

Large conservation gains possible for global biodiversity facets

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Different facets of biodiversity other than species numbers are increasingly appreciated as critical for maintaining the function of ecosystems and their services to humans^{1,2}. While new international policy and assessment processes such as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) recognize the importance of an increasingly global, quantitative and comprehensive approach to biodiversity protection, most insights are still focused on a single facet of biodiversity—species³. Here we broaden the focus and provide an evaluation of how much of the world's species, functional and phylogenetic diversity of birds and mammals is currently protected and the scope for improvement. We show that the large existing gaps in the coverage for each facet of diversity could be remedied by a slight expansion of protected areas: an additional 5% of the land has the potential to more than triple the protected range of species or phylogenetic or functional units. Further, the same areas are often priorities for multiple diversity facets and for both taxa. However, we find that the choice of conservation strategy has a fundamental effect on outcomes. It is more difficult (that is, requires more land) to maximize basic representation of the global biodiversity pool than to maximize local diversity. Overall, species and phylogenetic priorities are more similar to each other than they are to functional priorities, and priorities for the different bird biodiversity facets are more similar than those of mammals. Our work shows that large gains in biodiversity protection are possible, while also highlighting the need to explicitly link desired conservation objectives and biodiversity metrics. We provide a framework and quantitative tools to advance these goals for multi-faceted biodiversity conservation.

Protected areas are pivotal to biodiversity conservation, and globally coordinated plans to expand protected areas could vastly increase the protection of species^{4,5}. We know much less about how protected area expansion could benefit other facets of diversity, despite the potentially crucial role of these facets in representing biodiversity heritage under threat^{2,6,7} or ensuring locally stable and functioning ecosystems that provide services to humans^{1,8,9}. Thanks to rapid growth in available data, two of the main biodiversity facets—phylogenetic and functional diversity—have enabled transformational insights into fundamental questions in ecology and biogeography^{10,11}, but the looming question that has received far less attention is how best to protect this diversity. Ancestral relationships between species are crucial to conservation¹², and methods for using phylogenetic diversity in conservation planning were developed more than 20 years ago², but are still rarely considered in conservation efforts³. However, recent advances have enabled the use of phylogenetic diversity in more realistic conservation assessments with popular conservation planning software^{8,13–15}, including the use of species distribution models as inputs¹⁴ and incremental range protection of phylogenetic diversity (rather than the earlier limitation that a single occurrence of a phylogenetic branch is considered sufficient protection)^{8,14}. The use of functional diversity in conservation planning has typically been limited to broad vegetation or habitat types¹⁶, but

rapidly expanding datasets of functional traits and the development of dendrogram-based functional diversity metrics¹⁷ now allow for functional diversity estimates across broad spatial scales^{18,19}. Here, we combine emerging ideas from biodiversity science with spatial conservation planning approaches²⁰ to establish priority areas for facets of bird and mammal diversity across the globe, to explore conservation objectives (Fig. 1), and to show how biodiversity metrics match to these objectives. Specifically, we ask: (1) how effective is the current protected area system in covering species, functional, and phylogenetic diversity of birds and mammals; (2) how much more diversity could be protected if protected areas were expanded; and (3) how do different conservation objectives, different facets of diversity, and different animal groups influence the efficiency and spatial overlap of alternative solutions?

Across all three facets (species diversity, phylogenetic diversity, and functional diversity), protected areas have significant gaps, as previously shown for species^{21,22} and phylogenetic diversity^{15,23}. Around

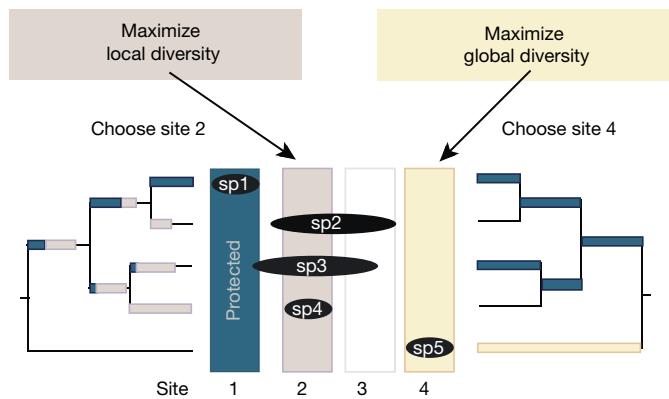


Figure 1 | How conservation objectives influence priorities for the phylogenetic or functional trees of life. With site 1 protected, the full range of species 1 (sp1) and a small part of the range of species 3 (sp3) are 'protected'. The protection of site 1 results in a different amount of the phylogeny originally considered to be protected (blue portions of branches on each phylogeny corresponding to the two objectives). If protection is expanded by only one additional site, the choice of site depends on the objective. To maximize global diversity, basic protection for all biodiversity units (that is, branches of different length in a dendrogram) is sought, and site 4 represents the greatest gain in phylogenetic or functional diversity (adding the yellow portion to the phylogeny on the right). By contrast, the maximize local diversity objective considers the composition within each local area alongside spatial range information for each phylogenetic/functional branch, which selects the area that maximizes the spatial representation of the phylogenetic or functional diversity (site 2; see Methods for additional explanation). Here, branches are represented incrementally as the proportion of the spatial range of each branch that is protected (blue portions of phylogenetic branches are already protected, and grey portions represent additional portions protected by protecting site 2).

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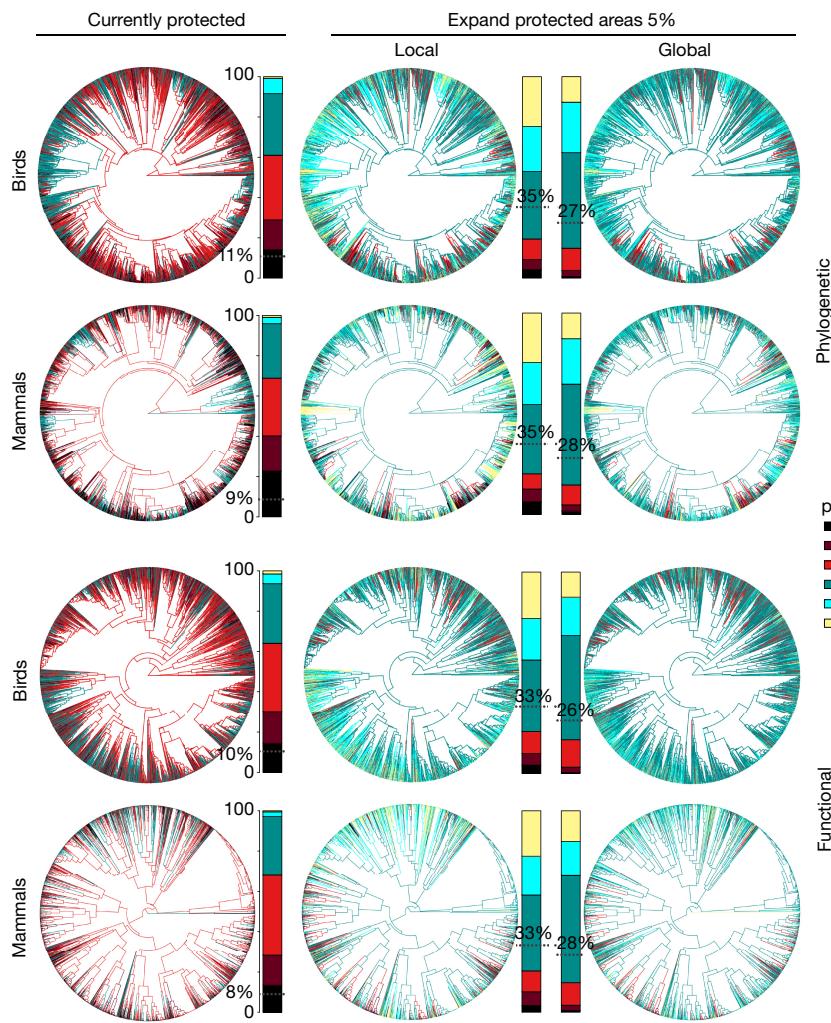


Figure 2 | Status of current protection and potential conservation gains for the phylogenetic and functional trees of life for birds and mammals. For each branch of each tree, protection is defined as the spatial range (per cent of the total branch occurrences) that is protected. Bar plots summarize the level of protection for all branches on a given tree by apportioning the total branch length into categories of protection. For example, if the black portion of the bar plot is 13%, this means that 13% of the total branch length of the phylogeny is <1% protected. The highlighted percentages (dotted lines) indicate the average protection of individual branches (that is, the spatial distribution of each branch found in protected areas, weighted by the branch length).

26% of species (3,850 species) are not reliably included in protected areas (having no terrestrial breeding range in cells with at least 17% of their land area in qualifying protected areas; see Methods) and many more do not meet more stringent thresholds for protection (Extended Data Fig. 1). Much of the bird and mammal trees of life are missing from protected areas including 13% of the phylogeny (that is, the total branch length) for birds and 23% for mammals (black segments; Fig. 2). The functional trees of life (defined by a suite of traits linked to trophic interactions and resource acquisition²⁴, including body mass, foraging height, activity time and diet) are faring slightly better (around 12% missing from protected areas for both birds and mammals; Fig. 2). In addition, protected areas hold, on average, less than 10% of the spatial range (for example, the per cent of total spatial occurrences that are protected) of bird and mammal species, and less than 10% of the average spatial range (weighted by the branch length) of phylogenetic and functional branches (Figs 2 and 3). This current layout of protected areas is far from optimal, as nearly every single species or the entire phylogeny or all functional diversity could be protected with the same amount of land that is currently protected (dotted lines in Fig. 3a). While this scenario is undesirable as existing protected areas serve many important roles, protected area expansions are stipulated by Aichi Target 11 of the Convention on Biological Diversity to benefit biodiversity.

The current outlook for bird and mammal diversity could vastly improve by expanding protected areas, but priorities depend on the objective, specifically whether to retain ‘global’ or ‘local’ diversity worldwide (Fig. 1). The ‘maximize global diversity’ approach aims to prevent extinctions of any biodiversity units—species, phylogenetic

or functional branch lengths—from the global pool with a particular focus on rare and under-represented diversity that would best broaden the range of diversity already protected. The ‘maximize local diversity’ approach also aims to protect rare and under-represented diversity, but with more emphasis on local assemblages (that is, it maximizes the biodiversity units that occur in a local grid cell scaled by the total spatial occurrences of each biodiversity unit). While the ‘local’ approach is more efficient, it can miss individual species or phylogenetic/functional branches of rare biodiversity in particular (Extended Data Figs 1 and 2). This influence of conservation objective on evaluating and designing protected areas is well-known for traditional species-based planning, with recent examples using either the global^{21,25} or local⁴ strategies. Here, in the first comparison for multi-faceted diversity, we show how these objectives can be tied to existing biodiversity metrics, how slight modifications of these metrics can be used to evaluate protected area expansions, and how the trade-offs between objectives are particularly severe for the conservation of different diversity facets.

Conservation planning for phylogenetic diversity typically adopts a form of the maximize global diversity objective^{2,8,14,23}, which matches a set of motivations for conserving phylogenetic diversity, such as preserving evolutionary heritage or protecting biomolecules, functions or ‘features’ that might be crucial for future human generations²⁶. Using the global objective, we find that an additional 5% of land area dedicated to protection would capture >99% of all bird and mammal biodiversity units as protected in at least one area, often more (Figs 2 and 3; Extended Data Fig. 3). This equates to protecting an additional 3,743 species or an additional 18,000 million years of evolutionary history. Only around 35% of these priority areas are identical between pairs of

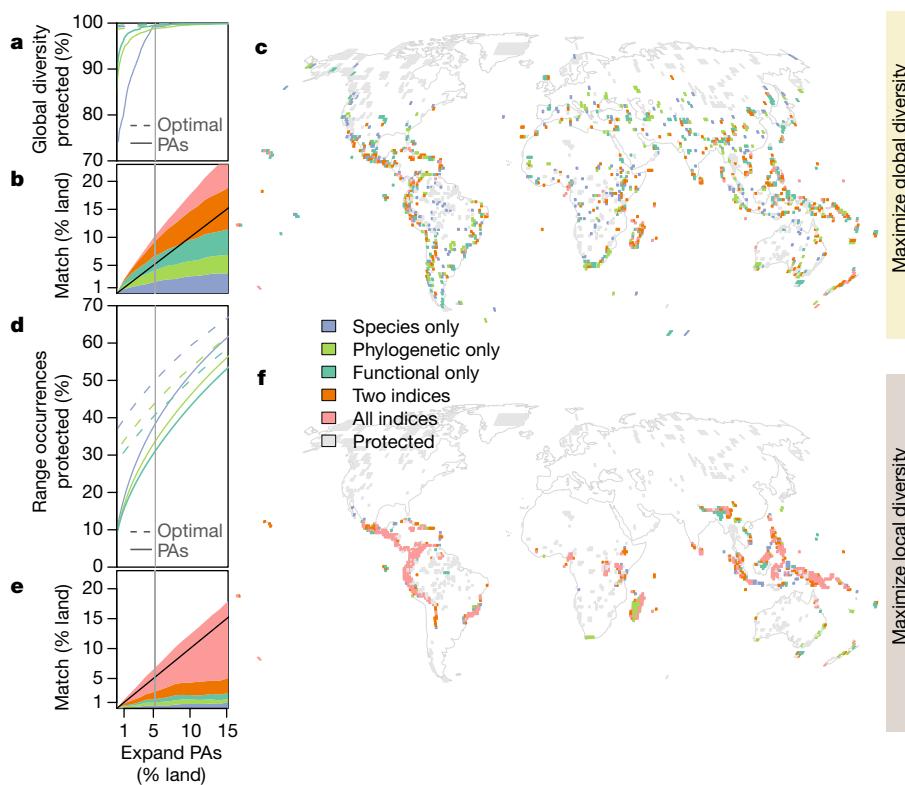


Figure 3 | Priorities for expanding protected areas to conserve species, phylogenetic and functional trees of life for birds and mammals. **a, d**, Biodiversity is gained as land is transferred into protection (expressed as a per cent of the total land area). **a–f**, Biodiversity gain is measured as the per cent of global diversity protected (that is, the amount of species diversity, phylogenetic diversity, or functional diversity protected in at least one cell) for the global objective (**a–c**) or the per cent of the spatial range of occurrences protected for the local objective (**d–f**). Solid lines are gains from the actual layout of protected areas, and dotted lines indicate the hypothetical case that both the new and existing protected area network were designed for this objective. Graphs in **b** and **e** are the spatial match in priorities between facets for protected area expansion scenarios. The maps in **c** and **f** show the priority areas for each facet (or multiple facets) for a 5% expansion scenario. For additional results that compare birds and mammals, see Extended Data Fig. 3 and <https://mol.org/patterns/facets>.

biodiversity facets (Figs 3b and 4), highlighting the efficiencies possible by focusing on a specific biodiversity facet. For example, the highly restricted range of the threatened Giant Ibis (*Thaumatinis gigantea*) in southeast Asia could be fully protected with a protected area expansion based on phylogenetic diversity, whereas an approach focused on species diversity alone would leave its estimated 57 million years of evolutionary history in essence unprotected (see Extended Data Table 1 for other bird and mammal examples). Further, the relative rates of biodiversity gain with land added into protection are steepest for functional diversity and shallowest for species diversity (Fig. 3a), confirming that the same general principles of how biodiversity facets scale with area^{6,19,27} apply to protected area expansion scenarios.

Not all conservation goals are best achieved with a sole focus on the global biodiversity pool, including the major aim of having diverse and functional ecosystems that provide services to humans. Intact ecosystems require local diversity, but are not necessarily impacted by the loss of an evolutionarily or functionally distinctive species from the global pool. The local approach considers cell diversity, spatial ranges and extinction risks based on those ranges. In other words, it prioritizes areas with diversity (similar to weighted species endemism²⁸ or phylogenetic endemism²⁹) not found and not protected elsewhere. This enables large biodiversity gains with much of the land required to achieve these gains being identical between facets. With a protected area expansion of 1% of land area, the amount of spatial range protected for species or phylogenetic or functional units could double (Fig. 3d), or it could even triple with a 5% expansion (from 9% to 38%; Fig. 3d). Further, over 80% of grid cells selected for a 5% expansion are priorities for multiple diversity metrics (Fig. 3f), and this spatial congruence increases as more land is protected (Fig. 3b, e).

The maximize global diversity approach and its focus on the global biodiversity pool is supported by its frequent prior use for setting priorities for species and phylogenies, its solid backing in conservation values, and the suggestion that local and regional diversity might not necessarily be declining with global species losses³⁰. However, the very efficient gains that can be made across facets with the local approach and its ties to ecosystem functioning³¹ suggest that there may be substantial practical conservation benefits to this approach. This warrants a

discussion on exactly which benefits are desired, and which biodiversity facets, metrics, and targets are key to achieving them.

Although many priority regions are well-known biodiversity hotspots such as Central and northwestern South America, eastern Madagascar, and southeast Asia (see Extended Data Table 2 for the top 20 areas across all facets and objectives), using diversity hotspots to assign conservation priorities vastly under-represents what could be gained with conservation planning. For example, over 1,500 more bird species or 8,236 million years more evolutionary diversity could be represented in protection if a 5% protected area expansion is done with optimized spatial conservation algorithms rather than prioritizing the most diverse areas, and the differences are even starker for rare species. Only approximately 30% of rare species would be protected by selecting diverse areas compared with around 90% with a spatial prioritization (Extended Data Fig. 1). A purely local approach of selecting the most diverse areas (that is, biodiversity hotspots) is an inefficient

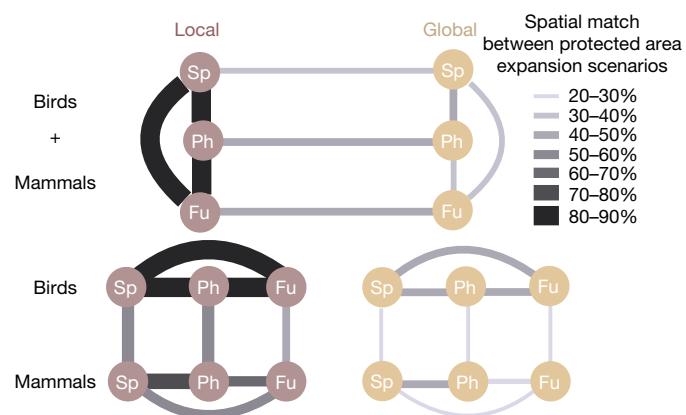


Figure 4 | Overlap of high priority areas for different objectives, facets and taxa. Species (Sp), phylogenetic (Ph), and functional (Fu) priorities are shown. Spatial congruity (spatial match) is the percentage of high priority cells out of the total number of cells in 5% of the land area (608 cells) that are shared between two combinations.

conservation solution for global species biodiversity²⁵, and here we show that this applies to phylogenetic and functional diversity also.

Beyond the choice of objective, there were some important differences in biodiversity facets. Functional priorities tend to diverge more than species and phylogenetic priorities, especially for mammals (Fig. 4). Rare mammal species in particular are very poorly represented with a functional-based prioritization (Extended Data Fig. 2). This discrepancy was previously shown in terms of neither species nor phylogenetic diversity predicting body mass variation for mammals³², and here we find this applies more generally to multi-trait functional diversity. Given our results and the tendency for certain functional types (for example, large animals) to be threatened³², functional diversity should probably be considered directly in conservation rather than relying on proxies such as species diversity or phylogenetic diversity. However, outcomes based on functional priorities are more uncertain than those based on phylogenetic diversity (Extended Data Fig. 4) owing to the influence of the choice of traits used to estimate diversity (Extended Data Fig. 5). Taken together, functional diversity is an important and potentially divergent axis of diversity to consider in conservation, but the traits used in functional diversity should be carefully considered. Our results broadly agree with previous work showing species and phylogenetic priorities are similar²², yet there are many exceptions, such as two biodiversity hotspots (the Cape Floristic Region, South Africa and southwestern Western Australia), which are more important from a phylogenetic, rather than species or functional, perspective (Fig. 3c, f).

By linking multi-faceted biodiversity with spatial conservation science, we show that the potential exists for large conservation gains that benefit a rich array of biological diversity with subsequent effects on ecosystems and humans. Across conservation objectives, two major animal groups, three facets of biodiversity, and variations of phylogenies, functional traits, and protected area definitions, a modest expansion in protected areas would vastly improve representation of species, phylogenetic and functional diversity. Further, many of the consistently top priority areas coincide with high-risk areas for mammals³³ and frequently occur in countries with low GDP, emphasizing the need for cross-national efforts to achieve Aichi Target 11 and to protect a robust array of diversity for the future.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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METHODS

No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assessment.

Data. We used IUCN range maps for 4,787 terrestrial mammal species and the Jetz *et al.*³⁴ range maps for 9,993 non-marine birds (breeding ranges only) (for details see <http://mol.org>). Ranges were converted to 110-km² equal-area grid cells, which was previously validated as the finest justifiable for these data globally without incurring false presences which would impose a geographic and ecological bias on spatial prioritization solutions^{35,36}. Mainland cells with >70% water were excluded but oceanic island cells with smaller land areas retained. We used 100 randomly selected phylogenies from the posterior distribution of phylogenies in Jetz *et al.*⁷ for birds and the phylogeny of Bininda-Emonds *et al.*³⁷ with updates^{38,39} for mammals. For simplicity, we present findings from a single bird and mammal phylogeny in the main text, and summarize results across all phylogenies in the Extended Data (Extended Data Figs 4–5). See Extended Data Table 3 for a full list of runs to assess uncertainty in phylogenetic, functional, and protected area definitions.

For functional prioritizations, we used species-level trait data for birds and mammals from Wilman *et al.*⁴⁰ to construct a functional trait dendrogram. We standardized the trait variation between birds and mammals and mammal with four equally weighted trait categories for each species: body mass, diet, activity cycle and foraging height. We used the same methods as Keil *et al.*¹⁹, but we substituted categorical variables for ordinal variables for activity cycle and foraging height. We calculated pairwise species dissimilarity with a generalized form of Gower's distance⁴¹, which accommodates various types of variables. We generated a dendrogram of all species in functional trait space using an UPGMA (unweighted pair group arithmetic mean), which is a hierarchical clustering method. To assess functional uncertainty in the results, we re-ran all analyses for birds and mammals with versions of the functional dendrogram that removed one trait at a time (Extended Data Fig. 5).

We considered reserves with International Union for Conservation of Nature (IUCN) category I–IV from the World Database on Protected Areas (<http://protectedplanet.net/>; accessed January 2015) as having sufficient protection status that increases the likelihood that species are well-protected. We also repeated analyses with all IUCN categories included, and found that although the potential for diversity gain is less (but still substantial—area coverage is doubled and nearly all species, phylogenetic and functional diversity is represented with a 5% protected area expansion) with more area originally considered protected, priority areas largely remain the same (Extended Data Fig. 6). We calculated the amount of polygon area in each of our grid cells and considered a cell to be protected if at least 17% of its area was under qualifying protection. We present a 17% cut-off in the main text following the global 17% coverage target in the Convention on Biological Diversity Aichi Target 11, but we found results were robust to the choice of an alternative 10% or 50% cut-off (Extended Data Fig. 6).

Spatial prioritization. Bird and mammal species distribution data, functional trait, and phylogenetic data were combined to produce input layers for the spatial prioritization. For the species-based prioritizations, the distribution of each species was represented as a raster layer of presences and absences across 110-km² grid cells. For the phylogeny-based prioritizations, the occurrence of each branch of the phylogeny must be calculated¹⁴. A branch was considered present if any of its descendent species occurs in that cell. The same method was used to assign values to each branch of the trait dendrogram. The final input layers consist of one raster layer for each species, each phylogenetic branch and each functional branch.

We used Zonation version 4.0 for all spatial prioritizations⁴². Zonation ranks the landscape from high to low conservation based on complementarity and irre-placeability. Starting with the entire landscape 'protected', the least valuable cells (that is, those that represent the least marginal loss of conservation value) are iteratively removed until all cells have been removed⁴³. The biodiversity conservation values for each cell depend on the biodiversity facet under consideration. For species, this value is the proportion of the total range of each species found in that cell (assuming species are weighted equally). For phylogenetic- and functional-based prioritizations, it is the proportion of the total range of each branch of the phylogeny/functional trait dendrogram found in that cell (weighted by the branch length).

Using these base conservation values, a marginal loss is calculated for each cell/iteration, and it differs depending on the conservation objective. For the 'maximize global diversity' objective, we used core-area zonation (CAZ), and for 'maximize local diversity', we used additive benefit function (ABF). For CAZ, marginal loss is based on the species (or phylogenetic/functional branch) with the greatest conservation value, and the cell with the lowest conservation value is removed⁴⁴. By contrast, in ABF, all species (or phylogenetic/functional branches) are considered in each cell. Marginal loss is determined by the sum of all biodiversity

features in each cell. The shape of the biodiversity gain with area added curves resemble a species-area curve. Assuming a reverse species-area curve can provide estimates of species extinctions, ABF has been interpreted as minimizing aggregate rates of local extinction rates⁴⁵. Using this reasoning, biodiversity loss is related to extinction risk by a power function with $e^2 = 0.25$ (ref. 45).

Broadly, these algorithms differ in that CAZ attempts to protect every species (or phylogenetic/functional branch), whereas ABF values diversity within cells (scaled by prevalence across the landscape). This results in ABF being more efficient in terms of protecting the greatest number of species or phylogenetic/functional cell occurrences (or average spatial range sizes) across all species, but at the risk of sacrificing individual species, especially in places that do not also contain occurrences for many other species (that is, in species-poor areas)⁴⁵.

Biodiversity units in Zonation need not be species. Phylogenies have been previously been included in spatial prioritizations by replacing species with phylogenetic branches that are weighted by the branch length^{8,13,14}. For functional-based prioritizations, we use the exact method as with phylogenies, but we replace the phylogeny with a trait dendrogram. All spatial prioritization settings are the same, with the exception that weights are used to scale each branch to match its evolutionary contributions. Although the general differences between CAZ and ABF algorithms are the same as prioritizations for species, here we show these algorithms tie to additional biodiversity metrics and contrasting conservation objectives.

Protecting global diversity. Here, the aim is to protect every species or every phylogenetic or functional branch unit. We evaluated the success of CAZ spatial prioritizations based the gain in protected global diversity (total species diversity, phylogenetic diversity, and functional diversity) with area added into protection. In the case of species, global diversity is the per cent of species minimally protected,

$$\text{global species diversity protected (\%)} = \frac{n}{N} \times 100$$

where n is the number of species protected (in a minimum of one cell) and N is the total number of species in the global pool.

For phylogenetic runs, global diversity is the length of the branches of the phylogeny that connect all protected species (Faith's phylogenetic diversity²) out of the total possible phylogenetic diversity,

$$\text{global phylogenetic diversity protected (\%)} = \frac{\sum_{i=1}^b L_i}{\sum_{i=1}^B L_i} \times 100$$

where b is branches of the phylogeny that are protected (in a minimum of one cell), B is the total number of branches, L is the length of branch i .

Global functional diversity is calculated exactly the same way as global phylogenetic diversity with the phylogeny being replaced with the functional dendrogram. In all cases, a species or branch is considered either fully protected (if a minimum of one cell of its distribution is protected) or fully unprotected (if no cells are protected). Here, we used the single occurrence threshold to match the original phylogenetic diversity prioritizations², but any threshold in terms of area protected or per cent of a species range protected could be used. Note that the global metrics used here do not exactly match the prioritization algorithm as they are target-based and the algorithm does not specify a target for each species as described above. See Extended Data Figs 1, 2, 4–6 for additional results with metrics targeted at rare species or phylogenetic/functional units.

Protecting local diversity. By contrast, the local approach favours concentrations of local diversity over protecting the global pool of biodiversity features. For species, areas are selected based upon local occurrences of species scaled by their total spatial occurrences. This results in a set of complementary areas that have concentrations of species diversity that is rarely found elsewhere. The biodiversity metric used to measure this range-restricted diversity in grid cells is weighted endemism²⁸. Weighted endemism in a cell is the proportion of the distribution of a species that is found in a cell (summed across all species). Therefore, cells with high endemism scores hold many range-restricted species. Here, we extend this metric for use in evaluating and contrasting conservation scenarios by calculating how much of the spatial range of species occurrences (that is, weighted endemism) is protected out of the total possible:

$$\text{range species occurrences protected (\%)} = \frac{1}{N} \times \sum_{i=1}^N \frac{\theta_i}{\Theta_i} \times 100$$

where N is the total number of species (that is, the global pool), θ_i is the number of protected cells where the species occurs, and Θ_i is the total number of cells where the species occurs. When all land cells are considered protected, the entire distribution of all species is protected and the per cent range of species occurrences and global species diversity are both 1.

We extend this idea to the phylogenetic-based prioritizations with the aim of finding complementary areas that maximize the amount of the tree of life not found elsewhere. Here, the ABF algorithm favours the combination of branch lengths and their spatial occurrence, which results in maximizing average cell-level phylogenetic diversity scaled by the spatial extent of phylogenetic units. Similar to the species case, this can be thought of as maximizing the phylogenetic endemism²⁹ protected. Our evaluation metric is calculated as:

$$\text{range occurrences protected (\%)} = \frac{1}{\sum_{i=1}^B L_i} \times \sum_{i=1}^B \left[L_i \times \frac{\theta_i}{\Theta_i} \right] \times 100$$

where B is the number of branches on the phylogeny, L is the length of branch i , θ_i is the number of protected cells where the species occurs, and Θ_i is the total number of cells where the species occurs. When all land cells are considered protected, all branches are fully represented and phylogenetic diversity (the sum of all branch lengths²) and the per cent range occurrences protected (the range-weighted sum of all branch lengths²⁹) are equal and both 1.

In the case of functional diversity, the aim is to maximize the amount of the functional tree of life that is not currently well-represented in the protected area system. Unlike the ‘protect global diversity’ prioritizations, the outcome for prioritizations that ‘protect local diversity’ is very similar to ranking grid cells by local weighted endemism values (Extended Data Fig. 7).

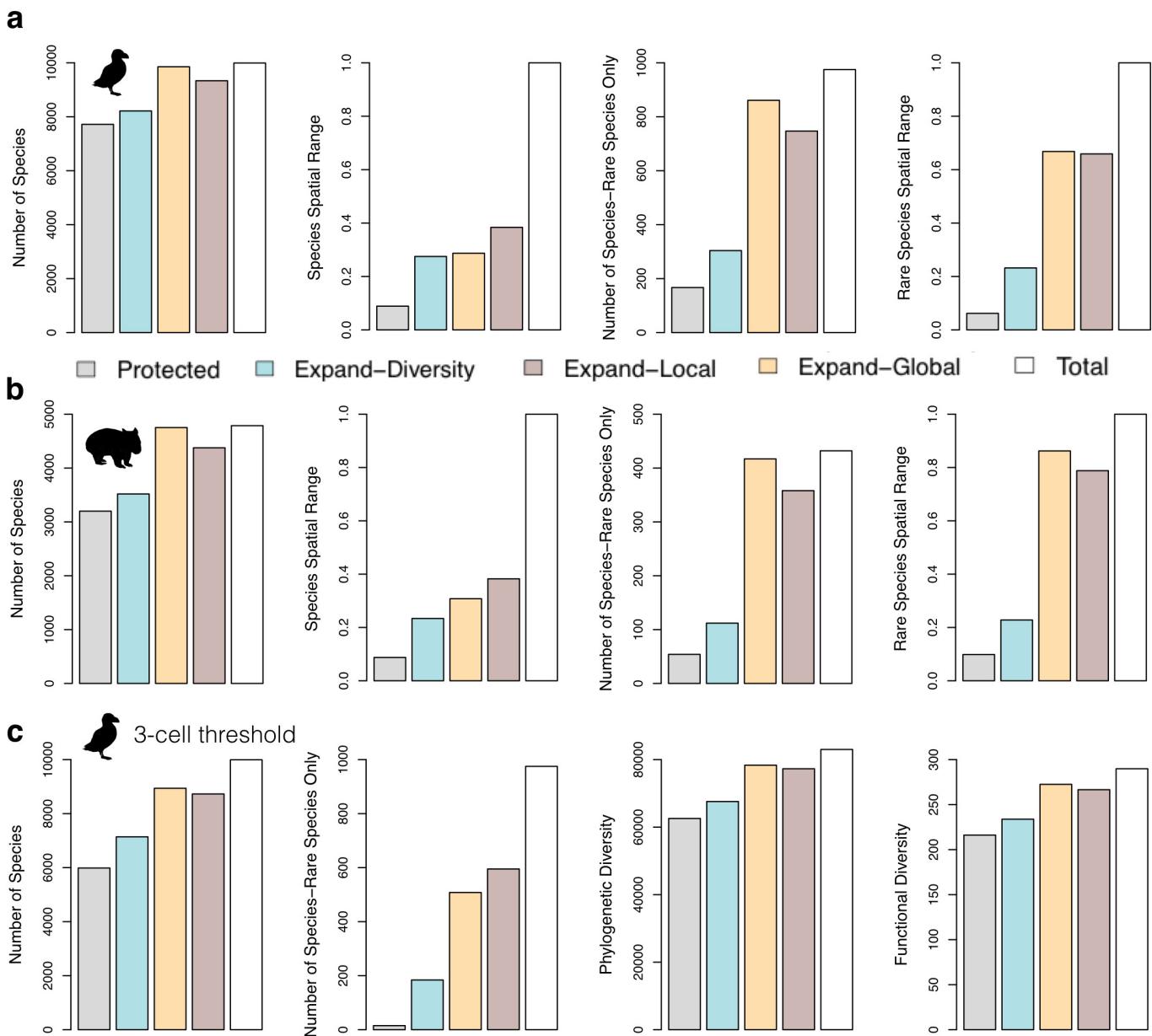
We ran each combination of objective and diversity facet for two scenarios—an optimal allocation of current protected areas and an expansion of current protected areas (Extended Data Table 3). Protected areas are included in the spatial prioritization by sequential ranking, in which all cells outside of protected areas are ranked first, followed by those in protected areas. Additionally, we compared how well prioritizations based on each conservation objective captured each type of evaluation metric (Extended Data Figs 1, 2, 4, 5).

We compared the similarity of each set of runs by calculating the spatial overlap of the highest priority areas between each combination expressed as a per cent of the land area at each increment of protected area expansion. Finally, we calculated

the spatial range of each branch of the phylogeny and functional tree under current protection and the amount that could be protected with a 5% expansion for both objectives. All R code is available upon request. For additional visualizations also see <https://mol.org/patterns/facets>.

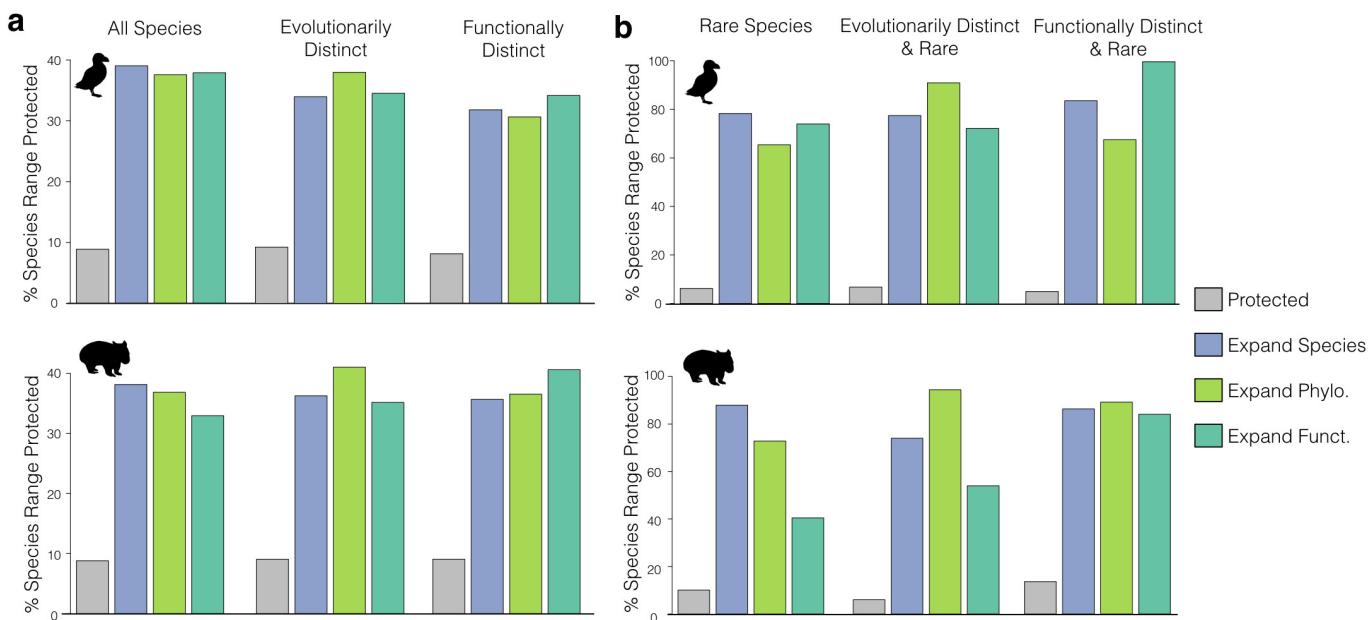
Data availability. The data that support the findings of this study are available from the corresponding author upon reasonable request.

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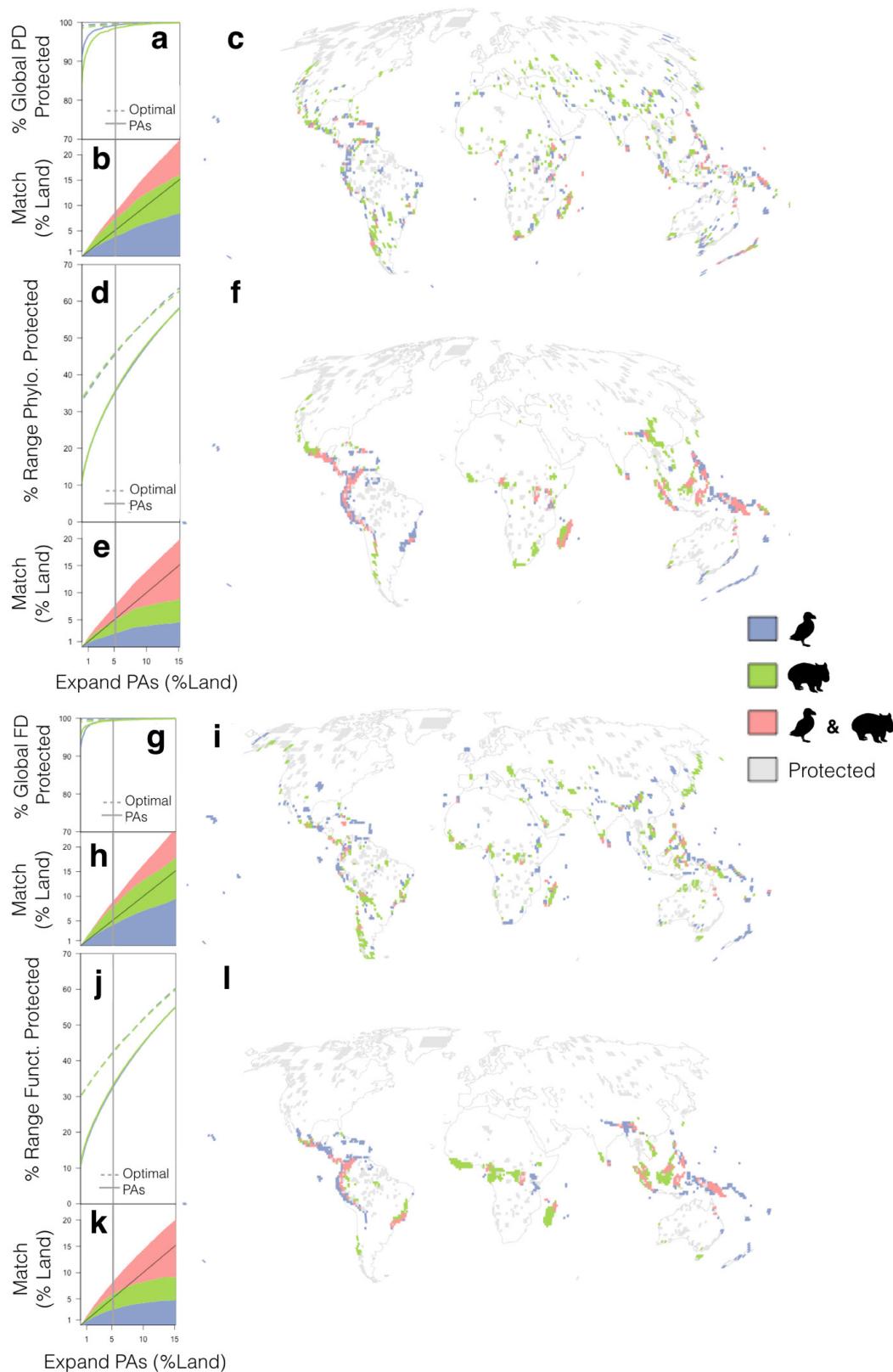
Extended Data Figure 1 | Which method is best for protecting diversity and how does the threshold for protection change the outcomes?
Spatial conservation algorithms versus selecting the most diverse areas (diversity hotspots) for protection. **a–c**, Bird (**a**, **c**) and mammal (**b**) diversity. Bars show how much of each metric is currently protected (grey) compared to how much could be protected with a 5% expansion in protected areas (colours) and the total possible (white). Protected areas are expanded by selecting the most diverse 5% of cells (Expand-Diversity) or spatial prioritizations that use the conservation principles of irreplaceability and complementarity. Priorities are shown for the maximizing global diversity (Expand-Global) and maximizing local diversity (Expand-Local) approaches. For the metrics that require a cell

threshold, **c** shows how much diversity is protected for birds in each scenario if a more stringent threshold of three cells protected (instead of the single-cell threshold used in **a**, **b**) is used. Species/phyletic/functional branches that occur in less than three cells are considered protected if all of their distribution is protected (for example, they occur in two cells and both are protected). Increasing the cell-based threshold substantially decreases the amount of diversity currently considered protected (77% of species protected for 1-cell versus 60% for 3-cell), but the rate of diversity increase with protected area expansion is steeper, meaning that this difference is partly made up for in a 5% expansion (90% of species could end up protected at the 3-cell threshold).



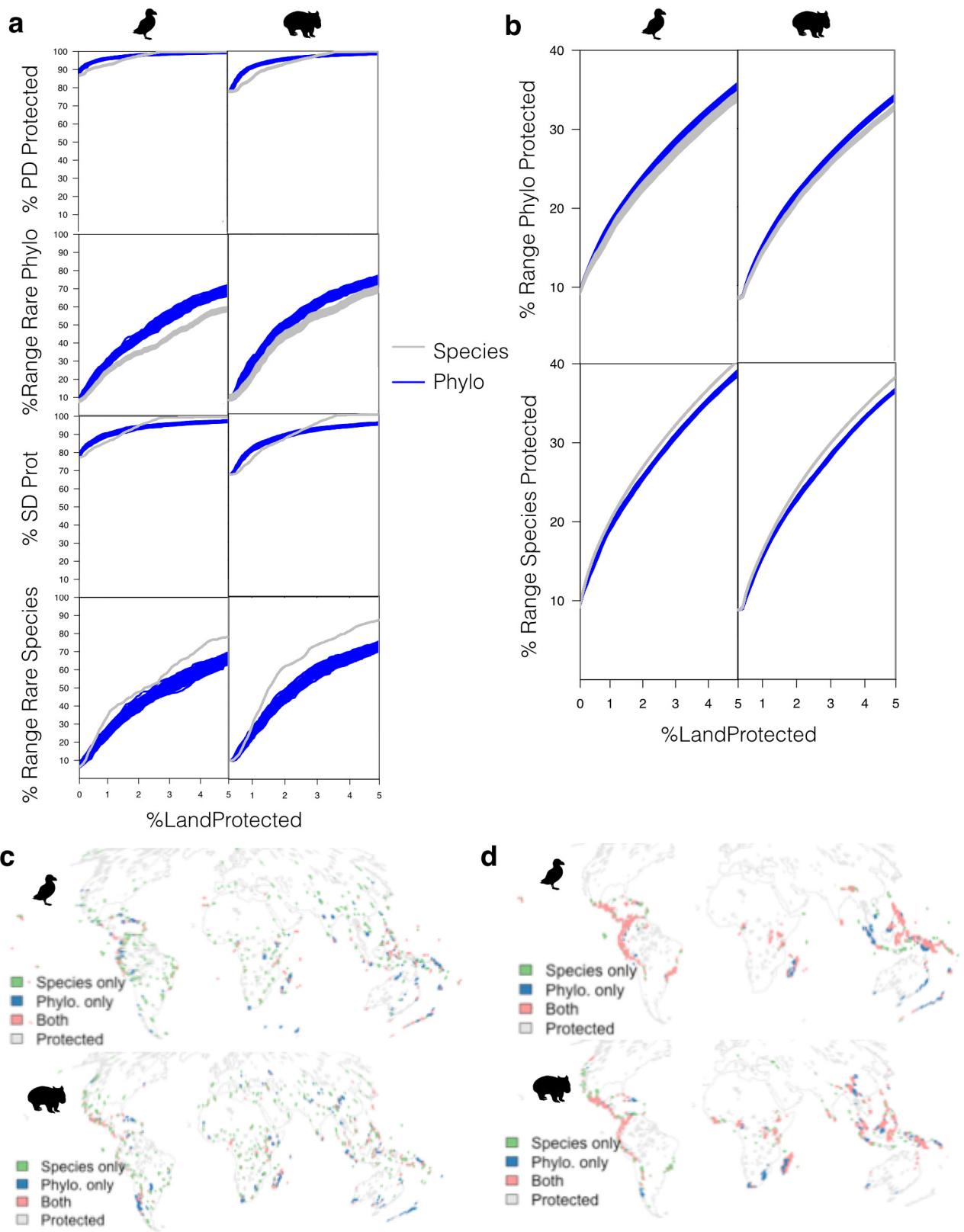
Extended Data Figure 2 | The outcome of protected area expansion for species, phylogenetic and functional prioritizations for different sets of bird and mammal species. The percentage of the total range occurrences protected (that is, the average spatial range of species that is protected) are shown for each species set: all bird or mammal species; species with the greatest evolutionary distinctiveness (top 10%);

distinct species (top 10%); the rarest species (top 10% most rare); species that are evolutionarily distinct and rare; and functionally distinct and rare species. Outcomes with the maximizing local diversity objective are shown in **a** for the full species sets, and maximizing global diversity for rare species in **b**.



Extended Data Figure 3 | Priorities for expanding protected areas to benefit the bird versus mammal phylogenetic and functional trees of life. **a–l**, Phylogenetic (**a–f**) and functional (**g–l**) trees of life are presented separately. **a, d, g, j**, Biodiversity gain is measured with per cent phylogenetic diversity (**a, d**) or per cent functional diversity (**g, j**) protected in at least one cell for the maximize global diversity objective, and per cent of the spatial range of occurrences protected (that is, the spatial representation of the functional or phylogenetic tree of life) for the

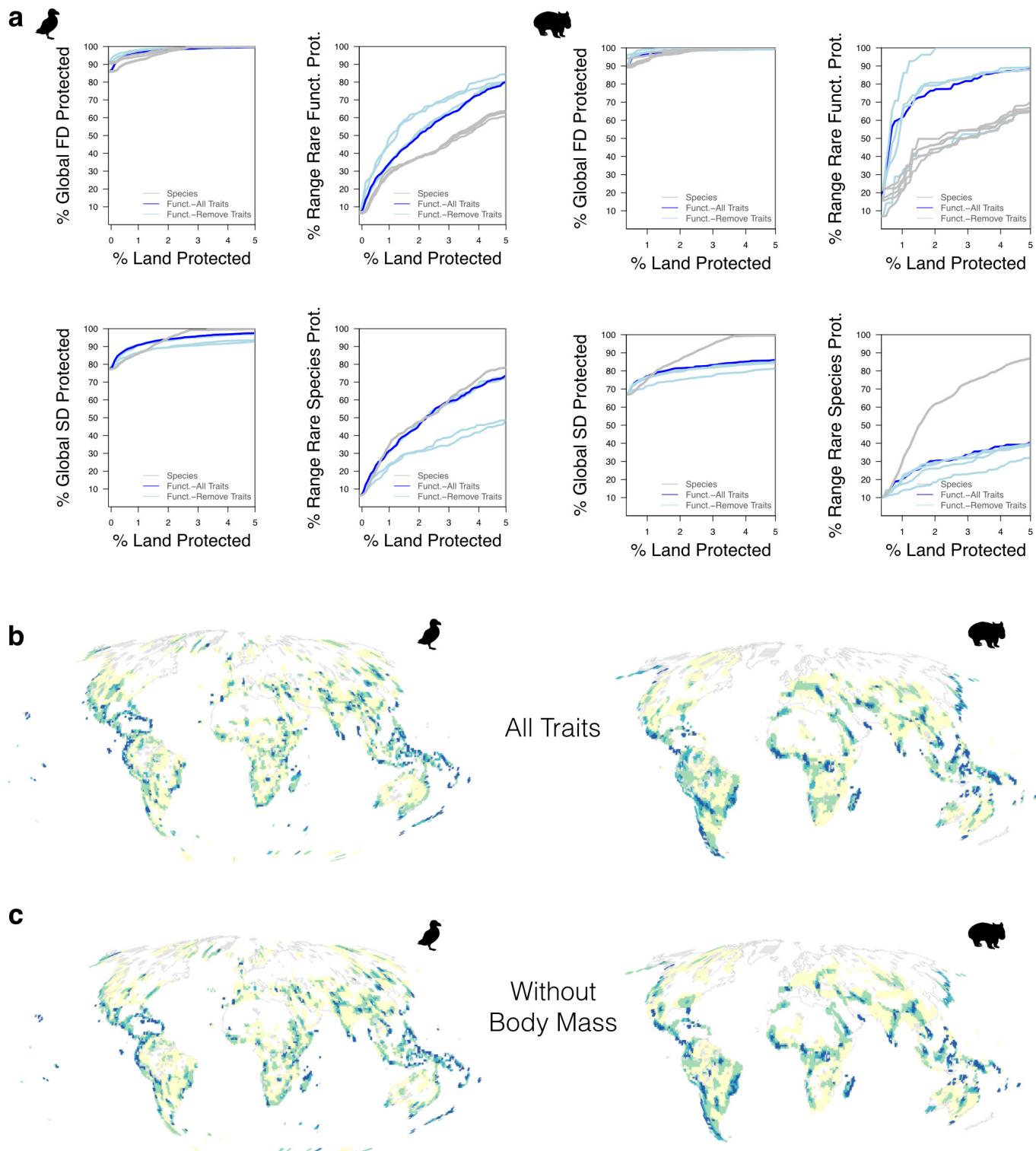
maximize local diversity objective. Solid lines are gains from the actual layout of protected areas, and dotted lines indicate the hypothetical case that both the new and existing protected area network were designed for this objective. **b, e, h, k**, Graphs of the spatial match in priorities for birds versus mammals with protected area expansion scenarios. **c, f, i, l**, Maps showing the priority areas for each group (bird priority only, mammal priority only, birds and mammals priority) for a 5% expansion scenario.



Extended Data Figure 4 | See next page for caption.

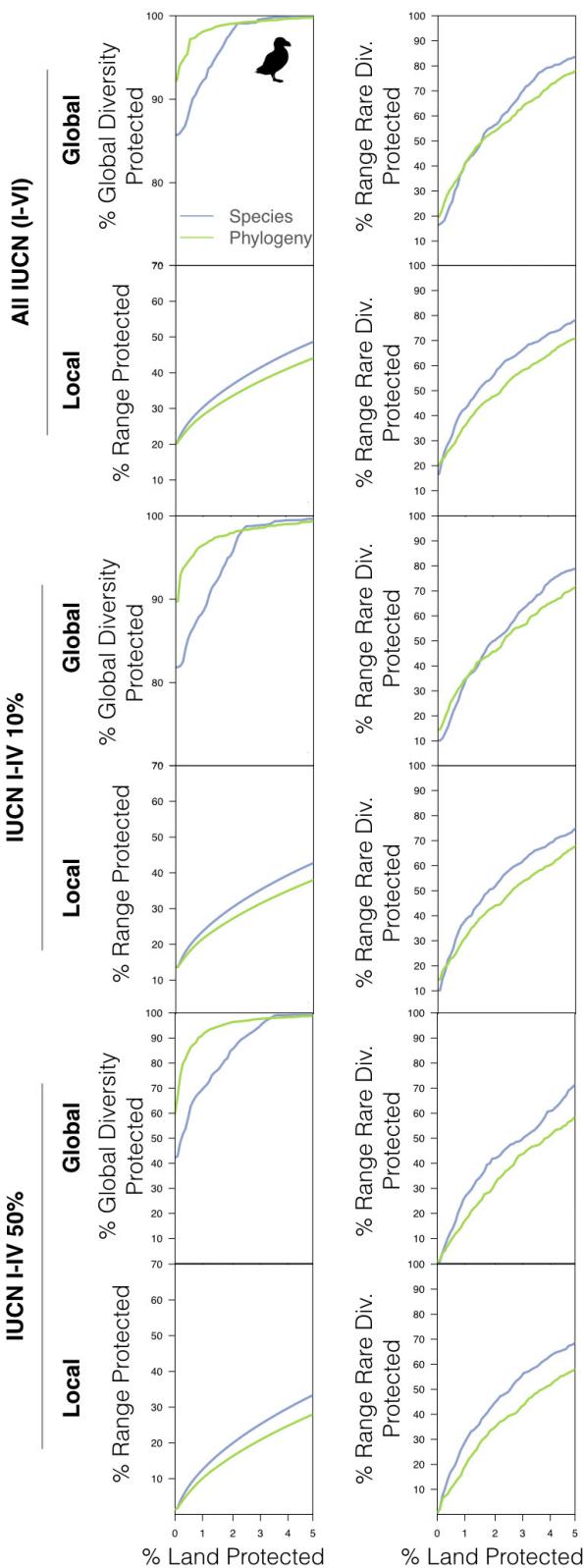
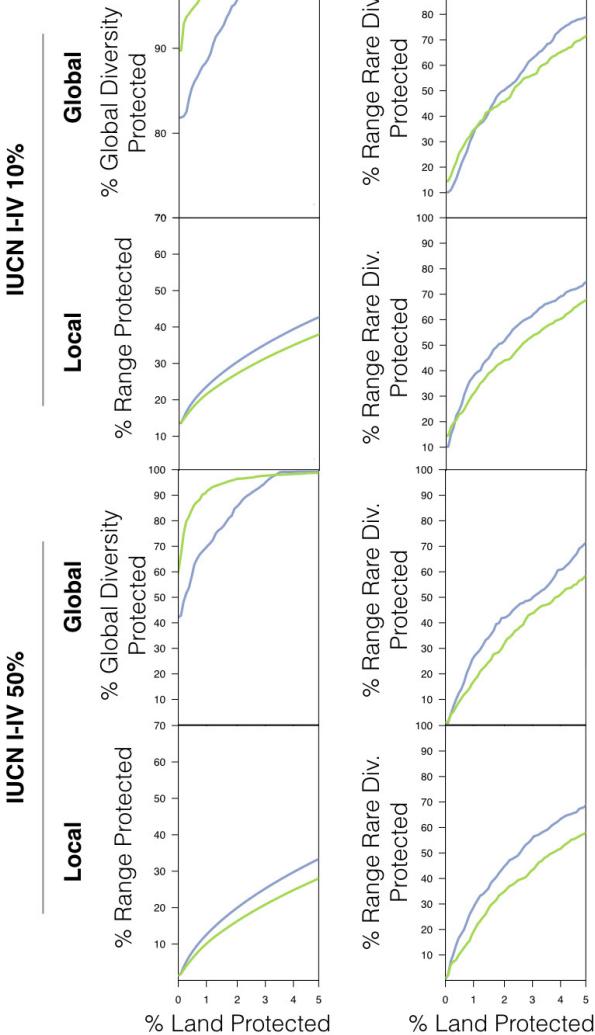
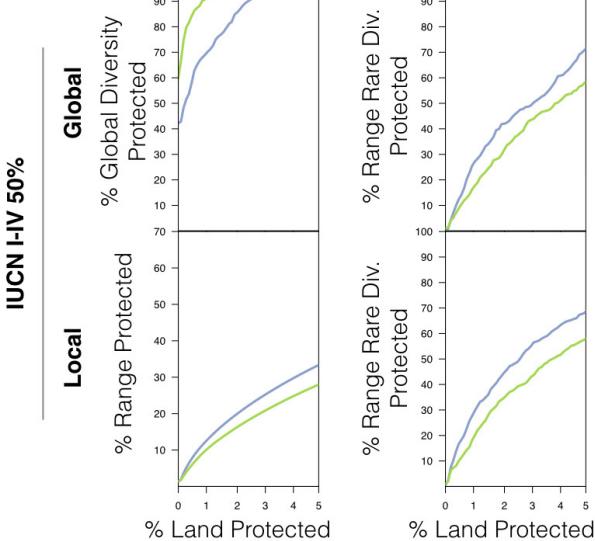
Extended Data Figure 4 | Uncertainty in species and phylogenetic priorities. **a–d**, Maximize global diversity (**a, c**) and maximise local diversity (**b, d**) strategies and their effect on different priorities for birds and mammals (across 100 phylogenies and 100 species replicates each). Graphs show the diversity that could be added into protection with an increase in land area protected for species (grey lines) and phylogenetic prioritizations (blue lines). ‘% Global PD Protected’ is the sum of phylogenetic branches (weighted by branch length) protected in at least one cell, and ‘% SD Prot’ is the number of species protected in at least one cell (both metrics expressed as a percentage of total possible diversity). Rare diversity is also considered. The ‘%Range Rare Species’ is the average spatial distribution that is protected for the rarest species (the rarest 10%)

and the ‘% Range Rare Phylo’ is the average spatial distribution of the rarest phylogenetic branches (rarest 10%) that are protected (weighted by the branch length). For the local objective (**b**), the tree of life is represented spatially as the per cent of the spatial range of the phylogeny that is protected ‘% Range Phylo Protected’ and species are represented as the average per cent of the spatial range of species ‘% Range Species Protected’ that are protected. Maps (**c, d**) show the similarities and differences in the top priorities for species and phylogenetic diversity for birds and mammals separately. The top priority is defined as cells that were consistently in the top 5% priority for protected area expansion across all species or phylogenetic runs.



Extended Data Figure 5 | Uncertainty in species and functional priorities for birds and mammals for the maximize global diversity strategy. **a**, Graphs show the diversity that could be added into protection with an increase in land in protection for species (grey lines) and functional prioritizations with all traits considered (dark blue lines). Light blue lines represent trait dendograms constructed without one trait (activity time, diet, foraging height and body mass). The '% Global FD Protected' is the sum of functional branches (weighted by branch length) protected in at least one cell, and '% Global SD Protected' is the number of species protected in at least one cell (both metrics expressed as a % of total possible diversity). FD, functional diversity; SD, species

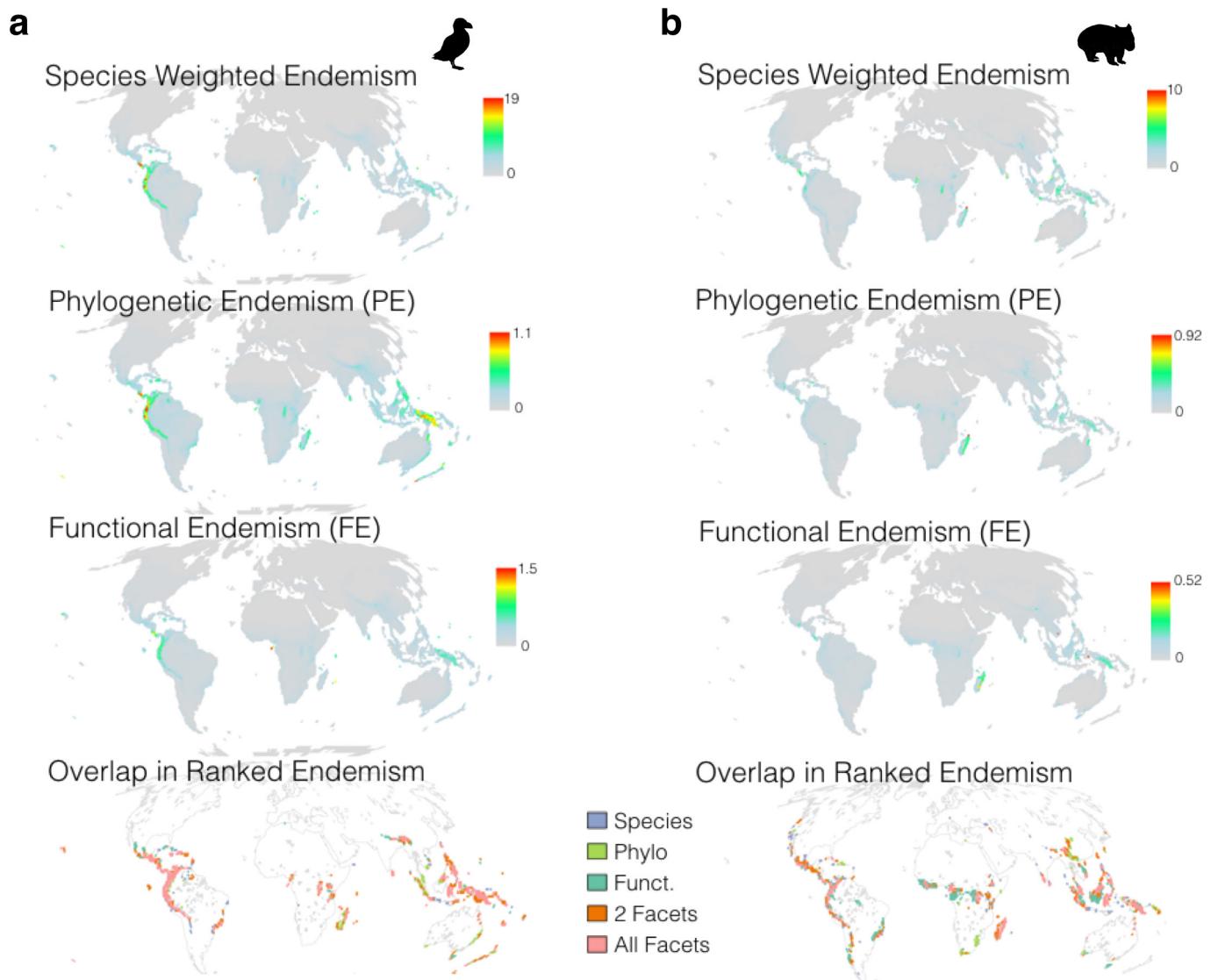
diversity. Rare diversity is also considered. The '% Range Rare Species Prot.' shows the average spatial distribution that is protected for the rarest species (the rarest 10%) and the '% Range Rare Funct. Prot.' is the average spatial distribution of the rarest functional branches (rarest 10%) that are protected (weighted by the branch length). Maps show how priorities change (or remain the same) when all traits are used (**b**) and when body mass is removed from consideration (**c**). Note that trait sensitivity to choice of traits was much lower with the local objective than for the global objective, and that spatial priorities are nearly identical. Additional results and/or graphs are available from the authors upon request.

a**b****c**

Extended Data Figure 6 | Uncertainty in definition of protected areas.

a–c, Uncertainty in definitions for birds from all IUCN categories with a 17% area threshold (a) and IUCN categories I–IV with a 10% (b) and 50% (c) threshold. Protected area thresholds are defined as those that have at least $x\%$ of the cell area in defined IUCN categories. Graphs show the diversity that could be added into protection with an extra 5% of the land area for species (blue) or phylogenies (green) and for ‘maximize local diversity’ or ‘maximize global diversity’ objectives. ‘% Global Diversity Protected’ is the sum of species or phylogenetic branches (weighted by

branch length) protected in at least one cell (both metrics expressed as a percentage of total possible diversity). Rare diversity graphs show the average spatial distribution that is protected for the rarest 10% of species or the average spatial distribution of the rarest 10% of phylogenetic branches that are protected (weighted by the branch length). The ‘% Range Protected’ is the average per cent of the spatial range of species or phylogenetic branches (weighted by the branch length) that is protected. Maps show the top priorities (that is, the top 5%) for bird species, phylogenetic diversity, and the match between the two.



Extended Data Figure 7 | Maps of weighted endemism (species, phylogenetic, and functional) for birds and mammals and comparisons between rankings produced by selecting grid cells with the highest endemism values for each biodiversity facet. a, b, Weighted endemism maps for birds (a) and mammals (b) show the raw values of species weighted endemism, phylogenetic endemism and functional endemism.

Maps of ranked endemism are calculated by selecting the top 5% of grid cells that have the highest weighted endemism values for each facet and that are not already protected. Colours indicate whether the grid cell is in the top 5% for one, two or all facets. For additional maps see <https://mol.org/patterns/facets>.

Extended Data Table 1 | How expanding protected areas by 5% could increase protected area coverage for the 20 most evolutionary and functionally distinct, rarest (<20 total occurrences), and least protected bird and mammal species (<1% of their range meeting the threshold protected area coverage)

Rank	Species Scientific	Species Common	RedList 2016	Rg	ED Mean	FD	D	% Spat. Range Protected with 5% PA expansions							
								Local Objective			Global Objective			Mean	
								Species	Phylo	Funct	Species	Phylo	Funct		
a															
1	<i>Rhynochetos jubatus</i>	Kagu	En	9	58.84	0.064	0.65	22	100	100	22	100	89	72	
2	<i>Oreophasis derbianus</i>	Horned Guan	En	10	13.15	0.211	0.61	100	100	100	20	29	100	75	
3	<i>Thaumatinis gigantea</i>	Giant Ibis	CrEn	4	56.89	0.051	0.60	0	99	0	0	100	100	50	
4	<i>Didunculus strigirostris</i>	Tooth-billed Pigeon	CrEn	2	27.77	0.140	0.56	100	100	100	100	100	100	100	
5	<i>Strigops habroptila</i>	Kakapo	CrEn	2	47.85	0.052	0.53	100	100	100	100	100	100	100	
6	<i>Notiomystis cincta</i>	Stitchbird	Vul	3	35.46	0.085	0.50	33	100	100	67	100	100	83	
7	<i>Aegotheles savesi</i>	New Caledonian Owlet-nightjar	CrEn	5	43.62	0.040	0.46	40	100	100	40	100	100	80	
8	<i>Eutriorchis astur</i>	Madagascar Serpent-eagle	En	15	33.58	0.066	0.44	73	97	80	33	77	33	66	
9	<i>Rigidipenna inexppectata</i>	Solomon Islands Frogmouth	NT	12	43.79	0.025	0.43	50	32	50	25	96	58	52	
10	<i>Callaeas cinereus</i>	Kokako	En	6	27.04	0.079	0.41	17	95	50	10	90	100	61	
11	<i>Habroptila wallacii</i>	Invisible Rail	Vul	8	13.91	0.124	0.41	100	59	100	25	38	100	70	
12	<i>Aegotheles tatei</i>	Starry Owlet-nightjar	DD	3	36.41	0.028	0.37	100	100	100	67	100	66	89	
13	<i>Mesitornis variegatus</i>	White-breasted Mesite	Vul	18	31.34	0.046	0.37	33	66	39	22	45	28	39	
14	<i>Fregetta grallaria</i>	White-bellied Storm-petrel	LC	7	30.24	0.049	0.37	43	42	42	86	94	86	66	
15	<i>Dasyornis broadbenti</i>	Rufous Bristlebird	LC	10	25.96	0.061	0.36	0	15	10	20	40	10	10	
16	<i>Hypsipetes crassirostris</i>	Seychelles Bulbul	LC	2	4.670	0.136	0.35	0	1	100	100	82	100	80	
17	<i>Hemignathus parvus</i>	Anianiau	Vul	1	4.420	0.137	0.35	100	100	100	100	100	100	100	
18	<i>Lugensa brevirostris</i>	Kerguelen Petrel	LC	13	37.12	0.018	0.35	15	16	10	31	94	39	33	
19	<i>Leptoptilos dubius</i>	Greater Adjutant	En	9	17.95	0.086	0.35	0	0	0	22	10	78	10	
20	<i>Nesoenas mayeri</i>	Pink Pigeon	En	1	9.260	0.117	0.35	100	52	100	100	100	100	92	
b															
1	<i>Solenodon cubanus</i>	Cuban Solenodon	En	2	61.53	0.057	0.63	100	100	0	0	100	100	67	
2	<i>Eulemur mongoz</i>	Mongoose Lemur	CrEn	5	10.78	0.211	0.57	100	60	100	60	42	100	77	
3	<i>Prolemur simus</i>	Greater Bamboo Lemur	CrEn	4	14.95	0.191	0.56	100	100	100	25	100	100	87	
4	<i>Urogale everetti</i>	Philippine Tree Shrew	LC	15	19.32	0.163	0.53	60	65	80	47	30	100	64	
5	<i>Rhinoceros sondaicus</i>	Javan Rhinoceros	CrEn	1	25.22	0.14	0.53	100	100	100	100	100	100	100	
6	<i>Pentalagus furnessi</i>	Amami Rabbit	En	3	29.05	0.102	0.47	67	98	0	67	100	100	72	
7	<i>Cryptotis peregrinus</i>	Oaxacan Broad-clawed Shrew	DD	4	10.05	0.167	0.46	100	100	100	50	68	100	86	
8	<i>Dendrogale melanura</i>	Bornean Smooth-tailed Treeshrew	DD	15	18.93	0.125	0.44	93	100	100	27	25	60	68	
9	<i>Hemitragus jayakari</i>	Arabian Tahr	En	10	5.57	0.147	0.38	0	0	0	10	5	100	19	
10	<i>Ailuropoda melanoleuca</i>	Giant Panda	Vul	15	38.28	0.031	0.38	53	85	7	20	71	27	44	
11	<i>Poiana leightoni</i>	West African Oyan	Vul	13	10.36	0.128	0.37	77	57	100	8	16	100	60	
12	<i>Sus ahoenobarbus</i>	Palawan Bearded Pig	Vul	11	10.53	0.127	0.37	73	54	73	36	43	100	63	
13	<i>Varecia rubra</i>	Red Ruffed Lemur	CrEn	3	14.79	0.112	0.37	100	100	100	67	87	100	92	
14	<i>Varecia variegata</i>	Black and White Ruffed Lemur	CrEn	11	14.79	0.112	0.37	100	100	100	36	88	100	87	
15	<i>Spalacopus cyanocephalus</i>	Coruro	LC	16	43.08	0.012	0.37	0	5	31	12	64	44	26	
16	<i>Salanoia concolor</i>	Brown-tailed Mongoose	Vul	7	16.01	0.092	0.34	100	100	100	43	88	100	88	
17	<i>Geogale aurita</i>	Large-eared Tenrec	LC	10	27.29	0.053	0.34	70	100	80	50	70	70	73	
18	<i>Podogymnura aureospinula</i>	Dinagat Moonrat	En	2	28.00	0.047	0.33	100	100	100	100	100	100	100	
19	<i>Podogymnura truei</i>	Mindanao Wood Shrew	LC	6	28.00	0.047	0.33	83	95	100	50	32	100	77	
20	<i>Biswamoyopterus biswasi</i>	Namadapha Flying Squirrel	CrEn	2	5.78	0.124	0.33	100	50	100	100	36	100	81	

Species (birds in **a**; mammals in **b**) are ranked by a distinctiveness index (D), which is the mean of the evolutionary distinctiveness across 100 phylogenies (ED mean) and the functional distinctiveness (FD), both scaled to between 0 and 1. Species scientific and common names and IUCN Red List status and species ranges (Rg; total occurrences in grid cells) are also included. The proportion of the spatial range of each species that could be protected with different protected area expansion scenarios are listed for each run (species, phylogenetic and functional) for both objectives and the mean per cent protected across all runs. Species and phylogenetic runs are averaged across 100 replicates.

Extended Data Table 2 | The top 20 grid cells that are the highest priorities for all facets, birds and mammals, and both conservation objectives

a

Rank	Bird SD	Bird PD	Bird FD	Bird Priority	Mammal SD	Mammal PD	Mammal FD	Mammal Priority	Priority All	Country
1	459	9736.7	36.4	0.99	168	4360	12.5	0.99	0.992	Cameroon
2	608	10609.2	43.9	0.99	193	4635	13.1	0.99	0.990	Costa Rica
3	224	6865.5	24	0.98	87	2893	7.5	1	0.990	Sri Lanka
4	570	10274.8	41.8	0.99	181	4543	13.1	0.99	0.989	Panama
5	616	11446.2	44.4	0.98	219	5292	14.7	0.99	0.986	Democratic Republic of the Congo
6	151	5009.7	17.4	0.98	64	1993	6.7	0.99	0.986	Madagascar
7	490	9999.9	37.7	0.98	169	4454	13	0.99	0.986	Cameroon
8	537	9982.7	40.4	0.99	183	4596	12.9	0.99	0.986	Costa Rica
9	129	4568.9	16	0.97	53	1824	5.4	1	0.984	Madagascar
10	486	9550.4	35.8	0.98	198	4785	13.2	0.98	0.983	Colombia
11	585	11239.5	43.1	0.97	224	5173	14.7	0.99	0.982	Democratic Republic of the Congo
12	521	9446.2	39.1	0.99	176	4497	13.1	0.98	0.981	Panama
13	193	5979.1	20.2	0.97	81	2471	6.3	0.99	0.981	Indonesia
14	199	5993	20.5	0.99	78	2411	6.2	0.98	0.981	Indonesia
15	250	7162.7	23.5	0.97	71	2354	6.5	0.99	0.981	Philippines
16	221	6817.6	23.8	0.99	80	2827	7.3	0.97	0.981	Sri Lanka
17	935	13902.8	51.5	0.98	235	5159	15.2	0.98	0.980	Ecuador
18	320	8265.6	28.9	0.98	85	2158	6.3	0.98	0.980	Papua New Guinea
19	250	7131.9	23.3	0.98	72	2387	6.6	0.98	0.980	Philippines
20	692	11122.8	44.8	0.99	197	4626	12.3	0.97	0.980	Ecuador

b

a. Priorities are the areas that would best benefit each facet of diversity with an expansion of protected areas by 5%. Grid cells are ranked by averaging the priority ranking across all individual runs (for example, bird phylogenetic priorities with a global objective or mammal functional priorities with a local objective). The overall averaged rank is 'Priority All', and averaged for mammal ('Mammal Priority') and bird runs ('Bird Priority'). A variety of diversity metrics are listed for each pixel (SD, species diversity; PD, phylogenetic diversity; FD, functional diversity) and the country where the pixel is found. **b.** The location of these pixels in red and its rank. Note that while in this multi-run summary, neighbouring pixels may see similar ranks due to their similarity in species and protection, single runs would identify only one or the other in a high priority set.

Extended Data Table 3 | List of conservation prioritization runs presented in the main paper and sensitivity analyses shown in Extended Data

Type	Group	Diversity Facet	Objective	Runs	Prot.Areas
Main Text	Birds+Mammals	Species, Phylo.,Funct.	Global, Local	1 each (6 total)	IUCN1-4 17%
	Birds Only	Species, Phylo.,Funct.	Global, Local	1 each (6 total)	IUCN1-4 17%
	Mammals Only	Species, Phylo.,Funct.	Global, Local	1 each (6 total)	IUCN1-4 17%
	Birds+Mammals	Species, Phylo.,Funct.	Global, Local	1 each (6 total)	Optimal
	Birds Only	Species, Phylo.,Funct.	Global, Local	1 each (6 total)	Optimal
	Mammals Only	Species, Phylo.,Funct.	Global, Local	1 each (6 total)	Optimal
Phylogenetic Uncertainty	Birds Only	Species, Phylo.	Global, Local	100 each (400 total)	IUCN1-4 17%
	Mammals Only	Species, Phylo.	Global, Local	100 each (400 total)	IUCN1-4 17%
Functional Uncertainty	Birds Only	Funct. (No Body Mass)	Global, Local	1 each (2 total)	IUCN1-4 17%
	Birds Only	Funct. (No Diet)	Global, Local	1 each (2 total)	IUCN1-4 17%
	Birds Only	Funct. (No Activity Cycle)	Global, Local	1 each (2 total)	IUCN1-4 17%
	Birds Only	Funct. (No Forage Ht.)	Global, Local	1 each (2 total)	IUCN1-4 17%
	Mammals Only	Funct. (No Body Mass)	Global, Local	1 each (2 total)	IUCN1-4 17%
	Mammals Only	Funct. (No Diet)	Global, Local	1 each (2 total)	IUCN1-4 17%
	Mammals Only	Funct. (No Activity Cycle)	Global, Local	1 each (2 total)	IUCN1-4 17%
	Mammals Only	Funct. (No Forage Ht.)	Global, Local	1 each (2 total)	IUCN1-4 17%
Prot. Areas Uncertainty	Birds+Mammals	Species, Phylo.,Funct.	Global, Local	1 each (6 total)	IUCN1-4 10%
	Birds+Mammals	Species, Phylo.,Funct.	Global, Local	1 each (6 total)	IUCN1-4 50%
	Birds+Mammals	Species, Phylo.,Funct.	Global, Local	1 each (6 total)	All IUCN 17%
	Birds+Mammals	Species, Phylo.,Funct.	Global, Local	1 each (6 total)	All IUCN 50%

For the main text, analyses include birds and mammals considered separately or combined for each biodiversity facet (species, phylogenetic, and functional diversity), each conservation objective (maximizing global or local diversity), and for 'Optimal' scenarios (currently non-existent protected areas that are hypothetically ideally located) and hypothetical expansions of the existing protected area network ('Prot.Areas' column). Additional spatial prioritization runs were run to assess uncertainty in three key areas: (1) phylogenetic uncertainty; (2) functional uncertainty; and (3) uncertainty in defining protected areas according to IUCN categories (IUCN I to IV, or all IUCN categories) and thresholds for protection (17% or 50%). For phylogenetic uncertainty, spatial priority results were re-run for 100 phylogenies for each of birds and mammals. Both species-based and phylogenetic-based prioritizations were run for each phylogenetic replicate (200 runs for each conservation strategy). We calculated how well both species-based and phylogenetic-based runs captured both species and phylogenetic diversity metrics.