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1 Conceptual and empirical bridges between micro and macroevolution

2

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35

36 **Keywords:** adaptive landscape, speciation, extinction, demography, molecular evolution,
37 phenotypic evolution

38 **Abstract**

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

51

52 **Main Text**

53 **Reconciling scales of evolution**

54 Since the modern synthesis¹, many evolutionary biologists have focused their attention on
55 evolution at one of two different time scales: microevolution, i.e., the evolution of populations
56 below the species level (in fields such as population genetics, phylogeography, and quantitative
57 genetics), or macroevolution, i.e., the evolution of species or higher taxonomic levels (e.g.,
58 phylogenetics, paleobiology, and biogeography). Patterns at the two scales often seem to
59 contradict one another. For example, accumulating evidence suggests that rates of evolution
60 seem to be faster at shorter time scales than at longer timescales². This discrepancy in rates has
61 been detected in molecular evolution, phenotypic evolution and even lineage diversification
62 rates², leading to several paradoxes and exposing conceptual gaps in current theory (see Figure
63 1). In the past few decades, attempts have been made to bridge these gaps and reconcile these
64 two scales³⁻¹². Nevertheless, the conceptual framework, terminology, and mathematical models
65 remain largely separate and opportunities exist to unite them. For example, speciation is often
66 described as a lengthy divergence between two populations at the microevolutionary scale and
67 as an instantaneous process in birth-death models at the macroevolutionary scale, but recent
68 efforts have sought to improve this e.g.¹³. Additionally, a known pitfall of comparative methods
69 is their inability to identify which microevolutionary mechanisms underlie associations
70 between phenotypic evolution and speciation-extinction dynamics. We argue here that solving
71 many long-standing questions in evolutionary biology will benefit from tighter conceptual
72 linkages between micro- and macroevolutionary approaches. We focus on four as yet unsolved
73 questions in evolutionary biology and propose avenues to tackle them.

74 *1- Why does the rate of evolution appear to accelerate close to present time?*

75 **Pattern** The paradox of stasis is the apparent discrepancy between the slow rate of phenotypic
76 evolution measured in the fossil record, over geological time scales and the fast rates of
77 evolution observed in populations at the present time¹⁴⁻¹⁸. The pattern can be decomposed in
78 two distinct components. The first is the acceleration of evolutionary rates close to the present
79 (Figure 1), which has been observed in molecular¹⁹⁻²¹, phenotypic^{7,22}, phylogenetic²³⁻²⁶ and
80 fossil data²⁷. The second component is the phenotypic stasis observed through long spans of
81 geological time, which we address in the next section (see section 2).

82 **Explanations** The perception of accelerated rates of molecular and phenotypic evolution, as
83 well as diversification, near the present might be due to methodological biases and/or biological
84 processes². Methodological bias can result from model misspecification, and from sampling or

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

99 One methodological bias that could contribute to the three patterns is our inability to
100 fully account for extinction and the incompleteness of the data in the past (Figure 2). Because
101 much of the past evolutionary history of a lineage is lost over time, there is much more data
102 sampled at the present time and more evolutionary change can be detected, which likely leads
103 to a perceived acceleration of the rates of evolution and diversification²⁹. An excess of lineages
104 sampled at present time has already been described as the “pull of the present” in the
105 phylogenetic birth-death model literature³⁰ or “the pull of the recent” in the paleontology
106 literature³¹, which is related to the probability that a (fossil) lineage is lost over time³². The
107 reconstructed birth-death process described in Nee et al.²⁹ is intended to explicitly account for
108 the pull of the present but only if rates are homogenous across time and among clades. While
109 a range of solutions have been derived to account for heterogeneous rates (e.g.,³³), estimating
110 extinction rates accurately, especially in the absence of fossil data, remains a challenging task³⁴.

111 Similarly, most past genetic polymorphisms are not recorded through time. This results
112 from both neutral processes, whereby many polymorphisms are lost through genetic drift and
113 selective processes that purge deleterious polymorphisms. Regardless of the cause, only a
114 fraction of polymorphisms will be fixed. The fact that many alleles are deleterious and short-
115 lived helps to explain why short-term rates of molecular evolution are much higher than longer-
116 term rates of substitution¹⁹ (Figure 1).

117 Finally, we can follow the same reasoning with phenotypic differences between
118 populations. Futuyma³⁵⁻³⁶ proposed that a large part of the variation in phenotypes observed at
119 present — ‘ephemeral divergences’ — will likely be lost over long time scales when
120 populations go extinct or merge. Reconstructing ancestral values based on a small fraction of
121 the phenotypic variance preserved in the fossil record from only persisting populations could
122 lead to biased phenotypic values on deeper timescales and lower estimated rates compared to
123 the present².

124 **Future** Future research should systematically assess the relative contribution of specific
125 methodological and biological biases to the perceived increase in evolutionary rates toward the
126 present. We identify two complementary avenues: (1) develop new approaches and (2) gather
127 more high-quality data. The development of new approaches will ideally span different time
128 scales, and include more complex models for both micro and macroevolution (see Box 1 for
129 some examples), using phylogenetic information, fossils or both. Current phylogenetic
130 methods are already correcting, to some extent, for the pull of the present³⁷, intraspecific
131 phenotypic variance³⁸⁻³⁹, the temporal sampling heterogeneity of the fossil record⁴⁰, and for the
132 fact that speciation is not instantaneous (protracted speciation models⁴¹). More complex
133 macroevolutionary models could be developed to account explicitly for phenotypic ‘ephemeral
134 divergences’ and the evolution of intraspecific genetic polymorphisms over long time scales
135 (i.e., at the clade level). Some attempts have already been made with the multispecies
136 coalescent and other recent genomic approaches⁴². To better account for extinction,
137 phylogenies can potentially be combined with the fossil record (see attempts⁴³⁻⁴⁷), at least for
138 the few clades for which both neontological and paleontological data are available (such as
139 mammalian lineages, Cetacea³⁷, Carnivora⁴³ or Rodentia⁴⁸). Importantly, these models of
140 molecular, phenotypic evolution, and diversification should be tested with individual-based
141 simulations on geological time scales (such as^{7,49}) to assess if they can tell apart the relative
142 contribution of methodological and biological biases in the increase of evolutionary rates near
143 the present.

144 Improving comparative methods may not be enough, given that they can only estimate a low
145 number of parameters, so we also need better data. Those data should allow a more precise and
146 unbiased estimation of rates from past populations that are comparable with modern
147 populations. Reanalysis of fine-scale fossil records, such as Bryozoa⁵⁰, Foraminifera⁵¹,
148 sticklebacks⁵² or diatoms⁵³ (reviewed in⁵⁴) or long-term lab experiments⁵⁵ may also help to

149 determine whether time-scaling patterns are artifactual and why. Fossil databases are also
150 important resources⁵⁶⁻⁵⁸. Finally, ancient genomes reconstructed for multiple individuals in past
151 populations may be used to estimate past polymorphism. Comparing these ancient with
152 present-day genomes could potentially make it possible to estimate how polymorphisms have
153 been lost and estimate variation in the rate of molecular evolution through time with higher
154 accuracy⁵⁹⁻⁶¹.

155 *2- Why is there stasis over long evolutionary time scales?*

156

157 **Pattern** The second part of the paradox of stasis consists of the observation that phenotypes in
158 the fossil record are not evolving gradually but rather seem to show long periods of stasis (i.e.,
159 a slow rate of evolution) punctuated by short bursts of rapid evolution. Although this
160 observation has received some support from fossil data (“stasis is data” from S. J. Gould¹⁶),
161 recent studies show results consistent with a large variety of scenarios, ranging from a slow
162 rate of phenotypic evolution on short time-scales (<1 Myrs) and cumulative evolutionary
163 changes over longer time-scales with bursts of evolution (e.g., every ~25 Myrs on average⁶²,
164 or every 1-100 Myrs depending on the size of the shift⁶³), or gradual evolution on both short
165 and long time-scales^{50,64}.

166 No paradox of stasis has been described for lineage diversification, as speciation and
167 extinction rates have been shown to be highly heterogeneous through time and among
168 clades^{33,37}. Only some small clades have been shown to fit a model of constant diversification
169 rates, while larger clades are generally highly heterogeneous^{33,37,65}. Nonetheless, in some cases,
170 net diversification may slow down when speciation decreases or extinction increases over time,
171 e.g. due to diversity-dependence or other reasons⁶⁶.

172 Similarly, stasis is not generally expected at the molecular level. Even 'living fossil'
173 clades, such as coelacanths and tuataras, show slow, but non-zero long-term average rates of
174 molecular substitution and phenotypic evolution⁶⁷⁻⁶⁹. Genome composition also changes at
175 heterogeneous rates among clades, via changing rates of inversion, translocation, chromosome
176 fusion, and polyploidization^{e.g. 70}.

177

178 **Explanations** Several biological processes may explain why we detect stasis in phenotypes.
179 These include oscillating directional selection around an optimum or stabilizing selection¹⁸,
180 which can be caused by genetic interactions between traits (epistasis, pleiotropy) or the
181 complexity of selective pressures acting on several traits simultaneously. Signals of adaptive

182 evolution may often be missed when measuring selection, for statistical and/or biological
183 reasons, such as phenotypic plasticity or age-specific response⁷⁰⁻⁷³. This may lead us to infer
184 stasis despite abundant genetic variation for functional traits and strong selection⁷⁰⁻⁷³.
185 Conversely, selection on skewed trait distributions can lead to signals of directional selection
186 when in fact it is stabilizing⁷³.

187

188 The tempo and mode of evolution over long time scales will be dictated by the shape of the
189 adaptive landscape (the mean fitness surface plotted in the phenotypic and genetic space, e.g.⁷⁵,
190 see Box 2, Figure 3 & 4). We can formulate the hypothesis that a lineage following a ‘stasis’
191 dynamic is often stuck at one peak of the adaptive landscape but is still evolving around this
192 peak at the same rate as other lineages. This hypothesis is consistent with previous results
193 showing that the distance traveled by the phenotype in morphospace was similar for all fossil
194 time series, with or without ‘stasis’⁷⁶. Therefore, macroevolutionary dynamics are thought to
195 be mainly related to changes in this landscape through time (“seascape”⁷⁷⁻⁷⁹), whereas short-
196 term evolution depends primarily on the current landscape.

197

198 **Future** To better describe adaptive phenotypic evolution, we have to understand
199 adaptive landscapes and how they change over time. Quantifying the topography of the
200 adaptive landscape and how it changes through time might help to explain why some traits are
201 evolving fast or slow in the long-term (Figure 3 & 4). A fast-evolving landscape or a flat
202 landscape would lead to relatively unconstrained evolution and high lability of the trait, such
203 as ovoviviparity in amphibians or migratory behavior in birds⁸⁰. Other traits may also have
204 landscapes with fitness valleys corresponding to “hard” boundaries — general limits caused by
205 physical properties of the organism (related to biomechanical constraints, maximum metabolic
206 rate, frost tolerance, e.g.⁸¹), biological interactions (traits that would make species vulnerable
207 to parasites or predators, such as maximum running speed for a given body mass⁸²) or simply
208 the properties of the phenotypes studied (proportion bounded between 0 and 1, latitude
209 bounded at 90°). For instance, the maximum critical temperature is thought to be very stable
210 through time, with the body temperature above 40-45°C representing a deep fitness valley
211 leading to a conserved maximum across most organisms⁸³.

212

213 Reconciling the multiple types of evolutionary landscapes that have been described and
214 their relation to each other would also be a fruitful bridge between evolution on shorter and
215 longer time scales (Figure 3). At least four types of “landscapes” have been envisioned: (1)
The fitness function describes fitness of individuals varying in phenotype⁸⁴. (2) The adaptive

216 landscape is defined as the mean fitness of a population over different combinations of trait
217 means⁸⁵ — or genotype frequencies⁷⁵ and so is closely connected to the fitness function. (3)
218 The macroevolutionary surface is a function representing a phylogenetic model of phenotypic
219 evolution at the species level (e.g., Ornstein Uhlenbeck model⁸⁶, Bounded Brownian Motion⁸⁷,
220 Surface⁸⁸). It describes the frequency distribution of species means over the long run. (4) The
221 species-selection surface describes how speciation and extinction rates depend on species
222 values in trait space (e.g., QuaSSE⁸⁹). The connections between those different representations
223 of selection are not yet well understood, but they might be key to predicting evolutionary
224 trajectories from one time scale to another. In theory, one could plot all the individuals of all
225 populations of all species in the same individual fitness landscape, and therefore all species
226 under the same adaptive landscape. However, in practice this is difficult because a fitness peak
227 for one species can be a valley for another, and because a peak at one scale might be a valley
228 at another scale⁹⁰⁻⁹¹(Box 3). For example, an increase in body size leading to a higher fitness
229 at the individual level could lead to a higher probability of extinction for the species (see also⁹²
230 for another example on the short and long-term effects of costly traits on fitness).

231 Finally, as a side note, we propose that the terminologies “stasis” and “punctuated
232 equilibrium” should be avoided when possible, as rates vary all the time with phases of bursts
233 and slow-downs. We encourage researchers to discuss and estimate variation in rates of
234 evolution and to investigate the causes for shifts in rates. For example, more factors potentially
235 contributing to slow rates of evolution should be investigated, such as covariance between traits
236 (G matrices⁸⁵ in a comparative context⁹³⁻⁹⁴), complex developmental processes (e.g., hourglass
237 model⁹⁵), traits with no intraspecific variation or complex adaptations to multiple correlated
238 selective pressures (e.g., humidity and temperature).

239

240 *3- Do bursts of phenotypic evolution and speciation occur at the same time?*

241

242 **Pattern** There is strong evidence that rates of evolution vary over time and along the branches
243 of the tree of life. Punctuated equilibrium theory proposed that bursts in phenotypic evolution
244 mainly occur with speciation events^{16,96}, an idea with little support from empirical fossil
245 data^{50,97}. Indirect evidence has been provided at the clade level from adaptive radiations (e.g.,
246 African cichlids, Anolis lizards, Galápagos finches⁹⁸), where speciation rate and phenotypic
247 evolution have been shown to increase concomitantly⁹⁹, but the exact synchrony between
248 phenotypic change and speciation has proved hard to test. At the lineage level, shifts in the rate

249 of phenotypic evolution and of molecular evolution in adaptive genes can occur during
250 ecological speciation: when lineages in a clade adapt to different niches (e.g., as in adaptive
251 radiations⁹⁸), respond to a changing environment⁶⁵, or fill ecological opportunities, e.g., after a
252 mass extinction¹⁰⁰. Interestingly, recent studies have also found evidence for an association
253 between major genetic changes: such as major genomic rearrangements (i.e., gene duplication)
254 associated with increased phenotypic innovation¹⁰¹ and potential speciation¹⁰². Contrastingly,
255 other modes of speciation do not require major changes in the molecular rate nor the phenotypic
256 rate of evolution. For instance, the evolution of Bateson-Dobzhansky-Muller incompatibilities
257 via genetic conflict might only involve a few genes and do not necessarily affect phenotypic
258 differences¹⁰³.

259

260 **Explanations** On the one hand, there are many reasons why phenotypic evolution should be
261 concentrated around speciation events. For example, sympatric speciation requires some form
262 of character displacement for incipient species to coexist¹⁰⁴⁻¹⁰⁵. During allopatric speciation,
263 geographic barriers to gene flow should lead to the accumulation of divergent mutations, which
264 should lead to faster phenotypic divergence than the average long-term rate. Futuyma³⁵⁻³⁶
265 proposed that most phenotypic divergence observed at the present time is ephemeral and might
266 not be recorded in long-term evolution, except when speciation events partition variation
267 between daughter species. This is because gene flow, which homogenizes phenotypic and
268 genetic differences between populations, diminishes during the emergence of reproductive
269 isolation. The process of partitioning of variation itself may be associated with an increase in
270 the rate of phenotypic evolution close to speciation events. In the case of asymmetric
271 segregation of traits at speciation, individuals of the two daughter species represent a non-
272 random draw of individuals from the parent population, driven by geography or traits involved
273 in the speciation process, which can lead to an apparent jump in trait evolution⁵⁰. The hypothesis
274 of ephemeral divergence is also consistent with the empirical observation that the accumulation
275 of phenotypic differences speeds up after a period, about one million years⁶² in vertebrates, that
276 is on the same order of magnitude as the expected waiting time between speciation events.
277 In terms of molecular evolution, a reduction in population size during speciation may increase
278 drift, or increased selective pressure on adaptive genes may lead to a higher substitution rate
279 associated with speciation events¹⁰⁶. Finally, speciation could also be largely a by-product of
280 genetic divergence¹⁰⁷, and consequently, speciation could be associated with bursts of
281 molecular genetic change. Polyploidization, for example, shows signs of clustering around

282 speciation events⁷¹, as expected from polyploid speciation and hybrid speciation. In those
283 cases, we may expect a correlation between genetic change, phenotypic change and speciation.

284 On the other hand, phenotypic change, substitution and speciation rates can be
285 disconnected in many cases. There are many examples of putatively non-adaptive radiations,
286 which unfold without any clear sign of ecological divergence (reported for some clades of
287 damselflies, snails, and salamanders¹⁰⁸). In a similar vein, key evolutionary innovations can
288 spread without changes in speciation rate (examples reviewed in¹¹⁰, such as the Australian
289 honeyeaters adapting from an arboreal/nectarivorous foraging strategy to a
290 terrestrial/insectivorous strategy). Additionally, it remains unclear whether substitution rates
291 accelerate at speciation events¹¹¹⁻¹¹². The association between mutation and speciation is at the
292 heart of classic theories, such as the metabolic theory of ecology¹¹³, which predicts that higher
293 rates of mutation at high temperature (such as in the tropics) should foster faster molecular
294 evolution and speciation. However, this theory has received relatively weak support, at least in
295 the context of the latitudinal diversity gradient¹¹⁴.

296

297 **Future** Overall, whether bursts of speciation and phenotypic evolution take place concurrently,
298 or whether one typically precedes the other, remains to be definitively demonstrated. To this
299 end, we first need to understand when and how rate shifts are happening at large
300 macroevolutionary scales. Data on molecular and phenotypic traits, as well as
301 speciation/extinction data, need to be compiled through time using fossil, ancient DNA and
302 genomes in order to identify the causes and the consequence of each speciation event, measured
303 over a long enough time scale to capture shifts. Fine-scale analysis of planktonic fossil
304 sequences¹¹⁵, long-term lab experiments⁵⁵ and resurrection experiments¹¹⁶ can help to test the
305 causes of shifts and speciation events. For example, comparison between ancient DNA in
306 sediments and present-day genomes of sticklebacks has led to the identification of genes under
307 selection during the transition from marine to freshwater habitat ~12,000 years ago⁶¹. Trait-
308 dependent models of diversification (e.g., ClaSSE¹¹⁷ distinguishing cladogenetic and
309 anagenetic trait evolution) and the development of models that combine fossil observations and
310 phylogenies¹¹⁸ allow for probabilistic tests of the correlation between speciation and trait
311 evolution at nodes and along the branches of the phylogenetic tree¹¹⁹. Finally, in order to better
312 understand how phenotypic variation is distributed between the two daughter lineages during
313 speciation and if jumps occur at speciation, current comparative models (such as BM, OU or

314 Levy flight⁶³) could be improved to account for asymmetrical inheritance of the intraspecific
315 variation during speciation for quantitative traits⁴⁹.

316 We are currently unsure under what circumstances macroevolution can predict
317 microevolution⁷⁻⁸ and vice versa (Box 3). We lack a framework to predict how adaptive
318 landscapes shift and the resulting impact on phenotypic evolution and diversification. A
319 striking example was the inability of researchers to predict the speed and the direction of
320 change leading to the emergence of new variants of the SARS-CoV-2 virus (but see¹²⁰). An
321 important factor complicating the prediction is that bursts of evolution strongly depend on the
322 environmental and the ecological context. For example, in the context of adaptive radiation,
323 phenotypic jumps to an alternative adaptive peak depends on whether the peaks (niches) are
324 already occupied^{85,88,98}. More generally, macroevolution could potentially be used to
325 understand when an adaptive jump will likely occur, by comparing mutations affecting fitness
326 in other related lineages at the clade level, and by estimating the probability of a beneficial
327 mutation to evolve given the sequence of the protein at a given time. Microevolution could also
328 be helpful to predict the rate of evolution and trajectory of evolution during the jump, using
329 population-based quantities such as intraspecific genetic variance (G matrix) for adaptive
330 traits⁷³. This gives hope that microevolution and macroevolution may soon be modeled jointly
331 to improve the predictive power of evolutionary biology concerning the probability of
332 speciation, extinction, and the adaptation of species.

333

334 *4- Do ecological interactions leave a predictable signature on macroevolution?*

335

336 **Pattern** Detecting the imprint of species interactions on macroevolution remains a difficult
337 task. Although evolution caused by ecological interactions is often thought to happen over short
338 time scales, interactions can influence evolutionary dynamics below and above the species
339 level¹²¹⁻¹²⁵. Although a number of potential biotic interactions (i.e., mutualism, symbiosis,
340 commensalism, antagonism) may impact both micro and macroevolution¹²⁶, previous studies
341 focused mostly on competition and predation. At the macroevolutionary scale, slowdowns in
342 diversification rates through time, are often inferred from small and medium-size phylogenetic
343 trees⁶⁵ and have often been interpreted as a potential signature of increased competition
344 accompanying the buildup of biodiversity reducing ecological opportunity. Speciation rates
345 should decline and extinction rates increase as the number of species increases over time, owing
346 to the increasing competition between the species for the limited resources. Under this process,
347 called diversity dependence^{25,127-128}, we expect that the rate at which new species accumulate

348 slows near the species “carrying capacity” of the environment. This process can be mitigated
349 when the resource limits are far from being reached or when evolutionary innovation
350 continually affords access to new resources. But the cause of observed slowdowns in
351 diversification is uncertain⁶⁸. Many other factors could cause slowdowns in diversification,
352 such as the temperature decline through the Phanerozoic⁶⁵, the effect of extinction and/or
353 protracted speciation at the tips of phylogenetic trees⁶⁶. Clade interactions could also influence
354 diversification dynamics on macroevolutionary scales, such as competition between Bivalves
355 and Brachiopods¹²⁹, Canids¹³⁰, or between Angiosperms and Gymnosperms¹³¹.

356

357 **Explanations** Many studies aimed at detecting the signal of biotic interactions on
358 macroevolution focus on the effect of interspecific competition. For instance, diversity-
359 dependent models assume that every environment can only carry a given number of species,
360 which is thought to be limited by the number of niches (a challenging concept to quantify¹⁰⁰)
361 or resource availability (see the discussion in¹³² and¹³³). Diversity-dependent diversification
362 models have been developed to estimate carrying capacity at the clade-level¹³⁴⁻¹³⁶, but these
363 models have important limitations.

364 First, these models do not account for all lineages potentially competing for resources.
365 They should account for interactions with lineages outside of the clade within the same
366 geographical region. Second, they do not explicitly include phenotypic data or pre-existing data
367 on species interactions. Species competing for the same niche are expected to show signs of
368 character displacement, which should be detectable with coexistence experiments¹⁰⁵, disparity
369 through time analysis of phenotypes (DTT¹³⁷) or other models of phenotypic evolution
370 (diversity-dependent, matching competition and early burst models¹¹⁹). These types of analyses
371 permit the detection of interspecific phenotypic interaction during species coexistence¹³⁸ and
372 across the latitudinal gradient¹³⁹. Interactions beyond temporal co-occurrence, such as
373 predation and spatial competition can be observed directly in the fossil record¹⁴⁰ and could
374 potentially be incorporated in modeling frameworks.

375 Finally, diversity-dependent macroevolutionary models do not account for the
376 demographic consequences of species interactions. At the microevolutionary scale, a
377 slowdown in population growth rate due to density dependence is often observed when
378 individuals compete for limited resources, so detecting this slowdown, i.e. using fossil density
379 estimates¹⁴¹, may help to validate the hypothesis that species are indeed interacting.

380

381 **Future** To better test whether biotic interactions leave a detectable imprint on macroevolution,
382 we propose that several lines of evidence from population trends, ecological experiments,
383 phenotypic data and birth-death models should be used to connect data at microevolutionary
384 and macroevolution scales. First, in order to understand the impact of direct ecological
385 competition on diversification, there is a need to improve our fundamental understanding of
386 the links between diversity-dependent and density-dependent processes¹⁴². In theory, if one
387 species is outcompeting another, it should experience an increase in effective population size,
388 while the other should decline. Correlations in abundance data through time are thus helpful to
389 understanding how species interact and if the fitness of the individuals from one species is
390 affected by other species. Fossil community data through time (such as pollen and macrofossil
391 database, e.g., *Neotoma*) could help to identify more such interactions between clades that were
392 coexisting in the past^{48,143}, given that species abundance can be obtained and compared through
393 time (from fossils¹⁴¹ or quantification of environmental DNA¹⁴⁴). Effective population size can
394 also be reconstructed, extending back for millions of years, either using ancient DNA or current
395 genomes with Pairwise Sequentially Markovian Coalescent¹⁴⁵. Interlinked patterns among
396 species could reveal the nature of interactions among them, keeping in mind that estimates of
397 effective population size can be biased and do not directly correspond to census population
398 size.

399 Although there are many microevolutionary models of species interactions, future
400 research should also investigate the demographic consequences of species interactions and
401 complex feedback loops between ecology and evolution across long time scales^{121,124,129-131}.
402 For instance, at the microevolutionary scale, the evolution of a predator can change the shape
403 of the adaptive landscape at a lower trophic level, which can, in turn, impact the evolution of
404 the predator¹⁴⁶. Such feedback can then affect speciation and extinction probabilities of all
405 interacting lineages. Similarly, as species alter their environment, they can create or destroy
406 niches of other species¹⁴⁷, altering diversification rates in the community. Interestingly, each
407 peak in the adaptive landscape defined by a resource can be stable over long time scales,
408 leading to the specialization of phenotypes, which in some extreme cases can lead to decreased
409 speciation and increased extinction risk (e.g., *X. morgani praedicta* feeding on *A.*
410 *sesquipedale*¹⁴⁸), or be more labile and related to the coexistence of species over short time
411 scales. A specific example is the coexistence of incipient species during speciation¹⁰⁵. The
412 strength of resource competition between two new species impacts both the probability that a
413 new isolated population forms and the persistence of isolated populations, two key parameters

414 rarely estimated in the literature^{11,149}. The appearance and persistence of populations should in
415 turn be linked to the probability of speciation and extinction at larger time scales^{9,129}. Recently
416 developed comparative models¹³⁹ have the potential to be used to study a large variety of
417 positive and negative species interactions (such as competition, mutualisms, symbiosis)¹²⁶.

418 Finally, through longer time scales, comparing similar environments at different places
419 on earth may also help to identify empty and occupied peaks in the adaptive landscape, in order
420 to better understand biotic constraints¹⁵⁰ and ecological opportunities for phenotypic evolution
421 and diversification.

422

423 *Concluding remarks*

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

433 Bridging scales of evolution will require using transdisciplinary approaches in order to
434 explain how combinations of microevolutionary processes produce macroevolutionary patterns
435 and to solve long-standing questions. In this review, we propose that future research should
436 move away from framing that ignores the dynamic interplay among processes. Quantifying
437 more precisely the tempo and mode of evolution among clades and through time promises to
438 unveil times when evolutionary rates change at the phenotypic and species level. We propose
439 that future research should (i) assess the relative contribution of methodological biases and
440 biological processes to understand why estimated molecular, phenotypic and diversification
441 rates appear to increase through time, (ii) attempt to measure adaptive landscapes across space
442 and time to explain changes in the tempo of evolution, (iii) measure more precisely variation
443 in rates and the causes of large shifts, especially near speciation events, and (iv) conduct further
444 tests of the impact of species interactions on macroevolution, combining abundance and
445 phenotypic data. Unification across scales in evolutionary biology seems more possible than
446 ever before. We anticipate that, in the next decades, researchers will likely revisit old questions

447 with new models and data in genomics, computational biology and paleontology in order to
448 better describe and understand evolution in all its complexity.

449

450

451

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477

478 Competing interest

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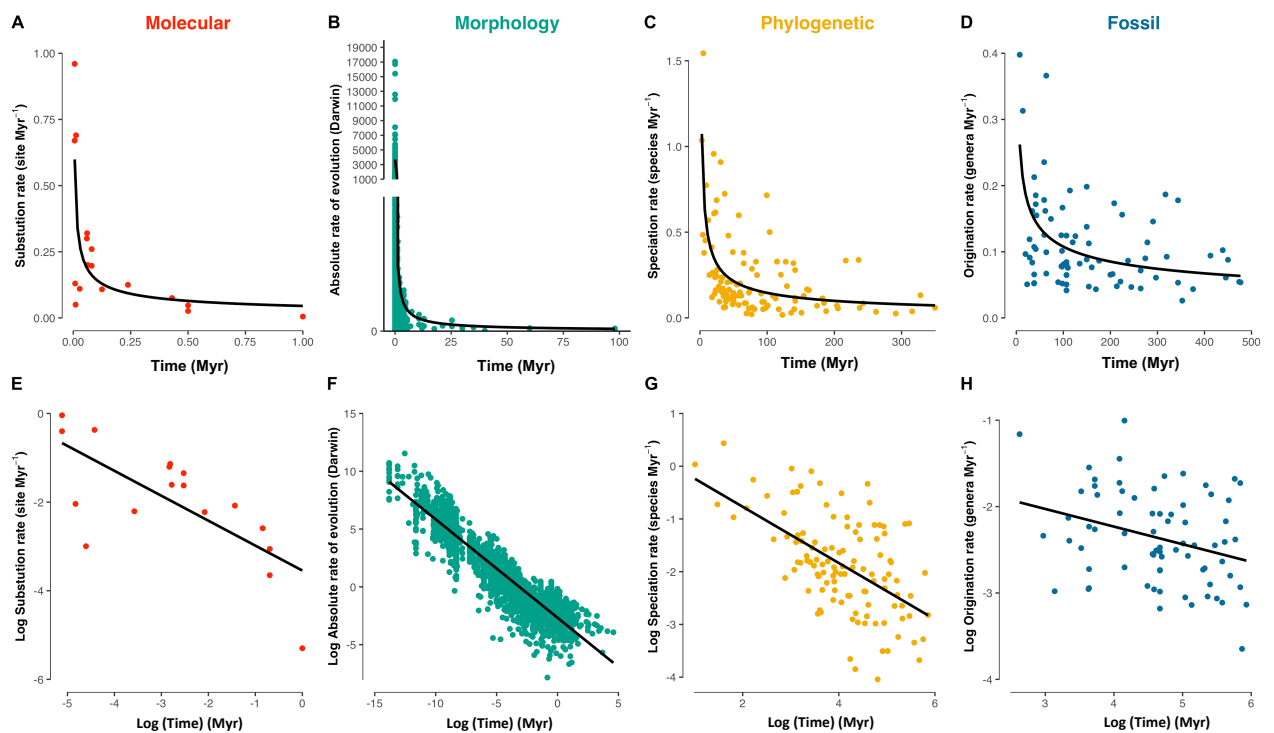
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1025 **Figure 1. Time-scale dependent rates of molecular evolution, phenotypic evolution, and**
1026 **speciation using phylogenetic or fossil data.** Molecular evolution is shown in panels A and
1027 E, phenotypic evolution in panels B and F, speciation rate using phylogenetic data in panels C
1028 and G and speciation rate using fossil data in panels D and H. All rates appear faster nearer the
1029 present and slower over longer timescales. Both axes in E, F, G, H have been log-transformed
1030 in order to show the long-term trend. This figure has been recreated from the data provided
1031 in^{19,27,62}. Darwin values of zero were removed in the panel F to avoid infinite values. Note that
1032 the timescales are different for each panel with an acceleration in the last 100kyr for genes, the
1033 last million of years for morphology, and the last tens of Myrs for speciation rates, while all
1034 relationships are linear when time is log-transformed. Why this pattern is shared between
1035 different measures of evolution is not well understood². In the literature, the “paradox of stasis”
1036 refers to morphological changes (panels B and F). The x-axis represents time intervals between
1037 calibration points (A and E), time intervals between measurements (B and F), clade ages (C
1038 and G), or clade durations (D and H).
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1044 **Figure 2. Current and fossil data represent past evolutionary processes incompletely.**
1045 Reconstructions of past molecular evolution, phenotypic evolution and diversification are
1046 biased because most of the information about past evolutionary changes is lost from molecular,
1047 phenotypic, phylogenetic and fossil history. Panel A shows how mutations in red cannot be
1048 reconstructed when several mutations affect the same position in the genome, a phenomenon
1049 called saturation. The comparison between a present-day genome and the genome of a sister
1050 species (or a sample of ancient DNA) only allows reconstructing mutations shown in green,
1051 biasing rate estimates if the method fails to take saturation into account, as shown in panel C,
1052 compared to the true rate in panel B. There may be other reasons why polymorphisms are not
1053 recorded over the long term, such as deleterious mutations not persisting or lost polymorphisms
1054 in extinct populations (not represented here). Similarly, phenotypic changes through geological
1055 time can only be accurately reconstructed when the fossil record is exceptionally well
1056 preserved. Reconstructed phenotypes based on phylogenies and fossils (panel E) will lead
1057 either to wrongly assigning a fossil to a branch when it belonged to another extinct lineage
1058 (e.g., fossil 1), or to missing shifts in phenotype that are not recorded in the fossil information.
1059 Phenotypes reconstructed only using phylogenetic data (F) will also largely miss past
1060 evolutionary changes. Finally, reconstructed phylogenies based on present-day data (H) are
1061 also likely missing most of the past speciation and extinction events (G). The observed lineage-
1062 through-time plot (I) obtained with the phylogenetic tree (black) is usually very far from the
1063 truth (blue).

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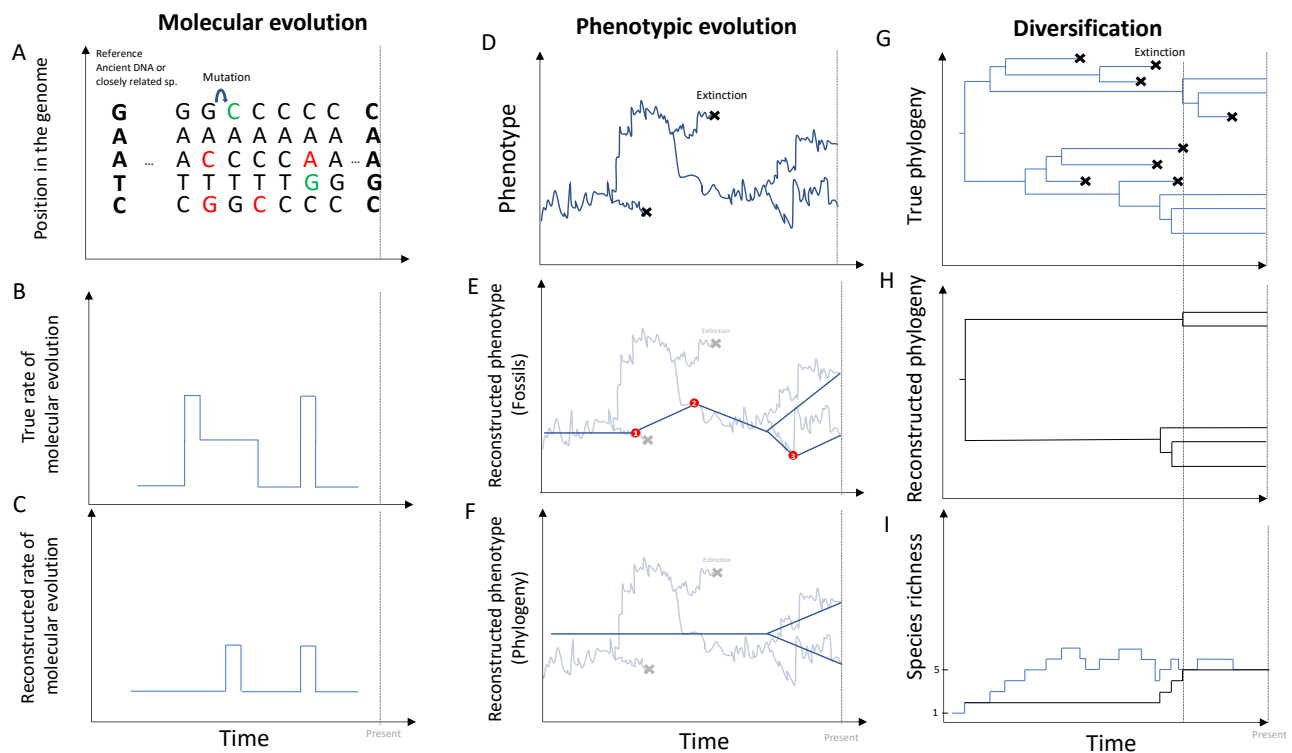
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1092 **Box 1. How to connect macroevolutionary trends to underlying population parameters?**

1093 The structure and the dynamics of evolving populations within species affect speciation and
1094 extinction rates. The probability of speciation is influenced by the probability of population
1095 establishment or splitting, the probability that populations persist long enough for speciation to
1096 occur, as well as the rate of evolution of reproductive barriers. The probability of species
1097 extinction is influenced by the number of populations and their size and genetic diversity. With
1098 the increasing availability of population parameters estimated for a large number of species
1099 (e.g. from population genomic datasets), there are growing opportunities to build more
1100 ‘mechanistic’ and potentially more informative comparative methods that include such details.
1101 Several comparative methods have already been developed to model trait evolution while
1102 accounting for intraspecific variance (jive model³⁸⁻³⁹) or to model diversification accounting
1103 for incipient lineages (protracted speciation model⁴¹), but they do not directly test the effects
1104 of population parameters on speciation and extinction rates. Trait-dependent diversification
1105 models (SSE models¹⁵¹) could be used for this exact purpose. SSE models were originally
1106 developed to test the effect of species traits on diversification¹⁵¹ with the probability of
1107 speciation and the probability of extinction at each point in time being a function of the species’
1108 trait value. They generally estimate the likelihood of trait-dependent speciation and extinction
1109 rates, given a phylogenetic tree and species’ traits measured at the present time. Transition rates
1110 between character states reflect both mutation and selection, although those two components
1111 are not explicitly modeled. One could thus treat microevolutionary parameters as species’ traits
1112 to estimate their impact on diversification rates. For instance, the probability of speciation is
1113 expected to depend on the rate of establishment of new populations and the probability of
1114 population splitting¹¹. Traits that could be used as microevolutionary proxies in diversification
1115 analyses include the number of populations within a species, the rate at which populations
1116 differentiate¹⁴⁹(e.g., using the slope of isolation by distance, estimated from F_{ST})⁹, or the rate
1117 at which reproductive isolation builds (e.g., via song evolution in birds¹⁵²). Similarly, the
1118 probability of species extinction is expected to be a function of the long-term population size¹⁵³
1119 and the probability that populations persist¹¹. Although estimates of persistence are rare, they
1120 are much needed and could be potentially estimated from high-quality fossil records or
1121 approximated from other traits implicated in extinction risk, such as effective population size,
1122 genetic diversity or range size. We thus need more studies to understand how those proxies
1123 relate to persistence/extinction and differentiation/speciation. Importantly, these comparative

1124 models provide insights on how those difficult-to-collect but crucial microevolutionary proxies
1125 could relate to differentiation/speciation and persistence/extinction.

1126

1127 **Box 2. Four evolutionary landscapes.** In the literature, four evolutionary landscapes have
1128 been described at different scales (Figure 3). At the microevolutionary level, one can either
1129 map the fitness of each individual onto trait values (the fitness function; e.g.,⁸⁴) or the mean
1130 fitness of a population as a function of gene frequencies or mean phenotype (adaptive
1131 landscape⁸⁵). The fitness function and adaptive landscape are usually measured from
1132 experiments¹⁵⁴ or more rarely in natural ecosystems^{84,77}. Peaks in the adaptive landscape
1133 represent genotypes/trait values where mean fitness is maximized, and valleys represent
1134 genotypes/phenotypes that are detrimental. The adaptive landscape concept is more
1135 complicated when selection is frequency-dependent, as when species interact.

1136 Macroevolutionary surfaces are functions that represent probabilities of phenotypic
1137 change over time. They lack a fitness interpretation but can be a useful summary of the outcome
1138 of the adaptive evolution of component species. The Brownian motion model, whereby
1139 instantaneous change is equiprobable in all directions, is represented by a flat
1140 macroevolutionary surface. It fits cases in which the squared difference between species
1141 increases linearly with time. The Ornstein-Uhlenbeck process fits data in which differences
1142 between species over time increasingly behave as though randomly sampled from a fixed
1143 underlying gaussian frequency distribution. The model can be represented by a concave
1144 downward surface with a single “peak” that is essentially the long-term mean of the underlying
1145 frequency distribution of species phenotype values. More complex surfaces can have multiple
1146 “peaks”, which fit data for which the long-term frequency distribution of species differences is
1147 best described by a mixture of probability distributions rather than a single distribution. For
1148 instance, Mahler et al.⁸⁸ showed that phenotypes of species in different lineages of the *Anolis*
1149 phylogeny clustered around the same set of “peaks” inferred from the distribution of species
1150 trait means, indicating convergence.

1151 “Species selection” surfaces describe the rates of speciation and extinction as a function
1152 of species mean trait values. The trait-dependent speciation and extinction can be estimated by
1153 fitting a model to data on trait means and branching rates in reconstructed phylogenetic
1154 trees^{89,151}. The concept can be applied to model speciation/extinction rates as a function of
1155 discrete or quantitative traits. The speciation and extinction rates are not interpretable on a
1156 fitness scale, but a lineage is more likely to persist if it splits often into daughter lineages and/or

1157 has a low extinction rate (see previous debates on species selection^{89,155}). A multi-trait
1158 framework still requires further development for quantitative characters (but see¹⁵⁶ for fossil
1159 data, and MuSSE for discrete traits¹⁵¹). Additionally, some methods based on the analysis of
1160 the fossil record also allow modeling a changing “species selection” surface (*evoTS* and
1161 *layeranalyzer* packages).

1162

1163 **Box 3. Why microevolution may not be coupled with macroevolution.** There are
1164 many reasons why all the details of microevolution would not predict macroevolution. The first
1165 reason is that large macroevolutionary patterns may emerge unpredictably from
1166 microevolutionary processes (e.g., the extinction risk of lineages may reflect unusual bouts of
1167 strong selection, rather than the average rate of selection). Classic philosophical discussions
1168 about challenges to the predictability of macroevolution from microevolution center on the
1169 hierarchical nature of biological organization, and the potential for properties to emerge at
1170 higher levels of organization (e.g. species) that cannot be explained at a lower organizational
1171 level¹⁵⁶⁻¹⁵⁹. A key element is that selection can change direction at different scales (section 2).
1172 Although the intensity of these debates has lessened, these issues remain and there is no
1173 consensus as to the relative frequency by which microevolutionary processes can predict
1174 macroevolution, and when they cannot.

1175 In his book *Wonderful life*¹⁶⁰, S.J. Gould proposed to “replay the tape of life” to know
1176 whether long-term evolution would follow the same trajectories over and over. Decades after
1177 this book, most evolutionary biologists would still argue that it is very unlikely that life will
1178 evolve following the same exact trajectory twice¹⁶¹. First, there is a large amount of
1179 stochasticity in any (complex) biological system, with survival, reproduction, and mutation all
1180 subject to chance¹⁶². For example, the COVID-19 pandemic hinged upon the chance of
1181 transmission of the virus in its first human hosts. Similarly, the time at which adaptations arise
1182 may be unpredictable, particularly for mutations that have arisen only once in the history of
1183 life¹⁶³. Second, there is a great deal of stochasticity and contingency in the abiotic environment,
1184 which affects both microevolutionary processes (e.g., lightning striking an individual) and
1185 macroevolutionary processes (e.g., a meteorite leading to a mass extinction¹⁵⁹). Another
1186 important problem is that several microevolutionary processes may lead to the same
1187 macroevolutionary pattern¹⁶⁴, which may lessen the identifiability of the models. Accounting
1188 for the microevolutionary processes underlying macroevolutionary patterns may also be
1189 challenging when several evolutionary processes operate simultaneously (e.g., population

1190 bottlenecks and periods of strong selection). Even if individual and population-level processes
 1191 may never totally explain broad-scale biodiversity patterns, we should strive to understand
 1192 which general rules at macroevolutionary scales can inform microevolution and vice versa.

1193

1194 **Figure 3. Four representations of evolutionary landscapes and surfaces at different scales**

1195 **related to phenotype.** Panel A and B represent the fitness function and the adaptive landscape

1196 at the microevolutionary scale. Panel A represents the fitness of all individuals in a population

1197 as a function of their trait values (e.g.,⁸⁴). Panel B represents the fitness averaged at the level

1198 of populations as a function of the mean trait value in a population (the so-called adaptive

1199 landscape⁸⁵). Panel C and D represent surfaces at the macroevolutionary scale. Panel C

1200 represents the likelihood of the parameter Θ , representing the attraction point of an OU process

1201 estimated using the frequency distribution of species trait values and a phylogeny or a time

1202 series. The peak is often interpreted as an “optimum” or “adaptive peak,” but it is better thought

1203 of as the mean of the underlying long-run frequency distribution of species’ trait values. Panel

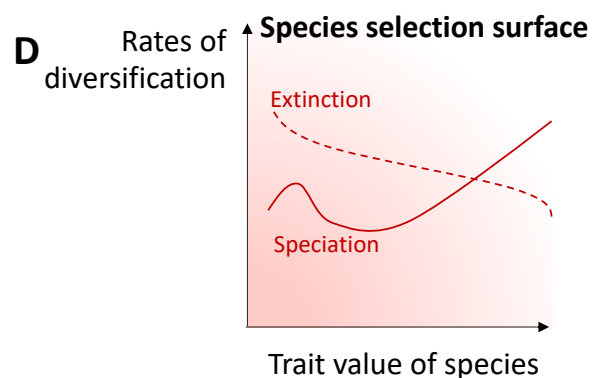
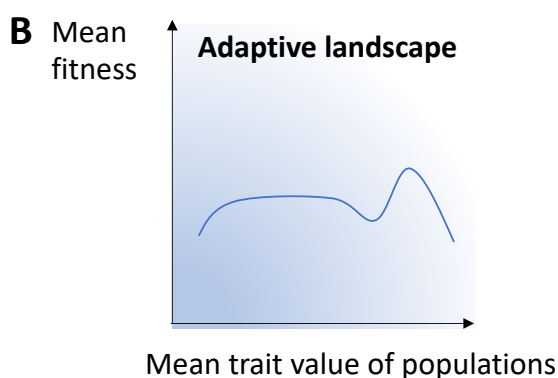
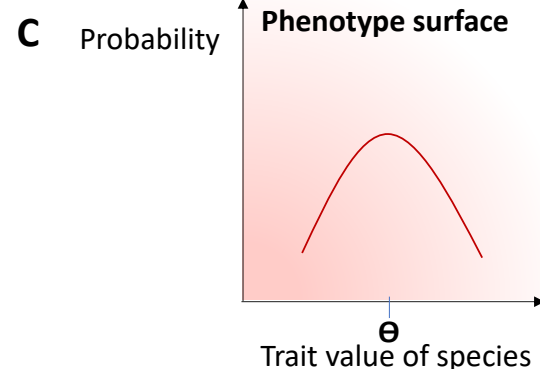
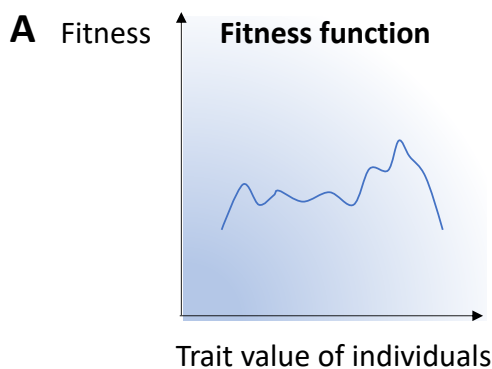
1204 D represents the rates of speciation and extinction as a function of lineage trait values, which

1205 are sometimes considered as parameters describing “species selection” on traits⁸⁹. The

1206 locations of “peaks” need not correspond between different landscapes.

MICROEVOLUTION

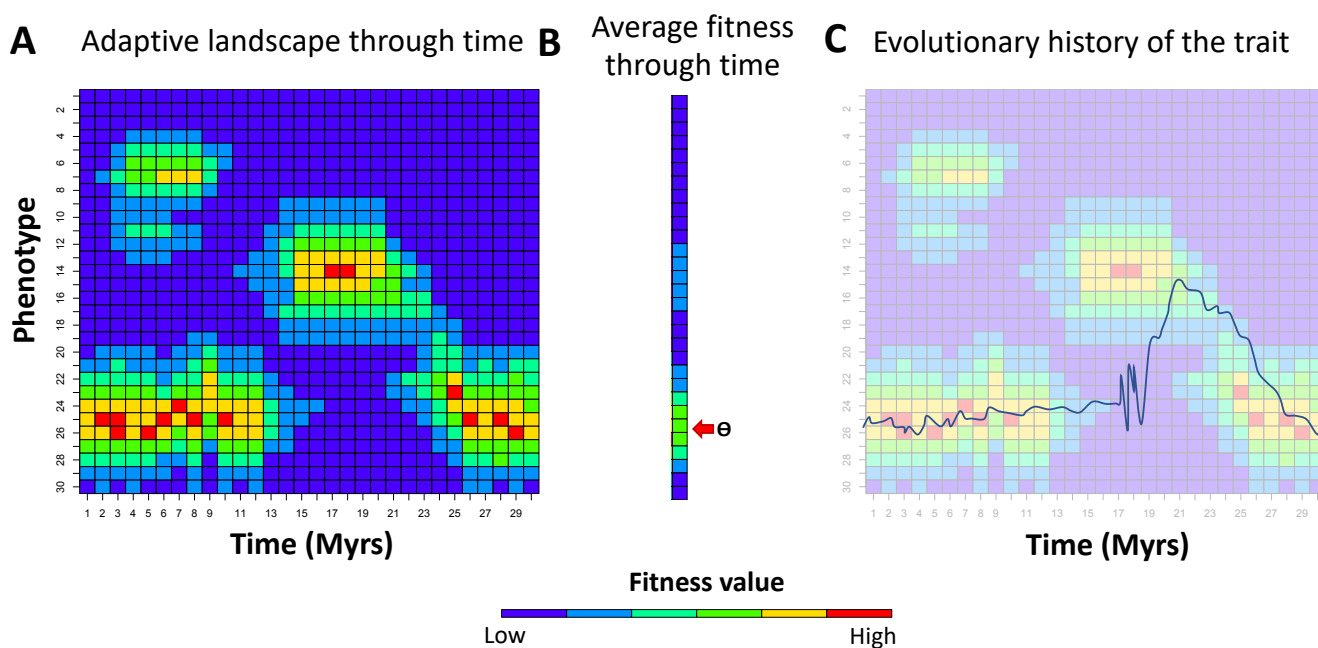
MACROEVOLUTION



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1208 **Figure 4. A changing microevolutionary adaptive landscape integrated over a**
 1209 **macroevolutionary time scale.** The relationship between the adaptive landscape, governing
 1210 the evolution of populations, to the macroevolutionary surface, representing probabilities of
 1211 change in species means over time, is not well understood. Panel A shows a hypothetical
 1212 adaptive landscape for a single trait at different slices of time. Each time slice describes mean
 1213 fitness of a single population (color goes from blue/low fitness to red/high fitness). Panel C
 1214 shows the ensuing changes in mean phenotype of the population over time, as it roughly tracks
 1215 the changing adaptive landscape (e.g., as recorded in a fossil sequence). Panel B represents the
 1216 average of the adaptive landscape through time, for each row of panel A over the entire time
 1217 period. The value of Θ , the attractor of the Ornstein-Uhlenbeck (OU) process is estimated by
 1218 fitting the model to the distribution of species values over time (not shown here). In this case,
 1219 Θ can be regarded as a summary of the outcome of adaptive evolution (e.g., as described across
 1220 a fossil sequence). In phylogenetics, Θ is usually estimated from a clade of species, each of
 1221 which might have its own unique adaptive landscape with a trajectory through time (one panel
 1222 A per lineage). Here too, Θ can be regarded as a summary of the outcome of lower-level
 1223 processes giving rise to the distribution of species values over the long run. This figure shows
 1224 how a macroevolutionary model of phenotypic evolution may be summarizing complex
 1225 microevolutionary processes.

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