Terrestrial conservation opportunities and inequities revealed by global multi-scale prioritization

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Abstract:

Area-based conservation through reserves or other measures is vital for preserving biodiversity and its functions for future generations[1–5], but its effective implementation suffers from a lack of both management-level detail[6] and transparency around national responsibilities that might underpin cross-national support mechanisms[7]. Here we implement a conservation prioritization[2,8] framework that accounts for spatial data limitations yet offers actionable guidance at a 1km resolution. Our multi-scale linear optimization approach delineates globally the areas required to meet conservation targets for all ~32,000 described terrestrial vertebrate species, while offering flexibility in decision management to meet different local conservation objectives. Roughly 48.5% of land is sufficient to meet conservation targets for all species, of which 60.2% is either already protected[9] or has minimal human modification[10]. However, human-modified areas need to be managed or restored in some form to ensure the long-term survival for over half of species.

This burden of area-based conservation is distributed very unevenly among countries, and, without a process that explicitly addresses geopolitical inequity, requires disproportionately large commitments from poorer countries. Our analyses provide baseline information for a potential intergovernmental and stakeholder contribution mechanism in service of a globally shared goal of sustaining biodiversity. Future updates and extensions to this global priority map have the potential to guide local and national advocacy and actions with a data-driven approach to support global conservation outcomes.

Main Text:

The current extinction crisis threatens biodiversity worldwide, driven primarily by loss of habitat due to human land use[5,11,12]. A decade after the Convention on Biological Diversity (CBD) created the strategic short-term Aichi Biodiversity Targets designed to promote and protect the planet's biodiversity, negotiations are underway for a post-2020 Global Biodiversity Framework that provides an improved set of biodiversity targets for the coming decade and beyond[4,6,13,14]. Key principles shaping the new framework include a grounding in scientific understanding of the planet's biodiversity, a focus on meaningful and measurable biodiversity outcomes, and development of mechanisms that support equitable management between parties[15]. Conservation policy and advocacy frequently features areal percentage targets – such as the 17% of land in Biodiversity Target 11 or the more ambitious 30% or 50% under discussion[15] – that have commonly been interpreted at the national or regional level, but generally fail to account for the uneven distribution of global biodiversity[6]. Other current CBD goals, by contrast, emphasize minimizing species extinctions and supporting global biodiversity persistence by enhancing perceptions of biodiversity importance. Thus, a good starting point for addressing issues of global conservation is one that reflects the multifaceted nature of these goals: given a shared objective to protect our planet's biodiversity, what and where are the baseline amounts of area required, and what actions are needed to achieve it? This perspective reframes the issue in terms of meaningful outcomes rather than area-based targets that lack this connection[6].

In support of these principles, here we identify priority areas for biodiversity conservation with a hierarchical framework that helps bridge the gap between global conservation objectives and local management practices. We used linear optimization[2,8] (see Supplementary Information) to allocate sufficient habitat for all terrestrial vertebrate species, accounting for currently protected areas (PAs)[9] and minimizing the amount of additional land needed and the degree of human modification (HM) contained within the network[10]. The spatial uncertainties of globally representative spatial distribution data impose hard analytical constraints on global conservation prioritization. Biodiversity data collated across large extents at grain sizes less than 100km inevitably suffer from geographically- and ecologically-variable false presences[16,17]. This directly affects spatial prioritization approaches by: i) preventing an unbiased and accurate quantification of each species' area of occupancy and reserve coverage; and ii) overstating the precision with which high priority conservation locations can be identified. We addressed these limitations by performing probabilistic downscaling of species distribution data to a 55km resolution (Fig. SI1) and applied it to all study species. Our hierarchical approach recommends the optimal proportion of area to protect in each of the 52,558 55km cells without immediately resolving or prescribing the fine-scale locations within. In identified areas, local management decisions will additionally be informed by more detailed species population data, and regional priorities.

We identify 48.5% of global inhabited terrestrial surface area as needed to meet area-based conservation targets for 31,904 vertebrate species, including the 12.2% of land that is already protected (Fig. 1). Optimization tended to prioritize locations of higher species rarity[18], endemism and richness[19]. 85.2% of cells that were in the 90th percentile of either richness, endemism or rarity were selected for some amount of additional conservation, compared to just 55.0% of cells in lower percentiles. We calculated the conservation priority rank of each cell in the conservation area network as the proportion of the protected range of a species found within the cell, and summed across all species. Priority rankings generally reflected global patterns of terrestrial vertebrate endemism, and their inter-taxonomic variation provides the taxon- and ultimately species-specific conservation hotspots that can help support advocacy or guide implementation at local levels[20].

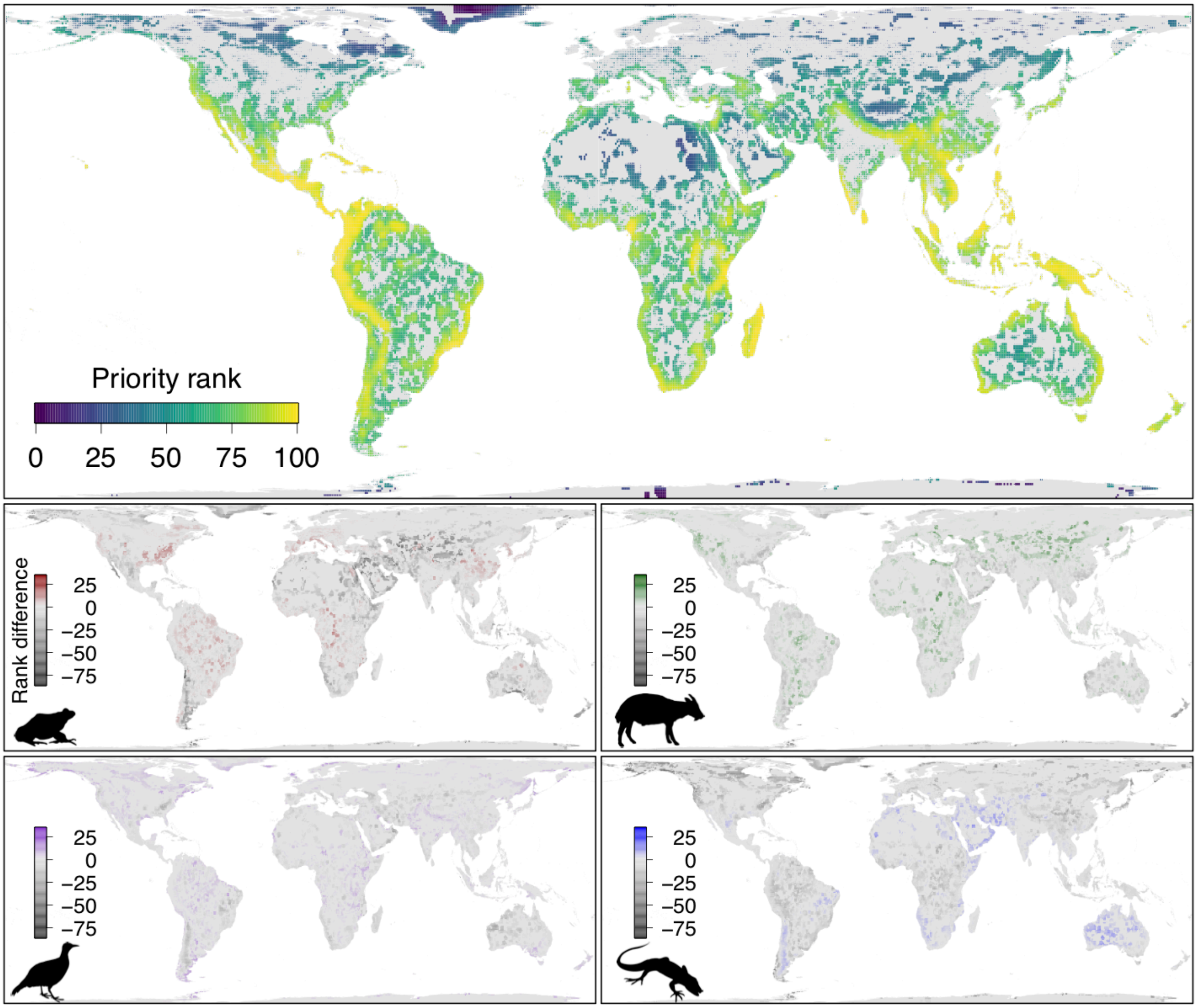

Figure 1. Conservation priority rank of locations in the network, calculated as the percentile rank of total network-size rarity, the proportion of the protected distribution of a species that is found in a cell (summed across all species). Cell size reflects the proportion of land needed within each cell. The rank difference of an individual taxon represents the difference between priority rank within each taxon and the priority rank of all taxa together. A positive rank difference value for a given taxon indicates that an area is of greater conservation importance for that taxon than for all taxa together.

These regions are further resolved by selecting the minimum number of 1km pixels to meet the area needs within each 55km cell. The selection process can reflect local management issues and concerns (Fig. 2A-C) such as connectivity, expansion of current PAs, areas of lesser HM, political desirability, economic feasibility, carbon sequestration, and greater protection of high-profile species[21]. Minimizing the amount of HM (Fig. 2), for example, the land needed for additional protection comprised 22.4% of all global areas with no HM, 39.8% with low, 52.8% moderate, and 33.1% high. This illustrates that comprehensive biodiversity conservation cannot be achieved simply by protecting areas of lower HM alone, but will require additional restoration efforts[10]. The extent of moderate- and high-HM land needed also highlights the importance of other effective area-based conservation measures (OECMs)[3,22], conservation in working lands, and efforts that include people[23,24] as essential approaches to protect biodiversity.

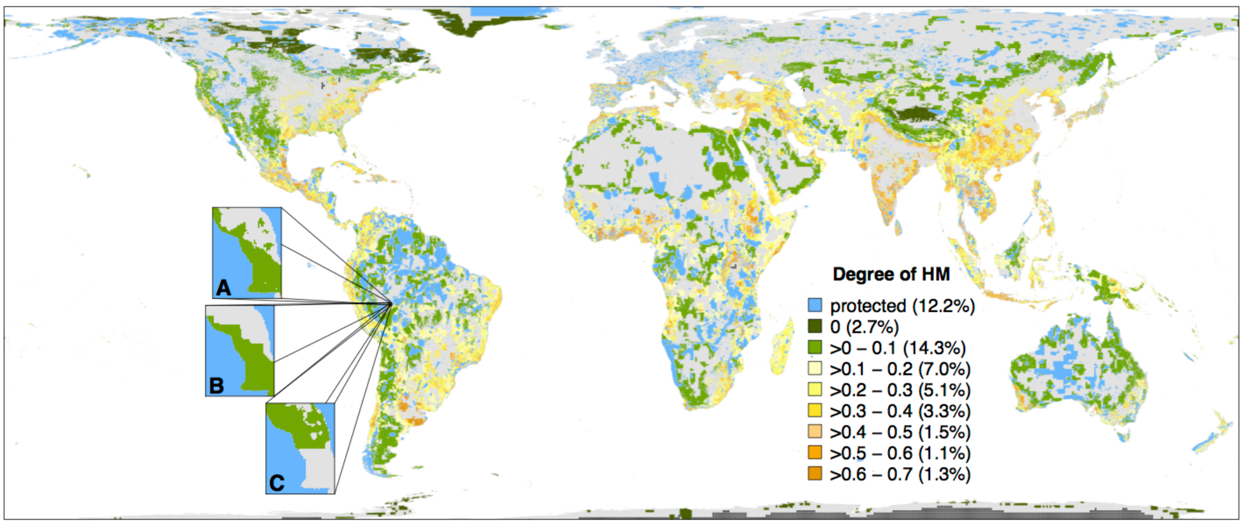

Figure 2. A putative 1km conservation area network that provides protection for all terrestrial vertebrates while minimizing the amount area of needed and the degree of human modification (HM) contained therein. Amounts in parentheses indicate the total percentage of habitable terrestrial surface area contained in the network by degree of HM. Dark grey cells denote the locations without species occurrences that were excluded from calculations of global area coverage. Inset panels show three possible examples of reserve network configuration within a single 55km grid cell, all with the same total area: (A) minimizes HM; (B) minimizes boundary length; (C) minimizes HM while ensuring network connectivity.

This minimum-HM approach suggests that current PAs alone are able to meet area-based conservation targets of only 18.8% of species (Fig. 3A). Adding areas of no and low HM (0 – 0.1) improves this to 43.6% of species, and further adding areas of moderate HM (>0.1 – 0.4) to 74.7% of species. The median range size of gap species (i.e., species that failed to meet targets) decreases as each category of HM is added (Fig. 3B), suggesting that the exclusion of areas with a greater degree of HM has a disproportionate effect on range-restricted species. Excluding areas of high HM (>0.4) fails to meet targets for 8,736 species, including 43.9% of amphibians, 10.8% of birds, 18.5% of mammals and 35.2% of reptiles, but half of these gap species are within 16.7% of their conservation targets (Fig. 3C). The largest gains in amount of range area protected comes from the inclusion of areas of moderate HM (Fig. 3D).

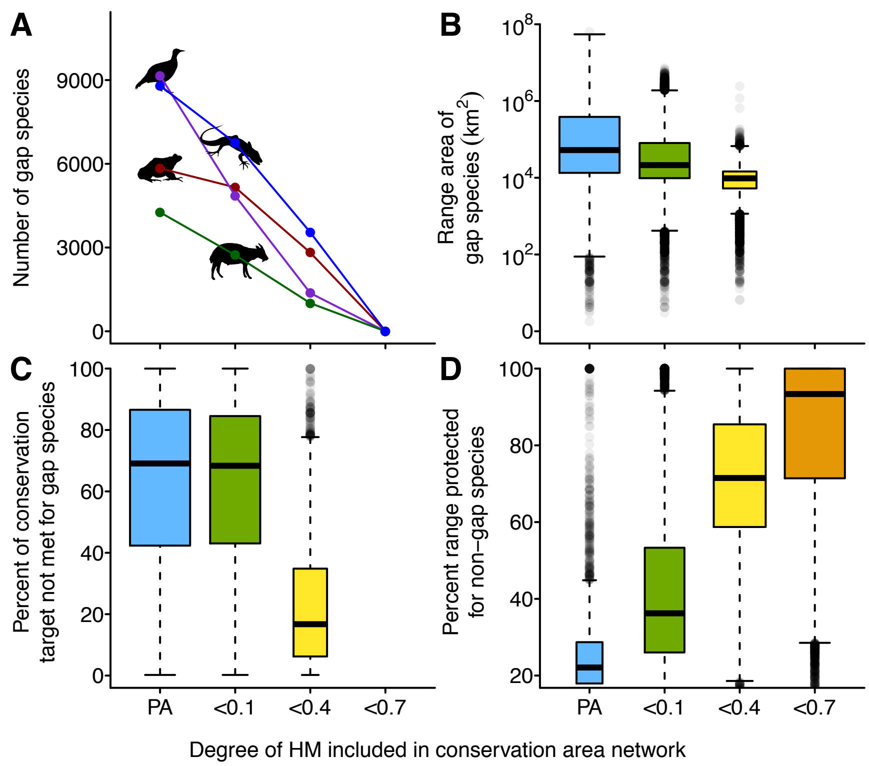

Figure 3. Variation in species coverage with the addition of increasingly modified areas. (A) The number of gap species when the network was constrained by differing degrees of HM. PA = currently protected areas only; <0.1 = PAs and areas with HM less than 0.1 (low); <0.4 = PAs and HM less than 0.4 (moderate); <0.7 = PAs and HM less than 0.7 (high). (B) Boxplots of range area in km^2 for gap species and for each network scenario. Boxplot width is proportional to the number of species represented. (C) Boxplots of the percent of conservation target that remains to be met for gap species. (D) Boxplots of the percent of range protected for species with conservation targets met. In all boxplots the center line indicates the median; box limits the quartiles; whiskers 1.5x the interquartile ranges; and points the outliers.

Both relative and total areas required across HM categories differed strongly between ecoregions (Fig. 4A) and biomes (Fig. 4B). Percent of ecoregion needed and ecoregion area correlated negatively (r_s = -0.42, n = 846), and so did percent of biome needed and biome area (r_s = -0.90, n = 14), with some of the smallest biomes requiring the greatest relative area for conservation management. This underscores the limitations and inefficiency of any conservation targets – such as 17%, 30% or 50% – that are uniform across ecoregions, as commonly inferred from the expiring Aichi Biodiversity Target 11 or others more recently proposed[14]. The degree of HM in the network also varied greatly, further emphasizing the heterogeneity of the extent and distribution of restoration efforts necessary to ameliorate habitat degradation.

Most relevantly, these considerable variances extend to political units: we found substantial disparities among countries and distinct administrative regions in the percent of land needed to meet conservation goals (Fig. 4C). Required commitments had a moderately negative correlation with country area (r_s = -0.37, n = 253), but were high for very small (e.g. island) nations. There was a similar relationship between countries in the amount of current HM in such a future conservation network, with a moderately negative correlation between area needed and mean HM (r_s = -0.36, n = 253). Generally, larger countries tended to have more low-HM land available for conservation.

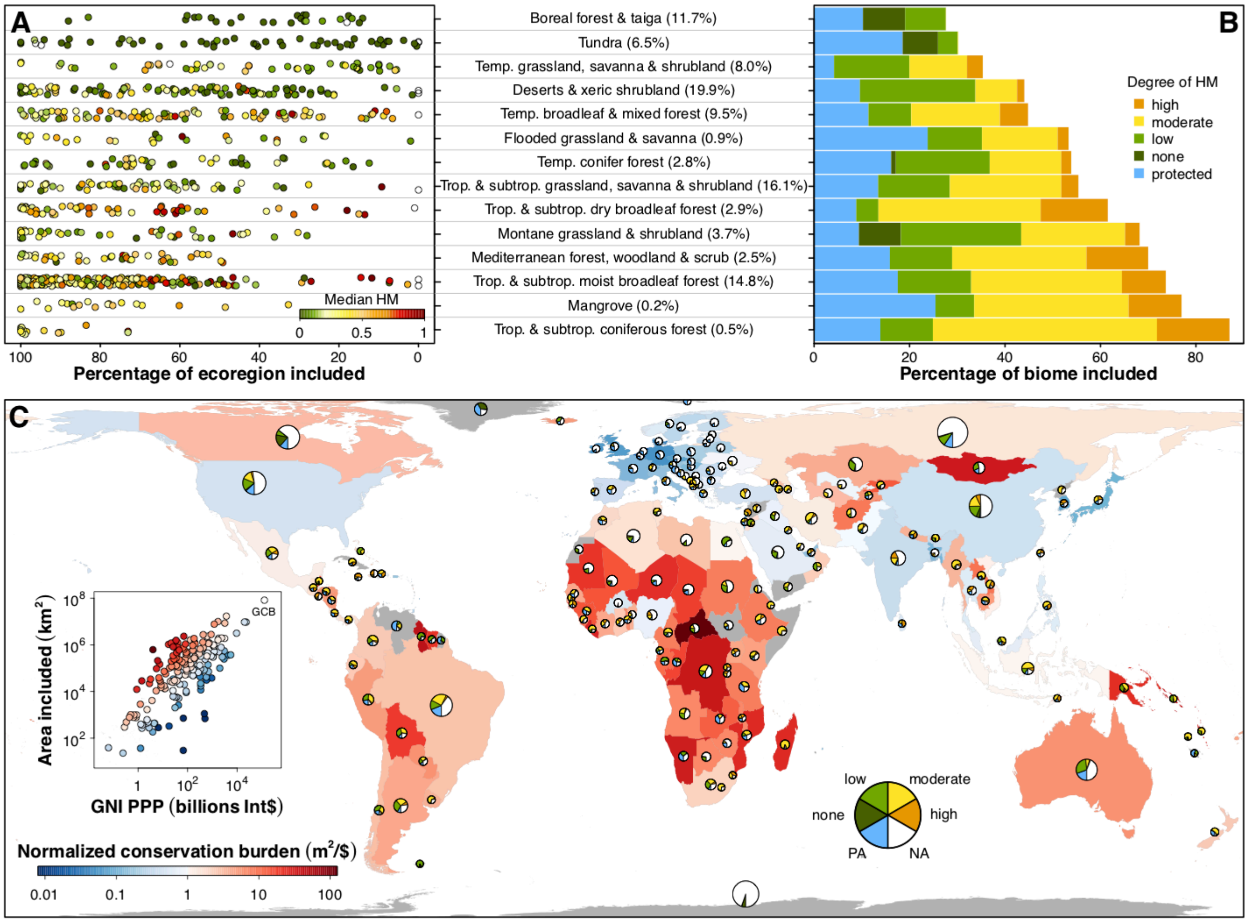

Figure 4. Conservation area network composition across ecoregions, biomes, and countries. (A) The percentage of each ecoregion contained in the network by biome category. Point colors indicate the median amount of HM in the network within each ecoregion. Percentages in parentheses indicate the total amount of global land area within each biome. (B) The percentage of each biome contained in the network by degree of HM and the amount currently protected. (C) Differences in conservation burden between countries, calculated as a ratio of a weighted sum of each country's area contained in the network and its gross national income adjusted for purchasing power parity (GNI PPP). The sum is weighted by HM category, with higher degrees of HM weighted more heavily. Burden is normalized by the global conservation burden (GCB), representing the weighted sum of the entire network divided by the sum of GNI PPP, and equal to 0.652. Countries in red have a higher burden than GCB, and countries in blue have a lower burden than GCB. Pie charts illustrate the proportion of each country contained in the network by degree of HM, the amount currently protected (PA), and the amount not in the network (NA). The radius of each pie chart is proportional to the total area of the country it represents. Countries in grey did not have recent estimates of GNI PPP available.

Differences between nations were further amplified by the economic feasibility of achieving conservation objectives (Fig. 4C). We characterized a country's conservation burden as the area of its required conservation area network divided by its gross national income adjusted for purchasing power parity (GNI PPP), with total network area weighted by HM category; higher HM was weighted more heavily to reflect the costs associated with restoration of degraded habitat[25]. The most extreme national burdens were more than a hundred-fold larger or smaller than the global burden (i.e., global weighted-area needed over global GNI PPP). Countries with relatively little monetary wealth, such as Papua New Guinea and the Democratic Republic of the Congo, for example, require large percentages of land, and this problem is further exacerbated by the disproportionately high amount of degraded habitat that is needed to meet these goals. By contrast, many European countries such as The Netherlands, Belgium, and Denmark require substantially smaller percentages of land, and have considerable financial resources to commit toward meeting conservation targets. Given that such disparities are often in part a direct result of a historical legacy and/or ongoing telecoupling of resource exploitation[26], this underscores a globally-shared ethical responsibility toward addressing these inequities. Recognizing the preservation of species as a globally shared goal, we could similarly apply the principle of "Common But Differentiated Responsibilities" from the United Nations Framework Convention on Climate Change to national targets for conservation in a framework that includes international support mechanisms[27].

Any successful and sustained conservation of the planet's biodiversity necessitates a cooperative, coordinated international effort. The discussions of the CBD's post-2020 Global Biodiversity Framework feature voluntary stakeholder contributions by Parties to the Convention and others as a vital mechanism for its implementation[15]. Our metric of conservation burden closely resembles the socioecological approach to intergovernmental biodiversity financing proposed by Droste *et al.*[7], who found that a framework that accounted for the Human

Development Index of countries best rewarded and incentivized global conservation action. In this light, conservation burden can be used as an implementation support mechanism of CBD goals by helping to guide intergovernmental fiscal subsidy agreements that encourage global conservation in the places it is most needed, while ensuring that economic and regulatory incentives promote biodiversity.

Our results are constrained by the still-limited knowledge of global biodiversity distributions[16,28,29], requiring a tradeoff between taxonomic coverage and spatial resolution reflected in our analyses. Invertebrate and plant groups are vital for ecosystem health and function[30] yet remain only partially mapped or are mapped over much coarser spatial units[31,32]. This prohibits their inclusion here, as any spatial differences in accuracy or representation would directly and non-transparently bias the resulting network. Previously identified similarities in endemism[19,33] suggest that our proposed conservation area network would also help protect rare plant species. But such cross-taxon congruence is known to decrease rapidly toward finer spatial grains[34,35], and both absolute and relative conservation burdens are expected to see slight shifts with the inclusion of other taxa. Efforts underway to develop the essential biodiversity information for species distributions for more groups and finer spatial grains through modeling and iterative feedback are poised to offer this vital support for outcome-focused global conservation[36].

The presented baseline results and future updates provide a spatial blueprint for policy targets (such as those currently under renegotiation in the CBD) and initiatives (such as Half Earth[37]) with stated goals of the preservation of species and their ecological diversity for future generations. Although area-based conservation measures may fall short of directly addressing drivers of biodiversity loss such as pollution and climate change[38], protecting land from habitat loss and fragmentation remains one of the most effective means of conservation[1]. The priority places highlighted here ensure baseline goals of adequate global biodiversity representation but can be readily combined with other priority areas that address additional considerations such as wilderness[39,40], carbon sequestration[41], land-use change[40,42], migration corridors[43], and climatic refugia[44], and can be revised to include other facets of biodiversity[45].

Our methods provide a rigorous, updatable approach for measuring both quantitative and qualitative progress toward meeting globally-informed area-based targets for nations, ecosystems, and species, while enabling local management decisions to reflect the world's heterogeneous landscape of cultural and social needs, values, and knowledge. While our work was explicitly designed to inform and support actions needed to achieve both the CBD's stated 2030 Agenda for Sustainable Development and their 2050 Vision for Biodiversity, the recommendations outlined here can be incorporated at any level of decision making, and the methods can be adapted to support more regionally-focused policy. Indeed, the successful implementation of a global strategy will require multi-faceted conservation efforts from a variety of actors at every scale.

Materials and Methods:

Species

We obtained range maps of 31904 terrestrial vertebrate species, comprising 6417 amphibians and 5433 mammals[32], 9991 birds[46], and 10063 reptiles[47]. We split the bird ranges by habitat use (resident, winter, or breeding) and treated these as separate species ranges, resulting in an effective total of 12635 bird species.

We used probabilistic downscaling to rasterize the range maps to a 55km grid of occurrences (Fig. 5). We first constructed four different global 110km Behrmann equal-area grids (approximately 1˚x1˚ at the standard parallels), each offset northwest, northeast, southwest or southeast around a 55km cell; the 110km resolution was chosen as appropriate for the uncertainty associated with range maps[16,17]. For each of the four 110km grids, we then created two rasterized versions of species occurrences. The first used a threshold of >50% range overlap with the cell to be considered occupied; this provides a conservative estimate of occupancy that may result in false absences. The second version used a threshold of >1% range overlap to be considered occupied; this provides a much more generous estimate of occupancy that may create false presences. The eight different occupancy rasters (i.e., >50% and >1% occurrence rasters of SE, NE, SW, NW grids) were then averaged by each 55km grid cell to obtain a probabilistic downscaling of the original range map. Finally, the probabilities were multiplied by 0.8, reflecting the detection probability at a 55km resolution[16]. Without this final step, all non-edge habitat of species with sufficiently large ranges would have occupancy probabilities of 1 because of 100% cell overlap with each of the eight grid versions.

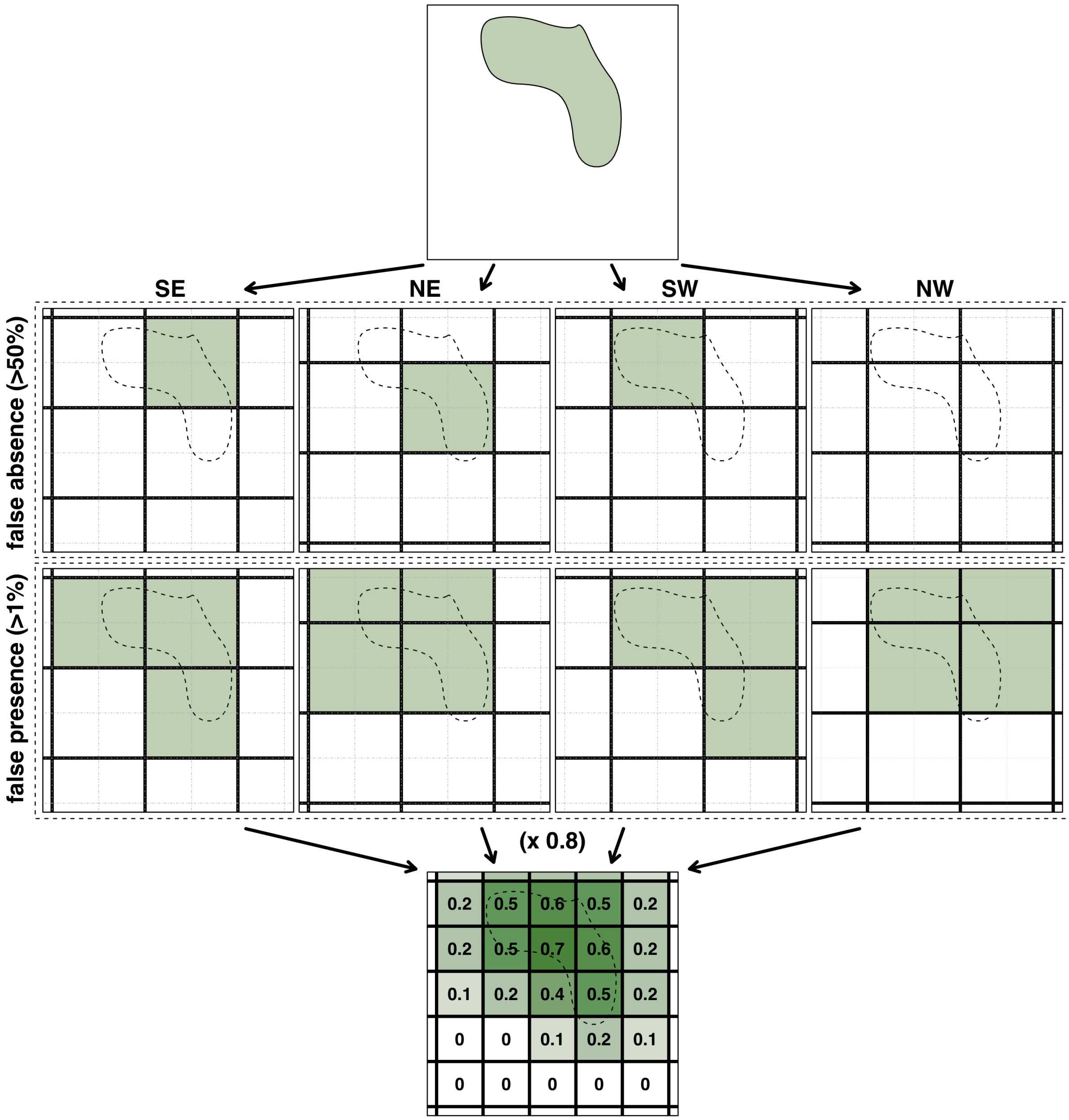

Figure 5. A conceptual diagram of the process of calculating species occurrence probabilities at a 55km resolution. A species range map is superimposed on four different 110x110 km grids, and discretized to indicate presence (light green) or absence (white) inside each grid cell. Two different thresholds of range overlap are used to determine occurrences: >50% as a stringent threshold for occurrence that may generate false absences; and >1% as a relaxed threshold for occurrence that may generate false presences. Occurrence probabilities are then calculated as the proportion of times a presence occurs in each 55x55km grid cell multiplied by 0.8, which represents the average occupancy probability at 55km.

Rare species – identified here by range maps with less than an area of occupancy of less than 2000km^2, per IUCN Red List Criterion B for Vulnerable species status – were downscaled with a slightly different approach than commonly occurring species. Reasoning that overprotection is a more desirable outcome than underprotection, we used no threshold of range overlap with grid cells to predict occurrences; any cell that overlapped with the range map of rare species was considered occupied. This resulted in only four occurrence rasters over which to average (SE, NE, SW, NW grids).

Our downscaling approach gained a four-fold increase in the resolution of the species data while still accounting for its spatial uncertainty. This approach easily extends to finer resolutions, and could be repeated at, e.g., 22.5km using 16 different offset grids. Each doubling of resolution will result in a quadrupling of the number of decision variables in the optimization problem, however, which will have computational costs. Given the global extent of our study, we chose not to pursue finer resolutions, but local- and regional-based conservation prioritization applications may benefit from further downscaling of global distribution data.

Protected areas and other effective area-based conservation measures

We used the World Database on Protected Areas to delineate current protected areas (PAs)[9]. Beginning with the January 2020 WDPA monthly release, we followed the WDPA's recommendations on cleaning data for calculations of global coverage: we excluded PAs that did not have designated, inscribed, or established status, points without a reported area, marine reserves, and UNESCO Man and Biosphere Reserves. A buffer was created around PA point data with the area of the buffer equal to the reported area of the PA[48]. The PA polygons and buffered points were dissolved together, and intersected with GADM 3.0 coastline. The results were then rasterized to a 1x1km grid using a Behrmann equal-area projection.

The January 2020 release of WDPA contained substantial updates from Brazil. Many of the new PA point data appeared to have misreported areas that were orders of magnitude larger than what might be expected, based on comparisons with previous WDPA versions. We opted to exclude Brazil's PA point data from the PA layer due to its unreliability, which may result in an underestimate of its amount of national protected area.

We also used the World Database on other effective area-based conservation measures (WD-OECM), which saw its inaugural release in December 2019. OECMs represent an important strategy for conservation, complementing PAs through active governance and management plans that result in sustained, positive conservation outcomes. Although WD-OECM as yet only contains spatial data for two different countries, it is worthwhile to recognize their contribution on principle, and were so included here despite currently incomplete global coverage. OECM data were cleaned using the same approach as PAs.

<u>Human pressures</u>

We used Kennedy *et al.*'s index of global human modification (gHM) to characterize the cumulative impact of human pressures on the landscape[10]. We reprojected the map to the same 1x1km Behrmann equal-area projection used for the PAs using bilinear interpolation for gHM values. We extended the map to cover the GADM 3.0 coastline, filling in any missing values (e.g., Antarctica) as 0, and masked out all current PAs. Values were then categorized into four levels of HM: none (gHM = 0), low ($0 < \text{gHM} \leq 0.1$), moderate ($0.1 < \text{gHM} \leq 0.4$), high ($0.4 < \text{gHM} \leq 0.7$), and highest ($0.7 < \text{gHM} \leq 1$).

Economic data

We used 2017 estimates of gross national income adjusted for purchasing power parity (GNI PPP) expressed in current (2019) international dollars as a measure of the financial wealth of countries, as calculated by The World Bank (https://data.worldbank.org/indicator/NY.GNP.MKTP.PP.CD).

Species representation targets

We used area-based representation targets to define the amount of habitat each species needed for protection in order to be considered safeguarded for the future. The amount of habitat potentially available for conservation was calculated by the count of 1km gHM pixels within each 55km grid cell and in each gHM category. Reasoning that the highest gHM category represented land either too degraded to be valuable habitat for most species or too encroached for possible restoration efforts, we excluded it from species area calculations. Similarly, the amount of currently protected habitat was calculated by the count of 1km PA pixels within each 55km grid. Species area was then calculated as the summed counts of PA and gHM pixels multiplied by each 55km grid cell's occurrence probability, and summed across all cells. The representation targets were then calculated as a function of a species' total range size with a piecewise log-linear function that specified representation targets of 100% for species with ranges up to 10,000km^2 and 15% for species with ranges greater than 250,000km^2, chosen *a priori* to reflect the 15% of global surface area currently protected[9]. Representation targets were capped at 1,000,000km^2, which prevented the optimization results from being overly influenced by the most widespread species.

Data availability

All datasets of species distributions, protected areas, and human modification used in this study are publicly available from their original sources. Detailed and interactive information on species distributions used in the analyses are also available at Map of Life (https://mol.org).

The global optimization results in Figure 1 (shapefile of 55km cells, with area needed and priority ranks of each cell) will be publicly shared in the ArcGIS Living Atlas of the World (https://livingatlas.arcgis.com/), and will be able to be explored interactively on Map of Life and the Half-Earth Project's mapviewer (https://www.half-earthproject.org/maps/) by date of publication.

The local optimization results in Figure 2 (raster of 1km HM values within the reserve network) will be publicly shared in the ArcGIS Living Atlas of the World (https://livingatlas.arcgis.com/), and will be able to be explored interactively on the Half-Earth Project's mapviewer (https://www.half-earthproject.org/maps/) by date of publication.

The species targets and gap data in Figure 3 will be deposited with the Environmental Data Initiative prior to publication.

The ecoregion, biome, and country data in Figure 4 are shared as supplementary tables with this manuscript.

Optimization

We formulated the optimization problem as a linear program (LP)[8] so that each of the $N = 53{,}253$ terrestrial cells in the global 55km grid was associated with four decision variables

α_i, β_i, γ_i, δ_i, indicating the proportion of land within cell *i* to protect by HM categories none, low, moderate, and high, respectively. The resulting LP was

$$\text{minimize} \quad \sum_{i=1}^{N} c_i^{\alpha}\alpha_i + c_i^{\beta}\beta_i + c_i^{\gamma}\gamma_i + c_i^{\delta}\delta_i, \tag{1}$$

subject to:

$$\sum_{i=1}^{N} q_{ij}^{\alpha}\alpha_i + q_{ij}^{\beta}\beta_i + q_{ij}^{\gamma}\gamma_i + q_{ij}^{\delta}\delta_i \geq T_j; \tag{2}$$

$$\sum_{i=1}^{N} q_{ij}^{\alpha}\alpha_i + q_{ij}^{\beta}\beta_i + q_{ij}^{\gamma}\gamma_i \geq T_j^{\gamma}; \tag{3}$$

$$\sum_{i=1}^{N} q_{ij}^{\alpha}\alpha_i + q_{ij}^{\beta}\beta_i \geq T_j^{\beta}; \tag{4}$$

$$\sum_{i=1}^{N} q_{ij}^{\alpha}\alpha_i \geq T_j^{\alpha}; \tag{5}$$

$$0 \leq \alpha_i, \beta_i, \gamma_i, \delta_i \leq 1. \tag{6}$$

Equation (1) minimizes the area of the reserve network. The costs c_i^{α}, c_i^{β}, c_i^{γ}, c_i^{δ} associated with protecting cell *i* reflected the amount of land in each HM category in the cell that was not currently protected and hence was theoretically "available" for conservation action. These were computed with 1km-pixel counts for each HM category and for each cell.

The inequality in Eq. (2) ensures that the amount of area protected by the reserve network is above the representation target T_j for each species *j*. The amount of habitat q_{ij}^{α} available for future protection for species *j* in cell *I* and HM category *x* was calculated as

$$q_{ij}^{x} = r_{ij}c_i^{x}, \tag{7}$$

where r_{ij} is the presence probability of species *j* in cell *i*. Species representation target T_j is given by

$$T_j = \rho_j \left(\sum_{i=1}^{N} q_{ij}^{\alpha} + q_{ij}^{\beta} + q_{ij}^{\gamma} + q_{ij}^{\delta} \right), \tag{8}$$

with ρ_j the proportion of range area determined by the representation target.

The inequalities in Eqs. (3-5) ensure that habitat with lower HM will be prioritized over habitat with higher HM. The thresholds T_j^x represent the amount of available habitat in HM category *x* or lower, and were calculated as

$$T_j^{\gamma} = T_j - \sum_{i=1}^{N} q_{ij}^{\delta}; \tag{9}$$

$$T_j^{\beta} = T_j^{\gamma} - \sum_{i=1}^{N} q_{ij}^{\gamma}; \tag{10}$$

$$T_j^{\alpha} = T_j^{\beta} - \sum_{i=1}^{N} q_{ij}^{\beta}. \tag{11}$$

Equation (6) constrains the decision variables to represent proportions between 0 and 1. Optimization was performed with Gurobi, a software package that employs the simplex and branch-and-bound algorithms for linear and mixed integer optimization[49]. All analysis was performed in R.

Supplementary discussion:

Richness, endemism, and rarity

Species richness describes the number of species occupying a given region[19], and is typically calculated by summing occurrences by grid cell. Because our probabilistic downscaling approach assigns a probability of occurrence to each 55km cell, summing occurrence probabilities by cell results in non-integer values of richness. Specifically, the species richness of cell *i* was calculated as

$$Richness_i = \sum_{j=1}^{J} r_{ij}, \tag{12}$$

where r_{ij} is the presence probability of species j in cell i and J is the total number of species (Fig. 6A).

Species endemism (also known as total range-size rarity or weighted endemism) describes the proportion of a species' range that is found in a given region, summed across all species within the region[19]. The species endemism of cell *i* was calculated as

$$Endemism_i = \sum_{j=1}^{J} \frac{L_i r_{ij}}{A_j}, \tag{13}$$

where L_i is the area of land in cell *i* and A_j is the total range area of species *j* (Fig. 6B). Species rarity (also known as average range-size rarity) is simply the endemism divided by the number of species present in each cell, and given by

$$Rarity_i = \frac{1}{J_i} \sum_{j=1}^{J} \frac{L_i r_{ij}}{A_j}, \tag{14}$$

where J_i is the number of species with a nonzero occurrence probability in cell *i* (Fig. 6C).

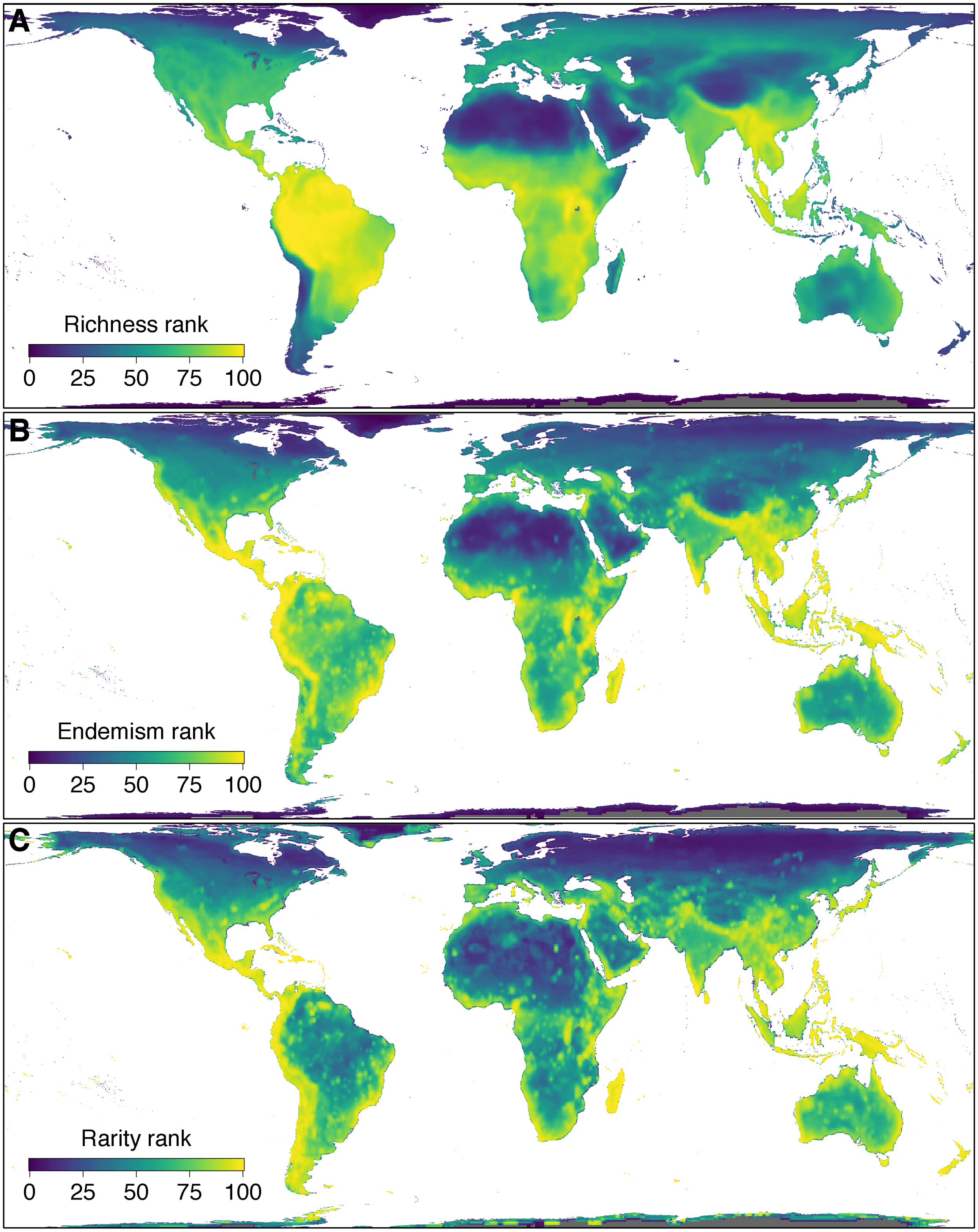

Figure 6: Percentile rank of species (A) richness, (B) endemism, and (C) rarity. Cells in grey did not contain any species occurrences, and were omitted from percentile rank calculations.

Conservation burden

We define the *conservation burden* of an administrative region as the ratio of the weighted sum of the region's area contained in the reserve network and the region's gross national income adjusted for purchasing power parity (GNI). We calculated two different formulations of burden: the first, denoted CB_P (or simply, present burden), includes the amount of currently protected area, and is calculated as

$$CB_P = \frac{\sum_{i \in K} PA_i + c_i^{\alpha}\alpha_i^* + 1.1 c_i^{\beta}\beta_i^* + 1.4 c_i^{\gamma}\gamma_i^* + 1.7 c_i^{\delta}\delta_i^*}{GNI}, \quad (12)$$

where PA_i is the amount of currently protected area in cell i, K is the set of cells that overlap with the region, and α_i^*, β_i^*, γ_i^*, δ_i^* are the decision variables at optimality. Land with higher HM is weighted more heavily to reflect additional expenses associated with restoration of more heavily degraded habitat. The weights were chosen to reflect the cutoffs for each HM category. The second formulation, denoted CB_F (or simply, future burden), excludes PAs and only sums across additional area needed, and is calculated by

$$CB_F = \frac{\sum_{i \in K} c_i^{\alpha}\alpha_i^* + 1.1 c_i^{\beta}\beta_i^* + 1.4 c_i^{\gamma}\gamma_i^* + 1.7 c_i^{\delta}\delta_i^*}{GNI}. \quad (13)$$

Both forms of conservation burden reflect the theoretical economic capacity of a country to achieve its national prescribed conservation objectives, and are expressed in square meters of land per dollar. Present burden considers the costs associated with maintaining land that is already protected, while future burden only considers costs associated with future additional conservation actions. In practice, the economic capacity of a country will be heavily influenced by local land costs and the proportion of GNI that a country chooses to invest toward conservation, in addition to other factors. Summing across all global area needed and all GNI, the global conservation burden (GCB) provides a useful reference point for individual regions;

GCB_P is 0.651 m^2/\$, and GCB_F is 0.516 m^2/\$. Countries with smaller present burdens generally had even smaller future burdens, sometimes by several orders of magnitude (Fig. 7). This suggests that most of the land requirements of countries with small present burdens come from areas that are already protected.

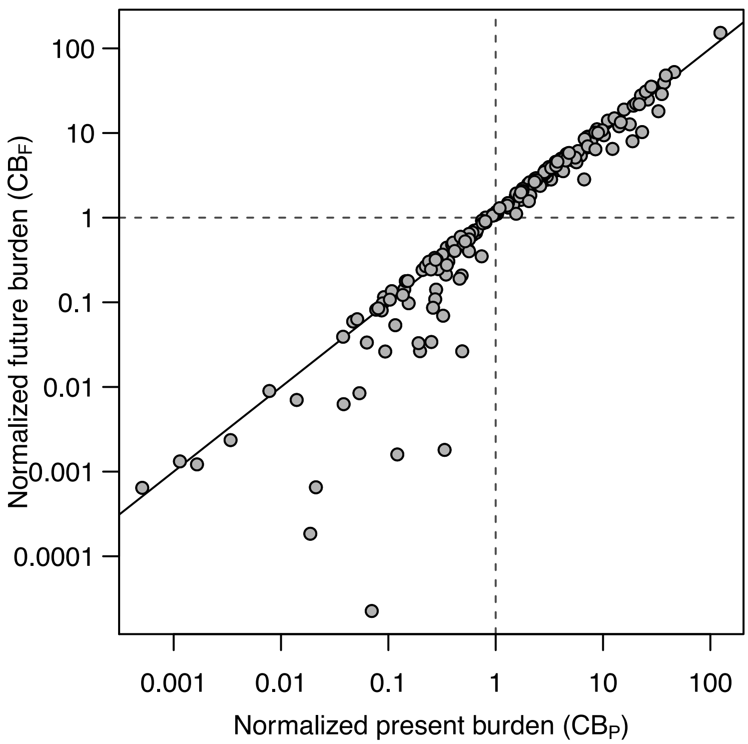

Figure 7: Present burden vs. future burden of countries, each normalized by GCB_P and GCB_F, respectively, so that values are expressed in magnitudes from the global conservation burden. GCB_P and GCB_F are indicated by the dashed lines.

Ecoregions and biomes

Achieving ecological representativeness in accordance with Aichi Biodiversity Target 11 is commonly interpreted as protecting at least 17% of each of the planet's distinct ecoregions. To assess the comprehensiveness of biogeographical representation in the reserve network we calculated the amount of land needed in 846 ecoregions, using the Ecoregions2017 dataset[50,51].

We note that this dataset was not created with GADM 3.6 as the base world layer, which led to occasional small rounding errors in ecoregion areas in places of border discrepancies. This resulted in some ecoregions needing an area slightly greater than 100%; such regions were rounded down to 100%.

We found that only 60 ecoregions required protection of 17% or less of their total area, illustrating that the terrestrial target suggested by the expiring Aichi Biodiversity Target 11 is woefully inadequate. Grouping broadly by biome, none of the 14 distinct biome categories required less than 17% of total area.

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D.S.R. and W.J. jointly conceived the project and figures and wrote the text. D.S.R. developed and implemented the modeling methodology and analyses with input from W.J. D.S.R. created the figures.