

1 Opinion Paper for Trends in Ecology and Evolution (TREE)

2

3 **Title:** Why does diversification slow down?

4

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11

12 **Abstract:** Studies of phylogenetic diversification often show evidence for slowdowns in  
13 diversification rates over the history of clades. Recent studies seeking biological explanations for  
14 this pattern have emphasized the role of niche differentiation, as in hypotheses of adaptive  
15 radiation and ecological limits to diversity. Yet many other biological explanations might  
16 underlie diversification slowdowns. Herein we focus on the geographic context of diversification,  
17 environment-driven bursts of speciation, failure of clades to keep pace with a changing  
18 environment, and protracted speciation. We argue that despite being currently underemphasized,  
19 these alternatives represent biologically plausible explanations that should be considered along  
20 with niche differentiation. Testing the importance of these alternative hypotheses might yield  
21 fundamentally different explanations for what influences species richness within clades through  
22 time.

23

24 **Keywords:** adaptive radiation; biogeography; diversification; ecological limits; extinction;  
25 speciation; wax-wane dynamics

## 26 **Reconsidering the causes of diversification slowdowns**

27 Understanding diversification dynamics – how and why speciation and extinction rates vary  
28 across time, space, and clades – has long interested evolutionary biologists [1]. Time-calibrated  
29 molecular phylogenies are increasingly used to characterize this diversification, particularly in  
30 groups with poor fossil records [1–3]. One emergent pattern is a slowdown of net diversification  
31 rates (see glossary) over the histories of clades [2–4], typically linked to a slowdown in  
32 speciation rates. Such slowdowns have been found with a variety of statistical methods (Box 1).  
33 A meta-analysis of 289 phylogenies spanning a variety of taxa estimated that slowdowns occur  
34 in as many as 63% of all clades [3]. Such slowdowns have strong implications for our  
35 understanding of the evolution of clades as well as global biodiversity patterns [5–7].

36       Why do many phylogenies show diversification slowdowns? Methodological biases can  
37 lead to such results and need to be controlled (Box 2). However, recent studies have avoided  
38 many biases and have still found strong support for slowdowns (e.g., [3,4,8]). Given that this  
39 appears to be a real and widespread pattern, studies now increasingly focus on the biological  
40 causes of diversification slowdowns (Figures 1,2). Many of these explanations are based on  
41 relatively old hypotheses put forward to explain diversification dynamics from the fossil record  
42 (e.g., [9–12]). Renewed interest results from the widespread availability and promise of time-  
43 calibrated molecular phylogenies and diversification rate methods for evaluating these  
44 hypotheses. Many recent papers have emphasized the role of competition for limited resources,  
45 adaptive radiation, and ecological limits on the number of species within a clade (e.g.,  
46 [2,4,5,8,13,14]). Here, we argue that current understanding of speciation, phenotypic evolution,  
47 and the fossil record suggests that for many clades alternative explanations might be more likely  
48 to have produced the observed diversification slowdowns than factors related to niche

49 differentiation. Possibilities as diverse as the influence of geography on diversification [15],  
50 environment-driven pulses of high speciation rate [9], and a failure to keep pace with a changing  
51 environment [16] should be considered more thoroughly. In some cases, these hypotheses may  
52 be initially teased apart by estimating whether diversification rates vary with the number of  
53 species in the clade (also called "diversity-dependence") or through time (Figure 1). However,  
54 distinguishing among hypotheses within these broad categories may be difficult without  
55 additional information, such as data on geographic distributions or phenotypes. We therefore  
56 detail the conceptual basis of these hypotheses, suggest how they may be tested with different  
57 forms of data, and indicate directions for future research.

58

#### 59 **Hypotheses based on niche differentiation**

60 The dominant explanation in the literature for diversification slowdowns is that they result from  
61 the influence of competition for limited resources or niches on diversification [2,8,13,17–19].  
62 This explanation, which falls in the category of diversity-dependent explanations (Figure 1), is  
63 often related to adaptive radiation [4,14,20–23], as authors have hypothesized that speciation rate  
64 would slow down after the initial rapid speciation and as niches are filled (Figure 2; [4,20,21,24]).  
65 The idea of niche filling has been expanded further to suggest that there are a limited number of  
66 ecological niches within a clade, putting an ecological limit on clade diversity [5,17,21,22]. The  
67 ecological theory of adaptive radiation, however, does not make the explicit prediction that  
68 slowdowns should follow radiations (but see [25]) nor that there should be a hard limit to the  
69 number of ecological niches [24].

70         Interpretations of diversification slowdowns in terms of adaptive radiation are regularly  
71 made with little or no testing of ecological diversification and adaptation [4,20,23,26], the key

72 components that distinguish adaptive from non-adaptive radiation [24]. And given that very few  
73 clades represent well-supported cases of adaptive radiation [24,26], it seems that far too many  
74 clades show diversification slowdowns to assume (without testing) that such slowdowns indicate  
75 adaptive radiation and niche differentiation [6,27]. While some studies of individual clades have  
76 shown strong support for early bursts of phenotypic evolution (i.e., those that might be expected  
77 in adaptive radiation; [28–31]), a meta-analysis of a wide array of animal clades found support  
78 for an early burst model in only two out of 88 datasets [32].

79         In even classic cases of adaptive radiation, other factors might strongly influence  
80 diversification. For example, phylogenetic analyses suggest that in Greater Antillean *Anolis*  
81 lizards, radiations on smaller islands (i.e., Jamaica and Puerto Rico) are “at or near equilibrium  
82 diversity” [33]. If niche-based differences led to this equilibrium diversity, clades on the islands  
83 should be at or near niche saturation as well. However, this does not seem to be the case.  
84 Decades of detailed ecological and evolutionary studies (summarized in [34]) have shown that  
85 the number of locally co-occurring and interacting *Anolis* species is represented by up to six  
86 distinct ecological types that are replicated across most islands (i.e., ecomorphs [34]). But clades  
87 on Jamaica and Puerto Rico have not reached these six ecomorphs, a clear case of “empty” or  
88 “unused” niches [35] (though it might be possible that smaller islands cannot support as many  
89 ecomorphs [34] or that the equilibrium number of occupied niches is below the maximum  
90 number of niches [11,36]). Moreover, there are multiple species of some ecomorphs (despite the  
91 absence of others) on each of these islands [34], and most *Anolis* speciation in the Greater  
92 Antilles (particularly on the largest islands) seems to have produced allopatric, ecologically  
93 equivalent sister species, at least in terms of resource competition [34,37]. These observations  
94 are not generally consistent with the hypothesis of ecological controls on species richness.

95 Indeed, geographic constraints on diversification (see below) and niche divergence may interact  
96 to produce these slowdowns [33].

97 Another challenge to the idea that niche availability limits diversity is the infrequent  
98 occurrence of clades at a supposed limit ([3], but see [36]). This observation has been suggested  
99 to be due (in part) to the continuous evolution of key innovations, each of which allows  
100 subclades to break away from the dynamics of their parent clade and prevents reaching a limit to  
101 diversity [7]. However, even in this case the broader parent clade should still show equilibrium  
102 dynamics [21]. Furthermore, the more general idea that bursts of diversification arise from  
103 greater niche availability early in a clade's history has been suggested as unlikely for many  
104 clades [27]. Therefore, other possible causes of diversification slowdowns should be considered  
105 much more thoroughly.

106

## 107 **Underemphasized biological explanations for diversification slowdowns**

### 108 *Geography of diversification*

109 Most speciation, particularly in animals, results from geographic isolation of populations with a  
110 lack of gene flow (i.e., allopatric speciation [38–42]). A common cause of such geographic  
111 isolation (and later speciation) is separation by a geographic barrier (i.e., vicariance [38]). These  
112 events are more likely to “miss” small range sizes, such that vicariant speciation is most likely at  
113 intermediate to large range sizes [15,38,42]. Hence, as diversification proceeds and ranges are  
114 subdivided within a geographically bound group, per-species rates of speciation decline (Figure  
115 2). In addition, extinction rates will increase as species range sizes (and thus population sizes)  
116 become smaller [38]. This geographic mode of diversification, which falls in the category of  
117 diversity-dependent explanations, could in principle lead to equilibrium diversity (Figure 1).

118           Recent studies lend support to the role of geography in explaining diversification  
119 slowdowns. First, Pigot *et al.* [15] used a simulation model of geographic range evolution and  
120 cladogenesis to show that ecologically neutral speciation, extinction, dispersal, and range-size  
121 evolution can produce diversification slowdowns. In addition, studies of island species have  
122 shown that probability of speciation increases with island size [43,44], and large, single-island  
123 assemblages show slowdowns while clades in archipelagoes of small, isolated islands show  
124 constant net diversification rates (i.e., spreading across islands leads to continual speciation  
125 opportunities [18]).

126           To produce diversification slowdowns, this explanation requires that range expansion  
127 after allopatric speciation is infrequent or delayed [15]. Such inhibition of range expansion on a  
128 macroevolutionary time scale can be linked to many factors unrelated to niche divergence,  
129 including low dispersal ability [45], conservatism in physiological traits [46], and reproductive  
130 interference [47]. These factors will not likely maintain species' ranges at equilibrium size over  
131 the full history of clades [45], but they will probably constrain ranges enough to significantly  
132 slow the average rate of speciation in a group. Thus the geographic context of diversification  
133 alone can lead to diversification slowdowns without niche differentiation [8,15].

134           In some cases, niches might also be important when considering the influence of  
135 geography on slowdowns [36]. For example, competition between sister species with similar  
136 niches might prevent range expansion [45,48], limiting further allopatric speciation and slowing  
137 speciation rate in a clade. However, in this case the maintenance of niche similarity – rather than  
138 niche divergence and the filling of a limited number of niches – is what leads to speciation rate  
139 slowdowns. In the case of hypotheses based on niche divergence, competition drives  
140 concomitant diversification of species and niches. When geography is important, competition

141 impedes diversification and there should be little or no niche divergence associated with the  
142 slowdown.

143 Two additional models are similar to the geographic hypothesis as described above. First,  
144 Wang *et al.* [49] developed a neutral model of diversification in which average speciation rate  
145 declines over time because abundance decreases at speciation, such that the most abundant  
146 species over time are those with low speciation rates. This model is analogous to the geographic  
147 hypothesis, with abundance substituting for geographic range size. Second, frequent peripatric  
148 speciation might lead to diversification slowdowns. Under this model, one species with a large  
149 geographic range size gives rise to many small-ranged species that are unlikely to further  
150 speciate, leading to a linear increase in species over time instead of the exponential increase  
151 expected under standard birth-death models of diversification. Pigot *et al.* [15] found that the  
152 peripatric model led to slowdowns as long as geographic range size was relatively stable.  
153 *Zosterops lateralis*, a bird species complex that has repeatedly colonized multiple south Pacific  
154 islands from Australia and has led to many incipient species (see [40,50]), may represent an  
155 empirical example of the peripatric model.

156

### 157 *Environment-driven pulses of high speciation rate*

158 Speciation rates might increase temporarily during periods of rapid environmental or geological  
159 change, then decrease after the period ends (Figure 2; [26,51]). Such changes can lead to  
160 speciation via simple population isolation or the creation of an environmental gradient (e.g.,  
161 climatic zonation along mountain slopes) along which speciation occurs due to climatic  
162 specialization [39]. Contrary to the previous hypotheses, where diversification slowdowns result  
163 from intrinsically negative diversity dependence (Figure 1), here the slowdown arises from the



164 slowing of extrinsic factors that lead to speciation (such as vicariance events). This idea was  
165 introduced by Vrba [9] to describe diversification in the fossil record, calling it the “Turnover  
166 Pulse Hypothesis.” In extant taxa this possibility was suggested by Lovette and Bermingham  
167 [20], who found evidence for high speciation rates in *Dendroica* warblers close to a period of  
168 climate cooling and drying in the late Miocene between 5–10 Mya. Ricklefs [51] later noted that  
169 many passerine bird clades with diversification slowdowns originated during this same time  
170 period [4], as well as many plant lineages in southern Africa [52]. Additionally, many Andean  
171 plant clades originated and diversified at a time of rapid uplift of the northern Andes [53,54]. In  
172 sum, evidence that environment-driven pulses of high speciation rate lead to diversification  
173 slowdowns is reasonable but largely anecdotal and awaits systematic testing.

174

#### 175 *Failure to keep pace with a changing environment*

176 An inability to keep pace with a changing biotic or abiotic environment may lead to  
177 diversification slowdowns (Figure 2) [16,55]. This hypothesis is distinct in that slowdowns may  
178 result in an actual decline in diversity after a period of expansion rather than lead to equilibrium  
179 diversity (Figure 2), a pattern sometimes called waxing-waning dynamics. This scenario falls in  
180 the category of time dependent explanations (Figure 1), with diversification slowing down such  
181 that net diversification rates switch from positive (corresponding to increasing diversity) to  
182 negative (corresponding to decreasing diversity) over a clade’s history. This could be due to  
183 speciation rates decreasing below extinction rates, extinction rates increasing above speciation  
184 rates, or both. Under this scenario, clades in both the expanding and the declining phase will  
185 show diversification slowdowns, thus potentially explaining the ubiquity of the pattern.

186 In terms of evidence, we know from the fossil record that most taxa go extinct [56], and  
187 recent paleontological studies have further shown that many genera symmetrically rise and fall in  
188 diversity [16,57], including groups that have extant representatives [16]. Recent studies have  
189 suggested that a changing environment may lead to the downfall of entire clades, particularly if  
190 they cannot tolerate abiotic environmental changes or if other expanding clades outcompete them  
191 [16,58]. Ricklefs [51] proposed a scenario of coevolutionary interactions between pathogens and  
192 their hosts that may fit this model. He suggested that initial speciation rate in a host clade may be  
193 high due to initial pathogen resistance (the “escape and radiate” hypothesis of Ehrlich and Raven  
194 [59]), but then rates would subsequently decline due to pathogens overcoming the resistance and  
195 limiting further diversification. The decline phase of a host clade’s history could lead to eventual  
196 extinction, as we discuss here, or it may lead to net diversification rates of zero until additional  
197 pathogen resistance evolved. This model remains to be tested.

198 Waxing-waning dynamics were not initially thought to explain observed diversification  
199 slowdowns – for example, those inferred via negative gamma values (Box 1; [56]) – because  
200 recent extinctions would erase the signal of earlier speciation slowdowns [60]. However, Quental  
201 and Marshall [61] demonstrated that clades in decline could in fact show negative gamma values.  
202 Waxing-waning dynamics have very rarely been inferred from phylogenies, but this results from  
203 a past lack of serious consideration because reconstructed phylogenies give the impression that  
204 species richness only increases through time [1,6,61]. A study of modern whales, however,  
205 illustrated that diversity declines can be recovered from reconstructed phylogenies ([62], see also  
206 [55]). Further studies will be necessary to determine the importance of waxing-waning dynamics  
207 for empirical phylogenies.

208

209 *Protracted speciation*

210 Under many speciation concepts, there is an expected lag time between the initial  
211 divergence of populations and when they have achieved reproductive isolation or gene flow  
212 completely stops [39,63,64]. However, the time at which sister species are inferred to have split  
213 in a phylogeny will date to the original population split, not the “completion” of speciation.  
214 Consequently, the presence of incipient species in a clade (and the failure to include them as  
215 distinct species in the phylogeny) will exclude the most recent branching points of a phylogeny.  
216 This concept, referred to as “protracted speciation” [63,64], may partly explain slowing  
217 diversification rates through time [65] because branching events near the tips will be excluded.

218 Protracted speciation is distinct from other hypotheses in that it only applies to a certain  
219 portion of the history of a group (i.e., near the present). This is a strength of the explanation  
220 because there is no reason for the present day to be a special time at which most clades show  
221 slowdowns [56,65], and indeed protracted speciation should only (and always) be applicable in  
222 the present day [65]. On the other hand, the explanation is somewhat limited in that the process  
223 will have no applicability to deep-time slowdowns. Many analyses have found slowdowns after  
224 removing the most recent branch lengths (e.g., [4,28]), and such slowdowns cannot be explained  
225 by protracted speciation.

226

### 227 **Identifying the biological causes of slowdowns in diversification rates: ways forward**

228 Novel phylogenetic diversification methods are increasingly making subtle differences among  
229 models differentiable [e.g., 3,8,17,19,62,66,67]. Yet it has become clear that very similar  
230 branching patterns in phylogenies can be the product of very distinct biological scenarios [3,27],  
231 and that comparing model fit alone often might not tease apart these scenarios [17,68]. As such,

232 here we propose ways to test the ecological, phenotypic, and geographic corollaries of these  
233 hypotheses, in addition to suggesting further needs in modeling diversification.

234

#### 235 *Testing diversification scenarios*

236 Many current alternatives to niche-divergence hypotheses have seen few explicit tests  
237 using diversification models. This is largely due to two reasons. First, few explicit inference  
238 approaches are available to directly compare the models of diversification discussed herein. For  
239 example, approaches do not exist to compare the model of peripatric speciation or the neutral  
240 model of Wang *et al.* [49] to other models such as constant rates, time-dependent diversification,  
241 and diversity-dependent diversification. Even rigorously testing among these latter models is still  
242 not very common, with the use of the gamma statistic still frequent (Box 1). However, at least  
243 simply testing for diversity-dependence versus time-variable diversification rates may eliminate  
244 some hypotheses (Figure 1), with additional data serving to further differentiate hypotheses (see  
245 below).

246 Second, many hypotheses simply have been under recognized. Waxing-waning dynamics  
247 can now be tested [55,62], as well as protracted speciation [65]. Tools are also available to  
248 evaluate the hypothesis that common environmental factors have led to bursts in speciation. To  
249 do so, one could simply first determine a priori events that might have lead to high speciation  
250 rates in a group, and then examine support for a model that allows a diversification rate shift at  
251 the time of the events (see, for example [69]). Alternatively, for a more complex history of  
252 diversification, one could use paleontological environmental data, specify a functional response  
253 of diversification rates to the environmental factors hypothesized to have had a strong influence

254 (e.g., rates of speciation increase during periods of geological activity or climatic change), and  
255 infer the likelihood support of this relationship [70].

256

257 *Additional data beyond phylogenies per se*

258         Given that examining the phylogeny alone might not be powerful enough to distinguish  
259 among hypotheses [3,17,68], incorporating other data into phylogenetic diversification analysis  
260 such as population size, traits, range size and overlap, and fossils would be useful and needs to  
261 be developed [56,70]. More simply, all hypotheses have other predictions beyond diversification  
262 per se and such predictions should be tested. For example, the most basic necessity for testing the  
263 influence of niche divergence on diversification is data on traits that affect competition among  
264 species within a clade (e.g. [28–31,68]), yet these data are not often presented. More refined  
265 statistical approaches that directly link tempo of species diversification to tempo of phenotypic  
266 evolution will also help in this endeavor (see [30,31]). Furthermore, information on range  
267 overlap is necessary to distinguish between geographic and niche divergence-based causes of  
268 slowdowns, and explicitly considering this might often be very simple. For example, even if the  
269 species in a given clade show niche divergence, if they do not occur in the same geographic area  
270 then there was probably little role for ecological differentiation in species diversification [6].  
271 Alternatively, the widespread co-occurrence of closely related species might indicate little  
272 importance for geographic factors, because slowdowns are not likely to be due to geographic  
273 factors under high rates of secondary range overlap [15]. Hence, a simple, initial test might be  
274 one that analyses the link between species' phylogenetic relatedness and co-occurrence.

275         The geographic vicariance hypothesis suggests that within a geographic area (e.g., a  
276 continent), sister clades (those of the same age) should show an inverse relationship between

277 species diversity in that area and average range size, and as far as we know this has not yet been  
278 tested. Alternatively, one could test the theoretical result that larger range sizes are those that are  
279 more likely to be bisected by vicariance to produce daughter species [38], as done by Price [42].  
280 The geographic peripatric model similarly yields testable predictions, such as an uneven  
281 distribution of range sizes across species [15] and a highly asymmetric phylogeny (due to many  
282 small-ranged species “budding off” a large-ranged species; Figure 2). Finally, given that the  
283 geographic models (both vicariant and peripatric) focus on range dynamics in general,  
284 understanding the determinants of range boundaries and expansion (e.g., [45]) would help  
285 resolve whether this model applies to a given clade.

286         Paleontological data can also offer a rich source of additional evidence [56]. Indeed, early  
287 hypotheses about the dynamics of macroevolutionary diversification came from the fossil record  
288 (e.g. [11,12]), though most such studies did not include ecological data, which limits their ability  
289 to provide support for the various hypotheses we outline above. However, ecological data are  
290 available for some fossil taxa (e.g. [71,72]) and morphology can be used as a proxy for  
291 ecological data for many fossils [73]. Such data can be combined with fossil-estimated speciation  
292 and extinction rates to test how niche-filling is associated with diversification rates. Geographic  
293 range data of fossils can similarly test the importance of geography on diversification rates. As a  
294 good example of such approaches, Ezard *et al.* [74] combined morphological, depth habitat, and  
295 paleoclimatic data with a complete phylogeny (i.e. including all extinct species) of the  
296 macroperforate planktonic foraminifera to test what factors have influenced their diversification  
297 in the Cenozoic. Finally, waxing and waning can be directly tested with origination and  
298 extinction rates over time in paleontological data [16], as can environment-driven bursts of  
299 speciation [9]

300

## 301 **Conclusions**

302 Many clades show diversification slowdowns. This pattern might be driven by many biological  
303 factors. No one hypothesis will apply to all groups that show a signal of declining diversification  
304 rates, and some clades might experience multiple factors that lead to diversification slowdowns.  
305 We simply argue here that the importance of the dominant explanation – that based on niche  
306 divergence– might be largely overstated. Other biological factors can explain why many groups  
307 show decreasing diversification rates through time, but much work remains to be done to  
308 distinguish among them. This will necessitate considering both the phylogenetic and non-  
309 phylogenetic predictions of various hypotheses and testing underlying assumptions.

310

## 311 **Acknowledgements**

312 We thank F. Condamine, P. Craze, H. Doll, J. Greene, J. Losos, A. Phillimore, A. Pigot, T.  
313 Quental, J. Rolland, J. Rosindell, J. Wiens, and an anonymous reviewer for insightful criticisms  
314 and helpful suggestions for this paper.

315

## 316 **References**

- 317 1. Ricklefs, R.E. (2007) Estimating diversification rates from phylogenetic information.  
318 *Trends Ecol. Evol.* 22, 601–610
- 319 2. McPeck, M.A. (2008) The ecological dynamics of clade diversification and community  
320 assembly. *Am. Nat.* 172, E270–E284
- 321 3. Morlon, H. *et al.* (2010) Inferring the dynamics of diversification: A coalescent approach.  
322 *PLOS Biol.* 8, e1000493

- 323 4. Phillimore, A.B. and Price, T.D. (2008) Density-dependent cladogenesis in birds. *PLOS*  
324 *Biol.* 6, 0483–0489
- 325 5. Rabosky, D.L. (2009) Ecological limits and diversification rate: alternative paradigms to  
326 explain the variation in species richness among clades and regions. *Ecol. Lett.* 12, 735–743
- 327 6. Wiens, J.J. (2011) The causes of species richness patterns across space, time, and clades  
328 and the role of "ecological limits". *Q. Rev. Biol.* 86, 75–96
- 329 7. Cornell, H.V. (2013) Is regional species diversity bounded or unbounded? *Biol. Rev.* 88,  
330 140–165
- 331 8. Rabosky, D.L. and Lovette, I.J. (2008) Density-dependent diversification in North  
332 American wood warblers. *Proc. R. Soc. B: Biol. Sci.* 275, 2363–2371
- 333 9. Vrba, E.S. (1985) Environment and evolution: Alternative causes of the temporal  
334 distribution of evolutionary events. *S. Afr. J. Sci.* 81, 229–236
- 335 10. Sloss, L.L. (1950) Rates of evolution. *J. Paleontol.* 24, 131–139
- 336 11. Walker, T.D. and Valentine, J.W. (1984) Equilibrium models of evolutionary species  
337 diversity and the number of empty niches. *Am. Nat.* 124, 887–899
- 338 12. Raup D.M. *et al.* (1973) Stochastic models of phylogeny and the evolution of diversity. *J.*  
339 *Geol.* 81, 525–542
- 340 13. Weir, J.T. (2006) Divergent timing and patterns of species accumulation in lowland and  
341 highland neotropical birds. *Evolution* 60, 842–855
- 342 14. Burbrink, F.T. *et al.* (2012) Evidence for determinism in species diversification and  
343 contingency in phenotypic evolution during adaptive radiation. *Proc. R. Soc. B: Biol. Sci.*  
344 279, 4817–4826



- 345 15. Pigot, A.L. *et al.* (2010) The shape and temporal dynamics of phylogenetic trees arising  
346 from geographic speciation. *Syst. Biol.* 59, 660–673
- 347 16. Quental, T.B. and Marshall, C.R. (2013) How the Red Queen drives terrestrial mammals to  
348 extinction. *Science* 341, 290–292
- 349 17. Etienne, R.S. *et al.* (2012) Diversity-dependence brings molecular phylogenies closer to  
350 agreement with the fossil record. *Proc. R. Soc. B: Biol. Sci.* 279, 1300–1309
- 351 18. Fritz, S.A. *et al.* (2012) Diversification and biogeographic patterns in four island radiations  
352 of passerine birds. *Evolution* 66, 179–190
- 353 19. Pyron, R.A. and Burbrink F.T. (2013) Phylogenetic estimates of speciation and extinction  
354 rates for testing ecological and evolutionary hypotheses. *Trends Ecol. Evol.* 28, 729–736
- 355 20. Lovette I.J. and Bermingham E. (1999) Explosive speciation in the New World *Dendroica*  
356 warblers. *Proc. R. Soc. B: Biol. Sci.* 266, 1629–1636
- 357 21. Etienne, R.S. and Haegeman, B. (2012) A conceptual and statistical framework for  
358 adaptive radiations with a key role for diversity dependence. *Am. Nat.* 180, E75–E89
- 359 22. Kennedy, J.D. *et al.* (2012) Ecological limits on diversification of the Himalayan core  
360 Corvoidea. *Evolution* 66, 2599–2613
- 361 23. Scantlebury, D.P. (2013) Diversification rates have declined in the Malagasy herpetofauna.  
362 *Proc. R. Soc. B: Biol. Sci.* 280, 20131109
- 363 24. Schluter, D. (2000) *The Ecology of Adaptive Radiation*, Oxford University Press
- 364 25. Gavrillets, S. and Vose, A. (2005) Dynamic patterns of adaptive radiation. *Proc. Natl. Acad.*  
365 *Sci. U.S.A.* 102, 18040–18045
- 366 26. Lieberman, B.S. (2012) Adaptive radiations in the context of macroevolutionary theory: a  
367 paleontological perspective. *Evol. Biol.* 39, 181–191

- 368 27. Rabosky, D.L. (2009) Heritability of extinction rates links diversification patterns in  
369 molecular phylogenies and fossils. *Syst. Biol.* 58, 629–640
- 370 28. Harmon, L.J. *et al.* (2003) Tempo and mode of evolutionary radiation in Iguanian lizards.  
371 *Science* 301, 961–964
- 372 29. Jønsson, K.A. *et al.* (2012) Ecological and evolutionary determinants for the adaptive  
373 radiation of the Madagascan vangas. *Proc. Natl. Acad. Sci. U.S.A.* 109, 6620–6625
- 374 30. Mahler, D.L. *et al.* (2010) Ecological opportunity and the rate of morphological evolution  
375 in the diversification of Greater Antillean anoles. *Evolution* 64, 2731–2745
- 376 31. Weir, J.T. and Mursleen, S. (2013) Diversity-dependent cladogenesis and trait evolution in  
377 the adaptive radiation of the auks (Aves: Alcidae). *Evolution* 67, 403–416
- 378 32. Harmon, L.J. *et al.* (2010) Early bursts of body size and shape evolution are rare in  
379 comparative data. *Evolution* 64, 2385–2396
- 380 33. Rabosky, D.L. and Glor, R.E. (2010) Equilibrium speciation dynamics in a model adaptive  
381 radiation of island lizards. *Proc. Natl. Acad. Sci. U.S.A.* 107, 22178–22183
- 382 34. Losos, J.B. (2009) *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of*  
383 *Anoles*, University of California Press
- 384 35. Losos, J.B. (1992) The evolution of convergent structure in Caribbean *Anolis* communities.  
385 *Syst. Biol.* 41, 403–420
- 386 36. Rabosky, D.L. (2013) Diversity-dependence, ecological speciation, and the role of  
387 competition in macroevolution. *Ann. Rev. Ecol. Evol. Syst.* 44, 481–502
- 388 37. Losos, J.B. *et al.* (2006) Adaptation, speciation, and convergence: a hierarchical analysis of  
389 adaptive radiation in Caribbean *Anolis* lizards. *Ann. Mo. Bot. Gard.* 93, 24–33

- 390 38. Rosenzweig, M.L. (1995) *Species Diversity In Space And Time*, Cambridge University  
391 Press
- 392 39. Coyne, J.A. and Orr, H.A. (2004) *Speciation*, Sinauer Associates
- 393 40. Price, T.D. (2008) *Speciation in Birds*, Roberts & Company
- 394 41. Phillimore, A.B. *et al.* (2008) Sympatric speciation in birds is rare: Insights from range  
395 data and simulations. *Am. Nat.* 171, 646–657
- 396 42. Price, T.D. (2010) The roles of time and ecology in the continental radiation of the Old  
397 World leaf warblers (*Phylloscopus* and *Seicercus*). *Phil. Trans. R. Soc. B: Biol. Sci.* 365,  
398 1749–1762
- 399 43. Losos, J.B. and Schluter, D. (2000) Analysis of an evolutionary species-area relationship.  
400 *Nature* 408, 847–850
- 401 44. Kisel, Y. and Barraclough, T.G. (2010) Speciation has a spatial scale that depends on  
402 levels of gene flow. *Am. Nat.* 175, 315–334
- 403 45. Pigot, A.L. and Tobias, J.A. (2013) Species interactions constrain geographic range  
404 expansion over evolutionary time. *Ecol. Lett.* 16, 330–338
- 405 46. Kozak, K.H. and Wiens, J.J. (2006) Does niche conservatism promote speciation? A case  
406 study in North American salamanders. *Evolution* 60, 2604–2621
- 407 47. Gröning, J. and Hochkirch, A. (2008) Reproductive interference between animal species. *Q.*  
408 *Rev. Biol.* 83, 257–282
- 409 48. Price, T.D. and Kirkpatrick, M. (2009) Evolutionary stable range limits set by interspecific  
410 competition. *Proc. R. Soc. B: Biol. Sci.* 276, 1429–1434
- 411 49. Wang, S. *et al.* (2013) Speciation rates decline through time in individual-based models of  
412 speciation and extinction. *Am. Nat.* 182, E83–E93

- 413 50. Moyle, R.G. *et al.* (2009) Explosive Pleistocene diversification and hemispheric expansion  
414 of a "great speciator". *Proc. Natl. Acad. Sci. U.S.A.* 106, 1863–1868
- 415 51. Ricklefs, R.E. (2010) Evolutionary diversification, coevolution between populations and  
416 their antagonists, and the filling of niche space. *Proc. Natl. Acad. Sci. U.S.A.* 107, 1265–  
417 1272
- 418 52. Verboom G.A. *et al.* (2009) Origin and diversification of the Greater Cape flora: Ancient  
419 species repository, hot-bed of recent radiation, or both? *Mol. Phylogenet. Evol.* 51, 44–53
- 420 53. Hughes C. and Eastwood R. (2006) Island radiation on a continental scale: Exceptional  
421 rates of plant diversification after uplift of the Andes. *Proc. Natl. Acad. Sci. U.S.A.* 103,  
422 10334–10339
- 423 54. Antonelli A. *et al.* (2009) Tracing the impact of the Andean uplift on Neotropical plant  
424 evolution. *Proc. Natl. Acad. Sci. U.S.A.* 106, 9749–9754
- 425 55. Pyron, R.A. and Burbrink, F.T. (2012) Extinction, ecological opportunity, and the origins  
426 of global snake diversity. *Evolution* 66, 163–178
- 427 56. Quental, T.B. and Marshall, C.R. (2010) Diversity dynamics: molecular phylogenies need  
428 the fossil record. *Trends Ecol. Evol.* 25, 434–441
- 429 57. Foote, M. (2007) Symmetric waxing and waning of marine invertebrate genera.  
430 *Paleobiology* 33, 517–529
- 431 58. Benton, M.J. (2009) The Red Queen and the Court Jester: species diversity and the role of  
432 biotic and abiotic factors through time. *Science* 323, 728–732
- 433 59. Ehrlich, P.R. and Raven, P.H. (1964) Butterflies and plants: a study in coevolution.  
434 *Evolution* 18, 586–608

- 435 60. Rabosky, D.L. and Lovette, I.J. (2008) Explosive evolutionary radiations: decreasing  
436 speciation or increasing extinction through time? *Evolution* 62, 1866–1875
- 437 61. Quental, T.B. and Marshall, C.R. (2011) The molecular phylogenetic signature of clades in  
438 decline. *PLOS One* 6, e25780
- 439 62. Morlon, H. *et al.* (2011) Reconciling molecular phylogenies with the fossil record. *Proc.*  
440 *Natl. Acad. Sci. U.S.A.* 108, 16327–16332
- 441 63. Avise, J.C. and Walker, D. (1998) Pleistocene phylogeographic effects on avian  
442 populations and the speciation process. *Proc. R. Soc. Lond. B* 265, 457–463
- 443 64. Rosindell J. *et al.* (2010) Protracted speciation revitalizes the neutral theory of biodiversity.  
444 *Ecol. Lett.* 13, 716–727
- 445 65. Etienne, R.S. and Rosindell, J. (2012) Prolonging the past counteracts the pull of the  
446 present: protracted speciation can explain observed slowdowns in diversification. *Syst. Biol.*  
447 61, 204–213
- 448 66. Stadler, T. (2011) Mammalian phylogeny reveals recent diversification rate shifts. *Proc.*  
449 *Natl. Acad. Sci. U.S.A.* 108, 6187–6192
- 450 67. Morlon, H. (In press) Phylogenetic approaches for studying diversification. *Ecol. Lett.*
- 451 68. Machac, A. *et al.* (2013) Ecological causes of decelerating diversification in carnivoran  
452 mammals. *Evolution* 67, 2423–2433
- 453 69. Condamine, F.L. *et al.* (2012) What causes latitudinal gradients in species diversity?  
454 Evolutionary processes and ecological constraints on swallowtail biodiversity. *Ecol. Lett.*  
455 15, 267–277
- 456 70. Condamine, F.L. *et al.* (2013) Macroevolutionary perspectives to environmental change.  
457 *Ecol. Lett.* 16, 72–85

- 458 71. Bush, A.M. and Bambach, R.K. (2011) Paleoeologic megatrends in marine Metazoa. *Ann.*  
459 *Rev. Earth Planet. Sci.* 39, 241–269
- 460 72. Novack-Gottshall, P.M. (2007) Using a theoretical ecospace to quantify the ecological  
461 diversity of Paleozoic and modern marine biotas. *Paleobiology* 33, 273–94
- 462 73. Roy, K. and Foote, M. (1997) Morphological approaches to measuring biodiversity. *Trends*  
463 *Ecol. Evol.* 12, 277–281
- 464 74. Ezard, T.H.G. *et al.* (2011) Interplay between changing climate and species' ecology drives  
465 macroevolutionary dynamics. *Science* 332, 349–351
- 466 75. Harvey, P.H. *et al.* (1994) Phylogenies without fossils. *Evolution* 48, 523–529
- 467 76. Pybus, O.G. and Harvey, P.H. (2000) Testing macro-evolutionary models using incomplete  
468 molecular phylogenies. *Proc. R. Soc. B: Biol. Sci.* 267, 2267–2272
- 469 77. Nee, S. *et al.* (1994) The reconstructed evolutionary process. *Phil. Trans. R. Soc. Lond. B*  
470 344, 305–311
- 471 78. Cusimano, N. and Renner, S.S. (2010) Slowdowns in diversification rates from real  
472 phylogenies may not be real. *Syst. Biol.* 59, 458–464
- 473 79. Pennell, M.W. *et al.* (2012) Trees of unusual size: biased inference of early bursts from  
474 large molecular phylogenies. *PLOS One* 7, e43348
- 475 80. Revell, L.J. *et al.* (2005) Underparameterized model of sequence evolution leads to bias in  
476 the estimation of diversification rates from molecular phylogenies. *Syst. Biol.* 54, 973–983
- 477 81. Rüber, L. and Zardoya, R. (2005) Rapid cladogenesis in marine fishes revisited. *Evolution*  
478 59, 1119–1127
- 479 82. Webster, A.J. *et al.* (2003) Molecular phylogenies link rates of evolution and speciation.  
480 *Science* 301, 478

481 83. Burbrink, F.T. and Pyron, R.A. (2011) The impact of gene-tree/species-tree discordance on  
482 diversification-rate estimation. *Evolution* 65, 1851–1861

483

484

485

486 **Glossary**

487 **Adaptive radiation:** the evolution of phenotypic and ecological diversity in a rapidly speciating  
488 clade [24].

489 **Diversification rate slowdown:** Higher net diversification rate earlier in a clade's history than  
490 later, with any functional form of decline (e.g., rates depend on time or species diversity).

491 **Diversity-dependent diversification:** Diversification rates vary with the number of species in  
492 the clade through time [8,12,17] (sometimes also coined "density-dependence" by analogy with  
493 population dynamics). On its own, this does not imply that there is a limit to the maximum  
494 number of species in a clade, nor that diversification is associated with niche divergence.

495 **Ecological limits:** Ecology-based limit on species diversity in a clade. Some papers have defined  
496 such limits as those imposed by a finite number of ecological niches (e.g., [18,22]); others have  
497 used the term less restrictively [5].

498 **Net diversification rate:** Speciation rate minus extinction rate

499 **Niche filling:** Process by which species fill niche space as diversification proceeds. On its own,  
500 this does not imply that there is a limit to the maximum number of species in a clade.

501 **Time-dependent diversification:** Diversification rates vary over time [8].

502 **Waxing-waning:** A pattern of diversification in which a clade first rises in diversity and then  
503 declines after reaching a peak in diversity.

504



505 **BOX 1: Ways to identify diversification slowdowns**

506 Researchers have identified slowdowns in diversification rate using many metrics. While we do  
507 not focus on computational details here, it is important to clarify what various metrics actually  
508 say about diversification and the factors that influence it.

509 Initial papers demonstrated slowdowns by showing concave lineage-through-time (LTT)  
510 plots [75], in which the accumulation of lineages on a phylogeny slowed through time. Later  
511 papers showed widespread evidence for speciation rate slowdowns by using the gamma statistic  
512 [2,4], a metric developed to identify departures from the constant rate pure-birth Yule model [76].  
513 However, despite its common use, gamma contains insufficient information to distinguish many  
514 types of diversification dynamics, from diversity-dependent diversification (e.g., [4]) to waxing-  
515 waning dynamics [61]. Pigot *et al.* [15] proposed a metric that, although potentially overcoming  
516 some limitations of the gamma statistic, is also a summary statistic of net diversification that is  
517 limited in its ability to test the importance of speciation versus extinction rates.

518 More recent diversification rate methods use likelihood to directly infer the relationship  
519 between diversification rates and other variables; their flexibility allows one to estimate the way  
520 that diversification slowdowns have occurred (e.g., slowdowns with time, species diversity, or  
521 environmental variables). Time-dependent models have been available since the earliest work on  
522 diversification methods [75,77], but have only recently been employed to test temporal variation  
523 in speciation and extinction rates [60]. Models are now available in which discrete rate shifts can  
524 occur during a clade's history and that can account for missing species ([66], see Box 2 for the  
525 consequences of ignoring incomplete sampling); these models can reveal long-term temporal  
526 trends, such as steady decline. Coalescent-based approaches can test explicit hypotheses about  
527 equilibrium dynamics and accommodate incomplete sampling [3]. Other models allow rate

528 heterogeneity across lineages, negative net diversification rates, and incomplete sampling and  
529 can recover hump-shaped diversity curves through time ([62], waxing-waning dynamics). Truly  
530 diversity-dependent pure birth (no extinction) models [8] have now been expanded to  
531 accommodate non-zero extinction [17]. Finally, a recent model allows explicit tests of the effect  
532 of the environment on diversification, such as a pulse and later decrease in speciation rates due to  
533 climatic or geological events [69].

534 **BOX 2: Slowdowns in diversification rates resulting from methodological biases**

535 Many biases in the methods used to estimate phylogeny and diversification rates can lead to  
536 apparent slowdowns in diversification rates. In many cases these biases can be controlled, but  
537 some might be difficult to resolve. We briefly summarize these potential biases to refer readers  
538 to more extensive discussions of them.

539         Investigators have long recognized that insufficient taxonomic sampling will lead (on  
540 average) to more branching deeper in a phylogeny [76,77]. If one assumes that the missing  
541 species are a random sample, some procedures can account for this bias [3,4,28,62,66,76].  
542 However, such approaches can be compromised if the number of missing species is unknown,  
543 and systematic sampling biases might exacerbate this problem [78]. Other biases might result  
544 from studying only large phylogenies, which are more likely than small phylogenies to show  
545 slowdowns just by chance [1,4,79].

546         Inaccurate estimation of phylogeny and branch lengths from DNA sequences can also  
547 lead to downstream biases when estimating diversification rates. Underparameterized  
548 substitution models [80], different methods for scaling molecular branch lengths into units of  
549 time [81], and the node-density effect [82] might all lead to greater amounts of branching deep in  
550 the phylogeny. Furthermore, deeper divergence times in gene trees than their associated species  
551 tree could lead to biases toward deeper nodes in a phylogeny [13,19,83]. Finally, the difficulty of  
552 delimiting species or a failure to sample cryptic species can lead to fewer branching events near  
553 the tips of a phylogeny and thus a signal of a slowdown in diversification rate [4,13]. Both of  
554 these possibilities can at least be partially resolved by only analyzing an initial portion of the  
555 phylogeny so as to exclude the region that is most susceptible to these types of errors (near the  
556 tips; e.g., [4,28]).

557

558 **Figure 1. Conceptual diagram showing how various explanations for observed**  
559 **diversification slowdowns fall into broad categories.** Potential methodological explanations  
560 are described in detail in Box 2. The explanations described in the text fall into two broad  
561 categories: diversity-dependent explanations, which can lead to equilibrium dynamics, and time-  
562 dependent explanations, which do not. Protracted speciation is neither diversity-dependent nor  
563 time-dependent, because rates of the initiation and completion of speciation are constant through  
564 time.  
565

566 **Figure 2. Different explanations for observed diversification slowdowns.** At the top left is a  
567 hypothetical phylogeny with a diversification slowdown that could correspond to four biological  
568 explanations (a–d), whereas two explanations are more easily illustrated with their own  
569 phylogenies on the right (e,f). Colors correspond to the graphics below the phylogeny, as do time  
570 slices. One extinction event is represented in the middle of the phylogeny and by the absence of  
571 that species at the third time slice in (a–c). Dotted grey branches represent additional branching  
572 and extinction events that only correspond to the bottom explanation (d). (a) In the case of niche  
573 differentiation, ecological and phenotypic diversification is expected to accompany speciation. In  
574 this hypothetical example, species diversify along a single phenotypic axis (e.g., that might  
575 correspond to resource use; the vertical axis is the frequency of individuals for a given  
576 phenotype). Speciation has slowed considerably by the third time slice because niche space has  
577 been filled. (b) The geographic model predicts that successive vicariance events affect relatively  
578 fewer and fewer species over time as their ranges get smaller, given limited range expansion.  
579 This leads to diversification slowdowns. Here, a mountain range and rivers divide geographic  
580 ranges to create new species. (c) In the case of environment-driven bursts of speciation, we  
581 expect significant geological or climatic events to lead to the rapid diversification of a group. In  
582 this example, initial mountain uprise leads to the isolation of four species at the second time slice,  
583 then those species subsequently speciate before the third time slice due to climatic specialization  
584 on different mountain slopes. (d) A clade might decline because its species cannot adapt to a  
585 changing biotic or abiotic environment. Under this scenario, a simple plot of the reconstructed  
586 lineages over time (blue) may show the slowdown but mask a more complex true history  
587 (orange). (e) Frequent peripatric speciation, wherein colonists from a large population give rise  
588 to new peripheral species that themselves fail to further speciate, may lead to slowdowns. In this

589 case the average rate of speciation for the entire clade decreases over time because most new  
590 species (e.g. those on small islands) do not speciate. (f) Protracted speciation might result in an  
591 underestimation of the branching events near the tips of a phylogeny, suggesting a slowing  
592 toward the present. The full history shows that protracted speciation (dotted orange lines) is a  
593 part of a clade's entire history, but the failure to complete speciation only near the tips leads to  
594 an underestimation of branching events near the present in the reconstructed history.

# Figure 1

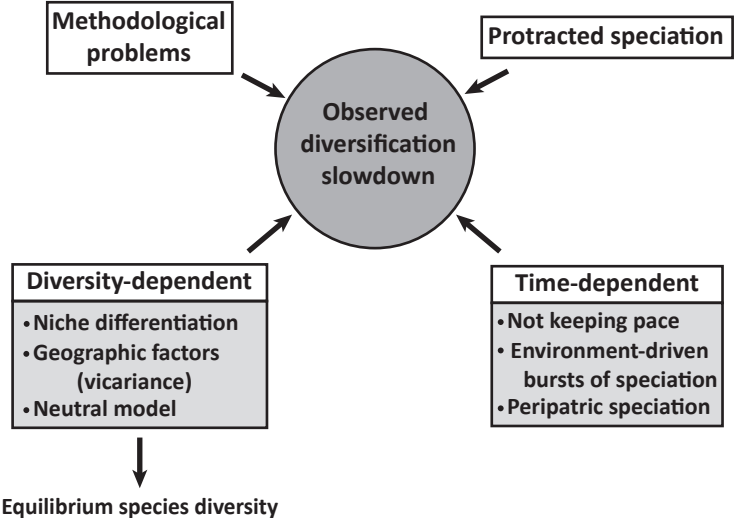
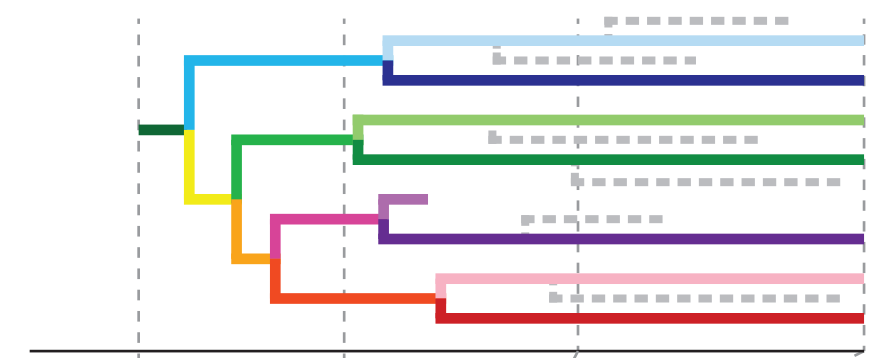
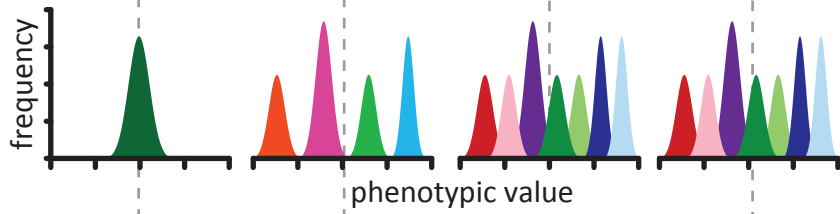


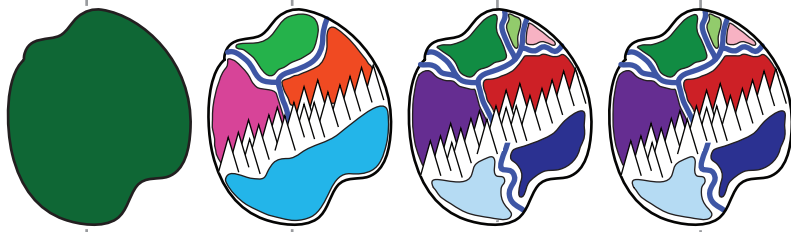
Figure 2



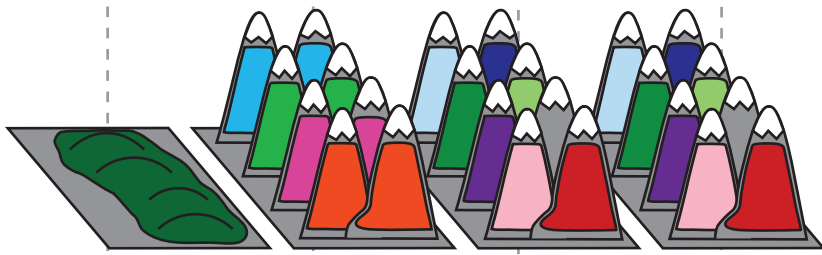
(a) Niche differentiation



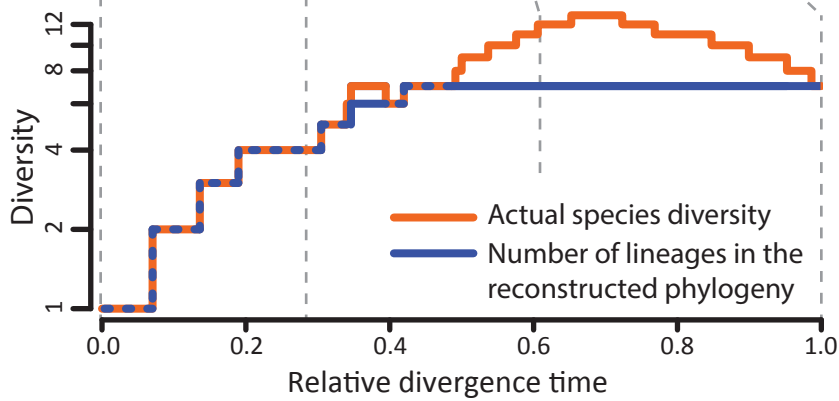
(b) Geographic factors



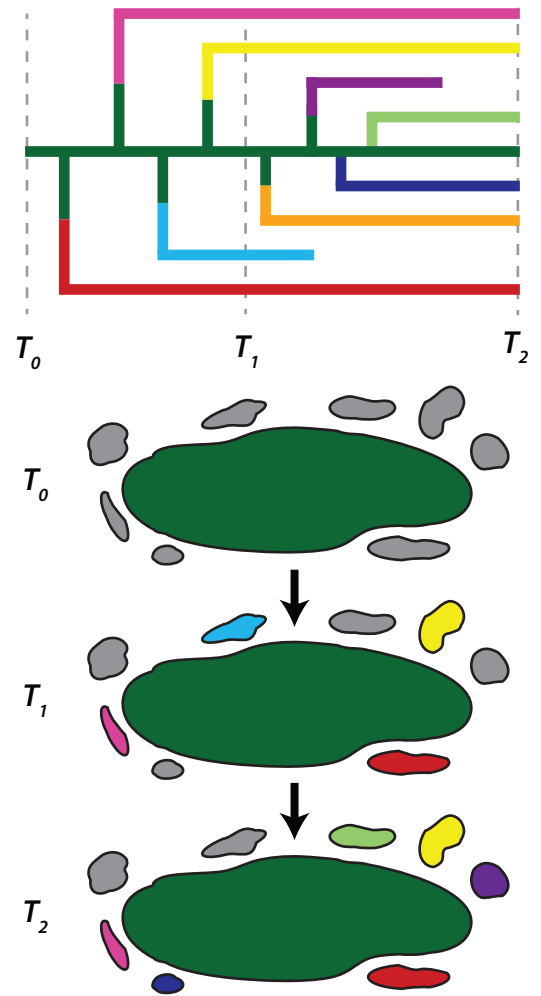
(c) Environment-driven bursts of speciation



(d) Not keeping pace with a changing environment



(e) Peripatric speciation



(f) Protracted speciation

