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Jonathan Rolland ¹✉, L. Francisco Henao-Diaz^{2,3}, Michael Doebeli ⁴, Rachel Germain ², Luke J. Harmon ⁵, L. Lacey Knowles ⁶, Lee Hsiang Liow ⁷, Judith E. Mank ², Antonin Machac^{2,8}, Sarah P. Otto ², Matt Pennell⁹, Nicolas Salamin ¹⁰, Daniele Silvestro ^{11,12,13}, Mauro Sugawara ^{2,14}, Josef Uyeda¹⁵, Catherine E. Wagner ¹⁶ & Dolph Schluter ²

Explaining broad molecular, phenotypic and species biodiversity patterns necessitates a unifying framework spanning multiple evolutionary scales. Here we argue that although substantial effort has been made to reconcile microevolution and macroevolution, much work remains to identify the links between biological processes at play. We highlight four major questions of evolutionary biology whose solutions require conceptual bridges between micro and macroevolution. We review potential avenues for future research to establish how mechanisms at one scale (drift, mutation, migration, selection) translate to processes at the other scale (speciation, extinction, biogeographic dispersal) and vice versa. We propose ways in which current comparative methods to infer molecular evolution, phenotypic evolution and species diversification could be improved to specifically address these questions. We conclude that researchers are in a better position than ever before to build a synthesis to understand how microevolutionary dynamics unfold over millions of years.

Since the modern synthesis¹, many evolutionary biologists have focused their attention on evolution at one of two different timescales: microevolution, that is, the evolution of populations below the species level (in fields such as population genetics, phylogeography and quantitative genetics), or macroevolution, that is, the evolution of species or higher taxonomic levels (for example, phylogenetics, palaeobiology

and biogeography). Patterns at the two scales often seem to contradict one another. For example, accumulating evidence suggests that rates of evolution seem to be faster at shorter timescales than at longer timescales². This discrepancy in rates has been detected in molecular evolution, phenotypic evolution and even lineage diversification rates², leading to several paradoxes and exposing conceptual gaps in current

¹CNRS, UMR5174, Laboratoire Evolution et Diversité Biologique, Université Toulouse 3 Paul Sabatier, Toulouse, France. ²Department of Zoology, and Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada. ³Department of Ecology and Evolution, University of Chicago, Chicago, IL, USA. ⁴Department of Zoology, and Department of Mathematics, University of British Columbia, Vancouver, British Columbia, Canada. ⁵Dept. of Biological Sciences, University of Idaho, Moscow, ID, USA. ⁶Department of Ecology and Evolutionary Biology, Museum of Zoology, University of Michigan, Ann Arbor, MI, USA. ⁷Natural History Museum, University of Oslo, Oslo, Norway. ⁸Laboratory of Environmental Microbiology, Institute of Microbiology of the CAS, Prague, Czech Republic. ⁹Departments of Quantitative and Computational Biology and Biological Sciences, University of Southern California, Los Angeles, CA, USA. ¹⁰Department of Computational Biology, University of Lausanne, Lausanne, Switzerland.

¹¹Department of Biology, University of Fribourg, Fribourg, Switzerland. ¹²Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden. ¹³Gothenburg Global Biodiversity Centre, University of Gothenburg, Gothenburg, Sweden. ¹⁴Mário Schenberg Institute, São Paulo, Brazil. ¹⁵Department of Biological Sciences, Virginia Tech, Blacksburg, VA, USA. ¹⁶Department of Botany, and Program in Ecology and Evolution, University of Wyoming, Laramie, WY, USA. ✉e-mail: jonathan.rolland@univ-tlse3.fr

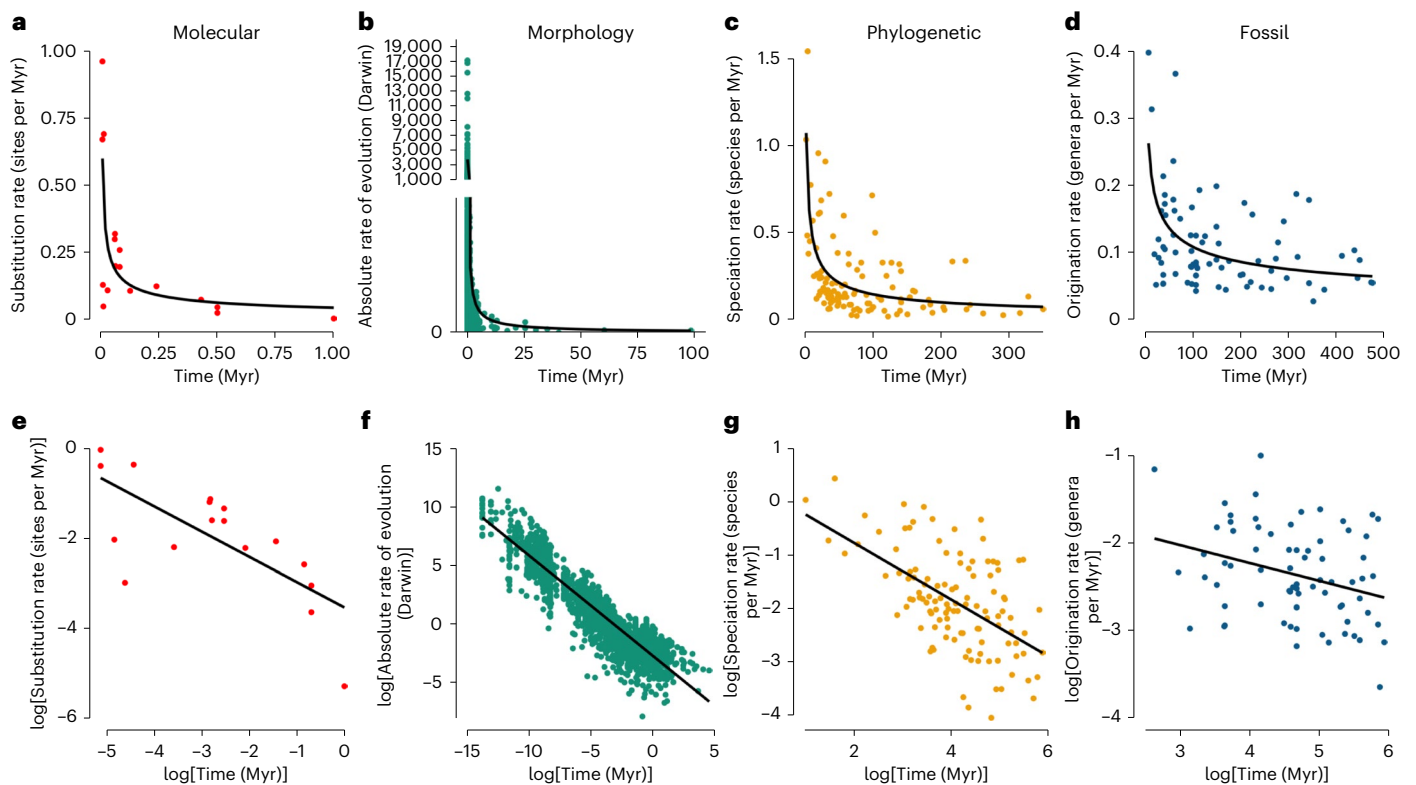


Fig. 1 | Timescale-dependent rates of molecular evolution, phenotypic evolution and speciation using phylogenetic or fossil data. a, e. Molecular evolution. **b, f.** Phenotypic evolution. **c, g.** Speciation rate using phylogenetic data. **d, h.** Speciation rate using fossil data. All rates appear faster nearer the present time and slower over longer timescales. Both axes in **e–h** have been log-transformed to show the long-term trend. This figure was recreated from the data provided in refs. 19,27,61. Darwin values of zero were removed in **f** to avoid infinite values. Note that the timescales are different for each panel, with an acceleration

in the past 100 thousand years for genes, the past million years for morphology and the past tens of million years for speciation rates, while all relationships are linear when time is log-transformed. Why this pattern is shared between different measures of evolution is not well understood². In the literature, the ‘paradox of stasis’ refers to morphological changes (**b, f**). The x-axis represents time intervals between calibration points (**a, e**), time intervals between measurements (**b, f**), clade ages (**c, g**) or clade durations (**d, h**).

theory (Fig. 1). In the past few decades, attempts have been made to bridge these gaps and reconcile these two scales^{3–12}. Nevertheless, the conceptual framework, terminology and mathematical models remain largely separate and opportunities exist to unite them. For example, speciation is often described as a lengthy divergence between two populations at the microevolutionary scale and as an instantaneous process in birth–death models at the macroevolutionary scale, but recent efforts have sought to improve this (for example, ref. 13). In addition, a known pitfall of comparative methods is their inability to identify which microevolutionary mechanisms underlie associations between phenotypic evolution and speciation–extinction dynamics. Here we argue that solving many long-standing questions in evolutionary biology will benefit from tighter conceptual linkages between micro- and macroevolutionary approaches. We focus on four yet-unsolved questions in evolutionary biology and propose avenues to tackle them.

Why does the rate of evolution appear to accelerate close to the present time? Pattern

The paradox of stasis is the apparent discrepancy between the slow rate of phenotypic evolution measured in the fossil record over geological timescales and the fast rates of evolution observed in populations at the present time^{14–18}. The pattern can be decomposed in two distinct components. The first is the acceleration of evolutionary rates close to the present (Fig. 1), which has been observed in molecular^{19–21}, phenotypic^{7,22}, phylogenetic^{23–26} and fossil data²⁷. The second component is the phenotypic stasis observed through long spans of geological

time, which we address in the next section (‘Why is there stasis over long evolutionary timescales?’).

Explanations

The perception of accelerated rates of molecular and phenotypic evolution as well as diversification near the present might be due to methodological biases and/or biological processes². Methodological bias can result from model misspecification and from sampling or parameter estimation errors^{2,22}. Errors in the estimation of a time interval biases rates upwards, particularly when the time interval (the denominator of a rate) is small. An example of model misspecification occurs when rate heterogeneity is ignored in a model, because more variability is expected over shorter time frames, resulting in younger clades exhibiting the highest rates of evolution^{2,28}. Similarly, phenotypic evolution over short time periods measures instantaneous rate, whereas measures over long timescales provide net rate, which need not be the same. Biological reasons include bounds on evolution, which become evident only at the macroevolutionary scale (for example, limits on the number of combinations of nucleotides for a genome sequence of a given length or bounded phenotypic traits) or simply, if unrealistically, that evolution might be accelerating towards the present day². Another potential factor is fluctuating selection, which yields measurable evolution in the short term but is recorded in the fossils only as time-averaged population variation. The fact that all rates tend to accelerate towards the present seems to suggest a common biological explanation and/or a sampling/methodological bias shared between subdisciplines of evolutionary biology.

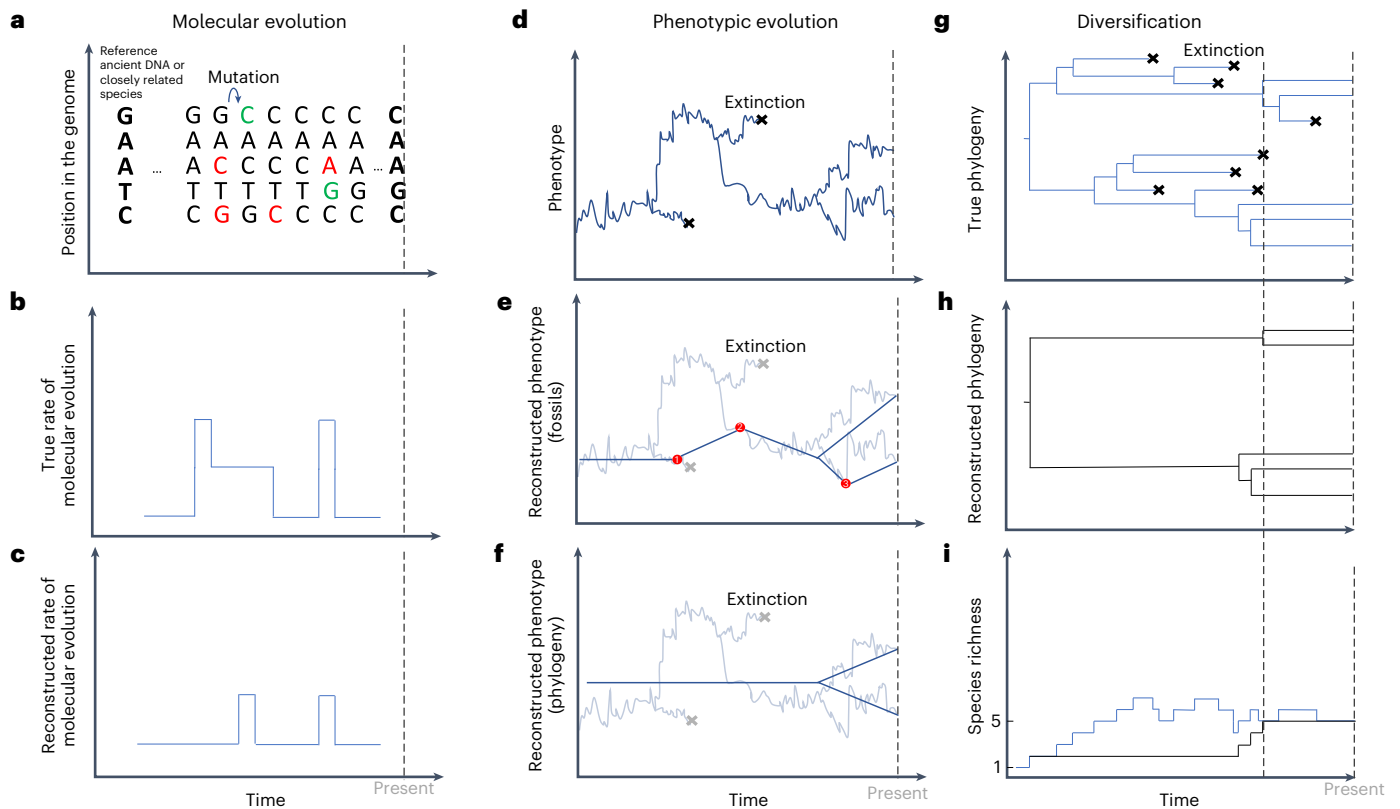


Fig. 2 | Current and fossil data represent past evolutionary processes incompletely. **a–c**, Reconstructions of past molecular evolution, phenotypic evolution and diversification are biased because most of the information about past evolutionary changes is lost from molecular, phenotypic, phylogenetic and fossil history. Panel **a** shows how mutations in red cannot be reconstructed when several mutations affect the same position in the genome—a phenomenon called saturation. The comparison between a present-day genome and the genome of a sister species (or a sample of ancient DNA) only allows reconstructing mutations shown in green, biasing rate estimates if the method fails to take saturation into account, as shown in **c**, compared with the true rate shown in **b**. There may be other reasons why polymorphisms are not recorded over the long term, such as deleterious mutations not persisting or lost polymorphisms in

extinct populations (not represented here). **d–f**, Similarly, phenotypic changes through geological time (**d**) can only be accurately reconstructed when the fossil record is exceptionally well preserved. Reconstructed phenotypes based on phylogenies (**f**) and fossils (**e**) will lead either to wrongly assigning a fossil to a branch when it belonged to another extinct lineage (for example, fossil 1 in **e**), or to missing shifts in phenotype that are not recorded in the fossil information. Phenotypes reconstructed only using phylogenetic data (**f**) will also largely miss past evolutionary changes. **g–i**, Finally, reconstructed phylogenies based on present-day data (**h**) are probably also missing most of the past speciation and extinction events (**g**). The observed lineage-through-time plot (**i**) obtained with the phylogenetic tree (black) is usually very far from the truth (blue).

One methodological bias that could contribute to the three patterns is our inability to fully account for extinction and the incompleteness of the data in the past (Fig. 2). Because much of the past evolutionary history of a lineage is lost over time, there is much more data sampled at the present time and more evolutionary change can be detected, which probably leads to a perceived acceleration of the rates of evolution and diversification²⁹. An excess of lineages sampled at the present time has already been described as the ‘pull of the present’ in the phylogenetic birth–death model literature³⁰ or ‘the pull of the recent’ in the palaeontology literature³¹, which is related to the probability that a (fossil) lineage is lost over time³². The reconstructed birth–death process described in ref. 29 is intended to explicitly account for the pull of the present but only if rates are homogeneous across time and among clades. While a range of solutions have been derived to account for heterogeneous rates (for example, ref. 33), estimating extinction rates accurately, especially in the absence of fossil data, remains a challenging task³⁴.

Similarly, most past genetic polymorphisms are not recorded through time. This results from both neutral processes, whereby many polymorphisms are lost through genetic drift, and selective processes that purge deleterious polymorphisms. Regardless of the cause, only a fraction of polymorphisms will be fixed. The fact that many alleles

are deleterious and short-lived helps to explain why short-term rates of molecular evolution are much higher than longer-term rates of substitution¹⁹ (Fig. 1).

Finally, we can follow the same reasoning with phenotypic differences between populations. Previous studies^{35,36} have proposed that a large part of the variation in phenotypes observed at present—‘ephemeral divergences’—will probably be lost over long timescales when populations go extinct or merge. Reconstructing ancestral values based on a small fraction of the phenotypic variance preserved in the fossil record from only persisting populations could lead to biased phenotypic values on deeper timescales and lower estimated rates compared with the present².

Future

Future research should systematically assess the relative contributions of specific methodological and biological biases to the perceived increase in evolutionary rates towards the present. We identify two complementary avenues: (1) develop new approaches and (2) gather more high-quality data. The development of new approaches will ideally span different timescales and include more complex models for both micro and macroevolution (see Box 1 for some examples), using phylogenetic information, fossils or both. Current phylogenetic methods are already

BOX 1

How to connect macroevolutionary trends to underlying population parameters?

The structure and the dynamics of evolving populations within species affect speciation and extinction rates. The probability of speciation is influenced by the probability of population establishment or splitting, the probability that populations persist long enough for speciation to occur, as well as the rate of evolution of reproductive barriers. The probability of species extinction is influenced by the number of populations as well as their size and genetic diversity. With the increasing availability of population parameters estimated for a large number of species (for example, from population genomic datasets), there are growing opportunities to build more ‘mechanistic’ and potentially more informative comparative methods that include such details. Several comparative methods have already been developed to model trait evolution while accounting for intraspecific variance (jive model^{38,39}) or to model diversification accounting for incipient lineages (protracted speciation model⁴¹), but they do not directly test the effects of population parameters on speciation and extinction rates. Trait-dependent diversification models (state-dependent speciation and extinction (SSE) models¹⁴⁹) could be used for this exact purpose. SSE models were originally developed to test the effect of species traits on diversification¹⁴⁹, with the probability of speciation and the probability of extinction at each point in time being a function of the species’ trait value. They generally estimate the likelihood of trait-dependent speciation and extinction rates, given a phylogenetic

tree and species’ traits measured at the present time. Transition rates between character states reflect both mutation and selection, although these two components are not explicitly modelled. One could thus treat microevolutionary parameters as species’ traits to estimate their impact on diversification rates. For instance, the probability of speciation is expected to depend on the rate of establishment of new populations and the probability of population splitting¹¹. Traits that could be used as microevolutionary proxies in diversification analyses include the number of populations within a species, the rate at which populations differentiate¹⁴⁷ (for example, using the slope of isolation by distance, estimated from a population differentiation metric such as F_{ST} ⁹ or the rate at which reproductive isolation builds (for example, via song evolution in birds¹⁵⁰). Similarly, the probability of species extinction is expected to be a function of the long-term population size¹⁵¹ and the probability that populations persist¹¹. Although estimates of persistence are rare, they are much needed and could potentially be estimated from high-quality fossil records or approximated from other traits implicated in extinction risk, such as effective population size, genetic diversity or range size. We thus need more studies to understand how these proxies relate to persistence/extinction and differentiation/speciation. Importantly, these comparative models provide insights into how these difficult-to-collect but crucial microevolutionary proxies could relate to differentiation/speciation and persistence/extinction.

correcting, to some extent, for the pull of the present³⁷, intraspecific phenotypic variance^{38,39}, the temporal sampling heterogeneity of the fossil record⁴⁰ and for the fact that speciation is not instantaneous (protracted speciation models⁴¹). More complex macroevolutionary models could be developed to explicitly account for phenotypic ‘ephemeral divergences’ and the evolution of intraspecific genetic polymorphisms over long timescales (that is, at the clade level). Some attempts have already been made with the multispecies coalescent and other recent genomic approaches⁴². To better account for extinction, phylogenies can potentially be combined with the fossil record (see attempts in refs. 43–47), at least for the few clades for which both neontological and palaeontological data are available (such as mammalian lineages, Cetacea³⁷, Carnivora⁴³ or Rodentia⁴⁸). Importantly, these models of molecular, phenotypic evolution and diversification should be tested with individual-based simulations on geological timescales (such as refs. 7,49) to assess whether they can tell apart the relative contributions of methodological and biological biases in the increase of evolutionary rates near the present.

Improving comparative methods may not be enough, given that they can estimate only a low number of parameters, hence we also need better data. These data should allow a more precise and unbiased estimation of rates from past populations that is comparable to that from modern populations. Reanalysis of fine-scale fossil records, such as Bryozoa⁵⁰, Foraminifera⁵¹, sticklebacks⁵² or diatoms⁵³ (reviewed in ref. 54) or long-term lab experiments⁵⁵ may also help to determine whether timescaling patterns are artefactual and why. Fossil databases are also important resources (<https://paleobiodb.org/> and refs. 56,57). Finally, ancient genomes reconstructed for multiple individuals in past populations may be used to estimate past polymorphism. Comparing these ancient with present-day genomes could potentially make it possible to

estimate how polymorphisms have been lost and estimate variation in the rate of molecular evolution through time with higher accuracy^{58–60}.

Why is there stasis over long evolutionary timescales?

Pattern

The second part of the paradox of stasis consists of the observation that phenotypes in the fossil record are not evolving gradually but rather seem to show long periods of stasis (that is, a slow rate of evolution) punctuated by short bursts of rapid evolution. Although this observation has received some support from fossil data (‘stasis is data’ from ref. 16), recent studies show results consistent with a large variety of scenarios, ranging from a slow rate of phenotypic evolution on short timescales (<1 Myr), cumulative evolutionary changes over longer timescales with bursts of evolution (for example, every ~25 Myr on average⁶¹ or every 1–100 Myr depending on the size of the shift⁶²) to gradual evolution on both short and long timescales^{50,63}.

No paradox of stasis has been described for lineage diversification, as speciation and extinction rates have been shown to be highly heterogeneous through time and among clades^{33,37}. Only some small clades have been shown to fit a model of constant diversification rates, while larger clades are generally highly heterogeneous^{33,37,64}. Nonetheless, in some cases, net diversification may slow down when speciation decreases or extinction increases over time, for example, due to diversity dependence or other reasons⁶⁵.

Similarly, stasis is not generally expected at the molecular level. Even ‘living fossil’ clades, such as coelacanths and tuataras, show slow but non-zero long-term average rates of molecular substitution and phenotypic evolution^{66–68}. Genome composition also changes at heterogeneous rates among clades, via changing rates of

BOX 2

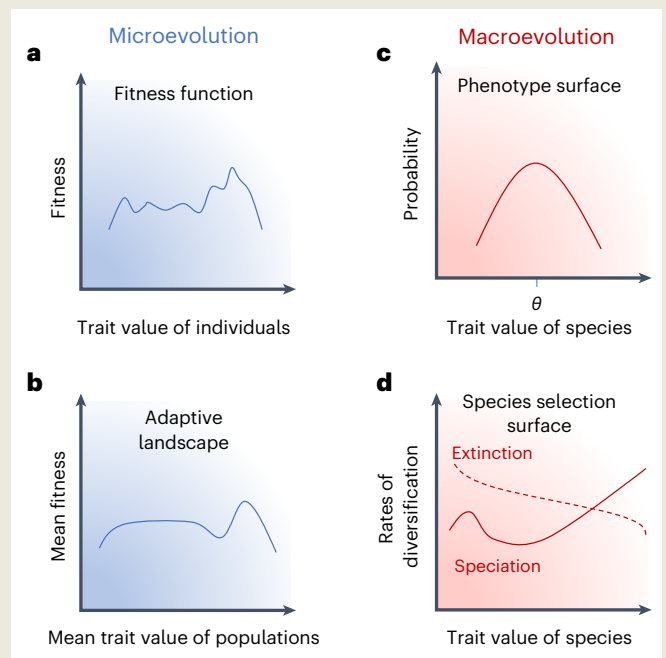
Four evolutionary landscapes

In the literature, four evolutionary landscapes have been described at different scales (see the figure). At the microevolutionary level, one can either map the fitness of each individual onto trait values (the fitness function; for example, ref. 83) or the mean fitness of a population as a function of gene frequencies or mean phenotype (adaptive landscape⁸⁴). The fitness function and adaptive landscape are usually measured from experiments¹⁵² or more rarely in natural ecosystems^{76,83}. Peaks in the adaptive landscape represent genotypes/trait values where mean fitness is maximized and valleys represent genotypes/phenotypes that are detrimental. The adaptive landscape concept is more complicated when selection is frequency dependent, as when species interact.

Macroevolutionary surfaces are functions that represent probabilities of phenotypic change over time. They lack a fitness interpretation but can be a useful summary of the outcome of the adaptive evolution of component species. The Brownian motion model, whereby instantaneous change is equiprobable in all directions, is represented by a flat macroevolutionary surface. It fits cases in which the squared difference between species increases linearly with time. The Ornstein–Uhlenbeck process fits data in which differences between species over time increasingly behave as though randomly sampled from a fixed underlying Gaussian frequency distribution. The model can be represented by a concave downward surface with a single ‘peak’ that is essentially the long-term mean of the underlying frequency distribution of species phenotype values. More complex surfaces can have multiple ‘peaks’, which fit data for which the long-term frequency distribution of species differences is best described by a mixture of probability distributions rather than a single distribution. For instance, ref. 87 showed that phenotypes of species in different lineages of the *Anolis* phylogeny clustered around the same set of ‘peaks’ inferred from the distribution of species trait means, indicating convergence.

‘Species selection’ surfaces describe the rates of speciation and extinction as a function of species mean trait values. The trait-dependent speciation and extinction can be estimated by fitting a model to data on trait means and branching rates in reconstructed phylogenetic trees^{88,149}. The concept can be applied to model speciation/extinction rates as a function of discrete or quantitative traits. The speciation and extinction rates are not interpretable on a fitness scale, but a lineage is more likely to persist if it splits often into daughter lineages and/or has a low extinction rate (see previous debates on species selection^{88,153}). A multi-trait framework still requires further development for quantitative characters (but see ref. 154 for fossil data and MuSSE for discrete traits¹⁴⁹). In addition,

some methods based on the analysis of the fossil record also allow modelling of a changing ‘species selection’ surface (‘evoTS’ and ‘layeranalyzer’ packages).



Four representations of evolutionary landscapes and surfaces at different scales related to phenotype. a, b, The fitness function and the adaptive landscape at the microevolutionary scale. a, Fitness of all individuals in a population as a function of their trait values (for example, ref. 83). b, Fitness averaged at the level of populations as a function of the mean trait value in a population (the so-called adaptive landscape⁸⁴). c, d, Surfaces at the macroevolutionary scale. c, Likelihood of the parameter θ , representing the attraction point of an Ornstein–Uhlenbeck process estimated using the frequency distribution of species trait values and a phylogeny or a time series. The peak is often interpreted as an ‘optimum’ or ‘adaptive peak’, but it is better thought of as the mean of the underlying long-run frequency distribution of species’ trait values. d, Rates of speciation and extinction as a function of lineage trait values, which are sometimes considered as parameters describing ‘species selection’ on traits⁸⁸. The locations of ‘peaks’ need not correspond between different landscapes.

inversion, translocation, chromosome fusion and polyploidization (for example, ref. 69).

Explanations

Several biological processes may explain why we detect stasis in phenotypes. These include oscillating directional selection around an optimum or stabilizing selection¹⁸, which can be caused by genetic interactions between traits (epistasis, pleiotropy) or the complexity of selective pressures simultaneously acting on several traits. Signals of adaptive evolution may often be missed when measuring selection for statistical and/or biological reasons, such as when measuring phenotypic plasticity or age-specific response^{69–72}. This may

lead us to infer stasis despite abundant genetic variation for functional traits and strong selection^{69–72}. Conversely, selection on skewed trait distributions can lead to signals of directional selection when in fact it is stabilizing⁷³.

The tempo and mode of evolution over long timescales will be dictated by the shape of the adaptive landscape (the mean fitness surface plotted in the phenotypic and genetic space, for example, ref. 74; see Box 2 and figure therein, and Fig. 3). We can formulate the hypothesis that a lineage following a ‘stasis’ dynamic is often stuck at one peak of the adaptive landscape but is still evolving around this peak at the same rate as other lineages. This hypothesis is consistent with previous results showing that the distance travelled by the phenotype in morphospace

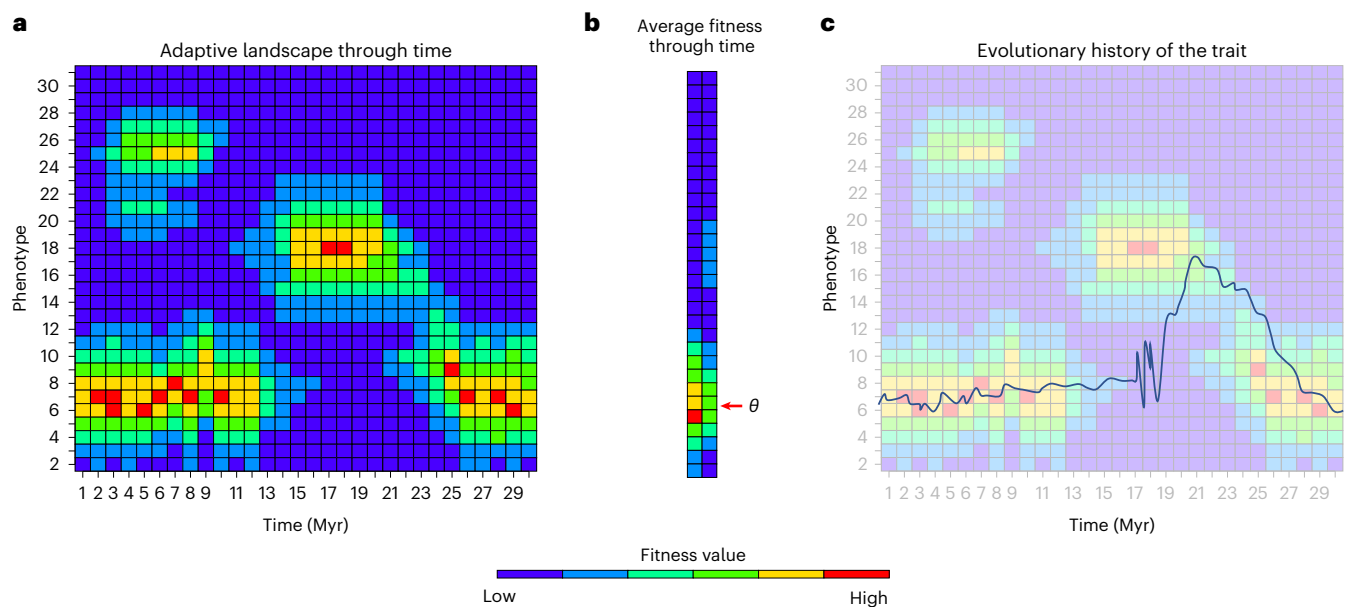


Fig. 3 | A changing microevolutionary adaptive landscape integrated over a macroevolutionary timescale. The relationship between the adaptive landscape, which governs the evolution of populations, and the macroevolutionary surface, which represents probabilities of change in species means over time, is not well understood. **a**, A hypothetical adaptive landscape for a single trait at different slices of time. Each time slice describes the mean fitness of a single population (blue to red colours indicate low to high fitness). **c**, The ensuing changes in mean phenotype of the population over time as it roughly tracks the changing adaptive landscape (for example, as recorded in a fossil sequence). **b**, The average of the adaptive landscape through time for each row in **a** over the entire time period. The value of θ , the attractor of the

Ornstein–Uhlenbeck process, is estimated by fitting the model to the distribution of species values over time (not shown here). In this case, θ can be regarded as a summary of the outcome of adaptive evolution (for example, as described across a fossil sequence). In phylogenetics, θ is usually estimated from a clade of species, each of which might have its own unique adaptive landscape with a trajectory through time (one panel **a** per lineage). Here too, θ can be regarded as a summary of the outcome of lower-level processes giving rise to the distribution of species values over the long run. This figure shows how a macroevolutionary model of phenotypic evolution may be summarizing complex microevolutionary processes.

was similar for all fossil time series, with or without ‘stasis’⁷⁵. Therefore, macroevolutionary dynamics are thought to be mainly related to changes in this landscape through time (‘seascape’, refs. 76–78), whereas short-term evolution depends primarily on the current landscape.

Future

To better describe adaptive phenotypic evolution, we have to understand adaptive landscapes and how they change over time. Quantifying the topography of the adaptive landscape and how it changes through time might help to explain why some traits are evolving fast or slow in the long term (figure in Box 2 and Fig. 3). A fast-evolving landscape or a flat landscape would lead to relatively unconstrained evolution and high lability of the trait, such as ovoviviparity in amphibians or migratory behaviour in birds⁷⁹. Other traits may also have landscapes with fitness valleys corresponding to ‘hard’ boundaries—general limits caused by physical properties of the organism (related to biomechanical constraints, maximum metabolic rate, frost tolerance; for example, ref. 80), biological interactions (traits that would make species vulnerable to parasites or predators, such as maximum running speed for a given body mass⁸¹) or simply the properties of the phenotypes studied (proportion bounded between 0 and 1, latitude bounded at 90°). For instance, the maximum critical temperature is thought to be very stable through time, with the body temperature above 40–45 °C representing a deep fitness valley leading to a conserved maximum across most organisms⁸².

Reconciling the multiple types of evolutionary landscape that have been described and their relation to each other would also be a fruitful bridge between evolution on shorter and longer timescales (figure in Box 2). At least four types of ‘landscape’ have been envisioned. (1) The fitness function describes fitness of individuals varying in phenotype⁸³.

(2) The adaptive landscape is defined as the mean fitness of a population over different combinations of trait means⁸⁴ or genotype frequencies⁷⁴, hence is closely connected to the fitness function. (3) The macroevolutionary surface is a function representing a phylogenetic model of phenotypic evolution at the species level (for example, Ornstein–Uhlenbeck model⁸⁵, bounded Brownian motion⁸⁶, surface⁸⁷). It describes the frequency distribution of species means over the long run. (4) The species-selection surface describes how speciation and extinction rates depend on species values in trait space (for example, QuaSSE⁸⁸). The connections between these different representations of selection are not yet well understood, but they might be key to predicting evolutionary trajectories from one timescale to another. In theory, one could plot all the individuals of all populations of all species in the same individual fitness landscape and therefore all species under the same adaptive landscape. However, in practice this is difficult because a fitness peak for one species can be a valley for another and because a peak at one scale might be a valley at another scale^{89,90} (Box 3). For example, an increase in body size leading to a higher fitness at the individual level could lead to a higher probability of extinction for the species (see also ref. 91 for another example on the short and long-term effects of costly traits on fitness).

Finally, as a side note, we propose that the terminologies ‘stasis’ and ‘punctuated equilibrium’ should be avoided when possible, as rates vary all the time with phases of bursts and slowdowns. We encourage researchers to discuss and estimate variation in rates of evolution and to investigate the causes for shifts in rates. For example, more factors potentially contributing to slow rates of evolution should be investigated, such as covariance between traits (G matrices⁸⁴ in a comparative context^{92,93}), complex developmental processes (for example, hourglass model⁹⁴), traits with no intraspecific variation or complex adaptations to multiple correlated selective pressures (for example, humidity and temperature).

BOX 3

Why microevolution may not be coupled with macroevolution

There are many reasons why all the details of microevolution would not predict macroevolution. The first reason is that large macroevolutionary patterns may emerge unpredictably from microevolutionary processes (for example, the extinction risk of lineages may reflect unusual bouts of strong selection rather than the average rate of selection). Classic philosophical discussions about challenges to the predictability of macroevolution from microevolution centre on the hierarchical nature of biological organization and the potential for properties to emerge at higher levels of organization (for example, species) that cannot be explained at a lower organizational level^{89,154–156}. A key element is that selection can change direction at different scales (see ‘Why is there stasis over long evolutionary timescales?’). Although the intensity of these debates has lessened, these issues remain and there is no consensus as to the relative frequency by which microevolutionary processes can predict macroevolution and when they cannot.

In his book¹⁵⁷, S. J. Gould proposed to “replay the tape of life” to know whether long-term evolution would follow the same trajectories over and over. Decades after this book, most evolutionary biologists would still argue that it is very unlikely that life will evolve following

the same exact trajectory twice¹⁵⁸. First, there is a large amount of stochasticity in any (complex) biological system, with survival, reproduction and mutation all subject to chance¹⁵⁹. For example, the COVID-19 pandemic hinged upon the chance of transmission of the virus in its first human hosts. Similarly, the time at which adaptations arise may be unpredictable, particularly for mutations that have arisen only once in the history of life¹⁶⁰. Second, there is a great deal of stochasticity and contingency in the abiotic environment, which affects both microevolutionary (for example, lightning striking an individual) and macroevolutionary (for example, a meteorite leading to a mass extinction¹⁵⁶) processes. Another important problem is that several microevolutionary processes may lead to the same macroevolutionary pattern¹⁶¹, which may lessen the identifiability of the models. Accounting for the microevolutionary processes underlying macroevolutionary patterns may also be challenging when several evolutionary processes operate simultaneously (for example, population bottlenecks and periods of strong selection). Even if individual and population-level processes may never totally explain broad-scale biodiversity patterns, we should strive to understand which general rules at macroevolutionary scales can inform microevolution and vice versa.

Do bursts of phenotypic evolution and speciation occur at the same time?

Pattern

There is strong evidence that rates of evolution vary over time and along the branches of the tree of life. Punctuated equilibrium theory proposed that bursts in phenotypic evolution mainly occur with speciation events^{16,95}, an idea with little support from empirical fossil data^{50,96}. Indirect evidence has been provided at the clade level from adaptive radiations (for example, African cichlids, *Anolis* lizards, Galápagos finches⁹⁷) where speciation rate and phenotypic evolution have been shown to increase concomitantly⁹⁸, but the exact synchrony between phenotypic change and speciation has proved hard to test. At the lineage level, shifts in the rate of phenotypic evolution and of molecular evolution in adaptive genes can occur during ecological speciation: when lineages in a clade adapt to different niches (for example, as in adaptive radiations⁹⁷), respond to a changing environment⁶⁴ or fill ecological opportunities, for example, after a mass extinction⁹⁹. Interestingly, recent studies have also found evidence for an association between major genetic changes: such as major genomic rearrangements (that is, gene duplication) associated with increased phenotypic innovation¹⁰⁰ and potential speciation¹⁰¹. Contrastingly, other modes of speciation do not require major changes in the molecular rate or the phenotypic rate of evolution. For instance, the evolution of Bateson–Dobzhansky–Muller incompatibilities via genetic conflict might only involve a few genes and do not necessarily affect phenotypic differences¹⁰².

Explanations

On the one hand, there are many reasons why phenotypic evolution should be concentrated around speciation events. For example, sympatric speciation requires some form of character displacement for incipient species to coexist^{103,104}. During allopatric speciation, geographic barriers to gene flow should lead to the accumulation of divergent mutations, which should lead to faster phenotypic divergence than the average long-term rate. Most phenotypic divergence observed at the

present time is proposed to be ephemeral and might not be recorded in long-term evolution, except when speciation events partition variation between daughter species^{35,36}. This is because gene flow, which homogenizes phenotypic and genetic differences between populations, diminishes during the emergence of reproductive isolation. The process of partitioning of variation itself may be associated with an increase in the rate of phenotypic evolution close to speciation events. In the case of asymmetric segregation of traits at speciation, individuals of the two daughter species represent a non-random draw of individuals from the parent population, driven by geography or traits involved in the speciation process, which can lead to an apparent jump in trait evolution⁵⁰. The hypothesis of ephemeral divergence is also consistent with the empirical observation that the accumulation of phenotypic differences speeds up after a period, ~1 Myr in vertebrates⁶¹, that is on the same order of magnitude as the expected waiting time between speciation events.

In terms of molecular evolution, a reduction in population size during speciation may increase drift, or increased selective pressure on adaptive genes may lead to a higher substitution rate associated with speciation events¹⁰⁵. Finally, speciation could also be largely a by-product of genetic divergence¹⁰⁶ and consequently, speciation could be associated with bursts of molecular genetic change. Polyploidization, for example, shows signs of clustering around speciation events⁷⁰, as expected from polyploid speciation and hybrid speciation. In these cases, we may expect a correlation between genetic change, phenotypic change and speciation.

On the other hand, phenotypic change, substitution and speciation rates can be disconnected in many cases. There are many examples of putatively non-adaptive radiations that unfold without any clear sign of ecological divergence (reported for some clades of damselflies, snails and salamanders¹⁰⁷). In a similar vein, key evolutionary innovations can spread without changes in speciation rate (examples reviewed in ref. 108, such as the Australian honeyeaters adapting from an arboreal/nectarivorous foraging strategy to a terrestrial/insectivorous strategy). In addition, it remains unclear whether substitution rates accelerate at speciation events^{109,110}. The association between mutation

and speciation is at the heart of classic theories, such as the metabolic theory of ecology¹¹¹, which predicts that higher rates of mutation at high temperature (such as in the tropics) should foster faster molecular evolution and speciation. However, this theory has received relatively weak support, at least in the context of the latitudinal diversity gradient¹¹².

Future

Overall, whether bursts of speciation and phenotypic evolution take place concurrently, or whether one typically precedes the other, remains to be definitively demonstrated. To this end, we first need to understand when and how rate shifts are happening at large macroevolutionary scales. Data on molecular and phenotypic traits, as well as speciation/extinction data through time, need to be compiled using fossil, ancient DNA and genomes to identify the causes and the consequence of each speciation event, measured over a long-enough timescale to capture shifts. Fine-scale analysis of planktonic fossil sequences¹¹³, long-term lab experiments⁵⁵ and resurrection experiments¹¹⁴ can help to test the causes of shifts and speciation events. For example, comparison between ancient DNA in sediments and present-day genomes of sticklebacks has led to the identification of genes under selection during the transition from marine to freshwater habitat ~12,000 years ago⁶⁰. Trait-dependent models of diversification (for example, ClaSSE¹¹⁵ distinguishing cladogenetic and anagenetic trait evolution) and the development of models that combine fossil observations and phylogenies¹¹⁶ allow for probabilistic tests of the correlation between speciation and trait evolution at nodes and along the branches of the phylogenetic tree¹¹⁷. Finally, to better understand how phenotypic variation is distributed between the two daughter lineages during speciation and whether jumps occur at speciation, current comparative models (such as Brownian motion, Ornstein–Uhlenbeck or Levy flight⁶²) could be improved to account for asymmetrical inheritance of the intraspecific variation during speciation for quantitative traits⁴⁹.

We are currently unsure under what circumstances macroevolution can predict microevolution⁷⁸ and vice versa (Box 3). We lack a framework to predict how adaptive landscapes shift and the resulting impact on phenotypic evolution and diversification. A striking example was the inability of researchers to predict the speed and the direction of change leading to the emergence of new variants of the severe acute respiratory syndrome coronavirus 2 virus (but see ref. 118). An important factor complicating the prediction is that bursts of evolution strongly depend on the environmental and the ecological context. For example, in the context of adaptive radiation, phenotypic jumps to an alternative adaptive peak depend on whether the peaks (niches) are already occupied^{84,87,97}. More generally, macroevolution could potentially be used to understand when an adaptive jump will probably occur, by comparing mutations affecting fitness in other related lineages at the clade level and by estimating the probability of a beneficial mutation to evolve, given the sequence of the protein at a given time. Microevolution could also be helpful in predicting the rate and trajectory of evolution during the jump, using population-based quantities such as intraspecific genetic variance (G matrix) for adaptive traits⁷². This gives hope that microevolution and macroevolution may soon be modelled jointly to improve the predictive power of evolutionary biology concerning the probability of speciation, extinction and adaptation of species.

Do ecological interactions leave a predictable signature on macroevolution?

Pattern

Detecting the imprint of species interactions on macroevolution remains a difficult task. Although evolution caused by ecological interactions is often thought to happen over short timescales, interactions can influence evolutionary dynamics below and above the species level^{119–123}. Although a number of potential biotic interactions (that is, mutualism, symbiosis, commensalism, antagonism) may impact both

micro and macroevolution¹²⁴, previous studies have focused mostly on competition and predation. At the macroevolutionary scale, slowdowns in diversification rates through time are often inferred from small- and medium-size phylogenetic trees⁶⁴ and have often been interpreted as a potential signature of increased competition accompanying the build-up of biodiversity, reducing ecological opportunity. Speciation rates should decline and extinction rates increase as the number of species increases over time, owing to the increasing competition between the species for the limited resources. Under this process, called diversity dependence^{25,125,126}, we expect that the rate at which new species accumulate slows near the species ‘carrying capacity’ of the environment. This process can be mitigated when the resource limits are far from being reached or when evolutionary innovation continually affords access to new resources. But the cause of observed slowdowns in diversification is uncertain⁶⁷. Many other factors could cause slowdowns in diversification, such as the temperature decline through the Phanerozoic⁶⁴, the effect of extinction and/or protracted speciation at the tips of phylogenetic trees⁶⁵. Clade interactions could also influence diversification dynamics on macroevolutionary scales, such as competition between bivalves and brachiopods¹²⁷, between canids¹²⁸ or between angiosperms and gymnosperms¹²⁹.

Explanations

Many studies aimed at detecting the signal of biotic interactions on macroevolution focus on the effect of interspecific competition. For instance, diversity-dependent models assume that every environment can only carry a given number of species, which is thought to be limited by the number of niches (a challenging concept to quantify⁹⁹) or resource availability (see discussion in refs. 130,131). Diversity-dependent diversification models have been developed to estimate carrying capacity at the clade level^{132–134}, but these models have important limitations.

First, these models do not account for all lineages potentially competing for resources. They should account for interactions with lineages outside of the clade within the same geographical region. Second, they do not explicitly include phenotypic data or pre-existing data on species interactions. Species competing for the same niche are expected to show signs of character displacement, which should be detectable with coexistence experiments¹⁰⁴, disparity through time analysis of phenotypes¹³⁵ or other models of phenotypic evolution (diversity-dependent, matching competition and early-burst models¹¹⁷). These types of analysis permit the detection of interspecific phenotypic interaction during species coexistence¹³⁶ and across the latitudinal gradient¹³⁷. Interactions beyond temporal co-occurrence, such as predation and spatial competition can be observed directly in the fossil record¹³⁸ and could potentially be incorporated in modelling frameworks.

Finally, diversity-dependent macroevolutionary models do not account for the demographic consequences of species interactions. At the microevolutionary scale, a slowdown in population growth rate due to density dependence is often observed when individuals compete for limited resources, hence detecting this slowdown, that is, using fossil density estimates¹³⁹, may help to validate the hypothesis that species are indeed interacting.

Future

To better test whether biotic interactions leave a detectable imprint on macroevolution, we propose that several lines of evidence from population trends, ecological experiments, phenotypic data and birth–death models should be used to connect data at microevolutionary and macroevolutionary scales. First, to understand the impact of direct ecological competition on diversification, there is a need to improve our fundamental understanding of the links between diversity-dependent and density-dependent processes¹⁴⁰. In theory, if one species is out-competing another, it should experience an increase in effective

population size, while the other should decline. Correlations in abundance data through time are thus helpful in understanding how species interact and whether the fitness of the individuals from one species is affected by other species. Fossil community data through time (such as pollen and microfossil database, for example, Neotoma) could help to identify more such interactions between clades that were coexisting in the past^{48,141}, given that species abundance can be obtained and compared through time (from fossils¹³⁹ or quantification of environmental DNA¹⁴²). Effective population size can also be reconstructed, extending back for millions of years, either using ancient DNA or current genomes with pairwise sequentially Markovian coalescent¹⁴³. Interlinked patterns among species could reveal the nature of interactions among them, keeping in mind that estimates of effective population size can be biased and do not directly correspond to census population size.

Although there are many microevolutionary models of species interactions, future research should also investigate the demographic consequences of species interactions and complex feedback loops between ecology and evolution across long timescales^{119,122,127–129}. For instance, at the microevolutionary scale, the evolution of a predator can change the shape of the adaptive landscape at a lower trophic level, which can, in turn, impact the evolution of the predator¹⁴⁴. Such feedback can then affect speciation and extinction probabilities of all interacting lineages. Similarly, as species alter their environment, they can create or destroy niches of other species¹⁴⁵, altering diversification rates in the community. Interestingly, each peak in the adaptive landscape defined by a resource can be stable over long timescales, leading to the specialization of phenotypes, which in some extreme cases can lead to decreased speciation and increased extinction risk (for example, *Xanthopan morgani praedicta* feeding on *Angraecum sesquipedale*¹⁴⁶), or be more labile and related to the coexistence of species over short timescales. A specific example is the coexistence of incipient species during speciation¹⁰⁴. The strength of resource competition between two new species impacts both the probability that a new isolated population forms and the persistence of isolated populations—two key parameters rarely estimated in the literature^{11,147}. The appearance and persistence of populations should in turn be linked to the probability of speciation and extinction at longer timescales^{9,127}. Recently developed comparative models¹³⁷ have the potential to be used to study a large variety of positive and negative species interactions (such as competition, mutualism, symbiosis)¹²⁴.

Finally, through longer timescales, comparing similar environments at different places on earth may also help to identify empty and occupied peaks in the adaptive landscape to better understand biotic constraints¹⁴⁸ and ecological opportunities for phenotypic evolution and diversification.

Concluding remarks

The four questions we address highlight many of the challenges but also the advantages to be gained by reconciling microevolution within species and macroevolution above the species level. Success is not assured and we have listed reasons why in some cases it may not be possible to bridge across evolutionary scales. Yet, many of the previous attempts have already been illuminating. Seeming discrepancies between rates of evolution over long and short timescales have indicated the existence of potentially key understudied processes, such as bounded evolution and ephemeral evolution. These examples illustrate how insights about microevolutionary processes may sometimes be revealed only after considering macroevolutionary data.

Bridging scales of evolution will require using transdisciplinary approaches to explain how combinations of microevolutionary processes produce macroevolutionary patterns and to solve long-standing questions. In this Perspective, we propose that future research should move away from framing that ignores the dynamic interplay among processes. Quantifying more precisely the tempo and mode of evolution among clades and through time promises to unveil times when

evolutionary rates change at the phenotypic and species level. We propose that future research should (1) assess the relative contribution of methodological biases and biological processes to understand why estimated molecular, phenotypic and diversification rates appear to increase through time, (2) attempt to measure adaptive landscapes across space and time to explain changes in the tempo of evolution, (3) measure more precisely variation in rates and the causes of large shifts, especially near speciation events and (4) conduct further tests of the impact of species interactions on macroevolution, combining abundance and phenotypic data. Unification across scales in evolutionary biology seems more possible than ever before. We anticipate that, in the coming decades, researchers will probably revisit old questions with new models and data in genomics, computational biology and palaeontology to better describe and understand evolution in all its complexity.

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Author contributions

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Competing interests

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Additional information

Correspondence should be addressed to Jonathan Rolland.

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