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Three-quarters of species' ranges have not been covered by protected areas in global borders

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Borderlands are increasingly recognized as critically important for biodiversity conservation owing to their ecological significance and high political profile. However, the species ranges covered by protected areas and their influencing factors in transboundary areas are still largely unknown worldwide. Here, based on the distributional ranges of 19,039 terrestrial vertebrates, we find that three-quarters of species' ranges in global borders remain uncovered by protected areas, particularly in tropical areas of Southeast Asia and West Africa. The average protected area coverage of species ranges is lower in transboundary areas than non-transboundary areas after accounting for geographical differences in sampling efforts. We also observe that protected area coverage of species ranges increases with governance effectiveness, collaboration abilities, protection levels, sizes and establishment years of protected areas, and topographic complexity, but decreases with human population density, human development index, and cropland expansion. Furthermore, protected areas simultaneously face threats of ongoing global challenges from climate change, land-use modification, and alien species invasion, and the proportions of borderlands threatened by global changes are higher than elsewhere. All these findings demonstrate that cross-border cooperation is urgently needed to achieve the ambitious goal of global biodiversity conservation by 2050.

Approximately one-third of terrestrial biodiversity hotspots and nearly 60% of IUCN-assessed terrestrial species are located at land borders[1,2] (details see Supplementary Table 1). Furthermore, under climate change, over half of terrestrial vertebrates may undergo range shift towards international borders[3–5]. However, the borders are being split by increasing physical barrier fences[3,6,7], and are also subject to armed political conflicts[8,9] and asymmetries in conservation efforts between countries[10]. In addition, neighboring nations usually implement resource management actions within their own boundaries, which might result in low percentage of species ranges covered by protected areas (PAs)[11]. Unfortunately, we still understand so little about the degree to which species ranges have been covered by PAs in transboundary areas and their influencing factors as well as comparisons with elsewhere, which is important to maximize transboundary conservation outcomes.

There might be several socioeconomic and ecological factors influencing the species ranges protected across borders[12]. First, previous studies found that richer, independent countries with higher levels of primary education had a greater amount of land protection[13]. We therefore expect that PAs might have better performances in regions with higher levels of human development and governance effectiveness. We assume that regions with high human population density may have low PA coverage, because these regions are likely associated with increased social and economic demands that could

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influence ecosystem conservation[14]. Meanwhile, global cropland has increased tremendously and is expanding inside many PAs[15–17], which could also pose a great threat to biodiversity conservation[18]. Second, transboundary areas with high topographic complexity could provide species a wide variety of habitats, which might attract more conservation attention[2]. Third, armed conflicts are increasing throughout the transboundary areas[9]. More frequent armed conflicts in regions may lead to overexploitation of natural resources and thus a lower PA coverage[8]. By contrast, neighboring countries with higher bilateral collaborations might be more likely to establish cross-border conservation alliances[4] and therefore have higher PA coverage. Lastly, we expect that characteristics of PAs including IUCN category, sizes, years after establishment, and government type could also affect the PA conservation coverage.

With accelerating human activities, the global transboundary areas are also facing emerging challenges from climate change[5], land use change[19] and alien species invasion[20,21]. Recent studies have shown that ongoing global changes may impede the success of PAs towards conservation targets[22,23]. However, it remains unclear about the vulnerability of PAs to different global change processes in transboundary areas, especially compared to non-transboundary areas, which is crucial for future conservation planning to improve decision-making and resource allocation under rapid global changes.

Here, we present a comprehensive study assessing the species ranges covered by PAs, the influencing factors, and vulnerability to global change factors in transboundary areas worldwide. Our analyses include a total of 19,039 terrestrial vertebrate species across 4 taxonomic groups (i.e., amphibians, reptiles, birds and mammals) that have any part of distributional ranges in transboundary areas. Terrestrial vertebrates are used because their distributions are most assessed by experts and mapped by IUCN[24]. We create buffer zones with three different distances (i.e., 25 km, 50 km, and 100 km) from the country edges to define the transboundary areas[11] and quantify the overlap of the distributions of PAs and species there. Importantly, in order to evaluate the conservation situation of PAs in transboundary areas, we also compare PA coverage of species ranges between transboundary and non-transboundary areas. Then we examine the role of different socioeconomic and environmental variables in explaining the observed PA coverage of species ranges after accounting for spatial and taxonomic sample pseudoreplications. Considering that there might be regional-specific circumstances across continents (e.g., illegal wildlife trade to fuel military actions in Africa, and avoidance of the area and subsequent natural resources use from the local communities in Southeast Asia), we also conduct continental scale analyses on influencing factors. Finally, we assess the vulnerability of transboundary PAs to major global change factors including climate change, land use change, and alien species invasion, and compare it with that in non-transboundary areas. Our analyses may not only help identify the biodiversity conservation gaps of PAs in transboundary areas, but also promote management strategies to prevent future threats from sustained global changes in the Anthropocene.

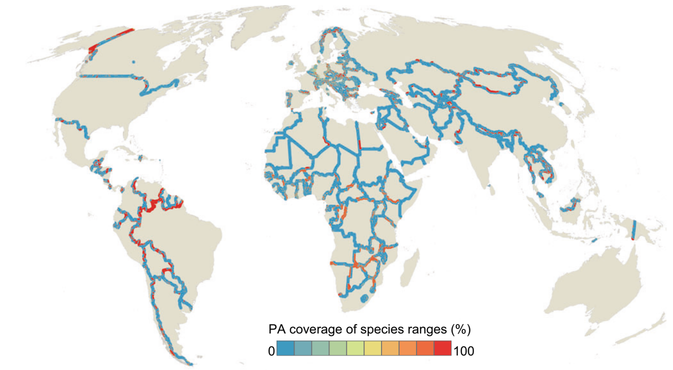

Fig. 1 | Spatial patterns of protected area (PA) coverage of species ranges in transboundary areas worldwide. The colors show the percentage of species ranges covered by PAs, with a warm color corresponding to a higher coverage in 5 km × 5 km grid cells. Source data are provided as a Source Data file.

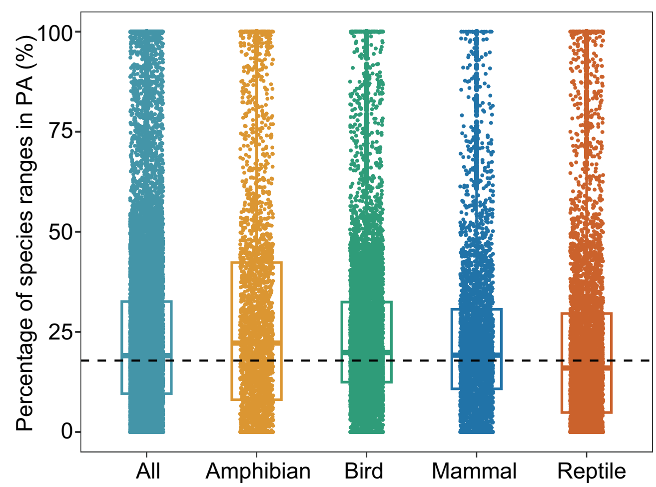

Fig. 2 | Conservation situation quantified as the protected area (PA) coverage of species ranges in transboundary areas across taxa. Different colors indicate taxonomic groups. The dashed line shows the overall percentage of the transboundary areas covered by PAs (17.9%). Box plots show the median (center line), interquartile range (IQR; box bounds), whiskers (1.5 × IQR), and outliers (points beyond whiskers) for the following groups: All (n = 19,039), Amphibian (n = 2943), Bird (n = 7710), Mammal (n = 3480), Reptile (n = 4906). Source data are provided as a Source Data file.

Results

Species ranges protected at global borders

At the global scale, we found that 17.1% of all assessed species had over 50% and 7.4% species had over 90% of their ranges in transboundary areas. The average percentage of species ranges covered by PAs in transboundary areas was 23.0% (Figs. 1 and 2), which was even higher than if PA distributions were random with respect to species ranges (i.e., 17.9%, the proportion of the land protected in transboundary areas; Fig. 2 and Supplementary Table 2). However, after controlling for PA availability and differences in sampling efforts quantified by various anthropogenic factors between the transboundary and non-transboundary areas, PA coverage of species ranges was lower in the transboundary areas (-17.7%) than in the non-transboundary areas both at the global scale (-20.9%) (in all cases, Kruskal-Wallis test, $P < 2.2 \times 10^{-16}$; Fig. 3a and Supplementary Table 3) and at the continent scale (in all cases, Kruskal-Wallis test, $P < 2.91 \times 10^{-11}$; Supplementary Fig. 1 and Supplementary Table 3). Specifically, there was a particularly low PA coverage in some Asian and African countries such as India (mean ± SEM, 4.5 ± 0.48%), Myanmar (12.1 ± 1.07%), and the Democratic Republic of the Congo (17.1 ± 0.99%), which are among regions with the richest terrestrial vertebrates (Supplementary Fig. 4 and Supplementary Data 1). Across taxa, there were also differences among the four vertebrate groups (Kruskal-Wallis test, $\chi^2 = 286.8$, $P < 0.001$), with reptiles having the smallest proportion of ranges covered by PAs (mean ± SEM, 21.6 ± 0.32%), followed by mammals (22.9 ± 0.32%), birds (24.3 ± 0.21%), and amphibians (29.7 ± 0.16%) (Fig. 2 and see Supplementary Data 2 for the full species list).

The threatened species (i.e., classified as Critically Endangered, Endangered, or Vulnerable by the IUCN Red List) had a larger proportion (27.5 ± 0.52%) of species ranges covered by PAs than those non-threatened species (NT and LC, 23.7 ± 0.15%) in transboundary areas (Kruskal-Wallis test, $\chi^2 = 10.59$, $P < 0.001$; Supplementary Fig. 5b).

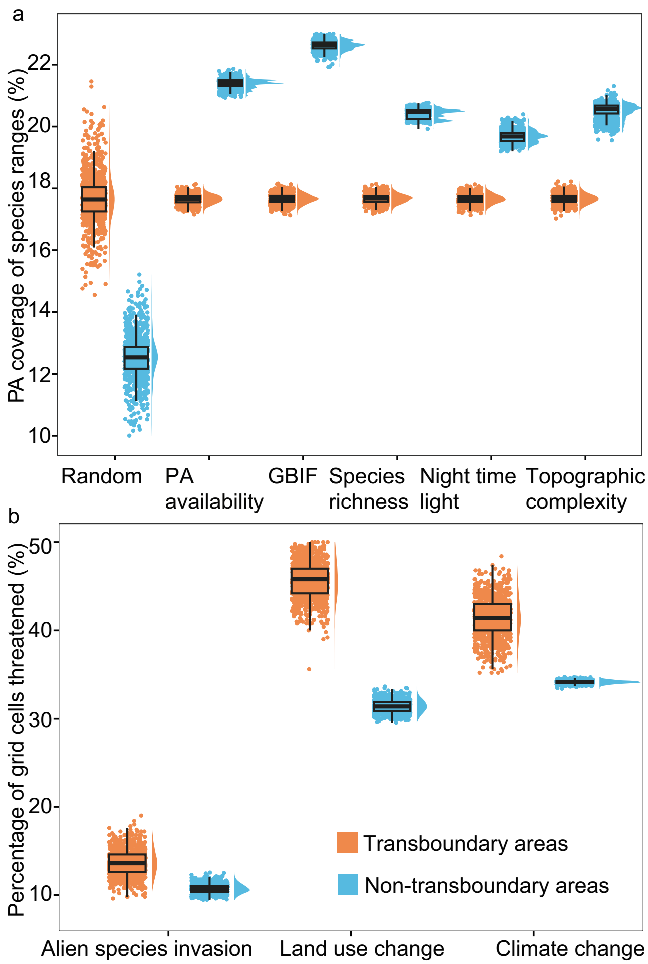

Fig. 3 | Comparison of mean protected area (PA) coverage of species ranges and global change threats in transboundary areas (orange) and non-transboundary areas (blue). The box plots were generated from 999 mean values, each calculated from 50,000 randomly selected grid cells of transboundary and non-transboundary areas, respectively. **a** PA coverage of species ranges. These grid cells were selected in the following ways: randomly (Random); selected from transboundary and non-transboundary areas with similar land areas covered by PAs (PA availability), sampling intensities as estimated by the number of GBIF records per grid cell (GBIF), mean species richness (Species richness), socio-economic condition (Night time light), and topographic complexity. After controlling for PA availability and geographical differences in sampling efforts, the PA coverages of species ranges in transboundary areas ($n = 999$) were lower than those in non-transboundary areas ($n = 999$) (in all cases, Kruskal-Wallis test, $P = 2.2 \times 10^{-16}$, two-sided). **b** Global change threats. All three global change threats in transboundary areas ($n = 999$) were higher than those in non-transboundary areas ($n = 999$) (Kruskal-Wallis test, $P = 2.2 \times 10^{-16}$, two-sided). The grid cells were selected with similar sampling intensities estimated by the number of GBIF records per grid cell, and other results are provided in Supplementary Fig. 2. Box plots show the median (center line), interquartile range (IQR; box bounds), whiskers (1.5 × IQR), and outliers (points beyond whiskers). Source data are provided as a Source data file.

However, we found that a much larger proportion (13.7%) of threatened species had not been covered by PAs at all than non-threatened species (4.9%). The PA coverage was even worse for species with all distributional ranges located in transboundary areas: nearly half (42.5%) of these species had less than 10% of their ranges within PAs, and one third (33.2%) of these species had no overlaps with PAs (Supplementary Fig. 6).

Our results were robust to data uncertainties, as sensitivity analyses obtained similar findings when we used different grid cell sizes or distances to borders defining transboundary areas (Supplementary Fig. 7).

Factors related with the species ranges coverage by PAs

We fitted linear mixed models (LMMs) based on 10 socioeconomic and ecological variables to investigate their relationships with species coverage by PAs in transboundary areas after accounting for spatial and taxonomic pseudoreplications. Globally, the best supported model (i.e., $\Delta AIC < 2$) contained 9 predictor variables (Supplementary Tables 4-5). We found that PA coverage of species ranges was negatively correlated with cropland expansion (estimate ± SEM, $-0.048 \pm 6.03 \times 10^{-4}$, $P < 0.001$), human development index ($-0.012 \pm 9.03 \times 10^{-4}$, $P < 0.001$), human population densities ($-0.02 \pm 5.37 \times 10^{-4}$, $P < 0.001$), but was positively correlated with PA size (0.056 ± 0.001, $P < 0.001$), years of establishment ($0.042 \pm 6.91 \times 10^{-4}$, $P < 0.001$), and protection level ($0.019 \pm 1.44 \times 10^{-3}$, $P < 0.001$). Moreover, PA coverage of species ranges was particularly greater in regions with higher governance effectiveness (0.014 ± 0.001, $P < 0.001$), bilateral cooperation abilities (0.054 ± 0.005, $P < 0.001$), and more complex topographies ($0.064 \pm 8.3 \times 10^{-4}$, $P < 0.001$; Fig. 4a). Furthermore, we found that collaboratively governed and local indigenous community-managed PAs performed better than other PAs (Kruskal-Wallis test, $\chi^2 = 5045.2$, $P < 0.001$; Supplementary Fig. 8). We obtained similar findings using generalized additive model to account for the spatial autocorrelation problem (Supplementary Fig. 9) and random forest model to account for the potential nonlinear relationships between predictor and response variables (Supplementary Fig. 10).

We found that there were variations in factors influencing species coverage by PAs in transboundary areas across continents (Fig. 4b–f; Supplementary Tables 6–10). Bilateral cooperation abilities and frequencies of armed conflicts were important only in Africa. Years of PA establishment were positively correlated with species ranges coverage in most continents except a negative correlation in Asia. Governance effectiveness was a positive predictor in Africa, Europe, and South America. As physical border barriers were mainly located in Eurasia, we analyzed the effect of physical fencings on PA coverage in Eurasia, which indeed showed that transboundary areas with physical fencings tended to have lower PA coverage of species ranges than those without physical fencings ($-0.033 \pm 5.51 \times 10^{-4}$, $P < 0.001$).

Global change threats to PAs at transboundary areas

We ultimately evaluated three main global change threats to PAs at global borders. These included climate change, land use change, and alien species invasion, which are all regarded as crucial stressors of global biodiversity[25,26]. We followed a previous approach[25] by aggregating 11 anthropogenic variables representing the three threats into a single metric to reflect overall global change threats (for details, see the "Method" section). Unfortunately, our results showed that PAs in transboundary areas were facing higher global change threats than those in non-transboundary areas (Kruskal-Wallis test, $P < 0.001$, Fig. 3b and Supplementary Figs. 2–3; Supplementary Table 11). Areas with intense threats from global changes were particularly located throughout Africa, Southeast Asia, Western Europe and North America, such as the Pakistan–India, Germany–Netherlands, and Canada–United States borders (Fig. 5).

We detected geographical variations in effects of the three threats. Specifically, threats from land-use change tended to be greater in Asia, South America and North America, such as in the Pakistan–India, Myanmar–Thailand and Brazil–Uruguay border areas. Climate changes were prominent in Africa. The risks of alien species invasion were particularly high in border areas of Europe (Fig. 5).

Discussion

Although both the number and area of PAs have been increasing markedly across the global land areas[27] and the percentage of PA coverage in transboundary areas (17.9%) has reached the Aichi 11 conservation target (17%)[28], we found that three-quarters of species'

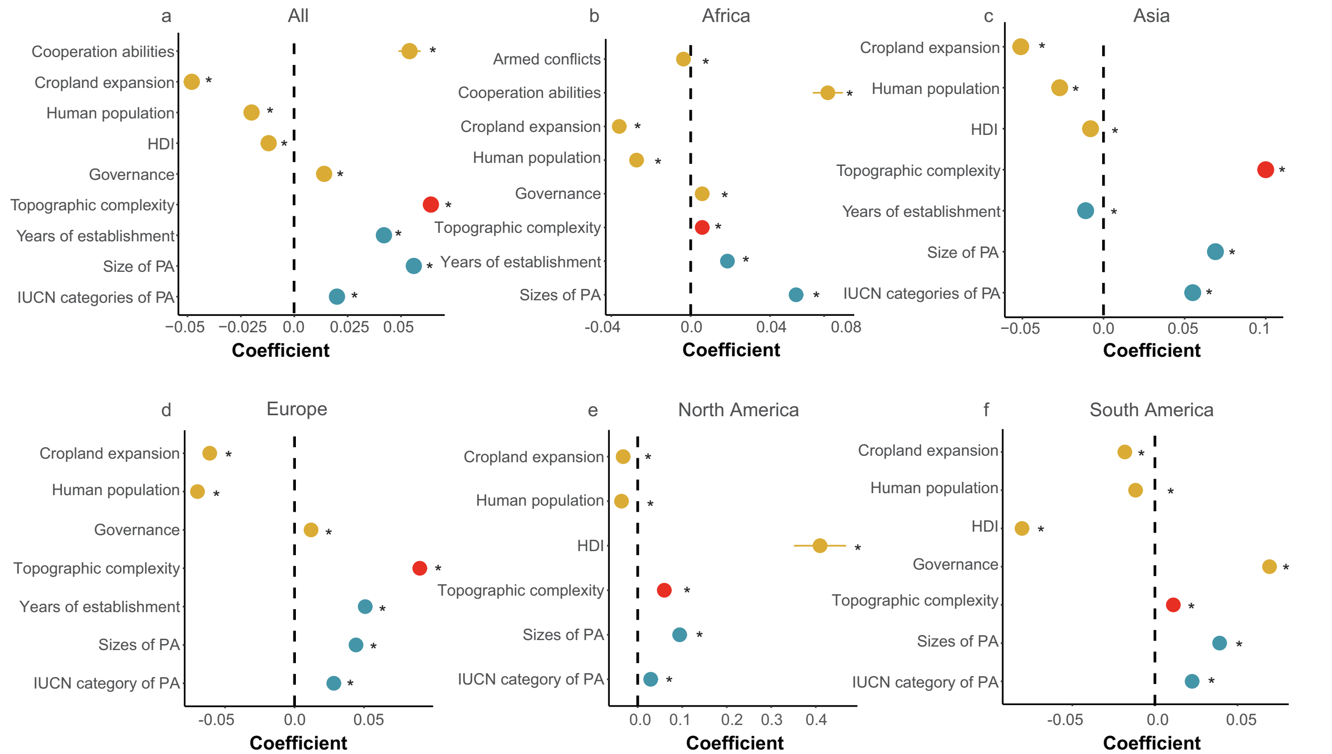

Fig. 4 | Relationships of different ecological and socioeconomic factors with the protected area (PA) coverage of species ranges in transboundary areas. Standardized regression coefficients for individual factors obtained from LMMs at the global (**a**) and continental (**b**–**f**) scales. Positive values indicate that PA coverage of species ranges increases with the variable, while negative values indicate that PA coverage of species ranges decreases with the variable. The yellow, red and blue dots indicate socioeconomic, ecological and PA characteristic factors, respectively. Asterisks indicate statistical support for the effects. The standard errors of the estimates are very small and not visible at this scale. HDI human development index. Source data are provided as a Source data file.

ranges have not been covered by PAs in global borders. Moreover, supporting previous studies[29,30], although we detected a better PA performance at covering species than if their distributions were random with respect to species ranges (Fig. 2; Supplementary Table 2), PA coverage of species ranges was in fact lower in transboundary areas than in non-transboundary areas after controlling for geographical sampling efforts (Fig. 3a). PA coverage of species ranges was particularly lower in transboundary areas with higher economic activities or cropland expansion, though there were some heterogeneities in influencing factors across continents. Further analysis revealed that PAs in transboundary areas were also facing higher degree of threats from ongoing global changes than non-transboundary areas.

There are several potential explanations for this low coverage. First, species do not recognize political boundaries[31], and their conservation outcomes are dependent mainly on the policies and actions of different countries[32]. Although both countries may establish PAs in the transboundary area on their own, the lack of cross-boundary collaboration may lead to less allocation of conservation resources to establish PAs near their border lines[33]. Indeed, our additional analysis showed that the percentage of PAs in transboundary areas increases with cooperation abilities (Supplementary Fig. 11). Second, there are spatial gaps in the distributions of the PAs and vertebrate diversity (Supplementary Figs. 12–13). In fact, many regions with high biodiversity, such as in the Nepal–India and Bhutan–India borders, have not been covered by any PAs. Furthermore, PAs are intended to be established to prioritize charismatic and threatened species[34], which thus could be one possible explanation for the higher coverage of threatened species than that of common species. However, the diversity distribution patterns could differ between the threatened and non-threatened species[35], PAs targeted to some threatened species may not have covered other species. Thus, we suggest that common species also need attentions as a previous study on European birds found that common species are facing rapid populations decline without effective conservation[36].

We observed a positive relationship between national governance level and PA's coverage of species ranges in transboundary areas. A potential explanation is that the national governance level can reflect the government commitment to biodiversity conservation, ensuring that protection is targeted to locations where it is most needed[37]. Our results showed that the PA coverage of species ranges decreases with human population density and cropland expansion across all continents. It may be explained by the fact that PAs are deliberately established in regions that are peripheral to economic activities, as there are trade-offs between biodiversity conservation and local livelihood demand[38,39]. Notably, recent studies show that the global human populations are increasing in transboundary areas[40]. This is especially true for many developing countries in Southeast Asia, such as India, Myanmar, Malaysia, and Vietnam, where we also found the lowest PA coverage across the globe. These regions, which harbor high biodiversity[1], could provide significant conservation gains if well protected. However, expanding protected areas there could increase conflicts, due to the economic growth requirements for local development. We suggest that future planning needs to balance biodiversity conservation with maintenance of ecosystem services for human well-being[41] and include other effective area-based conservation measures (OECMs) in transboundary conservation, which has been suggested as a good pathway to achieve 30 by 30 goal in the Kunming-Montreal Global Biodiversity Framework[42].

Our results also showed that collaboratively governed and local indigenous community-managed PAs performed better than other PAs, emphasizing the necessity to recognize tenure rights and

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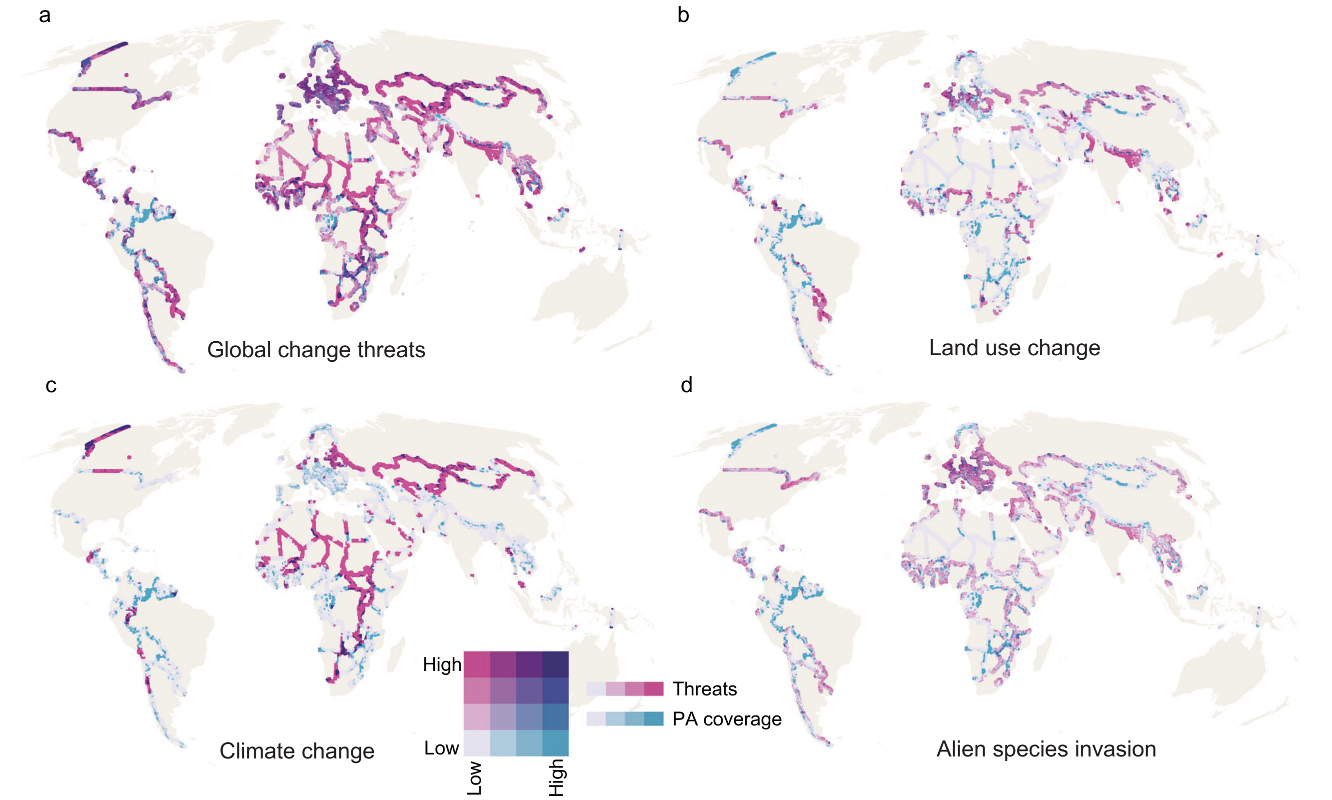

Fig. 5 | Global change threats and protected area (PA) coverage of species ranges in transboundary areas. Maps showing spatial patterns of the PA coverage of species ranges and the overall global change threats intensity (**a**), land use change (**b**), climate change (**c**), and alien species invasion (**d**) in transboundary areas. Darker colours correspond to higher threats based on quantile classes. Source data are provided as a Source Data file.

empower local communities in planning and management of PAs[43,44]. One potential explanation is that indigenous people often have deep spiritual and cultural ties with their land, which represent one of the oldest forms of conservation units[43]. Indigenous lands are increasingly recognized as critical for global biodiversity maintenance[45]. For example, Amazon indigenous lands with sustainable production systems were as effective as traditional PAs for medium- and large-sized vertebrates, including the emblematic jaguar, which moved across geopolitical borders[43]. In addition, recent studies show that PAs based primarily on enforcing penalties can be less effective than PAs where indigenous people and local communities are willing to engage in management[44].

Border areas are often hotspots of global armed conflicts, and a recent study showed that border conflicts accounted for 48.6% of the total global conflicts between 1992 and 2020[9]. Indeed, we detected a negative correlation between the frequency of armed conflicts and the percentage of species ranges covered by PAs especially in Africa. Armed conflicts can lead to direct biodiversity destruction and severe, immediate and long-lasting land-use changes such as forest loss[9,46]. The strongest negative effects are currently found in regions such as Crimea (Russia–Ukraine) and the Middle East (Israel–Palestinian Territories), which are experiencing armed conflicts that will pose a significant challenge for transboundary conservation[47]. Hopefully, we found that PA coverage of species ranges increased with bilateral cooperation ability. We notice that there have been some regional cross-boundary conservation initiatives (see Supplementary Table 12), which could serve as a promising way to protect transboundary biodiversity[48]. For example, the cross-border PA by Nicaragua and Costa Rica is one typical representative of a series of neighboring collaborations after decades of war in Central America[49].

We finally found that transboundary PAs are also facing higher threats from global change challenges than non-transboundary areas. This is especially for some tropical and subtropical regions, which are among the most biologically and culturally diverse regions of the earth[1]. Interestingly, we also observed global change pressures in some well protected regions such as western Europe. An explanation could be that European PAs are intentionally established in high-pressure areas as a "reactive" approach to protect threatened species in highly anthropogenic regions[50]. Border fencings might further exacerbate the global change threats, as they could make the range shifts of species tracking climate change or land use changes, more difficult in transboundary areas[5]. To safeguard PAs as effective refugia for biodiversity in transboundary areas, we suggest that active management may need to be prioritized towards PAs under global change threats.

We acknowledge that there are still some caveats in our present study. For example, many of IUCN maps may stop at the country boundaries due to limited understanding and lack of survey efforts in these areas. To address this potential issue, we conducted supplementary analysis by excluding those species with range maps stopping at the country boundaries and we obtained similar results (Supplementary Fig. 14), indicating that our findings may not be influenced by the potential IUCN range map limits.

The current Post-2020 Global Biodiversity Framework calls for a more ambitious expansion of PAs (covering 30% of land and sea by 2030)[51], which is considered key to prevent biodiversity loss. Our results indicate that PA expansion can consider not only the absolute area[12,32] but also need to pay attention to areas of particular concern, such as the border areas that are less protected but face more intense global change challenges than elsewhere. It thus requires imperative cross-national collaboration planning to achieve the win–win goal of biodiversity conservation and sustainable development.

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Methods

Protected area data

Terrestrial protected area data were derived from the February 2023 version of the World Database on Protected Areas (WDPA, accessible on: https://www.protectedplanet.net/en)[52]. In total, we had location data for 253,674 protected areas. We followed previous global studies[24] and the WDPA's recommendations (https://www.protectedplanet.net/c/calculating-protected-areacoverage) on cleaning data and used only the polygon boundary data layer. Point data layers, PAs without designated, inscribed, or established status, and the UNESCO Man and Biosphere Reserves were excluded from our analysis. We assigned PAs to each country based on the ISO3 code reported in the WDPA, which represents the country or territory in which the PA is located. For PAs that have more than one ISO3 code, we assigned the PA to each ISO3 code reported. The PA data were clipped to terrestrial areas, inland lakes and waterways by the polygons of Global Administrative Areas version 3.4 (GADM, 2020; https://www.gadm.org). For a few PAs lacking establishment time information, we randomly selected a year of establishment among PAs in the same country, following the approach used in previous studies[27]. Finally, we dissolved the overlapping polygons and retained larger areas for polygons with earlier establishment. Although there is variation in number of PAs in the WDPA, we did not include additional data from country-level or regional databases because the WDPA is the only authoritative dataset following globally consistent standards and is regularly validated and updated to maintain the highest data quality[21,53].

Species distribution data

Data on the species distributions and global conservation status of terrestrial mammals ($n = 5577$) and amphibians ($n = 7231$) were obtained from the IUCN Red List of Threatened Species[54]. Bird distribution data ($n = 10,987$) were sourced from BirdLife International and Handbook of the Birds of the World[55], and reptile data ($n = 10,899$) were collected from Roll et al.[56,57]. These distributional maps represent the most comprehensive spatial databases for different taxonomic groups based on expert reviews, especially for spatial boundaries of the distributions of each species[24]. Following Titley et al.[3], we included only the parts of each species' ranges where the species was considered to be "Extant" or "Probably Extant" ("Presence" codes 1 or 2), where the species was native ("Origin" code 1), and where the species had breeding or resident ranges ("Seasonality" code 1 or 2). We did not account for subspecies. Species are classified according to their Red List conservation status as Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), or Data Deficient (DD). Species classified as either Extinct (EX) or Extinct in the Wild (EW) were excluded from the analysis. Species classified as VU, EN, or CR are classed as "threatened".

Border area identification

We used data from the GADM and identified a total of 330 national terrestrial borders worldwide based on unique ISO3 codes, excluding coastlines. In addition, we use data from the Ministry of Natural Resources' standard mapping service (http://bzdt.ch.mnr.gov.cn/; No. GS (2016) 1666) as a reference in matters related to territorial boundaries. Our analyses did not include the Antarctic areas, Australia and New Zealand as they do not share terrestrial neighboring borders. Following Thornton et al.[11], we created three distances namely 25 km, 50 km, and 100 km on both sides to border lines as buffer zones. Next, we overlaid these buffer zones with grid cells of 5 km × 5 km resolution to define candidate transboundary areas.

Protected area coverage across species ranges

We overlaid the terrestrial species polygons ($n = 34,694$) onto the grid cells identified as transboundary areas, and included species in our analysis if any part of their range overlapped with transboundary areas. Finally, we obtained a dataset consisting of 2943 amphibians, 4906 reptiles, 7710 birds, and 3480 mammals, which accounts for 54.9% of all the 34,694 terrestrial species. The average proportion of their distributional ranges overlapping the transboundary areas was ~30.39% (Supplementary Data 2). Specifically, 3251 (17.1%) species had ≥ 50%, and 1409 (7.4%) species had > 90% of their ranges in transboundary areas. For threatened species, these proportion were 41.8% and 26.2%, respectively. Overall, the threatened species have a greater proportion of distributional ranges (48.1%) than the non-threatened species (24.0%) in transboundary areas (Kruskal-Wallis test, $\chi^2 = 590.51$, $P < 0.001$, Supplementary Fig. 5a).

Next, we overlaid the distributional boundaries of each species with the boundaries of PAs to identify proportion of their transboundary ranges protected. All geospatial data processing was carried out in the Mollweide equal-area projection using ESRI ArcGIS Pro version 3.0.1 (https://www.esri.com/).

For each species, we calculated the mean coverage C_i using the following formula (1):

$$Ci = \left(\sum_j c_{ij}\right)/n \tag{1}$$

where c_{ij} is the coverage by PAs of species i in cell j and n is the number of cells that overlap with species i's ranges.

c_{ij} is calculated using the following formula (2):

$$\frac{area_{protected}}{area_{range}} * 100 \tag{2}$$

where area$_{protected}$ is the size of species transboundary range covered by PAs and area$_{range}$ is the size of species' transboundary range in the grid cell. For each gird cell, species range coverage by PAs was defined by evaluating the average of the transboundary ranges of all species in that grid that were covered by PAs.

To compare PA coverage of species ranges between transboundary areas and non-transboundary areas, we applied a resampling approach by randomly selecting 50,000 pairs of grid cells from transboundary areas and from non-transboundary areas, respectively, and this process was repeated 999 times[58]. The grid cells were selected either randomly (Random), or with similar land areas (i.e., within a deviation of 10%) covered by PAs (PA availability), sampling intensities (GBIF), mean species richness (Species richness), socioeconomic conditions (Night time light) or topographic complexity (data source and references in Supplementary Table 13) to control for variations in the sampling efforts reflected by different anthropogenic factors.

Sensitivity analyses

We used buffer distances of 25 km and 100 km to test whether our results were sensitive to the buffer distance used to calculate the coverage of species ranges by PAs in transboundary areas, and obtained qualitatively similar results to the analyses using 50 km (Supplementary Fig. 7a–b). We also repeated the analysis using 10 km × 10 km and 25 km × 25 km grid cells and obtained similar results to the analyses conducted using 5 km × 5 km grid cells (Supplementary Fig. 7c–d). As our results were robust to different buffer classes and grid sizes, we show the results using the 5 km × 5 km grid cells with a buffer zone of 50 km in the main text and provide the results of additional analyses in the supplementary materials.

Ecological and socioeconomic variables related with PA coverage of species ranges

To explain spatial variations in PA coverage of species ranges across global borders, we selected 10 variables, namely, topographic complexity, governance, cropland expansion, human development index

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(HDI, which captures elements of life expectancy, education, and wealth at the country level), human population density, frequency of armed conflicts, bilateral cooperation abilities, size, years of establishment, and IUCN categories of PAs, which are considered potentially important variables that influence the PA coverage of species ranges in transboundary areas (see Supplementary Table 14 for rationales). We do not aim to indicate causal relationships between the outcome and the factors but instead aim to understand how the PA coverage of species ranges might vary across different socioeconomic and environmental contexts.

The difference between the maximum and minimum altitudes was used to measure the topographic complexity, because higher altitude differences can create a wide variety of habitats and environmental niches[59], and thus more biodiversity protection is expected. The 'Zonal Statistics' function in ESRI ArcGIS Pro was applied to extract the highest and lowest points of these altitudes from EarthEnv (https://www.earthenv.org/) at a 1 km resolution[60] in each grid cell polygon defined as transboundary areas. We included cropland expansion as an indicator of land-use needs using data from Potapov et al.[17] which is a global time series cropland maps from 2000 to 2019 at a spatial resolution of 30 m (available at https://glad.umd.edu/dataset/croplands). Human development index (HDI) values were derived from the 2022 Human Development Report published by the United Nations of Development Programme (https://hdr.undp.org/content/human-development-report-2021-22), which is measured annually from 1990 to 2022. The mean governance score for each country was calculated based on the Worldwide Governance Indicators (WGI, 2023; https://www.worldbank.org/en/publication/worldwide-governance-indicators), which includes voice and accountability, political stability and absence of violence/terrorism, government effectiveness, regulatory quality, rule of law, and control of corruption[61]. Following previous studies[3,62], we first calculated the mean score for each indicator for each country and then calculated the mean governance score for each country between 1996 and 2021. Human population density data were from the GPWv4 database[63] (https://doi.org/10.7927/H4F47M2C), which included UN-adjusted estimates of human population density data for the years 2000, 2005, 2010, 2015 and 2020. We obtained data of frequency of armed conflicts from the UCDP Georeferenced Event Dataset (GED) Global version 23.1 (UCDP, 2023; https://ucdp.uu.se/downloads/), which was developed by the UCDP at the PRIO to provide data to a wide range of users on armed conflicts that have occurred since 1946[64,65]. To quantify bilateral cooperation abilities between each neighboring country pair, we used a parameter of "Goldstein score", to determine the extent to which neighbors have been cooperative in the past years[4]. The Goldstein score was quantified as ranging from -10 to 10, with larger values indicating a higher bilateral cooperation ability. Physical fencing distribution is a unique and crucial conservation threat in the transboundary areas[6]. We collected this variable from previous global reports with either fully fenced or under constructions. As physical fencings were mainly located in Eurasia, our supplementary analyses incorporating this variable were only conducted in Eurasia (Supplementary Fig. 15). For bilateral cooperation abilities and physical fencing distribution data, we used the 'spatial join' function in ESRI ArcGIS Pro to group the grid cells by neighboring country pair, and assigned the grid cells with the same values of the nearest neighboring country pair. Sizes, years of establishment, and IUCN categories of PAs were extracted from the WDPA database. Previous studies showed that large reserves were more effective than smaller ones in attracting investment in conservation interventions[66] and protect larger species[67]. We thus included PA size in our model, by assigning grid cells a value of the "GIS_AREA" of their intersected PA. For the protection level of PAs, following the previous approach[13], we categorized PAs into two general levels: "strict" PAs (IUCN categories I–IV), which are well suited for protecting biodiversity and restricting human activities, and "multiple-use" PAs (IUCN categories V–VI and uncategorized), which permit multiple land uses and resource extraction.

One potential issue with the predictors we used is that there might be differences in the establishment time of PAs and the period of the predictors calculated (i.e., HDI, cropland expansion, human population density and bilateral cooperation ability). Therefore, we extracted the time-related predictor values for each 5 km × 5 km grid for the same period of time when a PA was established. For country-level HDI and governance score, we first identified the grid cells overlapping with the PAs and then extracted and calculated the mean values of HDI and governance score with the same period when the PA was established for each grid cell. For human population density data, we obtained data of the nearest year to the PA establishment for each grid cell.

All continuous predictor variables were normalized (scaled to mean = 0, s.d. = 1) to allow a direct comparison of effect sizes[68,69]. One potential issue in our data analysis is that PA coverage might be dependent on the variation in species richness among regions. To evaluate PA coverage by correcting for the effect of species richness, we first fitted a linear model of PA coverage as a function of species richness. Species richness indeed had a positive relationship with PA coverage (Linear Model, estimate ± SEM, $6.7 \times 10^{-4} \pm 2.5 \times 10^{-6}$, $F_{1,363214} = 71{,}160$, $P < 0.001$). We then extracted the residuals from the model above as a response variable for the further analysis. Species richness was measured as the number of species in each grid cell and was determined by overlaying IUCN range maps of all species recorded with grid cells. Each grid cell was assigned a country identity and neighboring country pair using 'spatial join' function in ESRI ArcGIS Pro. Autocorrelation between independent variables would lead to overfitting of models. Therefore, all continuous predictor variables were tested for multicollinearity (for all pairwise correlations, $-0.7 < r < 0.7$; see Supplementary Fig. 16). We applied linear mixed-effects models as implemented in the R package '*lme4*'[70] to identify the correlation of ecological and socioeconomic factors with PA coverage for species ranges. Species taxonomic class, country pairing, and country identity were included as random effects to account for the sample pseudoreplications. Specific to the taxonomic class, we calculated the proportion of species ranges protected in each grid cell for different taxa separately, and thus the species taxa information was identified into one of the four with an independent class ID. We then conducted a model averaging procedure to select the best model that explains species geographic ranges protected. To do this, we applied model selection analyses by generating all combinations of the initial variables using the dredge function of '*MuMIn*' package[71] and ranked them according to the information theory (Akaike's Information Criterion, AIC; see Supplementary Table 4 for the top models that were within 2 AIC units, i.e., $\Delta AIC < 2$). Our analyses were conducted at both the global scale and continental scale considering the fact that there might be regional heterogeneity in factors influencing the proportion of species ranges covered by PAs. All analyses were conducted in R version 4.2.0 (http://www.r-project.org).

As our analysis is based on grid analysis, we also conducted a sensitivity analysis to account for the potential problem of spatial autocorrelation on the estimation of regression coefficients by applying a generalized additive model using the R package '*mgcv*'[72] with the same combination of predictor variables as in the LMM plus a tensor product of the longitude and latitude of each grid cell. Furthermore, as relationships between predictor and response variables might be nonlinear, we conducted additional analyses by applying a random forest model using the R package '*randomForest*'[73] with the same combination of predictor variables as in the LMM. All analyses were conducted in R version 4.2.0 (http://www.r-project.org).

Global change threats to PAs at global borders

Threats from global changes can cause a large number of species to be threatened[14]. Here, we used the spatial overlap between the species ranges covered by PAs and threats from global changes to identify areas with high levels of human pressure but low PA coverage. We used global change maps from Bowler et al. 2020[25], which are cumulative indices of spatially explicit datasets of three major anthropogenic stressors: climate change, land use change, and alien species invasion. Climate change, as a recent and accelerating direct driver of biodiversity loss, has attracted attention in transboundary areas[3,74,75]. Other drivers, including land use change[16] and alien species invasion[21], also cause widespread biodiversity loss. These data were consisted of 11 associated variables[25] and were contained in numerical raster files at a spatial resolution of 100 km. All the raster files were resampled to a resolution of 5 km × 5 km to match the grid size used in the PA coverage analyses using a bilinear interpolation function that is widely regarded to be more realistic than the simpler nearest-neighbor method[76]. We calculated the mean global change threats for each grid cell by overlaying the grid cells with the anthropogenic stressors raster file. Grid cells were classed as impacted by the threat when they had a mean raster pixel value > 0. To compare the extent of global change threats to PAs between transboundary areas and non-transboundary areas, we applied the resampling approach as mentioned above again[58]. Then, we calculated the proportion of grid cells impacted by the global change threats.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Information files. The map data generated in this study using ESRI ArcGIS Pro version 3.0.1 are available in the Figshare database (https://doi.org/10.6084/m9.figshare.25627125). Source data are provided with this paper.

Code availability

Data analysis and plotting were processed with the "*tidyverse*", "*lme4*", "*MuMIn*", "*mgcv*", "*randomForest*", "*dplyr*", "*readxl*", "*tidyr*", "*ggplot2*", "*gghalves*", "*ggdist*" packages in R version 4.2.0. The R code to run the statistical analysis (Figs. 2 and 3) is available in the Figshare database (https://doi.org/10.6084/m9.figshare.25627125).

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