Spatial overlaps between the global protected areas network and terrestrial hotspots of evolutionary diversity

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Abstract

Aim: A common approach for prioritizing conservation is to identify concentrations (hotspots) of biodiversity. Such hotspots traditionally have been designated on the basis of species-level metrics (e.g., species richness, endemism and extinction vulnerability). These approaches do not consider phylogenetics explicitly, although phylogenetic relations reflect the ecological, evolutionary and biogeographical processes by which biodiversity is generated, distributed, and maintained. The aim of this study was to identify hotspots of phylogenetic diversity and compare these to hotspots based on species-level metrics, and to the existing protected areas network.

Location: Global.

Time period: Contemporary.

Major taxa studied: Terrestrial vertebrates (mammals, birds, and amphibians) and angiosperms.

Methods: We used comprehensive phylogenies and distribution maps of terrestrial birds, mammals, amphibians, and angiosperms to identify areas with high concentrations of phylogenetic diversity, phylogenetic endemism, and evolutionary distinctiveness and global endangerment. We compared the locations of these areas to those included within the current network of protected areas and concentrations of species-level indices: species richness, species endemism and species threat.

Results: We found spatial incongruence among the three evolutionary diversity metrics in each taxonomic group. Spatial patterns of diversity and endemism also differed among taxonomic groups, with some differences between vertebrates and angiosperms. Complementarity analyses of phylogenetic diversity identified the minimum area that

encapsulates the full branch lengths for each taxonomic group. The current network of protected areas and species-level hotspots largely do not overlap with areas of high phylodiversity.

Main conclusion: Overall, less than 10% of hotspot areas were designated as protected areas. Patterns of diversity, endemism, and vulnerability differ among taxonomic groups.

Keywords: amphibians, angiosperms, biodiversity hotspots, birds, complementarity, global conservation, mammals

Introduction

Areas with relatively high concentrations of species richness and endemism (*hotspots*) reflect ecological and evolutionary patterns and processes. Such hotspots can guide allocation of limited conservation resources (*e.g.,* Forest et al., 2007). Traditionally, hotspots have been designated on the basis of species-level metrics (*e.g.,* species richness, endemism, and extinction vulnerability; Myers et al., 2000; Orme et al., 2005; Ceballos & Ehrlich, 2006). These approaches do not capture important facets of biological diversity, such as phylogenetic diversity or latent risk of extinction (see Forest et al., 2007; Davies & Cadotte, 2011; Daru et al., 2015). Along these lines, studies have demonstrated that protected areas do not overlap with concentrations of avian or mammalian phylogenetic diversity (e.g. Brum et al., 2017; Pollock et al., 2017; Rosauer et al., 2017). As some species have more distinctive evolutionary histories than others (Vane-Wright et al., 1991; Faith 1992), non-random extinction of species can result in some clades losing a higher proportion of species than others (Davies & Yessoufou, 2013). Recent large-scale phylogenetic efforts make global quantification of such variation in evolutionary history possible, and the explicit incorporation of such information can facilitate more informed conservation decisions.

Phylogenetic information is increasingly integrated into the process of defining areas of conservation priority at various spatial and taxonomic scales (e.g., Sechrest et al., 2002; Devictor et al., 2010; Zupan et al., 2014; Daru et al., 2015; Pollock et al., 2015; Daru & le Roux, 2016; Brum et al., 2017; Pollock et al., 2017; Rosauer et al., 2017). However, previous attempts to integrate phylogeny into global hotspot designations have been limited in taxonomic scope, focusing solely on vertebrates (Sechrest et al., 2002;

Fritz & Rahbek, 2012; Mazel et al., 2014; Brum et al., 2017; Pollock et al., 2017; Rosauer et al., 2017), despite the fact that spatial patterns of phylogenetic diversity can differ among taxonomic groups (Park & Razafindratsima, 2018). Until recently, phylogenetic information has not been widely available for the majority of taxa hindering efforts to incorporate phylogeny into global-scale conservation efforts.

The phylogenetic equivalents of the traditional species-level hotspot metrics include phylogenetic diversity (PD, the phylogenetic equivalent of species richness) (Faith, 1992), phylogenetic endemism (PE, a variant of species endemism) (Rosauer et al., 2009), and evolutionary distinctiveness and global endangerment (EDGE, a phylogenetic equivalent of threats to a species) (Isaac et al., 2007). These metrics quantify different facets of evolutionary diversity (Tucker et al., 2017). PD is the sum of the lengths of branches that connect a set of species to the root of a phylogenetic tree (Faith, 1992). PE quantifies the degree to which a substantial proportion of phylogenetic diversity is restricted to the study area (Rosauer et al., 2009). EDGE combines evolutionary distinctiveness (ED; *i.e.,* phylogenetic isolation of a species) with global endangerment (GE) status as defined by the International Union for Conservation of Nature (IUCN) (Isaac et al., 2007).

PE and EDGE represent geographically- and threat-weighted variants of PD. Areas with high PE capture phylogenetic diversity not represented elsewhere, reflecting, for example, extinctions of ancient lineages (i.e., paleoendemics) (Purvis et al. 2000). On the one hand, this provides new opportunities for defining biodiversity hotspots more holistically (Redding & Mooers, 2006; Buerki et al., 2015; Daru et al., 2015), although the practicalities of implementation of conservation plans may limit the application of the

identified priorities. On the other hand, EDGE can be used to infer areas inhabited by taxa that are both evolutionarily distinct and globally endangered.

Here, we integrate data on the phylogeny and geographical distribution of three major groups of terrestrial vertebrates (amphibians, mammals, and birds) and angiosperms to explore congruence among biodiversity hotspots designated by different phylogenetic metrics. First, we contrast hotspots of PD, PE, and EDGE for each taxonomic group. We then compare our phylodiversity hotspots with the hotspots of Myers et al. (2000), which were based on species endemism and degree of threat, and test whether residuals from the regressions of species-level hotspots and their phylogenetic variants have strong spatial structure. We identify conservation gaps by assessing the coverage of the species-level hotspots and phylodiversity hotspots.

METHODS

Geographical distribution data

We obtained distributional data for vertebrates from the IUCN Red List database's maps of the native extent-of-occurrence of all terrestrial mammals (n = 5,283 species), amphibians (n = 6,337), and terrestrial birds (n = 10,079) (http://www.iucnredlist.org/technical-documents/spatial-data). We standardized taxonomic ranks with Frost (2009) and data from the American Museum of Natural History (AMNH; http://research.amnh.org/vz/herpetology/amphibia/index.php) for amphibians, Gill et al. (2009) for birds, and Wilson & Reeder (2005) for mammals.

Because there were no species-level global data on the distributions of angiosperms, we assembled data on the global distribution of angiosperms at the genus

level. Although we recognize that species richness among genera may differ across taxonomic groups, in the absence of sufficient species-level data, we considered a genus-based analysis to be the best alternative. First, we compiled a worldwide genus checklist from a list of 32,223 angiosperm species within 8,179 genera for which phylogenetic information was available (Zanne et al., 2014). We used The Plant List (www.plantlist.org) as our taxonomic authority. Second, to generate geographic distributions, we used the R package rgbif (Chamberlain et al., 2015). We extracted locality records from the Global Biodiversity Information Facility (http://www.gbif.org) for 6,483 of the 8,179 angiosperm genera for which more than 10 spatially explicit records remained after data cleaning. We cleaned the data by removing points in the sea, duplicate records, and records with inverted latitude and longitude coordinates. We also restricted the data to the native ranges of each genus, which we estimated by searching the literature and then assigning each genus to one or more of the following continental classes: the Americas (North and South America), Eurasia (Europe and Asia), Africa, Australia, Australasia (Asia and Australia), and Oceania.

We used the cleaned locality records (presence-only data), 10,000 background points, and Maxent (Phillips et al., 2006) to model the distribution of each angiosperm genus. We used eigenvector-based spatial filters to account for the restricted distribution of most taxa (Blach-Overgaard et al., 2010). To generate spatial filters, we used the coordinates of each grid cell's centroid to generate a pairwise geographical connectivity matrix among grid cells that covered all land on Earth (except Antarctica) at a grain of 1° × 1°. We then used the default settings in SAM (Spatial Analysis in Macroecology; Rangel et al., 2010) to establish a truncation distance for the eigenvector-based spatial

filtering, resulting in a total of 150 spatial filters. These filters were subsequently resampled to a resolution of 5 minutes. We included the first 14 spatial filters (see Figure S1) and 19 bioclimatic variables (also at 5 minute resolution) from WorldClim (Hijmans et al., 2005) as predictor variables (following the approach of Blach-Overgaard et al., 2010). We used the equal training sensitivity and specificity threshold (Liu et al., 2005) to create presence-absence maps for each genus in Maxent. We evaluated model performance with the area under the receiver operator curve (Bewick et al., 2004). We aggregated the final outputs from Maxent at a resolution of 110 × 110 km to match the resolution of the vertebrate data.

Because sampling effort is spatially unequal, we tested the sensitivity of our analyses to incomplete sampling of angiosperm genera. We mapped the genera for which geographical data were missing (or inadequate for inclusion) onto the global phylogeny to assess whether their phylogenetic distributions were random or clustered (Figure S2). We also analyzed the three groups of vertebrates at the genus level (Figure S3) and found strong correlations between hotspots defined at the genus level versus species-level.

Phylogenetic data

We used a dated amphibian phylogeny from Isaac et al. (2012), derived from the amphibian generic-level supertree (Frost et al., 2006) and updated with species-level taxonomy (Frost, 2007) and molecular phylogeny (Roelants et al., 2007). Our mammal phylogeny was a supertree derived from Bininda-Emonds et al. (2007), which is the most recent time-calibrated phylogeny of the world's mammals. We used a consensus phylogeny for all land and non-pelagic bird species, which was based on a distribution of

500 phylogenies from Jetz et al. (2012; downloaded from birdtree.org). Our angiosperm phylogeny was a dated molecular phylogeny for 32,223 angiosperm species inferred from seven genes (Zanne et al., 2014). We sampled one species from each angiosperm genus for our analyses (following Forest et al., 2007).

Data Analyses

We overlaid each taxon's range map on equal-area grids (each cell approximately 110 × 110 km; see also Rosauer & Jetz, 2015) to record the presence or absence of the species or genus within grid cells. We considered a species or genus present if any of its range overlapped a grid cell. We removed coastal grid cells with less than 50% land from analyses. We included only taxa that were represented in both the phylogeny and the distribution maps. The data we analyzed included 25,229 taxa: 4732 mammal species, 9886 bird species, 5314 amphibian species, and 6483 angiosperm genera.

To map phylodiversity hotspots, we chose metrics that closely followed Myers et al. (2000): PD, PE, and EDGE, which were calculated for each grid cell.

We expressed phylogenetic diversity (PD) as

$$PD = \sum_{i \in I} L_i,$$

where L_i is the length of branch i in the set of branches I in the phylogeny pool.

We expressed PE as

$$PE = \sum_{\{i \in I\}} \frac{L_i}{R_i},$$

where $\{I\}$ is the set of branches connecting species to the root of a phylogenetic tree; L_i is the length of branch i, expressed as proportion of the total length of the tree; and R_i is the area inhabited by the clade.

We expressed EDGE as

$$EDGE_i = \ln (1 + ED_i) + GE_i \times \ln (2),$$

where ED was calculated with the *evol.distinct* function in the R library picante (Kembel et al., 2010) and represents the partitioning of phylogenetic branch lengths by the total number of species subtending them, then weighting species on the basis of the amount of unique evolutionary history they represent (Isaac et al., 2007; Cadotte & Davies, 2010). GE represents species threat, calculated as the expected probability of extinction over 100 years of each taxon i in the phylogeny (Redding & Mooers, 2006), scaled as follows: least concern = 0.001, near threatened and conservation dependent = 0.01, vulnerable = 0.1, endangered = 0.67, and critically endangered = 0.999. Because PD and PE are sums, and are properties of an area, whereas EDGE represents species values per cell, we summed EDGE values for each grid cell (see Safi et al., 2013 for a similar approach). Thus, to quantify EDGE, we calculated ED on the basis of the full phylogeny of the group, combined with GE scores from IUCN (see equation above), before taking the sum per cell. We could not compute EDGE for angiosperms because the IUCN does not provide threat categories for them; therefore, we only calculated and summed ED values per grid cell.

We calculated species richness (SR) as the total number of species (or genera) in each grid cell. We used the *weighted endemism* function in BIODIVERSE (Laffan et al., 2010) to calculate species-weighted endemism (WE) as the sum of the number of species present in each cell in a local neighbourhood, weighting each by the fraction of the area they inhabit (Laffan & Crisp, 2003). We calculated PD with the *pd* function in the R package picante (Kembel et al., 2010), and PE with the R function *phylogenetic.endemism* (Guerin & Lowe, 2015). To calculate both PD and PE, we used the species × row matrix and the phylogenetic tree of the species.

We used residuals from a local regression (LOESS) to identify areas in which evolutionary diversity was higher or lower than expected by running LOESS of PD against SR, PE against WE, and EDGE against GE. Expectations were based on SR (or genus richness for angiosperms), WE, and GE.

We defined hotspots for each metric as the 2.5% of grid cells with the highest values (Orme et al., 2005; Ceballos & Ehrlich, 2006). We also conducted a sensitivity analysis to investigate the effect of variation in the size of hotspots by steadily increasing the hotspot threshold percentage (from 1%, 2.5%, 5%, 7.5%, 10%, 12.5% to 50%), examining if different threshold percentage values altered the areas identified as hotspots during our analyses.

In addition to mapping the phylodiversity hotspots, we mapped hotspots of complementarity with a greedy algorithm that maximizes species richness and phylogenetic diversity in as few grid cells as possible. The complementarity analysis calculates the degree to which an area contributes unrepresented species or shared

phylogenetic branches to a set of areas. We then compared the complementarity cells against a random selection of cells.

We tested the overlap between the global terrestrial network of reserves and the phylodiversity hotspots with the most recent (December 2015) version of the World Database on Protected Areas (IUCN, 2015). We conducted our analysis on the basis of all terrestrial protected areas in IUCN categories I through VI, and determined the proportion of protected area overlapping each hotspot and complementary cell for each taxonomic group.

We conducted statistical analyses in R (R Core Team, 2015) and used the Research Computing Clusters of Harvard University (https://rc.fas.harvard.edu/).

RESULTS

Hotspots of amphibians, mammals, birds, and angiosperms that were based on PD, PE, and EDGE were concentrated in 29 clusters (covering 4 – 6% of the geographic ranges of these taxonomic groups; Figure 1). These phylogenetically informed hotspots (phylodiversity hotspots) are chiefly located in Mesoamerica, the Tropical Andes, West Africa, Central Africa, the Maputo-Pondoland-Albany Centre of Endemism, Madagascar, Eastern Australia, Papua New Guinea, New Caledonia, and South-Central China (Figure 1). The locations of many phylodiversity hotspots were similar to those of hotspots defined by species-level methods (Figure S4), but several were not, including Central Chile, Honshu, New Caledonia, Appalachia, and Texas.

There was low spatial congruence among the various evolutionary diversity metrics for the different taxonomic groups. Between 8 and 23% of hotspot grid cells were

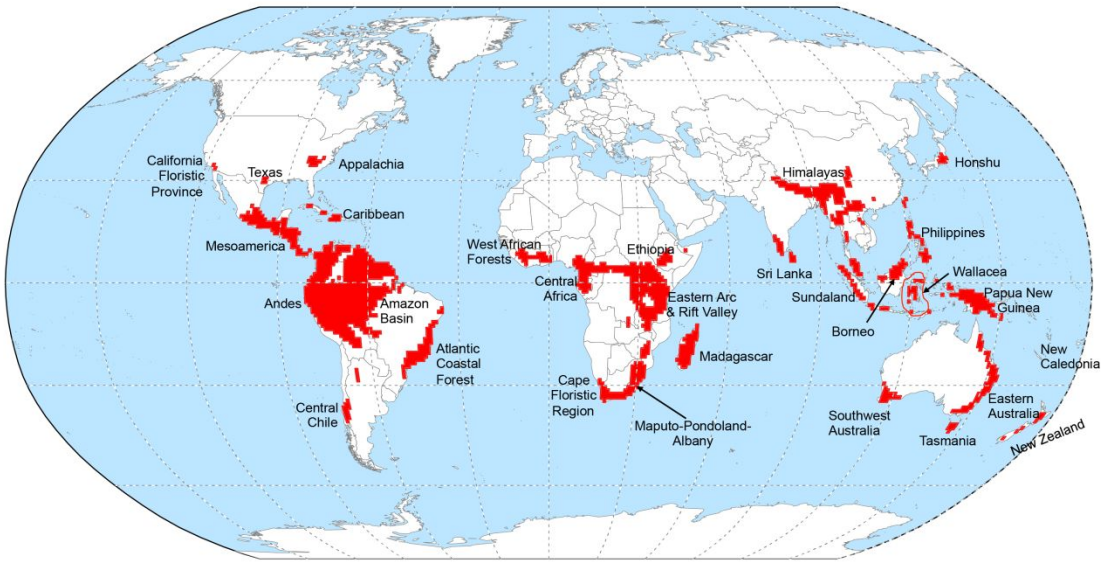

Figure 1. Phylodiversity hotspots generated by identifying the equal-area grid cells (ca. 110 km × 110 km) with the highest 2.5% of phylogenetic diversity, phylogenetic endemism, and evolutionary distinctiveness and global endangerment for each taxonomic group. The map is in equal-area Behrmann projection. See SI Appendix, Figs S6-9 for taxon-specific hotspots.

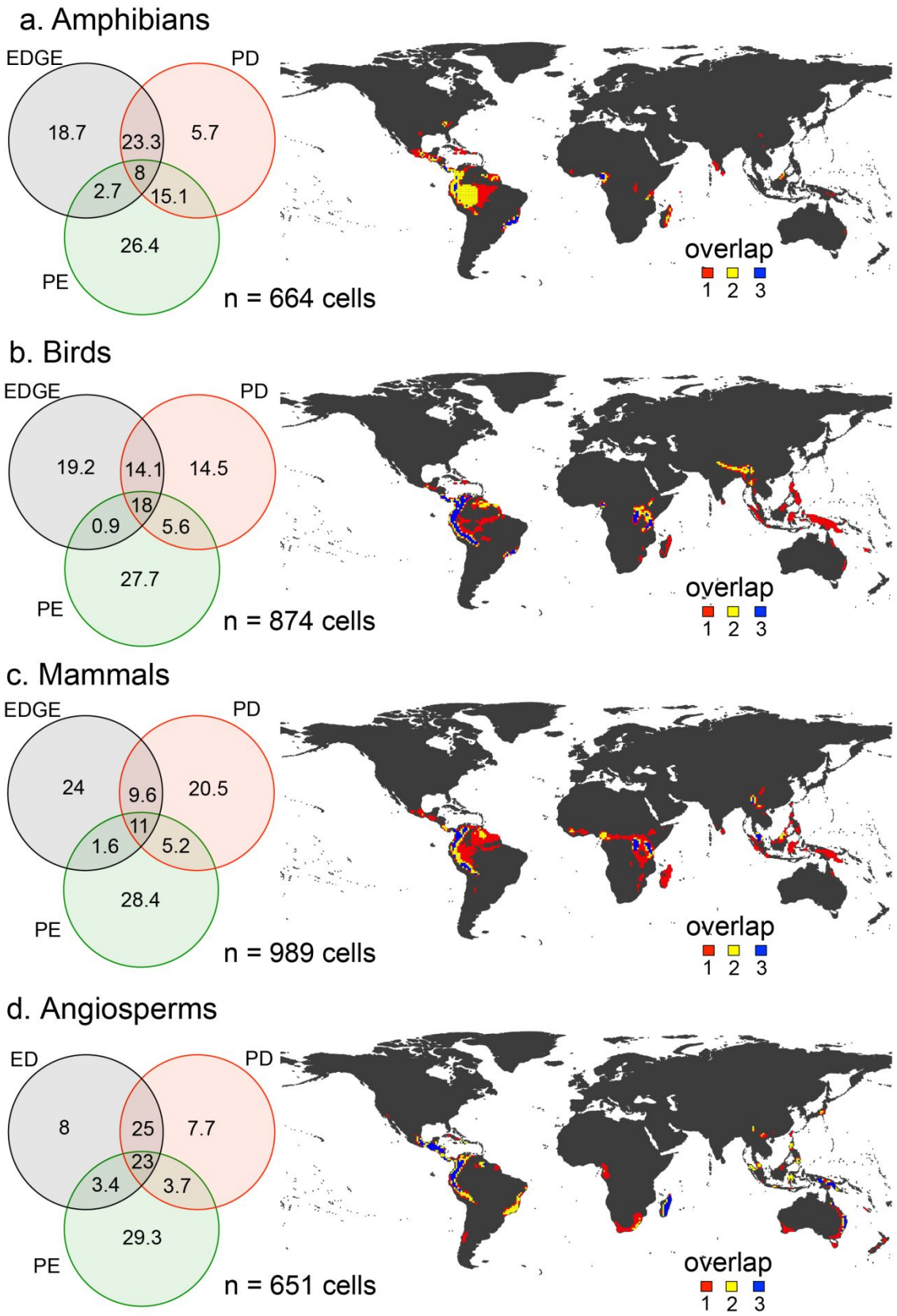

Figure 2. Spatial congruence among phylodiversity hotspots based on phylogenetic diversity (PD), phylogenetic endemism (PE), and evolutionary distinctiveness and global endangerment (EDGE) for **(a)** amphibians, **(b)** mammals, **(c)** birds, and **(d)** angiosperms. Values in Venn diagrams are percentages of the total number of hotspot grid cells (highest 2.5%). Overlap references the number of phylogenetic metrics.

identified as hotspots by all three metrics (Figure 2). The low congruence could reflect the small size of the hotspots. Increasing the percentage of cells considered as phylodiversity hotspots did not increase overlap appreciably until 10% were designated as hotspots (Figure S5). Nonetheless, values of the diversity metrics for each grid cell were positively correlated, with r = 0.6 to 0.7 for all metrics and for each taxonomic group (Tables S1-4). All three diversity metrics for each taxonomic group were concentrated in the tropics, including South America, Africa, and Southeast Asia (Figures S6-9).

Given that values of species-level metrics for designating biodiversity hotspots covary with values of phylogenetic metrics (Rodrigues & Gaston, 2002; Morlon et al., 2011) (Figure S10), decoupling phylogenetic patterns from species-level indices is challenging. Our LOESS analysis indicated that, after accounting for species richness, areas of exceptionally high evolutionary diversity for each taxonomic group are widely dispersed (Figure S11) and have low degrees of spatial congruence (Figure S12).

Our complementarity analysis indicated that all amphibians' phylogenetic branch lengths could be represented once in a set of 855 cells, mammal branch lengths in 739 cells, birds in 467 cells, and angiosperm genera in 312 cells (Figure S13). These sets of cells are geographically dispersed, including in regions that were not identified as hotspots.

The percentage of hotspot cells not included within the existing global network of reserves ranged from 24% (angiosperms) to 36% (mammals) (Figure 3a). Eighteen percent (mammals) to 22% (angiosperms) of hotspot cells had < 2% overlap with protected areas (Figure 3a). At least 10% of the area of 9% of amphibian, 10% of

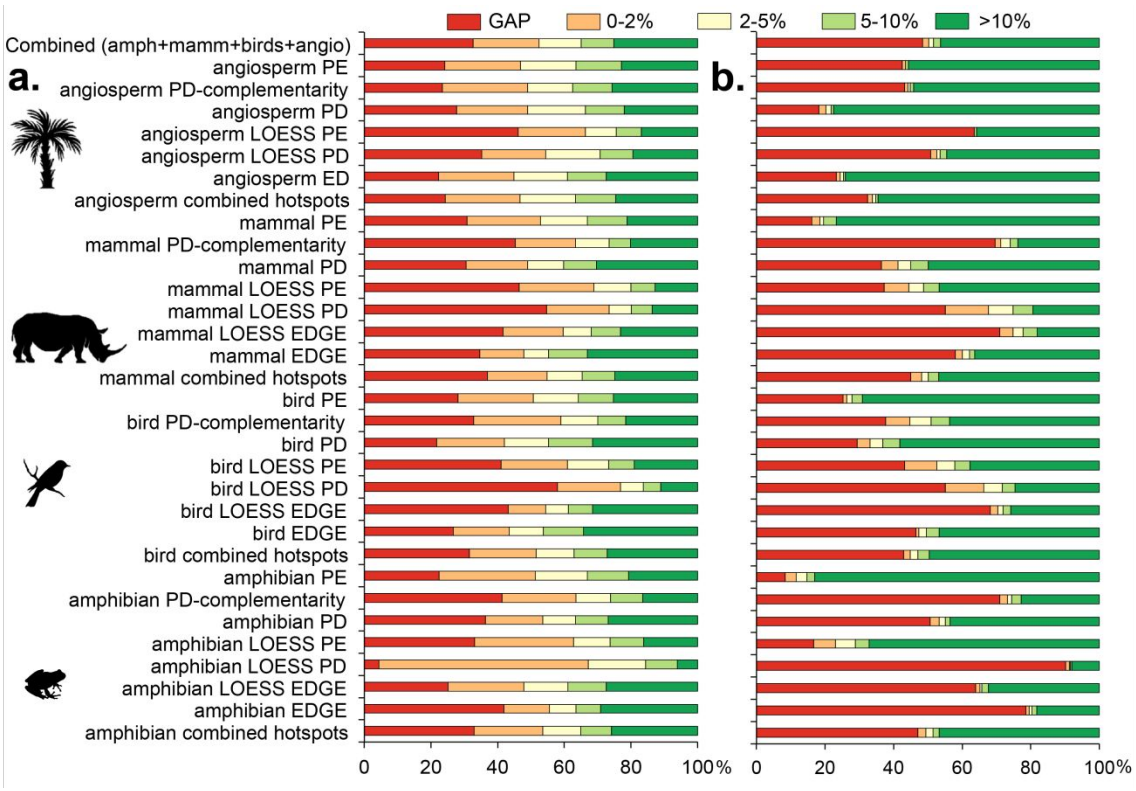

Figure 3. Percentage of overlap between phylodiversity hotspots and **(a)** current protected areas **(b)** biodiversity hotspots identified by Myers et al. (2000). GAP indicates the proportion of phylogenetic hotspot cells that do not overlap protected areas or biodiversity hotspots. Phylogenetic diversity: PD; phylogenetic endemism: PE; evolutionary distinctiveness and global endangerment: EDGE.

mammal and bird, and 12% of angiosperm hotspot cells overlapped protected areas (Rodrigues et al., 2004; Venter et al., 2014) (overlap increased as the size of hotspots increased). The percentage of phylodiversity hotspot cells that did not overlap those of Myers et al. (2000) ranged from 32% (angiosperms) to 47% (mammals) (Figure 3b). At least 10% of the area of 47% of amphibian and mammal, 50% of bird, and 65% of angiosperm phylodiversity hotspot cells overlapped the hotspots of Myers et al. (2000).

DISCUSSION

We conducted the first global evaluation of the spatial distribution of terrestrial phylogenetic diversity of amphibians, mammals, birds and angiosperms. Our method is consistent with Myers et al.'s (2000) vision for biodiversity hotspots – to maximally represent all taxonomic groups.

Although there was low spatial congruence among three evolutionary diversity metrics for the different taxonomic groups, we found that the three types of diversity overlap in some areas in the tropics (South America, Africa, and Southeast Asia). These areas reflect a complex biogeographic history of speciation, extinction, and dispersal (Rosenzweig, 1995; Chown & Gaston, 2000; Daru et al., 2017). The general lack of spatial overlap suggests that one diversity metric cannot reliably be used as a surrogate for others.

Areas such as the Andes and Amazon in South America, and Madagascar, often emerge as high priority conservation areas for vertebrates (e.g. Rosauer & Jetz, 2015; Brum et al., 2017; Pollock et al., 2017). However, high-priority areas for the conservation of other taxonomic groups may differ. For instance, the hotspots in East Africa overlap

several important biodiversity areas including the Eastern Arc mountains, Albertine Rift Mountains and Kenya Highlands that provide unique habitats for endemic birds (Stattersfield et al., 1998; Jetz et al., 2004), plants (Lovett, 1988; Yessoufou et al., 2012), and mammals (Olson & Dinerstein, 1998; Davenport et al., 2006). As these East African regions are associated with mountain areas, they might indicate the role of past and present barriers facilitating speciation and beta-diversity in the region (Graves, 1988; Rahbek, 1997). Similarly, the Cape Floristic region of southern Africa has very high species richness and endemism of angiosperms, reflecting the radiation of 33 angiosperm clades about 18-8 million years ago (Linder, 2003). Southeast Australia is another angiosperm phylodiversity hotspot (due to the presence of long phylogenetic branches resulting from historical extinctions; Thornhill et al., 2016) that does not correspond to hotspots of vertebrate phylodiversity. The Atlantic coastal forest of southeastern Amazonia is a phylodiversity hotspot for amphibians, birds and angiosperms, potentially reflecting areas of special evolutionary history such as high in situ speciation, with low dispersal rates (Jønsson & Holt, 2015). Central Chile and Honshu also have high concentrations of angiosperm phylodiversity. Southern Chile has high paleo-endemism, whereas northern Chile is a center of neo-endemism (Scherson et al., 2017). Although tropical rainforests have high species richness of amphibians (Fritz & Rahbek, 2012), our analysis also highlights the Appalachian Mountains and mesic regions of Texas in North America as hotspots for amphibians driven mainly by the presence of mole salamanders (Ambystomatidae) and lungless salamanders (Plethodontidae) endemic to these regions. Another feature of interest is the phylodiversity hotspots across the West African Forests. These hotspots are driven mainly by a concentration of distinct clades of mammals (e.g.

Hippopotamidae) and amphibians, and might suggest that a large proportion of the unique evolutionary history in the region can be explained by biogeographic barriers such as the formation of the Dahomey Gap, a rainforest fragmentation in West Africa during the late Holocene (Salzmann & Hoelzmann, 2005).

Although PE and EDGE both have properties of PD (Figure S14), we found that these two metrics were not highly correlated. For instance, evolutionarily distinct species tend to have distinct traits (Redding et al., 2010). An analysis of PE demonstrated that past climate and geographic isolation at the Last Glacial Maximum might have generated and maintained deep lineages with narrow ranges in mammals (Rosauer & Jetz, 2015). Thus, if the goal is to protect areas of exceptional phylogenetic history, it may be worthwhile to protect areas with disproportionately high phylodiversity relative to their species-level variants.

To enable comparison of ED (which represents species values) with PD and PE (which both represent summations and are properties of areas), we summed EDGE per cell. In this study, summed EDGE values per cell were correlated strongly with the number of threatened taxa present in the same cell. Therefore we believe that summed EDGE may be a phylogenetic equivalent of species threat. Irrespective of the correlation between summed EDGE values and the number of threatened species per cell (or other standard environmental variables; see e.g. Safi et al. 2013), summed EDGE values may identify high concentrations of the world's phylogenetically distinctive and most endangered vertebrates and angiosperms.

Similarly, although the summations of ED and PD are expected to be correlated, the two metrics are calculated differently and represent distinctly different components of

phylodiversity. We calculated ED on the basis of the full phylogeny of the group before taking the sum per cell. Therefore, ED is independent of clade size, whereas PD is sensitive to differences in species richness (i.e., number of tips present). Thus, summed ED in a cell will not equal PD, except where all species in the phylogeny are present in the cell. Variation in evolutionary processes such as extinction rates or speciation of lineages can result in substantial differences in the distributions of ED and PD. Given that EDGE is associated with species, not grid cells, it does not encapsulate complementarity explicitly. Jensen et al. (2016) proposed i-HEDGE (iterative heightened evolutionary distinctiveness and global endangerment) as a means of representing the extinction risk of all species. i-HEDGE accounts for complementarity by iteratively down-weighting species at high risk of extinction if closely related species are less threatened. This approach could be applied across areas (as demonstrated for PD complementarity in our study).

Consistent with suggestions that mountain ranges often represent hotspots of species richness and endemism (Hoorn et al., 2013; Quintero & Jetz, 2018), we found that many phylodiversity hotspots (e.g., the Drakensberg in southern Africa, Eastern Arc, Hengduan, Himalayas, Andes) were montane. Some of these mountain ranges, including the Drakensberg, which abuts Maputo-Pondoland-Albany in southern Africa, and the Hengduan Mountains in China, are hotspots for angiosperms but not vertebrates. We acknowledge the spatial resolution of our global analyses was coarse and did not address fine resolution environmental heterogeneity (which often is pronounced in montane areas).

Phylodiversity hotspots as units for real-world conservation

Hotspots analyses have not been well integrated into on-the-ground conservation decision-making for reasons ranging from data unavailability and budget constraints to social, economic, and political factors (Balmford, 2003). However, as more phylogenetic information and species distribution data become available, phylodiversity increasingly may inform real-world conservation planning. For instance, the Australian government intends to expand conservation areas, and facilitated a partnership among researchers, local communities, and private land managers to identify priority areas on the basis of evolutionary heritage (Laity et al., 2015; Rosauer et al. 2018). Similarly, although Conservation International (CI; www.conservation.org) adopted Myers' concept of hotspots (Myers et al., 2000) as the blueprint for their conservation activities, CI's mission has expanded to include other facets of biodiversity (Olson, 2010).

Although phylodiversity hotspots are not necessarily more informative than hotspots based on species endemism or species richness, phylodiversity hotspots can represent evolutionary history and, potentially, adaptive capacity. However, the overlap between hotspot cells and protected areas did not meet the 10% threshold, the minimum percentage of a range that must be overlapped by protected areas in order for the species to be considered covered (Rodrigues et al., 2004; Venter et al., 2014).

Despite the potential of phylodiversity hotspots for preserving evolutionary heritage, there are gaps and potential biases in phylogenetic data and analytical methods. The results of global analyses of other taxonomic groups (e.g., insects or fungi) might differ from the results in this study, but data on those taxonomic groups are not comparable to the data we used here. Museum collections – the source of our data on

angiosperms and vertebrates – are extensive but rarely reflect systematic sampling (Meyer et al. 2016; Daru et al. 2018). As more data become readily available through ongoing digitization efforts and as new methods of phylogenetic analysis are developed, some gaps and biases may be reduced.

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Author contributions

B.H.D. designed the study and ran the analyses with help from P.C.R. and M.G. B.H.D. wrote the manuscript with substantial contributions from all co‐authors.

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