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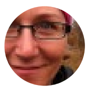
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Global protected area expansion is compromised by projected land-use and parochialism

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Protected areas are one of the main tools for halting the continuing global biodiversity crisis[1–4] caused by habitat loss, fragmentation and other anthropogenic pressures[5–8]. According to the Aichi Biodiversity Target 11 adopted by the Convention on Biological Diversity, the protected area network should be expanded to at least 17% of the terrestrial world by 2020 (http://www.cbd.int/sp/targets). To maximize conservation outcomes, it is crucial to identify the best expansion areas. Here we show that there is a very high potential to increase protection of ecoregions and vertebrate species by expanding the protected area network, but also identify considerable risk of ineffective outcomes due to land-use change and uncoordinated actions between countries. We use distribution data for 24,757 terrestrial vertebrates assessed under the International Union for the Conservation of Nature (IUCN) 'red list of threatened species'[9], and terrestrial ecoregions[10] (827), modified by land-use models for the present and 2040, and introduce techniques for global and balanced spatial conservation prioritization. First, we show that with a coordinated global protected area network expansion to 17% of terrestrial land, average protection of species ranges and ecoregions could triple. Second, if projected land-use change by 2040 (ref. 11) takes place, it becomes infeasible to reach the currently possible protection levels, and over 1,000 threatened species would lose more than 50% of their present effective ranges worldwide. Third, we demonstrate a major efficiency gap between national and global conservation priorities. Strong evidence is shown that further biodiversity loss is unavoidable unless international action is quickly taken to balance land-use and biodiversity conservation. The approach used here can serve as a framework for repeatable and quantitative assessment of efficiency, gaps and expansion of the global protected area network globally, regionally and nationally, considering current and projected land-use pressures.

Habitat loss and fragmentation due to intensifying land-use is one of the major drivers of biodiversity loss[7,8]. The global protected area (PA) network is one of the most important means to halt such loss[1–4]. Adoption of the strategic Aichi Biodiversity Target 11 of the Convention of Biological Diversity (CBD; http://www.cbd.int/sp/targets) provides a unique opportunity for expanding the current PA network to cover 17% of the terrestrial areas by 2020. At present, global patterns in biodiversity and global priority areas for conservation at the regional scale are relatively well known[1,6,8,12–16], but spatial assessments are essential[13,14] to maximize global conservation outcomes from PA expansion.

Here, we carried out a comprehensive assessment of priority areas for expanding the current global PA network, and quantified their potential contribution to global conservation. We present a prioritization of the global PA network expansion to 17% that shows the performance and spatial pattern of alternative expansions of the current PA network, delivering balanced, complementary coverage across a breadth of ecoregions (827) and species (24,757), for present and future (2040) land-use conditions, and comparing the outcomes of a globally coordinated expansion against nationally prioritized expansion areas. Our analyses and maps are informative at the global, regional and national levels.

We used newly developed prioritization methods and software that follow principles and approaches from systematic conservation planning and spatial conservation prioritization[17,18]. As urbanization, agricultural land-use, desertification and deforestation are rapidly increasing[8,11], we integrated information about projected land-use change[11] and discounted the distributions of species and ecoregions, to produce effective ranges at present and by 2040 (Supplementary Information). We address three questions that are crucial for the effective implementation of the Aichi Biodiversity Target 11: (1) what is the potential performance of the expanded PA network in terms of increased coverage of species ranges and ecoregions; (2) how will land-use change by 2040 effect the performance and spatial pattern of the best PA expansion areas; and (3) what is the efficiency gap between globally and nationally identified priority areas.

First, our results show that there is a high potential to increase coverage of ecoregions and species, which could be harnessed with complementarity-based prioritization. If placed efficiently (Fig. 1 and Extended Data Fig. 1), additional protection could triple the average protection of vertebrate species ranges (Fig. 2, labels *A* and *B*, and Extended Data Fig. 2). Furthermore, it would increase average protection of ecoregions by a factor of 3.3, helping to address the continuing biome crisis[19] and providing a broader bioclimatic coverage and representativeness under climate change[20] (Supplementary Information). This high potential is a result of the presently largely unprotected status of a considerable proportion of species and ecoregions that have narrow ranges. Globally, the highest priorities for expanding PAs are located in the Neotropics (Central America, along the Andes and the Brazilian coast), Africa (Madagascar, the Eastern Arc Mountains and the forests of west Africa) and southeast Asia (the Himalayan slopes, Indonesia, Papua New Guinea and the Philippines) (Fig. 1 and Supplementary Information). The locations of the top 17% priorities are relatively consistent at a regional scale (Supplementary Information), regardless of the land-use scenario and/or parameters being used. This highlights the importance of the top priority areas and the robustness of our results in identifying some well-known areas[1,12,13].

Second, regarding the effects of projected land-use change on the performance of the expanded PA network, we show that intensification may lead to considerable biodiversity loss by 2040 (Fig. 2, label *C*). Although the expansion to 17% could on average account for ~61% of the current ranges of species and ecoregions (Fig. 2), the level of protection would drop to ~54% by 2040, even if projected land-use change is accounted for in the PA network expansion. Globally, terrestrial vertebrates could lose on average ~12 to 16% of their current effective range by 2040 (Supplementary Information), with more than 50% habitat loss for more than 2,600 species (Extended Data Fig. 3 and Extended Data Table 1). Furthermore, a loss of 15% in the average range of threatened species would occur by 2040 (Extended Data Table 2), and among threatened species, over 4,880 would lose more than 30% of their current range, 990 more than 50%, and 110

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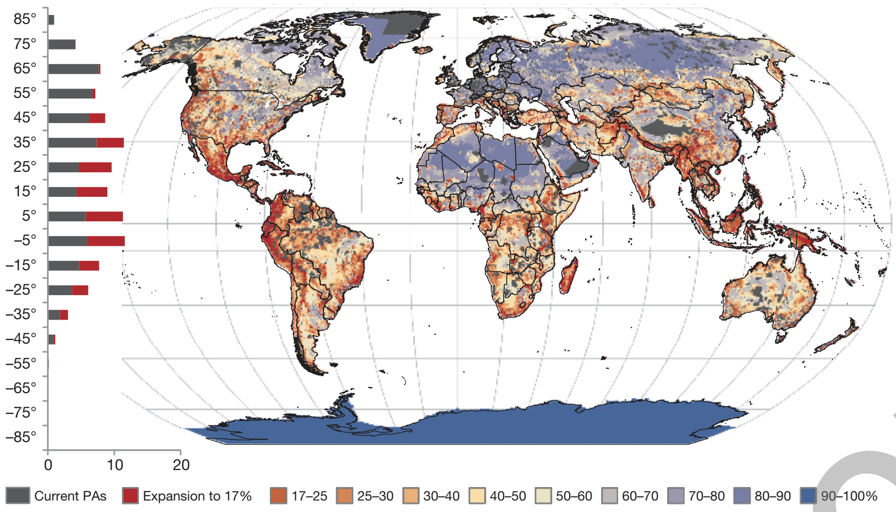

Figure 1 | Global priority map for the expansion of the PA system. Prioritization of the global PA network expansion, taking future (2040) projected land-use into account. The bars on the left show the distribution of current (grey) and proposed (red) expansion areas by latitude bins. Currently designated PAs are quite evenly distributed across latitudes (55% of global PAs are in latitudes $\geq -30°$ and $\leq 30°$), whereas the expansion effort would be concentrated in the tropics to maximize coverage of species and ecoregions (75% of the expansion areas are between latitudes $-30°$ and $+30°$). Analysis data sources: International Union for the Conservation of Nature (IUCN), World Database on Protected Areas (WDPA), and Database of Global Administrative Areas (GADM).

more than 70% (Extended Data Table 1 and Supplementary information). Prioritizing on the basis of threatened species would improve the average coverage of threatened species ranges by only 4%, but causing an average loss of 5% across all non-threatened species and 22% across ecoregions (Extended Data Table 2, Extended Data Fig. 4 and Supplementary Information). Consequently, actions should be taken quickly to reduce land-use changes or palliate their effect in the highest priority areas. Furthermore, to reach the currently possible protection levels, if conservation planning would consider projected future land-use (Fig. 1), the global protection target would need to be increased from 17% to 21% to compensate for land-use intensification (Fig. 2, label *C*).

Third, we show that global to continental scale conservation planning and international cooperation is vital for reaching high conservation outcomes. We demonstrate this by conducting analyses separately for each country and analysing the resulting global pattern and performance. We find that a lack of international coordination would cause an efficiency loss much greater than expected from projected land-use change by 2040 (Fig. 2 and Extended Data Table 2). The national top 17% areas could at best cover on average ~70% of the amount of species' ranges and ecoregions covered in the global prioritizations (Fig. 2, label *C*). Although marked overlaps between global and national priorities occur in large tropical countries such as Brazil, Congo and India (Fig. 3 and Extended Data Fig. 5), many highly irreplaceable biodiversity areas in Central America, Madagascar and southeast Asia would be left unprotected in national prioritizations, and over 450 threatened species would lose more than 50% of their effective range (Supplementary Information). Nevertheless, the fraction (38%) in which the global and national priorities overlap (Fig. 3) undoubtedly identifies key areas for Aichi Biodiversity Target 11. In other regions, conservation partnerships across country borders are crucial[21]. This is particularly relevant for the connectivity or compactness of PAs: the global prioritization produces a network in which the number and size of new PAs are comparable to the current network, whereas national prioritization would lead to a more fragmented network, duplicating the number of PAs and decreasing their average size by 60% (see Supplementary Information).

We have made use of several sources of information, including spatial patterns of PAs of all sizes[22], high-resolution human-driven land-use scenarios[11,23], and spatial patterns of thousands of narrow-range species and distinctive ecoregions[9,10]. To meet our study objectives, it has been crucial to be able to account for detailed spatial patterns of PAs and biodiversity (Supplementary Information). Considering the dynamic nature of PA designations, and the numerous downgrading, downsizing and degazettement events recently observed[24], there is a need for recurrent following-up on previous studies that have provided insight into the effectiveness and gaps of the global PA network[1,4,13,15]. Further development of global data resources are required to consider other aspects of biodiversity and additional taxa[25,26], such as invertebrates[14] or plants[16]. Fine-scale conservation planning assessments using more local information should be carried out in priority areas identified by this study[2]. In particular, high-resolution data can be used on sites of confirmed importance for biodiversity, such as 'important bird areas', 'important plant areas', 'alliance for zero extinction sites', or key biodiversity areas (KBAs) generally[2] (see Supplementary Information for an analysis of KBAs in three countries). Furthermore, fair estimation of opportunity costs, dynamic monitoring of

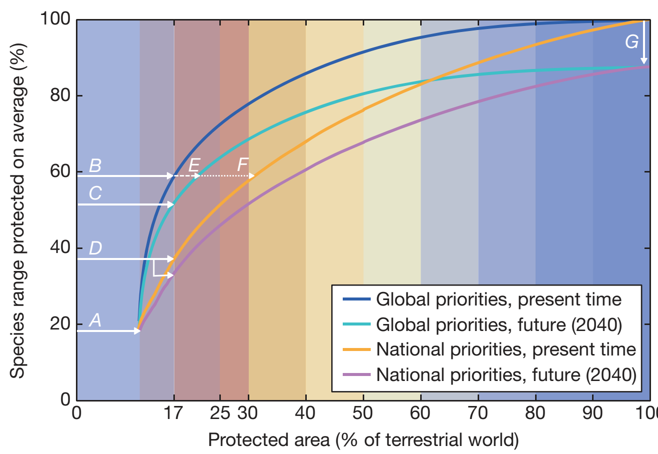

Figure 2 | Cumulative average coverage of species ranges in different fractions of terrestrial land. Terrestrial land fractions are listed in priority order, from current PAs (grey) to 17% expansion (red), and over entire terrestrial land. Background colours match the priority map (Fig. 1). The present PAs cover ~19% of species ranges (*A*). Expansion to 17% could increase coverage to ~61% (*B*) or ~56% with 2040 land use (*C*). National priorities perform much poorer (*D*). A further expansion would be required to compensate land-use change (to 21%, *E*) and/or national-scale planning (to 32%, *F*). Globally, land-use change may cause over ~12% species' range loss (*G*).

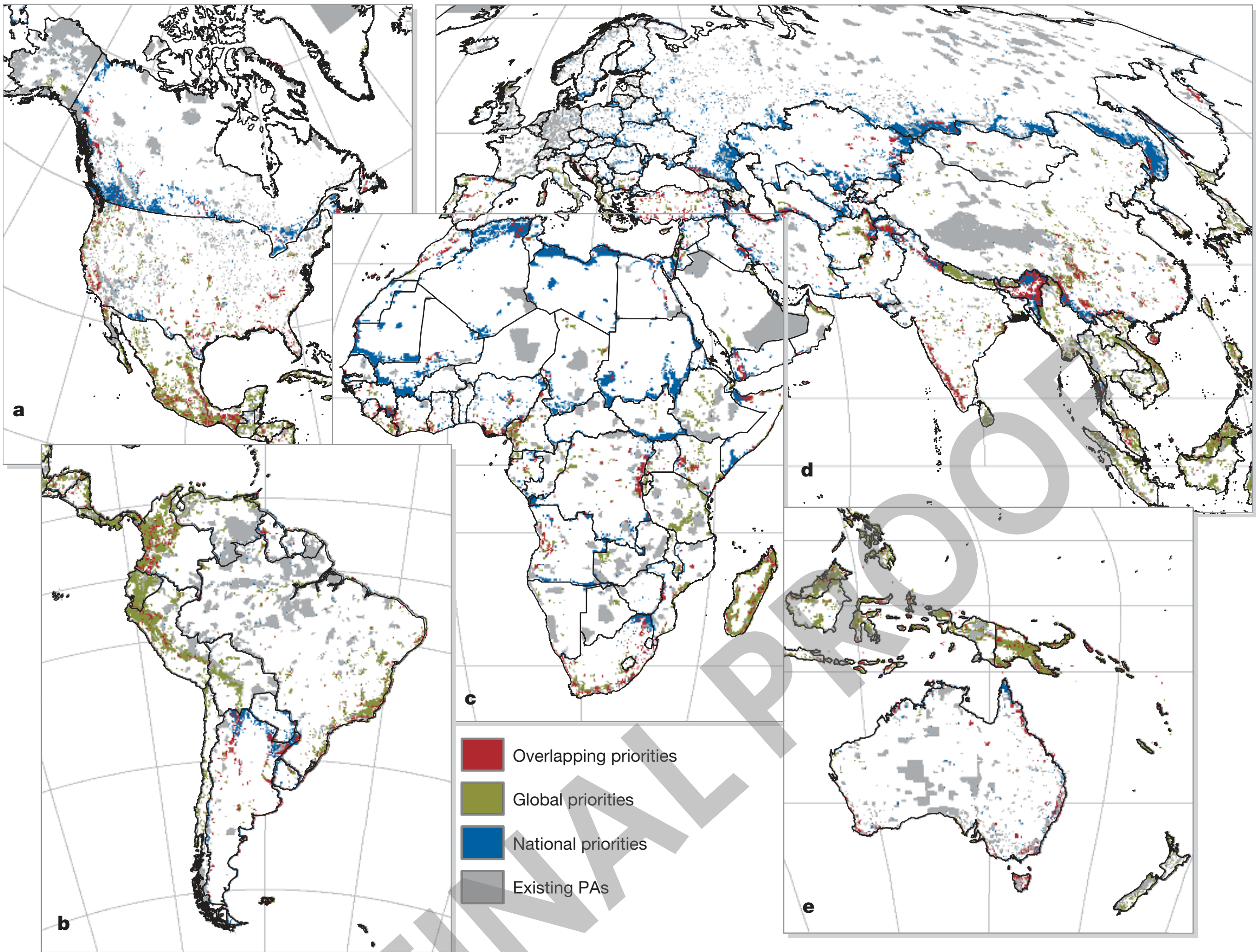

Figure 3 | Global and national priority expansion areas (2040), and their overlap (38% of top 17% priority areas). There is a clear difference between the areas with relatively higher national priority (blue) and higher global priority (green). The edge effects in the national prioritization originate primarily from latitudinal gradients in species diversity. Notably, the congruent areas (red) overlap with many previously identified biodiversity hotspots in large countries: Atlantic forest/Brazil, Himalaya and mountains of southwestern China and eastern Afromontane/Congo. While this map is visualized for a strict top 17% threshold, our results provide continuous rankings of the whole land surface of the Earth. For a global map projection, see Supplementary Information. Analysis data sources: IUCN, WDPA and GADM.

threats, update of land-use scenarios, and integration of species-specific habitat requirements would benefit recurrent systematic assessments of biodiversity patterns. While our study focuses on relatively short-term changes due to land-use, climate change is a major issue that needs to be addressed in forward-looking conservation prioritization. For longer-term projections, priorities should be defined considering recent advances in climate change scenarios[27], and recent results that model the vulnerability of species[28] and ecoregions[20] to climate change.

Implementing PA network expansion could be more challenging in areas that are less economically developed, resource limited and/or have weaker governance[29]. Our global solution (Fig. 1) shows that most of the priority areas for expanding the PA network are concentrated in the global south (Extended Data Fig. 6 and Supplementary Information), whereas only 25% of the global expansion responsibility lies at higher latitudes ($\leq 30^\circ$ and $\geq -30^\circ$). Continentally, Asia has the highest responsibility, with 37% of the total expansion areas, while 18% are in Africa and 31% in Central and South America. In these areas of highest responsibility, support mechanisms are needed to address governance challenges, overall feasibility, development and population growth, and the burden of additional management costs of PAs[29]. It would also be important to reconcile future land-use with national and global conservation priorities. If every country is to contribute the same percentage of area, priority areas are more evenly distributed globally, less concentrated in Central and South America and more in Africa and Asia, less in tropical forests and more in temperate forest, and especially in grassland, savannah and shrubland (Extended Data Fig. 6 and Supplementary Information).

Robust, reproducible assessments are pivotal for well-informed and iterative decision-making towards an effective and balanced expansion of the global PA network. Our analysis is based on published data, and a well-documented, newly developed, and publicly available dedicated software tool. We have also shared the files required to implement the analyses, and the resulting spatial data layers in the hope that they will stimulate further analyses and interpretation. Here, we have quantitatively shown the considerable potential that is at stake. Halting biodiversity loss requires global planning and implementation of support mechanisms for the PA network expansion. Furthermore, good coverage of species' ranges in PAs does not guarantee their persistence. The effectiveness of PAs depends on several ecological and societal factors. While the national level implementation is not efficient in terms of global coverage of biodiversity, it is socially more acceptable and increases the local benefits of conservation, that is, the several positive aspects of parochialism[30]. The Aichi Biodiversity Target 11 opens a unique window of opportunity with political commitment to address biodiversity loss. It is important that decision-makers and other stakeholders take action to implement platforms for effective and balanced protected area expansion at global, continental and regional scales, and use these to reduce land-use pressures on biodiversity.

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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Supplementary Information is available in the online version of the paper.

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Author Contributions F.M.P., T.T. and A.M. designed the study and wrote the manuscript, with contributions from all authors. A.M. conceived and led the study. F.M.P. and T.T. analysed the data and prepared the figures and tables. F.M.P. implemented prioritization algorithms and analyses. T.T., E.D.M., A.K., P.K., J.K., J.L., H.T. and F.M.P. collected and processed the data. P.H.V. contributed land-use models and data.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to F.M.P. (federico.montesino-pouzols@stfc.ac.uk), T.T. (tuuli.toivonen@helsinki.fi) or A.M. (atte.moilanen@helsinki.fi).

METHODS

Below, we describe the steps of our analysis from spatial data collection and pre-processing to spatial prioritization.

Data processing. We based our analysis on a set of 25,588 spatial data layers collected from different sources and in different formats. This data set consisted of two basic administrative delineations (protected areas and country borders), 25,584 biodiversity feature distributions (species and ecoregions) and two land cover layers (present and projected future), as described below. The pre-processing was the same for all layers: we converted all input data to latitude/longitude coordinate system and rasterized them to global resolution grids (latitude/longitude coordinate system), using ArcGIS 10.1 software, harmonized to different resolutions: 0.01667° (equalling 1.7 km at the Equator), 0.05°, 0.1° and 0.2°. The content of the data was restricted to terrestrial areas using a binary land/water mask that contained all continental terrestrial areas, excluding large water bodies[31]. The land/water mask was originally downloaded from and processed by WorldGrids (http://www.worldgrids.org).

Basic administrative delineations. The data on protected areas was based on the June 2013 release of the WDPA[22] (retrieved from http://www.protectedplanet.net, produced by the United Nations Environment Programme's World Conservation Monitoring Centre). We extracted the protected areas from the WDPA database by selecting only areas belonging to IUCN protected area categories I to VI and having as status 'designated' or alike (such as 'desingated'). These areas cover approximately 11% of the Earth's land surface (including Antarctica) at the time of this study. We included only protected areas having detailed geographic information in the database (105,369), excluding the ones represented with a point only. This meant excluding in total 21,248 protected areas that did not have polygon boundaries, totalling 817,321 km^2 (6.9% of all protected areas). One common approach would have been to represent the PAs with only point information by a circle that has the surface of the PA as presented in the WDPA. This would have, however, added extra noise to the shapes of the PAs, as many PAs are elongated or otherwise of particular shape. We rasterized the protected areas to the analysis resolution with an intersect rule, thus labelling all cells touching a protected area polygon as protected areas. This way, we were also able to include the smallest and narrowest protected areas to the analysis. National boundaries were rasterized from the polygons of the GADM based on the unique country codes. This resulted in a raster layer identifying 253 countries or autonomous regions in the world.

Ecoregions. We used spatial distributions of all 827 terrestrial ecoregions, grouped into 14 biomes or major habitat types, as defined by the World Wildlife Fund (http://worldwildlife.org/biomes). On the basis of regional analyses and information from hundreds of experts, the ecoregion boundaries delimit areas within which ecological and evolutionary processes interact most strongly[10]. The same ecoregion classification has previously been used in analysis of, for example, broad patterns of biodiversity, habitat loss and conservation status of different areas[15,19,20].

Species. We based our analysis on terrestrial vertebrates included in the IUCN red list of threatened species[9,32–35]. Produced by the IUCN Global Species Programme, the IUCN Species Survival Commission, and the IUCN Red List Partnership, this is the most comprehensive global assessment of the conservation status of animal, plant and fungi species. We retrieved the species range data for mammals, amphibians and reptiles from the 'spatial data download' area of the IUCN red list website (http://www.iucnredlist.org/)[9]. Data for birds was obtained from the BirdLife International data zone webpage[32] (http://www.birdlife.org/datazone/home).

Distribution data for species were available as geographic information system (GIS) polygons, covering known or inferred areas where species occur. These distribution polygons are in practice positioned somewhere between the extent of occurrence and the true area of occupancy of the species[36,37]. They are far from perfect and may overestimate the species' true area of occupancy[4,37–40], as they may include areas from which the species is absent, such as large freshwater bodies within terrestrial species' distributions. Therefore, the present analyses should be interpreted in terms of coverage of species' ranges, not in terms of coverage of the true distributions of species. Nevertheless, the range maps reduce geographical biases and fill gaps that exist in point locality data[37,40]. In addition, these species distribution polygons represent the best frequently updated and publicly available information of the distribution limits of vertebrate species[4]. These data have been widely used previously[4,6,34,35,41–44]. Here, we refined these range distribution maps to obtain effective ranges by land-use models, as further described below. At the time of this study, a considerable fraction of reptiles remains unassessed and range distribution data are not available[45]. The main results reported here have been generated including the available spatial data on reptiles, which are geographically biased[45]. See Supplementary Information for an analysis of the sensitivity of our results to this factor, and prioritization results generated excluding reptiles from the analysis. From the IUCN species database[9], we selected terrestrial species only, leaving out 79 entirely marine mammals in families Otariidae, Phocidae, Odobenidae, Balaenidae, Balaenopteridae, Delphinidae, Eschrichtiidae, Iniidae, Monodontidae, Neobalaenidae, Phocoenidae, Physeteridae, Platanistidae, Ziphiidae and Sirenia. We processed all species similarly and rasterized the range of each species to a separate raster layer. With the information facilitated by the IUCN red list of threatened species, the breeding and non-breeding portions of the ranges of migratory birds could also be treated separately[46].

In the rasterizing process, we assigned the pixel values according to the certainty of species presence in the polygon, as reported by the IUCN. We used four categories with a continuous scale from 1 to 0, with less reliable occurrence categories translated into lower values: extant = 1.0; probably extant and uncertainly extant = 0.5; possibly extinct = 0.1; and extinct = 0.0. Several arguments coming from the field of biogeography suggest the use of spatial resolutions comparable to the highest resolution of the available distribution maps[37,47,48]. We made the polygon to raster conversion originally using a pixel size of 0.00833° (equalling roughly 0.85 km at the equator) and aggregated the data up to 1.7-km resolution (0.01667°), 0.05°, 0.1° and 0.2° by summing up the original pixel values in blocks of 4, 36, 144 and 576 cells, respectively. This way, we were able to include even the smallest ranges without exaggerating their size.

Land-use data. We considered land-use effects on ecoregion extents and species ranges by discounting the ranges by land use for present time and 2040 (refs 7, 11). This process reduces one of the most common sources of commission errors in species' range maps: areas that fall inside range polygons but are unsuitable for species, as they have been transformed by human activities. For present land-use conditions, species' ranges were discounted by an average of 14.12% (s.d.: 13.37%, median: 9.558%), whereas for future conditions their ranges were discounted by 23.99% on average (s.d.: 19.03%, median: 18.22%). The land-use scenarios for 2040 is based on the Organisation for Economic Co-operation and Development (OECD) environmental outlook baseline scenario[49]. The scenarios were generated using the CLUMondo model at a resolution of 5 arcmin (9.25 km). In the models, land-use changes are driven by regional demand for goods and influenced by local factors that either promote or constrain land-use change. CLUMondo has the highest thematically relevant land-use information for the purpose, distinguishing different land systems that can have a mixed composition and contains relevant information from the perspective of biodiversity analyses. In particular, these models include quantitative information of land-use intensity for different land-use classes[11]. We first converted the original land-use maps from 2000 (present) and 2040 (future) to numerical data by giving different land-use classes values between 1 and 0 reflecting their naturalness and different intensities of farming[50,51]. The following naturalness values were given for different land uses, from most to least natural.

Dense forest, mosaic grassland and forest, mosaic grassland/bare and natural grassland = 1.0; open forest/few livestock, open forest, grassland/few livestock, grassland, bare/few livestock = 0.9; mosaic cropland and grassland, mosaic cropland and forest = 0.8; mosaic cropland (extended) and grassland/few livestock, mosaic cropland (extended) and open forest/few livestock = 0.7; mosaic cropland (medium intensive) and grassland/few livestock, mosaic cropland (medium intensive) and forest/few livestock = 0.6; mosaic cropland (intensive) and grassland/few livestock, mosaic cropland (intensive) and forest/few livestock = 0.5; cropland extensive/few livestock, cropland extensive = 0.4; cropland medium intensive/ few livestock, cropland medium intensive = 0.3; cropland intensive/few livestock, cropland intensive = 0.2; bare, peri-urban and villages = 0.1; urban = 0.0. In a more restrictive scale, we defined the naturalness value as 0 for all intensive land uses (see Supplementary Information for additional results obtained for this scale).

To produce estimates of effective ranges for present and future, we multiplied the values in the original species range and ecoregion maps using the naturalness map for present and future, respectively. Technically, the calculations were implemented in zonation by using the condition transformation[52,53] In the later analyses for the present and future, we used the respectively transformed sets of distribution layers.

These values were defined as a reasonable first approximation. However, we made several assumptions, and especially we assume the same effects across all taxonomic groups. Refinement of this processing step in a reliable manner would require models and evidence on the effects of different land uses on species, which are only recently becoming available for some taxonomic groups[54]. Alternative approaches used in the literature include the use of habitat suitability models[55] or habitat classification schemes from the IUCN red list of threatened species[56] to constrain species' range distributions, or the use of additional data[57]. Such approaches would probably reduce commission errors resulting from broad range maps but would not be trivial to combine with high-resolution land-use data, and could potentially introduce omission errors and other artefacts resulting from the fact that land-use classes do not match habitat classes.

Spatial prioritization method and process. Priority maps were generated as rankings of landscape elements (cells), iteratively ranked from lowest to highest priority for conservation (Fig. 1). Together with ranking maps, we produced performance curves that describe the extent to which each feature or species is retained in any given high- or low-priority fraction of the landscape (Fig. 2). We implemented priority ranking with the zonation methods and software for spatial conservation planning[53,58,59], which produce ranking maps and performance curves as main outputs. We used the newly developed zonation 4 software tool, introducing methods capable of processing problems four or more orders of magnitude bigger than previously possible[14,21,59,60], of the order of 10^4 species or features and 10^9 landscape elements[53]. Zonation produces a balanced ranking in which balanced denotes that for any given rank level, such as top 17% areas, these areas are complementary and jointly achieve a well-balanced level of representation across all biodiversity features. Complementarity is a key concept in spatial conservation prioritization and it can be loosely defined as a property of the solution that sites work together efficiently in achieving conservation objectives[4,17,61,62].

We used the additive benefit function analysis variant of zonation[53,58,63], which can be interpreted as minimization of aggregate extinction rates via feature-specific species-area curves. This method can produce a high return on investment[64] in terms of average coverage of biodiversity features per amount of area protected, and does not require targets or thresholds that necessarily have a degree of arbitrarity[41]. To prioritize expansion areas starting from the current global PA network, we used a technique[14,53,59] in which the priority ranking is generated in two stages, with the ranking of expansion areas being generated in the first stage and current PA landscape elements remaining in the second stage. The method also induces aggregation of cells into compact PAs or PA expansions by favouring cells that are found in the neighbourhood of areas retained for protection to the detriment of more scattered cells[53].

The results reported here correspond to seven different set-ups or analysis variants (columns of Extended Data Table 2), which have been made publicly available, with raster maps available for a resolution of 0.2°. Each set-up defines a set of spatial data layers and prioritization analysis parameters based on which a unique priority ranking (together with performance curves) is produced in a deterministic manner. Ecoregions were weighted so that their aggregate weight is equal to the aggregate weight of all species. Species were weighted according to their category of extinction risk on the IUCN red list of threatened species[65], with highest weights assigned to critically endangered species (least concern: 1, near threatened: 2, vulnerable 4, endangered: 6, critically endangered: 8, data deficient: 2). This weighting scheme induces a relatively higher coverage of more endangered species while the prioritization method maintains an overall balanced representation of different species and groups of species (Supplementary Information). In the seven different prioritization set-ups we analysed the implications of: (1) different land-use conditions (present and future, 2040); (2) whether all assessed species or only threatened species are considered as priorities for conservation; and (3) the context of planning, that is, defining global priorities in a globally coordinated manner versus strictly nationally developed priorities. Alternative analysis variants excluding reptiles were also evaluated. In these, although the data on reptile species' distributions is strongly geographically biased, the figures of global expansion responsibility by latitude change only slightly, with a 0.4% decrease of responsibility in latitudes between 30° and −30° (see Supplementary Information).

The analysis presented here implicitly assumes that costs (acquisition, management and opportunity) of protected areas are uniform across the world, whereas in practice costs vary enormously[66]. Different approaches to integrate costs into conservation planning have been proposed in the literature[67]. Costs can be integrated in a zonation prioritization analysis in different ways[53], and global data on conservation costs are publicly available[68], although these have several limitations[44]. The integration of costs also requires careful consideration of other factors that can have a major influence on spatial conservation prioritization, such as governance[69], funding issues[70] or the dynamic nature of other societal factors in a changing world with areas experiencing an increase in public demand for conservation and willingness to pay for conservation, especially in tropical countries[71].

The main results presented here correspond to analyses carried out for input grid layers with a resolution of 0.2°, or approximately 20 km at the equator. This low resolution was used in our main results to reflect the limitations in the original input data on species' distributions, reducing potential misuse of our results. In particular, the data limitations should be carefully considered when making decisions at a local scale. See Supplementary Information for additional analysis results corresponding to different, higher analysis resolutions up to 1.7 km. We found that our results, when aggregated globally, continentally or nationally, or by species groups or latitude bins are robust with respect to the analysis resolution used in the range explored here (from 0.01667° to 0.2° degrees).

The spatial prioritization approach used here uses two kinds of data: distribution data of biodiversity features and costs (where relevant), and structural data elements. The first class includes input data digitized to polygons at various scales. With high resolution it is possible to mimic the shapes of the original species distributions without introducing an additional bias in early analysis stages. The second class of data includes mask layers, such as those defining spatial units, such as country borders and protected area boundaries. These are typically known and digitized as spatial data with high precision.

Accounting for land-use change. Three set-ups were used to analyse the implications of projected land-use change on global priorities for expanding the PA network: global priorities present time, global priorities (2040), and global priorities (restrictive 2040) (Extended Data Table 2). Here and in general, the set-up for present time uses effective ranges of species and extents of ecoregions according to present land-use conditions, whereas the set-up for 2040 uses effective distributions for projected future (2040) land-use conditions (Supplementary Information). The third set-up, global priorities (restrictive 2040), uses effective distributions that were calculated from projected future (2040) land-use conditions following stronger or more negative impacts of land use on species and ecosystems (Supplementary Information). We also analysed the potential effect that projected land-use change could have on priorities for threatened species. To this end, we defined two additional set-ups: global priorities for threatened species (present time), and global priorities for threatened species (2040) (Extended Data Table 2). In both, only threatened species (extinction risk categories vulnerable, endangered and critically endangered) are assigned standard weights as described above, whereas ecoregions and all other species are not included in the prioritization.

National analyses. To analyse the influence of national planning as opposed to globally coordinated planning[21,72–75], we used additional methods that produce country-specific priorities on the basis of the ranges of species and extents of ecoregions exclusively within the country boundaries[21,53,76]. A similar approach has been used previously, at a much coarser resolution, to reveal a severe loss of performance and the emergence of edge artefacts in national conservation planning when compared to continentally coordinated planning[21]. However, the present analysis addressed a different problem: the expansion of the current global PA network, considering the effects of land-use on species distributions for present and projected future (2040) conditions. Two prioritization set-ups were defined to investigate national priorities: national priorities (present time) and national priorities (2040) (Extended Data Table 2). In both, national priorities were developed for every country considering separately the distributions of all ecoregions and species occurring in each of them, using the strong administrative priorities analysis type[76], delimited by the national boundaries derived from the GADM.

Interpreting and comparing analyses. Results were compared statistically, spatially and against well-known regional-scale global priority maps, such as the map of biodiversity hotspots revisited, 2011 revision[13,77–79], and the centres of plant diversity[80]. The plots and statistics provided for small-range species concern those species with range size smaller than 50,000 km^2. In the figures and Supplementary Information, all the box plots include median, twenty-fifth and seventy-fifth percentiles (boxes), whiskers and outliers. The whiskers are extremes that are 1.5 times the height of the boxes (or interquartile range) above or below the boxes.

The maps presented here have been generated as continuous rankings of the whole land surface of the Earth. The spatial priorities resulting from our analyses are continuous estimations of the importance of the contribution of cells or sites to the global PA network. These data should not be interpreted as if they prescribed hard thresholds or decisions. Also, robust decision-making requires careful consideration of the different types of uncertainties that necessarily affect such priority maps. Two intertwined issues that are further analysed below deserve special attention: effective spatial resolution and omission and commission errors.

Maps of uncertainty corresponding to our main results are provided in Supplementary Information, showing that the spatial location of priorities is fairly consistent even when as much as 33% of additional, simulated, commission error is introduced into the species' distribution data. The degree of uncertainty in the ranking of sites or cells is considerably higher in national priorities as compared to global priorities, especially around borders of countries with edge effects.

Comparison with KBAs and other site-scale prioritizations. To test the reliability and usefulness of the priority ranking maps presented here when considering additional taxonomic groups, we compared these maps with important sites for biodiversity conservation. We compared our results with KBAs[81,82]. These sites have been identified as the result of processes that follow an essentially different methodology and are based on partially different data, with better access to local expertise and sources of information. We analysed three national lists of KBAs: Madagascar, Myanmar and the Philippines[83]. The list of KBAs of the Philippines[84,85] contains 284 sites (151 terrestrial), ranging from 8 to 339,000 ha of area. The KBAs of Myanmar[86] retrieved from Myanmar Biodiversity (http://www.myanmarbiodiversity.org) are a total of 132 sites of size ranging from 0.4 to 11,300 km^2. In Madagascar, a total of 1,218 sites of high or potential interest for conservation have been identified, with areas ranging from <1 to 372,000 ha (ref. 87), in which sites of high potential for conservation have been identified as KBAs. In all cases, we restricted our analysis to terrestrial areas. Results (see Supplementary Information) confirm that the priority ranking maps presented here would target KBAs to a large extent, effectively inverting the trend towards less representation of important sites that has been observed in recent PA network expansion. This also provides evidence that to a notable extent, the global PA network expansion areas identified here can be efficient and representative for other biodiversity not directly considered in this study[26,88]. This comparison with important sites is an example that the high-resolution priority ranking maps presented here can help to bridge the gap between large-scale conservation planning assessments, regional scale assessments, and site-scale assessments.

Spatial resolution. The spatial resolution[89] or grain size[47] has a notable effect on the outcomes of systematic conservation planning assessments[89], and a comparison between different results obtained for different resolutions is not strictly possible. Notwithstanding this, we analysed how our results would vary when using range maps of species and ecoregions scaled at different coarser resolutions, taking as reference the results obtained for a resolution of 0.01667°. We compared these with results obtained for different resolutions: 0.05°, 0.1° and 0.2°. Previous related studies have used species range distributions at comparable resolutions: 0.125° (ref. 43), 0.333° (ref. 44), 10 × 10 km, approximately equivalent to 0.1°, or even polygons and ellipses with their full resolution[4]. We analysed the correlation between the different rankings obtained as well as the overlap between the areas identified as best candidates for expansion of the global PA network to 17% of the terrestrial world (Supplementary Information). The coarser resolution priority ranking maps were compared with upscaled versions of the reference priority ranking maps, generated by calculating median values of blocks of cells. We also compared the distribution of these expansion areas by latitude bins (Supplementary Information).

We used three measures of correlation: the Pearson correlation coefficient, the Spearman's rank correlation and the Kendall tau[90]. The Pearson product-moment correlation coefficient is a measure of linear correlation between two priority rankings in this context. It takes values between −1 and +1, with +1 denoting total positive correlation. The Spearman's rank correlation coefficient is in contrast a nonparametric measure of statistical dependence that evaluates to what extent the relationship between two rankings can be described by a monotonic function. Perfect correlation of +1 or −1 indicates that each ranking is a perfect monotone function of the other. The Kendall tau correlation coefficient is an alternative nonparametric statistic that measures the rank correlation between two rankings, or similarity in the ordering of the rankings. We also compared aggregated results, such as the distribution of expansion areas by latitudinal bins, finding that our conclusions are robust with respect to the analysis resolution.

Omission and commission errors. There are different issues associated with different types of species occurrence data[47,55]. In particular, different types of occurrence data, such as point localities, range maps and predicted distributions, are more or less likely to present omission and commission error. The species' range maps used here are very likely to contain important commission errors because of the nature of such maps[37–39,47]. By contrast, omission errors can be expected to be very infrequent in these maps[91]. This can lead to a systematic overestimation of occurrence and representation of biodiversity in spatial prioritization. When using range maps, it is recommended to assess the sensitivity to commission errors when selecting areas for conservation in systematic conservation planning[37].

We performed an assessment of the sensitivity of our results to potential commission errors. We added random omissions to all the effective range maps, that is, in addition to the constraining of original range maps by land-use models, we introduced a varying percentage or rate of artificial omissions ranging from 5 to 15%, choosing coordinates and species at random. These random omissions are introduced in addition to the discounting of species' ranges by an average of 14.12% (present) and 23.99% (future, 2040) from the original range maps, reflecting human land use. We then evaluated the correlation between the different ranking maps, and the overlap between the different expansion areas obtained for different rates of artificial omission rates. These results (see Supplementary Information) give an indication of the sensitivity of our results to potential commission errors in the distribution maps. For rates of random omissions between 3.3 and 25%, the difference in average coverage of species in top 17% areas is <2.5% and the difference in expansion areas ranges between 1 and 10%. On the basis of this analysis we also generated maps of uncertainty that show, for different confidence intervals, how the ranking of top 17% areas would change owing to commission errors (Supplementary Information). This is a simple quantitative sensitivity analysis with two unrealistic assumptions that make it demanding. First, artificial omissions are generated randomly, producing a scattered cloud of omissions in addition to a discounting pattern that reflects human land use, whereas real commission errors can be expected to follow a non-random pattern. Second, we use the same rate of randomly introduced commission errors for all species (while larger range species tend to have lower rates of commission errors[39,55]). Also, the uncertainty maps presented in the Supplementary Information were generated for the highest rate of commission error introduced into the species' distribution data (33%).

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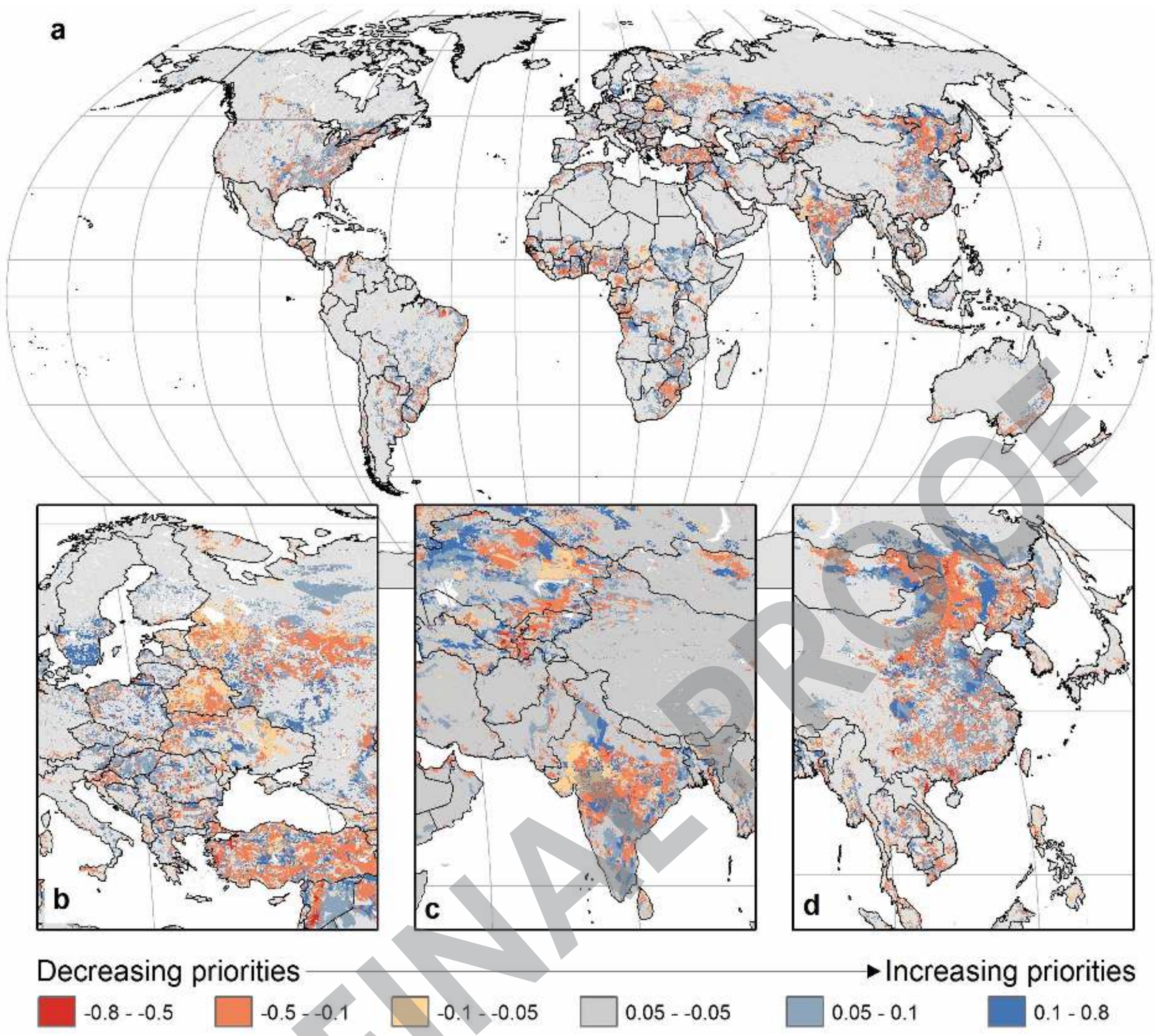
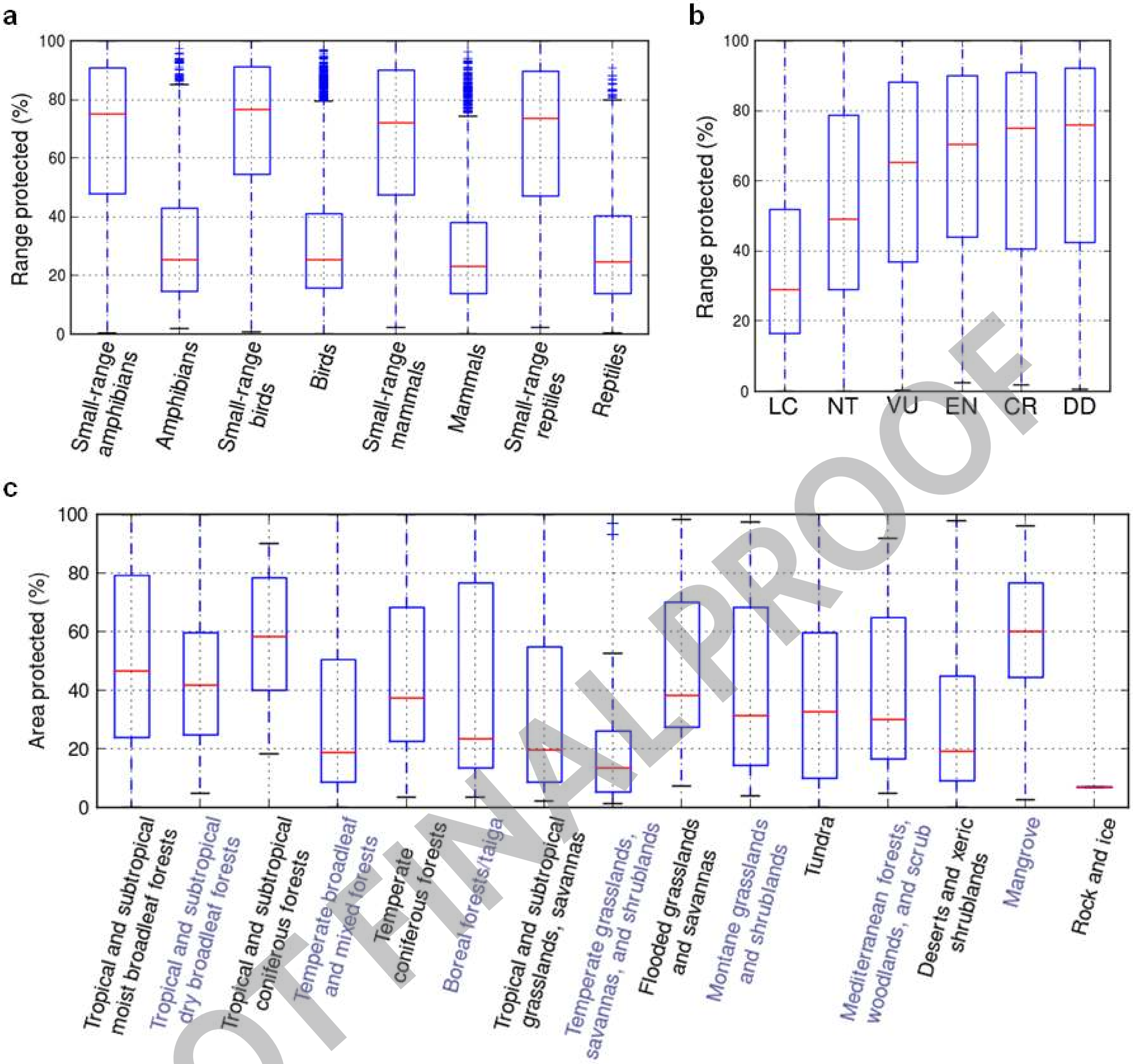
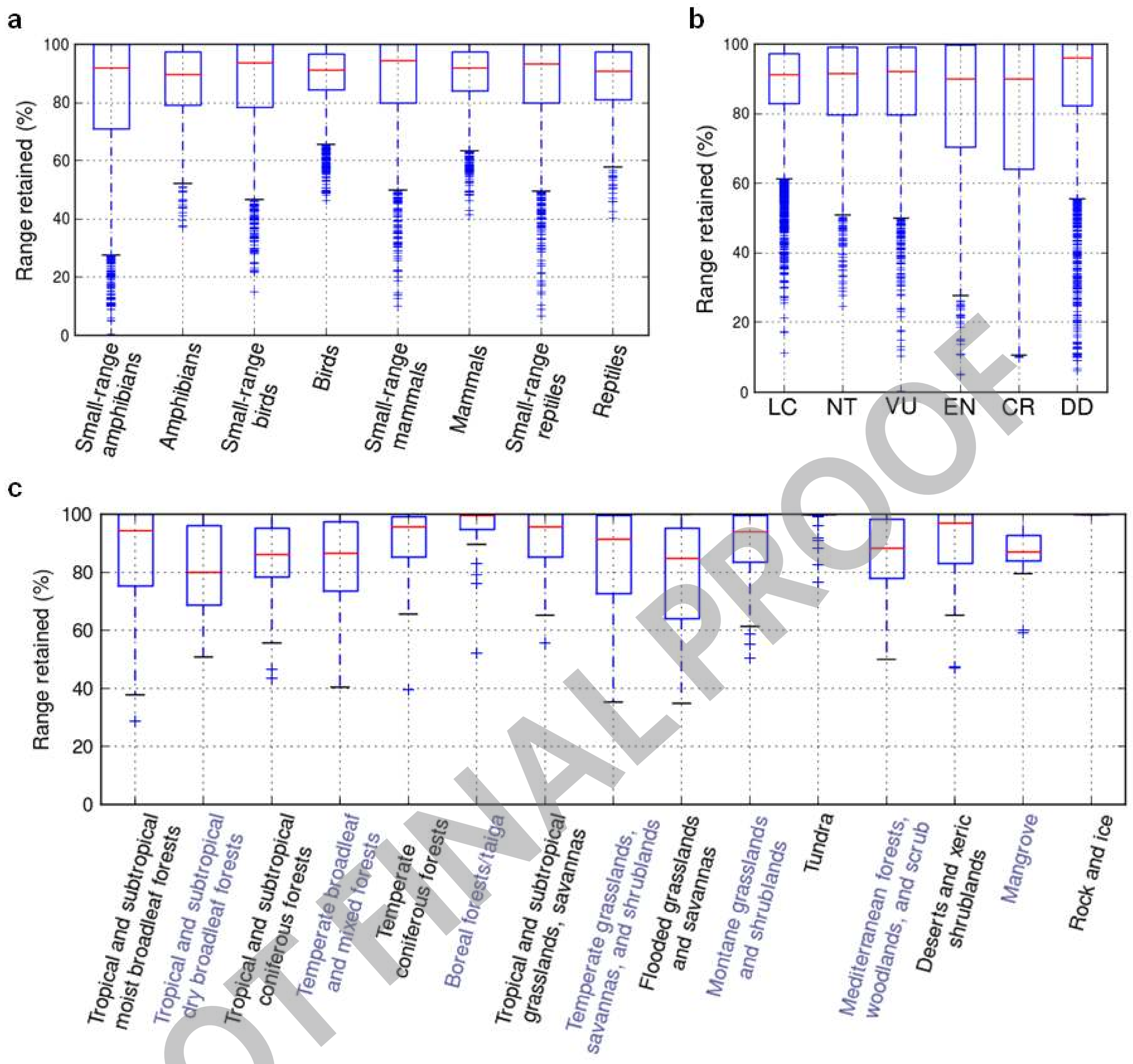


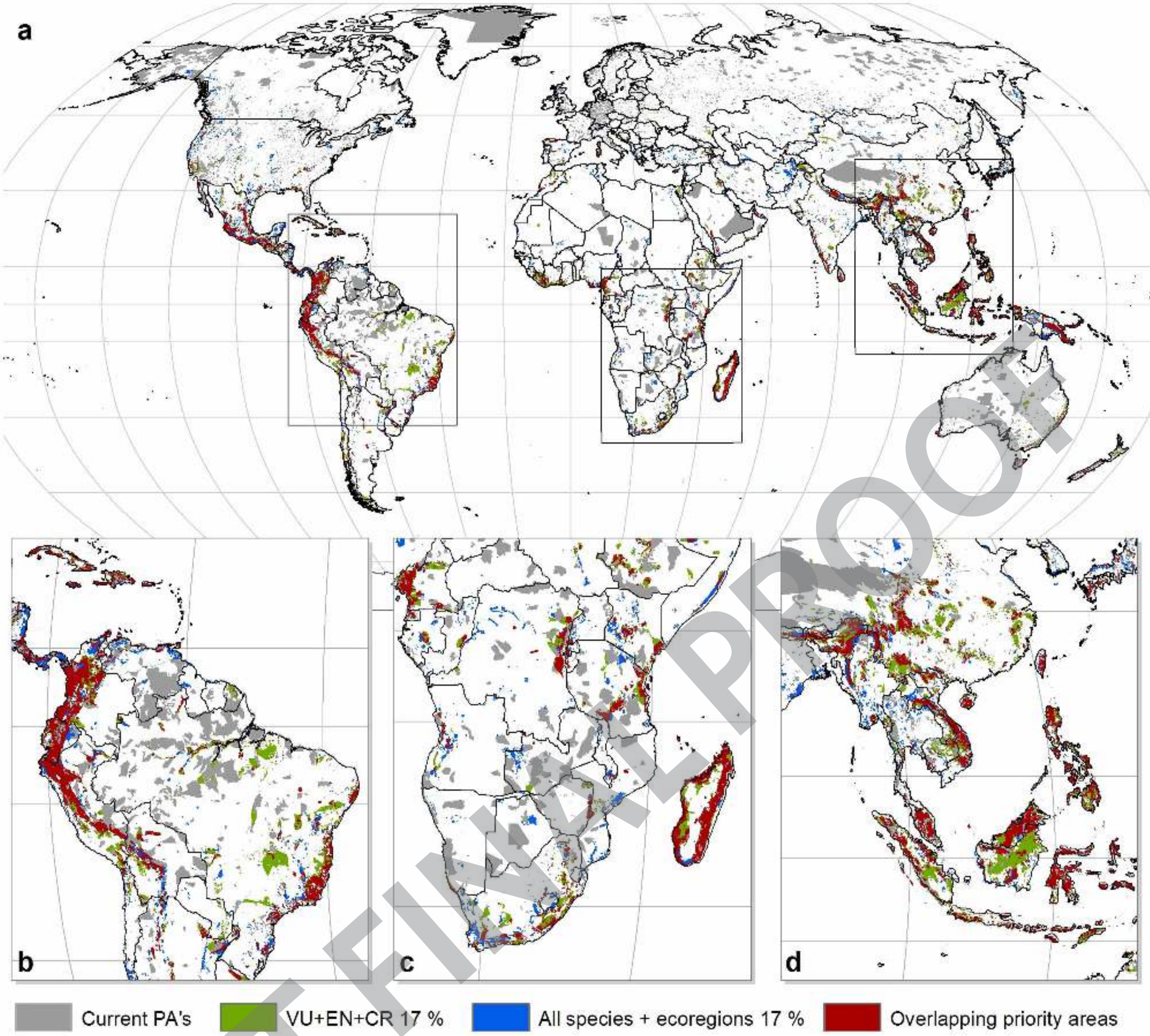
Extended Data Figure 1 | Changes in spatial conservation priority between present and future (2040). The top areas for PA expansion remain relatively stable: the congruence between priority expansion areas for present and projected future land use is 77.9%. Despite relatively high congruence (Supplementary Information), there are important localized differences. The biggest declines in priority would happen in China, India, eastern Europe and Turkey, whereas the changes are more subtle in sub-Saharan Africa and the Americas.



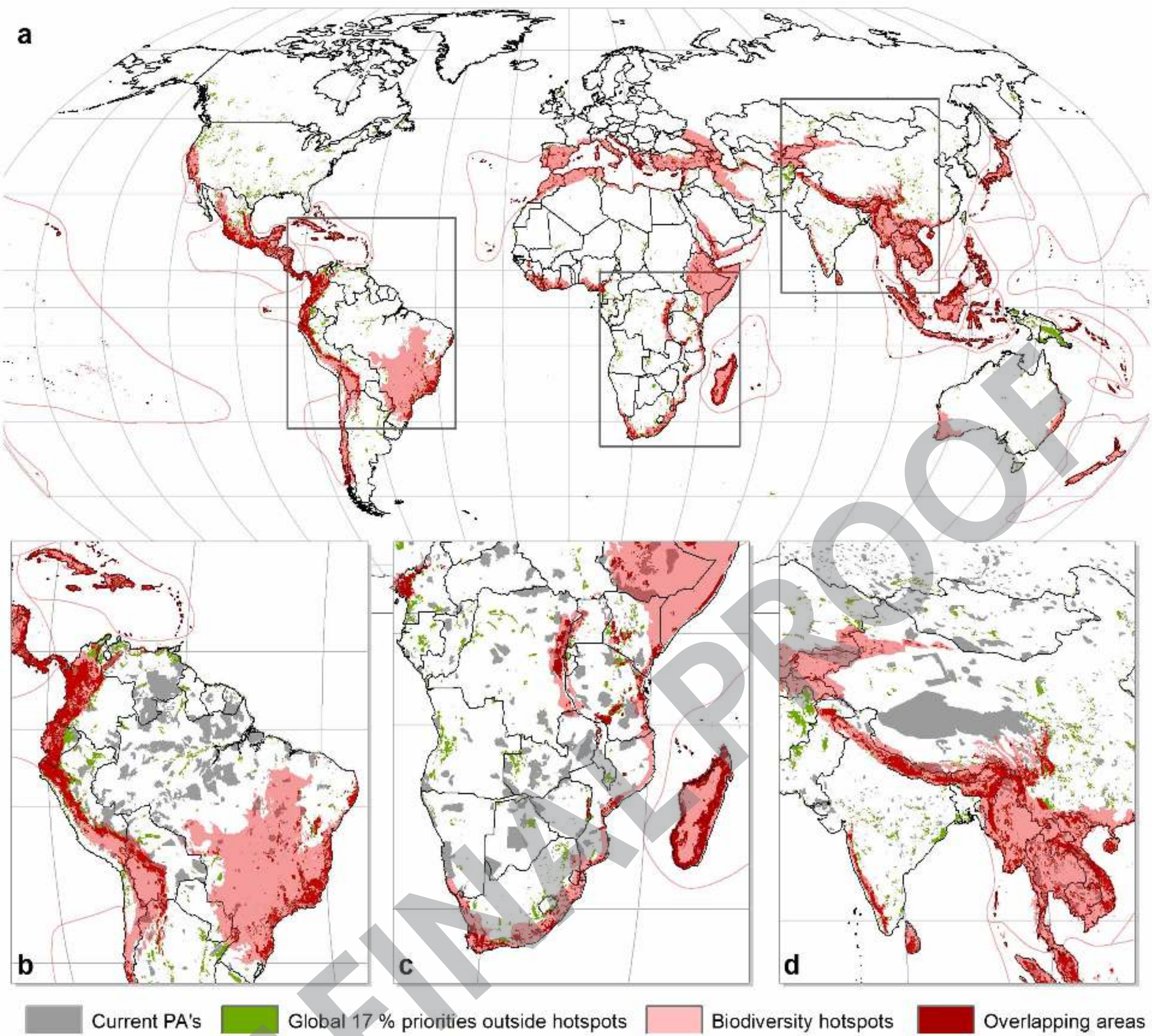
Extended Data Figure 2 | Box plots of protection of effective range (species) and effective extent (ecoregions) in the expanded global PA system, under projected future (2040) land-use conditions. **a**, **b**, Summaries of coverage for species grouped by taxonomic groups (classes) (**a**) and IUCN status (**b**). **c**, Ecoregions grouped by biome. These box plots show median values, twenty-fifth and seventy-fifth percentiles (boxes), whiskers (1.5 times the interquartile range) and outliers. Protection levels are well balanced for different species groups, and between species and ecoregions. Protection levels tend to be lower for less threatened species, as these tend to have wider ranges.



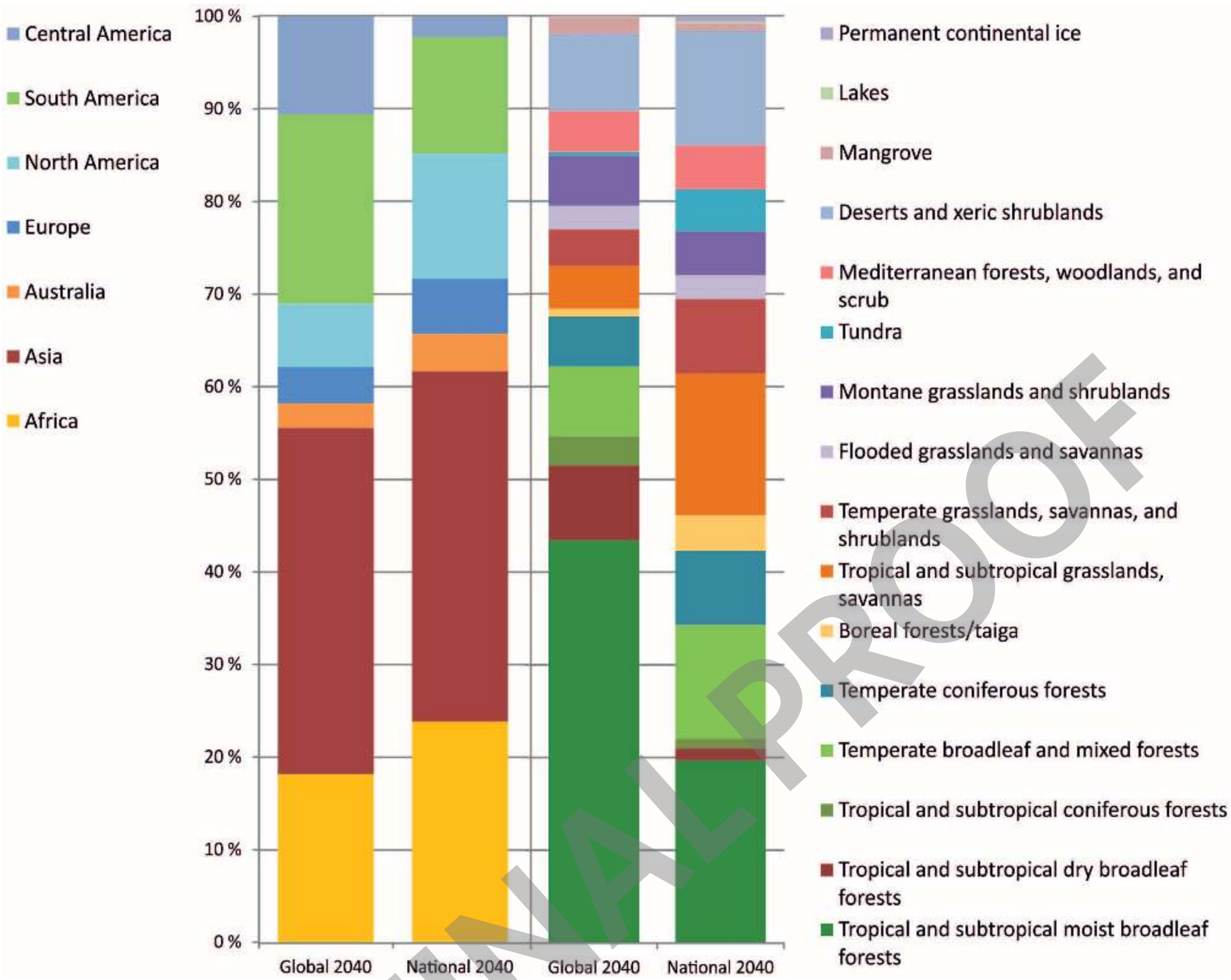
Extended Data Figure 3 | Box plots of loss of effective range (species) and effective extent (ecoregions) from projected land-use changes by 2040. **a**, Species grouped by taxonomic groups (classes), distinguishing small-range species (range size <50,000 km^2). **b**, Species grouped by IUCN threat status. **c**, Ecoregions grouped by biome. The proportion of species that lose a significant fraction of their habitat is higher for species with a higher threat status.



Extended Data Figure 4 | Comparison of priority areas for threatened species, and all species and ecoregions, both considering projected future land-use (2040). The overall overlap of the respective top 17% priority areas is 62%. Priorities are highly congruent in most biodiversity hotspots of the world. More top priority areas are identified for threatened species in the tropics, whereas there are more top priority areas in higher latitudes for ecoregions and all vertebrate species. IUCN threat categories: critically endangered (CR), endangered (EN) and vulnerable (VU).



Extended Data Figure 5 | Global expansion priority areas for projected future (2040) land-use. **a–c**, Some of the areas in which the largest spatially contiguous overlaps occur are highlighted. Areas that overlap with biodiversity hotspots (full red) and those outside hotspots (green) are shown.



Extended Data Figure 6 | Stacked bar plot showing the distributions of 17% expansion areas across different continents (left) and biomes (right), for future (2040) land-use. When following national priorities, the distribution of expansion areas tends to be more balanced between biomes, at the expense of lower average protection of species and ecoregions, particularly favouring grasslands over tropical forests. The continental responsibility for Asia is virtually independent on whether national or global priorities are followed, whereas if planning is made nationally, responsibility clearly increases in Africa and North America and decrease in Central and South America. These patterns are stable across time (Supplementary Information).

Extended Data Table 1 | Species with effective range loss above 30, 50 and 70% for land-use change projected for 2040

Threat status	Number of species	Species with >30% effective range loss	Species with >50% effective range loss	Species with >70% effective range loss
LC	14978	953	192	11
NT	1783	234	51	4
VU	2092	320	103	14
EN	1804	443	180	33
CR	986	277	161	66
DD	2954	439	207	93

Species are grouped by their category of extinction risk on the IUCN red list of threatened species. The values shown reflect changes in the effective range of species as a consequence of projected future (2040) land-use intensification.

Extended Data Table 2 | Summary of protection levels of species ranges and ecoregions area for the expanded (17%) PA system

	global priorities (present time)	global priorities (2040)	global priorities (pessimistic 2040)	global priorities for threatened species (present time)	global priorities for threatened species (2040)	national priorities (present time)	national priorities (2040)
LC	46.8	42.5	42.0	45.7	41.2	30.0	27.7
NT	68.7	61.3	59.6	67.3	60.2	42.5	38.6
VU	80.7	70.8	68.4	86.4	75.4	54.9	48.9
EN	92.1	77.3	72.6	94.7	79.7	73.6	62.9
CR	95.8	77.4	78.3	97.2	78.8	85.4	69.5
DD	86.2	77.3	76.3	76.0	69.3	71.3	64.7
All non-threatened vertebrates	54.7	49.4	48.6	51.8	46.7	37.3	34.2
All threatened vertebrates	87.9	74.5	71.7	91.6	77.6	67.8	58.1
All vertebrates	61.2	54.3	53.0	59.7	52.9	43.3	38.9
All ecoregions	55.4	48.9	47.4	42.8	38.2	36.6	33.8

Protection levels are reported as average percentages of the (effective) global range size (species) or area (ecoregions), covered by 17% top priority areas for present and projected future (2040) land-use conditions.