



High exposure of global tree diversity to human pressure

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Safeguarding Earth's tree diversity is a conservation priority due to the importance of trees for biodiversity and ecosystem functions and services such as carbon sequestration. Here, we improve the foundation for effective conservation of global tree diversity by analyzing a recently developed database of tree species covering 46,752 species. We quantify range protection and anthropogenic pressures for each species and develop conservation priorities across taxonomic, phylogenetic, and functional diversity dimensions. We also assess the effectiveness of several influential proposed conservation prioritization frameworks to protect the top 17% and top 50% of tree priority areas. We find that an average of 50.2% of a tree species' range occurs in 110-km grid cells without any protected areas (PAs), with 6,377 small-range tree species fully unprotected, and that 83% of tree species experience nonnegligible human pressure across their range on average. Protecting high-priority areas for the top 17% and 50% priority thresholds would increase the average protected proportion of each tree species' range to 65.5% and 82.6%, respectively, leaving many fewer species (2,151 and 2,010) completely unprotected. The priority areas identified for trees match well to the Global 200 Ecoregions framework, revealing that priority areas for trees would in large part also optimize protection for terrestrial biodiversity overall. Based on range estimates for >46,000 tree species, our findings show that a large proportion of tree species receive limited protection by current PAs and are under substantial human pressure. Improved protection of biodiversity overall would also strongly benefit global tree diversity.

biodiversity | conservation frameworks | land use | protected areas | tree species

Trees play a vital role in the biosphere. As key agents in the flow of energy and matter, they protect catchments and stabilize drainage areas, sequester carbon, and regulate climate on a local-to-global scale (1–3). Trees also provide habitat for a large proportion of the diversity of the world's vertebrates, invertebrates, and fungi (4–9). The magnitude of many of these functions and services increases as tree diversity increases, and greater functional diversity of tree assemblages enhances ecosystem productivity and stability (10–12). However, continued global forest loss and degradation (13–20) have decimated biodiversity among tree and tree-dependent organisms (8, 21–23). Tree diversity loss diminishes ecosystem resilience and contributions to coregulating the changing climate system (24–26). While policy makers and land managers are increasingly aware of the importance of trees, an in-depth global assessment of the adequacy and effectiveness of existing protections for tree diversity is lacking. A comprehensive assessment of protection and pressures on tree diversity would provide important input for establishing conservation and restoration priorities to bend the curve of biodiversity loss (27).

Protected areas (PAs) represent a first-order conservation strategy for preventing biodiversity loss, aimed to preserve natural ecosystems (28–30) and their inherent services, such as carbon sequestration (31). At present, PAs cover 15.8% of the Earth's land (World Database on Protected Areas; WDPA*). This value remains below the 17% of Earth's land area recommended by the Convention on Biological Diversity (CBD) 2020 target (see *SI Appendix, Box S1* for a detailed explanation). However, it is not well-understood how well existing PAs cover tree species diversity.

Significance

Earth's tree diversity is crucial for biodiversity and ecosystem functions and services. Using species range estimates for 46,752 tree species, we find that an average of 50.2% of a tree species' range occurs in 110-km grid cells without any protected areas, with a total of 6,377 small-range tree species entirely unprotected, and that 83% of tree species experience nonnegligible human pressure across their range on average. Protecting additional areas selected to optimally cover multiple dimensions of tree diversity would strongly improve this situation. Our results highlight the need for strengthening efforts to protect tree diversity via increased coverage of protected areas through well-targeted conservation actions as well as integration of tree diversity into restoration efforts in human-dominated landscapes.

The authors declare no competing interest.

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*<https://www.protectedplanet.net/en>, accessed 30 May 2022.

Given the current pace of biodiversity loss, debate has arisen regarding the post-2020 PA targets (32–34). One initiative that has gained significant momentum is E. O. Wilson’s “Half-Earth” proposal (35), which argues that half of the Earth’s surface needs to be protected in order to avoid major biodiversity loss and safeguard major ecosystem processes and services (36–39). This proposal aligns with the 2050 Vision for Biodiversity, proposed by CBD parties for the Post-2020 Global Biodiversity Framework (40). Different frameworks may suggest different priority areas (*SI Appendix, Box S1*) for future PAs, but effective, coordinated global conservation measures require a strong consensus. While various organizations may establish global conservation targets and areas of priority based on different considerations (29, 41), the realized network of PAs should ideally effectively represent overall biodiversity as identified through systematic analyses (28).

Recent studies have highlighted the need to consider multiple biodiversity dimensions, including phylogenetic and functional diversity, and their roles in providing ecosystem services in spatial conservation planning (42–44). Unlike taxonomic diversity, which is still most often used in biodiversity assessments, functional and phylogenetic diversity represent critical ecological and evolutionary aspects of biodiversity not fully captured by species composition alone (45–50) (but see ref. 51). Given the pivotal role of trees in global terrestrial ecosystems, questions surrounding how well their multiple diversity dimensions are and could be protected by major biodiversity policy targets are critical to the domains of both conservation and the broader sustainability agenda, such as the rising global interest in tree restoration (3) and integration of trees into agricultural production systems (52, 53).

While foundational to conservation efforts, PAs are seldom free from anthropogenic pressures. For example, a recent study found that approximately one-third of global PAs experience intensive human pressure (54). Anthropogenic pressures on PAs may increase as human activity near existing PAs intensifies, and as new PAs are increasingly established in proximity to global population centers (30, 55). Many regions that host high biodiversity overlap with human settlements. As a result, future PAs will be confronted with other land-use demands (56, 57), given the rising global human population and natural resource requirements. Examining human pressure within existing PAs and priority areas for tree diversity is important for assessing both the effectiveness of current PAs in protecting the tree species they harbor, and the need for increasing protection of currently unprotected priority areas for tree diversity.

Here, we analyze a recently developed global database of 46,752 tree species’ ranges to 1) assess range protection and anthropogenic pressures for tree species, 2) identify priority areas for conservation of tree diversity considering multiple diversity dimensions, and 3) assess the geographic distribution of current PAs and different potential conservation prioritization scenarios and their respective coverage of global tree species diversity. We used complementarity analysis [Zonation (58, 59)] and integration of taxonomy, phylogenetic relatedness, and functional traits to assess whether priority areas for tree conservation overlapped or diverged spatially according to different diversity dimensions (42, 44). Taxonomic diversity was represented by species identities. Phylogenetic diversity was represented by phylogenetic eigenvectors computed from a genus-level phylogeny (60). Functional diversity was represented using similar eigenvectors, based on eight commonly measured, ecologically important traits including maximum

height, wood density, specific leaf area, leaf area, leaf nitrogen concentration, leaf phosphorus concentration, leaf dry matter content, and seed dry mass (*SI Appendix, Table S1*).

We used these diversity data to estimate overlaps in the priority areas for three diversity dimensions for the top 17 and 50% area targets, representing the CBD 2020 target and the Half-Earth proposal, respectively. By comparing the tree species’ range parts covered by existing PAs (as documented by the WDPA) with those covered by the top 17 and top 50% priority areas identified through the Zonation algorithm, we quantified the coverage of existing and potential PAs with respect to global tree diversity. We further quantified anthropogenic pressures on species by estimating the Human Modification Index (HMI) (61) for each species’ range inside and outside existing PAs, as well as for areas covered by potential future PAs for the different conservation targets. As a cumulative measure of human alteration of terrestrial areas based on 13 anthropogenic layers, HMI is a unitless index that ranges from 0 to 1, with $0 \leq \text{HMI} \leq 0.1$ as low (e.g., a value of 0.007 for wildlands), $0.1 < \text{HMI} \leq 0.4$ as moderate (e.g., 0.12 for seminatural lands and 0.37 for croplands), and $0.4 < \text{HMI} \leq 1.0$ as high to very high (e.g., 0.58 for dense settlements and 0.65 for villages), following ref. 61.

We also tested coverage of existing PAs and top-priority areas for tree diversity in relation to the different existing frameworks for biodiversity conservation (*SI Appendix, Box S1*), covering three global biodiversity conservation priority frameworks proposed by leading conservation nongovernmental organizations (NGOs). These included the Global 200 Ecoregions (G200), Biodiversity Hotspots (BH), and Last of the Wild (LW) (29) (*SI Appendix, Box S1*; hereafter “NGO frameworks”). These NGO frameworks prioritize either areas of high vulnerability (BH), the most intact areas (LW), or areas of highest irreplaceability (G200) (29). We identified gaps and overlaps between current conservation efforts (PAs), our estimated priority areas for tree diversity, and these existing NGO frameworks to assess their utility for protecting Earth’s tree diversity and guiding future funding and conservation efforts.

Results

Global Protection Coverage and Pressures on Tree Species.

Across all 46,752 tree species in our dataset, an average of 50.2% of a species’ range occurred in 110-km grid cells without existing PAs. A total of 6,377 species (13.6% of the tree species evaluated) experience no protection anywhere in their range (Fig. 1A and *SI Appendix, Table S2*), and 10,987 (23.5% of tested) tree species have less than 25% of their ranges in such PA cells (*Dataset S1*). Most tree species experience at least moderate human pressure within their ranges, with an average HMI of 0.25 across all species (a value comparable to the HMI across most of Wales; Fig. 1A and *SI Appendix, Table S2*). A total of 14.8% of tree species experience high to very high average human pressure within their range ($0.4 < \text{HMI} \leq 1.0$), and an additional 68.5% experience moderate average human pressure ($0.1 < \text{HMI} \leq 0.4$) (following ref. 61). For the portions of species’ ranges inside protected cells (110-km cells with PAs), human pressure is relatively low, with an average HMI of 0.11. In contrast, the unprotected portion of tree species’ ranges (110-km cells without PAs) are exposed to considerably higher human pressure, with a mean value of 0.25, and 7,776 species experiencing high to very high HMI in these areas (Fig. 1A). The global patterns described above largely reflect relatively wide-ranged tree species (*SI Appendix, Fig. S1 and Table*

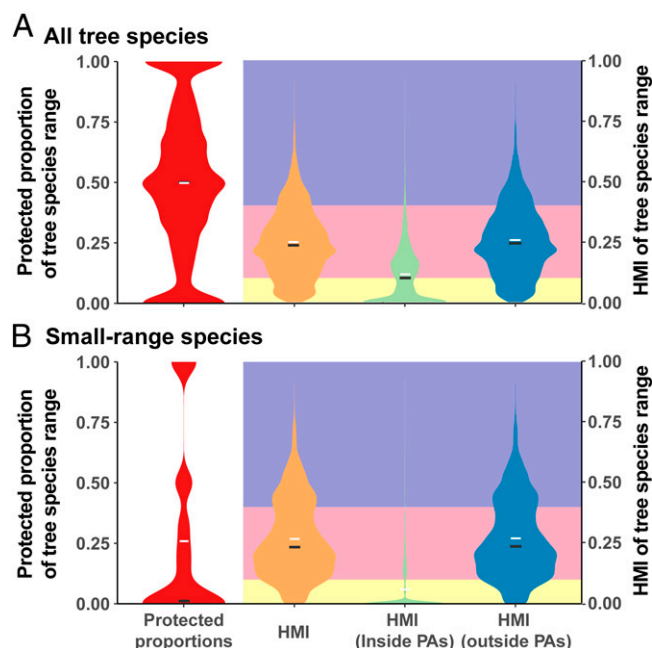


Fig. 1. Current protection status and pressures on tree species' ranges for all (A) and small-range tree species (B) (the first range size quantile). Protected proportions show the proportion of each tree species' range within existing PAs; HMI indicates the mean Human Modification Index within a tree species' range, overall, or just the range part within or outside PAs. Mean and median values are indicated by white and black solid lines in the violin density plots, respectively. Colored panes in yellow, pink, and purple, respectively, indicate low ($0 \leq \text{HMI} \leq 0.1$), moderate ($0.1 < \text{HMI} \leq 0.4$), and high to very high ($0.4 < \text{HMI} \leq 1.0$) levels of human modification (61). *SI Appendix, Table S2* lists the mean, median, and first and third quartiles for each variable.

S2). By contrast, small-range tree species (the first quintile of tree species' range sizes) have overall greater unprotected range proportions (mean value of 74.1%), and all of the 6,377 species that are completely unprotected are such small-range species. Compared with species with larger ranges, small-range species have lower HMI (a mean of 0.06) within PA cells but slightly higher human pressures outside PAs (Fig. 1B and *SI Appendix, Fig. S1* and *Table S2*).

Global Priority Areas for Tree Conservation across Three Dimensions of Diversity. The top-priority areas for the 17 and 50% targets show considerable spatial divergence when selected separately considering taxonomic, phylogenetic, and functional diversity dimensions (Fig. 2 and *SI Appendix, Fig. S2*). The 48.2% of the 17% top-priority areas for the different diversity dimensions are selected according to all three dimensions. Another 43.5% of the 17% target priority areas selected based on taxonomic diversity differ from those based on phylogenetic and functional diversity (Fig. 2B). By contrast, the 17% top-priority areas determined according to phylogenetic or functional diversity largely overlapped, reflecting the strong correlation between the two dimensions (Fig. 2A and B and *SI Appendix, Fig. S2* and *Table S3*). Overlaps were stronger for the top 50% priority areas but otherwise similar (Fig. 2C and D and *SI Appendix, Fig. S2*).

Areas prioritized according to all three diversity dimensions occur primarily in the tropical rainforest regions of the Americas, Africa, Indo-Malaya, and Australasia, as well as in subtropical Asia for the 17% target, but also cover subtropical and warm-temperate regions more broadly under the 50% target. Generally, areas prioritized by just two diversity dimensions mainly occur in tropical and subtropical savanna areas (e.g., the

Cerrado in Brazil) for the 17% target, but also include temperate areas in North America and Europe as well as in arid areas, notably in Australia, for the 50% target (Fig. 2A and C). High-priority sites only selected according to a single diversity dimension show a scattered global distribution (Fig. 2A and C).

Protection Coverage and Pressures Associated with Global Priority Areas. Protecting the 17 and 50% area targets based on priority areas according to taxonomic diversity would increase the average coverage of a species' range to 65.5% (top 17%) and 82.6% (top 50%), strongly exceeding the average range proportion covered by existing PA cells (49.8%) (red dashed lines in *SI Appendix, Fig. S3A* and *Table S4*). Expanding current PAs to either the 17 or 50% top-priority areas would furthermore increase tree species' protection status (*SI Appendix, Figs. S3A* and *S4*). For example, of the 13.6% of tree species in our dataset that are small-range and currently lack any protection, a majority (66.2%) would become partly or fully covered by 110-km grid cells with potential PAs corresponding to the 17% top-priority areas (yellow flow ribbons in *SI Appendix, Fig. S3A*). The proportion of species whose entire range falls within 110-km grid cells with PAs would increase to 24.8 and 42.5% if the 17 and 50% target top-priority areas were protected, respectively. Mean HMI values for the priority areas under the 17 and 50% targets exceed those estimated for existing PAs (red dashed lines in *SI Appendix, Fig. S3B* and *Table S4*), reflecting that ca. 30% more species experience moderate to high HMI values within these top-priority areas relative to the proportion within current PAs.

Protection coverage and current pressure for prioritizations based on functional and phylogenetic diversity resemble those based on taxonomic diversity (*SI Appendix, Table S4*), with only minor differences (*SI Appendix, Fig. S3A* vs. *C* and *E*). However, we found important differences in the degree of protection in wide- vs. small-range species, particularly for the top 17% priority area scenario. Specifically, the priority areas obtained considering taxonomic diversity would greatly increase the protection coverage of small-range species to 75% of the mean proportion of ranges, while the protection coverage of small-range species would only reach ca. 53% if using the priority areas obtained from the other two dimensions (*SI Appendix, Fig. S4*).

Global priority areas identified using all three diversity dimensions simultaneously largely match results from the single dimensions, especially those from taxonomic diversity (Figs. 3 and 4). Many of the areas designated as top 17% priority areas experience moderate human pressure. These areas include southern and eastern Asia, South America outside the Amazon Basin, and Madagascar (Fig. 4). Many of the top 50% priority areas are subject to high human pressure (Fig. 4). They include many European countries, India, eastern China, Indonesia, Nigeria, Ethiopia, central North America, and eastern Argentina.

Congruence among Top Tree Conservation Priority Areas, Existing PAs, and NGO Frameworks. Grid cells with existing PAs cover only about half of the top 17 or 50% priority areas for tree conservation as jointly defined by taxonomic, phylogenetic, and functional diversity (51.2 and 44.6%, respectively, the proportion of "current PAs only" + "shared" in Fig. 5). In terms of overlap between PAs and the three NGO frameworks (*SI Appendix, Fig. S5*), G200 showed the greatest degree of overlap with the top 17% priority areas (45.4%). The BH framework showed 34.8% overlap, and the LW framework showed only 7.3% overlap with the top 17% priority areas (Fig. 5A). Expansion of PAs based on the G200

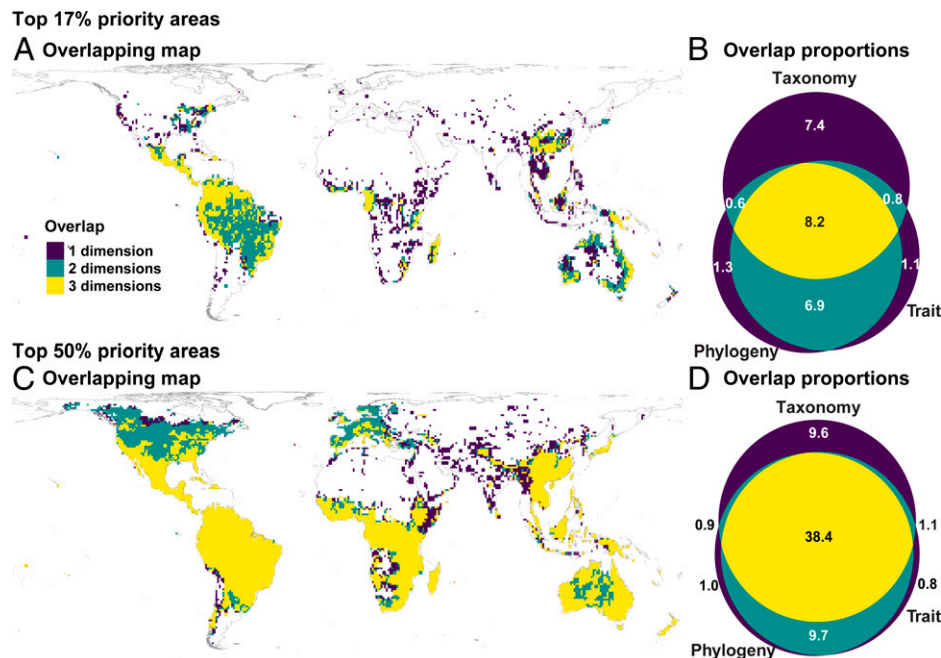


Fig. 2. Top 17% and top 50% priority areas (A and C) according to species taxonomic, phylogenetic, and functional diversity dimensions defined by the Zonation prioritization. The Venn diagrams show overlapping and unique areas for prioritizations for the 17% target (B) and 50% target (D) based on either taxonomic, phylogenetic, or functional diversity dimensions. Colors indicate overlap between combinations of two of the three dimensions (green), between all three dimensions (yellow), or no overlap (purple).

framework would protect ~91 or 83% of the top 17 and 50% priority areas for trees, respectively. The LW framework would only protect about 50% of the top-priority areas (57 and 53% for the top 17 and 50% priority areas, respectively), thus representing only minor improvements to current tree diversity and range protection. The BH framework offers an intermediate case and would protect 77 and 67% of

the top 17 and 50% priority areas for the three diversity dimensions for trees.

Discussion

Our results demonstrate that, conservatively estimated, on average approximately half of a tree species' range lacks protection

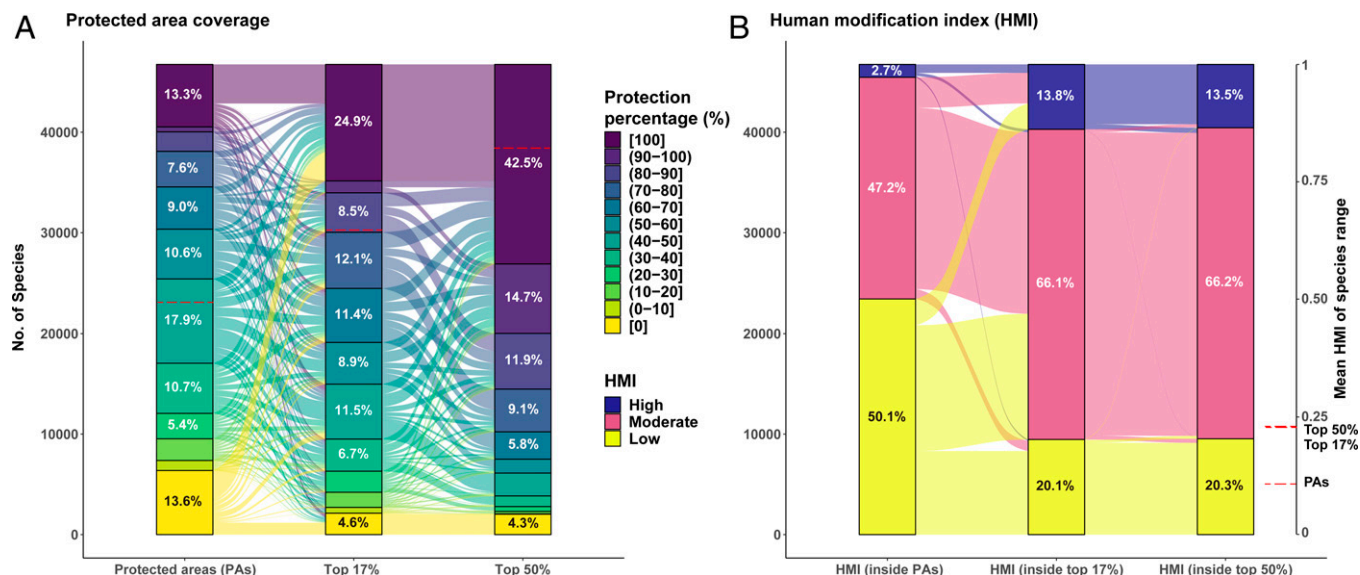


Fig. 3. Proportional changes in the number of tree species with (A) a certain proportion of the species range protected and (B) a certain level of human influence within the protected species range, computed for existing PAs, the top 17% priority areas, and between the top 17% and top 50% priority areas. The prioritization jointly considers taxonomic, phylogenetic, and functional diversity; results for prioritizations for taxonomic, phylogenetic, and functional diversity separately are shown in *SI Appendix, Fig. S3*. Ribbons represent proportional flows of species in terms of changing scores (i.e., either protection coverage [A] or human influence level [B]) between two consecutive grouping bars. (A) Protection percentage categories indicate the proportion of a species' range inside 110-km grid cells overlapping current PAs or the top 17% or top 50% priority areas, respectively. Red dashed lines indicate mean protection percentages for all tree species, with exact values given in *SI Appendix, Table S4*. (B) HMI categories based on the mean HMI value for the proportion of each species' range overlapping with existing PAs or the top 17% or top 50% priority areas. HMI values were divided into three categories following ref. 61 representing low ($0 \leq \text{HMI} \leq 0.1$), moderate ($0.1 < \text{HMI} \leq 0.4$), and high to very high ($0.4 < \text{HMI} \leq 1.0$) degrees of human modification. The y axis and dashed red lines (Right) show the average HMI values across all tree species' range proportions overlapping with either existing PAs or the top 17% or top 50% priority areas, respectively. *SI Appendix, Table S4* provides exact values.

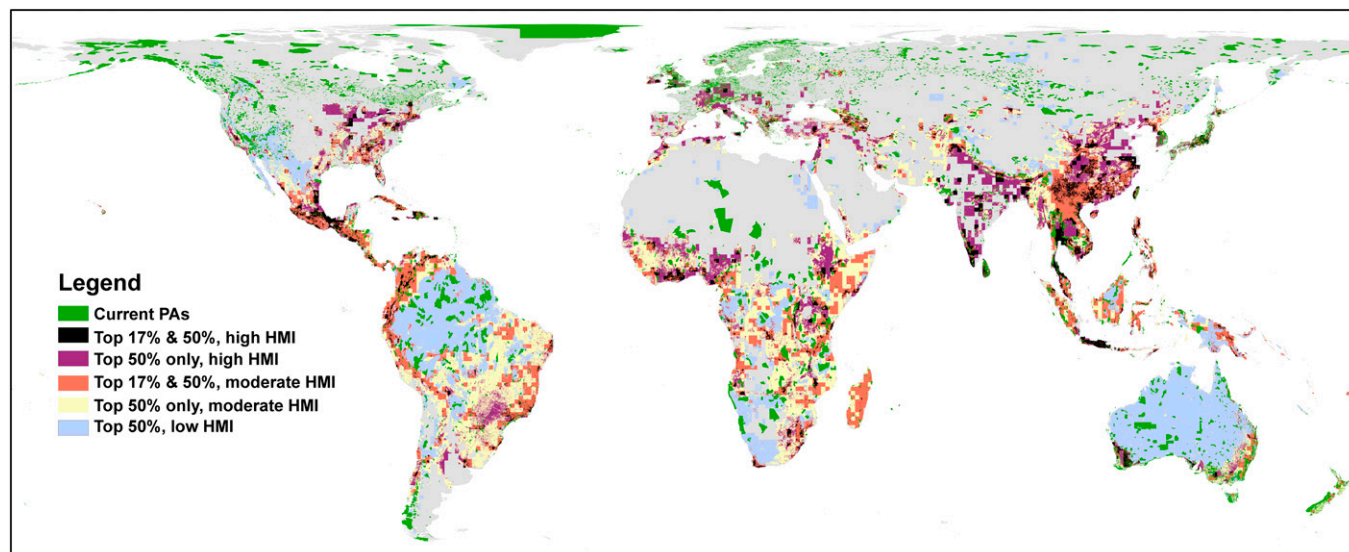


Fig. 4. Overlap between current PAs, top-priority areas for 17% and 50% targets, and the HMI. The priority areas for tree conservation are jointly defined according to taxonomic, phylogenetic, and functional diversity. HMI is categorized into low ($0 \leq \text{HMI} \leq 0.1$), moderate ($0.1 < \text{HMI} \leq 0.4$), and high to very high ($0.4 < \text{HMI} \leq 1.0$) levels(61). The HMI layer is shown at a resolution of 1 km².

under the current PA network. A majority of species' ranges experience moderate (32,003 species) or high (6,928 species) human pressure, even for species with ranges that are fully covered with existing PA grid cells. About 13.6% of tree species, all of which are small-range species, occur completely outside grid cells with existing PAs. Compared with average PA coverage (49.8% of species range in grid cells with PAs), the ranges of small-range tree species are only about half as well-covered

(25.9%) (*SI Appendix, Table S2*). In addition, nearly one-quarter of the 46,752 tree species have less than 25% of their ranges overlapping protected cells (i.e., grid cells with existing PAs). Overall, our results indicate that, even when optimistically equating PA presence in a 110-km grid cell as PA coverage (*Methods*), the current PA network is insufficient to protect Earth's tree diversity, particularly for small-range trees, given the fact that a large proportion of Earth's total tree species are estimated to be small-range, as found in our analysis. Further, a recent analysis estimates ca. 9,000 further undiscovered tree species, which will be mostly small-range species (62). However, our results also show that protecting the top 17 and 50% priority areas would strongly improve protection coverage and would include large numbers of areas of global importance for tree diversity that are currently exposed to moderate to high human pressure (Fig. 3 and *SI Appendix, Fig. S4*). Importantly, species with limited ranges would also be better protected (Fig. 3 and *SI Appendix, Fig. S4*), which is crucial as they experience greater anthropogenic pressures and extinction risk (63, 64).

Critically, 49.2% of tree species experience moderate to very high human pressure even within protected cells (Fig. 1*A*), highlighting the need to enhance protection effectiveness within and around PAs. Furthermore, half of the high-priority areas for tree diversity conservation currently have moderate to high human pressures. Here, pressures such as habitat conversion, overharvesting, or overgrazing by livestock threaten tree populations and may also negatively influence conservation efforts in nearby PAs (17, 18, 65–67). Our analysis thus identifies vulnerable areas in which protection efforts, mitigation of human pressure, and restoration efforts (*sensu ref. 29*), including cost-effective approaches such as natural regeneration of degraded habitat (68, 69), would yield high returns in terms of biodiversity protection goals (57). Mechanisms such as payments for ecosystem services programs could help achieve the reduction in human pressures in these critical areas identified in our study.

Studies of conservation priorities have often used taxonomic diversity or other singular dimensions (70–72) as a surrogate for other aspects of biodiversity or ecosystem function (50, 51, 73) (but see *ref. 45*). In the present study, we found that

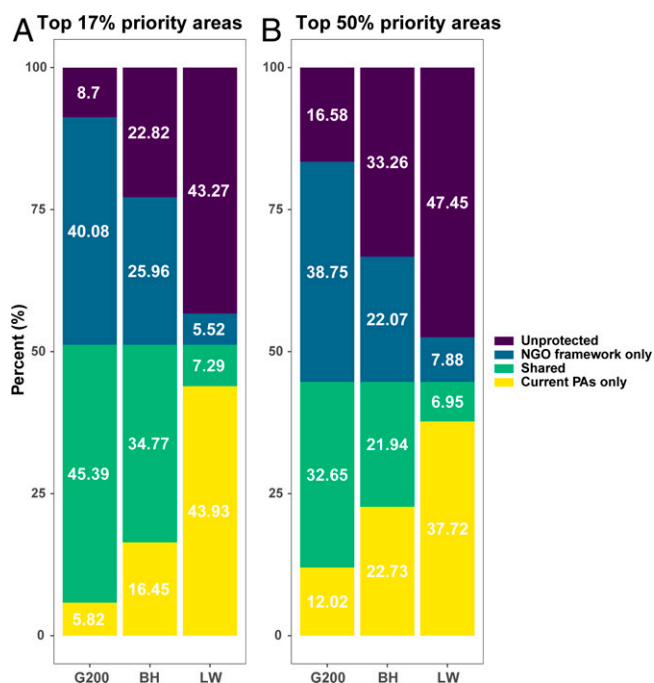


Fig. 5. Percentages of the (A) top 17% and (B) top 50% priority areas for tree diversity covered by existing PAs or by each NGO framework (G200, BH, and LW) for global biodiversity conservation. Colors indicate overlaps between combinations. Unprotected: areas not overlapping with either PAs or a conservation priority framework; NGO framework only: areas overlapping only with the considered NGO framework; shared: areas overlapping with both PAs and a given NGO framework; current PAs only: areas only overlapping with PAs. Priority areas for tree conservation are jointly defined according to taxonomic, phylogenetic, and functional diversity.

different diversity dimensions resulted in substantially different spatial prioritizations (Fig. 2 and *SI Appendix*, Figs. S2 and S3) and distinct relationships between species' range sizes and protection percentages (*SI Appendix*, Fig. S4), demonstrating the importance of considering multiple aspects of biodiversity in conservation planning (42, 44). Specifically, in using a comprehensive view of trees beyond only species in forests (74), we found certain regions usually not considered as tree diversity hotspots (e.g., tropical and subtropical savanna, temperate areas in North America and Europe, arid areas in Australia) are also priority areas within one- or two-dimensional priority analyses (Fig. 2). This finding apparently owes to certain traits or phylogenetic lineages evolved in situ, such as Cerrado woody species in Brazil (75) and the family Gyrostemonaceae, endemic to Australia and concentrated in the drier parts of the continent. In addition, phylogenetic and functional diversity dimensions support more spatially continuous priority areas than those determined by taxonomic diversity (Fig. 2; similar to ref. 44). Growing recognition of the importance of ecological integrity of large PAs supports the usefulness of phylogenetic and functional diversity dimensions in conservation planning (28, 35, 76). Further, priority areas defined by these dimensions include more temperate areas (*SI Appendix*, Fig. S2) and areas with less human pressure (*SI Appendix*, Fig. S3 and Table S4).

Organizations such as the International Union for Conservation of Nature (IUCN) have conducted similar conservation status evaluations for other, mostly smaller taxonomic groups. The IUCN Red List reports that 18% of vertebrates are threatened. The Global Tree Assessment has used the IUCN approach to evaluate the global conservation status of 58,497 tree species and found that 30% (17,510 species) are threatened (77). Based on quantitative range estimates for >46,000 tree species, we report that 83.3% of tree species experience moderate to high human pressure, in which 14.8% of species are exposed to high or very high human pressure. The differing risk estimates clearly arise from diverging approaches used by the different evaluations. The IUCN system considers population loss and decline of range size as indicators of extinction risk (78), while our analysis evaluates conservation status according to PA coverage and human pressure within species' ranges. Despite the differences, the estimations are not incompatible and consistently show that much stronger conservation efforts for trees are needed to reduce the risk of losing large proportions of tree species diversity. Both approaches also highlight the need to have special focus on small-range tree species, in line with a global assessment for plants overall (79). Similarly, a regional study on the Brazilian Amazon found that tree species with small-range sizes are more likely to become extinct from rising human pressures (80), supporting the conclusion that better PA coverage is especially needed for the world's many small-range tree species.

As a cornerstone of biodiversity conservation, PAs are established to protect biodiversity and ecosystem services. However, as species, ecosystems, and PAs are experiencing dynamic changes and pressures (54–56) from land use and climate change, alien species introductions, and pollution, other conservation actions are increasingly proposed and realized outside PAs, such as restoration and reforestation through natural regeneration (81), active promotion of rare species in restoration and reforestation (82), stronger integration of tree diversity into forest management (11, 81), and integration of tree diversity into agricultural landscapes via agroforestry (e.g., ref. 83). Those implementations are not only critical for preserving and enhancing tree diversity but also for mitigating climate change

(3, 83, 84) and enhancing rates of provisioning of other ecosystem services such as biomass productivity (11). Indeed, PA roles have been transforming, and are increasingly extended to cover ecosystem services (85, 86). PAs are thus increasingly regarded as a multipurpose solution to ensure biodiversity while providing key ecosystem services (87), a view that is supported by high associations between biodiversity, carbon stocks, and other key ecosystem services (84, 86, 88). Thus, a comprehensive evaluation of existing PAs and proposed conservation prioritization frameworks using key organismal groups is critical for understanding their effectiveness and for guiding future PA expansions (89).

Addressing this need, we here focus on a key organismal group, namely trees, to test the global effectiveness of multiple influential biodiversity conservation frameworks. The high degree of overlap between the NGO frameworks and the top-priority areas for tree diversity (particularly the G200 and BH frameworks) demonstrates that tree diversity is fairly congruent with that of broader sets of organisms, because these frameworks are assumed to select ecoregions that are most crucial (either highly irreplaceable or vulnerable) to the global biodiversity and include socioecological factors (90, 91). Importantly, this finding shows that enhanced protection of biodiversity overall would also strongly benefit tree diversity. The LW framework showed the smallest degree of overlap with tree conservation priority areas, because this NGO framework primarily captures remote wilderness areas, which are often located in arid or cold high-altitude or -latitude regions, which have limited suitability for trees and inherently harbor low tree species diversity (92). Such areas have also historically experienced lower levels of human pressure, allowing large natural areas to persist and reducing opportunity costs of conservation (29, 32, 54, 93).

Despite the coverage and quality of the tree species dataset analyzed here, limitations such as a necessary coarse spatial resolution (110-km grid cells), limited geographical coverage in parts of Russia and southern Asia (94), and limited data for many functional traits introduce uncertainties. Phylogenetic and functional diversity often correlate strongly (44, 95), and we also found significant phylogenetic signals for four out of the eight functional traits analyzed in this study (*SI Appendix*, Table S1). However, this correlation was certainly enhanced by imputing functional traits using phylogenetic eigenvectors. Nevertheless, functional and phylogenetic diversity dimensions gave somewhat distinct priority areas (Fig. 2 and *SI Appendix*, Fig. S3), indicating that these diversity dimensions still provided unique information. Even though range size is generally a good proxy to represent species' vulnerability (96, 97) and is commonly used in conservation status assessments (78), further research is clearly needed to expand our understanding of geographical distributions. Better data coverage for tree functional traits is also important for conserving or restoring tree diversity, as tree species with different sets of traits have distinct ecological demands and functions; for example, large seeds and animal pollination are positively related to tree species' extinction risk (96). Further, our prioritization analysis did not consider socioeconomic costs and local or regional social or political contexts (98), factors which are important for systematic conservation planning (99). Moreover, as the goal of our study is to understand pressures and protections of tree species, we did not specifically consider primary vs. secondary forest. Notably, the top-priority areas under high pressure would inherently tend to be or develop as secondary forests if such protection was realized, with expected time lags in developing their full biodiversity and ecosystem benefits.

Conclusions

Globally, 83.8% of the 46,752 tree species evaluated in our analysis are subject to moderate to very high human pressure, with PA grid cells covering only $\leq 25\%$ of the ranges for 23.5% of tree species. Further, a total of 6,377 small-range tree species remain completely unprotected. At the same time, a total of 14.8% tree species experience high to very high human pressure even within existing PAs. Our analysis further found existing PA grid cells are estimated to cover only about half of the critical areas for tree diversity, as quantified by taxonomic, phylogenetic, and functional diversity dimensions. These results highlight the pressing need for stronger protection of Earth's tree diversity. Our results also show that expanding PAs according to the top 17% and especially the 50% priority areas would yield strong improvements in PA coverage of trees, as would implementing some of the major proposals for increased general biodiversity protection, notably the G200 framework. Such efforts are critically needed to counter expanding human pressure on natural and seminatural areas in many parts of the world (100), and also require effective protection of current and future PAs as pressures may penetrate into the PAs despite formal protection (3, 41, 80). We further suggest that promoting protection and inclusion of tree diversity, notably rare and threatened species, into land-sharing approaches such as small-scale nature areas, sustainable forestry, multiuse reforestation, and agroforestry (e.g., ref. 82) would help to achieve adequate protection of tree diversity and facilitate contributions to ecosystem services in rural and urban landscapes broadly (101). Given the enormous importance of tree diversity for biodiversity overall, for people, and for the functioning of the biosphere, it should be a major priority for environmental policy to bend the curve from biodiversity loss to recovery (27) for Earth's rich flora of trees.

Methods

Tree Species, Their Occurrence Records, and Range Estimates. We used the world tree species list and species occurrence data compiled and cleaned in ref. 94. Briefly, they extracted the records from the world tree species checklist [GlobalTreeSearch; GTS (74)] and further standardized the taxonomic names via the Taxonomic Name Resolution Service online tool (102). The GTS employed the definition of the tree-type growth habit agreed by IUCN's Global Tree Specialist Group, namely "a woody plant with usually a single stem growing to a height of at least two meters, or if multi-stemmed, then at least one vertical stem five centimeters in diameter at breast height" (74). An initial list of 54,020 tree species was left (94).

Occurrence data for tree species were compiled from five widely used and publicly accessible occurrence databases: the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org>), public domain Botanical Information and Ecology Network, version 3 [BIEN; <https://bien.nceas.ucsb.edu/bien/> (79, 103)], Latin American Seasonally Dry Tropical Forest Floristic Network [DRYFLOR; <http://www.dryflor.info/> (104)], RAINBIO database [<http://rainbio.cesab.org/> (105)], and Atlas of Living Australia (ALA; <https://www.ala.org.au/>). Due to well-documented problems of biases and errors in global plant occurrence datasets (106), we applied a workflow for occurrence data quality assessment (94) to the initially gathered 9,032,654 occurrence records. Our final list of species was lowered to 46,752 species with a total occurrence dataset of 7,066,785 records.

We then constructed alpha hulls (107) to estimate the range of each species with 20 or more occurrence records using the ashape function of the alphahull package (108) implemented in R [version 3.5.1 (109)]. For species with fewer than 20 occurrences or with disjunct records, a 10-km buffer was given to each point record and then merged with the alpha-hull range to estimate species ranges. Previously, several alpha levels were recommended for the estimation of species range (e.g., refs. 110–113); four alpha degrees (2, 4, 6, and 10) were applied to each species here after external validation of the different alpha levels tested. To validate the range maps using different alpha levels (alpha values of 2, 4, 6, and 10), we performed three types of external validation, as described in

SI Appendix, Methods, External Validation and Figs. S6–S10. Based on those validations, we selected the alpha-hull range maps with an alpha parameter of 6 degrees for subsequent analyses, as recommended and applied in similar studies (112, 113), and with the highest *R*-squared in our validation (*SI Appendix, Fig. S6*). The obtained estimated range maps were rasterized to 110-km equal-area grid cells, a resolution commonly used in global diversity studies (e.g., refs. 99, 114, and 115), using the *letsR* package (116). Even though the estimated range can reduce the geographical bias and fill gaps of the occurrence records, it may overestimate the species' true area of occupancy and they should therefore not be interpreted as a detailed coverage of species' realized distribution, but rather as an estimate of its extent of occurrence (cf refs. 41 and 117).

Phylogeny. We extracted phylogenetic information for the tree species with range maps from the largest seed plant phylogeny that is currently available (the ALLMB tree in ref. 118). This phylogeny combines a backbone tree (119) reflecting deep relationships with sequence data from public repositories (GenBank) and previous knowledge of phylogenetic relationships and species names from the Open Tree of Life (synthetic tree release 9.1 and taxonomy version 3; <https://tree.opentreeoflife.org/about/synthesis-release/v9.1>). We matched this phylogeny to our tree dataset by first removing any species that were not in our data, and then manually adding some species that were missing from the phylogeny (due to different taxonomic concepts) following the same approach that ref. 119 used to add missing species. The resulting phylogeny contained 46,752 species (*SI Appendix, Fig. S11* and *Dataset S2*).

We calculated phylogenetic eigenvectors (60) to represent the phylogenetic position of each species in our dataset using the PVR package (60, 120). Because we were mostly interested in the deep structure of the phylogeny, and phylogenetic eigenvector calculation for large phylogenies is computationally prohibitive, we calculated eigenvectors at the genus level (4,031 genera). To accomplish this, we randomly chose one species per genus, removed all other species, and computed phylogenetic eigenvectors using the resulting phylogenetic tree. All species were then assigned the eigenvector values of their genus. In the following analysis, we used the first 15 eigenvectors, excluding those that captured very little phylogenetic variation (eigenvalues $< 1\%$, following ref. 44). These selected eigenvectors accounted for 40.6% of the total phylogenetic variation, representing the deep evolutionary history of our study species.

It is possible to use the phylogenetic diversity [like Faith's PD (121)] directly in a prioritization algorithm (e.g., Zonation); however, the use of this alpha-diversity layer will diminish the advantages of the complementarity, which is derived from beta diversity and makes the priority ranking based on all biodiversity features directly, rather than the species-rich hotspots only (122) (see *Prioritization Analyses*). To accommodate this, we adapted from the framework in refs. 42 and 44. First, we evenly divided each eigenvector into 20 bins. Then, we created a binary variable for each bin, scoring all species with values within the range of the bin as 1, and all others as 0. This resulted in 20 binary variables for each of the 15 eigenvectors, that is, a matrix of 46,752 species $\times$ 300 binary variables. We multiplied this matrix with the grid cells $\times$ species matrix to generate a presence-absence matrix of phylogenetic groups in grid cells (44). This matrix showed which parts of the phylogeny—as represented by the binary variables derived from the eigenvectors—were present in each grid cell. We used this matrix in the following prioritization analysis to find priority regions for the conservation of tree phylogenetic diversity.

Functional Trait Data. Twenty-one functional traits (*SI Appendix, Table S1*) were compiled from major trait databases (*SI Appendix, Functional Traits and Imputation*). As many of the traits had missing values, we imputed trait values applying a gap-filling technique using Bayesian hierarchical probabilistic matrix factorization (123) (*SI Appendix, Fig. S12*). We finally selected eight key functional traits for further functional diversity analyses, including leaf nitrogen concentration, wood density, leaf phosphorus concentration, leaf dry matter content, plant maximum height, seed dry mass, specific leaf area, and leaf area. We used the *beanplot* package (124) to visually compare the observed original and imputed data, and found they generally had similar distribution patterns for each functional trait (*SI Appendix, Fig. S13*). We further tested the phylogenetic signal for each imputed trait with the function *phylosig* in the *phytools* package (125), and found four of the eight traits showed significant phylogenetic signals (*SI Appendix, Table S1*).

We performed a similar procedure as for phylogenetic eigenvectors to obtain trait diversity dimensions for our conservation prioritization analysis. We first split each trait into 20 equal bins, and then converted it into a binary species $\times$ trait matrix for each trait (46,752 species $\times$ 20 bins). For each of the 20 bins, we multiplied it by the 110-km grid cells $\times$ species matrix to obtain a trait $\times$ grid cell matrix, in which each 110-km grid cell contained the number of species of trait values within the trait interval. In total, we obtained 160 trait $\times$ grid cell matrices, a distribution map was generated for each of them, and then all the 160 distribution maps were used in the prioritization analysis to locate the priority regions for trait dimension.

Protected Areas. PA distribution was extracted from the December 2019 release of the WDPA via the *wdpar* package (126, 127). The release includes 244,869 PAs globally. According to previous similar global studies (e.g., ref. 54), we extracted the PAs from the WDPA database by selecting terrestrial areas belonging to IUCN PA categories I to VI and having a status of “designated,” “inscribed,” or “established” and areas not designated as man and biosphere reserves by the UN Educational, Scientific, and Cultural Organization. We also excluded the PAs represented as points. A final list of 95,506 PAs was kept. We then resampled PAs at the 110-km grid level following ref. 38, that is, labeling all cells intersecting a PA polygon as PAs to include any small or narrow PAs. Thus, the PA layer used here provides a very optimistic estimate of existing PA coverage.

Global Biodiversity Conservation Priority Frameworks (NGO Frameworks). Many NGOs have proposed frameworks for global biodiversity conservation prioritization, such as the BH by Conservation International (90), LW by the Wildlife Conservation Institute (128), and G200 by the World Wide Fund for Nature (91). However, these frameworks vary in both location and coverage, largely due to the emphasis on different facets of nature conservation. Although irreplaceability and vulnerability, the two central aspects of systematic conservation planning (28), are equally important, some frameworks concentrate only on irreplaceability, while others focus more on vulnerability (29). Under the framework of irreplaceability and vulnerability, ref. 29 summarized nine major NGO frameworks, dividing them into three groups: prioritizing high vulnerability (regions of high threat, purely reactive, e.g., BH), low vulnerability (regions of low threat, purely proactive, e.g., LW), or high irreplaceability (e.g., G200).

We selected three NGO frameworks of global biodiversity conservation prioritizations (29) (*SI Appendix, Fig. S5*) encompassing the three major groups of the irreplaceability–vulnerability gradient. Specifically, we selected the BH (ref. 90 and Conservation International), G200 (91), and LW (128). BH prioritizes high vulnerability, LW prioritizes low vulnerability, and G200 prioritizes high irreplaceability. A detailed description of the three selected frameworks can be found in *SI Appendix*. The BH data layer was obtained from ref. 129; the upgraded LW data layer was obtained from ref. 130; and the G200 terrestrial ecoregion layer was from the World Wildlife Fund (<https://www.worldwildlife.org/publications/global-200>). We aggregated all the three spatial layers to 110-km grid spatial resolution.

Human Pressure Data. We used the recently proposed Human Modification map (61) as a proxy of human pressure. Compared with the commonly used Human Footprint map (100, 128), the Human Modification map was modeled with the incorporation of 13 recent global-scale anthropogenic layers (with a median year of 2016) to account for the spatial extent, intensity, and co-occurrence of human activities, many of which show high direct or indirect impact on biodiversity. HMI values were extracted at a resolution of 5 km² to ease the calculation burden. Based on ref. 61, we categorized the HMI into three groups representing different intensity levels of human pressure: low ($0 \leq \text{HMI} \leq 0.1$); moderate ($0.1 < \text{HMI} \leq 0.4$); and high to very high ($0.4 < \text{HMI} \leq 1.0$).

Prioritization Analyses. We used Zonation systematic conservation prioritization software, version 4 (59, 131) to identify global priority areas for tree diversity in each of the three biodiversity dimensions (taxonomic, phylogenetic, and functional). Zonation is based on the principle of complementarity, by balancing a set of biodiversity features to jointly achieve the most effective representation in a given region, and evaluating the spatial priority areas through the priority ranking (59). We used the core-area Zonation (CAZ) algorithm as a cell removal rule. The CAZ ranking algorithm emphasizes species (or any biodiversity feature)

rarity to ensure high-quality locations for all features, even if these features occur in species-poor areas (58).

We ran the Zonation spatial conservation prioritization procedure on species, phylogenetic groups, and functional trait groups separately to compare the mismatch or congruence between the resulting priority areas. We first assessed each of the obtained priority rankings on both the top 17 and 50% of the highest conservation value areas (i.e., the cells with ranking values greater than or equal to 0.83 or 0.50). These percentages were chosen to reflect current and future targets for Earth's PAs (33, 35). However, merging the top-priority areas issued from the separate analysis of the three diversity dimensions led to total greater PAs than the 17 and 50% targets, namely 26.3 and 61.5%, respectively (Fig. 2). Thus, to obtain prioritizations made jointly across the three diversity dimensions but consistent with the two biodiversity targets, we ran a joint analysis using the three diversity dimensions (taxonomic, phylogenetic, functional) as input layers of Zonation, and selected the top 17 and top 50% priority areas for further analyses. In addition, we also performed a sensitivity analysis by comparing the resulting priority areas with those derived from simply combining the priority areas from the prioritizations on the separate diversity dimensions. We found the two analyses generated similar results, namely similar percentages of overlap with existing PAs and conservation priority frameworks (Fig. 5 vs. *SI Appendix, Fig. S14*), and similar HMI values of the priority areas inside and outside existing PAs (*SI Appendix, Fig. S15* vs. *Fig. S16*). Thus, we report the joint results in the main text (Figs. 3, 4, and 5), that is, given that only these adhere to the 17 and 50% PA targets.

Spatial Analysis. The relationships among the three priority areas were tested after accounting for spatial autocorrelation using the *SpatialPack* package (132). We evaluated the degree of spatial overlap of the top 17 and 50% priority areas generated from the three dimensions using a Venn diagram. We divided the priority areas based on the ranking scores into two categories: areas with priority scores higher than 0.83 (top 17%), and between 0.50 and 0.83 (top 17 to 50%).

The species' protection proportion was calculated as the overlap ratio between species' range and existing PAs and the top 17 and 50% priority areas, respectively. Then, the protection percentages for each species were grouped into 12 levels, for example, no overlap as the group of “0,” (0, 10] for less than 10% of species' range within PAs, and “100” for a species' range completely inside the PAs. Species' HMIs were calculated separately as the mean HMI value for the whole species' range, outside PAs, and inside PAs. These steps were repeated also treating the top 17% priority areas and the top 50% areas as PAs, respectively. The Sankey diagrams were plotted via the *ggalluvial* package (133) in Fig. 3 and *SI Appendix, Fig. S3*.

Congruence between PAs, top-priority areas, and NGO frameworks was assessed through gap analyses. We overlaid the three layers (i.e., the top-priority areas, PAs, and each conservation priority framework) to calculate the level of protection in PAs, potential protection in the priority framework, and shared protection of the two global high-priority areas (both 17 and 50%).

Data Availability. All species occurrences reported in this article have been deposited in the BIEN database (<https://bien.nceas.ucsb.edu/bien/>) and can be accessed via the RBIEN package. In addition, species' alpha-hull ranges at the 110-km resolution, which were the input data for analyses in the study, have been deposited in GitHub (https://github.com/wyeco/TC_conservation), together with the relevant R codes. The phylogeny and imputed trait data and phylogeny are available in *Datasets S2* and *S3*.

All other study data are included in the article and/or supporting information.

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