APPLIED ECOLOGY

Identifying global centers of unsustainable commercial harvesting of species

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Overexploitation is one of the main threats to biodiversity, but the intensity of this threat varies geographically. We identified global concentrations, on land and at sea, of 4543 species threatened by unsustainable commercial harvesting. Regions under high-intensity threat (based on accessibility on land and on fishing catch at sea) cover 4.3% of the land and 6.1% of the seas and contain 82% of all species threatened by unsustainable harvesting and >80% of the ranges of Critically Endangered species threatened by unsustainable harvesting. Currently, only 16% of these regions are covered by protected areas on land and just 6% at sea. Urgent actions are needed in these centers of unsustainable harvesting to ensure that use of species is sustainable and to prevent further species' extinctions.

INTRODUCTION

Habitat transformation, unsustainable harvesting, invasive species, pollution, and climate change are often reported as the main human causes of global biodiversity loss (1). Among those taxonomic groups where extinction risk has been assessed for all species by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (2), unsustainable harvesting is now the most prevalent threat affecting threatened marine species and is the second most prevalent (after agriculture/aquaculture) for terrestrial and freshwater species (3). On land, unsustainable harvesting for food and other uses is threatening the persistence of not only high-profile species, such as rhinoceroses (4) and elephants (5), but also many lesser-known species (6). Similarly, one-third of commercial wild fish stocks are currently being overfished (7), and global marine fisheries catches are declining despite increasing fishing effort (8). Unsustainable harvesting jeopardizes global food security (9) and can have negative consequences on food webs, ecosystem functioning, and human well-being (10).

No previous global assessment has investigated the distribution and vulnerability of global centers of unsustainable commercial harvesting (11, 12). Here, we therefore assess how the intensity of unsustainable harvesting varies across concentrations of species threatened by unsustainable harvesting.

Our analysis uses the approaches of spatial conservation planning (13, 14) to find the global top 20% highest conservation priority grid cells for species threatened by unsustainable harvesting (see fig. S1 for a flow chart of the analysis). We carried out separate analyses for marine species and terrestrial and freshwater species, given that the drivers of threats are very different in the two environments and the United Nations (UN) Sustainable Development Goals treat these groups separately (15). Overall, 4543 threatened (Critically Endangered, Endangered, and Vulnerable) and Near Threatened species were included from those taxonomic groups in which all species have been assessed in the IUCN Red List (2): birds, mammals, amphibians, chameleons, sharks and rays, tarpons and ladyfishes, parrotfishes and surgeon fishes, groupers, tunas and billfishes, hagfishes, angelfishes, blennies, butterflyfishes, picarels, porgies, pufferfishes, sea breams, sturgeon, wrasses, reef-building corals, freshwater caridean shrimps, cone snails, freshwater crabs, freshwater crayfish, lobsters, cacti, sea grasses, and mangroves (see fig. S2 for number of species per taxon) (16). All selected species had range maps available and have been coded as threatened by biological resource use (hunting and collecting terrestrial animals, gathering terrestrial plants, logging and wood harvesting, and fishing and harvesting aquatic resources) (17). A species may be coded as threatened by "biological resource use" (unsustainable harvesting) if the species is directly targeted or indirectly affected (e.g., as "bycatch" or as species affected by timber extraction, etc.).

We then overlaid the identified grid cells with a high-medium-low–threat intensity classification map to identify vulnerable regions. We did this to assess the relative intensity of threat experienced by concentrations of species threatened by unsustainable harvesting. We used accessibility to urban areas and transport infrastructure to supply national and international markets (18) as a proxy for potential intensity of unsustainable harvesting on terrestrial and freshwater species, given that commercial harvesting pressure has been found to be higher in areas with greater accessibility to major towns (19–21). Similarly, we used average fishing catch rate standardized by productivity as a proxy for intensity of unsustainable fishing in the oceans because excessively high overfishing rates cause stock collapses and have the greatest impact on regions with lower productivity (22, 23). For both the accessibility map and the fishing catch map, we classified grid cells into low, medium, and high intensity of unsustainable harvesting

using tertiles (see Materials and Methods). Next, we calculated species representation and protected area coverage in the low-, medium-, and high-threat intensity grid cells.

We conducted additional spatial conservation planning analyses to see if avoidance of threat and poor governance would be possible without compromising the biodiversity values of the global top 20% highest conservation priority grid cells for species threatened by unsustainable harvesting. We accounted for socioeconomic factors in spatial conservation planning, seeking to minimize conflicts while maintaining same species representation. Specifically, we sought to identify a new set of centers of species threatened by unsustainable harvesting, where (i) threat intensity was lower and threat reversibility, therefore, is potentially higher and (ii) in countries where the capacity to implement the rule of law (e.g., protected area establishment, effective protected area management, and controls on harvesting and trade) would potentially be greater.

RESULTS

On land, our results show that 43% of the global top 20% highest centers of species threatened by unsustainable harvesting are found in highly accessible terrestrial and freshwater systems (corresponding to 4.3% of all terrestrial land; red areas in Fig. 1). These cells occur across all continents but are overwhelmingly concentrated in Asia and North and South America (Fig. 1 and fig. S3). Compared to previous assessments, such as the global biodiversity hotspots (24), we identify new regions as centers of unsustainably harvested terrestrial and freshwater species in China, South Asia, the Amazon basin, North America, and southern Africa. At sea, 30% of the areas holding the greatest complements of species threatened by unsustainable harvesting are found in marine areas with the highest levels of fisheries catch (corresponding to 6.1% of all sea; red areas in Fig. 1). These cells are most concentrated not only in Asian seas but also in regions not recognized by previous studies [e.g., (25)], such as in the Eastern coast of the United States and Brazil; in the Gulf of Guinea; in the Arabian Sea; and in the North, Norwegian, and Mediterranean seas (Fig. 1 and fig. S3). The distribution of these overlaps, both on land and at sea, varies little between taxonomic groups (fig. S4). However, there are geographical differences between top priority areas under each type of unsustainable harvesting (fig. S5), even if there is high overlap between top priority areas for terrestrial species threatened by hunting and collection and top priority areas for species threatened by logging and wood harvesting (table S1). Our results are stable at different spatial analysis resolutions for cell sizes of 0.1°, 0.2°, 0.5°, and 1° (fig. S6). Furthermore, the identified areas are those where the species are most likely harvested, considering that the species included in the analysis mostly have small ranges (fig. S7).

Overall, 82% of all species threatened by unsustainable harvesting occur in areas of high intensity of threat (red in Fig. 1), which together contain a median of ~50% of their ranges (marine species: 53%; terrestrial and freshwater species: 46%; table S2). In contrast, locations of low-threat intensity contain only a median of 13.5% of the ranges of all species threatened by unsustainable harvesting (marine species: 13%; terrestrial and freshwater species: 14%). Worryingly, high-threat intensity areas contain a median of 80% (interquartile range of 35 to 100%) of the ranges of Critically Endangered species, which, by definition, face the highest risk of extinction (Fig. 2A). At the taxonomic level, these overlapping areas contain a median of more than 50% of the ranges of plants, reptiles, amphibians, invertebrates, and cartilaginous fishes (Fig. 2B). However, only 6% of these marine areas and 16% of these terrestrial areas are covered by protected areas (fig. S8).

Looking at the species representation in Fig. 3, it becomes apparent that there is minimal scope for guiding conservation efforts away from threats and poor governance. Attempting to do so would markedly compromise the performance of conservation plans: The reason is that large fractions of the ranges of most of the species threatened by unsustainable harvesting occur where threat is high. Species representation would decrease substantially were conservation efforts directed toward regions where threat intensity is lower (37% lower representation for marine species and 20% lower for terrestrial and freshwater species) or in countries where the capacity to implement the rule of law is greater (60% lower representation for marine species and 26% lower for terrestrial and freshwater species) (Fig. 3).
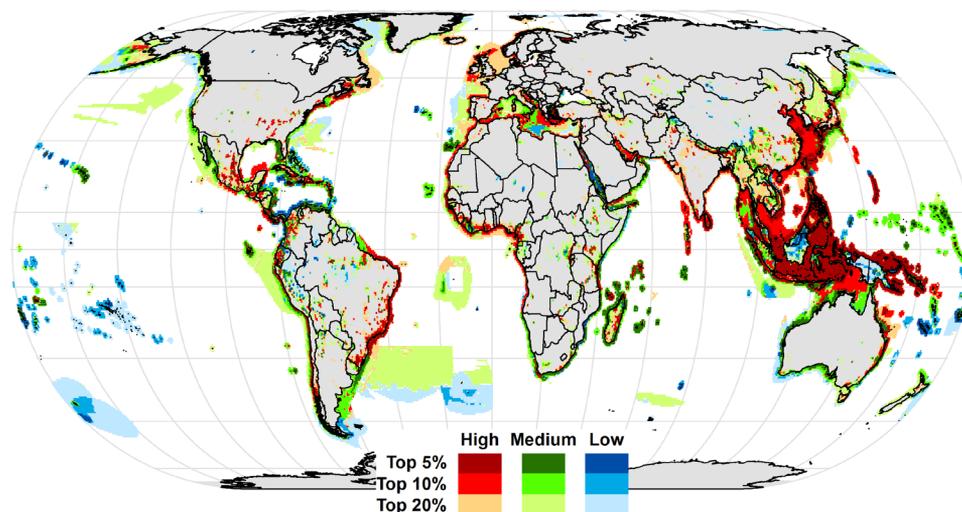
Fig. 1. Vulnerability of global conservation priority areas to unsustainable commercial harvesting. Different colors correspond to high (red, 33% upper tertile), medium (green, 33% medium tertile), and low (blue, 33% lower tertile) intensity of unsustainable commercial harvesting. Different hues correspond to different priorities for the conservation of species threatened by unsustainable commercial harvesting (top 5, 10, and 20% of the landscape or seascape).
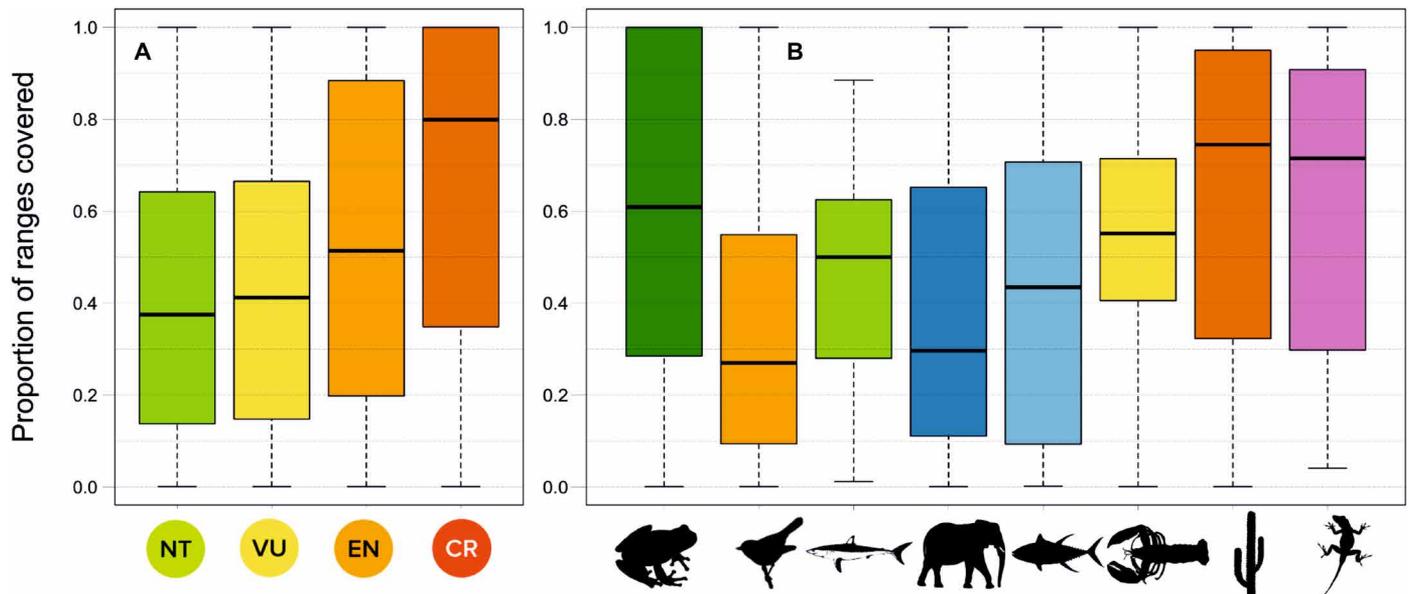
Fig. 2. Species representation in global conservation priority areas under high intensity of unsustainable commercial harvesting. Box-and-whisker plots show representation of species threatened by unsustainable harvesting and are grouped by (**A**) IUCN Red List category and (**B**) taxonomic group. NT, Near Threatened; VU, Vulnerable; EN, Endangered; CE, Critically Endangered. In (B), from left, the images are for amphibians, birds, cartilaginous fishes (sharks and rays), mammals, bony fishes, invertebrates, plants, and reptiles. Colors for each taxonomic group match those in fig. S1, where the number of species for each taxonomic group is also reported.

For marine species, the top 20% centers of species threatened by unsustainable harvest cover as high a proportion of the species' respective ranges as the remaining 80% of the seascape (Fig. 3). Similarly, for terrestrial species, the top 20% of these centers cover as much species ranges as the next 20 to 74% of the world (Fig. 3).

DISCUSSION

As with other global analyses (*26*, *27*), there are a number of caveats to our work. The species range maps used in the analysis represent coarse-resolution distributional boundaries of species, not fine-resolution area of habitat. While our results were consistent across a range of spatial resolutions, they are, nonetheless, too coarse to inform on-the-ground planning of actions across specific locations of land and water management. Although market accessibility and fishing catch are imperfect proxies for harvesting pressure, the areas identified in this study are congruent with previous regional conservation assessments (*28–32*). Because direct information on the local demand for all species is currently missing, future studies should also assess relationships between demand and supply for all species to better account for the intensity of unsustainable harvesting. When additional taxonomic groups become assessed and mapped for the IUCN Red List, they should be added to future updates of this assessment. Nevertheless, the present set of species represents an extensive set of higher taxa.

Enhancing the survival of species threatened by unsustainable harvesting will be challenging, as they are concentrated in areas where harvesting intensity is the highest and governance and political stability are the lowest (Figs. 1 and 3). Even so, our results highlight the necessity of prioritizing conservation efforts in these areas, as this is where Critically Endangered species are largely concentrated. Protected areas are an essential part of the solution to tackling unsustainable exploitation, if they are effectively managed (*33*), including

private and community-based approaches. Strict species and site protection, for example, play a crucial role in enhancing future persistence of species of high commercial value (*4*, *5*). However, as our results show, the areas at highest risk are currently poorly covered by protected areas. Hence, complementary conservation strategies are also needed, including (i) reducing consumer demand where appropriate (*34*) and promoting sustainable resource use both globally and locally (*35*); (ii) enhancing legislation and better enforcement of laws to control harvest levels, bycatch, and indirect impacts; and (iii) strengthening compliance with trade regulation, both domestically and internationally, including through the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Underpinning all of these, improved monitoring is needed of both the intensity of pressure from different forms of unsustainable exploitation (e.g., intensity of legal and illegal killing and bycatch levels) (*11*) and the abundance, distribution, and trends of the species affected. Our results confirm that major threats, such as deforestation and commercial trade, may well act together in some of the identified regions (*36*) and that conservation actions that target both threats might be needed. These responses must be particularly targeted within Asia and North and South America and, given the geographic pattern of our results, especially in areas that were not identified in previous analyses.

Our results inform how best to achieve aspects of the UN Sustainable Development Goal targets (e.g., 12.2: "Achieve sustainable management and efficient use of natural resources; 14.4: "Regulate harvesting and end overfishing, illegal, unreported, and unregulated fishing; and 15.7: "End poaching and trafficking of protected species of flora and fauna") and other intergovernmental commitments such as CITES and Aichi Target 6 of the Strategic Plan for Biodiversity 2011–2020. Losing populations and species to overharvesting will compromise ecosystem functioning, food security, and human well-being. Investing resources to support the conservation of
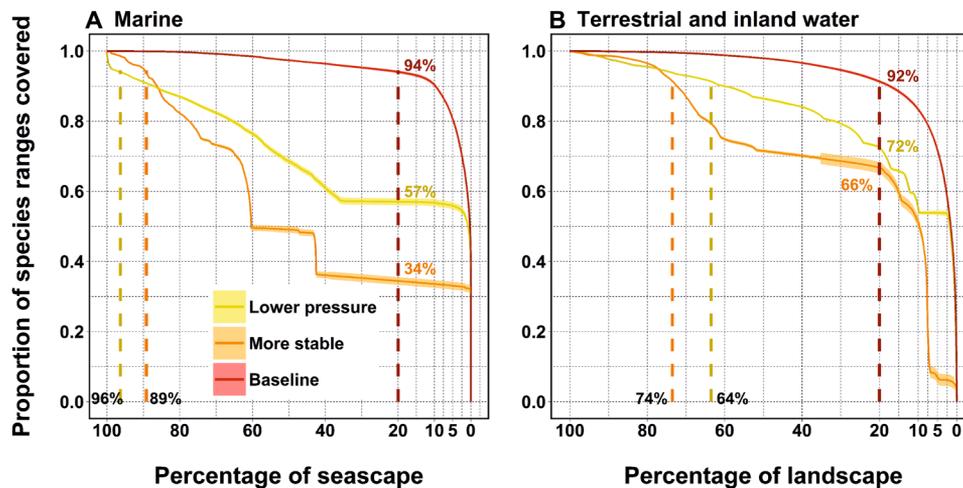
Fig. 3. Average representation for 4543 species threatened by unsustainable commercial harvesting at each percentage of the seascape and landscape. Curves quantify the proportion of the species' ranges represented at each percentage of the seascape (**A**) and landscape (**B**) under different scenarios. "Baseline" curves show representation when only species range maps were included in the analysis. "Lower pressure" is for the scenario in which maps of accessibility and fisheries catch were additionally included in the analysis as cost layers to implement avoidance of areas with high-threat intensity. "More stable" curves are for analysis in which the Fragile State Index was included as a cost layer to implement avoidance of areas where the rule of law is lowest. The red dashed vertical line shows species representation at the top 20% ranked areas. Yellow and orange dashed lines show the percentage of landscape and seascape needed to achieve same species representation as in the baseline scenario under the lower pressure and more stable scenarios, respectively. Black numbers report the percentage of landscape and seascape needed to achieve such representation. Red, yellow, and orange numbers show mean species representation within the top 20% ranking areas under the baseline, lower pressure, and more stable scenarios, respectively.

unsustainably harvested species will decrease risks to human societies in the future.

MATERIALS AND METHODS
Figure S1 shows a flowchart of the analysis, which is composed of three main steps, namely, preprocessing of data, spatial conservation planning, and postprocessing of the outputs of spatial conservation planning. We described each step in detail below.

Preprocessing
We based our analysis on a set of 5349 spatial data layers collected from different sources and in different formats. This dataset was composed of 5344 range maps, two threat maps, two governance maps, and a protected area map. All layers were converted to global grids in different resolutions (latitude/longitude coordinate system), with cell sizes of 0.1° (equal to 10 km at the equator), 0.2°, 0.5°, and 1°. Data preprocessing was done using ArcGIS software v.10.2 (*37*) and the Python programming language v.2.7 (*38*).

Species range maps
We focused our analysis on species that are listed as Critically Endangered, Endangered, Vulnerable, and Near Threatened in the IUCN Red List. Specifically, we selected species that the IUCN have coded as threatened by biological resource use (hunting and trapping terrestrial animals, gathering terrestrial plants, logging and wood harvesting, and fishing and harvesting aquatic resources for intentional use and motivation unknown or unrecorded) in 2016 (www.iucnredlist.org/resources/threat-classification-scheme). We only selected species from those species groups on the IUCN Red List that have received comprehensive assessment, namely, birds, mammals, amphibians, chameleons, sharks and rays, tarpons and ladyfishes, parrotfishes and

surgeon fishes, groupers, tunas and billfishes, hagfishes, angelfishes, blennies, butterfly fishes, picarels, porgies, puffer fishes, sea breams, sturgeon, wrasses, reef-building corals, freshwater caridean shrimps, cone snails, freshwater crabs, freshwater crayfish, lobsters, cacti, sea grasses, and mangroves (*16*). In addition, we only used species for which range maps were available or about to become available from the IUCN Red List portal (www.iucnredlist.org/) and from the BirdLife International Data Zone webpage (www.birdlife.org/datazone/home). This resulted in a total of 4543 species belonging to eight broad taxonomic groups (birds, mammals, amphibians, reptiles, cartilaginous fishes, bony fishes, invertebrates, and plants) in terrestrial and freshwater and marine systems. For birds, we split up the original range maps to consider the breeding, nonbreeding, passage, and resident ranges of each species. This resulted in a total of 4765 range maps included in the analysis in representation of 4543 species. For all species, we excluded all portions of the ranges where the species were identified as extinct, introduced, or of uncertain origin. In addition, we further considered 579 Data Deficient species, which are coded as threatened by unsustainable harvesting in the IUCN Red List, from the same range of taxonomic groups. We did this to generate a measure of uncertainty for the average range coverage of data sufficient species in additional analyses, as we explain below. Hence, Data Deficient species were not included in spatial conservation planning. Overall, a total of 5344 range maps (4765 for threatened and Near Threatened species and 579 for Data Deficient species) were processed.

Threat maps
We used two threat maps in the analysis, one for terrestrial areas and one for marine areas. We used a map for market accessibility for terrestrial analyses and a layer for fisheries catch for marine analyses. No map reporting the spatial distribution of unsustainable harvesting pressure is available at a global resolution (*11*). Instead, we used

market accessibility as a proxy for intensity from unsustainable harvesting on land. Specifically, we used a global map of market accessibility, where accessibility is defined as the travel time to a location of interest using land-based (road/off-road) or water-based (navigable river and lake) travel (*18*). Accessibility was computed using a cost-distance algorithm, which computes the "cost" of traveling between two locations on a regular raster grid.

To create the marine threat map, we combined five separate commercial fishing catch layers for 2013: demersal destructive, demersal nondestructive high bycatch, demersal nondestructive low bycatch, pelagic high bycatch, and pelagic low bycatch (*22*). Methods and data sources were explained by Halpern *et al.* (*22, 23*), and original data can be downloaded from https://knb.ecoinformatics.org/#view/doi:10.5063/F1S180FS. Following Halpern *et al.* (*22*), we log[X+1]-transformed each layer. By doing so, the effect of extreme outliers when rescaling the data was reduced. Each layer was then rescaled between 0 and 1 to ensure comparability across layers with different units of measurement (*22*). The layers were then combined by taking the mean value for each pixel in ArcMap 10.2 (*37*).

Both threat maps were classified into low, medium, and high intensity by using tertiles in R (tertiles are the two points that divide an ordered distribution into three parts, each containing a third of the population) (*39*). In this case, splitting the two layers into three categories, each using tertiles, allowed us to simplify the interpretation and visual presentation of results.

Governance maps

We used two separate governance maps in the analysis: one for terrestrial areas and one for marine areas. For the terrestrial analysis, the governance map was created by assigning the 2016 Fragile State Index value to each spatial pixel of the country, as mapped by the Database of Global Administrative Areas (www.gadm.org/). The Fragile State Index (http://fundforpeace.org/fsi/) aims to assess the vulnerability of a country to conflict or collapse. It ranks all sovereign states with UN membership on a continuous scale from sustainable (more stable) to alert countries (least stable). Specifically, the index is based on 12 indicators of state vulnerability, grouped by three categories: social (four indicators), economic (two indicators), and political (six indicators). The Fragile State Index represents an aggregate measure summarizing various aspects of governance, therefore offering a more realistic measure of the capacity of countries to implement the rule of law.

For the marine prioritization, we created the governance map by merging the Exclusive Economic Zones of each country and a layer with the regional fishing bodies' boundaries in high seas, that is, the waters beyond national jurisdiction. In the resulting layer, each Exclusive Economic Zone pixel reported the Fragile State Index value of the country the Exclusive Economic Zone belonged to. For high seas, instead, we used the average Fragile State Index value across the contracting countries of each regional fishing body (www.fao.org/fishery/rfb/en). Our approach might be considered optimistic, as many of the high seas are, in reality, hotspots of illegal fishing (*8*). Exclusive Economic Zone boundaries were downloaded from the Marine Regions data portal (www.marineregions.org/downloads.php), while the regional fishing bodies' boundaries were obtained from the World Food Program data portal (www.fao.org/geonetwork/srv/en/metadata.show?id=31675). A few countries (Taiwan, the Palestinian territories, Kosovo, and Western Sahara) were not yet ranked by the Fragile State Index. In the absence of data, they were therefore assigned an average value across all countries ranked by the index.

Protected areas

The data on protected areas were based on the May 2016 release of the World Database on Protected Areas (retrieved from www.protectedplanet.net and produced by the UN Environment World Conservation Monitoring Centre) (*40*). We only selected areas belonging to IUCN protected area categories I to VI and having status as "designated," "inscribed," "established," or "adopted" (all meaning that the protected area is designated). Areas marked as "Proposed" were removed, as well as all protected areas lacking polygonal representation. To prevent overestimation of the areal coverage of protected areas caused by overlapping designations, we merged polygons into a single layer.

Spatial conservation planning

Priority maps showing the grid cells with the highest complements of species were generated by iteratively ranking of grid cells from lowest to highest priority for conservation. Together with ranking maps, we produced performance curves that describe the extent to which each species is retained in any given high- or low-priority fraction of the landscape and seascape. We implemented complementarity-based, balanced, priority ranking with the Zonation software for spatial conservation planning (*13, 14*), which produces the ranking maps and performance curves as main outputs. Specifically, we used the Zonation software v.4 (*13, 14*).

Zonation produces a ranking that is balanced in the sense that, irrespective of landscape fraction chosen, the areas are complementary and jointly achieve a well-balanced representation across all species. We used the additive benefit function analysis variant of Zonation (*13, 14*), 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 in terms of average coverage of species per grid cell and does not require targets or thresholds that are necessarily arbitrary to a degree (*41*). Species were weighted according to their IUCN Red List category of extinction risk, with highest weights assigned to Critically Endangered species (Near Threatened: 2, Vulnerable: 4, Endangered: 6, and Critically Endangered: 8) (*26, 42*). This weighting scheme induces a relatively higher coverage of more threatened species, while the prioritization method maintains an overall balanced representation across different species and groups of species (*26, 42*).

We carried out two separate assessments, one for terrestrial and freshwater species only and one for marine species only. For each assessment, we developed three different prioritization setups: (i) Baseline, based on species range maps only to understand where the unconstrained priorities for the conservation of the species threatened by unsustainable harvesting are; (ii) lower pressure, based on species range maps and the threat maps, mentioned above, included as cost layers; and (iii) more stable, based on species range maps and the governance maps, mentioned above, included as a cost layers. In the second and third prioritizations, threat maps and the governance maps were negatively weighted, and the aggregate weight of each layer was equal to the aggregate weight of all species together. We did so to produce a spatial priority ranking that reduced the overlap between priority regions for the species and regions either under high human pressure (lower pressure) or with lower rule of law (more stable).

For the baseline prioritization, we carried out four analyses at different spatial resolutions (0.1°, 0.2°, 0.5°, and 1°) to assess the sensitivity of our results to different spatial resolutions. We analyzed the overlap of the different resolution rankings by comparing 20% priority

areas identified by different analyses using the Jaccard similarity index. Specifically, the coarser-resolution priority ranking maps were compared with upscaled versions of the reference priority ranking maps (0.1°), generated by calculating the median values of the blocks of cells. We also carried out separate assessments for each taxonomic group included in the analysis and for each type of threat (hunting and collecting terrestrial animals, gathering terrestrial plants, logging and wood harvesting, and fishing and harvesting aquatic resources).

For each setup, we produced performance curves for all species. In addition, we further included 579 Data Deficient species, which are coded as threatened by unsustainable harvesting in the IUCN Red List, to generate a measure of uncertainty for the average range coverage of data sufficient species by assuming that unsustainably harvested Data Deficient species are threatened in the same proportion as are unsustainably harvested threatened and Near Threatened Data Sufficient species. We sampled this proportion at random 1000 times from among unsustainably threatened Data Deficient species to generate confidence intervals for the curves in R (39).

Postprocessing and gap analysis
Results were compared statistically and spatially. First, we identified the areas under highest harvesting intensity on land and at sea, as the areas of overlap between the 20% priority regions holding the greatest complements of species and the grid cells within the 33% upper quantile of the threat maps in ArcMap (37). Last, we used the areas under highest harvesting intensity, as well as medium and low intensity, as hierarchical masks in Zonation to evaluate what percentage of species ranges is represented in those areas. We did so to assess species representation for each taxonomic group and IUCN Red List category. We visualized these results by using parallel boxplots to display the median, quartiles, and minimum and maximum of original total range remaining.

SUPPLEMENTARY MATERIALS
Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/5/4/eaau2879/DC1

Fig. S1. Flowchart of the analysis.
Fig. S2. Pie chart showing the number of species per taxonomic group included in the analysis.
Fig. S3. Percentage of each continent and sea in global conservation priority areas under high intensity of unsustainable commercial harvesting.
Fig. S4. Global conservation priority areas (for taxonomic groups) under high intensity of unsustainable commercial harvesting.
Fig. S5. Vulnerability of global priority areas for the conservation of species threatened by each type of unsustainable harvesting.
Fig. S6. Robustness of identified global priority areas for the conservation of species threatened by unsustainable commercial harvesting to spatial resolutions.
Fig. S7. Histogram of range sizes of species included in the analysis, with a bin size of 10,000 km^2.
Fig. S8. Protected areas found in global conservation priority areas under high intensity of unsustainable commercial harvesting.
Table S1. Percentage area overlap between global priority areas for the conservation of species threatened by each type of unsustainable harvesting.
Table S2. Species representation in global conservation priority areas under low, medium, and high intensity of unsustainable commercial harvesting.

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Science Advances

Identifying global centers of unsustainable commercial harvesting of species

Enrico Di Minin, Thomas M. Brooks, Tuuli Toivonen, Stuart H. M. Butchart, Vuokko Heikinheimo, James E. M. Watson, Neil D. Burgess, Daniel W. S. Challender, Bárbara Goettsch, Richard Jenkins and Atte Moilanen