



Global priorities for conservation across multiple dimensions of mammalian diversity

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Conservation priorities that are based on species distribution, endemism, and vulnerability may underrepresent biologically unique species as well as their functional roles and evolutionary histories. To ensure that priorities are biologically comprehensive, multiple dimensions of diversity must be considered. Further, understanding how the different dimensions relate to one another spatially is important for conservation prioritization, but the relationship remains poorly understood. Here, we use spatial conservation planning to (i) identify and compare priority regions for global mammal conservation across three key dimensions of biodiversity—taxonomic, phylogenetic, and traits—and (ii) determine the overlap of these regions with the locations of threatened species and existing protected areas. We show that priority areas for mammal conservation exhibit low overlap across the three dimensions, highlighting the need for an integrative approach for biodiversity conservation. Additionally, currently protected areas poorly represent the three dimensions of mammalian biodiversity. We identify areas of high conservation priority among and across the dimensions that should receive special attention for expanding the global protected area network. These high-priority areas, combined with areas of high priority for other taxonomic groups and with social, economic, and political considerations, provide a biological foundation for future conservation planning efforts.

complementarity | phylogenetic dimension | spatial conservation prioritization | taxonomic dimension | trait dimension

Human activities are rapidly transforming the planet and are the primary causes of biodiversity loss (1–4). In response to growing concern about the future of biodiversity, the 10th Convention on Biological Diversity developed a strategic plan for 2011–2020 that introduced protection targets called the “Aichi Targets” to facilitate conservation action (5). One of the primary targets is to protect 17% of the global land surface (6), focusing on areas of particular importance for biodiversity and ecosystem services (7, 8). Traditionally, global priority areas have been identified based on richness, species endemism, and vulnerability (9, 10). Although these features are important in identifying key biodiversity regions, they focus on only one dimension of biodiversity—taxonomic diversity. Selecting regions based on species richness may not be the best conservation strategy, because richness does not reflect complementarity and thus could lead to priority areas with similar assemblage composition, at the cost of protecting unique assemblages (11, 12). Species are a product of ecological and evolutionary processes, and the species that we observe today represent only the tips of the tree of life. If we measure only species numbers, we might miss unique ecological and evolutionary information. Therefore the taxonomic dimension may not sufficiently capture other

facets of diversity, such as evolutionary history and functional traits (13–15). Evolutionary history captures the uniqueness of lineages through deep time (16) and can influence species’ susceptibility to extinction, because extinction risk is phylogenetically nonrandom (17–19). The trait dimension reflects ecological, morphological, and physiological strategies of species (20). Therefore losses in all three dimensions could have large consequences for biodiversity and ecosystem function (13).

There is clearly a need for spatial conservation priorities that account for multiple dimensions of biological diversity, including taxonomy, phylogeny, and traits (15, 21, 22). However, the relationships among these dimensions across the globe are poorly understood and vary depending on the metric used and the scale of the analysis (15, 23). Some studies have shown a high correlation among taxonomic, phylogenetic, and trait diversity of global mammals (23, 24), especially when using diversity indices affected by species richness, i.e., phylogenetic diversity (14) and functional diversity (20). For example, species richness was an effective surrogate for the functional and phylogenetic dimensions of local rodent assemblages in Manu (25). In contrast, Mazel et al. (15) identified strong geographical mismatches among global hotspots of taxonomic, phylogenetic, and functional diversity of mammals. Low geographical congruence was also found in prioritization analyses based on taxonomic, phylogenetic, and trait diversity of birds and mammals in Brazil (21).

Significance

Approximately a quarter of all land mammals are currently threatened, mostly by human activities including habitat loss and harvesting. Here, we provide the first biological map of priority areas that captures all three dimensions of mammalian biodiversity: taxonomic, phylogenetic, and traits. We find limited overlap in priority regions across the three dimensions and with currently protected areas, indicating that conservation planning should consider multiple dimensions of biodiversity to maximize biodiversity conservation. Our complementarity-based prioritization provides a conservation solution that can be incorporated in future conservation planning efforts aimed at helping protect not only species but also evolutionary potential and ecosystem function.

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The problem with the lack of congruence among dimensions is that conservation planning based on only one dimension does not fully represent biodiversity (26, 27). Policy responses to biodiversity loss require knowledge of how these dimensions relate to each other and should use a more integrated approach by considering each dimension independently and all three jointly.

Global priority regions for mammal conservation have been identified (9, 10, 28, 29), but few have included different [i.e., taxonomic, phylogenetic, and functional (15, 21)] dimensions of mammal biodiversity simultaneously, and few have used a complementarity-based prioritization framework globally (30–33). Further, all prioritization analyses for mammals incorporate taxonomic, phylogenetic, and functional information by using alpha diversity indexes (15, 21, 23). Selecting priority areas for conservation based on high alpha diversity could omit some species/lineages/traits, because alpha diversity indices do not take into account the differences in composition among sites (12). Complementarity is derived from beta diversity and is considered a core principle of systematic conservation planning to ensure that conservation actions are directed to all species, not just to those occurring in species-rich hotspots (7, 34). Complementarity-based selection of priority areas allows the representation of all biological features without much duplication of sites with similar species, resulting in a more cost-effective conservation solution (12). For example, Strecker et al. (22) performed the first complementarity-based prioritization, considering separately taxonomic, phylogenetic, and trait diversity in freshwater fish, highlighting the use of this approach for the optimal allocation of limited conservation resources that incorporates multiple dimensions of biodiversity.

Here we present a spatial conservation prioritization for terrestrial mammals using taxonomic, phylogenetic, and trait information

and a complementarity-based approach to site selection. Our aims were (i) to identify and compare priority regions for global terrestrial mammal conservation, based on taxonomic, phylogenetic, and trait dimensions and (ii) to evaluate how those priority areas relate to threatened species' distribution and existing protected areas. Our work on the global prioritization of mammalian biodiversity across the dimensions can be used as a biological layer from which priority areas can be identified and subsequently combined with political, social, and economic considerations (e.g., ref. 31).

Results and Discussion

Priority Areas for Global Mammal Conservation Across the Three Dimensions of Biodiversity. We found that important areas for mammal conservation had strikingly different spatial patterns for the three dimensions of biodiversity (Figs. 1 and 2). For the top 17% of sites with the highest conservation values, priority areas based on taxonomic dimension were spatially scattered, whereas the phylogeny- and trait-based priority areas were more contiguous (Fig. 1; for maps with all values see Fig. S1). Similarly, Carwardine et al. (35) and Dobrovolski et al. (32) found a scattered pattern of global priority areas for mammals, and Albuquerque et al. (36) also found the same diffused priority areas for mammals, birds, and amphibians. The areas we identified by using the taxonomic dimension were likely spatially scattered because of the prioritization algorithm we used. The core-area algorithm reduces biological loss by retaining the core of each species' geographic range, even when they occur in species-poor regions, and it favors species with restricted ranges in the final solution.

In our study, priority areas based on phylogeny and traits were generally similar, but there were important differences as well.

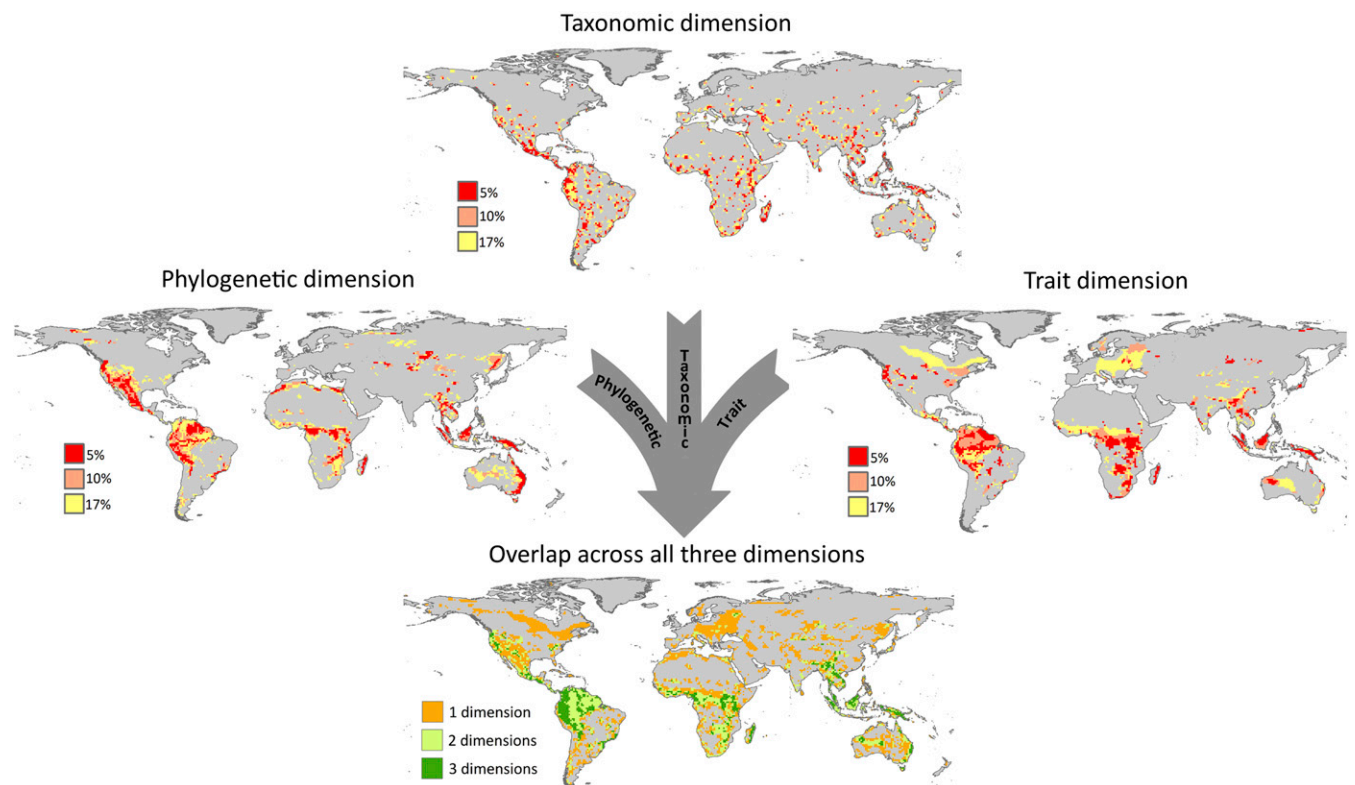


Fig. 1. The top 17% of cells selected according to zonation prioritization based on the taxonomic dimension, phylogenetic dimension, trait dimension and on the overlap across the three dimensions. In the overlap map, cells in which all three dimensions overlap are shown in dark green, those in which two dimensions overlap are shown in light green, and those selected only by one dimension are shown in orange.

Overlap among the top 17% priority areas, across the three dimensions of biodiversity

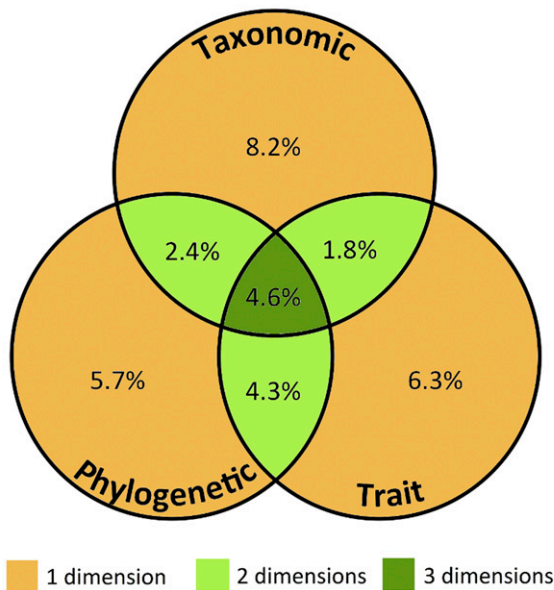


Fig. 2. Venn diagram showing the proportion of the land surface where we can observe the overlap between the top 17% priority areas across the taxonomic, phylogenetic, and trait dimensions of biodiversity, referent to the overlap map presented in Fig. 1. For example, only 1.8% of the land was selected as an area of priority for both the taxonomic and trait dimensions. The color scheme is that used in the overlap map in Fig. 1.

For example, parts of Australia were more valuable in the phylogeny-based solution than in the trait-based solution. Almost half of the native land mammals from Australia are either monotremes or marsupials, lineages that diverged early in mammalian evolution and have a unique evolutionary history, making them phylogenetically distinct. However, the ecological traits of Australian marsupials are functionally similar to those of placentals and are classic examples of ecological convergence (37). The preponderance

of these distinct lineages may explain why Australia had more areas of importance when we considered priorities for the phylogenetic dimension rather than trait dimension, and the results suggest we are successfully capturing different facets of biodiversity in our prioritization analyses.

The overlap of important areas across the three dimensions of biodiversity was low, only 4.6% of the global land area (Figs. 1 and 2). Many of the overlapping regions have been identified previously as important areas for conservation because of their high species richness and number of threatened and restricted-range species, including mammals and other vertebrates, invertebrates, and trees (10, 31–33, 36, 38). These areas also were included in the global priority map for the expansion of protected areas to achieve the goals of 17% of global protected land and triple the average protection of vertebrate species' ranges (39). Further, some of the areas that we identify here as important for all dimensions of mammal biodiversity are already recognized as Biodiversity Hotspots (40) and High Biodiversity Wilderness Areas (41). For example, the Tropical Andes in the Neotropics, Madagascar, Sundaland and Indo-Burma regions in Indo-Malay realm, and the forest of eastern Australia are biodiversity hotspots because of their high vulnerability and irreplaceability (40). Likewise, the Amazon and New Guinea are identified by Conservation International as High-Biodiversity Wilderness Areas because of their mostly intact original vegetation cover and high species richness and endemism (41). We found that these areas are important for all three dimensions of biodiversity and that they harbor not only high species richness and endemism but also unique evolutionary lineages and distinct ecological traits, underscoring the importance of protecting these regions.

The conservation values according to our prioritization analysis for each of the different dimensions were correlated (Table 1 and Fig. S2), but correlation values were small, and the correlation plots did not show clear trends, again indicating the low congruence of conservation priorities among the three dimensions of mammal biodiversity. The conservation values were also positively correlated with species richness and with the number of threatened species, showing that places with higher conservation values for all dimensions usually had higher species richness (Table 1 and Fig. S3), and consistently harbored a greater number of threatened species (Table 1 and Fig. S4). The spatial mismatch among the taxonomic, phylogenetic, and functional components

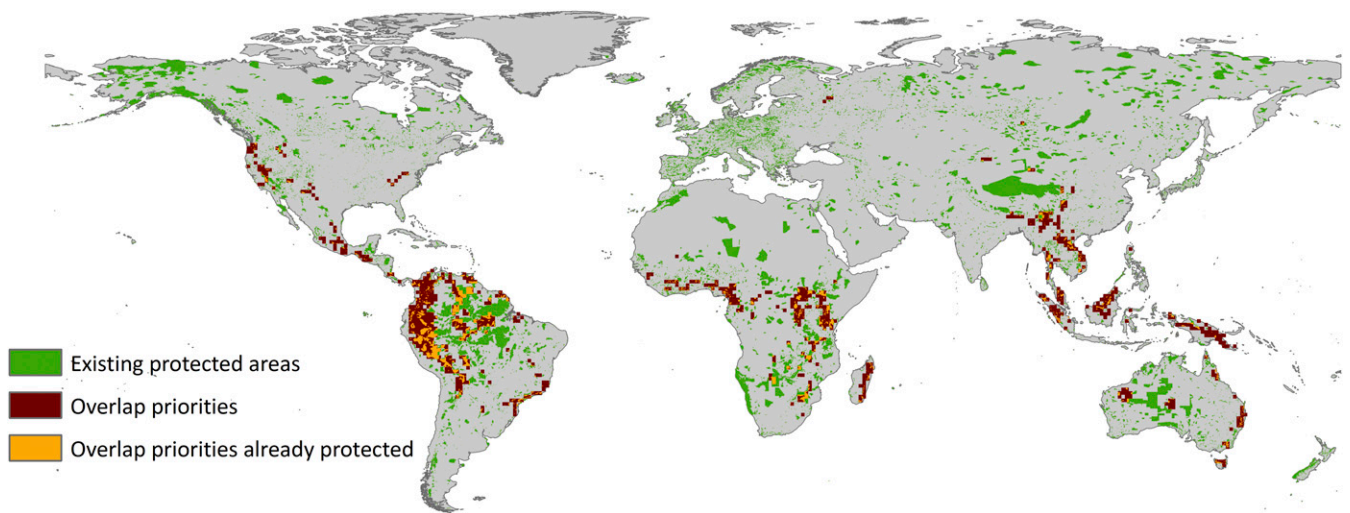


Fig. 3. The overlap across areas important for the taxonomic, phylogenetic, and trait dimensions (brown), the current network of protected areas (green), and areas of overlap that are already protected (orange).

Table 1. Kendall rank correlation coefficients (τ) between the conservation priority values given by the spatial prioritization analysis for each pair of dimension of biodiversity (species, phylogeny, and traits) and with species richness and the number of threatened mammal species

	Conservation priority				Number of threatened species
	Taxonomic dimension	Phylogenetic dimension	Trait dimension	Species richness	
Conservation priority for taxonomic dimension	1.00	0.30	0.25	0.34	0.44
Conservation priority for phylogenetic dimension	0.30	1.00	0.43	0.46	0.37
Conservation priority for trait dimension	0.25	0.43	1.00	0.50	0.34

All correlation coefficients were significant for $P < 0.001$.

of biodiversity has been observed globally for birds (26), freshwater fishes (22), and mammals (15). Such lack of congruence triggers a conservation conflict, because conservation strategies based only on taxonomic diversity do not include important phylogenetic and functional hotspots (15, 26).

Priority Areas and Currently Protected Areas. Currently protected areas performed poorly in terms of protecting the species, phylogenetic diversity, trait dimensions of mammal biodiversity and also in protecting threatened species (Table 2). The average conservation values of cells currently under protection were significantly lower than would be expected by randomly selecting areas around the globe, and this finding was consistent for each of the three dimensions and for all three dimensions jointly (Fig. S5). Similarly, Guilhaumon et al. (27) found that the Mediterranean marine protected areas system did not harbor more taxonomic diversity, phylogenetic diversity, or functional diversity of coastal fish than would be expected by chance. Jenkins et al. (38) showed that location of protected areas in the United States contrasts with regions where high numbers of endemic and threatened species are located, leaving unique species unprotected. Some of the priority areas highlighted by Jenkins et al. (38) concur with those that we identify as important across the three dimensions of mammal biodiversity, especially in the western United States. Several studies (e.g., refs. 42–44) have shown that the global network of protected areas is ineffective and is biased toward residual locations; these places are considered cheap to protect because they are remote or of low economic value, making it easier to set them aside for protection (7, 44, 45). Our findings combined with these other studies at local and regional scales demonstrate that currently protected areas are not maximizing the coverage of biodiversity.

Of the 4.6% of the area that we indicated as having priority for conservation across all dimensions of mammal biodiversity

(consensus map, Fig. 3), only 1% is currently protected, leaving vulnerable 3.6% of the most important areas for all three dimensions of mammal diversity conservation. Considering that ~14% of the Earth's land area is already protected (46), the 3.6% of unprotected land that we identified here as key areas for mammal conservation could inform efforts to expand the system of currently protected areas to achieve the Aichi Target 11. However, setting aside areas for conservation incurs socioeconomic and political costs, such as land acquisition value, social conflicts, and political willingness (7, 35). Therefore, the priority areas provide a key biodiversity layer for future conservation planning that should be considered along with the priority areas of other taxonomic groups and economic, social, and political considerations (7, 12, 35). They also highlight biologically important, unprotected regions of the globe that can be used to guide future conservation planning at both regional and global scales.

Conclusion

We show that priority areas for taxonomic, phylogenetic, and functional dimensions of biodiversity are strongly spatially mismatched, suggesting that conservation planning based in only one dimension of biodiversity could undermine the conservation of the other two. Effective conservation planning should maintain taxonomic, phylogenetic, and functional diversity to ensure biodiversity persistence in a changing world (47). Here, we identify a set of areas that are high conservation priorities across all three dimensions; this information can be used to inform conservation actions to expand the current network of protected areas to achieve the 17% target proposed by the Convention on Biological Diversity strategic plan for 2011–2020. The current system of protected areas poorly protects species richness, phylogenetic diversity, functional diversity, and threatened species; the important areas that we identified could perform better for

Table 2. Percentage of global total of species richness, phylogenetic diversity (14), trait diversity (20), and number of threatened species that are retained within the top 17% of the important regions for each dimension (taxonomic, phylogenetic, and functional) and across all three dimensions (overlap priorities) from the zonation prioritization analyses and in currently protected areas

% of the global total	Zonation prioritization				Currently protected areas, %
	Taxonomic dimension, %	Phylogenetic dimension, %	Trait dimension, %	Overlap priorities	
Species richness	99	83	71	70	62
Phylogenetic diversity	99	90	87	80	74
Trait diversity	99	91	80	80	78
Threatened species	99	72	56	57	37

all these aspects of biodiversity. The small fraction of areas (4.6%) where there was overlap across the dimensions should receive special conservation attention. Those areas retain many restricted-range species that have distinct evolutionary history and unique traits. Our work presents a global effort to identify important areas for terrestrial mammal conservation across the taxonomic, phylogenetic, and functional dimensions of biodiversity using a complementarity-based analysis. The key areas identified here can be used as a biological foundation for future conservation planning, which also would have to account for other factors such as opportunity costs, social/political considerations, and funding for land purchase. Conserving biodiversity beyond species identity (13, 48, 49) is crucial to ensure the provision of ecosystem services and their contribution to human well-being, the evolutionary potential for species to evolve and adapt, and the extraordinary diversity that exists across mammalian lineages.

Methods

Occurrence Data. We used maps of “extent of suitable habitat” that were generated based on species’ ranges and habitat preferences (50) to calculate mammal species occurrence. We aggregated the occurrence information into distribution maps (presence/absence) of $1^\circ \times 1^\circ$ ($\sim 110 \times 110$ km at the equator) and identified priority regions for the mammal taxonomic dimension using geographic distribution maps for 4,547 terrestrial mammals.

Traits. We compiled a species-level traits database for 4,547 terrestrial mammals (17, 51–54). From a total of 23 traits available, we used 14 intrinsic biological traits in the analyses. We chose these traits based on ecological importance, the correlation among them, and the percentage of missing values. Traits were related to resource use (activity cycle, habitat mode, trophic level, diet breadth), speed of life history (body mass, litter size, litters per year, gestation length, weaning age, neonate body mass, maximum life span), and population characteristics (social group size, population density). Because removing species for which some trait data are lacking can cause statistical bias and interpretation error (55), we imputed missing trait values using missForest [Package missForest in R (56)], a nonparametric approach based on random forests. This method performs well on large databases with correlated variables (56, 57). Phylogeny was not used in the imputation analysis. Because some of the traits had high proportions of data missing, we ran the prioritization analysis removing traits with more than 60% of missing data as a robustness check. We found that removing traits that had high proportions of missing data before imputations did not change our main results.

To represent the trait dimension in the prioritization analyses, we followed the framework of Strecker et al. (22), using a grid cells \times traits matrix. To create this matrix, all trait variables were converted into binary format. For categorical traits, we assigned the presence/absence of each category. We split quantitative traits into 5% quantiles and then converted them into binary variables. (We choose to use 5% to incorporate more trait variability in our analysis.) Once our dataset was converted to binary format, we created a binary species \times traits matrix. By multiplying the species \times traits and species \times grid cells (obtained from occurrence data) matrices, we obtained a trait \times grid cells matrix in which each $1^\circ \times 1^\circ$ grid cell contained the number of species exhibiting a trait value (e.g., the number of nocturnal species in that cell). Then we generated a distribution map for each trait value and used those maps in the prioritization analysis to find the priority regions for mammal trait dimension.

Phylogeny. We used phylogenetic eigenvectors to represent the phylogenetic dimension in our analyses, thereby avoiding nonindependence issues associated with phylogenetic trees (58). We used an interpolated, smoothed phylogenetic tree of mammals (59) to obtain a phylogenetic distance matrix among all species. Then we synthesized the phylogenetic information in eigenvectors by conducting a principal coordinate analysis (PCoA) based on phylogenetic distances between species (PVR package in R; refs. 58, 60). Eigenvectors from a phylogenetic distance matrix reflect the different phylogenetic relationships among species in independent vectors (60). The first eigenvectors tend to represent larger distances among species, expressing divergences closer to the root of the phylogeny (60), and subsequent eigenvectors tend to capture phylogenetic relationships closer to the terminal nodes. For each species, we generated multiple eigenvector scores that represent relatedness of each species to all other species at different

phylogenetic levels. We used only axes that presented eigenvalues larger than 1%, because axes with eigenvalues less than 1% contain only a small fraction of the total variation of the whole phylogeny, and we wanted to avoid including low-representative axes in the analysis. From 4,546 phylogenetic axes generated by the PCoA, we only used 16 eigenvectors in our analyses. These eigenvectors contained 63% of the total variation in the phylogenetic distance matrix. We also tested whether our results were sensitive to the number of eigenvectors by using 16, 100, 200, and 250 eigenvectors. Because the results generated by the different sets were highly correlated, the inclusion of more eigenvectors appeared not to provide any significant new information in the analyses.

We split the first 16 phylogenetic eigenvectors into 5% quantiles, as we did for the continuous traits. For each eigenvector, species were split into 20 same-size phylogenetic groups in which species were grouped based on their phylogenetic affinity in a given phylogenetic level. Then we multiplied the binary matrix of species \times phylogenetic groups by the grid cells \times species matrix, resulting in a matrix of site \times phylogenetic groups in which each $1^\circ \times 1^\circ$ grid cell contained the number of species belonging to a particular phylogenetic group. Next, we generated a distribution map for each phylogenetic group and used those maps in the prioritization analysis to find the priority regions for the mammal phylogenetic dimension.

Prioritization Analyses. We identified the important areas for mammal conservation across the dimensions of biodiversity using Zonation (61). Zonation produces a hierarchical prioritization of the study region based on the biological value of sites (cells), accounting for complementarity by considering the representation level of all species (or other biodiversity features). Zonation iteratively removes cells whose removal causes the smallest loss in biodiversity representation across the overall remaining region until no cell is left in the region. The hierarchical prioritization of the region is based on the order of cell removal, which is recorded and can be used later to select any given top fraction (e.g., best 10%) of the region. This order of cell removal is called “conservation value” and ranges from 0 to 1, with 0 being the first cell removed (i.e., the least important for retaining biodiversity representation) and 1 being the last cell removed from the region (the most important).

The basic cell-removal rule is the Core-Area Zonation (CAZ) algorithm. The CAZ algorithm calculates the conservation values of each cell based on the marginal loss (i.e., the relative contribution to total diversity) of the species/phylogenetic group/trait value with the higher proportion of its range in that cell. CAZ prioritizes sites by gathering a higher proportion of each dimension distribution, thus favoring rare species/phylogenetic groups/trait values in the final solution, even when they occur in otherwise species-poor regions. We analyzed each dimension separately because we wanted to evaluate the individual solution generated by each dimension and to determine how much they converge. Following the Convention on Biological Diversity (5), which proposed that 17% of the terrestrial areas should be protected by 2020, we focused our analyses on the 17% of the world with the highest conservation value (i.e., cells with conservation value greater than or equal to 0.83). In addition, we provide the full results in Fig. S1.

Protected Areas. To compare the priority areas across the three dimensions with currently protected areas, we used the International Union for the Conservation of Nature (IUCN) and United Nations Environmental Programme World Conservation Monitoring Center (UNEP-WCMC) data on global protected areas (62). We included only restricted protected areas classified as I–IV by the IUCN in our analyses. We resampled protected areas at the $1^\circ \times 1^\circ$ grid cell level.

Congruence Among Dimensions. We assessed the congruence among dimensions and between each dimension and species richness and the number of threatened species in two ways: (i) by evaluating how the conservation values generated in our prioritization analysis related between dimensions and (ii) by calculating how much of the global amount of taxonomic/phylogenetic/trait diversity was captured by each spatial priority. First, we calculated the Kendall rank correlation to evaluate how the conservation priority values of the cells for the prioritization based on each dimension (taxonomic/phylogenetic/trait) related to each other and to species richness and to the number of threatened species. Then, to evaluate how much the spatial priorities of each dimension captured the existing taxonomic, functional, and phylogenetic diversity of terrestrial mammals, we calculated the global amount of species richness, the number of threatened mammals, phylogenetic diversity (the PD index) (14), and functional diversity (the FD index) (20). Last, we assessed how much of the global total of each index was captured proportionally by the conservation solution for each dimension

and by the overlapping areas among all dimensions. We also performed the same calculation to determine how much of the global total of species richness, number of threatened mammals, phylogenetic diversity, and functional diversity are protected by the currently protected area network. The analyses were performed in R, using the “stats” package (63) for correlation analysis and the “picante” package (64) to calculate phylogenetic and functional diversity indexes.

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