologically meaningful across disciplines.

Consider the **Ornstein–Uhlenbeck (OU) models** [38], which capture a conceptually realistic depiction of the dynamics of adaptation of a phenotypic trait to an optimal state [39,40]. The OU

on trait distributions, while $\lambda = 1$ indicates as much phylogenetic signal as Brownian motion.

Phylogenetic comparative methods (PCMs): a suite of different approaches that use relationships of lineages (i.e., phylogenies) and temporal information of the same lineages to test evolutionary hypotheses. These hypotheses can be focused on the history of traits born by the lineages and/or directed toward the diversification rates or the history of the lineages.

Timetrees: phylogenies with branching times and branch lengths usually inferred using molecular sequence data from extant species and calibrated using fossil relatives of the extant species. Timetrees estimated using extant species are termed 'extant timetrees'. Note that timetrees can also be inferred using data other than molecular sequences, including morphological data. Their calibration can also be performed using other temporal information, such as geological events or temporal samples, as in viral phylogenies [93]. Extant timetrees show genealogical relationships among living species and timings of their branching from one another.

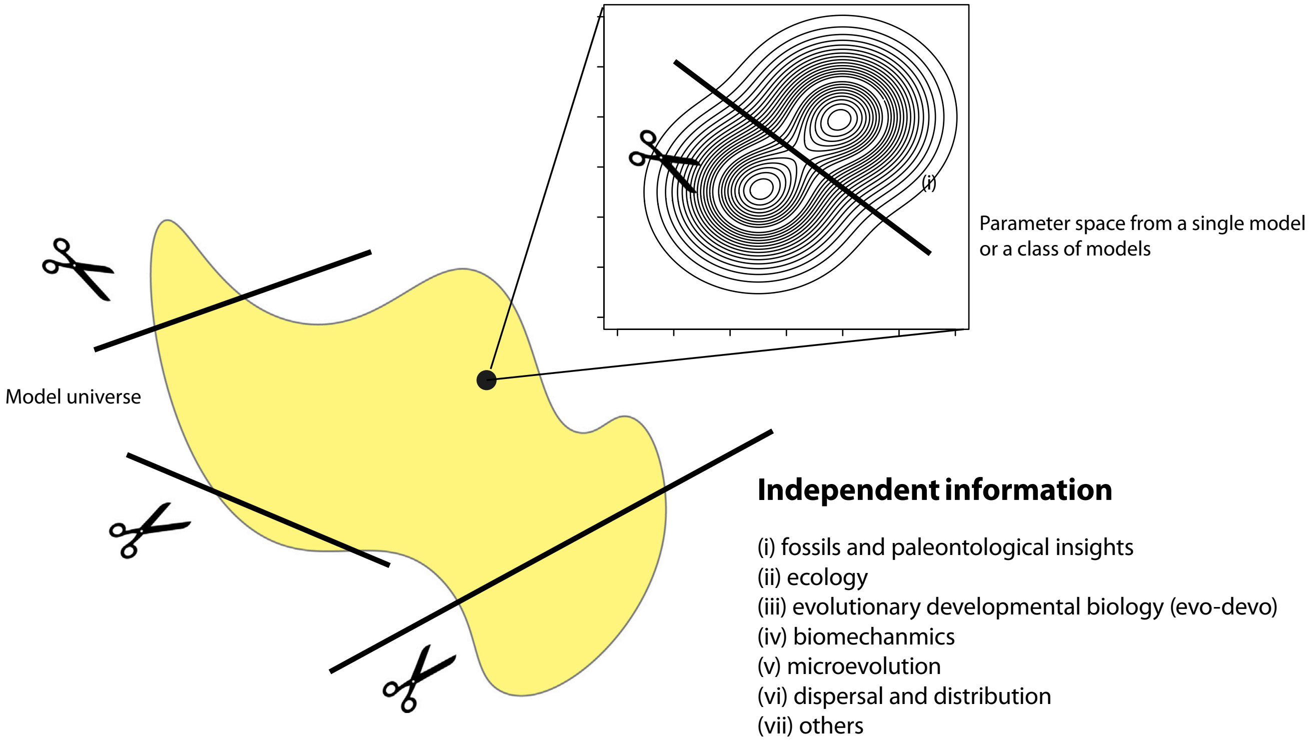

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Figure 1. Constraining the collection of macroevolutionary models: we have what we need. The yellow shape represents a collection of macroevolutionary models that contains what could represent a true underlying model for a given empirical system(s). We can chip away parts of this model space that are of low plausibility using independent data and insights (scissors), which may or may not stem from the same empirical system. These include, but are not limited to, (i) fossil data and paleontological insights, (ii) ecological data and theory, (iii) evolutionary developmental biology, (iv) biomechanics, (v) quantitative genetics and microevolutionary theory, (vi) dispersal and distributions and others. For example, beyond our own paleontological examples (e.g., Box 1), ecological limits and coexistence theory could be used to constrain diversification estimates via variation in standing richness as tantalizingly shown using simulations [68]. Likewise, the nature of individual-level interactions seems to have predictable effects on diversification [69] and could, with more in-depth study, be used to rein in a universe of plausible models. The black dot in the yellow shape represents a single (class of) model(s) within the collection of models. The contour plot represents parameter space in which we originally had two equally probable peaks, but the peak at the bottom left can be disregarded as we gain independent insights (see Box 2 for an example using fossils).

model allows researchers to test hypotheses regarding the macroevolutionary drivers of adaptation, and to estimate how long such adaptation takes to occur. However, OU models have been criticized [41,42]. Specifically, different crucial parameters in the model could interact in complex ways and generate weakly identifiable **likelihood surfaces**. For example, estimating the rate of adaptation to the optimum will be difficult if adaptation is too rapid relative to the branching events in the phylogeny (Box 2). However, the introduction of even a small number of fossil data points separated by intermediate timescales (i.e., shorter than the youngest divergence times in the phylogeny) can restore our ability to estimate evolutionary parameters (Box 2), even when those fossils cannot themselves be placed within the phylogeny. In other words, even short, fragmented sequences of phenotypic measurements from fossils can facilitate the modeling of trait evolution across a phylogeny. Importantly, neither fossils nor comparative data alone can provide good answers; each dataset provides different views that jointly illuminate the dynamics of the adaptive process. Improvements in such cross-disciplinary connection would help overcome the statistical challenges of fitting trait evolution models to phylogenetic data, and potentially enable continued development of previously unidentifiable models, such as models that incorporate biologically realistic levels of heterogeneity. Although both phylogenies and timeseries are available to paleontologists, surprisingly, only a handful of studies combine these data types into a joint analysis of evolution (e.g., [43–45]).

Box 1. Fossil priors on diversification

Here, we present an empirical example on establishing informative priors on extinction. We consider extinction fraction (= extinction rate divided by speciation rate), which is commonly used to parameterize extinction in diversification models. We estimated speciation and extinction rates using the Pradel seniority model [70] using data from species-level fossil observations of bryozoans [71] (Figure I). Speciation and extinction were assumed to be constant within families, where we follow family assignments using the World Register of Marine Species (https://www.marinespecies.org); preservation rates were allowed to vary across geological stages but were assumed to be shared among families. Speciation and extinction parameters were estimated separately in the 53 extant families that had at least 25 formally described species represented in the dataset (informal species were omitted), and extinction fractions were computed from the maximum likelihood estimates of speciation and extinction rates. To emphasize a similar qualitative feature of fossil estimates regardless of organismal group or estimation method, we added extinction fractions from rates for six mammal clades [22], using the rate estimates inferred under that paper's 'incompatible rates' method (their Supplementary Table 10; see [22] for details). These paleontologically derived extinction fractions were compared to those from a compilation of molecular phylogenies, including chordates, plants, arthropods, n = 140 clades, reported in Figure 2 of [72] (Figure I).

Consistent with general paleontological predictions, speciation and extinction rates tend to be nearly balanced when estimated in fossil bryozoans and fossil mammals (Figure I; median extinction fractions = 0.83 and 0.86, respectively). By contrast, the extant-taxa-based phylogenetic estimates indicate much lower extinction (median extinction fraction = 0.28), with only modest overlap between the two distributions. In phylogenetic studies, an extinction fraction of 0.9 is often taken to represent a high extinction scenario, but the fossil data suggest that this scenario is typical, rather than unusually high (Figure I).

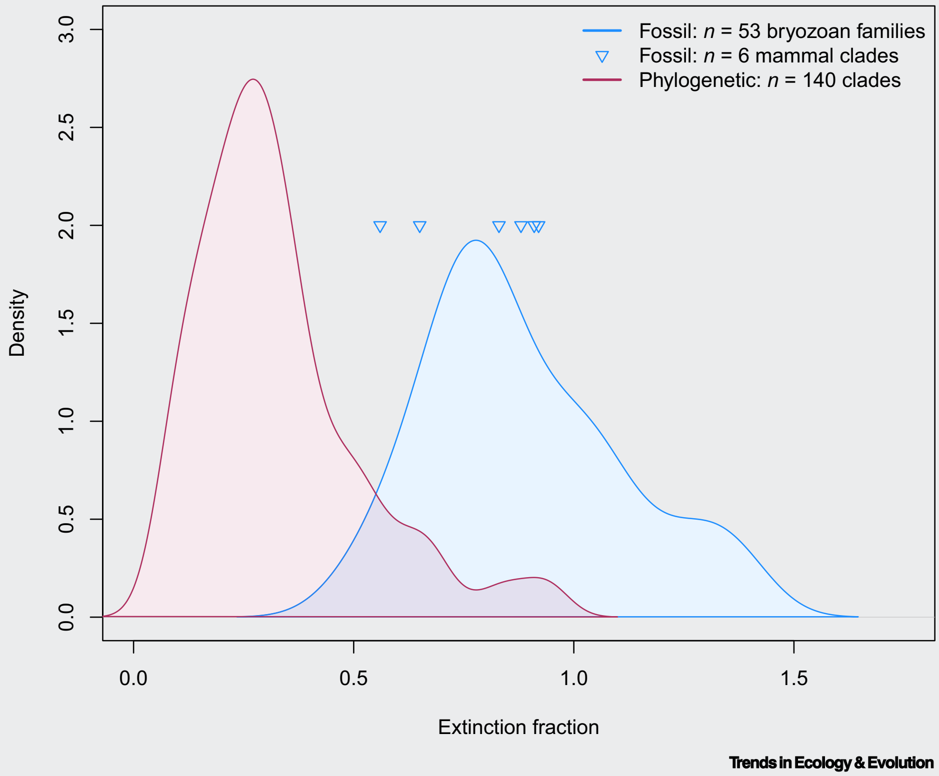

Figure I. Density plots of extinction fraction (= extinction rate divided by speciation rate) for families of bryozoans using data from fossil occurrences (in blue) [71] and for six mammal clades (blue triangles) [22]. Shown in red are extinction fractions estimated from molecular phylogenies of extant species from many different higher taxa compiled in [72]. Code and data can be retrieved at https://doi.org/10.5281/zenodo.7078649.

Box 2. Trait evolution models: priors and constraints

We present an example to illustrate how even a few fossils of uncertain placement in a phylogeny can be helpful in constraining model space in phenotypic evolution. OU models are often used to model the adaptation of continuous phenotypes to an optimal state. Nevertheless, they have been criticized for the difficulties in independently estimating their parameters in ways that may impact biological inference [41,42]. Specifically, the estimate of the rate of adaptation (α) toward the optimal state (θ) forms a weakly identifiable ridge in the likelihood surface with the estimate of the stochastic evolutionary diffusion rate (σ^2), as well as other parameters in the model, in complex ways. Since the rate of adaptation is related to, for example, the breadth of the **adaptive zone** or the distance to the adaptive peak, such uncertainties can have consequences for the interpretation of a particular adaptive scenario. To demonstrate this effect – and a potential solution – we simulated trait evolution under conditions similar to that in Figure 7 in [42], using an OU model, only differing in exploring in higher α-values, to tune the problem to standard differences in timescales between clade-wide phylogenies and fossil timeseries. As in [42], trait evolution was simulated on down-sampled datasets using the mammal tree from [3] for 10, 50, 100, and 500 tips (Figure I). In a second set of simulations, we added five observations for a hypothetical fossil timeseries evolving under the same OU model and parameters, but that is ‘detached’ from the rest of phylogeny. Each fossil observation is separated by 0.2 my (i.e., total timeseries length = 0.8 my). This addition of a modest fossil timeseries, even without placement on the phylogeny, turns a weakly identifiable likelihood ridge into an identifiable likelihood peak. This is because constraints imposed by sequential fossils over shorter timescales gives a resolution on the process absent from the rest of the phylogeny. This exercise shows that even weakly informative prior information derived from fossil traits could greatly improve the fitting of OU models to extant-only datasets, and that two-way communication between phylogenetic and paleontological views of the process can better converge on the true process and history.

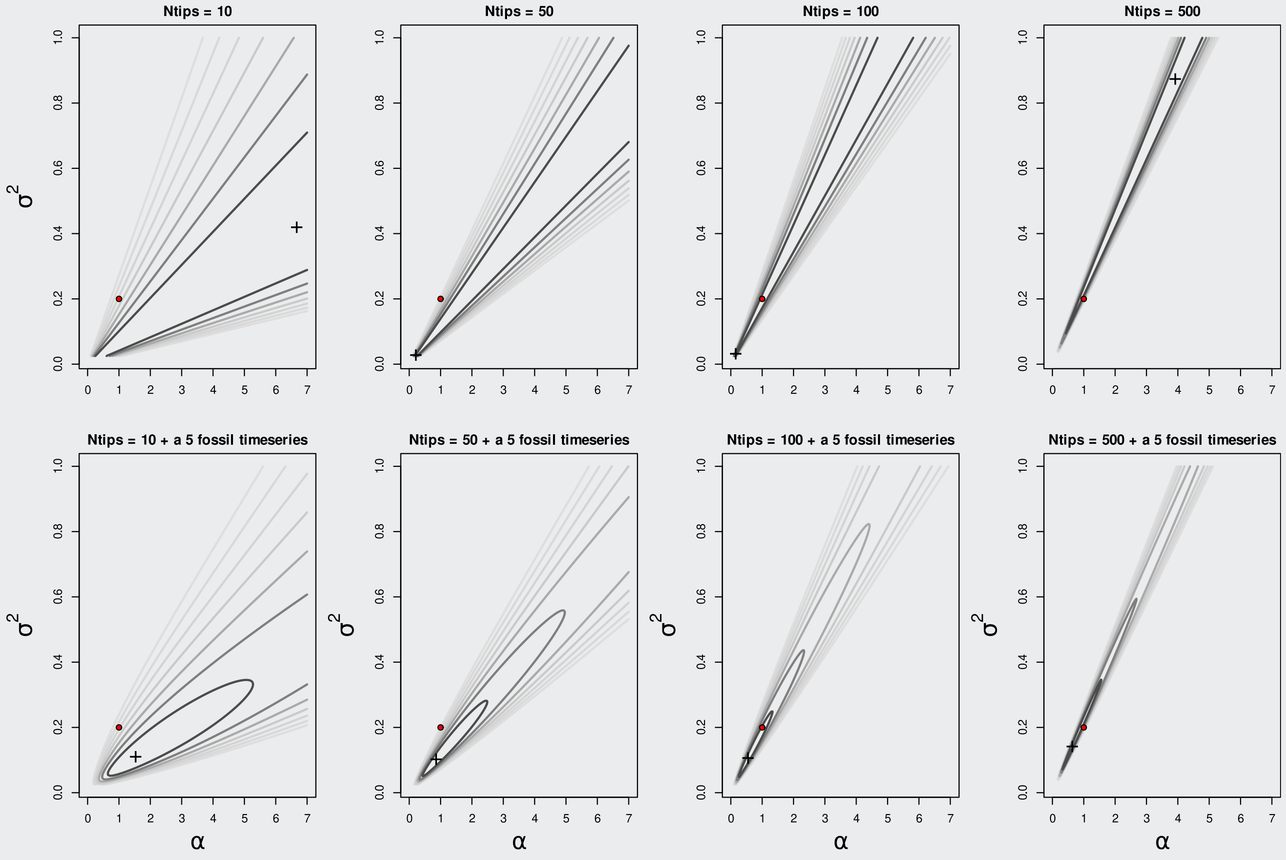

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Figure I. Likelihood surfaces for α and σ^2 parameters, with and without fossils. Columns show down-sampled datasets for 10, 50, 100, and 500 tips, where $\alpha = 1$ my^{-1} and $\sigma^2 = 0.2$. Bottom row adds an additional five data points that are detached from the rest of phylogeny. The red dot shows the true value in each panel, and + symbol indicates the highest point of the grid search on the likelihood surface. Code and data can be retrieved at https://doi.org/10.5281/zenodo.7078649. Abbreviation: Ntips, number of tips.

In general, macroevolutionary models should be first parameterized in process-based terms that are connected to data observed in other contexts (e.g., the parameters of an OU model can be estimated independently from either phylogenetic or timeseries data in ways that a model using

Pagel's λ cannot). Second, we must compile data that allow a connection between the observations and the parameters of the model: in this example, by assigning ancestor–descendent pairs with estimates of divergence in units of years. Third, considerable additional work must be conducted to understand whether and how the parameters estimated from independent data such as fossil timeseries are connected to **macroevolutionary parameters** estimated from comparative studies. While it may seem to be relatively straightforward to make such connections, attempts to quantitatively link datasets across scales may uncover underappreciated paradoxes and conflicts between scales (e.g., [16]) which will nevertheless present additional research questions that will likely drive the field forward.

While the fossil record can clearly facilitate the reconstruction of trait histories and dynamics through time, other sources of knowledge and data integration can also help to constrain macroevolutionary parameters. Data from quantitative genetics [18], developmental biology [46,47], biomechanics [48], and field studies [49] might not inform history as directly as fossils, but they nevertheless give key insights into the plausibility of parameters governing evolutionary dynamics. For example, trait models that can incorporate knowledge of anatomical dependencies and development can change our inferences when viewed at the phylogenetic scale by rejecting or accepting combinations of character states that a developmental biologist would deem implausible or plausible, respectively [47]. Enhancing existing PCMs in ways that facilitate the usage of data from these other views of the evolutionary process should be a primary target among method developers, one that will require cross-disciplinary, community efforts.

Community databases that serve multiple disciplines for breaking down cross-disciplinary barriers

A major barrier to synthesis is a cross-community awareness. For example, it is likely that the paleontologists with the expertise to effectively collect and appropriately interpret fossil information are mostly unaware of this potential need for their data in macroevolutionary modeling. Similarly, comparative biologists who work with extant taxa may not be aware that established insights and empirical parameters derived from the fossil record may help them constrain and understand models and parameters (e.g., Box 1). Crucially, cross-disciplinary data should be applied with the relevant sets of expertise. Recent studies that integrated phylogenetic modeling with fossil data found that individual fossils could have large, spurious effects on analyses when the temporal or taxonomic assignment of those fossils was doubtful [50,51]. Specialists will be able to recognize and vet these cases, but, in the absence of such interventions, problematic occurrences will be present in data harvested uncritically from published literature. The success of studies that integrate fossils and phylogenies [52] argues for the power of this approach, but collaboration and communication between fields will be key to leveraging expertise from both of these domains.

Building the infrastructure for such work will be facilitated by targeted community databases for fossil phenotypic timeseries and diversification rates, and goal-oriented cross-disciplinary networks that can train a new generation of interdisciplinary researchers. For example, expert vetted libraries of empirical origination (speciation)–extinction rates estimated from the fossil record where appropriate taxonomic data and reasonable models of sampling and preservation were applied should be compiled (Box 1). It should be noted that the great majority of fossil compilations and diversification analyses are focused at the genus level or above, thus complicating direct data exchange between comparative biology and paleontology. However, species-level fossil databases are attainable in some cases and should be developed collaboratively. Additionally, the development of theory to link genus-level data to species-level parameters [53] has been mostly neglected, but should be revisited. Likewise, compilations of phenotypic timeseries are needed for fossil data, even when those timeseries comprise only single or fragmentary ancestor–descendant pairs. Such libraries cannot be cobbled together without deeper knowledge of the sedimentological processes, and should be jointly designed, populated, and maintained by teams invested directly in the fossil record and macroevolutionary modeling. Cross-disciplinary database work for macroevolution is not without precedence: the Fossil Calibration Database [54] came about as a result of the need for the joint expertise of molecular phylogeneticists and paleontologists to understand the timing of the origination of clades.

Connecting between disciplines and timescales: a plea for expertise and uncommon data

In our experience, connections between disciplines are not accomplished by simply placing experts from different domains in a room together. Rather, we need scientists whose expertise is not strictly in either field, but rather in how those fields connect. Indeed, the great opportunities for innovation in macroevolutionary research in the future will likely be found by young scientists trained in working in these discipline gaps.

For example, the connection between microevolution and macroevolution has long been contentious, and it is reasonable to expect that their links have varying amounts of explanatory power. Nevertheless, efforts to strengthen the relationship between scales have opened new paths for understanding and improving macroevolutionary analyses. Research programs as varied as connecting macroevolutionary trait divergence to variability or evolvability of those traits [18,55], comparing geographic or temporal variation within species to differences between species in a clade [56], and determining whether speciation and extinction rates correlate with population-level attributes such as reproductive isolation [57,58], geographic isolation [59], geographic range size [60], or sexual selection [61,62] all work toward linking patterns and processes that unfold on different timescales.

However, encouraging research on the connections between micro- and macroevolutionary timescales requires more than interest; it requires data. Often, the missing link for studies of diversification and trait evolution are data on ‘intermediate’ temporal scales (10^1 to 10^4 years or even 10^5 years). Such timescales are often too long for all but the most devoted monitoring efforts, and yet shorter than can be resolved in more commonly available paleontological data. But they are not unattainable (Box 3). Indeed, establishing and/or consolidating empirical study systems involving diverse nonmodel organisms with ‘uncommon datasets’ and existing micro- to macroevolutionary resources should be a research priority (Box 3).

What do we gain by filling in the intermediate timescale data gap? Such observations will foster continued development of hierarchical models based on evolutionary and sampling processes operating at different sites and on multiple temporal scales [63], and will provide a clearer picture of what, exactly, macroevolutionary parameters are measuring. They would allow us to test more detailed hypotheses of how and when mechanistic short-timescale models of evolution [18,64] operate or break down when extrapolated to longer-term scales, both within and across species lineages [65–67]. And ultimately, providing the data and infrastructure needed to bridge across scales will foster a new generation of evolutionary thinkers capable of better bridging across disciplines and timescales.

Concluding remarks

The past couple of decades has seen excellent progress in macroevolutionary research, yet our awareness of model unidentifiability urges us to recast our questions and rethink our data compilation and modeling efforts (see Outstanding questions). We believe continued progress in

Outstanding questions

What are the independent sources of information we can use to constrain macroevolutionary models and parameters beyond those suggested here?

Are there certain kinds of external or independent evidence that will be most useful for constraining macroevolutionary models?

How do we build and what do we include in community databases of macroevolutionary data and parameters?

Can we develop models and evolutionary parameters that can be estimated meaningfully across disciplines?

How do we boost under-sampled timescales and taxa to consolidate diverse model systems to link micro- and macroevolution and hence to constrain macroevolutionary models?

On which timescales (and why) can we detect the influence of microevolutionary principles on phenotypic evolution in a macroevolutionary context and on diversification rates?

Box 3. Uncommonly studied timescales and organisms

Uncommonly studied timescales

Observations of individuals – and hence also changes in phenotypes within a population – are readily tracked over a few generations (10^0–10^1 years) in extant populations [73,74]. However, observations of individuals and their phenotypes within species-level lineages are usually captured at million-generation intervals (10^5–10^7 years) in the fossil record [75,76]. Timescale-specific patterns of phenotypic change are relatively well characterized for both types of timeseries [74,76]. However, phenotypic timeseries on intermediate timescales of decades to millennia (10^1–10^4 years) while uncommon are sometime achievable and are exceptionally valuable for linking micro- and macroevolutionary studies. Some studies tracing phenotypic changes have taken advantage of high-resolution environments, including lakes [77,78], marine regions that concentrate sediments [79], and Quaternary caves [80,81], but many more timeseries are needed, and other sedimentological environments need to be explored. It is also fruitful to distill observations from paleontological, archeological, and historical records [82], each with their own characteristic spans and resolutions [83,84]. There is similar power to be gained in understanding speciation and extinction dynamics in studies that use high-resolution stratigraphy to more finely resolve originations and extinctions in the fossil record [85,86].

Uncommonly studied organisms

Mineralized marine invertebrates and plankton commonly studied in paleontology are rarely studied by comparative phylogeneticists reliant on molecular data. Whereas phylogenetic comparative data and generational timescale insights from well-studied groups such as birds and plants have been instrumental in helping us understand evolutionary processes, the data gap in the intermediate timescale for many such taxa will be impossible to fill because of their poor fossil record. We suggest that one way forward is to invest in sequencing and molecular or whole-evidence phylogenetic construction of understudied groups with a good fossil record.

Many taxa, of course, have little or no useful fossil record. Moreover, even when a group has a rich fossil record, it may be that the morphology preserved in fossils will not capture the information needed to answer a particular question. Many aspects of behavior, life history, and ecology, for example, will simply be unknowable from fossils, and insight into their evolution will come from phylogenetically informed studies of their modern representatives. Select clades, however, can preserve surprisingly rich biological information in their mineralized fossil remains. For example, sex ratios and sexual dimorphism can be estimated in fossil ostracodes and linked to extinction rates [62], and fecundity can be estimated and hence used to study fitness components in fossil populations in bryozoans [87]. Population structure and demographic change [88] can also be estimated from well-picked fossil groups for a more nuanced view of extinction processes, which ultimately stem from negative population growth. Larval mode can be routinely inferred in mollusks and some other taxa [89], and sexually versus asexually produced individuals can be distinguished in benthic foraminifera [90] and bryozoans [91]. A combined effort in acquiring molecular, fossil and extant phenotypic, spatial observation, and ecological data from plankton [92], bryozoans, ostracodes, bivalves, and other such groups is ‘low hanging fruit’.

macroevolutionary research will come ‘between disciplines’, and require new infrastructure, resources, datasets, and training to facilitate the connection between complementary domains of expertise.

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Declaration of interests

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