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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 synthesis<sup>1</sup>, 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 timescales<sup>2</sup>. This discrepancy in rates has  
61 been detected in molecular evolution, phenotypic evolution and even lineage diversification  
62 rates<sup>2</sup>, 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 scales<sup>3-12</sup>. 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.<sup>13</sup>. 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 time<sup>14-18</sup>. 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 molecular<sup>19-21</sup>, phenotypic<sup>7,22</sup>, phylogenetic<sup>23-26</sup> and  
80 fossil data<sup>27</sup>. 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 processes<sup>2</sup>. Methodological bias can result from model misspecification, and from sampling or

85 parameter estimation errors<sup>2,22</sup>. 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<sup>2,28</sup>. 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 day<sup>2</sup>. 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 diversification<sup>29</sup>. 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 literature<sup>30</sup> or “the pull of the recent” in the paleontology  
106 literature<sup>31</sup>, which is related to the probability that a (fossil) lineage is lost over time<sup>32</sup>. The  
107 reconstructed birth-death process described in Nee et al.<sup>29</sup> 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.,<sup>33</sup>), estimating  
110 extinction rates accurately, especially in the absence of fossil data, remains a challenging task<sup>34</sup>.

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 substitution<sup>19</sup> (Figure 1).

117 Finally, we can follow the same reasoning with phenotypic differences between  
118 populations. Futuyma<sup>35-36</sup> 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 present<sup>2</sup>.

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 present<sup>37</sup>, intraspecific  
131 phenotypic variance<sup>38-39</sup>, the temporal sampling heterogeneity of the fossil record<sup>40</sup>, and for the  
132 fact that speciation is not instantaneous (protracted speciation models<sup>41</sup>). 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 approaches<sup>42</sup>. To better account for extinction,  
137 phylogenies can potentially be combined with the fossil record (see attempts<sup>43-47</sup>), at least for  
138 the few clades for which both neontological and paleontological data are available (such as  
139 mammalian lineages, Cetacea<sup>37</sup>, Carnivora<sup>43</sup> or Rodentia<sup>48</sup>). Importantly, these models of  
140 molecular, phenotypic evolution, and diversification should be tested with individual-based  
141 simulations on geological time scales (such as<sup>7,49</sup>) 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 Bryozoa<sup>50</sup>, Foraminifera<sup>51</sup>,  
148 sticklebacks<sup>52</sup> or diatoms<sup>53</sup> (reviewed in<sup>54</sup>) or long-term lab experiments<sup>55</sup> may also help to

149 determine whether time-scaling patterns are artifactual and why. Fossil databases are also  
150 important resources<sup>56-58</sup>. 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 accuracy<sup>59-61</sup>.

## 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. Gould<sup>16</sup>),  
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 average<sup>62</sup>,  
164 or every 1-100 Myrs depending on the size of the shift<sup>63</sup>), or gradual evolution on both short  
165 and long time-scales<sup>50,64</sup>.

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<sup>33,37</sup>. Only some small clades have been shown to fit a model of constant diversification  
169 rates, while larger clades are generally highly heterogeneous<sup>33,37,65</sup>. 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 reasons<sup>66</sup>.

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 evolution<sup>67-69</sup>. Genome composition also changes at  
175 heterogeneous rates among clades, via changing rates of inversion, translocation, chromosome  
176 fusion, and polyploidization<sup>e.g. 70</sup>.

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 selection<sup>18</sup>,  
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 response<sup>70-73</sup>. This may lead us to infer  
184 stasis despite abundant genetic variation for functional traits and strong selection<sup>70-73</sup>.  
185 Conversely, selection on skewed trait distributions can lead to signals of directional selection  
186 when in fact it is stabilizing<sup>73</sup>.

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.<sup>75</sup>,  
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’<sup>76</sup>. Therefore, macroevolutionary dynamics are thought to  
195 be mainly related to changes in this landscape through time (“seascape”<sup>77-79</sup>), 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 birds<sup>80</sup>. 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.<sup>81</sup>), biological interactions (traits that would make species vulnerable  
207 to parasites or predators, such as maximum running speed for a given body mass<sup>82</sup>) 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 organisms<sup>83</sup>.

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 phenotype<sup>84</sup>. (2) The adaptive



216 landscape is defined as the mean fitness of a population over different combinations of trait  
217 means<sup>85</sup> — or genotype frequencies<sup>75</sup> 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 model<sup>86</sup>, Bounded Brownian Motion<sup>87</sup>,  
220 Surface<sup>88</sup>). 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., QuaSSE<sup>89</sup>). 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 scale<sup>90-91</sup>(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 also<sup>92</sup>  
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 matrices<sup>85</sup> in a comparative context<sup>93-94</sup>), complex developmental processes (e.g., hourglass  
237 model<sup>95</sup>), 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<sup>16,96</sup>, an idea with little support from empirical fossil  
245 data<sup>50,97</sup>. Indirect evidence has been provided at the clade level from adaptive radiations (e.g.,  
246 African cichlids, Anolis lizards, Galápagos finches<sup>98</sup>), where speciation rate and phenotypic  
247 evolution have been shown to increase concomitantly<sup>99</sup>, 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 radiations<sup>98</sup>), respond to a changing environment<sup>65</sup>, or fill ecological opportunities, e.g., after a  
252 mass extinction<sup>100</sup>. 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 innovation<sup>101</sup> and potential speciation<sup>102</sup>. 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 differences<sup>103</sup>.

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 coexist<sup>104-105</sup>. 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. Futuyma<sup>35-36</sup>  
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 evolution<sup>50</sup>. 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 years<sup>62</sup> 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 events<sup>106</sup>. Finally, speciation could also be largely a by-product of  
280 genetic divergence<sup>107</sup>, and consequently, speciation could be associated with bursts of  
281 molecular genetic change. Polyploidization, for example, shows signs of clustering around

282 speciation events<sup>71</sup>, 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 salamanders<sup>108</sup>). In a similar vein, key evolutionary innovations can  
288 spread without changes in speciation rate (examples reviewed in<sup>110</sup>, 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 events<sup>111-112</sup>. The association between mutation and speciation is at the  
292 heart of classic theories, such as the metabolic theory of ecology<sup>113</sup>, 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 gradient<sup>114</sup>.

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 sequences<sup>115</sup>, long-term lab experiments<sup>55</sup> and resurrection experiments<sup>116</sup> 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 ago<sup>61</sup>. Trait-  
308 dependent models of diversification (e.g., ClaSSE<sup>117</sup> distinguishing cladogenetic and  
309 anagenetic trait evolution) and the development of models that combine fossil observations and  
310 phylogenies<sup>118</sup> allow for probabilistic tests of the correlation between speciation and trait  
311 evolution at nodes and along the branches of the phylogenetic tree<sup>119</sup>. 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 flight<sup>63</sup>) could be improved to account for asymmetrical inheritance of the intraspecific  
315 variation during speciation for quantitative traits<sup>49</sup>.

316 We are currently unsure under what circumstances macroevolution can predict  
317 microevolution<sup>7-8</sup> 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 see<sup>120</sup>). 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<sup>85,88,98</sup>. 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 traits<sup>73</sup>. 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 level<sup>121-125</sup>. Although a number of potential biotic interactions (i.e., mutualism, symbiosis,  
340 commensalism, antagonism) may impact both micro and macroevolution<sup>126</sup>, 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 trees<sup>65</sup> 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<sup>25,127-128</sup>, 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 uncertain<sup>68</sup>. Many other factors could cause slowdowns in diversification,  
352 such as the temperature decline through the Phanerozoic<sup>65</sup>, the effect of extinction and/or  
353 protracted speciation at the tips of phylogenetic trees<sup>66</sup>. Clade interactions could also influence  
354 diversification dynamics on macroevolutionary scales, such as competition between Bivalves  
355 and Brachiopods<sup>129</sup>, Canids<sup>130</sup>, or between Angiosperms and Gymnosperms<sup>131</sup>.

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 quantify<sup>100</sup>)  
361 or resource availability (see the discussion in<sup>132</sup> and<sup>133</sup>). Diversity-dependent diversification  
362 models have been developed to estimate carrying capacity at the clade-level<sup>134-136</sup>, 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 experiments<sup>105</sup>, disparity  
369 through time analysis of phenotypes (DTT<sup>137</sup>) or other models of phenotypic evolution  
370 (diversity-dependent, matching competition and early burst models<sup>119</sup>). These types of analyses  
371 permit the detection of interspecific phenotypic interaction during species coexistence<sup>138</sup> and  
372 across the latitudinal gradient<sup>139</sup>. Interactions beyond temporal co-occurrence, such as  
373 predation and spatial competition can be observed directly in the fossil record<sup>140</sup> 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 estimates<sup>141</sup>, 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 processes<sup>142</sup>. 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<sup>48,143</sup>, given that species abundance can be obtained and compared through  
393 time (from fossils<sup>141</sup> or quantification of environmental DNA<sup>144</sup>). 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 Coalescent<sup>145</sup>. 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<sup>121,124,129-131</sup>.  
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 predator<sup>146</sup>. 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 species<sup>147</sup>, 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*<sup>148</sup>), 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 speciation<sup>105</sup>. 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<sup>11,149</sup>. The appearance and persistence of populations should in  
415 turn be linked to the probability of speciation and extinction at larger time scales<sup>9,129</sup>. Recently  
416 developed comparative models<sup>139</sup> have the potential to be used to study a large variety of  
417 positive and negative species interactions (such as competition, mutualisms, symbiosis)<sup>126</sup>.

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 constraints<sup>150</sup> 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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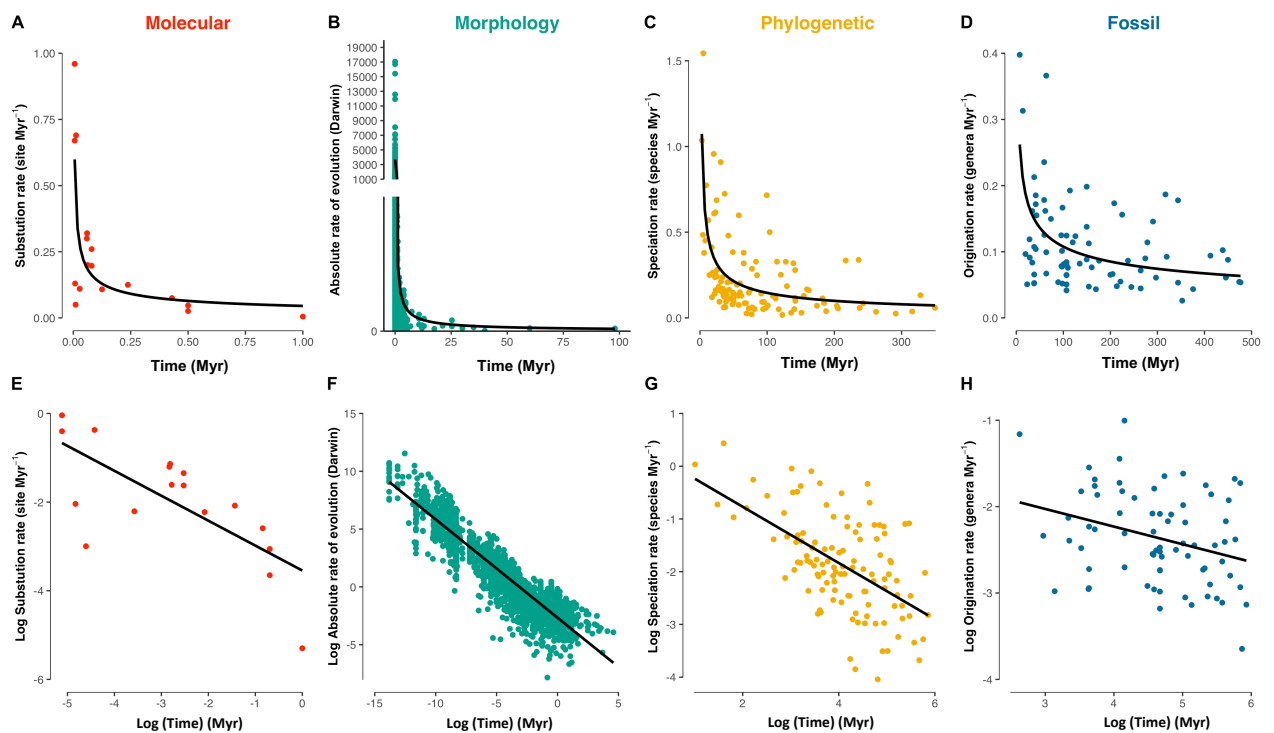
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1025 **Figure 1. Time-scale dependent rates of molecular evolution, phenotypic evolution, and**  
1026 **speciation using phylogenetic or fossil data.** Molecular evolution is shown in panels A and  
1027 E, phenotypic evolution in panels B and F, 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<sup>19,27,62</sup>. 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 understood<sup>2</sup>. 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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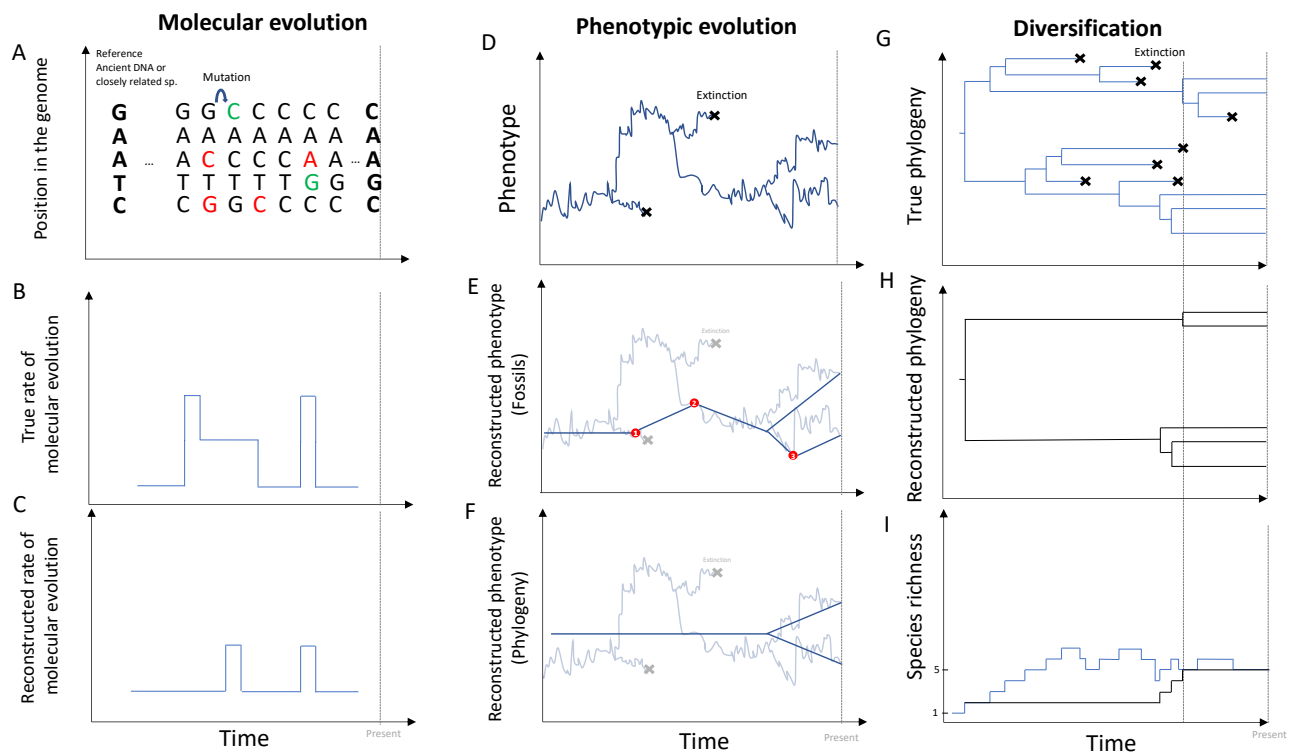
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1092 **Box 1. How to connect macroevolutionary trends to underlying population parameters?**

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 model<sup>38-39</sup>) or to model diversification accounting  
1103 for incipient lineages (protracted speciation model<sup>41</sup>), but they do not directly test the effects  
1104 of population parameters on speciation and extinction rates. Trait-dependent diversification  
1105 models (SSE models<sup>151</sup>) could be used for this exact purpose. SSE models were originally  
1106 developed to test the effect of species traits on diversification<sup>151</sup> 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 splitting<sup>11</sup>. 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 differentiate<sup>149</sup>(e.g., using the slope of isolation by distance, estimated from  $F_{ST}$ )<sup>9</sup>, or the rate  
1117 at which reproductive isolation builds (e.g., via song evolution in birds<sup>152</sup>). Similarly, the  
1118 probability of species extinction is expected to be a function of the long-term population size<sup>153</sup>  
1119 and the probability that populations persist<sup>11</sup>. 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.,<sup>84</sup>) or the mean  
1130 fitness of a population as a function of gene frequencies or mean phenotype (adaptive  
1131 landscape<sup>85</sup>). The fitness function and adaptive landscape are usually measured from  
1132 experiments<sup>154</sup> or more rarely in natural ecosystems<sup>84,77</sup>. 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.<sup>88</sup> 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<sup>89,151</sup>. 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<sup>89,155</sup>). A multi-trait  
1158 framework still requires further development for quantitative characters (but see<sup>156</sup> for fossil  
1159 data, and MuSSE for discrete traits<sup>151</sup>). 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 level<sup>156-159</sup>. 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*<sup>160</sup>, 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 twice<sup>161</sup>. First, there is a large amount of  
1179 stochasticity in any (complex) biological system, with survival, reproduction, and mutation all  
1180 subject to chance<sup>162</sup>. 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 life<sup>163</sup>. 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 extinction<sup>159</sup>). Another  
1186 important problem is that several microevolutionary processes may lead to the same  
1187 macroevolutionary pattern<sup>164</sup>, 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.,<sup>84</sup>). 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 landscape<sup>85</sup>). Panel C and D represent surfaces at the macroevolutionary scale. Panel C

1200 represents the likelihood of the parameter  $\Theta$ , 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

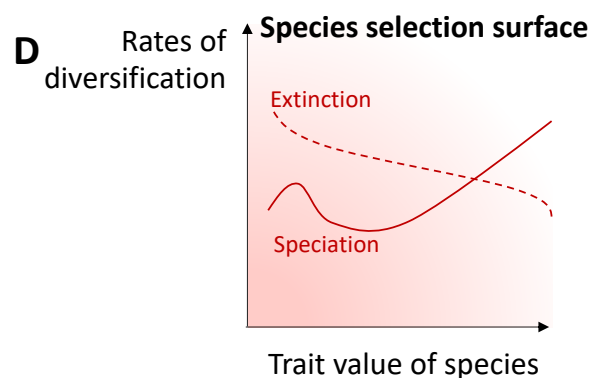
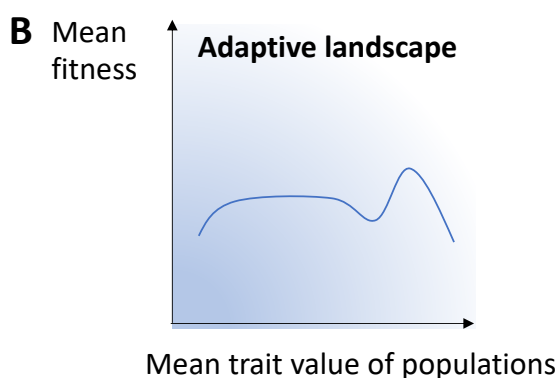
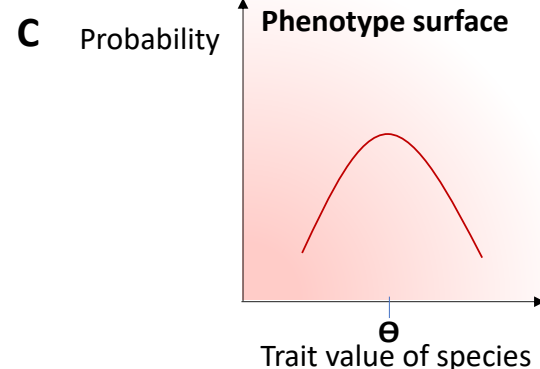
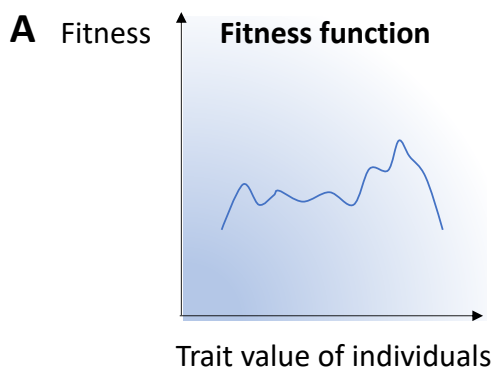
1204 D represents the rates of speciation and extinction as a function of lineage trait values, which

1205 are sometimes considered as parameters describing “species selection” on traits<sup>89</sup>. The

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

### MICROEVOLUTION

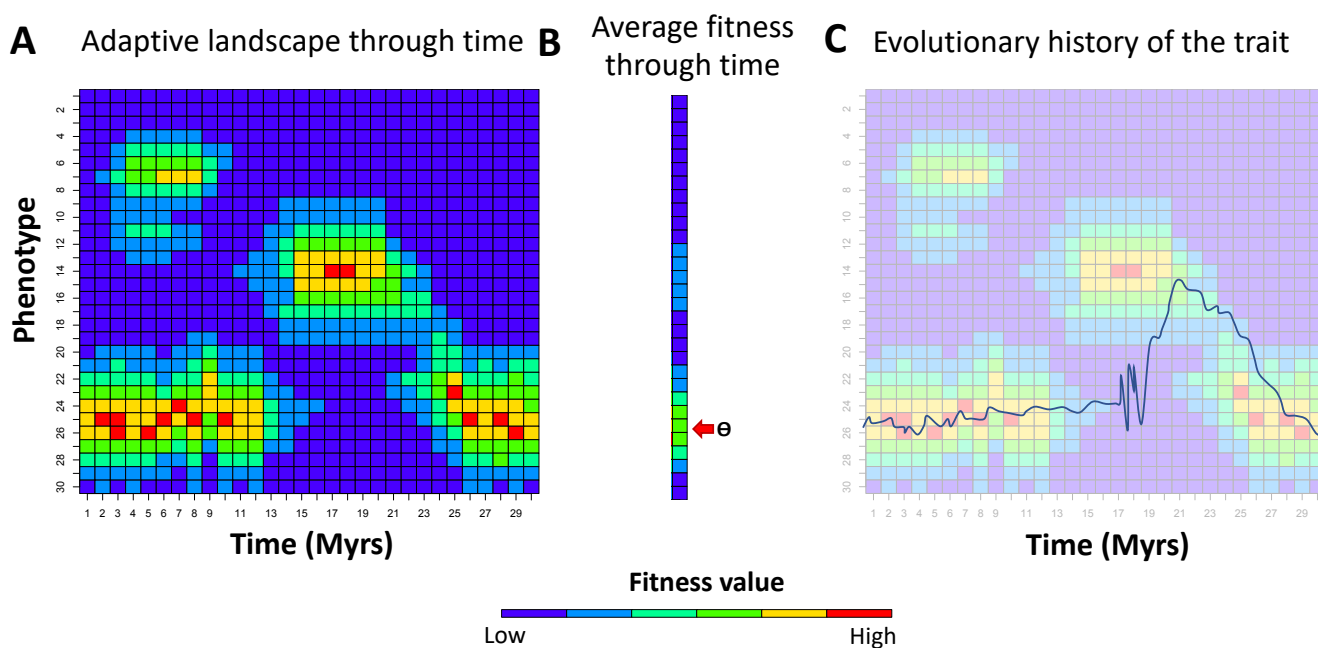
### MACROEVOLUTION



1207

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  $\Theta$ , 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  $\Theta$  can be regarded as a summary of the outcome of adaptive evolution (e.g., as described across  
 1220 a fossil sequence). In phylogenetics,  $\Theta$  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,  $\Theta$  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.

1226  
1227



1228  
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