

# 1 **Phylogenetic scale in ecology and evolution**

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## 23 SUMMARY

24 It has been widely acknowledged that many phenomena in ecology and evolution depend on  
25 spatial and temporal scale. However, important patterns and processes may vary also across the  
26 phylogeny and depend on phylogenetic scale. Though phylogenetic scale has been implicitly  
27 considered in some previous studies, it has never been formally conceptualized and its potential  
28 remains unexplored. Here, we develop the concept of phylogenetic scale and, building on  
29 previous work in the field, we introduce phylogenetic grain and extent, phylogenetic scaling and  
30 the domains of phylogenetic scale. We use examples from published research to demonstrate how  
31 phylogenetic scale has been considered so far and illustrate how it can inform, and possibly  
32 resolve, some of the longstanding controversies in evolutionary biology, community ecology,  
33 biogeography and macroecology. To promote the concept of phylogenetic scale empirically, we  
34 propose methodological guidelines for its treatment.

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## 53 INTRODUCTION

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55 Numerous patterns in ecology and evolution vary across the phylogenetic hierarchy (Fig. 1).  
56 Species diversity declines with latitude across higher taxa but not necessarily across their  
57 constituent families and genera (Buckley *et al.* 2010) that often conform to very different  
58 diversification dynamics (Phillimore & Price 2008; Morlon *et al.* 2010; Rabosky *et al.* 2012).  
59 Phylogenetic delimitation of species pools determines our inferences about the processes that  
60 form local communities (Cavender-Bares *et al.* 2009). Many other, similar examples can further  
61 illustrate that patterns in ecology and evolution often depend on phylogenetic scale (Fig. 1). Yet,  
62 unlike the extensively developed and widely recognized concepts of spatial and temporal scale  
63 (e.g. Wiens 1989; Levin 1992; Schneider 2001), phylogenetic scale remains largely unnoticed and  
64 its importance has only recently been emerging. Here, we formalize and develop the concept of  
65 phylogenetic scale, summarize how it has been considered across disciplines, provide empirical  
66 guidelines for the treatment of phylogenetic scale, and suggest further research directions.

67         Inspired by the concept of spatial scale (e.g. Wiens 1989; Levin 1992; Schneider 2001), we  
68 define phylogenetic scale in terms of phylogenetic grain and phylogenetic extent. Phylogenetic  
69 grain refers to the elementary unit of analysis, defined in terms of tree depth, taxonomic rank,  
70 clade age, or clade size. Phylogenetic extent refers to the entire phylogeny encompassing all these  
71 units (Box 1). The grain and extent of biological patterns might provide relevant insights about  
72 the mechanisms that have produced the patterns. For example, the number of families in the fossil  
73 record seems to stay constant while the number of genera seems to increase continually over  
74 geological time, suggesting that different mechanisms produce genus-level and family-level  
75 diversity (Benton & Emerson 2007). In community ecology, clade-wide analyses typically suggest  
76 that communities have been shaped by environmental filters (Parra *et al.* 2011) while focused  
77 analyses of narrowly defined clades often uncover a suite of additional mechanisms (e.g.  
78 competition, mutualisms, dispersal limitation) (Parra *et al.* 2011; McGuire *et al.* 2014). Different  
79 patterns, and by extension different inferences about the underlying processes, might therefore  
80 emerge across the continuum of phylogenetic scales.

81         The concept of phylogenetic scale seems particularly pertinent, given the growing body  
82 of research and statistical methods to explore the increasingly accurate and ever more complete

83 phylogenetic data (e.g. phylogenetic comparative methods, community phylogenetics,  
84 diversification analysis). Yet, few studies have extended the explorative strategies to  
85 systematically investigate scale-dependence of phylogenetic patterns (e.g. scaling coefficients,  
86 upscaling, downscaling), delimit biologically consistent domains of scale (e.g. morphologically,  
87 ecologically, geographically distinct segments of the phylogeny), or test the universal laws of  
88 ecology (e.g. species-abundance distributions, latitudinal gradients). We therefore contend that  
89 the full potential of the phylogenetic data and the methods at hand has not yet been realized, and  
90 further progress might be precipitated by a more focused and formalized treatment of  
91 phylogenetic scale, akin to the one commonly applied across temporal and spatial scales (e.g.  
92 Wiens 1989; Levin 1992; Schneider 2001).

93         Here, we summarize the variety of ways in which different disciplines have either  
94 implicitly or explicitly considered phylogenetic scale, highlighting their respective benefits and  
95 pitfalls. We further propose how these efforts might be consolidated under one conceptual and  
96 empirical framework that would provide the common ground for cross-disciplinary discussion.  
97 In particular, we define and formalize the concept of phylogenetic scale, distinguish between  
98 phylogenetic grain and extent, scale-dependence, phylogenetic scaling and the domains of scale.  
99 We also provide practical guidelines for the treatment of phylogenetic scale across empirical  
100 studies, using the data and statistical methods currently available. We hope this will inspire  
101 further debate, draw more focused attention to the subject, and advance the notion of  
102 phylogenetic scale in ecology and evolution.

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## 104 **PHYLOGENETIC SCALE IN ECOLOGY AND EVOLUTION**

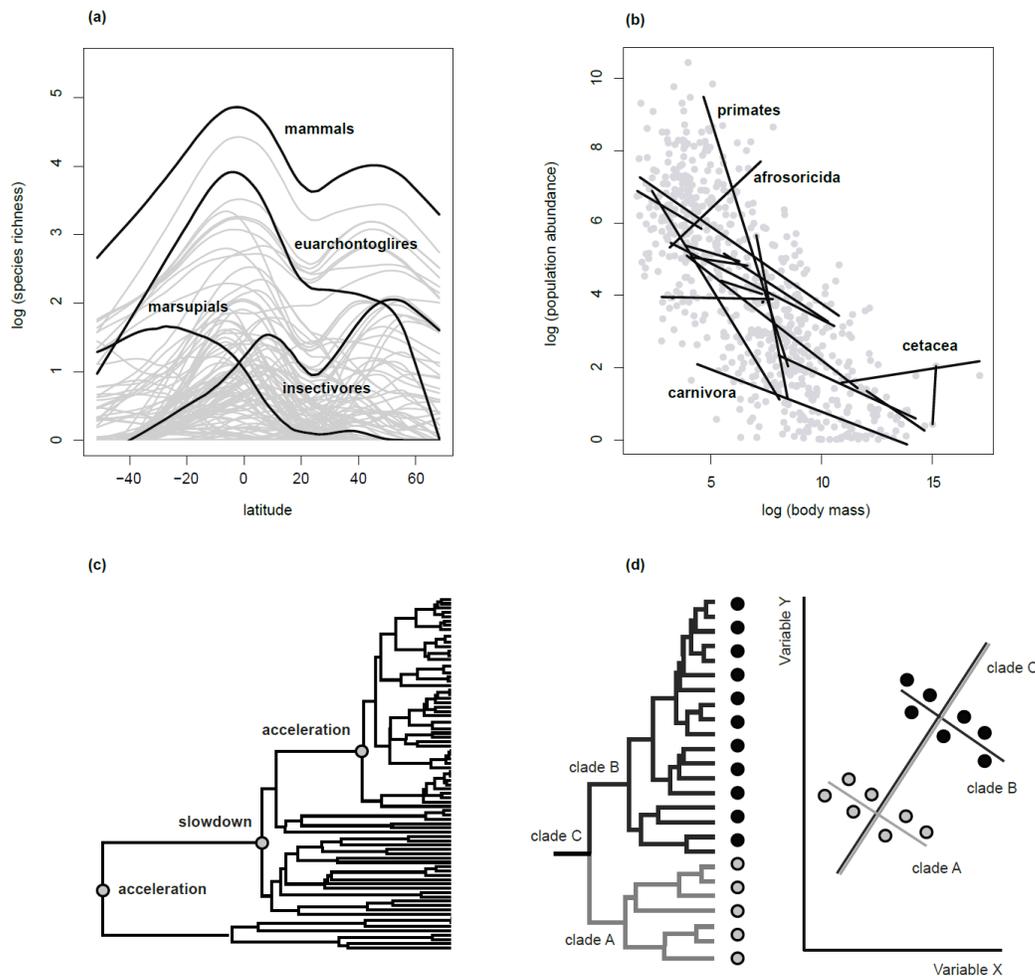
105 Phylogenetic scale has been considered to varying degrees in ecology and evolution, from being  
106 largely neglected to being relatively well-developed. In this section, we describe previous  
107 research that has implicitly or explicitly considered phylogenetic scale but also how the core  
108 disciplines in the field might further benefit from this concept (e.g. macroevolution, community  
109 ecology, biogeography, macroecology).

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113 **Figure 1.** Examples of patterns that vary across phylogenetic scales. (a) The latitudinal diversity  
114 gradient. Mammal diversity decreases with latitude across large clades but many other patterns  
115 emerge across small clades, including inverse ones (select clades depicted in black). (b) The  
116 dependence of population abundance on body mass. The dependence is negative across large  
117 phylogenetic scales (mammals depicted in grey) but varies substantially across small scales (select  
118 orders depicted in black). (c) Diversification dynamics. Slowdowns detected over some  
119 phylogenetic scales might be accompanied by accelerations over both larger and smaller scales.  
120 (d) Statistical correlations. Even though the depicted variables are negatively correlated within  
121 each of the two subclades, the correlation becomes positive when the subclades are studied  
122 together. The data were taken from the IUCN (2016) and PanTHERIA (2016).



## 123 **BOX 1: The concept of phylogenetic scale**

124 The concept of scale is based on the fact that some entities can be ordered, or placed on a scale  
125 (*scala* means *ladder* in Latin). For example, continents contain biomes, ecoregions, and localities,  
126 giving rise to spatial hierarchy. Similarly, large clades contain small clades, creating phylogenetic  
127 hierarchy which defines phylogenetic scale. However, clades are not always nested, in which case  
128 standard measures might be needed to order the clades along the scale continuum. These  
129 measures might include time (clade age) but also clade size (number of species within a clade) or  
130 the degree of molecular, phenotypic, or ecological divergence within a clade. These measures will  
131 be inherently correlated across mutually nested clades but might become decoupled across non-  
132 nested clades (e.g. old clades will not necessarily be most diverse) (Box 2).

133 In the concept of spatial scale, **grain** and **extent** are usually distinguished. Grain refers to the area  
134 of the basic unit analyzed (e.g. ecoregion) while extent refers to the total area analyzed (e.g.  
135 continent). Phylogenetic scale can be defined analogically, such that phylogenetic grain refers to  
136 the basic unit of analysis (e.g. species, genera, families) and phylogenetic extent to the total  
137 phylogeny that would encompass all the units analyzed (e.g. class, phylum).

138 Even though taxonomic ranks are commonly used to define phylogenetic scale, they are not  
139 always comparable (e.g. genera in mammals are not comparable to genera in insects), and  
140 standard measures might be better suited to define phylogenetic scales across distant taxa (e.g.  
141 taxon age, taxon size), but even these measures might not ensure entirely that the analyzed taxa  
142 are fully comparable. For example, clade age might reflect the degree of phenotypic divergence  
143 across clades, but some clades might be more diverged than others despite being of similar age.

144 The same limitations apply to the measures of spatial scale because spatial grains of standardized  
145 sizes might not ensure comparability across species of dramatically different home range sizes  
146 (Wiens 1989). Therefore, the most suitable measure and definition of the phylogenetic scale  
147 should be dictated by the biological properties of the organismal system (e.g. body size,  
148 generation time, rates of phenotypic evolution) and the question under study (e.g. phenotypic  
149 divergence, diversification dynamics, diversity patterns).

150 In some cases, it may be useful to work with non-standardized grains which represent more  
151 natural units of analysis (e.g. islands in spatial scaling or island faunas in phylogenetic scaling).

152 The extents will then be defined correspondingly, so as to cover all of the units analyzed (e.g. all  
153 islands or the entire biotas across islands). Finally, grain and extent are defined only in relation  
154 to each other. The grain from one study can therefore act as an extent in another study, or vice  
155 versa.

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## 158 **Evolution and diversification**

159 Evolutionary diversification and disparification are known to vary across phylogenetic scales but  
160 have rarely been thoroughly studied in this context. Even though a suite of methods are  
161 commonly used to explore these processes across the phylogeny (e.g. Rabosky et al. 2012, Alfaro  
162 et al. 2009) (see Table 1), most studies report the recovered patterns without a focused  
163 examination of their scale-dependence. Focused examination of patterns across scales may  
164 precipitate the resolution of several outstanding controversies in the field.

165 One such controversy revolves around the dynamics of diversity and diversification. It  
166 has been debated whether the dynamics are expansionary, such that regional and clade diversity  
167 accumulate constantly over time (Benton & Emerson 2007; Wiens 2011; Harmon & Harrison  
168 2015), or whether the dynamics are ecologically limited, such that diversity tends toward an  
169 equilibrium (Rabosky 2009; Rabosky & Hurlbert 2015). Empirical evidence suggests that genera  
170 with dozens of species often expand in terms of their diversity (McPeck 2008; Morlon *et al.* 2010)  
171 whereas higher taxa with thousands of species are mostly saturated at their equilibrium diversity  
172 (Vamosi & Vamosi 2010; Rabosky *et al.* 2012). Island radiations and fossil evidence also indicate  
173 that clades often expand, seemingly without bounds, during the initial phases of their  
174 diversification but eventually reach an equilibrium and saturate (Alroy 1996; Benton & Emerson  
175 2007; Glor 2010; Quental & Marshall 2013). It is therefore possible that diversification varies  
176 systematically across phylogenetic scales such that seemingly contradictory dynamics (i.e.  
177 expansionary and equilibrial) might be detected even within the same phylogenetic tree. If that  
178 were the case, the debate as to whether the dynamics are expansionary or equilibrial might not  
179 prove particularly productive and should perhaps be reframed in terms of phylogenetic scale  
180 (e.g. phylogenetic scales over which the different dynamics prevail, scale-related factors that

181 determine the shift between the dynamics, how the dynamics combine across scales and across  
182 nested clades of different ages and sizes).

183 Evolutionary disparification may also vary across the phylogeny because traits  
184 (phenotypic, behavioral, but also molecular) diverge at different rates and therefore are  
185 conserved over different phylogenetic scales (Freckleton *et al.* 2002; Blomberg *et al.* 2003; Wiens &  
186 Graham 2005). Even though the dynamics of trait divergence and niche conservatism have been  
187 the subject of much research (e.g. Blomberg *et al.* 2003, Freckleton *et al.* 2002), clear  
188 generalizations about their scale-dependence have not yet emerged. In most cases, physiological  
189 traits that largely determine the extent of species distributions seem conserved over extensive  
190 phylogenetic scales (Freckleton *et al.* 2002; Blomberg *et al.* 2003) while habitat- and diet-related  
191 traits that mediate species coexistence locally seem generally labile and conserved over small  
192 scales (Ackerly *et al.* 2006; Buckley *et al.* 2010). However, the opposite pattern has also been  
193 observed where physiological tolerances were conserved over small scales while habitat, diet,  
194 body size, and feeding method remained unchanged for most of a clade's history (Kennedy *et al.*  
195 2012; Price *et al.* 2014).

196 These mixed results suggest that temporal scale may be insufficient to fully capture the  
197 variance in niche conservatism. Phylogenetic scale, in contrast, captures the fact niches and traits  
198 may evolve at different rates even across closely related clades (e.g. due to clade-specific selection  
199 regimes, genetic architecture, pleiotropy) than span similar temporal scales but different  
200 phylogenetic scales (e.g. one clade has undergone an explosive radiation on an island while the  
201 other has accumulated only limited morphological, ecological, and species diversity on the  
202 mainland). In these cases, time will not capture the phylogenetic hierarchy as well as phylogenetic  
203 scale would (e.g. phylogenetic domains defined in terms of clade size, phenotypic and ecological  
204 divergence; see below). The concept of phylogenetic scale may therefore encourage a more  
205 realistic and potentially more accurate way of thinking about trait evolution and niche  
206 conservatism.

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## 208 **Community ecology**

209 Patterns of community phylogenetic structure, and hence the inferred processes that shape  
210 communities, can vary with phylogenetic scale (Webb *et al.* 2002; Cavender-Bares *et al.* 2009;

211 Vamosi *et al.* 2009, Münkemüller *et al.* 2014). Even though community phylogeneticists have long  
212 been aware of this fact (Webb *et al.* 2002; Cavender-Bares *et al.* 2009), most studies routinely do  
213 not recognize the influence of phylogenetic scale on their results.

214 To study the phylogenetic structure of a community, researchers calculate standardized  
215 community metrics (e.g. the net relatedness index, NRI) that compare the observed values to the  
216 null expectation based a model in which species are drawn randomly from the regional species  
217 pool. Phylogenetic delimitation of the species pool can influence the results and provide insights  
218 into the mechanisms that mediate local coexistence of different suites of species (Cavender-Bares  
219 *et al.* 2009; Jean-Philippe Lessard 2012; Cornell & Harrison 2014). For example, environmental  
220 filters seem to form the communities that consist of mutually unrelated species selected from a  
221 broadly defined regional species pool (Parra *et al.* 2011; Cavendar-Bares review) while narrowly  
222 defined pools typically uncover signatures of competition, mutualism, or dispersal limitation  
223 among closely related and locally coexisting species (Swenson *et al.* 2007; Cavender-Bares *et al.*  
224 2009; Parra *et al.* 2011).

225 The interpretation of community structure has been under increasing scrutiny lately  
226 because different processes can produce very similarly structured communities (e.g. Mayfield  
227 and Levine 2010; Gerhold *et al.* 2015) and a single metric may not capture community structure  
228 well enough to identify the processes that may have been at play (Gerhold *et al.* 2015). We argue  
229 that using multiple metrics across phylogenetic scales along the lines of some recently developed  
230 statistical approaches (Leibold *et al.* 2010; Pavoine *et al.* 2010; Borregaard *et al.* 2014) might prove  
231 to be a particularly powerful strategy to capture community structure more completely and  
232 disentangle the interplay of processes that produced the community. Moreover, we would also  
233 recommend that the results are complemented by experimental work whenever possible (Cadotte  
234 *et al.* 2013; Godoy *et al.* 2014). Community ecology represents one of the disciplines where  
235 patterns and processes have already been analyzed in relation to phylogenetic scale, illustrating  
236 the theoretical and empirical potential of the concept. Further advances on this front are certainly  
237 possible (e.g. analysis of multiple community metrics across phylogenetic scales) and hold the  
238 promise of a more conclusive interpretation of community-level patterns and the ecological  
239 processes behind them.

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## 241 **Biogeography and niche conservatism**

242 Biogeographic patterns, such as species distributions and diversity gradients, are largely shaped  
243 by the conservatism of the ecological niche (Wiens & Graham 2005; Wiens *et al.* 2010), which  
244 varies across the different dimensions of the niche and across phylogenetic scales (Freckleton *et*  
245 *al.* 2002; Wiens & Graham 2005). Instead of studying whether niches are conserved or not  
246 (Freckleton *et al.* 2002; Wiens & Graham 2005; Losos 2008; Wiens 2008), we should perhaps  
247 identify the scales over which they are conserved and study the imprints of these phylogenetic  
248 scales in biogeographic patterns.

249 Diversity gradients vary dramatically across taxa (Fig. 1), presumably because the taxa's  
250 climatic niches are conserved over different phylogenetic scales (Wiens & Donoghue 2004;  
251 Buckley *et al.* 2010). In mammals, many of the ancient lineages have failed to colonize high  
252 latitudes (e.g. treeshrews, sloths, armadillos) presumably because their physiological tolerances  
253 have been conserved over larger phylogenetic scales than those of the lineages that have not only  
254 invaded high latitudes but also accumulated most of their diversity there (e.g. rabbits and hares)  
255 (Buckley *et al.* 2010), producing reverse latitudinal gradients (e.g. Cook 1969; Owen & Owen 1974;  
256 Buckley *et al.* 2003; reviewed in Kindlman *et al.* 2007). The occasional breakdowns of niche  
257 conservatism, which typically span only a short period in the history of a clade and limited  
258 phylogenetic scales, sometimes precipitate diversification episodes that significantly enrich the  
259 diversity of the regional biota (e.g. African cichlids, Madagascan vangas, or ray-finned fishes and  
260 angiosperm plants) (Gavrilets & Losos 2009; Glor 2010; Jonsson *et al.* 2012; Rabosky *et al.* 2013).  
261 The phylogenetic scale over which niches are conserved, or break away from the conservatism,  
262 may consequently contribute to the formation of diversity patterns.

263 Diversity patterns may be further influenced by the effects of niche conservatism on  
264 regional extinctions (Cahill *et al.* 2012). Many genera whose climatic niches were conserved over  
265 phylogenetic scales that extended beyond the timeframe of the climatic changes during the  
266 Pleistocene were wiped out by these changes (e.g. North American trees, European megafauna)  
267 (Stuart 1991; Jackson & Weng 1999). Yet, the Pleistocene changes in climate have exterminated  
268 only few families, perhaps because climatic niches are less conserved at the family-level than at  
269 the genus-level (Freckleton *et al.* 2002; Blomberg *et al.* 2003). The extinction footprint of climate  
270 change therefore likely depends on the phylogenetic scale at which climatic niches are conserved.

271 Evaluating scale-dependent vulnerability to extinction seems particularly relevant in the face of  
272 the on-going worldwide changes in climate and land use, and the results of such research might  
273 afford insights into the patterns of loss of phylogenetic diversity. Even though it has long been  
274 recognized that niches are conserved to varying degrees, few studies have systematically  
275 investigated this variation across the phylogeny despite the potentially promising insights that  
276 such an investigation could contribute to the study of biodiversity patterns.

277

## 278 **Macroecology**

279 Macroecologists, concerned mostly with statistical patterns across large spatial and temporal  
280 scales, rarely consider phylogenetic scale in their research. Yet, cross-scale comparisons can  
281 identify statistical patterns (e.g. latitudinal diversity gradient, body size distributions, species-  
282 area relationship, species-abundance distributions) that are truly universal and those that  
283 disintegrate over certain phylogenetic scales (Marquet *et al.* 2004; Storch & Šizling 2008).  
284 Phylogenetic scale may therefore inform us about the generality of statistical patterns in ecology  
285 and about the mechanisms (e.g. mathematical, geometric, random sampling, or biological) that  
286 likely produced them (Marquet *et al.* 2004; McGill 2008).

287         Some of the patterns originally considered to be universal have later been reported to  
288 disintegrate across phylogenetic scales. The latitudinal diversity gradient provides a very  
289 intuitive example, where the pattern holds across most higher taxa (e.g. mammals, birds,  
290 amphibians, reptiles, plants) but often breaks down across their constituent lower taxa that  
291 encompass limited phylogenetic scales (e.g. penguins, hares, aphids, ichneumonids, Proteacea)  
292 and produce a variety of diversity gradients, including reverse ones (e.g. Cook 1969; Owen &  
293 Owen 1974; Buckley *et al.* 2003; reviewed in Kindlman *et al.* 2007) (Fig. 1a). Likewise, species  
294 abundance and body mass are negatively correlated across birds and mammals (Damuth 1981),  
295 but the correlation disappears across narrowly defined taxa (Isaac *et al.* 2011) and becomes even  
296 positive in some tribes of birds (Cotgreave 1994) (Fig. 1b). These changes in correlation  
297 coefficients across phylogenetic scales implicate the mechanisms behind the correlation. Within  
298 large phylogenetic extents, small-bodied species are locally abundant because their low metabolic  
299 requirements raise the carrying capacities of their populations (Gaston and Blackburn 1997).  
300 However, within restricted extents, local abundance becomes constrained by competition

301 between closely related species, and large-bodied species become locally abundant because of  
302 their competitive superiority, thus reversing the directionality of the correlation between body  
303 size and population abundance across phylogenetic scales (Cotgreave 1994) (Fig. 1b).

304 Moreover, the species-area relationship (SAR) and species-abundance distribution (SAD)  
305 were traditionally believed to universally conform to certain mathematical forms (the power-law  
306 function and the lognormal distribution, respectively) (Preston 1948; Rosenzweig 1995).  
307 However, if two sister clades follow power-law SARs and lognormal SADs which differ in their  
308 parameters, it can be proven mathematically that the clade containing both sister taxa cannot  
309 follow either the power-law SAR or the lognormal SAD (Storch & Šizling 2008; Šizling *et al.* 2009).  
310 Even though some of these patterns represent classic examples of ecological laws, cross-scale  
311 analyses indicate that they are not truly universal and sometimes provide insights into the  
312 biological mechanisms behind them.

313 The fact that some statistical patterns disintegrate across phylogenetic scales implies that  
314 the theories to explain these patterns based on the universal principles of geometry and  
315 mathematics might be fundamentally ill-founded (Storch & Šizling 2008). It is also possible that  
316 the theories pertain to certain phylogenetic scales only. This would suggest that phylogenetic  
317 scales form phylogenetic domains (Box 2) within which the processes hypothesized by our  
318 theories operate, and the explicit delimitation of these domains might further inform the theory  
319 (see Box 2).

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331 **BOX 2: Research across phylogenetic scales**

332 Many attributes, such as diversification rate, niche conservatism, or community structure, vary  
333 across phylogenetic scales (Table 1). They may vary in three different ways:

334 **(a) Scale dependence** refers to the situation when the studied attribute varies across phylogenetic  
335 scales without any obvious trend. In this case, the suitable scale of investigation should be defined  
336 a priori, based on the objective of the study. The results from one scale will be difficult to  
337 extrapolate to other scales.

338 **(b) Scaling** occurs when the attribute of interest varies systematically along the scale axis. The  
339 interpretation of scaling is at least threefold, depending on the underlying mechanism (note that  
340 only one of the interpretations is biological):

341 1. **Statistical scaling** is a sample-size effect whereby the statistical power of the analysis increases  
342 with clade size. Consequently, the attribute under study appears to change systematically  
343 from small clades to large clades (Machac et al. 2012). While the inferred values of the  
344 attribute itself may be technically correct, their systematic variation across scales is  
345 biologically irrelevant.

346 2. **Methodological artifacts** result when a statistical analysis becomes increasingly misleading  
347 toward the deep nodes of the phylogeny, resulting in incorrect and potentially biased  
348 estimates for the attribute of interest (e.g. ancestral reconstructions under dispersal-  
349 vicariance models tend to suggest that the ancestor occupied all of the regions examined)  
350 (Ronquist 1997). Methodological artifacts can be mitigated under various statistical  
351 corrections or when the results are validated using supplementary data, such as fossils.

352 3. **Phylogenetic scaling in the strict sense** occurs when the studied attribute changes across scales  
353 because the underlying biological process changes. True scaling can therefore inform us  
354 about the processes which generate the patterns observed across scales. If the scaling can be  
355 described mathematically, it allows to extrapolate across scales, even those not included in  
356 the original study, i.e. *downscale* or *upscale* the patterns under study.

357 **(c) Domains of scale** refer to the segments of the phylogeny (e.g. taxonomic units, tree depth,  
358 distinct clades) within which the attribute of interest appears relatively unchanged. The attribute  
359 might change abruptly between domains, indicating changes in the underlying biological

360 processes. Therefore, it should be possible to extrapolate across phylogenetic scales within  
361 domains, but not across scales between them.

362

363 **FIGURE (BOX 2):** Numerous attributes can be studied across phylogenetic scales. These may  
364 include diversification measures, statistical relationships between ecological variables,  
365 parameters of frequency distributions, metrics that describe community phylogenetic structure,  
366 or measures of niche conservatism (see Table 1). Phylogenetic scale can be defined in terms of  
367 clade age, clade size, taxonomic rank, the degree of molecular or phenotypic divergence, etc.,  
368 depending on the question under study.

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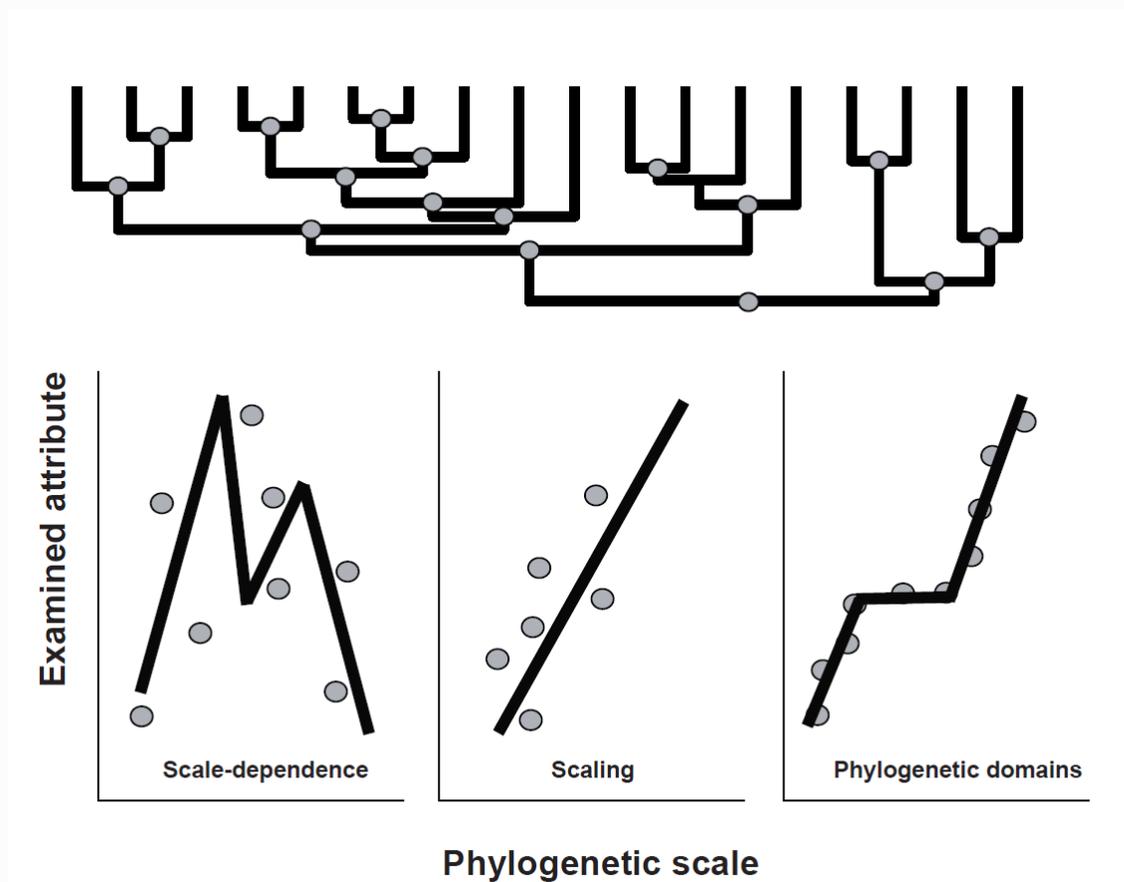
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## 390 **PHYLOGENETIC SCALE IN PRACTICE**

391 The above overview demonstrates that the consideration of phylogenetic scale varies across  
392 fields, both in terms of the approach used to consider phylogenetic scale and the vocabulary used  
393 to describe it. Therefore, there is value in developing a common language to discuss and study  
394 phylogenetic scale. There are two general approaches with which phylogenetic scale can be  
395 considered in ecological and evolutionary research. One is exploratory, where patterns are  
396 identified across a range of phylogenetic scales and then explained in the light of specific events  
397 or mechanisms. The other approach relies on testing a priori hypotheses, which are based on  
398 mechanisms that presumably take place at a given phylogenetic scale. Both approaches have their  
399 strengths and either may be appropriate, depending on the objective of a given study; however,  
400 we advocate the hypotheses testing approach for most questions.

401 To study the effects of phylogenetic scale, one can evaluate how a specific attribute of  
402 interest (such as diversification rate, niche conservatism, geographic distribution, statistical  
403 relationships) changes with phylogenetic scale. These attributes may vary randomly or  
404 systematically across the phylogeny, be more prevalent at particular scales, or stay unchanged  
405 across a discrete set of mutually nested clades (Box 2). We refer to the latter as a domain of  
406 phylogenetic scale which, in analogy to spatial domains (Wiens 1989), corresponds to a segment  
407 of phylogeny that reveals homogeneity in the attribute of interest. In this section, we consider  
408 conceptual and methodological approaches to explore patterns which are phylogenetic scale-  
409 dependent.

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### 411 **Choice of phylogenetic scale**

412 While most researchers are aware that the choice of scale can influence inferences about patterns  
413 or processes, all too often the choice of scale, be it spatial, temporal or phylogenetic, is influenced  
414 by data availability or other logistical concerns. Instead, the scale of an investigation should be  
415 chosen based on a specific objective or question whenever possible. For example, phylogenies of  
416 higher taxa may not be appropriate for evaluating the processes of community assembly that  
417 typically take place across small phylogenetic scales. To test the hypothesis that competition  
418 reduces species coexistence locally, for example, small phylogenetic scales (e.g. genera, or  
419 generally clades where species can reasonably compete) should be preferred to large scales where

420 most species are unlikely to compete (e.g. the entire classes, such as birds and mammals).  
421 However, even with a specific question at hand, it can be difficult to choose a single most  
422 appropriate phylogenetic scale. Therefore, evaluating multiple phylogenetic extents or grains  
423 should be considered.

424

### 425 **Multiple phylogenetic scales**

426 Simultaneous consideration of multiple phylogenetic scales may be particularly important in  
427 large phylogenies because different clades within such phylogenies may show different patterns  
428 with respect to the attribute of interest (e.g. diversification rate, the strength of niche  
429 conservatism, patterns of community phylogenetic structure) (Figure 1). For example, Cetacean  
430 systematists had long been perplexed as to why there is little correspondence between  
431 diversification dynamics estimated from the fossil record and phylogenetic trees (Quental &  
432 Marshall 2010; Slater *et al.* 2010; Morlon *et al.* 2011). The correspondence between the two datasets  
433 emerged only when diversification dynamics were evaluated independently for clades within  
434 cetaceans (whales, dolphins, and porpoises) as opposed to cetaceans as a whole. In this case, each  
435 clade appeared to have its own dynamics which were obscured when the entire tree was  
436 evaluated (Morlon *et al.* 2011).

437 In some cases, it may be difficult or even undesirable to specify, a priori, a specific set of  
438 scales. It might be instead more illuminating to study how the attribute of interest varies across  
439 an inclusive range of scales. There are several approaches, originating in community  
440 phylogenetics, which allow for such cross-scale analyses and return results for each node of the  
441 phylogenetic tree (Leibold *et al.* 2010; Pavoine *et al.* 2010; Borregaard *et al.* 2014). For example, the  
442 method developed by Borregaard *et al.* (2014) identifies nodes whose descendant clades  
443 underwent conspicuous geographic, phenotypic, or ecological shifts. In evolutionary research,  
444 evaluation of all nodes is not uncommon, and multiple tools have been developed to identify  
445 shifts in diversification rates and clades with conspicuously fast or slow diversification (Alfaro *et al.*  
446 2009; Rabosky 2014) (Table 1). However, statistical analyses that would include all nodes of  
447 the phylogeny remain relatively scarce (e.g. Machac *et al.* 2012; Machac *et al.* 2013), and most  
448 studies analyze select clades only, despite the often cited concerns that the selection of clades is

449 rarely random, reflects our prior biases, and might influence the analysis profoundly (e.g.  
450 Phillimore and Price 2008; Cusimano and Renner 2010; Pennell et al. 2012).

451 Two potential issues associated with the evaluation of all nodes are data non-  
452 independence and nestedness. Non-independence can be readily accommodated by the widely  
453 used comparative methods (e.g. PIC, PGLS) (Hurlbert 1984; Felsenstein 1985; Freckleton *et al.*  
454 2002; Rohlf 2006). These methods typically estimate the same parameters as their conventional  
455 counterparts (e.g. intercepts, regression slopes, group means) but adjust the confidence intervals  
456 for these parameters based on the inferred degree of phylogenetic correlation in the data  
457 (Hurlbert 1984; Felsenstein 1985; Freckleton *et al.* 2002; Rohlf 2006). The nestedness of the data is  
458 more difficult to accommodate. For example, the diversification rate of a clade is inherently  
459 determined by the rate values across its constituent subclades. Nestedness therefore extends  
460 beyond the phylogenetic correlation of rate values and reflects how the value for a clade is  
461 produced by the subclade values. This information cannot be readily accommodated under the  
462 currently available comparative methods whose phylogenetic corrections consequently cannot  
463 guarantee proper estimates of statistical significance across nested data. For these reasons, we  
464 argue that parameter estimates can be extracted, compared, and analyzed across nested clades,  
465 but their significance needs to be interpreted cautiously. New theory that would illuminate how  
466 different attributes of interest (e.g. diversification rates, regression slopes, phylogenetic signal)  
467 combine and compound across nested hierarchies, as well as the methods to capture these  
468 correlations, are clearly needed.

469

### 470 **Phylogenetic scaling**

471 Statistical methods that evaluate all clades (nodes) in a given phylogeny (Leibold *et al.* 2010;  
472 Borregaard *et al.* 2014; Rabosky 2014) can be used to explore phylogenetic scaling. Scaling is a  
473 systematic trend along the scale axis in the attribute of interest. For example, diversification rate  
474 or net relatedness index (NRI) (Webb *et al.* 2002) may change systematically with increasing  
475 phylogenetic scale (Cavender-Bares *et al.* 2009; Vamosi *et al.* 2009).

476 Phylogenetic scaling should be most prevalent across mutually nested clades because the  
477 patterns associated with larger clades are determined by the patterns of clades nested within them  
478 (or vice versa). For example, diversification rate of a clade is determined by the rate values of its

479 subclades, similarly as species richness of a spatial plot is determined by the richness of its  
480 subplots. Consequently, it should be possible to predict the value of an attribute (e.g.  
481 diversification rate, regression slopes, phylogenetic signal) at a particular phylogenetic scale from  
482 the knowledge of those values across other scales, much like it is possible to estimate species  
483 richness within large geographic areas, based on the knowledge of richness within small areas  
484 (Harte *et al.* 2009; Storch *et al.* 2012). When characterized mathematically, phylogenetic scaling  
485 should allow for predictions across phylogenetic scales not covered by the phylogeny at hand  
486 (i.e. upscaling or downscaling).

487

### 488 **Domains of phylogenetic scale**

489 When moving along the scale axis, the values of an attribute might sometimes change abruptly.  
490 Such discontinuities provide the opportunity to delimit the domains of phylogenetic scale (Box  
491 2). Domains are discrete segments of a phylogeny, such as monophyletic clades, taxonomic ranks,  
492 or tree depth, which show homogeneity in the attribute of interest (i.e. diversification rate,  
493 statistical correlation, or phylogenetic signal). By definition, the attribute does not vary  
494 substantially within a domain but changes between domains. Phylogenetic domains may  
495 therefore provide insights into the processes which operate over different segments of a  
496 phylogenetic tree.

497 Traditionally, phylogenetic domains were delimited by taxonomists whose objective was  
498 to organize species into biologically meaningful units, such as families, orders, or classes. These  
499 units are based mostly on morphological and ecological attributes. However, phylogenetic  
500 domains can also consist of clades that show diversification homogeneity, similar rates of  
501 morphological evolution, or similar life-history trade-offs. Therefore, the domains may be  
502 delimited based on key innovations, episodes of historical dispersals, or extinction events, but  
503 also statistically, using quantitative methods without the prior knowledge of the evolutionary  
504 history of a clade. While the statistical approach may be more transparent and reproducible, the  
505 resulting domains may be harder to interpret biologically. Nonetheless, statistically delimited  
506 domains may reveal otherwise unnoticed evolutionary events and potentially important breaks  
507 in the clade's history that may have shaped its extant diversity.

508 Phylogenetic domains may further facilitate statistical inference, given that most  
509 comparative methods assume that the analyzed attributes are largely homogeneous (e.g.  
510 regression slopes do not vary across genera within the analyzed family, diversification is  
511 homogenous across the analyzed lineages) and return spurious results when applied to clades  
512 that show a mixture of patterns and processes (Morlon *et al.* 2011; O'Meara 2012; Rabosky &  
513 Goldberg 2015). Phylogenetic domains may therefore identify when comparative methods report  
514 reasonably reliable results and when their conclusions must be interpreted with caution because  
515 the results span different domains and the underlying assumptions have been violated.

516

## 517 CONCLUSION

518 It is well established that different processes dominate over different spatial and temporal scales.  
519 Phylogenetic scale, however, has received limited attention although much research in ecology  
520 and evolution relies on molecular phylogenies (Table 1). Explicit consideration of phylogenetic  
521 scale, scale dependence, phylogenetic scaling, and the domains of phylogenetic scale can  
522 therefore inform multiple disciplines in the field (e.g. diversification analysis, community  
523 ecology, biogeography and macroecology).

524 We have discussed phylogenetic scale largely in isolation from spatial and temporal  
525 scales, but these types of scale will often be related. For instance, competitive exclusion may be  
526 prominent among closely related species within local communities over short time periods  
527 (Cavender-Bares *et al.* 2009). In contrast, plate tectonics might influence deeper nodes in a  
528 phylogeny and operate over broad geographic and temporal scales (Ricklefs 1985; Willis &  
529 Whittaker 2002). In some notable cases, however, the scales may not be related. Diversity  
530 anomalies, such as New Caledonia or Madagascar, represent examples of decoupling where rich  
531 biotas that encompass extensive phylogenetic scales diversified in a relatively small region  
532 (Warren *et al.* 2010; Espeland & Murienne 2011). In contrast, recent radiations within grasses and  
533 rodents have had a large geographic footprint but encompass only limited phylogenetic scales  
534 (Edwards *et al.* 2010). Evaluating when different types of scale are coupled (or decoupled) may  
535 yield new insights into the evolutionary history of different clades and regions (Willis &  
536 Whittaker 2002).

537 We hope that the perspective presented here will spur further theoretical, empirical, and  
538 methodological research. Explicit consideration of phylogenetic scale may turn our focus away  
539 from the importance of particular mechanisms (diversification, trait evolution, niche  
540 conservatism) toward the appreciation for the interplay of multiple processes which together, but  
541 over different phylogenetic scales, shape the diversity of life.

542

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546

## 547 **REFERENCES**

- 548 Ackerly, D. D., D. W. Schwilk, and C. O. Webb. 2006. Niche evolution and adaptive radiation: testing the order of trait  
549 divergence. *Ecology* 87:50–61.
- 550 Alfaro, M. E., F. Santini, C. Brock, H. Alamillo, A. Dornburg, D. L. Rabosky, G. Carnevale, et al. 2009. Nine exceptional  
551 radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy  
552 of Sciences of the United States of America* 106:13410–13414.
- 553 Benton, M. J., and B. C. Emerson. 2007. How did life become so diverse? The dynamics of diversification according to  
554 the fossil record and molecular phylogenetics. *Palaeontology* 50:23–40.
- 555 Blomberg, S. P., T. Garland, and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits  
556 are more labile. *Evolution* 57:717–745.
- 557 Borregaard, M. K., C. Rahbek, J. Fjeldså, J. L. Parra, R. J. Whittaker, and C. H. Graham. 2014. Node-based analysis of  
558 species distributions. *Methods in Ecology and Evolution* 5:1225–1235.
- 559 Buckley, H. L., T. E. Miller, A. M. Ellison, and N. J. Gotelli. 2003. Reverse latitudinal trends in species richness of pitcher-  
560 plant food webs. *Ecology Letters* 6:825–829.
- 561 Buckley, L. B., T. J. Davies, D. D. Ackerly, N. J. B. Kraft, S. P. Harrison, B. L. Anacker, H. V. Cornell, et al. 2010.  
562 Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society  
563 of London B: Biological Sciences*: rspb20100179.
- 564 Cadotte, M., C. H. Albert, and S. C. Walker. 2013. The ecology of differences: assessing community assembly with trait  
565 and evolutionary distances. *Ecology Letters* 16:1234–1244.
- 566 Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, X. Hua, C. J. Karanewsky, H. Y. Ryu, G. C. Sbeglia, et al. 2012.  
567 How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*: rspb20121890.
- 568 Cavender-Bares, J., A. Keen, and B. Miles. 2006. Phylogenetic structure of Floridian plant communities depends on  
569 taxonomic and spatial scale. *Ecology* 87:S109–122.
- 570 Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and

- 571 phylogenetic biology. *Ecology Letters* 12:693–715.
- 572 Cook, R. E. 1969. Variation in species density of North American birds. *Systematic Zoology* 18:63–84.
- 573 Cornell, H. V., and S. P. Harrison. 2014. What are species pools and when are they important? *Annual Review of*  
574 *Ecology, Evolution, and Systematics* 45:45–67.
- 575 Cotgreave, P., and P. Stockley. 1994. Body size, insectivory and abundance in assemblages of small mammals. *Oikos*  
576 71:89–96.
- 577 Damuth, J. 1981. Population density and body size in mammals. *Nature* 290:699–700.
- 578 Daniel L Rabosky, G. J. S. 2012. Clade age and species richness are decoupled across the Eukaryotic Tree of Life. *PLoS*  
579 *biology* 10:e1001381.
- 580 Edwards, E. J., C. P. Osborne, C. A. E. Strömberg, S. A. Smith, C4 Grasses Consortium, W. J. Bond, P.-A. Christin, et al.  
581 2010. The origins of C4 grasslands: integrating evolutionary and ecosystem science. *Science* 328:587–591.
- 582 Espeland, M., and J. Murienne. 2011. Diversity dynamics in New Caledonia: towards the end of the museum model?  
583 *BMC Evolutionary Biology* 11:254.
- 584 Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.
- 585 Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of  
586 evidence. *American Naturalist* 160:712–726.
- 587 Gaston, K. J., T. M. Blackburn, and J. H. Lawton. 1997. Interspecific Abundance-Range Size Relationships: An Appraisal  
588 of Mechanisms. *Journal of Animal Ecology* 66:579–601.
- 589 Gavrillets, S., and J. B. Losos. 2009. Adaptive radiation: Contrasting theory with data. *Science* 323:732–737.
- 590 Gerhold, P., J. F. Cahill, M. Winter, I. V. Bartish, and A. Prinzing. 2015. Phylogenetic patterns are not proxies of  
591 community assembly mechanisms (they are far better). *Functional Ecology* 29:600–614.
- 592 Glor, R. E. 2010. Phylogenetic insights on adaptive radiation. *Annual Review of Ecology, Evolution, and Systematics*  
593 41:251–270.
- 594 Godoy, O., N. J. B. Kraft, and J. M. Levine. 2014. Phylogenetic relatedness and the determinants of competitive  
595 outcomes. *Ecology Letters* 17:836–844.
- 596 Gould SJ. 2002. *The Structure of evolutionary theory*. Harvard University Press, Cambridge, MA.
- 597 Hansen, T. F. 1997. Stabilizing selection and the comparative analysis of adaptation. *Evolution* 51:1341–1351.
- 598 Harmon, L. J., and S. Harrison. 2015. Species diversity is dynamic and unbounded at local and continental scales.  
599 *American Naturalist* 185:584–593.
- 600 Harte, J., A. B. Smith, and D. Storch. 2009. Biodiversity scales from plots to biomes with a universal species–area curve.  
601 *Ecology Letters* 12:789–797.
- 602 Heath, T. A., J. P. Huelsenbeck, and T. Stadler. 2014. The fossilized birth–death process for coherent calibration of  
603 divergence-time estimates. *Proceedings of the National Academy of Sciences* 111:2957–2966.
- 604 Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–  
605 211.
- 606 Isaac, N. J. B., D. Storch, and C. Carbone. 2011. Taxonomic variation in size–density relationships challenges the notion

- 607 of energy equivalence. *Biology Letters* 7:615–618.
- 608 IUCN 2016. The IUCN Red List of Threatened Species.
- 609 Jackson, S. T., and C. Weng. 1999. Late Quaternary extinction of a tree species in eastern North America. *Proceedings*  
610 *of the National Academy of Sciences of the United States of America* 96:13847–13852.
- 611 Lessard, J. P. 2012. Inferring local ecological processes amid species pool influences. *Trends in Ecology & Evolution*  
612 27:600–607.
- 613 Jones, K. E., J. Bielby, M. Cardillo, S. A. Fritz, J. O'Dell, C. D. L. Orme, K. Safi, et al. 2009. PanTHERIA: a species-level  
614 database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90:2648–2648.
- 615 Jönsson, K. A., P.-H. Fabre, S. A. Fritz, R. S. Etienne, R. E. Ricklefs, T. B. Jørgensen, J. Fjeldså, et al. 2012. Ecological and  
616 evolutionary determinants for the adaptive radiation of the Madagascan vangas. *Proceedings of the National*  
617 *Academy of Sciences of the United States of America* 109:6620–6625.
- 618 Kennedy, J. D., J. T. Weir, D. M. Hooper, D. T. Tietze, J. Martens, and T. D. Price. 2012. Ecological limits on  
619 diversification of the Himalayan Core Corvoidea. *Evolution* 66:2599–2613.
- 620 Kindlman, P., Schodellbauerova, I. & Dixon, A.F.G. (2007). Inverse latitudinal gradients in species diversity. In: *Scaling*  
621 *Biodiversity*, eds. Storch, D., Marquet, P.A. & Brown, J. H. Cambridge University Press, Cambridge.
- 622 Kindlman, Schodellbauerova, and Dixon. 2007. Inverse latitudinal gradients in species diversity. In: *Scaling*  
623 *Biodiversity*, ed. David Storch, Pablo A. Marquet and James H. Brown. Cambridge University Press.
- 624 Kozak, K. H., and J. J. Wiens. 2010. Accelerated rates of climatic-niche evolution underlie rapid species diversification.  
625 *Ecology Letters* 13:1378–1389.
- 626 Laland, K., T. Uller, M. Feldman, K. Sterelny, G. B. Müller, A. Moczek, E. Jablonka, et al. 2014. Does evolutionary theory  
627 need a rethink? *Nature* 514:161–164.
- 628 Leibold, M. A., E. P. Economo, and P. Peres-Neto. 2010. Metacommunity phylogenetics: separating the roles of  
629 environmental filters and historical biogeography. *Ecology Letters* 13:1290–1299.
- 630 Levin, S. A. 1992. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. *Ecology*  
631 73:1943–1967.
- 632 Losos, J. B. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic  
633 relatedness and ecological similarity among species. *Ecology Letters* 11:995–1003.
- 634 Machac, A., Graham, C.H. & Storch, D. Ecological controls of mammalian diversification vary with phylogenetic scale,  
635 in review.
- 636 Machac A., Storch D., Wiens J. J. (2013) Ecological causes of decelerating diversification in carnivoran mammals.  
637 *Evolution* 67: 2423-2433.
- 638 Machac A., Storch D., Zrzavy J., Smrckova J. (2012) Temperature dependence of evolutionary diversification:  
639 differences between two contrasting model taxa support the metabolic theory of ecology. *Journal of Evolutionary*  
640 *Biology* 25: 2449-2456.
- 641 Marquet, P.A., M. Fernández, S.A. Navarrete & C. Valdovinos (2004) Diversity emerging: Towards a deconstruction of  
642 biodiversity patterns. In: *Frontiers of Biogeography: New Directions in the Geography of Nature*. Cambridge

- 643 University Press, Cambridge.
- 644 May, R. M. 1974 Patterns of species abundance and diversity. Harvard University Press.
- 645 Mayr E. 1942. Systematics and the origin of species. Dover, New York.
- 646 McGill, B. J., A. E. K. Roy, and E. M. C. Whitlock. 2008. Exploring Predictions of Abundance from Body Mass Using  
647 Hierarchical Comparative Approaches. *American Naturalist* 172:88–101.
- 648 McGuire, J. A., C. C. Witt, J. V. Remsen Jr., A. Corl, D. L. Rabosky, D. L. Altshuler, and R. Dudley. 2014. Molecular  
649 phylogenetics and the diversification of hummingbirds. *Current Biology* 24:910–916.
- 650 McPeck, M. A. 2008. The ecological dynamics of clade diversification and community assembly. *American Naturalist*  
651 172:270–284.
- 652 Morlon, H., T. L. Parsons, and J. B. Plotkin. 2011. Reconciling molecular phylogenies with the fossil record. *Proceedings*  
653 *of the National Academy of Sciences* 108:16327–16332.
- 654 Morlon, H., M. D. Potts, and J. B. Plotkin. 2010. Inferring the dynamics of diversification: a coalescent approach. *PLoS*  
655 *biology* 8.
- 656 Münkemüller, T., L. Gallien, S. Lavergne, J. Renaud, C. Roquet, S. Abdulhak, S. Dullinger, et al. 2014. Scale decisions  
657 can reverse conclusions on community assembly processes. *Global ecology and biogeography* 23:620–632.
- 658 Munoz, F., B. R. Ramesh, and P. Couteron. 2014. How do habitat filtering and niche conservatism affect community  
659 composition at different taxonomic resolutions? *Ecology* 95:2179–2191.
- 660 Ndiribe, C., L. Pellissier, S. Antonelli, A. Dubuis, J. Pottier, P. Vittoz, A. Guisan, et al. 2013. Phylogenetic plant  
661 community structure along elevation is lineage specific. *Ecology and Evolution* 3:4925–4939.
- 662 Nilsson, M. A., U. Arnason, P. B. S. Spencer, and A. Janke. 2004. Marsupial relationships and a timeline for marsupial  
663 radiation in South Gondwana. *Gene* 340:189–196.
- 664 O'Meara, B. C. 2012. Evolutionary inferences from phylogenies: a review of methods. *Annual Review of Ecology,*  
665 *Evolution, and Systematics* 43:267–285.
- 666 Owen, D., and J. Owen. 1974. Species diversity in temperate and tropical Ichneumonidae. *Nature* 249:583–584.
- 667 PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals.  
668 *Ecology* 90:2648
- 669 Parra, J. L., J. A. McGuire, and C. H. Graham. 2010. Incorporating clade identity in analyses of phylogenetic community  
670 structure: an example with hummingbirds. *American Naturalist* 176:573–587.
- 671 Parra, J. L., C. Rahbek, J. A. McGuire, and C. H. Graham. 2011. Contrasting patterns of phylogenetic assemblage  
672 structure along the elevational gradient for major hummingbird clades. *Journal of Biogeography* 38:2350–2361.
- 673 Pavoine, S., M. Baguette, and M. B. Bonsall. 2010. Decomposition of trait diversity among the nodes of a phylogenetic  
674 tree. *Ecological Monographs* 80:485–507.
- 675 Pigliucci, M. 2007. Do we need an extended evolutionary synthesis? *Evolution* 61:2743–2749.
- 676 Preston, F. W. 1948. The commonness, and rarity of species. *Ecology* 29:254–283.
- 677 Price, T. D., D. M. Hooper, C. D. Buchanan, U. S. Johansson, D. T. Tietze, P. Alström, U. Olsson, et al. 2014. Niche filling  
678 slows the diversification of Himalayan songbirds. *Nature* 509:222–225.

- 679 Quental, T. B., and C. R. Marshall. 2010. Diversity dynamics: molecular phylogenies need the fossil record. *Trends in*  
680 *Ecology & Evolution* 25:434–441.
- 681 — — —. 2013. How the Red Queen drives terrestrial mammals to extinction. *Science* 341:290–292.
- 682 Rabosky, D. L. 2009. Ecological limits and diversification rate: alternative paradigms to explain the variation in species  
683 richness among clades and regions. *Ecology Letters* 12:735–743.
- 684 — — —. 2014. Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees.  
685 *PLoS ONE* 9:e89543.
- 686 Rabosky, D. L., and E. E. Goldberg. 2015. Model inadequacy and mistaken inferences of trait-dependent speciation.  
687 *Systematic Biology* syu131.
- 688 Rabosky, D. L., and A. H. Hurlbert. 2015. Species richness at continental scales is dominated by ecological limits. *The*  
689 *American Naturalist* 185:572–583.
- 690 Rabosky, D. L., and D. R. Matute. 2015. Macroevolutionary speciation rates are decoupled from the evolution of  
691 intrinsic reproductive isolation in *Drosophila* and birds.
- 692 Rabosky, D. L., F. Santini, J. Eastman, S. A. Smith, B. Sidlauskas, J. Chang, and M. E. Alfaro. 2013. Rates of speciation  
693 and morphological evolution are correlated across the largest vertebrate radiation. *Nature Communications* 4: 2958-  
694 2961.
- 695 Rabosky, D. L., G. J. Slater, and M. E. Alfaro. 2012. Clade age and species richness are decoupled across the eukaryotic  
696 tree of life. *PLoS biology* 10:e1001381.
- 697 Rohlf, F. J. 2001. Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution*  
698 55:2143–2160.
- 699 Rohlf, F. J. 2006. A comment on phylogenetic correction. *Evolution* 60:1509–1515.
- 700 Ronquist, F. 1997. Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography.  
701 *Systematic Biology* 46:195–203.
- 702 Rosenzweig. 1995. *Species diversity in space and time*. Cambridge University Press.
- 703 Scheiner, S. M. 2000. Species richness, species–area curves and Simpson’s paradox. *Evolutionary Ecology Research*  
704 2:791–802.
- 705 Schneider, D. C. 2001. The rise of the concept of scale in ecology the concept of scale is evolving from verbal expression  
706 to quantitative expression. *BioScience* 51:545–553.
- 707 Šizling, A. L., W. E. Kunin, E. Šizlingová, J. Reif, and D. Storch. 2011. Between geometry and biology: the problem of  
708 universality of the species-area relationship. *American Naturalist* 178:602–611.
- 709 Slater, G. J., S. A. Price, F. Santini, and M. E. Alfaro. 2010. Diversity versus disparity and the radiation of modern  
710 cetaceans. *Proceedings of the Royal Society of B: Biological Sciences* 277:3097–3104.
- 711 Storch, D., P. Keil, and W. Jetz. 2012. Universal species-area and endemics-area relationships at continental scales.  
712 *Nature* 488:78–81.
- 713 Storch, D., and A. L. Šizling. 2008. The concept of taxon invariance in ecology: Do diversity patterns vary with changes  
714 in taxonomic resolution? *Folia Geobotanica* 43:329–344.

- 715 Stuart, A. J. 1991. Mammalian extinctions in the late Pleistocene of northern Eurasia and North America. *Biological*  
716 *Reviews of the Cambridge Philosophical Society* 66:453–562.
- 717 Swenson, N. G., B. J. Enquist, J. Pither, J. Thompson, and J. K. Zimmerman. 2006. The problem and promise of scale  
718 dependency in community phylogenetics. *Ecology* 87:2418–2424.
- 719 Swenson, N. G., B. J. Enquist, J. Thompson, and J. K. Zimmerman. 2007. The influence of spatial and size scale on  
720 phylogenetic relatedness in tropical forest communities. *Ecology* 88:1770–1780.
- 721 Vamosi, J. C., and S. M. Vamosi. 2010. Key innovations within a geographical context in flowering plants: towards  
722 resolving Darwin’s abominable mystery. *Ecology Letters* 13:1270–1279.
- 723 Vamosi, S. M., S. B. Heard, J. C. Vamosi, and C. O. Webb. 2009. Emerging patterns in the comparative analysis of  
724 phylogenetic community structure. *Molecular Ecology* 18:572–592.
- 725 Warren, B. H., D. Strasberg, J. H. Bruggemann, R. P. Prys-Jones, and C. Thébaud. 2010. Why does the biota of the  
726 Madagascar region have such a strong Asiatic flavour? *Cladistics* 26:526–538.
- 727 Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. J. Donoghue. 2002. Phylogenies and community ecology. *Annual*  
728 *Review of Ecology and Systematics* 33:475–505.
- 729 Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.
- 730 Wiens, J. J. 2008. Commentary on Losos (2008): Niche conservatism *deja vu*. *Ecology Letters* 11:1004–1005.
- 731 — — —. 2011. The causes of species richness patterns across space, time, and clades and the role of ecological limits. *The*  
732 *Quarterly Review of Biology* 86:75–96.
- 733 Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V. Cornell, E. I. Damschen, et al. 2010. Niche  
734 conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13:1310–1324.
- 735 Wiens, J. J., and M. J. Donoghue. 2004. Historical biogeography, ecology and species richness. *Trends in Ecology &*  
736 *Evolution* 19:639–644.
- 737 Wiens, J. J., and C. H. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology.  
738 *Annual Review of Ecology, Evolution, and Systematics* 36:519–539.
- 739 Willis, K. J., and R. J. Whittaker. 2002. Species diversity - scale matters. *Science* 295:1245–1248.
- 740
- 741

742 **Table 1.** Ecological and evolutionary attributes that often vary across phylogenetic scales. Each  
 743 attribute is listed along with examples of methods for its evaluation.

<b>Field</b>	<b>Examined attribute</b>	<b>Examples of evaluation methods</b>
<b>Evolution and diversification</b>	diversification mode	coalescent inference to distinguish between accelerations, slowdowns, and saturation (Morlon <i>et al.</i> 2010)
	diversification rate	product-moment estimators (Magallon & Sanderson 2001), equal-splits measures (Jetz <i>et al.</i> 2012)
	slowdown strength	gamma statistic (Pybus & Harvey 2000)
<b>Community ecology</b>	community structure	phylometrics (NRI, NTI, MNND, MPD) (Webb <i>et al.</i> 2002)
	phylogenetic diversity	Faith's PD (Faith 1992)
<b>Biogeography and macroecology</b>	form of the relationship	linear, polynomial, exponential, lognormal functions
	strength of the relationship	Pearson's correlation, Spearman's correlation, regression slope
<b>Niche conservatism</b>	phylogenetic signal	Pagel's lambda (Freckleton <i>et al.</i> 2002), Blomberg's K (Blomberg <i>et al.</i> 2003)
	evolutionary rates	Brownian motion model (Felsenstein 1985), Ornstein-Uhlenbeck model (Hansen 1997) of trait evolution