

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**

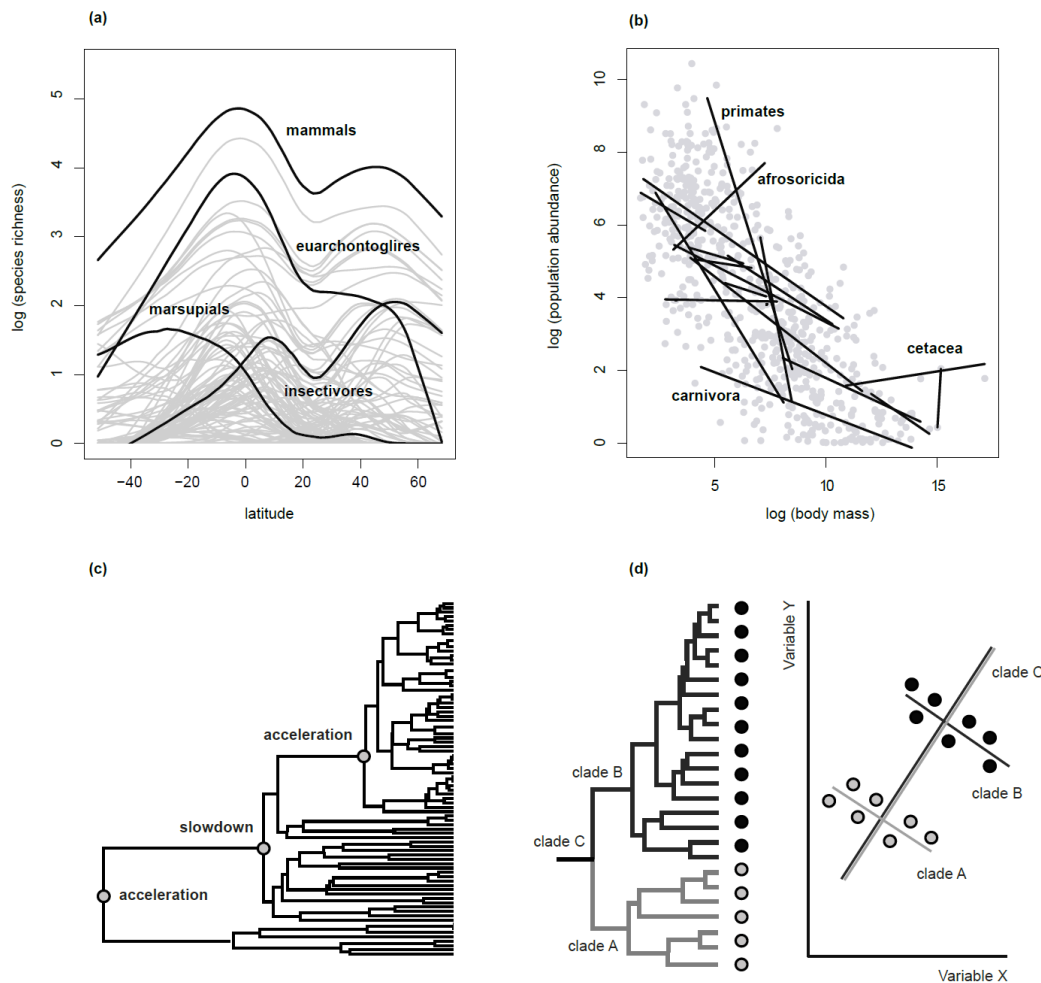
105 Phylogenetic scale has been considered to varying degrees in ecology and evolution, from being
106 largely neglected to being relatively well-developed. In this section, we describe previous
107 research that has implicitly or explicitly considered phylogenetic scale but also how the core
108 disciplines 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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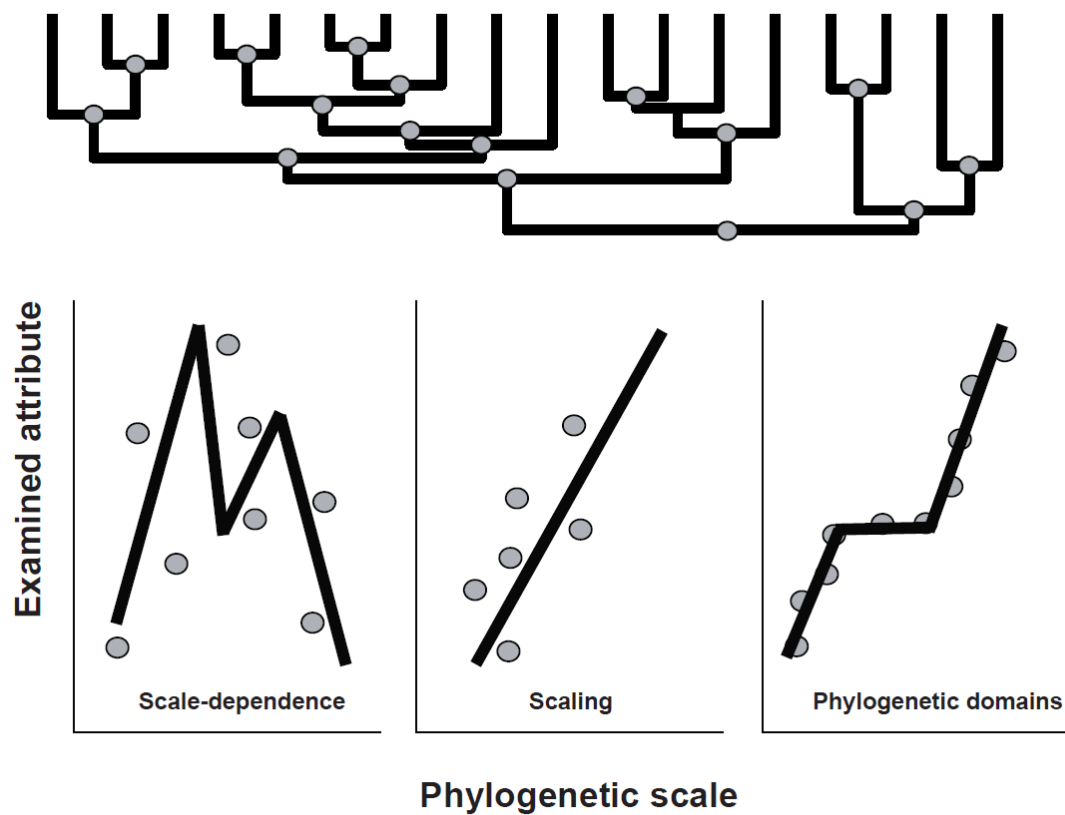
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390 **PHYLOGENETIC SCALE IN PRACTICE**

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

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- 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.

Field	Examined attribute	Examples of evaluation methods
Evolution and diversification	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)
Community ecology	community structure	phylogenetics (NRI, NTI, MNND, MPD) (Webb <i>et al.</i> 2002)
	phylogenetic diversity	Faith's PD (Faith 1992)
Biogeography and macroecology	form of the relationship	linear, polynomial, exponential, lognormal functions
	strength of the relationship	Pearson's correlation, Spearman's correlation, regression slope
Niche conservatism	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