

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

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Biodiversity is ultimately the outcome of millions of years of evolution; however, due to increasing human domination of the Earth, biodiversity in its multiple dimensions is changing rapidly. Here, we present “phylogenetic completeness” (PC) as a concept and method for safeguarding Earth’s evolutionary heritage by maintaining all branches of the tree of life. Using data for five major terrestrial clades, we performed a global evaluation of the PC approach and compared the results to an approach in which species are conserved or lost at random. We demonstrate that under PC, for a given number of species extinctions, it is possible to maximize the protection of evolutionary innovations in every clade. The PC approach is flexible, may be used to conduct a phylogenetic audit of biodiversity under different conservation scenarios, complements existing conservation efforts, and is linked to the post-2020 UN Convention on Biodiversity targets.

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For 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 genomes and forms 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: innovations that not only support current NCP but are also necessary for future benefits to humanity, including those yet to be 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 that evolution has generated and can be used to inform approaches to species conservation with the goal of minimizing extinction of evolutionary innovations (Faith 2002; Mace *et al.* 2003; Diniz-Filho *et al.* 2013; Larkin *et al.* 2016). Close relatives typically have a high proportion of shared genetics because 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 evolutionary-based metrics of diversity are applied to community or regional phylogenies and represent different amounts of shared ancestry between taxa (sometimes accounting for other factors, such as probability of extinction). The canonical example is “phylogenetic diversity” (PD; Faith 1992), which, for a subset of species, is defined as the sum of all branch lengths required to connect those species or the total amount of evolutionary history contained by those species (Faith 1992, 2002). Since its introduction in 1992, PD has been used in ecological and

In a nutshell:

- In an era of rapid global change and biodiversity loss, conservation efforts face the reality that saving all species on Earth is a monumental challenge
- We propose the “phylogenetic completeness” (PC) framework for informing biodiversity conservation that focuses on maintaining the accumulated evolutionary innovations across the tree of life
- Using five major terrestrial clades (seed plants, amphibians, squamates, birds, and mammals), a global evaluation reveals that more than 97% of evolutionary heritage can be safeguarded under the PC conservation scenario

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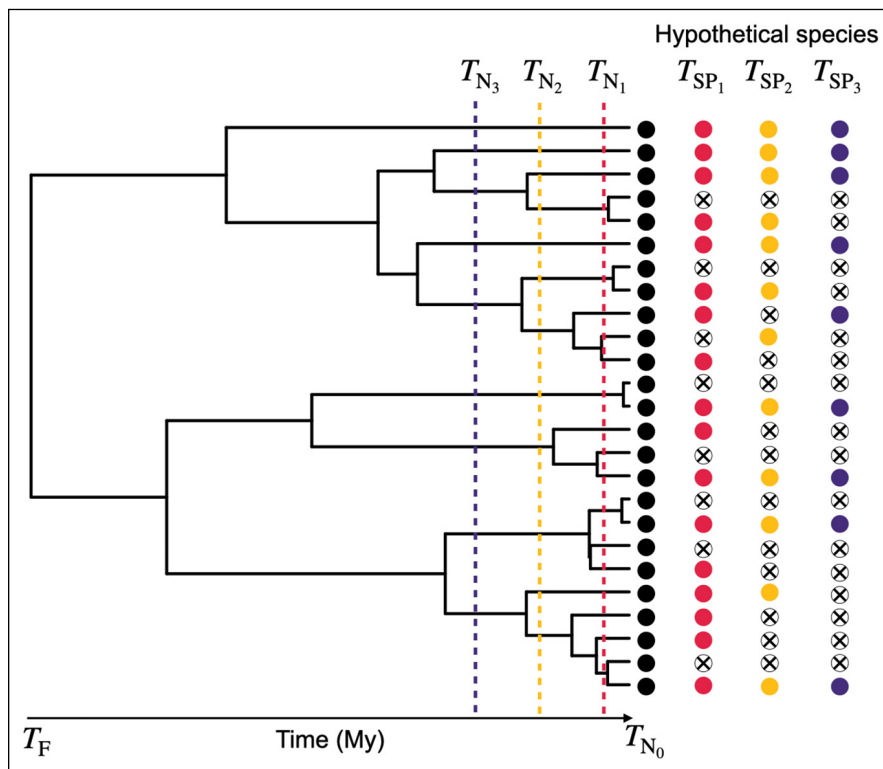


Figure 1. Schematic diagram of the phylogenetic relationships of species within a lineage, showing the hierarchical nesting of hypothetical species. The number of preserved species required to prevent the extinction of any branches in the tree depends on the depth in the phylogeny where the branch is defined. Dashed vertical lines represent different ages (T_N), or depths in the phylogeny, used to define branches: the number of species preserved (T_{SP}), if one species per branch is conserved, is colored the same as the dashed line. Solid black circles represent species at T_{N_0} . Circles with an “x” indicate extinct species at a specific T_N . My = million years. T_F = finish time.

conservation studies as a measure of biodiversity that captures information about the number of accumulated features in the branches of the tree of life (Scherson and Faith 2018).

In the current era of rapid biodiversity loss (Tilman *et al.* 2017; Díaz *et al.* 2019; IPBES 2019), retaining all species—the tips of the tree of life—is not realistic, and indeed is practically unfeasible given recent extinction rates (Crozier 1997; Rounsevell *et al.* 2020). However, it may still be possible to conserve most of the branches of the tree of life, assuming it is possible to meaningfully define those branches (Figure 1). This notion is the principle behind “phylogenetic completeness” (PC), a concept and method we propose here that aims to preserve Earth’s evolutionary heritage (Mooers *et al.* 2005) by maintaining all branches across the tree of life. The approach aims to facilitate a phylogenetic audit of biodiversity. The central goal is to track all of life’s variation that has arisen over the course of evolution, and that still remains, in both early diverged lineages and recently derived lineages in each of the major living clades and across the entire tree of life. The underlying goal of both PC and PD is to maintain as many branches as possible from the tree of life, recognizing that 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 (Vane-Wright *et al.* 1991; Diniz-Filho *et al.* 2013; Scherson and Faith 2018). 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 cutoff (Figure 1), using a phylogenetic accounting framework to identify and audit all distinctive branches in the tree of life at local, regional, or global scales, rather than only maximizing phylogenetic breadth.

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” PC approach or in which species conserved or lost to extinction occurred randomly.

Methods

The phylogenetic completeness 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, then a total of 25 slice points are obtained (see also Figure 1). These slice points are then used to drop all but one of the terminal tips—or operational taxonomic units (OTUs)—from the phylogeny, an approach that ensures that at least one descendant OTU of each lineage at a specific time (T_N) is retained. 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 PD (T_{PD}) as the simple sum of branch lengths at the specific slice point (T_N).

Empirical assessment

The empirical assessment focused on five major terrestrial clades (seed plants, amphibians, squamates [Squamata, the largest order of reptiles], birds, and mammals). Descriptions of the data and software used are provided in Appendix S1: Panel S1.

We tested the reliability of the PC approach by slicing each phylogeny every $T_N = 100$ thousand years until $T_F = 100$ million years ago (Ma) and calculated the T_{SP} and T_{PD} at every slice point. Given the size of the seed plants' phylogeny and computational constraints, we sliced this phylogeny every $T_N = 250$ thousand years. These metrics were then used to identify change points in the PD and the number of species over time. Change points were evaluated using Bayesian multiple changing points (MCP) regressions. The first changing point and its credible intervals (CIs) identified by the MCP analysis were used as the cutoff thresholds to estimate the number and identities of the OTUs to be kept. This procedure allowed us to identify different change points or cutoff thresholds in the PD and the number of species over time for each clade separately and consequently prevent us from establishing a fixed arbitrary cutoff threshold (eg setting a changing point at 2 Ma as cutoff threshold) for all clades.

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

Finally, using the OTUs' identities from both the PC and the RAND scenarios, we mapped the PD of seed plants and terrestrial vertebrates globally. These maps were used to estimate the difference (ΔPD) between the observed PD (PD_{OBS}) and the expected PD (PD_{EXP}) under the PC (PD_{PC}) and RAND (PD_{RAND}) approaches:

$$\Delta PD = \frac{PD_{EXP} - PD_{OBS}}{PD_{OBS}} \times 100 \quad (\text{Equation 1}).$$

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

Results

Bayesian MCP models revealed variable cutoff thresholds for each clade (Appendix S1: Figure S1 and Table S1).

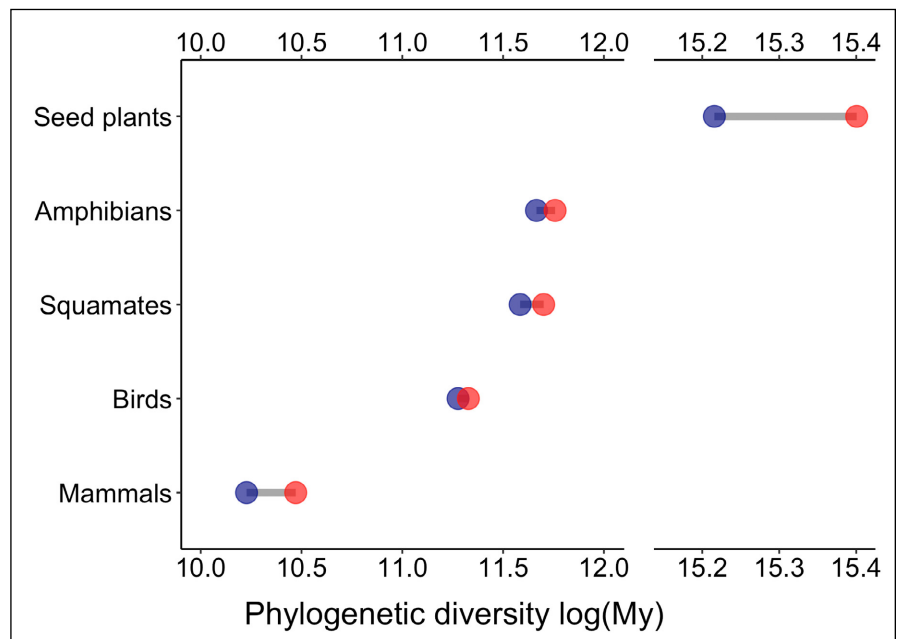


Figure 2. Difference between the remaining phylogenetic diversity (PD) under the phylogenetic completeness (PC, red) and random loss (RAND, blue) scenarios for five major terrestrial clades (seed plants, amphibians, squamates, birds, and mammals). The x axis was log-transformed for plotting purposes. In all cases, PD is higher under the PC approach. My = million years.

Based on these thresholds, losses of species ranging from 1.34% to 18.11% were estimated to occur in each of the major clades (seed plants, amphibians, squamates, birds, and mammals) (Appendix S1: Table S1) while still safeguarding between 97.27% and 99.97% of the PD (ie of the evolutionary history of each clade; Figure 2; Appendix S1: Table S1). If the lower credible interval (LCI, or the 2.5% quantile of the posterior distribution) of our Bayesian model estimates was used to define the phylogenetic branches to be conserved (Figure 2; Appendix S1: Table S1), then 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 2 shows the comparison between the estimates of PD under both the PC and RAND scenarios. Under PC, more branches (Table 1) and a greater degree of evolutionary history in each clade are preserved for a given number of species extinctions (Figure 2; Appendix S1: Figure S2).

Spatial patterns of ΔPD under the PC and RAND scenarios (Figure 3; Appendix S1: Figure S3) reflected how conservation informed by PC safeguards a greater proportion of evolutionary history even with the same number of species extinctions (Appendix S1: Figure S2). For example, for seed plants in tropical regions across the world, conservation

Table 1. Number of branches conserved under the phylogenetic completeness (PC) and random loss (RAND) conservation scenarios

Clade	Number of species		Threshold (Ma)	Number of branches		
	observed	threshold		all species	PC	RAND
Seed plants	353,185	312,540	1.76	438,863	397,974 (90.68%)	391,851 (89.29%)
Amphibians	7238	5927	4.43	14,474	12,614 (87.15%)	11,852 (81.88%)
Squamates	9755	8141	2.61	19,508	17,186 (88.10%)	16,280 (83.45%)
Birds	9993	9859	0.33	19,984	19,716 (98.66%)	19,716 (98.66%)
Mammals	5911	5802	0.31	11,820	11,602 (98.16%)	11,602 (98.16%)

Notes: Ma = million years ago. Values in the observed number of species column correspond to the number of species sampled in each phylogenetic tree and might not represent each clade's true number of species. The number of branches conserved under the PC approach is higher than the RAND scenario for the same number of species, except for birds and mammals. Percentages of the number of branches under the PC and RAND scenarios appear in parentheses. Number of branches within a clade assuming no extinction (number of branches "all species" column) is displayed for reference. The threshold number of species under either the PC or RAND scenarios corresponds to the number of species at the lower credible interval identified using multiple changing points regressions.

informed by PC resulted in PD loss below 10%, whereas the RAND scenario resulted in 10–20% of PD loss. Extinction patterns of terrestrial biodiversity under the PC and RAND scenarios at the biome level (Appendix S1: Figure S4) also exhibited greater preservation of accumulated evolutionary innovations when conservation is targeted toward maintaining branches of the tree of life. Nevertheless, we found that the tundra and taiga biomes are susceptible to high losses in PD, especially for seed plants, amphibians, and mammals, even under PC scenarios. Indeed, further statistical analyses revealed small to no evidence in favor of the PC over RAND approaches (evidence ratio < 5) in these biomes (Appendix S1: Table S2). In contrast, tropical biomes (for both forests and grasslands) experienced only limited losses in PD for the same threshold values used to define branches as in tundra and taiga biomes (Appendix S1: Figure S4 and

Table S2). These results indicate that for a given number of species extinctions, tropical biomes will lose fewer branches of the tree of life and are therefore less susceptible to loss of evolutionary history.

Discussion

Our PC framework for informing biodiversity conservation focuses on 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 rather than specific species

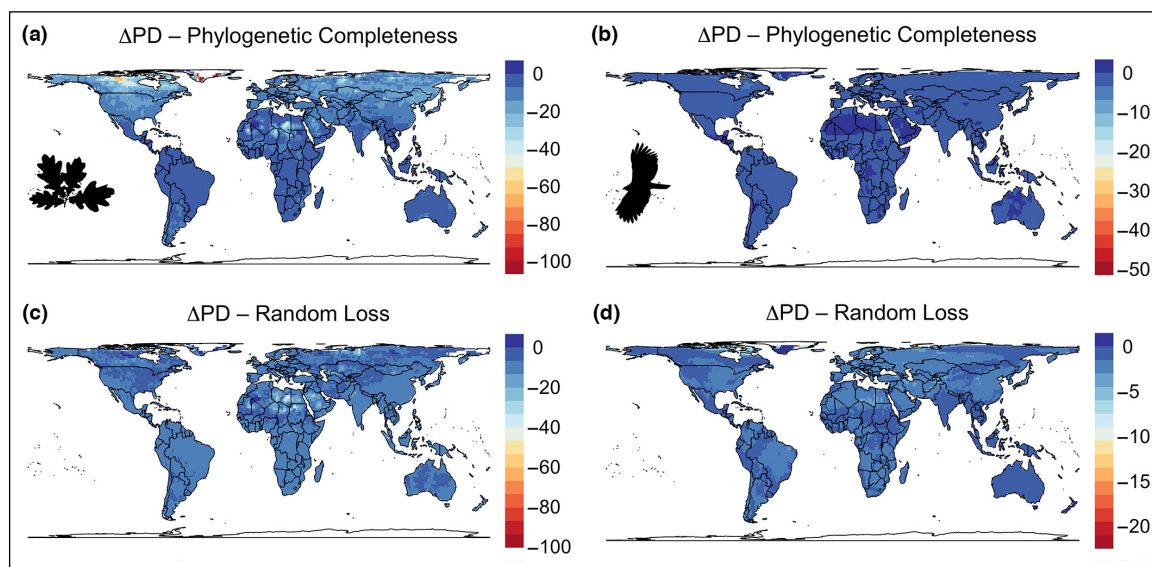


Figure 3. Mapped phylogenetic diversity (PD) for (a, c) seed plants and (b, d) birds globally under the phylogenetic completeness (PC) and random loss (RAND) scenarios. Legends indicate the proportional loss of phylogenetic diversity (Δ PD). Blue tones indicate that more branches of the tree of life were preserved and red tones that more branches were lost. Comparing the two scenarios globally, more branches of the tree of life are conserved in the PC scenario for the same number of species extinctions. Maps for amphibians, squamates, and mammals can be found in Appendix S1: Figure S3. Silhouettes courtesy of PhyloPics (www.phylopic.org).

or OTUs. By defining these branches and the species contained within them, the PC approach provides critical information about branches at risk of extinction where redundancy is low, as well as flexibility in which species could be targeted for conservation in cases of high redundancy (Mooers *et al.* 2005).

The approach is particularly useful in developing priorities for ex situ conservation, as well as for in situ conservation within protected areas, by tracking which branches of the tree of life are currently safeguarded and by identifying branches at highest risk: those not currently protected or with the least amount of their range protected. Recently adopted by the Convention on Biological Diversity (CBD), the Kunming-Montreal Global Biodiversity Framework aims for a tenfold reduction in the extinction rate and risk for all species by 2050 (Goal A; CBD 2022), but does not explicitly include the tree of life. Yet calls by the international scientific community to set ambitious goals for biodiversity recognize that not all extinctions have equal consequences and that phylogenetic dimensions of biodiversity need to be recognized among the criteria for implementation (Díaz *et al.* 2020). The PC approach is consistent with the overall CBD agenda because, at a given overall extinction rate, it can help identify which species or clades will represent disproportionately large or small losses of evolutionary history. In addition to having self-evident intrinsic value, evolutionary history is considered a major basis of “maintenance of options”, one of the major categories of NCP recognized by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES 2019).

Increasing human domination of Earth's ecosystems is rapidly changing biodiversity patterns and negatively impacting the biosphere's capacity to provide essential contributions to humanity (Tilman *et al.* 2017; Díaz *et al.* 2019). Safeguarding all remaining biodiversity, although ideal, is unrealistic on the basis of virtually all projections (Pimm *et al.* 2014; Tilman *et al.* 2017; Scherson and Faith 2018); the footprint of humanity is currently too large to prevent further extinctions. Given the complexity of stakeholder interests (including those of managers and indirect actors), scientists have recognized the challenge of developing effective conservation solutions as a “wicked problem” for which there is no straightforward solution (Vane-Wright *et al.* 1991; Crozier 1997; Mace 2014). Focusing on the conservation of evolutionary history has been hailed as an integrative way to safeguard most of the world's biodiversity and its functions (Faith 1992; Mooers 2007; Mishler *et al.* 2014; Larkin *et al.* 2016). For example, a recent study by Molina-Venegas *et al.* (2021) found strong evidence that plant evolutionary history is tightly linked to multiple plant use categories and therefore to human well-being. These findings, among others, support the idea that conserving evolutionary history is critical for future human well-being (Forest *et al.* 2007; Molina-Venegas *et al.* 2021).

Our analysis demonstrates that the loss of evolutionary history—measured as the total branch lengths in the tree of life—can be minimized under the PC framework (Figures 2 and 3). Our results show that the loss of evolutionary heritage for five major terrestrial clades is lower than the loss of heritage from phylogenetically random extinctions (Figure 2; Appendix S1: Figure S2). In addition, although current species extinctions are non-random (Purvis *et al.* 2000), evidence suggests that the impact of random extinctions erases more evolutionary history on clades with imbalanced phylogenetic trees (Heard and Mooers 2002) such as the ones assessed in this study.

By assessing the loss of evolutionary history at the biome level (Appendix S1: Figure S4), we found that the PC approach does not outperform the conservation scenario of random extinction in biomes at high latitudes (eg tundra and taiga), especially for seed plants, amphibians, and squamates (Appendix S1: Table S2). At the scale of the biome, the loss of evolutionary history under the PC framework seems to have acted selectively, with extinctions concentrated in specific taxa, causing already depauperate lineages in those biomes to become even more depauperate. Indeed, at high latitudes an individual species frequently represents an entire phylogenetic branch, whereas at low latitudes (tropics) many species are likely contained within a branch. This pattern is largely the consequence of more recent divergence and higher rates of speciation in the tropics. However, the spatial scale (grain size) must also be considered; for example, in a tropical forest a single hectare can hold ~650 tree species, which is more than the total number of tree species that occur at high latitudes (Coley and Kursar 2014). Despite this high diversity, tropical forests are usually hyper-dominated by a fraction of tree species (~1.4% of about 16,000 tree species estimated in the Amazon Basin are considered hyper-dominant) that are specialists to their habitats and have large geographical ranges (ter Steege *et al.* 2013). The less abundant or more poorly known tree species with small geographical ranges are potentially threatened.

Although beyond the scope of this study, PC audits at local and regional scales could help to identify which species may be prioritized to prevent losing branches of the tree of life at local and regional scales. To demonstrate scaling our approach to local sites, we assessed plant-community-level phylogeny at the Cedar Creek Ecosystem Science Reserve in Minnesota (Pinto-Ledezma *et al.* 2020). This analysis revealed which taxa are unique and which taxa present evolutionary redundancy (ie red branches in Appendix S1: Figure S5). Moreover, using plant community composition ($n = 987$ plots of 40 m × 40 m) from the National Ecological Observatory Network (NEON), we found that under scenarios where extinctions are predicted to occur all branches are preserved according to our phylogenetic accounting framework. Our results demonstrate that PD is nearly equivalent to that calculated from observed data where no extinctions are assumed to have occurred (Appendix S1: Figure S6). This

additional analysis reveals that, despite variation in the number of species lost (Appendix S1: Figure S6a), focusing on branches as units of conservation aids in maintaining the evolutionary history of local communities.

Multiple approaches have been proposed to assess changes in biodiversity focusing on “hotspot” areas (spatial prioritization) or taxa (taxonomic prioritization) for conservation purposes (Margules and Sarkar 2007). These approaches rely on the use of metrics that capture different dimensions of biodiversity: for instance, metrics that capture (i) evolutionary changes among a set of taxa (Rodrigues *et al.* 2005; Margules and Sarkar 2007) or (ii) the variation in form and function of taxa within communities (Díaz and Cabido 2001; Petchey and Gaston 2006). Despite their usefulness for assessing the state and fate of biodiversity, most if not all of these metrics are sensitive to information (in)completeness. Missing information can result in misleading metric calculations and inappropriate interpretations of spatial or taxonomic comparisons (Isaac 2004; Rodrigues *et al.* 2011; Diniz-Filho *et al.* 2013; Weedop *et al.* 2019). The PC framework introduced here represents a complementary approach to counting numbers of species or comparing levels of PD to assess biodiversity under alternative conservation scenarios. It provides an accounting framework that prioritizes conservation of branches of the tree of life rather than individual taxa (Table 1; Figure 3). It also facilitates identification of areas susceptible to high losses of evolutionary heritage (Figure 3; Appendix S1: Figure S3), which can be used as baseline information for spatial prioritization, providing a broader context for local decision making (Mace *et al.* 2003; Mishler *et al.* 2014; Chaplin-Kramer *et al.* 2022; Silvestro *et al.* 2022).

Moreover, given that the PC framework focuses on the branches of the tree of life, in the context of spatial prioritization, our approach may enhance the capacity of existing spatial phylogenetic approaches (eg categorical analysis of neo- and paleo-endemism [Mishler *et al.* 2014; Thornhill *et al.* 2016] and phylogenetic endemism [Rosauer *et al.* 2009]) to address the issue of missing data. To illustrate this point, if we consider protecting at least one descendant taxon from a specific node in the phylogeny, this taxon contains information—genes, traits, functions—that captures most of the evolutionary history of the lineage (ie the evolutionary history of the taxon plus its common ancestor; Figure 1; Appendix S1: Figure S5). If species within the branch have not yet been identified or are not readily observed, the branch itself is still preserved, with the caveat that phylogenetic information remains imperfect (ie Darwinian shortfall in biodiversity and conservation; Diniz-Filho *et al.* 2013). By focusing on branches of the tree of life as an additional conservation criterion beyond those prioritized in other ways, it is possible to reduce the impact of missing data and taxonomic inflation on evolutionary diversity estimations and conservation planning (Isaac 2004; Rodrigues *et al.* 2011; Diniz-Filho *et al.* 2013; Allen and Mishler 2022).

Although incomplete, the data in our empirical evaluation represent the best phylogenetic and geographical data

available at present. While our estimations are robust, more research may be needed to fully understand the potential of the PC framework in biodiversity conservation. In addition, this study is limited to terrestrial biodiversity; thus, evaluations of aquatic biodiversity are required. Future studies focusing on aquatic systems or terrestrial biodiversity not considered here (eg Hexapoda) may help to refine PC's potential in biodiversity assessment and conservation. These studies should also investigate the relative impact of branch selection (that is, “the agony of choice”, or which branch should be prioritized and what would be the conservation implications of that selection): in other words, where efforts should be focused to minimize the loss of evolutionary heritage. Finally, we emphasize that PC is not a metric of PD but rather an accounting framework that identifies targets (unique branches) for eco-evolutionary or conservation questions in a phylogenetic context. Once the unique branches are identified, existing metrics can be used (Appendix S1: Figure S6) to estimate the impact of lineage loss on biodiversity estimations, conservation scenarios, or ecological research.

Moving forward

The PC approach provides a means to account for phylogenetic branches and facilitates the safeguarding of evolutionary heritage, adding to but not replacing other priorities for conservation. For example, the approach highlights when a single species is the lone member of a branch, increasing its conservation priority. The spatial scale of evaluation is important to consider, and application at local scales in coordination with regional scales is critical. It would be dangerous to consider that maintaining only one species in a branch is adequate at large scales, mainly because some species are locally extirpated and currently inhabit a mere fraction of their original geographic distribution (eg hyacinth macaw [*Anodorhynchus hyacinthinus*], African lion [*Panthera leo*]). However, informed and coordinated conservation strategies may allow individual protected areas to focus on conservation of species that maintain all branches locally, emphasizing particular species within a branch based on other conservation criteria. An auditing procedure with appropriate tools would enable coordination at regional scales to ensure that most or all species in a particular branch are being managed. By focusing on branches of the tree of life as an additional conservation criterion beyond those prioritized in other ways, we will be less likely to overlook the importance of management for taxa that alone represent an evolutionary branch (Mace *et al.* 2003; Mace 2014; Allen and Mishler 2022).

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■ Data Availability Statement

All data used in this manuscript are publicly available. Main sources are provided in Appendix S1: Panel S1. R functions and examples for data analyses are available at <https://github.com/jesusNPL/FITBITs>.

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