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No branch left behind: tracking terrestrial biodiversity from a phylogenetic completeness perspective

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24 **Abstract**

25 Biodiversity, as we see it today, ultimately is the outcome of millions of years of evolution;
26 however, biodiversity in its multiple dimensions is changing rapidly due to increasing human
27 domination of Earth. Here, we present the “phylogenetic completeness” (PC) a concept and
28 methodology that intends to safeguard Earth’s evolutionary assets that have arisen across the tree
29 of life. We performed a global evaluation of the PC approach using data from five major
30 terrestrial clades and compared the results to an approach in which species are conserved or lost
31 randomly. We demonstrate that under PC, it is possible to maximize the protection of greater
32 evolutionary assets of each clade for a given number of species extinctions. The PC approach is
33 flexible and can be used to assess biodiversity under different conservation scenarios. The PC
34 approach complements existing conservation efforts and is linked to the post-2020 Convention of
35 Biodiversity targets.

36

37

38 **Introduction**

39 Over more than 3.5 billion years of life on Earth, evolution has generated and honed a vast array
40 of innovations represented by the diversity of forms and genomes across the tree of life.
41 Contemporary species collectively represent the genetic assets that contribute to the functioning
42 of the current biosphere, and these functions in turn serve as the foundation of Nature's
43 Contributions to People (NCP) (Díaz *et al.* 2019). Put another way, species embody evolutionary
44 innovations that represent complex and unique approaches to life on Earth. These innovations
45 not only support current NCP, but are also necessary for future benefits to humanity, including
46 those not yet discovered.

47 Phylogenetic trees depict the hierarchy of life in which species are nested in larger and
48 larger clades, each descended from a more distant common ancestor (Figure 1). They provide
49 information on the breadth and variation of innovations evolution has generated and can be used
50 to inform approaches to species conservation with the goal of minimizing extinction of
51 evolutionary innovations (Faith 2002; Larkin *et al.* 2016). Close relatives typically have a high
52 proportion of shared genetics since they arose from a common ancestor at some point in the
53 comparatively recent past, and thus share many of the same innovations.

54 A wide range of phylogenetic metrics exist that capture diversity across the tree of life
55 (Tucker *et al.* 2017) and are relevant to discerning how much variation is captured under
56 different conservation scenarios. Most metrics of phylogenetic diversity are applied to
57 phylogenetic trees and represent a sum over phylogenetic branch lengths (possibly after
58 augmentation to account for other factors, such as probability of extinction). The canonical

59 example is phylogenetic diversity (PD, *sensu* (Faith 1992)), which, for a subset of species, is
60 defined as a sum of all branch lengths required to connect those species (Faith 1992, 2002).

61 In our era of rapid biodiversity loss (Tilman *et al.* 2017; Díaz *et al.* 2019) (Tilman *et al.*
62 2017; Díaz *et al.* 2019), keeping all species—the tips of the tree of life—is not realistic, and
63 indeed is impossible given recent extinction rates (Rounsevell *et al.* 2020). However, it may still
64 be possible to conserve all branches of the tree of life, depending on how deeply we define the
65 branches. This concept is the principle behind phylogenetic completeness, a concept and
66 methodology we propose here that aims to preserve Earth’s evolutionary assets that have arisen
67 across the entire tree of life. Phylogenetic completeness (PC) and phylogenetic diversity (PD)
68 both aim to maintain as many branches as possible from the tree of life, recognizing it is not
69 possible to retain all species. But given the hierarchical nature of phylogenetic trees, how a
70 lineage is circumscribed—or what constitutes a “branch” that should be protected—can
71 influence the outcome. PC differs from PD in that it slices across the tree at a given point in
72 evolutionary history and defines a set of branches based on this cut off (Figure 1), using an
73 accounting framework, rather than merely maximizing phylogenetic breadth.

74 Here we conducted a series of analyses to explore the implications for conservation
75 depending on the depth in the tree of life where a “branch” is defined. The goal was to develop
76 and apply a framework for conservation of species that minimizes hemorrhaging of Earth’s
77 evolutionary assets, given a fixed level of species loss that is assumed to be unavoidable. We
78 then compared the loss of PD under conservation scenarios in which the set of species targeted
79 for conservation was based on an “informed” phylogenetic completeness approach or in which
80 species conserved or lost to extinction occurred randomly.

81

82 **Methods**

83 *Phylogenetic completeness (PC) approach*

84 We developed an approach in which a phylogeny is iteratively sliced at different periods of time
85 (T_N) until a specified finish time (T_F). For example, if a phylogeny is sliced every $T_N = 2$ million
86 years until $T_F = 50$ million years, a total of 25 slice points is obtained (see also Figure 1). These
87 slice points are then used to drop all but one terminal tips—or operational taxonomic units
88 (OTU)—from the phylogeny; with this approach, we ensure that at least one OTU of each
89 lineage at a specific time (T_N) is kept. In other words, by keeping at least one OTU from each
90 lineage in the tree of life, we aim to maximize the preservation of the deepest evolutionary
91 history. At each slice point (T_N) we additionally calculated the number of species (T_{SP}) and
92 phylogenetic diversity (T_{PD}) as the simple sum of branch lengths at the specific slice point (T_N).

93

94 *Empirical assessment*

95 The empirical assessment was focused on five major terrestrial clades (seed plants, amphibians,
96 squamates, birds, and mammals). Description of the data can be found in the WebPanel 1.

97 We tested the reliability of the PC approach by slicing each phylogeny every $T_N = 100$
98 Ky until $T_F = 100$ My and calculated the T_{SP} and T_{PD} at every slice point. These metrics were
99 then used to identify change points in the phylogenetic diversity over the 100 My time period.
100 Change points were evaluated using Bayesian Multiple Changing Points (MCP) regressions. The
101 first changing point plus its credible intervals (CIs) identified by the MCP analysis were used as
102 cutoff thresholds to estimate the number and identities of OTUs to be kept. This procedure
103 allowed us to identify different change points or cutoff thresholds in the phylogenetic diversity

104 over 100 My for each clade separately and consequently prevent us establishing a fixed arbitrary
105 cutoff threshold (e.g., setting a changing point at 2 My as cutoff threshold) for all clades.

106 We compared the diversity in each clade for a PC conservation scenario, in which species
107 were managed to maintain all phylogenetic branches to random losses (RDM). In other words,
108 we removed OTUs at random until the identified cutoff threshold for each clade separately. This
109 procedure was repeated 1000 times, and at each step the T_{SP} and T_{PD} were estimated.

110 Finally, using the OTUs identities from both the PC and the random loss scenarios we
111 mapped the phylogenetic diversity of seed plants and terrestrial vertebrates globally. These maps
112 were used to estimate the difference (ΔPD) between the observed PD (PD_{OBS}) and the expected
113 PD (PD_{EXP}) under either the phylogenetic completeness (PD_{PC}) and the random loss approach
114 (PD_{RDM}).

$$115 \quad \Delta PD = \frac{PD_{EXP} - PD_{OBS}}{PD_{OBS}} \times 100$$

116 These maps represent the proportional difference between the observed (PD_{OBS}) and
117 expected (PD_{PC} or PD_{RDM}) phylogenetic diversity, where negative values suggest that a grid cell
118 will lose a proportion of its PD according to a specific conservation scenario, e.g., under the PC
119 scenario. Note that the lower CI from the Bayesian MCP regressions were used as variable cutoff
120 thresholds for each clade for mapping purposes.

121

122 *Protected areas assessment*

123 We were also interested in evaluating the role of protected areas (PAs) in protecting the
124 evolutionary history of terrestrial biodiversity. To do so, we overlaid the PAs with the
125 vertebrate and seed plants PAMs to obtain the presence-absence of species within the PAs
126 (PAM_{PA}) globally (WebPanel 1). These PAM_{PA} were then used to estimate the number of

127 species and phylogenetic diversity within each PA. Using this information, we estimate and map
128 the ΔPD between the observed PD (PD_{OBS}) and the PD within PAs (PD_{PA}). The resulting maps
129 show how much evolutionary history are currently protected within the PAs.

130

131 **Results**

132 *Phylogenetic completeness*

133 Bayesian MCP models revealed variable cutoff thresholds for each clade (Figure 2; WebTable
134 1). Based on these thresholds, losses of species ranging from 1.34% to 18.11% are estimated to
135 occur in each of the major clades (seed plants, amphibians, squamates, birds, and mammals)
136 (WebTable 1) while still safeguarding between 97.27% to 99.97% of the phylogenetic
137 diversity—i.e., of the evolutionary history of each clade (WebTable 1; Figure 2). If the lower
138 credible interval (LCI) of our Bayesian model estimates were used to define the phylogenetic
139 branches to be conserved (Figure 2; WebTable 1), a higher number of species and branches in
140 the tree of life would be safeguarded (Table 1).

141 These analyses demonstrate that if conservation efforts are focused on maintaining
142 defined branches of the tree of life it is possible to maximize the accumulated evolutionary
143 innovations that are safeguarded across all clades even when individual species go extinct.
144 Figure 3 shows the comparison between the estimates of PD under both phylogenetic
145 completeness (PC) and random loss (RDM) scenarios. Under PC, a higher number of branches
146 (Table 1) and greater evolutionary history in each clade is preserved for a given number of
147 species extinctions (Figure 3).

148 Spatial patterns of ΔPD under PC and RDM scenarios (Figure 4; WebFigure 1), show
149 how conservation informed by PC safeguards a greater proportion of evolutionary history even

150 with the same number of species extinctions. For example, for seed plants in tropical regions
151 across the world, conservation informed by PC resulted in PD loss below 10%, whereas the
152 RDM scenario resulted in 10-20 % of PD loss. Extinction patterns of terrestrial biodiversity
153 under PC and RDM scenarios at the biome level (WebFigure 2) also show greater preservation
154 of accumulated evolutionary innovations when conservation is targeted to maintain branches of
155 the tree of life. Nevertheless, we find that Tundra and Taiga biomes are susceptible to high losses
156 in PD, especially for seed plants, birds, and mammals, even under PC scenarios. In contrast,
157 tropical biomes (for both forest and grasslands) show limited losses in PD for the same threshold
158 values used to define branches, as in Tundra and Taiga biomes (WebFigure 2). These results
159 indicate that for the a given number of species extinctions, tropical biomes will lose fewer
160 branches of the tree of life and are thus less susceptible to loss of evolutionary history.

161

162 *Protected areas assessment*

163 The currently implemented PAs across the world cover an area of approximately 26,775,820
164 km²—~18% of the land surface. Collectively, ~97% of the species in our dataset overlap their
165 ranges with the system of PAs globally (Table 2). Although the proportion of likely protected
166 species is high, a large proportion of the Earth’s land surface, and thus most of the ranges of
167 most of these species, is not protected (Figure 4; WebFigure 3) and is threatened by land use
168 change and other human activities.

169

170 **Discussion**

171 Our “phylogenetic completeness” framework for informing biodiversity conservation focuses on
172 maintaining the accumulated evolutionary innovations across the tree of life with the intent of

173 leaving no branch behind. We introduce a rigorous approach for defining branches across clades
174 of terrestrial organisms to ascertain where in the tree of life there is high evolutionary
175 redundancy and where a single species may represent an entire branch. In doing so, we establish
176 phylogenetic branches as units of conservation priority. By defining these branches and the
177 species contained within them, the phylogenetic completeness approach provides critical
178 information on branches at risk of extinction where there is low redundancy as well as flexibility
179 in which species can targeted for conservation in cases of high redundancy. The approach is
180 particularly useful in developing conservation priorities in relation to protected areas by tracking
181 which branches of the tree of life are currently safeguarded and by identifying the branches that
182 are at highest risk—those not currently protected or with the least amount of their range
183 protected. This approach is consistent with the Convention on Biodiversity draft Milestone A.2,
184 that *the increase in the extinction rate is halted or reversed, and the extinction risk is reduced by*
185 *at least 10 per cent, with a decrease in the proportion of species that are threatened, and the*
186 *abundance and distribution of populations of species is enhanced or at least maintained*. Yet it
187 also captures elements of diversity not delineated by the CBD by accounting for the breadth of
188 evolved variation in plant and vertebrate-animal life.

189 Increasing human domination of Earth and its ecosystems is rapidly changing
190 biodiversity patterns and negatively impacting the capacity of ecosystems to provide goods and
191 services to humanity (Tilman *et al.* 2017; Díaz *et al.* 2019). Safeguarding all remaining
192 biodiversity, although desirable, is unrealistic on the basis of virtually all projections (Pimm *et*
193 *al.* 2014; Urban 2015; Tilman *et al.* 2017); the footprint of humanity is currently too large to
194 completely avoid further extinctions. Scientists have recognized the challenge of developing
195 logical conservation solutions given the complexity of stakeholders, managers, and indirect

196 actors as a ‘wicked problem’ that has no straightforward solution (Vane-Wright *et al.* 1991;
197 DeFries and Nagendra 2017). Focusing on the conservation of evolutionary history has been
198 hailed as an integrative way to safeguard most of the biodiversity and its functions (Faith 1992;
199 Mooers 2007). For example, a recent study by Molina-Venegas and collaborators (Molina-
200 Venegas *et al.* 2021) (Molina-Venegas *et al.* 2021) found strong evidence that plant evolutionary
201 history is tightly linked to multiple plant use categories and therefore to human well-being
202 (Molina-Venegas *et al.* 2021). These findings, among others, support the idea that conserving
203 evolutionary history is critical for future human well-being (Forest *et al.* 2007; Molina-Venegas
204 *et al.* 2021).

205 Multiple approaches have been proposed to assess changes in biodiversity focusing on
206 “hotspot” areas (spatial prioritization), or taxa (taxonomic prioritization) for conservation
207 purposes (Margules and Sarkar 2007). These approaches rely on the use of metrics that capture
208 different dimensions of biodiversity, e.g., metrics that capture evolutionary changes among a set
209 of taxa (Margules and Sarkar 2007) or the variation in form and function of taxa within
210 communities (Díaz and Cabido 2001; Petchey and Gaston 2006). Despite their usefulness for
211 assessing the state and the fate of biodiversity, most of these metrics, if not all, are sensitive to
212 information completeness. Missing information can result in misleading metric calculations and
213 inappropriate interpretations of spatial or taxonomic comparisons (e.g., Weedop *et al.* 2019). The
214 PC framework introduced here represents a complementary approach to counting numbers of
215 species or comparing levels of phylogenetic diversity to assess biodiversity under alternative
216 conservation scenarios. It provides an accounting framework that prioritizes conservation of
217 branches of the tree of life rather than individual species (Table 1; Figure 2). It also allows the
218 identification of areas susceptible to high losses of evolutionary assets (Figure 4; WebFigure 1),

219 which can be used as baseline information for spatial prioritization, providing a broader context
220 for local decision making (Chaplin-Kramer *et al.* 2022). Moreover, in the context of spatial
221 prioritization, the PC framework may be less susceptible to missing data given that it focuses on
222 the branches of the tree of life. To illustrate this point, if we consider protecting at least one
223 descendant taxon from a specific node in the phylogeny, this taxon contains genetic information
224 that captures most of the evolutionary history of the entire branch (see Figure 1). If species
225 within the branch have not yet been identified or are not readily observed, the branch itself is still
226 preserved, with the caveat that phylogenetic information remains imperfect.

227 Substantial efforts have been invested to prevent the extinction of biodiversity. In
228 particular, the establishment, expansion, and enhancement of protected areas (PAs) have
229 received considerable attention due to their critical role in protecting Earth's biodiversity and
230 preventing the erosion of its benefits to humans (Naughton-Treves *et al.* 2005; Watson *et al.*
231 2014). Despite important progress in establishing terrestrial PAs around the world (Table 2),
232 several critical areas are still unprotected, leaving many branches of the tree of life vulnerable to
233 extinction (Figure 4; WebFigure 3). Note that in our evaluation we used the species presence
234 within current PAs to estimate which species are less vulnerable to extinction for the purposes of
235 deciphering which branches of the tree of life are most at risk. We thus assume that species not
236 present in PAs are the most vulnerable to extinction and in greatest need of conservation or
237 assistance.

238 At high latitudes (tundra) an individual species frequently represents an entire
239 phylogenetic branch while at low latitudes (tropics), a branch is likely to contain many species.
240 This pattern is largely the consequence of more recent divergence times and higher speciation
241 rates in the tropics. However, the spatial scale (grain size) must also be considered, for example,

242 one hectare in a tropical forest can hold ~650 tree species more than all tree species that occur at
243 high latitudes (Coley and Kursar 2014). Despite this high diversity, tropical forests are usually
244 hyperdominated by a fraction of species (~1.4% of about 16,000 tree species estimated for the
245 Amazonian Forest are considered as hyperdominant) that are specialists to their habitats and
246 have large geographical ranges (ter Steege *et al.* 2013). The less abundant species or poorly
247 known species with small geographical ranges are potentially threatened. Although it is beyond
248 the scope of this article, PC evaluations at local and regional scales could help to identify which
249 species may be prioritized to prevent losing branches of the tree of life at local and regional
250 scales.

251 Furthermore, the combined effects of climate and land-use changes are likely to limit the
252 role of PAs in safeguarding biodiversity (Hoffmann *et al.* 2019; Asamoah *et al.* 2021). About
253 one-quarter of the PAs globally are projected to suffer rapid climate change, with small PAs
254 being the most impacted (Hoffmann *et al.* 2019; Asamoah *et al.* 2021). Advancing projections of
255 combined limits to species tolerance to climate change and migration capability without
256 assistance could be oriented towards understanding which branches of the tree of life currently
257 protected are most likely to be lost. Doing so, could help inform costly efforts to establish
258 corridors for movement within human-dominated landscapes (Gibson *et al.* 2011; Wintle *et al.*
259 2019) and assisted migration plans to target the protection of species that maintain all the
260 branches of the tree of life.

261

262 **Conclusion**

263 In our era of rapid global change and rapid biodiversity loss, conservation efforts must reckon
264 with the reality that we will not succeed in saving all species on Earth. We outline an approach

265 for conservation, which we call phylogenetic completeness, that focuses on saving the
266 accumulated innovations that have evolved in Earth's biota by counting individual branches in
267 the tree of life as units of conservation priority. The approach benefits from detailed information
268 of the tree of life that is only now sufficiently resolved to be applicable to all of life on Earth.
269 The approach complements other conservation efforts and is directly relevant to the targets of the
270 post-2020 Convention of Biodiversity.

271

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277

278 **Statement of Authorship**

279 All authors contributed intellectually to the manuscript. J.C.-B. and J.N.P.-L. conceived of and
280 framed the manuscript. J.N.P.-L. performed all the statistical and spatial analyses with input from
281 J.C.-B. All authors edited the manuscript.

282

283 **Open Research**

284 *Data Availability Statement*

285 All data used in this manuscript are publicly available. Main sources are provided in the
286 WebPanel 1. R functions and examples for data analyses are publicly available at
287 <https://github.com/jesusNPL/FITBITS>.

288

289 **References**

290

291 Asamoah EF, Beaumont LJ, and Maina JM. 2021. Climate and land-use changes reduce the
292 benefits of terrestrial protected areas. *Nat Clim Chang* **11**: 1105–10.

293 Chaplin-Kramer R, Brauman KA, Cavender-Bares J, *et al.* 2022. Conservation needs to integrate
294 knowledge across scales. *Nat Ecol Evol* **6**: 118–9.

295 Coley PD and Kursar TA. 2014. On Tropical Forests and Their Pests. *Science* **343**: 35–6.

296 DeFries R and Nagendra H. 2017. Ecosystem management as a wicked problem. *Science* **356**:
297 265–70.

298 Díaz S, Settele J, Brondízio ES, *et al.* 2019. Pervasive human-driven decline of life on Earth
299 points to the need for transformative change. *Science* **366**: eaax3100.

300 Díaz S and Cabido M. 2001. Vive la différence: plant functional diversity matters to ecosystem
301 processes. *Trends in Ecology & Evolution* **16**: 646–55.

302 Faith DP. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation*
303 **61**: 1–10.

304 Faith DP. 2002. Quantifying Biodiversity: a Phylogenetic Perspective. *Conservation Biology* **16**:
305 248–52.

306 Forest F, Grenyer R, Rouget M, *et al.* 2007. Preserving the evolutionary potential of floras in
307 biodiversity hotspots. *Nature* **445**: 757–60.

- 308 Gibson L, Lee TM, Koh LP, *et al.* 2011. Primary forests are irreplaceable for sustaining tropical
309 biodiversity. *Nature* **478**: 378–81.
- 310 Hoffmann S, Irl SDH, and Beierkuhnlein C. 2019. Predicted climate shifts within terrestrial
311 protected areas worldwide. *Nat Commun* **10**: 4787.
- 312 Larkin DJ, Jacobi SK, Hipp AL, and Kramer AT. 2016. Keeping All the PIECES:
313 Phylogenetically Informed Ex Situ Conservation of Endangered Species (N Cellinese,
314 Ed). *PLoS ONE* **11**: e0156973.
- 315 Margules CR and Sarkar S. 2007. Systematic conservation planning. Cambridge ; New York:
316 Cambridge University Press.
- 317 Molina-Venegas R, Rodríguez MÁ, Pardo-de-Santayana M, *et al.* 2021. Maximum levels of
318 global phylogenetic diversity efficiently capture plant services for humankind. *Nat Ecol*
319 *Evol* **5**: 583–8.
- 320 Mooers AØ. 2007. The diversity of biodiversity. *Nature* **445**: 717–8.
- 321 Naughton-Treves L, Holland MB, and Brandon K. 2005. THE ROLE OF PROTECTED AREAS
322 IN CONSERVING BIODIVERSITY AND SUSTAINING LOCAL LIVELIHOODS.
323 *Annu Rev Environ Resour* **30**: 219–52.
- 324 Petchey OL and Gaston KJ. 2006. Functional diversity: back to basics and looking forward. *Ecol*
325 *Letters* **9**: 741–58.
- 326 Pimm SL, Jenkins CN, Abell R, *et al.* 2014. The biodiversity of species and their rates of
327 extinction, distribution, and protection. *Science* **344**: 1246752.

- 328 Rounsevell MDA, Harfoot M, Harrison PA, *et al.* 2020. A biodiversity target based on species
329 extinctions. *Science* **368**: 1193–5.
- 330 Steege H ter, Pitman NCA, Sabatier D, *et al.* 2013. Hyperdominance in the Amazonian Tree
331 Flora. *Science* **342**: 1243092.
- 332 Tilman D, Clark M, Williams DR, *et al.* 2017. Future threats to biodiversity and pathways to
333 their prevention. *Nature* **546**: 73–81.
- 334 Tucker CM, Cadotte MW, Carvalho SB, *et al.* 2017. A guide to phylogenetic metrics for
335 conservation, community ecology and macroecology: A guide to phylogenetic metrics for
336 ecology. *Biol Rev* **92**: 698–715.
- 337 Urban MC. 2015. Accelerating extinction risk from climate change. *Science* **348**: 571–3.
- 338 Vane-Wright RI, Humphries CJ, and Williams PH. 1991. What to protect?—Systematics and the
339 agony of choice. *Biological Conservation* **55**: 235–54.
- 340 Watson JEM, Dudley N, Segan DB, and Hockings M. 2014. The performance and potential of
341 protected areas. *Nature* **515**: 67–73.
- 342 Weedop KB, Mooers AØ, Tucker CM, and Pearse WD. 2019. The effect of phylogenetic
343 uncertainty and imputation on EDGE Scores. *Anim Conserv* **22**: 527–36.
- 344 Wintle BA, Kujala H, Whitehead A, *et al.* 2019. Global synthesis of conservation studies reveals
345 the importance of small habitat patches for biodiversity. *Proc Natl Acad Sci USA* **116**:
346 909–14.
- 347

348 **Tables**

349

350 Table 1. Number of branches (NB) conserved under the scenarios of phylogenetic completeness
351 (PC) and random loss (RDM) conservation scenarios. The number of branches conserved under
352 the phylogenetic completeness approach is higher than the random loss scenario for the same
353 number of species except for birds and mammals. Percentages of NB under PC and RDM
354 scenarios are displayed within brackets. Number of branches for all species within a clade
355 assuming no extinction is displayed for reference. The number of species under PC/RDM
356 correspond to the number of species at the minimum threshold (lower credible interval)
357 identified using the Bayesian MCP regressions. Note that the observed number of species
358 (second column) corresponds to the number of species sampled in each phylogenetic tree and
359 might not represent each clade's true number of species.

360

Clade	Observed N species	PC/RDM N species	Threshold (My)	NB all species	NB-PC	NB-RDM
Seed plants	353185	312540	1.76	438863	397974 [90.68%]	391851 [89.29%]
Amphibians	7238	5927	4.43	14474	12614 [87.15%]	11852 [81.88%]
Squamata	9755	8141	2.61	19508	17186 [88.10%]	16280 [83.45%]
Birds	9993	9859	0.33	19984	19716 [98.66%]	19716 [98.66%]
Mammals	5911	5802	0.31	11820	11602 [98.16%]	11602 [98.16%]

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363

364 Table 2. Summary of terrestrial biodiversity within protected areas. Table summarizes the
365 number and percentage of species currently protected in protected areas. Our estimations of
366 %protected and % of loss are based on the number of species available in the geographical
367 ranges and phylogenetic datasets (see methods). Note that the number of seed plant species with
368 available geographic ranges is 207,146, so the estimations of %protected and % of loss may be
369 underestimated. The observed number of species (second column) corresponds to the number of
370 species sampled in each phylogenetic tree and might not represent each clade's true number of
371 species.

372

Clade	Observed N species	WPA N species	%Protected	%Loss
Seed plants	353,185	191,830	92.61	7.39
Amphibians	7,238	6,630	91.60	8.40
Squamata	9,755	8,872	90.95	9.05
Birds	9,993	9,710	97.17	2.83
Mammals	5,911	5,661	95.77	4.23

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375

376 **Figure legends**

377 Figure 1. Schematic diagram of the phylogenetic relationships of species within a lineage of
378 organisms, showing the hierarchical nesting of hypothetical species. The number of species that
379 need to be conserved in order to prevent the extinction of any branches in the tree depends on the
380 depth in the phylogeny we define the branch. Dashed lines represent different ages (T_N) or
381 depths in the phylogeny used to define branches—the corresponding number of species
382 preserved (T_{SP}), if one species per branch is conserved, is colored the same as the dashed line.
383 For example, purple circles (fewer branches and species with a deep slice at T_{N3}) to red ones
384 (more branches and species with a more recent slice at T_{N1}). The deeper we “slice” the
385 phylogeny, the fewer the species need to be saved in order to preserve all branches of the
386 phylogeny at that slice. Black circles represent species at T_{N0} , i.e., the current species, assuming
387 no extinction. Open circles filled with “x” indicate species that went extinct at a specific T_N .

388

389 Figure 2. Changes in the phylogenetic diversity and number of species over 100 million years for
390 terrestrial biodiversity, including seed plants (A), woody plants (B), amphibians (C), squamates
391 (D), birds (E), and mammals (F). Black dashed vertical lines represent the first changing point
392 identified by the Bayesian Multiple Changing Points (MCP) regressions. Black dotted vertical
393 lines represent the 95 credible intervals. Red long-dashed horizontal lines represent the observed
394 number of species for each clade. Red dashed horizontal lines are the number of species expected
395 under the first changing point. Red dotted horizontal lines represent the expected number of
396 species under the lower bound (or credible interval) of the first changing point. See WebTable 1

397 for a comprehensive numerical summary of the changing points. Silhouettes obtained from
398 Phylopic (<http://phylopic.org>).

399

400 Figure 3. Difference between the remaining phylogenetic diversity under phylogenetic
401 completeness (red) and random loss (green) scenarios. X-axis was log-transformed for plotting
402 purposes. In all cases, the phylogenetic diversity is higher for the phylogenetic completeness
403 approach.

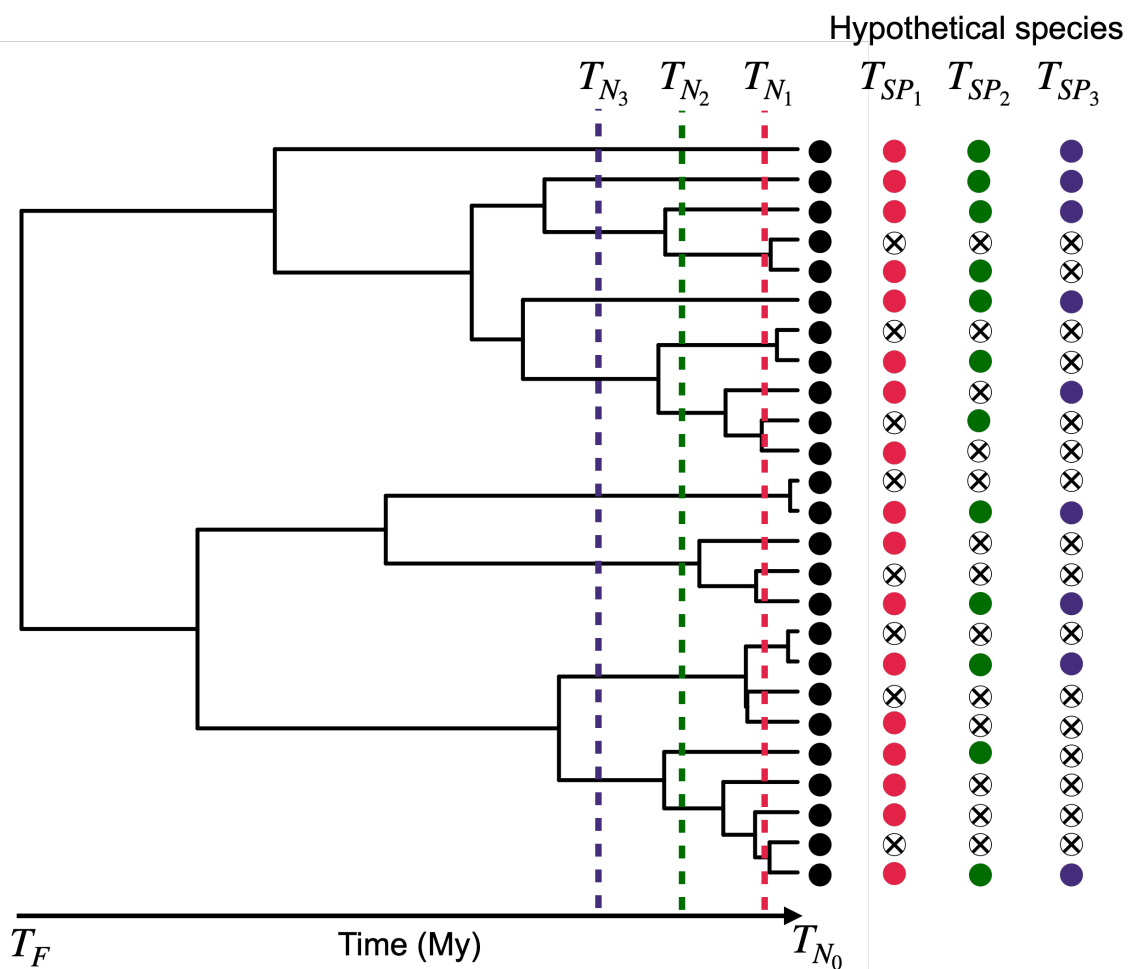
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405 Figure 4. Mapped phylogenetic diversity for seed plants (A-B) and birds (D-E) globally under
406 scenarios of phylogenetic completeness and random loss. Legends indicate the proportional loss
407 of phylogenetic diversity (ΔPD). Blue tones indicate that more branches of the tree of life have
408 been preserved and red tones that more branches have been lost. Comparing the two scenarios,
409 globally more branches of the tree of life are conserved in the phylogenetic completeness
410 scenario for the same number of vertebrate species extinctions. Bottom panels (C and F) show
411 the differences in phylogenetic diversity (ΔPD) in 1° grid cells between the species currently
412 estimated to occur in those cells and the fraction of those estimated to occur in protected areas
413 globally. Red colors represent greater ΔPD , meaning more branches of the tree of life are not
414 currently protected. Continental China is shaded gray given that protected area information is
415 currently unavailable in the WDPA for this country. Maps for amphibians, squamates, and
416 mammals can be found in the supplementary material.

417

418 **Figures**

419 Figure 1



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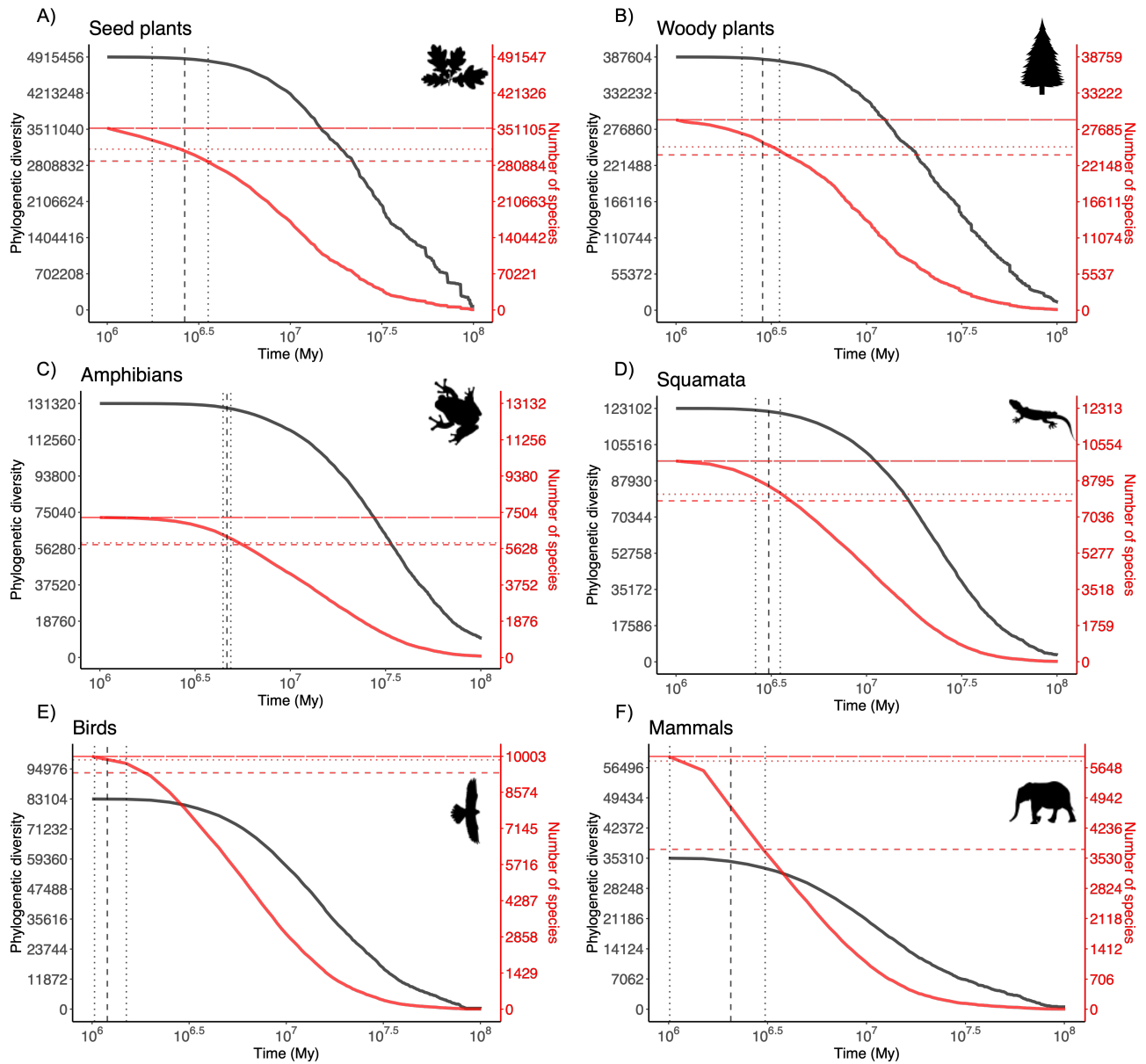
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423 Figure 2

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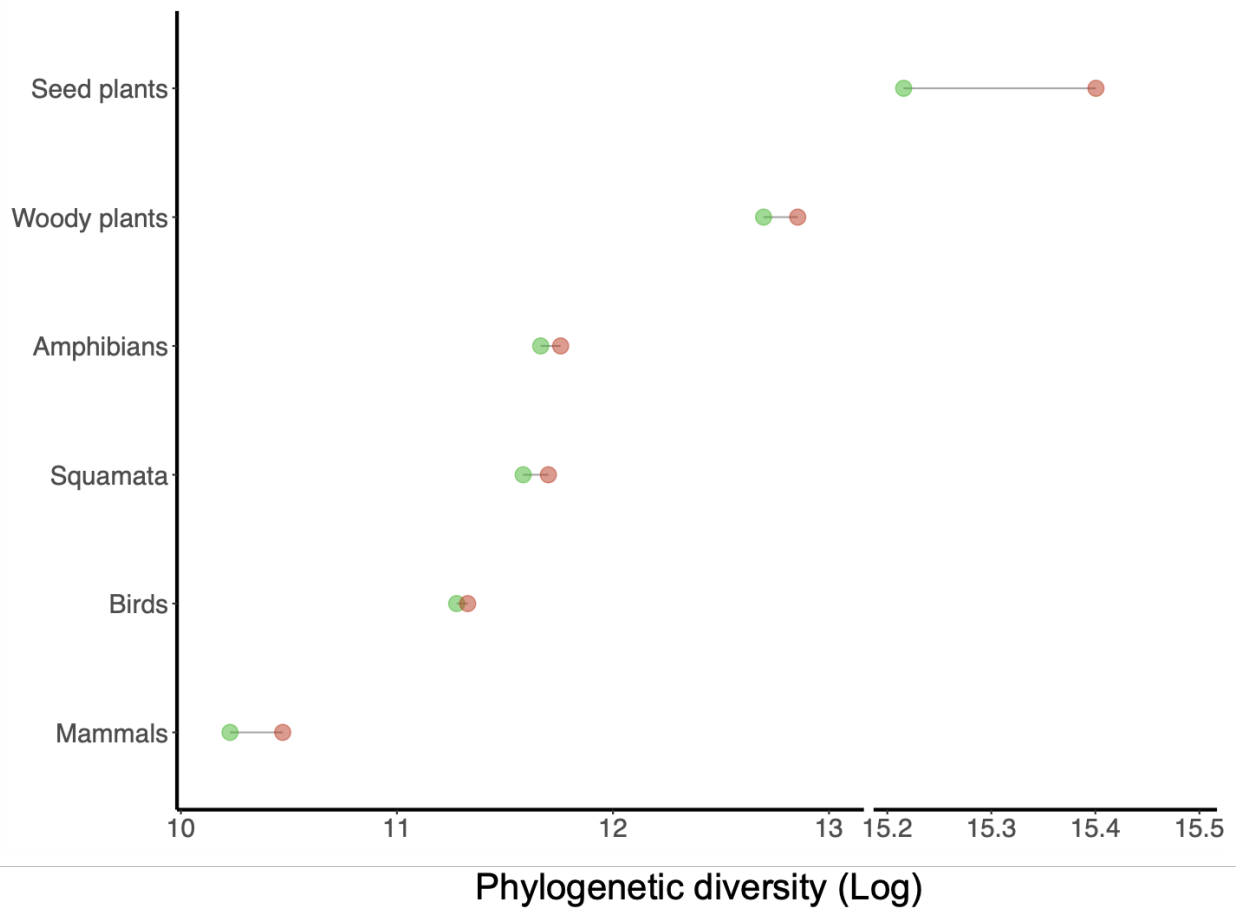
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429 Figure 3

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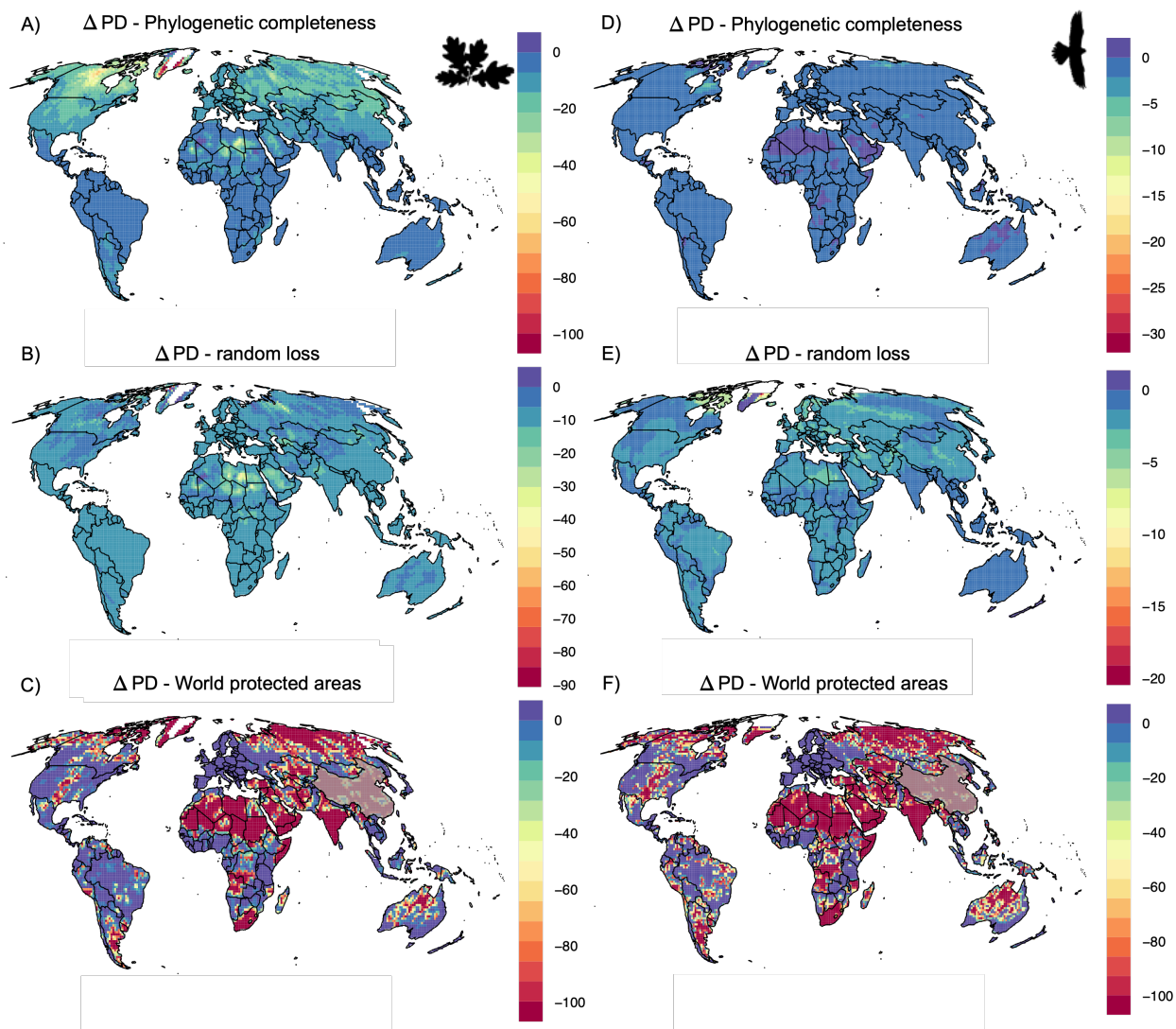


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433 Figure 4

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