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1 *H1THE USE OF PHYLOGENETIC DIVERSITY IN CONSERVATION BIOLOGY AND
2 COMMUNITY ECOLOGY: A COMMON BASE BUT DIFFERENT APPROACHES

3

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KEYWORDS

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55 phylogenetic diversity, ecosystem services, evolutionary potential, feature variation, option

56

values, spatial planning

57

58 *AB1 abstract

59

60 *AB2The use of phylogenetic tools and studies has strongly increased in the last two
61 decades especially in conservation biology and community ecology. Phylogenetic trees have been
62 essential to understand the processes of community or network assembly, to identify centers of
63 diversification, and to help protect Earth's evolutionary heritage. Despite two decades of research
64 and syntheses, there are still many discussions on how phylogenetic diversity (PD) methods
65 should be effectively applied to those fields. In particular, conservation approaches based on PD
66 have become similar to these used in community ecology. Thus, the main benefit of using PD
67 calculations in conservation biology may have been ignored or misinterpreted. Our goal is to
68 discuss and provide guidelines to the use of PD in biodiversity conservation so that its benefits
69 are not hidden or lost in the approaches employed. We also aim that benefits and uses are better
70 recognized and more easily understood by researchers or practitioners who would like to include
71 PD in their studies and conservation planning.

72

73 *S1Introduction

74

75 *T1The development of humanity has impacted Earth, causing damage to ecosystems, species
76 extinction, and habitat loss that—among the many potential impacts—may in turn threaten
77 human societies. It has become urgent to establish appropriate actions that could mitigate this
78 “crisis” affecting humankind. However, conserving representative populations of all species is
79 generally perceived to be unrealistic due to limited resources and, therefore, effective decisions
80 are needed to best protect biodiversity. Conservation strategies based on species richness and
81 abundance (which aim to preserve species and habitats at a broad scale) have been the rule rather
82 than the exception. For example, the influential “hotspots” of biodiversity have been identified
83 based on endemic and threatened species (Myers et al. 2000). Moreover, these approaches were
84 easier to implement than those based on functions or phylogenies (e.g., no need to collect time-
85 consuming and expensive traits or molecular data nor to estimate functional/phylogenetic
86 relationships between species). However, approaches that consider all species as equal are limited
87 when conservation priorities have to be defined because they fail to recognize their
88 distinctiveness (Avice 1989; Vane-Wright et al. 1991; Faith 1992). On the contrary, progress in
89 phylogenetic inference has enabled the prioritization of conservation efforts based on the
90 evolutionary history of species (Mace et al. 2003). Similarly, in community ecology and
91 biogeography, considering all species ecologically equal is inherent to neutral hypotheses
92 (Hubbell et al. 2001), whereas other methodologies, such as phylogenetic approaches, consider
93 that species assemblage may be guided by species niches (Webb et al. 2002).

94 In the 1980s, the International Union for the Conservation of Nature (IUCN) emphasized
95 the interest of taxonomic distinctiveness for conservation by stating that “the greater the gap
96 between the nearest related family (or genus) . . . and therefore the more distinct” (IUCN
97 1980:22; Faith 2016a, 2018a). From this, “taxonomic hierarchy provides the only convenient rule
98 of thumb for determining the relative size of a potential loss of genetic material” because
99 “different positions in this hierarchy reflect great or lesser degrees of genetic difference” (IUCN

100 1980:22). The significance of the taxonomic distinctiveness concept prompted its use by several
101 state agencies in Australia at the end of the 1980s and through research in systematics and
102 conservation biology (Avice 1989; Faith 1994, 2018a). Quantitative measures of taxonomic
103 distinctiveness for conservation originated in the 1990s with studies from May (1990) and Vane-
104 Wright et al. (1991). Vane-Wright et al. (1991) introduced a measure of taxonomic distinctness
105 that ranks species according to the number of cladistic groups they belong to, a perspective that
106 was later refined by other authors (e.g., Erwin 1991; Brooks et al. 1992; Crozier 1992; Faith
107 1992, 1994; Weitzman 1992; Crozier and Kusmierski 1994; Williams and Humphries 1994;
108 Witting and Loeschke 1995). However, taxonomic distinctiveness did not allow for the ability to
109 measure the diversity of a set of species (Vane-Wright et al. 1991). Faith (1992) proposed to link
110 diversity and distinctiveness by introducing the notion of phylogenetic diversity (PD) as the sum
111 of the branch lengths of the minimum spanning path joining a set of taxa on a tree. Phylogenetic
112 diversity is assumed to represent the relative feature diversity of organisms so that maximizing
113 PD may be a sound strategy for conservation because it would, *on average*, maximize the
114 protection of feature diversity (a “feature” is a particular trait characteristic of a taxa). Due to
115 their high number and because many are unknown, all taxon features cannot usually be accounted
116 for (Faith 1992, 1994, 2016a; Pavoine et al. 2005). This relation was based on an evolutionary
117 model in which shared features are inherited from shared ancestry (Faith 1992), which was later
118 shown to have important implications not only in conservation, but also in community ecology
119 and biogeography (e.g., Webb et al. 2002; Gerhold et al. 2015; Saito et al. 2018). Indeed, this
120 assumption resulted in the use of phylogenetic information to unravel the process at the origin of
121 diversity patterns and community assembly (Webb et al. 2002; Davies et al. 2011). For example,
122 it was hypothesized that the occurrence of distantly related species in a given area might indicate
123 potential competition exclusions of evolutionary close species with similar niches. On the other
124 hand, communities composed of closely related species may indicate possible environmental

125 filtering of species adapted to a similar environment (Webb et al. 2002). From this, the use of
126 phylogenetic information in conservation biology and community ecology became on occasion
127 indistinguishable, whereas the purposes of each domain highly differ in general. This resulted in
128 the absence of consideration of one of the main goals of the use of phylogenetic information in
129 conservation for many studies: the preservation of features' variations that may allow to maintain
130 future options for humanity (Faith 1992).

131 This review aims to reinforce the rationale for the use of phylogenetic metrics in
132 biodiversity conservation and their direct link with practical strategies while identifying some
133 limitations and areas requiring further development in the existing methods. A parallel will be
134 drawn with the use of phylogenetic information in community ecology to highlight how different
135 assumptions and objectives, which are discussed for both biodiversity conservation and
136 community ecology, may result in different uses of phylogenetic information. Finally, limitations
137 for those uses in both fields are discussed in detail and we highlight how they may be alleviated.

138

139 *S1Basic Principles For the Use of PD in Conservation Biology

140

141 *T1The reason to use PD in conservation relies heavily on its link with feature diversity
142 (Faith 1992). Here we present the principles at the basis of this relationship and some of the
143 resulting implications for conservation biology. We focus on the main arguments that justify the
144 use of PD, although some others can be found elsewhere (e.g., Maclaurin and Sterelny 2008;
145 Tribot et al. 2016; ~~Faith 2017~~ Faith 2016b). The aim here is to guide readers to understand the
146 value of PD in regard to practical applications such as the ones proposed in the following
147 sections. We also referred to studies that have investigated the mechanisms at stake to explain the
148 relationships between phylogenetic and functional diversity in macro-organisms, but also in
149 micro-organisms (e.g., Goberna and Verdú 2016; Faith 2018a).

150

151 *S2Phylogenetic Diversity and Feature Diversity: A Relationship Based on Evolutionary

152 Principles

153

154 *T1Darwin observed that “species of the same genus have usually, though by no means
155 invariably, some similarity in habits and constitution” (Darwin 1859:76). This observation has
156 been one of the main justifications behind the use of phylogenies in conservation biology, but is
157 also a matter of debate (Faith 2018a,b; Mazel et al. 2018). Many phylogenetic metrics used in
158 conservation were assumed to capture the variability or the scarcity of morphological or
159 functional traits (e.g., Faith 1992; Redding and Mooers 2006; Davies et al. 2016). This
160 assumption is inherent to Darwin’s theory that introduced the principle of filiation with
161 modification in which shared characters can be explained by shared ancestry. This principle on
162 which PD (among other measures) relies, have several implications: first, closely related species
163 may share more characters than distantly related species; second, species descending from long
164 branches are more likely to capture more ancient characters than species descending from shorter
165 branches; and, third, summing the branch lengths that join species on a tree (a calculus from
166 which the set of PD-based indices originates) captures, on average, their feature variation. Yet,
167 some approaches missed this pattern-process model, which led to some misinterpretations (Kelly
168 et al. 2014).

169

170 *S2Can Evolutionary History Reveal Future Benefits to Societies?

171

172 *T1Biodiversity provides multiple services to humanity (Gascon et al. 2015) that have
173 been classified under the notion of “ecosystem services.” These services include regulation,
174 production, habitat, and information functions (Millennium Ecosystem Assessment 2005). Going

175 further, Faith (1992, 1994) introduced the primary goal of PD for conservation: by measuring
176 feature diversity, PD maintains unanticipated and future benefits of biodiversity to human well-
177 being, i.e., option values. Although ecosystem services are useful at focusing on current rapidly
178 sensible benefits, option values consider long-term, human well-being that may depend on overall
179 and more complex biodiversity sets (Faith 2012). The concept of option values dates back to the
180 1970s: at this time it was already predicted that high rates of species extinction may cause the
181 loss of options to humanity (Iltis 1972; see Faith 2018a for a review). For Bishop, “[t]he loss of
182 any species irreversibly reduces the reservoir of future resources” (Bishop 1978:17) where
183 resources “are not, they become” (Bishop 1978:11), depending on human tastes, preferences, and
184 needs, among others. Bishop (1978) showed that resources are uncertain and may irreversibly be
185 lost with species extinctions. Today, preserving those unexpected future benefits appears crucial
186 in the face of the many threats accelerating species extinctions and population loss such as
187 climate change (Faith and Richards 2012). Indeed, it is almost given that uncertainties linked to
188 the consequences of biodiversity losses will always persist, but the best conservation decisions
189 have to be taken in spite of those uncertainties (Forest et al. 2015; Oliver 2016).

190 The unanticipated services of biodiversity may be provided by species evolutionary history
191 and potential and, thus, captured by a measure such as PD that may help to maximize a variety of
192 features on which future services depend (Mouillot et al. 2016). Biodiversity conservation
193 strategies based on PD are a “form of risk analysis that involves estimating patterns of variation,
194 and then trying to conserve as much of that estimated variation as possible—as a way to retain
195 ‘options’ (possible values) for the future” (Faith and Baker 2006:121). A well-known example of
196 option values and PD was presented by Forest et al. (2007) who found through experimentation
197 that maximizing PD is the best way to conserve the medicinal and economic uses of the Cape
198 flora, whereas a strategy based on species richness alone was less efficient. Oka et al. (2019)
199 found that phylogenetic distant tree species in Japan tended to provide different provisioning,

200 regulating, and cultural services and, therefore, it may be expected that PD could capture the
201 variation of these services. In a similar logic, Faith (2018a) highlighted the insurance value of PD
202 at the scale of ecosystems. The identification of species allowing for the preservation of
203 ecosystem resilience is uncertain, but PD may help to maintain a variety of features that may
204 permit ecosystem to respond to the disturbance. Another striking example is the emerging
205 positive contribution of PD to human health. Indeed, maintaining bacterial phylogenetic diversity
206 could have important consequences on the resilience of those bacterial communities and their
207 metabolic potential (Blaut and Clavel 2007; Lozupone et al. 2012; see also Faith 2018a for some
208 other examples). Although most of this review is built from studies on macro-organisms, PD has
209 also huge implications in the field of microbiology, especially because phenotypes of
210 microorganisms are largely unknown, but their variation may be predicted through phylogenetic
211 information (Goberna and Verdú 2016).

212 The potential surrogacy of PD for option values has encouraged its use for regional and
213 global conservation programs (Millennium Ecosystem Assessment 2005; IPBES 2018). In
214 particular, it may support the definition of a global measure of biodiversity based on a PD metric,
215 which would guide conservation efforts in the long term in the context of uncertainties regarding
216 environmental change (Faith 1992, 2016b; Forest et al. 2015). Indeed, conservation based on PD-
217 based measures should on average provide more goods to societies than those based on other
218 measures of biodiversity (Forest et al. 2007; Lean and Maclaurin 2016). Measures based on
219 phylogenies were also proposed as planetary boundaries in order to maintain a safe operating
220 system in which biodiversity benefits to societies would be preserved (Faith et al. 2010; Mace et
221 al. 2014). The rationale for using phylogenetic information as a planetary boundary is that it may
222 provide long-term ecological and evolutionary potential (but see below) and, as previously stated,
223 future benefits for societies. Last but not least, the Intergovernmental Science-Policy Platform on
224 Biodiversity and Ecosystem Services (IPBES) called to maintain the options provided by nature

225 to humankind facing future needs (Díaz et al. 2015). From this, IPBES drew a framework based
226 on PD to estimate those “option values” and their threats (Faith et al. 2018; IPBES 2018). All of
227 these proposals based on “option values” make PD a powerful approach for conservation goals
228 that aim to maintain human well-being.

229 Although conserving PD may allow an increase in the probability that features providing
230 unexpected benefits to humankind are maintained, the relationship between PD and option values
231 would be even stronger if phylogenetic trees could reveal the evolutionary potential of species
232 (Mouquet et al. 2012). Indeed, this would help predict which set of species would best adapt or
233 diversify in the face of ecological changes and would be more likely to provide or preserve future
234 ecosystem functions and services (Sarrazin and Lecomte 2016).

235

236 *S2Do Phylogenetic Trees Reflect Opportunities For Future Evolution?

237

238 *T1Past and current human activities, besides species domestication, have imposed a
239 strong selection on species, their genetic diversity, and on their number (Hendry et al. 2011).
240 Estimating and preserving the possibilities for species to evolve, as a single unit and in
241 communities, appears crucial for the maintenance of biodiversity, especially in the face of
242 impending global environmental changes. Conserving species with high evolutionary potential
243 would contribute to maintaining biodiversity into the future and would help to preserve the
244 functions and associated services it provides to humans (Sarrazin and Lecomte 2016).

245 How can phylogenies help identify the evolutionary potential of species? First, using PD to
246 maximize feature variation would in principle increase the probability that feature diversity,
247 which is vital for species to be able to adapt to future environmental changes, will be maintained,
248 consequently providing evolutionary potential. This assumption has been introduced by Faith
249 who noted that PD ensures “that one or more members of the subset can adapt to changing

250 conditions” (Faith 1992:2). Later, Forest et al. stated that features useful for the adaptation of
251 species to change are not known such that “maximizing PD will in turn maximize the options for
252 future diversification” (Forest et al. 2007:759). Yet, the relationship between PD and evolutionary
253 potential require further investigation.

254 Evolutionary history of species influences their phenotype and genotype, which then may
255 impact on the direction and speed of contemporary evolution (Hendry et al. 2011). In the absence
256 of specific selection pressures, species with a long history of evolutionary independence are more
257 likely to harbor unique genetic variation that, in turn, may allow them to adapt to change in
258 different ways from other species. Indeed, due to random mutations they may become either more
259 vulnerable or more resistant than other species (Hendry et al. 2011). In contrast, young lineages
260 may evolve more rapidly and have a greater capacity to diversify or adapt and could serve as the
261 source of long-term evolution (Hendry et al. 2011; Mouquet et al. 2012). However, whether long
262 or short branches best represent the possibilities of future evolution is still poorly understood and
263 further research on this topic is needed to guide conservation practices (Rolland et al. 2012).
264 Some authors suggested that estimating past diversification rates across current lineages might
265 indicate which lineages would be more prone to diversify in the future (Rolland et al. 2012). The
266 potential for future evolution of a species might also be assessed by combining information on
267 rates of trait evolution and diversification (Morlon et al. 2010). However, several researchers do
268 not support the idea of using phylogenies for estimating the future possibilities of evolution in
269 particular because empirical proofs are lacking, which paves the way for new research (Rolland et
270 al. 2012; Winter et al. 2013). Thus, in spite of some authors arguing that PD is related to
271 evolutionary potential (e.g., Voskamp et al. 2017), there are no stringent proofs, to our
272 knowledge, that it is actually the case.

273

274 *S2Can Phylogenetic Information Reveal Ecosystem Processes?

275

276 *T1Although the primary goal of using PD for conservation is the maintenance of feature
277 variation and “option values,” some authors have been interested in the relationship between PD
278 and the diversity of some functional traits (e.g., Loreau et al. 2001; Hooper et al. 2005). Given
279 that phylogenetic variation may represent variation in species traits, based on the principle of
280 “filiation with modification,” it has been argued that PD could be a good surrogate of functional
281 diversity (Faith called this the proxy value of PD; Faith 2018a) and capture ecosystem functions
282 (Srivastava et al. 2012; Davies et al. 2016). The main idea follows the community ecology
283 framework (Webb et al. 2002): communities with high mean phylogenetic distance among
284 species (i.e., communities composed of distantly related species) should comprise species with
285 high niche complementarity owing to the evolution of different traits, implying high niche
286 differentiation among distantly related species (Srivastava et al. 2012). Given this higher niche
287 difference, and consequently higher complementarity, the resources in the environment would be
288 more efficiently used, providing higher yields of given processes such as productivity in plants
289 (Srivastava et al. 2012).

290 Moreover, communities composed of distantly related species should have lower levels of
291 exploitative competition due to niche differentiation and, thus, would be more buffered against
292 competitive exclusions (Webb et al. 2002). Second, as phylogenetic difference may relate to
293 feature difference and ecological functions are generally provided by interrelated multiple traits, a
294 community of distantly related species may be functionally highly diverse, and this was shown to
295 increase the ecosystem functions provided (Cadotte 2015; Cadotte and Davies 2016). Contrary to
296 the rationale for the use of PD to conserve option values, the relationship between PD and
297 ecosystem functions is thus not based on the preservation of biodiversity units but rather on the
298 maintenance of ecological integrity (Faith 2018a). However, the relationship between PD,

299 functional diversity, and ecosystem functions is not always well supported, a topic we discuss
300 further (see the section titled When Phylogenetic and Feature Variation Are Not Congruent:
301 Limitations and Solutions).

302 A conclusion that can be drawn from this section is that the surrogacy between PD and
303 feature diversity is well founded: it relies on basic evolutionary principles that tend to make
304 closely related species more similar in traits than distantly related ones. Many assumptions that
305 use PD in conservation depend on this relationship. The conservation logics presented here
306 comprises the proxy value (PD may reveal ecosystem processes), the option value (PD may
307 capture unexpected future benefits to humanity), and the insurance value (PD may preserve the
308 resilience of an ecosystem; Faith 2018a). The option value argument is certainly the best-
309 supported reason for the use of PD in conservation. Further, we will discuss appropriate
310 conservation practices that correctly consider the relationship between PD and feature diversity,
311 and others that fail to account for this surrogacy, leading to the loss of benefits linked to the use
312 of PD. In particular, we will emphasize approaches based on evolutionary distinctiveness that,
313 although they may not allow to maximize feature variation, have a high practical interest.

314

315 *S1 Practical Use of Phylogenetic Information in Conservation

316

317 *S2 Conserving PD and Feature Variation

318

319 *S3 The PD Calculus

320

321 *T1 As stated above, the main benefits linked to the use of measures based on phylogenies
322 in conservation is to capture feature variations, which is beneficial to society faced with
323 unpredictable change and may help for the adaptation of biodiversity to change (Faith 1992).
324 Justified by the rationale that shared features are due to a shared ancestry, optimizing the

325 conservation of feature variation may be achieved by securing the species that capture the highest
326 proportion of a phylogenetic tree. This aim is reached by maximizing the sum of branch lengths
327 of a phylogenetic tree that is protected, i.e., maximizing the PD calculus (the PD of a set of
328 species is equal to the sum of the lengths of all the branches from the corresponding minimum
329 spanning path; Faith 1992), whereas measures that preserve some branch lengths several times do
330 not maximize feature variation (Faith et al. 2004; Faith and Baker 2006). A direct consequence is
331 that in a scenario where only a limited number of species can be rescued, those capturing the most
332 PD should be prioritized. On the contrary many metrics based on phylogenetic trees may
333 not be suitable to achieve this goal (see for example “*T1Another strategy is to give priority
334 to the threatened diversity of a region. Several PD-based measures have been developed with this
335 specific aim in mind (e.g., Faith 2008; Rosauer et al. 2009). A crucial aspect to consider is that
336 the risk of losing a deep branch depends on the risk of losing all of the species it supports (i.e., the
337 phylogenetic complementarity of extinction risks). If this complementarity is not accounted for,
338 the risk of losing deep branches will be incorrectly assessed and, consequently, so is the risk of
339 losing PD (Steel et al. 2007; Faith 2008; Veron et al. 2016, 2017). Extinction risks are generally
340 based on probabilities of extinctions (Faith 2008) or on the restricted range of species (Rosauer et
341 al. 2009). Estimating PD on a phylogenetic tree where branches are weighted by those extinction
342 risks may represent how much feature diversity is threatened. In spatial planning, those measures
343 can be included in a PD gain strategy as described above. One would prioritize the sites that
344 would secure the maximum threatened PD of a region while considering its phylogenetic
345 complementarity (Veron et al. 2018). This may result in very different conservation strategies
346 than when extinction risks are not accounted for. Finally, information about land use, probability
347 of strategy success, or conservation costs could also be used together with a PD gain approach to
348 comply with the requisites for conservation planning assessments (e.g., Billionnet 2013).

349 In conclusion, the approaches described above are not exhaustive and several strategies
350 may be adopted to conserve PD in spatial planning or in species prioritization strategies (other
351 measures are described by Faith 2008). However, assuming that shared traits are due to shared
352 ancestry, the rationale to preserve feature variation and potential option values should rely on the
353 phylogenetic complementarity of sites and/or species. This may help to clarify the use of PD in
354 conservation (Winter et al. 2013) and to consider the criteria of evolutionary history in the
355 implementation of practical conservation actions.

356 Figure 1. THREE PRIORITIZATION STRATEGIES BASED ON PD. PD is measured as the sum of
357 branch lengths on the spanning path joining taxa on a tree to the root. In all scenarios we assume
358 that only three sites out of four can be protected due to limited resources. Protected sites are
359 represented by red squares and safe branches are shown in black. 1) The conservation value of a
360 site is represented by its total PD. The first site to be chosen includes species A, B, and D (PD =
361 26 Ma). The second site selected comprises species A and B with PD = 20 Ma, although no
362 additional branch length is protected. Finally, the third site to protect harbors species C and D
363 (PD = 13 Ma). 2) Sites are selected in function of their local PD gain: branch lengths are
364 weighted by the proportion of their range that is safe following the protection of a site. The order
365 of selection of sites is 1, 4, and 2. 3) Sites are prioritized following a global PD gain strategy: the
366 protection of one occurrence of a species conduct to the gain of all branches supporting that
367 species. Only two sites, those numbered 3 and 2, are needed to protect the entire tree.

368

369 *S2THE ED FRAMEWORK”). Going further, and by considering reasonable that
370 phylogenetic variation is a good surrogate of feature variation, PD, and PD-like measures
371 (e.g. Faith 1992; Faith 2008; Rosauer et al. 2009; Veron et al. 2017), are likely to be the
372 only existing measures based on phylogenetic trees that may help to preserve feature
373 diversity of conservation interest (Faith and Baker 2006; Faith et al. 2004).

374

375

376 *S3PD Gain

377

378 *T1 Various measures have been proposed to extend the PD framework (Faith 2008). In
379 particular, we highlight here a method that allows the preservation of feature variation based on
380 PD gain (Faith 1992; Faith et al. 2018a). Phylogenetic diversity gain is defined as the amount of
381 branch length a species adds to the PD already represented by a given set of species, also known
382 as PD complementarity or PD endemism value, when the set of species is all other species (Faith
383 1992; Faith et al. 2004). In a conservation strategy, PD gain is the additional branch length that is
384 secured after the protection of species and/or sites. Consequently, PD gain is of great interest for
385 conservation planning because it helps to unravel how sites complement each other in order to
386 represent the overall diversity of a region. However, several regional studies have used the total
387 PD of a given site (often a grid cell) as its conservation value and thus did not consider that
388 branches can be shared among sites. This departure from the basic framework of conservation
389 planning based on the complementarity of sites (Margules and Pressey 2000) may originate from
390 the community ecology framework where the total PD of a site is of interest (e.g., Gómez-Ortiz et
391 al. 2017; see the section titled Why Approaches in Community Ecology and Conservation
392 Biology Should Be Different). Yet, in conservation biology, the purpose to maximize the
393 protection of a region's diversity is not achieved with this method because sites with the highest
394 total PD will most likely share branches and thus redundant information (Figure 1; Pollock et al.
395 2017; Faith et al. 2018a). This could lead to the prioritization of sites that add little branch length
396 (i.e., little PD gain) and, consequently, little feature diversity to a set of already protected sites.

397 Considering phylogenetic complementarity of sites and species is thus more appropriate to
398 capture feature variation. A recent set of works have incorporated PD gain as a strategy to protect

399 biodiversity (e.g., Pollock et al. 2017; Rosauer et al. 2017; Veron et al. 2018). Interestingly,
400 Pollock et al. (2017) showed how PD gain could be used for conservation objectives at both
401 global and local scales. At global scale, securing one occurrence of a given species results in a
402 gain equivalent to the full length of the branches supporting that species (Figure 1). On the other
403 hand, when the aim is to emphasize local assemblages, the PD gained at a local site is measured
404 on a phylogenetic tree where each branch is weighted by the proportion of its protected range
405 (Figure 1; Pollock et al. 2007). Thus, a strategy to spatially protect PD would be to prioritize the
406 minimum number of sites that maximize the gain in PD (Figure 1; see also Faith et al. 2018 to
407 define an order of priority among these sites). Whether conservation objectives are local or global
408 may cause the identification of priority sites to differ (Figure 1).

409 One drawback of this PD gain approach is that it defines an effective *set* of protected sites yet, in
410 practice, protected areas are rarely implemented as a set. Thus, it remains essential to identify
411 sites that are likely to be important to include over many possible sets even though they do not
412 optimize the overall PD of a region. Those sites could be based on a hotspot approach as
413 proposed by Veron et al. (2018). Moreover, the PD gain approach for macro-organisms has
414 mainly been used at global or regional scales with the view of preserving “option values” (e.g.,
415 Mouillot et al. 2016). This approach could be extended at the scale of ecosystems where PD may
416 provide an “insurance value” (Faith 2018a). Species in the ecosystem that may be useful for its
417 resilience are unknown, but maximizing their PD and feature diversity may maximize its chance
418 to resist and/or recover from perturbations.

419

420 *S3PD At Risk

421

422 *T1Another strategy is to give priority to the threatened diversity of a region. Several PD-
423 based measures have been developed with this specific aim in mind (e.g., Faith 2008; Rosauer et

424 al. 2009). A crucial aspect to consider is that the risk of losing a deep branch depends on the risk
425 of losing all of the species it supports (i.e., the phylogenetic complementarity of extinction risks).
426 If this complementarity is not accounted for, the risk of losing deep branches will be incorrectly
427 assessed and, consequently, so is the risk of losing PD (Steel et al. 2007; Faith 2008; Veron et al.
428 2016, 2017). Extinction risks are generally based on probabilities of extinctions (Faith 2008) or
429 on the restricted range of species (Rosauer et al. 2009). Estimating PD on a phylogenetic tree
430 where branches are weighted by those extinction risks may represent how much feature diversity
431 is threatened. In spatial planning, those measures can be included in a PD gain strategy as
432 described above. One would prioritize the sites that would secure the maximum threatened PD of
433 a region while considering its phylogenetic complementarity (Veron et al. 2018). This may result
434 in very different conservation strategies than when extinction risks are not accounted for. Finally,
435 information about land use, probability of strategy success, or conservation costs could also be
436 used together with a PD gain approach to comply with the requisites for conservation planning
437 assessments (e.g., Billionnet 2013).

438 In conclusion, the approaches described above are not exhaustive and several strategies
439 may be adopted to conserve PD in spatial planning or in species prioritization strategies (other
440 measures are described by Faith 2008). However, assuming that shared traits are due to shared
441 ancestry, the rationale to preserve feature variation and potential option values should rely on the
442 phylogenetic complementarity of sites and/or species. This may help to clarify the use of PD in
443 conservation (Winter et al. 2013) and to consider the criteria of evolutionary history in the
444 implementation of practical conservation actions.

445 Figure 1. THREE PRIORITIZATION STRATEGIES BASED ON PD. PD is measured as the sum of
446 branch lengths on the spanning path joining taxa on a tree to the root. In all scenarios we assume
447 that only three sites out of four can be protected due to limited resources. Protected sites are
448 represented by red squares and safe branches are shown in black. 1) The conservation value of a

449 site is represented by its total PD. The first site to be chosen includes species A, B, and D (PD =
450 26 Ma). The second site selected comprises species A and B with PD = 20 Ma, although no
451 additional branch length is protected. Finally, the third site to protect harbors species C and D
452 (PD = 13 Ma). 2) Sites are selected in function of their local PD gain: branch lengths are
453 weighted by the proportion of their range that is safe following the protection of a site. The order
454 of selection of sites is 1, 4, and 2. 3) Sites are prioritized following a global PD gain strategy: the
455 protection of one occurrence of a species conduct to the gain of all branches supporting that
456 species. Only two sites, those numbered 3 and 2, are needed to protect the entire tree.

457

458 *S2The ED Framework

459

460 *S3Evolutionary Distinctiveness Does Not Allow the Protection of Feature Variation

461

462 *T1Evolutionary distinctiveness (ED) is another type of measure based on phylogenetic
463 trees that has been widely used in conservation biology. It quantifies the number of relatives a
464 species has, how phylogenetically distant they are, and assigns an individual score to each species
465 in the phylogenetic tree. For example, the widely used fair proportion index partitions the branch
466 lengths of a phylogenetic tree (i.e., PD) among all of the species it supports (Isaac et al. 2007).
467 Species are then prioritized according to their ED value. This also implies that the sum of all ED
468 scores measured on a phylogeny is equal to the total PD of all taxa comprised in this tree.

469 The ED order of prioritization is, however, not as efficient as the PD calculus at capturing
470 the variations of features (Figure 2). This is mainly because ED measures do not account for the
471 phylogenetic complementarity among species (i.e., by conserving species with the highest ED,
472 some deep branches are likely to be represented several times whereas others may not be
473 represented at all; Figure 2). Feature variation is therefore not properly captured. For example,
474 Isaac et al. (2007) argued that the species with the highest ED scores, and thus the highest

475 priority, would be two closely related species. However, the choice of those two species does not
476 look to be the best strategy to maximize feature variation as it does not represent the highest
477 protected proportion of the tree of life (see the section titled *S2Conserving PD and Feature
478 VARIATION). In a PD-based strategy, two distantly related species would have been selected to
479 protect most feature variation.

480 Similarly, some spatial planning research has focused on preserving sites with the highest
481 ED values, especially by summing/averaging ED scores of the species occurring in each site and
482 prioritizing sites with the highest cumulative ED (e.g., Daru et al. 2013; Safi et al. 2013; Jetz et al.
483 2014). This method should also not be viewed as a conservation planning strategy that maximizes
484 feature variation because phylogenetic complementarity is not taken into consideration. These
485 arguments related to spatial planning can be applied to all types of ED measures even those that
486 include extinction risks or endemism such as Evolutionary Distinctiveness and Global
487 Endangerment (EDGE; Isaac et al. 2007), Heightened Evolutionary Distinctiveness and Global
488 Endangerment (HEDGE; Steel et al. 2007), Biogeographical weighted Evolutionary
489 Distinctiveness (Cadotte and Davies 2010), Loss-significant Evolutionary Distinctive Globally
490 Enduring (LEDGE; Faith 2015), or After Downlisting Expected Phylogenetic Diversity (ADEPD;
491 Nunes et al. 2015).

492

493 *S3Evolutionary Distinctiveness Remains a Useful Measure For Practical Conservation

494

495 *T1Although an approach based on preserving species with high ED may not be the best
496 strategy to capture feature variation, this measure is still valuable for conservation biology. First,
497 the rationale of protecting species with high ED values is linked to their isolation from all other
498 species and to the fact that they may represent long branches capturing old features shared by
499 very few species (Magnuson-Ford et al. 2009; Redding et al. 2010; Collen et al. 2011; Stein et al.

500 2018; but see Grandcolas and Trewick 2016). From this, conservation of species with a high ED
501 generally would be able to capture a lot of PD (although it is not the maximum PD) and would
502 contribute to the maintenance (but not the maximization) of feature variation (Faith et al. 2018).

503 Other arguments to preserve highly evolutionary distinct species are essentially practical
504 (e.g., Faith 2015; Forest et al. 2018; Stein et al. 2018; Thévenin et al. 2018). Isaac et al. justified
505 the protection of species with the highest ED values, despite the fact that they are closely related,
506 because “the extinction of either would leave a single descendant of the oldest and most unusual
507 lineage in the phylogeny” (Isaac et al. 2007:2). For Redding and Mooers (2006), real-world
508 conservation practice is based on lists of threatened species, and PD does not offer an order of
509 conservation prioritization, especially because there will be as many possible rankings of species
510 as there are PD maximizing solutions in a set of species. A species list based on PD may be
511 difficult to implement at the management level (Redding and Mooers 2006). Moreover, strategies
512 based on maximizing PD are based on a set of species (or sites). Consequently, the conservation
513 of a species outside this set may lead to the identification of a new and very distinct set to
514 preserve PD, and management actions are rarely implemented on a set of species or sites (e.g.,
515 Thévenin et al. 2018). Thus, it remains important to identify species that may capture large
516 amounts of PD independently of a given set. To this aim, because they may be evolutionarily
517 isolated and descending from long branches, species with high ED may capture more branch
518 lengths and more PD than species with low ED as showed by Redding et al. (2008).

519 Regarding extinctions, Chaudhary et al. (2018) showed that summing the ED scores of
520 extinct species was strongly correlated to PD loss. By looking at the calculus of ED and expected
521 loss of PD, Faith et al. (2018) showed that the sum of ED scores of threatened species was
522 approximately the total expected loss of PD, assuming that the probabilities of extinctions of
523 threatened species were close to 1.

524 To summarize, the ED approach has many advantages, but future research based on this
525 measure should be aware that it does not maximize feature variation and option values. High ED
526 species may capture rare features and have practical interest to capture more PD than expected
527 when the protection of a set of species maximizing PD cannot be set up in real-world
528 conservation actions.

529 Figure 2: Comparison of PD and ED in maximizing feature variation This figure represents the
530 selection of species based on A) evolutionary distinctiveness (estimated here through the fair
531 proportion index) and B) the PD value. Developing a conservation strategy based on ED does not
532 maximize feature variation. Marks on branches represent the unique features it captures based on
533 the simplified assumption that the number of unique features is proportional to branch length. In
534 A, species E and F are prioritized due to their high ED scores. This represents 15 Ma of branch
535 length and 15 unique features. In B, species B and F (or E), which maximize PD, are selected,
536 and they capture 20 Ma of PD and 20 unique features.

537 The rationale to preserve feature variation and related conservation benefits may be
538 reached by a PD calculus that maximizes the proportion of the Tree of Life protected. However,
539 some PD approaches were erroneously thought to protect feature variation whereas they may be
540 more informative in the field of community ecology. In the next section we will underline what
541 these approaches are and how different goals in conservation biology and community ecology
542 require different uses of PD.

543

544 *S1 Why Approaches in Community Ecology and Conservation Biology Should Be Different

545

546 *T1 Some approaches using PD in conservation biology have likely been influenced by
547 those applied in community ecology (or at least they became similar on occasions) resulting in
548 wrong interpretations and practices. Although we previously discussed what phylogenies can tell

549 us about feature variation and its potential for conservation, in this section we discuss what PD
550 can tell us about species interactions influencing community and network assembly. By doing so
551 we will show why and when approaches in conservation biology and community ecology should
552 differ.

553

554 *S2Some Phylogenetic Information of Interest in Community Ecology: Niche Conservatism and
555 Community Assembly

556

557 *T1As previously mentioned, the idea that phylogenetic distance should be related to
558 species interaction can be traced back to Darwin (1859). He hypothesized that, because of their
559 common ancestry, congeners should have many similar characters, increasing the chances of
560 exploiting the environment in a similar fashion—what would be later known as the competition-
561 relatedness hypothesis (Cahill et al. 2008). Gause (1934), inspired by Darwin’s ideas and by
562 Lotka (1925) and Volterra (1926), established the foundations for the theory of competitive
563 exclusion. This theory proposes that two species occupying the same ecological niche cannot
564 coexist in a stable manner. It was later complemented by the limiting similarity model—
565 introduced by MacArthur and Levins (1967) and revised by Abrams (1983)—that demonstrates
566 mathematically how species coexistence could be limited by their degree of niche overlap. Works
567 by Felsenstein (1985) and Harvey and Pagel (1991) introduced the first formal discussions
568 surrounding the concept of niche conservatism. Because a species is expected to not easily adapt
569 to conditions outside its fundamental niche, evolutionary changes are likely to be an inherently
570 conservative process (Holt and Gaines 1992; Wiens and Graham 2005). Thus, closely related
571 species should fundamentally overlap in their niches.

572 Based on the concepts of niche conservatism and limiting similarity, Webb et al. (2002)
573 proposed the use of phylogenetic relatedness as a surrogate for niche overlap, which allowed for

574 the understanding of community assembly through the analysis of patterns of phylogenetic
575 structure. According to their logic, when closely related species co-occur more often than
576 expected by chance (i.e., phylogenetic clustering), one could infer the predominance of
577 environmental filtering, whereas when closely related species co-occur less than expected by
578 chance (i.e., phylogenetic overdispersion), one could infer the predominance of competitive
579 exclusion due to the limited similarity among closely related species. This concept has been
580 widely used due to the straightforward way that observed patterns can be interpreted and the
581 increasing availability of comprehensive data sets (Cavender-Bares et al. 2004; Vamosi and
582 Vamosi 2007; Emerson and Gillespie 2008).

583 Although environmental filtering and competitive exclusion are only a part of the story
584 explaining how species could coexist (Gerhold et al. 2015; Saito et al. 2018), these assumptions
585 foster the use of PD in community ecology that, therefore, relies on very different logic than in
586 conservation biology.

587

588 *S2Phylogenetic Diversity in Community Ecology—A Generalization

589

590 *T1From the logic described above, several metrics based on phylogenetic trees have been
591 developed in community ecology that are related to divergence, diversity, and evenness (Tucker
592 et al. 2017). We will here focus on the use of PD to show how it differs from its use in
593 conservation biology; reviews on other measures are available elsewhere (e.g., Pavoine and
594 Bonsall 2011; Tucker et al. 2017).

595 The PD value (Faith 1992) of a set of species found at a given site has been employed as a
596 measure of phylogenetic alpha diversity (e.g., Chai et al. 2016) to assess the coexistence or
597 functional differences among species (Cadotte et al. 2010). One particular approach has been to
598 compare the PD and species richness (SR) at a given site. High PD compared to SR would relate

599 to the occurrence of distantly related species and indicate potential competitive exclusions, while
600 low PD over SR may reveal communities composed of closely related species and possible
601 environmental filtering (overdispersion versus clustering; see above). For example, Chai et al.
602 (2016) used this approach to reveal the deterministic and stochastic process at the origin of
603 diversity patterns in a long-term study of forest succession. Moreover, relative PD might provide
604 insights into evolutionary processes, including the balance between speciation and extinction that
605 affect community assembly (Pavoine and Bonsall 2011). Davies and Buckley (2011) measured
606 the mammal relative PD in individual sites to disentangle areas where speciation has been rapid
607 and immigration rare (low PD relative to species richness) and areas where diversification has
608 been slow and long-distance immigrations frequent (high PD relative to species richness).

609 This is, of course, a very general view of the use of PD in community ecology that is often
610 employed in combination with other measures (Cadotte et al. 2010; Pavoine et al. 2013).
611 However, this shows that PD is used for different purposes in community ecology and
612 conservation biology and should not be confused. Although the PD of a given site may be of
613 interest to understand community assembly, it may be less important in conservation biology
614 where, to preserve feature variation, the phylogenetic complementarity of sites and species is
615 considered. There are cases when community ecology and conservation ecology meet, for
616 example, to predict the effect of invasions (Yguel et al. 2011, 2014) or ecosystem functioning, as
617 discussed above. Yet, we prefer to highlight the main differences and avoid sources of confusion
618 in both fields of ecology.

619

620 *S1When Phylogenetic and Feature Variation Are Not Congruent: Limitations and Solutions

621

622 *T1A common point in conservation biology and community ecology frameworks is the
623 use of PD under the assumption that large evolutionary distances among species indicate more

624 feature differences among them. All of the benefits that can result from this relationship make it
625 likely that many studies based on PD will be conducted in the future. Yet, existing limitations and
626 misinterpretations to this assumption have fuelled the ongoing debate on the use of phylogenetic
627 information in both conservation biology and community ecology (e.g., Cadotte et al. 2017;
628 Mazel et al. 2018). As stated by Faith and from what is clear in the original PD paper (Faith
629 1992) “PD should not be expected to magically make inferences about every favorite character or
630 feature” (Faith 2018a:6). This implies that, despite clear benefits, some conclusions from PD
631 investigations should be drawn with care. We present some of the most common sources of
632 limitations in the PD and feature diversity relationship, their consequences, and how they may be
633 alleviated. Some limitations have also been treated in depth by other authors, so the general
634 overview we present here may be complementary to previous work (e.g., Cadotte et al. 2017; Box
635 1). We focus our attention on how these limitations may (or may not) weaken the conclusions
636 drawn from PD analyses in conservation and community ecology presented in the section above.

637

638 *S2A General Overview of Existing Limitations

639

640 *S3Phylogenetic Reconstruction

641

642 *T1Modern phylogenetic trees originated from cladistics, a set of methods used to
643 reconstruct relationships between organisms established by Hennig (Hennig 1950, 1965).
644 Phylogenetic trees enable the grouping of species/organisms based on the analysis of homologous
645 characters (i.e., characters inherited from a common ancestor). Currently, this method is the
646 preferred principle to classify organisms and numerous statistical and computational tools have
647 been developed (Box 1; e.g., maximum parsimony, maximum likelihood, and Bayesian methods)
648 in the quest to find the most accurate phylogenetic trees (Huelsenbeck et al. 2001; Tamura et al.
649 2011).

650 All of the tools available for phylogenetic tree reconstruction have advantages, drawbacks,
651 and limitations that should be carefully considered. In Box 1 we relate sources of uncertainties in
652 some of the most employed methods for phylogenetic reconstruction. This shows that the
653 relationship between phylogenetic variation and feature variation may already be blurred by these
654 reconstruction methods.

655

656

BOX 1

657

Phylogenetic tree reconstruction methods as source of uncertainties

658

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*S1Distance-Based Methods

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672

*S2Unweighted Pair Group Method with Arithmetic Means (UPGMA)

673

674 *T1UPGMA is one of the simplest methods for tree reconstruction. The clustering works by
675 searching for the smallest pairwise distance value between OTUs in the matrix that will form a
676 new cluster. Then a new distance matrix is calculated between the newly formed cluster and the
677 remaining OTUs. The process continues until all OTUs are clustered. The tree is formerly
678 additive and thus all nodes are equally distant from the root. UPGMA assumes that evolutionary
679 rates in all branches are similar, which is generally not the case (Nei 1991).

680

681 *S2Neighbor Joining (NJ)

682

683 *T1This method differs from UPGMA in that there is no assumption about the distance
684 between OTUs. The NJ algorithm does not construct clusters, but minimizes the length of all
685 internal branches (Saitou and Nei 1987). The process begins with an estimation of evolutionary
686 distances correcting for multiple substitution events at the same site. In a second step, the
687 minimal distance is used to introduce a new node that groups a pair of OTUs for which
688 evolutionary distance is minimal. Then a new matrix is calculated from the new node to each
689 other's terminal node. The process is repeated until an unrooted tree is constructed. A distantly
690 related taxon (outgroup) can be chosen to root the tree.

691

692 A serious weakness for distance methods such as NJ and UPGMA is that the observed differences
693 between sequences are not accurate reflections of the evolutionary distances between them,
694 especially due to non-constant evolutionary rates. In that case, corrections must be applied, but
695 there is no consensus on what correction could be the best. NJ and UPGMA appear as suitable
696 methods when sequences have diverged recently, but could be particularly misleading when
697 estimating old relationships (Holder and Lewis 2003). Other distance-based methods are Fitch-
698 Margoliash, minimum evolution, or least-squares algorithms.

699

700 *S1Character-Based Models

701

702 *T1Character-state methods use variation in a set of discrete characters (e.g., sequence
703 data) to construct phylogenetic trees. In contrast to distance-matrix methods, they can be used to
704 reconstruct ancestral character states because they retain the original character status of the taxa.

705

706 *S2Maximum Parsimony (MP)

707

708 *T1Under the maximum parsimony criterion, the best tree is one that requires the minimum
709 number of character changes (e.g., nucleotide substitutions) to produce the data (e.g., a set of
710 homologous sequences). However, there are many plausible scenarios that could have produced a
711 group of sequences and considering a single mutational path, as MP does, may be misleading
712 (Holder and Lewis 2003). MP assumes that common characteristics are inherited from a common
713 ancestor, but when homoplasy (parallelisms, convergences, and reversal events) is present, the
714 most parsimonious method may underestimate the actual evolutionary divergences. The MP
715 algorithm usually finds more than one tree with the same parsimonious length. A consensus
716 approach is then built up to combine all of the most parsimonious trees. The MP method does not
717 consider the fact that the number of character changes may vary on each branch of the tree. Long-
718 branch attraction occurs when rapidly evolving taxa are placed together on a tree because they
719 have many mutations (Rizzo and Rouchka 2007). Yet, parsimony performs relatively well if the
720 amount of convergence is rare compared with the number of mutations that are conveying useful
721 information (Holder and Lewis 2003). There are other different parsimony algorithms such as
722 weighted, transversion, or Dollo parsimony.

723

724 *S2Maximum Likelihood (ML)

725

726 *T1This method allows for the correction of multiple mutational events at the same location.

727 Likelihood methods measure the probability of the data given the hypothesis (i.e., it prefers the

728 tree with the highest probability to fit the observed sequences). ML optimizes the likelihood of

729 observing data given a tree topology and a model of nucleotide evolution (Egan and Crandall

730 2006). ML assumes a model of evolution and the tree returning the highest likelihood is

731 considered the best tree. An advantage of ML is that it accounts for the possibility of unseen

732 events such as back mutations or complex pathways (Holder and Lewis 2003). As for MP, it

733 examines different tree topologies. This method is very robust for reconstructing old relationships

734 and fast evolutionary events, but is one of the most computationally demanding and may be

735 inappropriate for relatively large data sets. To tackle those computer load issues, more recent

736 methods based on ML have been developed, in particular PhyML (Guindon et al. 2010), RAxML

737 (Stamatakis 2006), and IQ-TREE (Nguyen et al. 2014), among others.

738

739 All of the methods described above require a form of confidence assessment for the

740 relationships inferred in the tree. The most common tool to establish this confidence is called

741 “bootstrapping,” which consists of creating pseudo-replicate data matrices by randomly

742 resampling the original data set (with replacement) and reconstructing phylogenetic trees for each

743 (Lemey et al. 2009). Bootstrap values provide a measure of support for the monophyly of clades

744 and the relationships among studied taxa.

745

746 *S2Bayesian Methods

747

748 *T1 Bayesian methods simultaneously estimate trees and measures of support for every
749 branch. This approach searches for a set of trees representing the data by using a prior probability
750 for the distribution of each parameter of the model (or equal probabilities if we do not have prior
751 information). The optimal tree is the one that maximizes the posterior probability that is
752 proportional to the likelihood multiplied by the prior probability. The posterior probabilities
753 specify the probability of each tree given a model, a prior, and the data. A technique called
754 Markov chain Monte Carlo (MCMC) is used to explore tree space. An advantage of Bayesian
755 techniques is that they allow the implementation of complex models of sequence evolution.
756 Moreover, contrary to ML, Bayesian approaches may be reliable even when the ratio of data
757 points over the number of parameters is low. Unfortunately, Bayesian methods are very
758 computationally demanding and selecting an uninformative prior may result in serious issues.

759

760 *S3 Different Rates of Feature Evolution and Convergences Can Blur Phylogenetic Signals

761

762 *T1 Evolutionary rate variation among features may influence how similar closely related
763 species are in a phylogenetic tree. Fast evolving features may tend to be very different between
764 closely related species and reveal little about evolutionary history (Losos 2011). Phylogenetic
765 signals in features can thus be revealed only when the rates of character evolution are low relative
766 to rates of clade evolution (Losos 2011).

767 Another reason why phylogenetic similarity may not reflect feature similarity is because of
768 convergent evolution (Faith 1992). This is the process by which evolutionarily unrelated
769 organisms show similar features as a result of natural selection and adaptation. Because of
770 convergences, several features in different clades do not show any phylogenetic signal (Mazel et
771 al. 2017). As stated by Faith (1992), the PD index does not capture convergent features because
772 they depart from the assumption that shared traits are due to a common evolutionary history.

773 Although this principle is inherent in the evolutionary model on which PD is based, it has been
774 missed in some studies (e.g., Kelly et al. 2014). Therefore, convergent features should be
775 considered through other metrics, such as shared habitats as suggested by Faith and Walker
776 (1996).

777

778 *S3Species Descending From Long Branches Do Not Always Retain Old Features

779

780 *T1Species descending from deep nodes do not always exhibit features older than species
781 found in shallower nodes (Grandcolas and Trewick 2016). There are two potential reasons for this
782 situation. First, all characters of a species that have been in an evolutionary stasis are not in a
783 primary state. Grandcolas and Trewick (2016) showed that species found on long branches may
784 also have features considered more modern. Second, isolated species on long branches can be
785 remnants from a lineage formerly much more diverse that was decimated by subsequent
786 extinction events. Thus, the species that are remnants from an ancient group previously
787 comprising more species represent a combination of features of this group, but not always the
788 character states present in its ancestor (Grandcolas et al. 2014; Grandcolas and Trewick 2016).
789 The conservation interest of evolutionary distinct species and long branches, capturing large
790 amounts of PD, may not always rely on their unique features and possible related functions in an
791 ecosystem, but also to their level of endangerment and symbolic value (Isaac et al. 2007;
792 Grandcolas and Trewick 2016; Trewick and Morgan-Richards 2016).

793

794 *S3Uncertainties Due to the Model of Feature Evolution

795

796 *T1The expectation that greater evolutionary distances indicate that species have
797 accumulated more ecological differences assumes a very particular evolutionary model (i.e., the
798 Brownian motion model). Phylogenies are often built following a Brownian motion model

799 (Diniz-Filho et al. 2013). This model assumes that features continue to diverge linearly over time
800 and that convergence is rare. This supports the rationale to use PD in conservation and
801 community ecology (i.e., that shared features may be explained by shared ancestry; Cadotte et al.
802 2017). Cadotte et al. (2017) showed that under the Brownian motion model the relationship
803 between ecological and phylogenetic distance was linear only when multiple features (or
804 ecological traits) were considered, whereas this was not true for a single feature. PD may be a
805 good surrogate for variation of multiple features, but this surrogacy may weaken when the
806 number of features decrease (Diniz-Filho et al. 2013; Cadotte et al. 2017; Tucker et al. 2018), as
807 stated in the original paper introducing PD (Faith 1992). Yet, evolutionary, physiological, or
808 ecological constraints tend to make evolution models more complex than a Brownian motion
809 model. Many studies show that only a small proportion of features (or ecological traits) followed
810 a linear model of evolution and a model of bounded evolution was generally favored (Davies
811 2015). From this, the relationship between phylogenetic distance and ecological distance and
812 between the sum of branch lengths joining species and their feature variation can take many
813 forms (Cadotte et al. 2017; Tucker et al. 2018). For example, if evolution slows down over time,
814 phylogenetic diversity may capture little feature variation, whereas if evolution occurs in bursts,
815 much feature variation may be captured (Davies 2015). A useful review of the issues related to
816 the model of evolution can be found in Cadotte et al. (2017), and some practical solutions have
817 been proposed by Pagel (1999), Diniz-Filho et al. (2012), Letten and Cornwell (2015), Davies
818 (2015), and Mazel et al. (2016).

819 Yet, despite numerous possible evolutionary models, if “large numbers of species [are
820 examined] and combine multiple traits, which have been subject to different selection regimes,
821 then the pattern of evolution is likely to be indistinguishable from BM [Brownian motion model]”
822 (Cadotte et al. 2017:537–538). When this condition is met, PD may then still be a good predictor

823 of feature (or ecological traits) diversity, independent of the evolutionary model of features
824 (Cadotte et al. 2017).

825

826 *S2Consequences For the Use of Phylogenetic Information in Conservation Biology...

827

828 *T1One main benefit for the preservation of PD highlighted in this review is its
829 relationship with ecosystem processes and option values (Kraft et al. 2007). Up until now, some
830 studies have found that ecosystem processes were related to species richness, with a small
831 fraction of increase due purely to higher phylogenetic diversity (Venail et al. 2015; but see
832 Cadotte 2015). From the discussion above, it is clear that there are many reasons why
833 phylogenetic diversity itself may not be able to forecast functional diversity or the value of
834 ecosystem services (Venail et al. 2015). First, traits that control ecological functions are not
835 phylogenetically conserved, so that maximizing PD may not maximize feature variation.
836 Moreover, this implies that closely related species do not have similar ecological functions and
837 distantly related species do not complement each other's function. Second, closely related species
838 do not compete more strongly than distantly related ones, given all of the reasons discussed above
839 (see Mayfield and Levine 2010). Thus, communities composed by distantly related species do not
840 have more niche complementarity and better productivity than communities formed by closely
841 related species. Third, closely related species commonly experience facilitative interactions
842 (Cianciaruso et al. 2009). Thus, communities composed by closely related species can have
843 higher productivity when these species facilitate each other, in comparison with communities of
844 distantly related species that face competitive interactions. In spite of all these possible imitations,
845 PD was shown to be a strong predictor of ecosystem functioning (Cadotte 2015). This is likely
846 because by summing the phylogenetic distances of species in a community, PD represents the
847 variation (and not the difference) in species traits (i.e., the total niche space occupied; Cadotte et

848 al. 2017). Moreover, when the additional benefits of using PD over other measures to capture
849 ecosystem processes are not clear, phylogenetic information may still be valuable (Cadotte 2015).
850 For instance, Yguel et al. (2016) argued that, even if PD remained useful for predictions related to
851 ecosystem processes, it may be too simple to depict differences in the phylogenetic structure of
852 communities. These authors then proposed a measure called Evolutionary Legacy of
853 Diversification, which describes branching patterns and may better predict ecosystem processes
854 than other commonly used metrics such as PD. Besides, ecological functions may not always be
855 provided by feature diversity but rather by key innovations (Davies et al. 2016). In that case
856 phylogenetic placement, for example, measured by metrics that describe the connectedness or
857 centrality of nodes and edges within a network, may better represent those functions than PD does
858 (Davies et al. 2016).

859 In addition, many studies showed that PD was not a good proxy for functional diversity
860 and that spatial patterns were incongruent most of the time (Devictor et al. 2010; Pavoine et al.
861 2013; Pollock et al. 2017; Cadotte and Tucker 2018; Mazel et al. 2018). Again, these results were
862 expected because only a few traits were considered, convergence may occur or models were not
863 convenient (see discussion in Faith 2018b). Appropriate measures to estimate functional diversity
864 and spatial priorities, which separately consider functional and phylogenetic diversity, are
865 therefore necessary (e.g., Cadotte and Tucker 2018).

866 Although some limitations and improvements can be found regarding the relationship
867 between PD and ecosystem processes and that some features do not show any phylogenetic
868 signals (Faith 1992), PD remains an important calculus to maintain option and insurance values.
869 PD may *on average* capture feature diversity that may be the best way to maintain unexpected
870 benefits to humanity and for the resilience of ecosystems. As shown above, this relationship does
871 not rely on only a few existing traits, but on the overall features of species with unknown
872 variation and unknown future values. Analyses based on a few traits have sometimes led to the

873 wrong interpretation that PD does not capture option values (Faith 2018b). On the contrary,
874 “option values” is the primary argument for the use of PD calculus in conservation such that
875 “maximizing the retention of phylogenetic diversity (PD) should also maximize option value”
876 (Larsen et al. 2012).

877 In conclusion, despite the fact that niche conservatism provides the foundation for the PD
878 ecosystem services agenda, it has some limitations that should be acknowledged. Although PD
879 has been shown to be a strong predictor of ecosystem functioning, the key to understanding the
880 processes that explain this prediction is to go deeper into the phylogenetic signature of species
881 interactions that may result in the definition of new metrics based on phylogenies. Studies
882 investigating the relationship of PD and ecosystem functions and services will be more fruitful if
883 we acknowledge the underlying premises of phylogenetic signals and niche complementarity,
884 otherwise studies will have strong contingency and with low generalization for conservation
885 purposes.

886

887 *S2...and in Community Ecology

888

889 *T1From the limitations described above (see the section titled *S1When Phylogenetic and
890 Feature Variation Are Not Congruent: Limitations and SOLUTIONS), assuming that niche
891 conservatism indicates the maintenance of the fundamental niche over time a priori and to link it
892 directly to competition between closely related species may sometimes be flawed (Kraft et al.
893 2007). Although many features are more conserved through evolutionary history than expected,
894 in cases of convergent or divergent evolution, the interpretation of phylogenetic patterns in the
895 face of assembly processes becomes confused (Losos 2008, 2011). For example, species from
896 distinct lineages where trait evolution is predominantly convergent can be assembled in
897 communities driven by environmental filters and yet their phylogenetic pattern can be

898 overdispersed. In this case, if we assume niche conservatism, phylogenetic patterns, such as the
899 relationship between PD and SR, would be erroneously interpreted as competition between
900 closely related species. Moreover, when species are assembled by asymmetric competition—i.e.,
901 species have different competitive abilities—communities can have phylogenetically clustered
902 structures due to the competitive exclusion of distantly related species with inferior competitive
903 abilities (Mayfield and Levine 2010; Gerhold et al. 2015; Saito et al. 2016, 2018). From this,
904 relationships between phylogenetic overdispersion/clustering and competition/environmental
905 filtering is also not uniform across clades (Pearse et al. 2018). Cadotte et al. (2017) provides a
906 review on how to interpret the lack of phylogenetic signals in community assembly. Other points
907 for the weakness and strengths of inferring assembly processes from phylogenetic information,
908 such as understanding how coexistence leads to the macroevolutionary diversification of habitat
909 lineage pools or, on the contrary, how macroevolutionary contingency of habitat lineage pools
910 affects present-day species coexistence (Gerhold et al. 2015) were explored by others (Mayfield
911 and Levine 2010; Mason and Pavoine 2013; Gerhold et al. 2015; de Bello et al. 2017).

912 The use of PD in conservation biology and community ecology relies on a strong
913 theoretical background. Limitations exist that may blur or nullify the relationship between
914 phylogenetic variation and variation in some traits (e.g., Cadotte and Tucker 2018), potentially
915 influencing the conclusions that can be drawn from PD approaches. In particular, this may
916 influence the predictions of species interactions so that niche complementarity, species
917 assemblage, and ecosystem functioning can sometimes be difficult to interpret through PD. As
918 stated above, this situation could be improved by a clearer understanding of the phylogenetic
919 signature of species interactions. Finally, the relationship between genotypes and phenotypes and
920 how it affects the use of PD has received, to our knowledge, nearly no attention. Still, the
921 limitations regarding the use of PD in conservation and community ecology are better understood
922 (e.g., Cadotte et al. 2017) and incorrect interpretations occasionally arise from unfit analyses or

923 inaccurate understanding of the rationale of PD usage (e.g., Kelly et al. 2014; Venail et al. 2015).
924 Several corrections, but also additional applications, have been proposed (e.g., Cadotte 2015;
925 Gerhold et al. 2015; Yguel et al. 2016). Although conclusions about the use of PD should
926 sometimes be mitigated, we believe that such improvements and good practices will allow the
927 appropriate use of phylogenetic information as a powerful tool for the future of conservation
928 biology and community ecology.

929

930 *S1Conclusions

931 *T2

- 932 1. The use of phylogenetic information in conservation biology and community ecology
933 relies highly on the assumption that shared features are due to a shared evolutionary
934 history.
- 935 2. Up until now, confusion between the conservation biology and community ecology
936 frameworks may have resulted to a misuse of phylogenetic information in many cases.
- 937 3. In conservation biology, the interest is to maintain option values through feature
938 variation. Strategies that do not consider the phylogenetic complementarity of sites and
939 species do not allow maximizing the chances to preserve option values, but some may
940 have a practical interest.
- 941 4. In community ecology, phylogenetic information may help to disentangle the process at
942 the origin of diversity patterns and community assembly in a given area, but phylogenetic
943 complementarity among sites is not always essential.
- 944 5. Yet, it should be noted that limitations in the relationship between features and
945 evolutionary history may lead to misunderstandings and misinterpretations in both
946 conservation biology and community ecology.

- 947 6. Understanding and considering the conditions to use phylogenies for conservation and
948 community ecology purposes is challenging, but recent progress has been made. For
949 example, alternative indices to phylogenetic diversity have been proposed to include
950 factors at the origin of shifts in the relation between evolutionary and trait variation.
- 951 7. Improving our knowledge on the relation between evolutionary history and trait variation
952 is important as it has implications in various fields of ecology such as the understanding
953 of ecological interactions, ecological functions, and the potential future benefits of
954 biodiversity to societies.

955

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1484

1485 APPENDIX 1

1486

1487

Glossary

1488 **Character:** All observable characters of an organism, including morphological, anatomical,
1489 chemical, and molecular.

1490 **Diversification:** The process that lead species to diversify; the sum of speciation and extinction
1491 events.

1492 **Evolutionary History:** The history of species evolution that links all species on Earth in a
1493 unique natural classification.

1494 **Extinction:** In its modern definition, a species is considered extinct when there is no reasonable
1495 doubt that the last individual has died.

1496 **Natural Selection:** Darwin's natural selection theory stated that the most useful variations of
1497 species in their environment (i.e., a new fitness) favored the individuals and thus persisted, and
1498 that those advantageous variations were inheritable.

1499 **Niche Complementarity:** This hypothesis states that for coexistence to occur high overlap in one
1500 dimension of the niche must be compensated by low overlap in another.

1501 **Option Value:** Biodiversity values that provide benefits and uses, often unanticipated, for future
1502 generations.

1503 **Operational Taxonomic Unit (OTU):** An operational definition used to classify groups of
1504 closely related individuals.

1505 **Phylogenetic Root:** The root represents the common ancestor to all taxa on a tree and is their
1506 oldest ancestor.

1507 **Phylogenetic Signal:** The tendency for related species to resemble each other more than they
1508 resemble species drawn at random from the phylogenetic tree.

1509 **Species:** Defined for language convention as reproductively isolated populations.

1510 **Speciation:** Lineage-splitting event that produces two or more separate species.

- 1511 **Trait:** The diversity of morphological, biochemical, behavioral, and physiological characters of
1512 species.
- 1513 **Tree of Life:** Phylogenetic tree depicting the links uniting all of the species on Earth.