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

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Abstract

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

Introduction

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

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

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

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

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

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

Methods

Phylogenetic completeness (PC) approach

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

Empirical assessment

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

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

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 overlayed 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

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

Results

Phylogenetic completeness

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

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

Spatial patterns of ΔPD under PC and RDM scenarios (Figure 4; WebFigure 1), show 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 km—~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

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

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

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

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Statement of Authorship

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

Open Research

Data Availability Statement

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

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Tables

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

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%]

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

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

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.
404
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

Figures

Figure 1

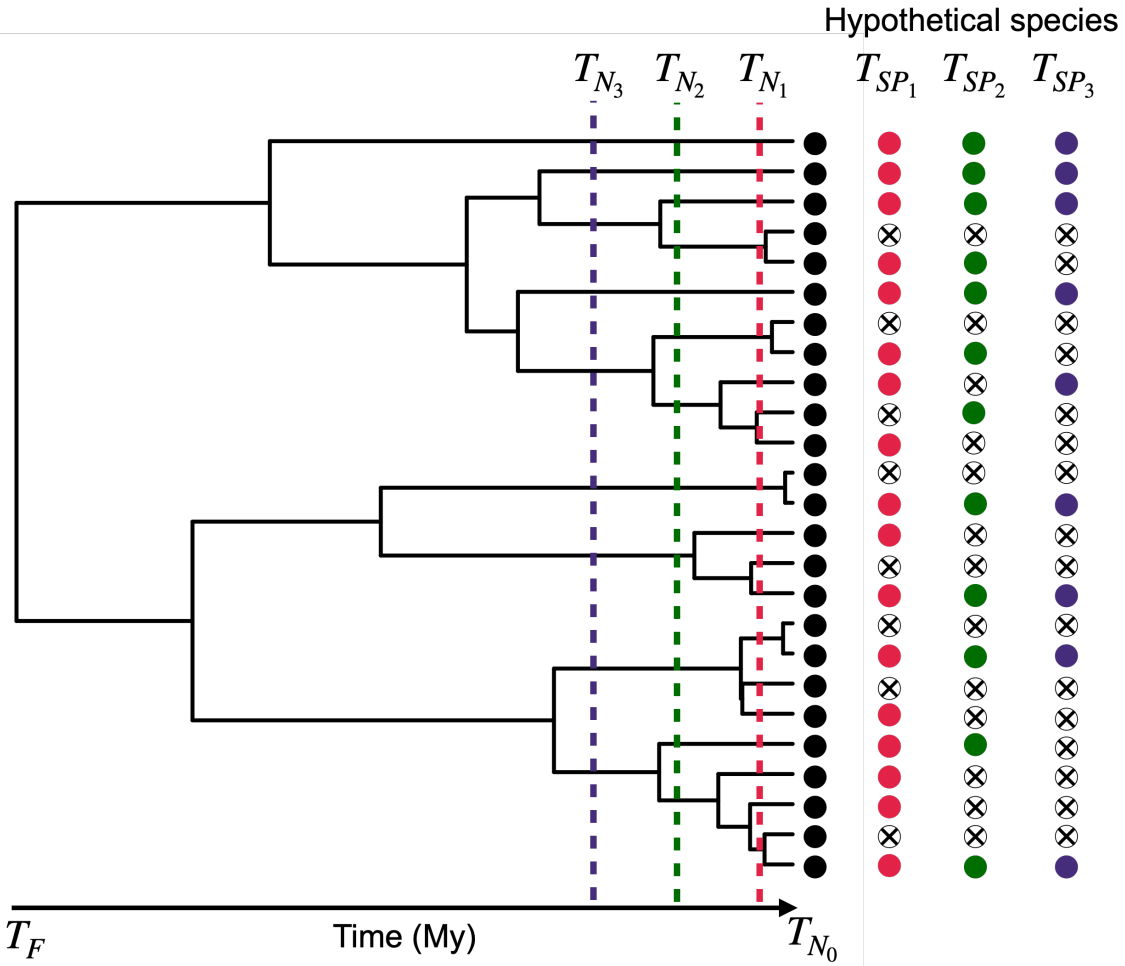
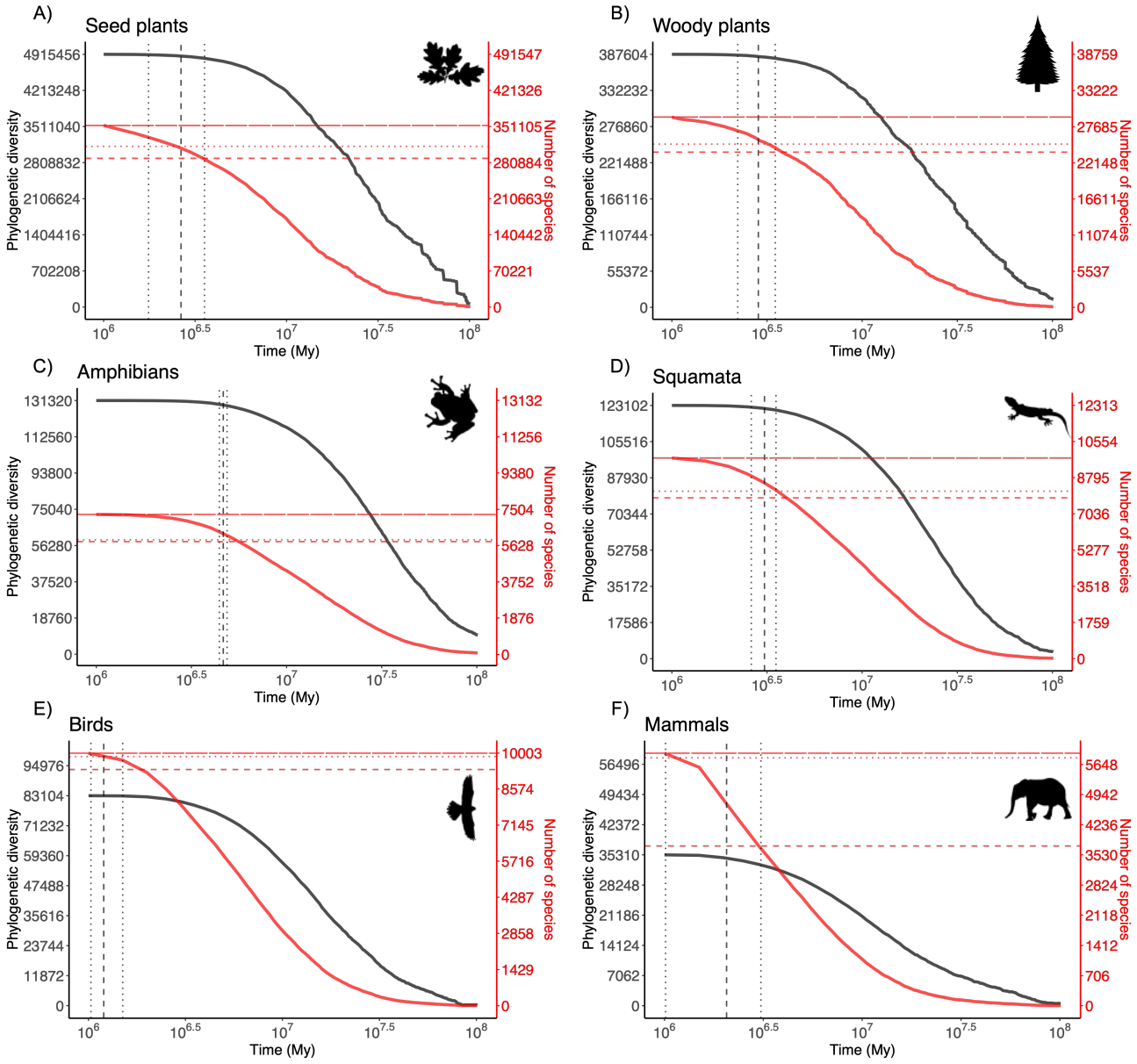
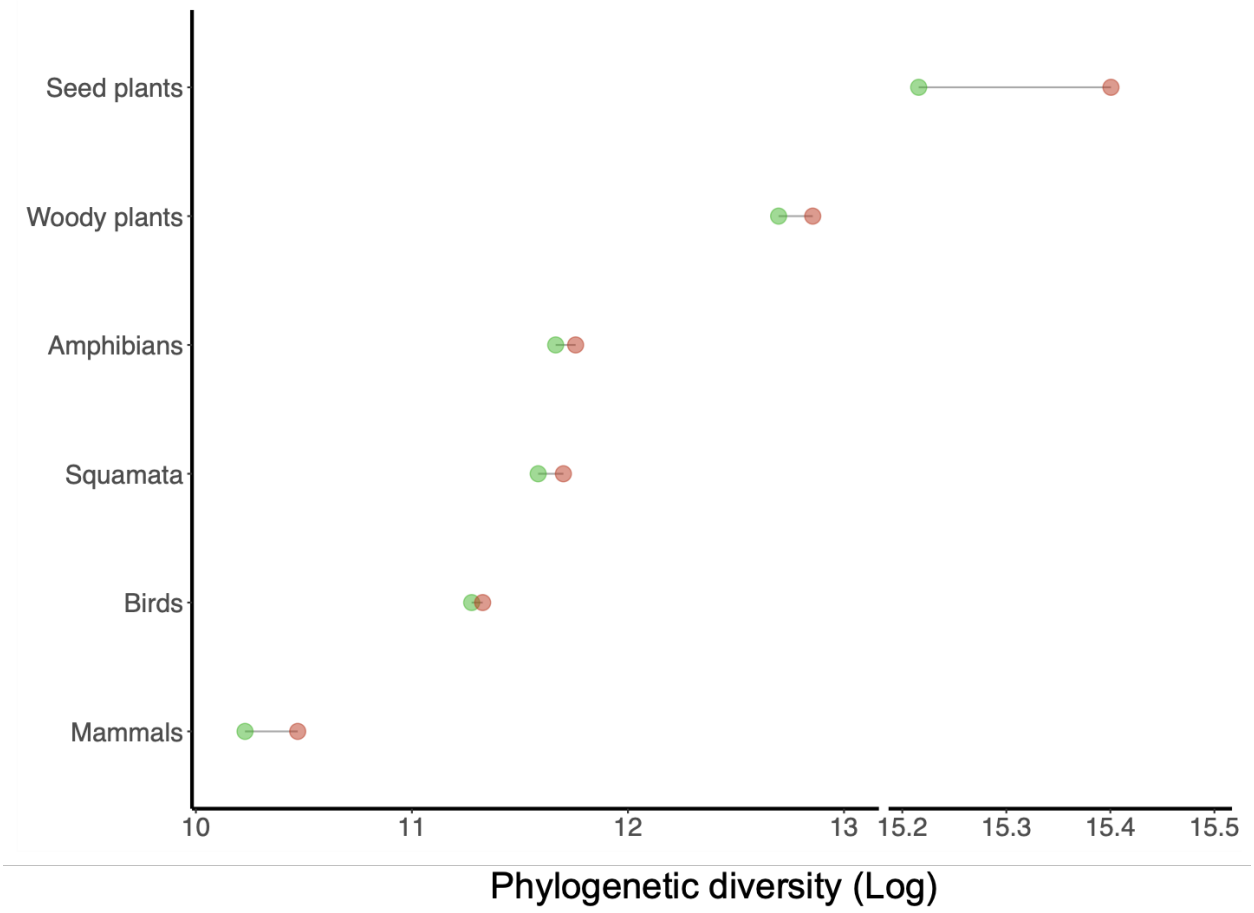


Figure 2


A)
Seed plants
Phylogenetic diversity
4915456
4213248
3511040
2808832
2106624
1404416
702208
0
Number of species
491547
421326
351105
280884
210663
140442
70221
0
Time (My)
B)
Woody plants
387604
332232
276860
221488
166116
110744
55372
0
38759
33222
27685
22148
16611
11074
5537
0
C)
Amphibians
131320
112560
93800
75040
56280
37520
18760
0
13132
11256
9380
7504
5628
3752
1876
0
D)
Squamata
123102
105516
87930
70344
52758
35172
17586
0
12313
10554
8795
7036
5277
3518
1759
0
E)
Birds
94976
83104
71232
59360
47488
35616
23744
11872
0
10003
8574
7145
5716
4287
2858
1429
0
F)
Mammals
56496
49434
42372
35310
28248
21186
14124
7062
0
5648
4942
4236
3530
2824
2118
1412
706
0

429 Figure 3

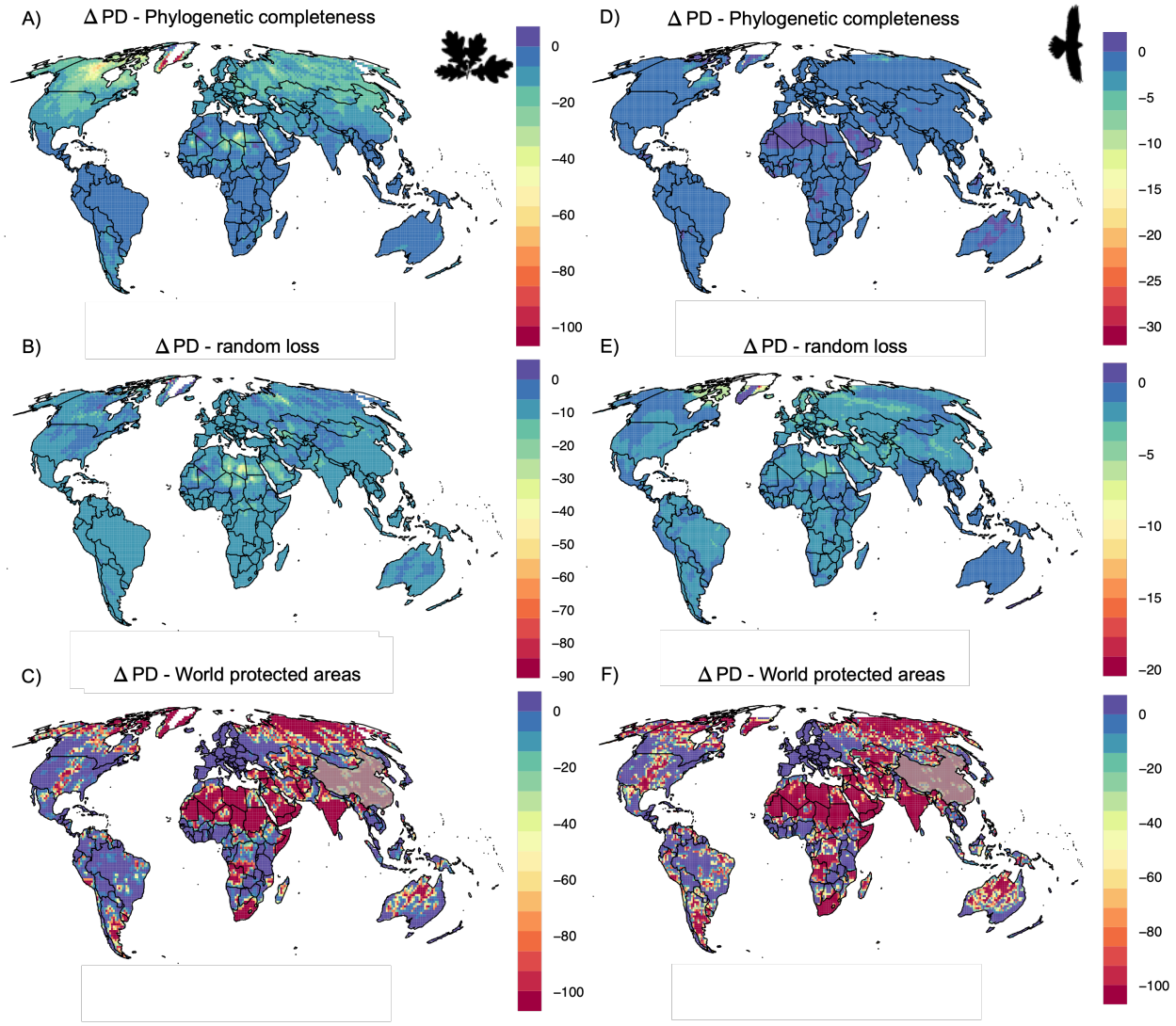
430



431

432

Figure 4


A)
Δ PD - Phylogenetic completeness
0
−20
−40
−60
−80
−100
B)
Δ PD - random loss
0
−10
−20
−30
−40
−50
−60
−70
−80
−90
C)
Δ PD - World protected areas
0
−20
−40
−60
−80
−100
D)
Δ PD - Phylogenetic completeness
0
−5
−10
−15
−20
−25
−30
E)
Δ PD - random loss
0
−5
−10
−15
−20
F)
Δ PD - World protected areas
0
−20
−40
−60
−80
−100