ECOLOGY

Global scale assessment of the human-induced extinction crisis of terrestrial carnivores

Erik Joaquín Torres-Romero[1,2]*, Timothy M. Eppley[3,4], William J. Ripple[5,6], Thomas M. Newsome[7], Miha Krofel[8], Neil H. Carter[9], Andrés Ordiz[10], Tadeu G. de Oliveira[11], Nuria Selva[12,13], Vincenzo Penteriani[14]

Human impacts on carnivores are a persistent conservation challenge worldwide. We present a global analysis showing the overlap of conservation lands and the cumulative impact of humans on the distribution ranges of 257 terrestrial carnivore species. Our findings reveal that 64% of carnivore ranges overlap with areas characterized by high human pressures. We found that Indigenous peoples' lands emerge as crucial for carnivore population viability, potentially safeguarding 26% of carnivore ranges globally, while protected and wilderness areas cover roughly 10 and 16% of carnivore ranges, respectively. These three areas combined cover 35% of the global range of carnivores. Reducing human pressure on conservation lands and managing them to protect carnivores are therefore critical, yet challenging. The extent of carnivore ranges outside these areas underscores the necessity to expand the network of conservation lands, which are a pivotal component of global conservation planning, alongside broader proactive species-specific conservation measures.

INTRODUCTION

Human impact threatens wildlife populations and is hastening the extirpation of numerous species (*1*, *2*). The gravity of this biodiversity crisis is underscored by alarming statistics, with extinction rates currently estimated to be 100 to 1000 times higher than Holocene background rates, a trajectory that may persist into the future (*3*, *4*). To illustrate the global challenge, among the 5400 vertebrate genera (excluding teleost fishes) comprising 34,600 known species, 73 genera (1.4%) have become extinct since 1500 CE, while it would have presumably taken approximately 18,000 years in the absence of human beings (*5*). The loss of wildlife is propelling us toward a critical juncture in the coexistence of human development and the preservation of ecosystem services provided by biodiversity (*2*, *6*, *7*).

Mammals currently grapple with a severe extinction crisis, with approximately a quarter of existing species at risk of extinction (*8*). Within this imperiled cohort, carnivore species stand out as one of the most diverse and widely distributed mammalian orders, inhabiting every continent and habitat type (*9*, *10*). The order Carnivora presents an exceptional range of body sizes, from the least weasel (*Mustela nivalis*) weighing around 50 g to the male polar bear (*Ursus maritimus*) tipping the scales at ≥300 kg of body mass (*11*, *12*). These species play a pivotal role in shaping the structure and function of diverse ecosystems, often carrying local cultural significance (*12*–*15*). However, this taxonomic group is particularly vulnerable to extinction, facing diverse threats from human activities [e.g., (*16*, *17*)], such as habitat loss due to deforestation and agricultural expansion [e.g., (*18*)], pressure from invasive and exotic species [e.g., (*19*)], and direct mortality resulting from legal hunting, poaching, trade, and retaliation arising from conflicts over domestic livestock (*20*–*22*). Especially vulnerable are the large carnivores (body mass > 15 kg) due to their large spatial requirements, increased sensitivity to human presence, disproportionally higher levels of human-caused mortality, and lower adaptability to such mortality linked with their apex trophic position during evolution (*12*, *15*, *23*).

Looking forward, the capacity of most carnivores to persist seems to be critically reduced by projections of increasing anthropogenic pressures on natural habitats, including the ongoing reduction of conservation lands worldwide (*14*, *24*–*27*). Conservation lands, i.e., areas of land managed and preserved for the protection and conservation of biodiversity, geological features, and cultural heritage, play a pivotal role in sustaining life on Earth (*28*, *29*). Yet, as natural habitats undergo fragmentation and transformation into human-modified landscapes, they become less suitable for carnivore population viability (*25*, *30*, *31*), as local populations diminish into smaller and isolated units. This phenomenon also heightens carnivore vulnerability to threats such as hunting, poaching, persecution, vehicle collisions, and human-wildlife conflicts (*29*).

Efforts to address pervasive habitat loss and transformation include establishing conservation lands. For example, there are ~250,000 terrestrial protected areas (PAs) covering 22 million km^2 (*32*), which are formally protected and designated for their natural, ecological, and associated cultural values, as defined by the International Union for Conservation of Nature (IUCN). In addition to the PAs, species protection is also bolstered by lands managed or owned by Indigenous people, which constitute the majority of recognized

[1]Ingeniería en Biotecnología-Universidad Politécnica de Puebla, San Mateo Cuanalá, Juan C. Bonilla, C.P. 72640 Puebla, México. [2]División de Biología, Subdirección de Investigación y Posgrado, Tecnológico Nacional de México, Instituto Tecnológico Superior de Zacapoaxtla, Carretera Acuaco-Zacapoaxtla Km. 8, Col. Totoltepec, C.P. 73680 Zacapoaxtla, Puebla, México. [3]Wildlife Madagascar, San Diego, CA 92106, USA. [4]Department of Anthropology, Portland State University, Portland, OR 97297, USA. [5]Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA. [6]Conservation Biology Institute, Corvallis, OR 97333, USA. [7]School of Life and Environmental Sciences, University of Sydney, Sydney, NSW 2006, Australia. [8]Biotechnical Faculty, University of Ljubljana, Jamnikarjeva 101, 1000 Ljubljana, Slovenia. [9]School for Environment and Sustainability, University of Michigan, Ann Arbor, MI 48109, USA. [10]Departamento de Biodiversidad y Gestión Ambiental, Área de Zoología, Facultad de Ciencias Biológicas y Ambientales, Universidad de León, Campus de Vegazana, 24071 León, Spain. [11]Department of Biology, Universidade Estadual do Maranhão, São Luís, Brazil. [12]Institute of Nature Conservation, Polish Academy of Sciences, Adama Mickiewicza 33, 31-120 Krakow, Poland. [13]Departamento de Ciencias Integradas, Facultad de Ciencias Experimentales, Centro de Estudios Avanzados en Física, Matemáticas y Computación, Universidad de Huelva, 21071 Huelva, Spain. [14]Department of Evolutionary Ecology, National Museum of Natural Sciences (MNCN), Spanish National Research Council (CSIC), Madrid, Spain.
*Corresponding author. Email: ejtr23@hotmail.com

terrestrial conservation lands, protected habitats, and ecologically intact landscapes globally (*33*). Presently, Indigenous peoples' lands (IPLs) cover at least ~38 million km^2 in 87 countries or politically distinct areas across all inhabited continents, representing more than a quarter of the world's land surface, and intersect with ~40% of all terrestrial protected areas and ecologically intact landscapes (*33*). Furthermore, approximately 30.1 million km^2, equivalent to 23.2% of terrestrial areas worldwide, are currently classified as "wilderness areas or wildlands" [henceforth, wilderness areas (WAs)] characterized by ecologically intact landscapes devoid of human pressures, with the majority located in North America, North Asia, North Africa, and the Australian continent (*34*). Although conservation lands play a pivotal role in sustaining life on Earth, persistent species loss suggests that these lands alone may be insufficient for safeguarding mammals such as carnivores amidst increasing human pressures (*27*, *29*). Therefore, there is a pressing need to assess how the geographic ranges of the world's carnivores overlap with human pressures and conservation lands to identify and address gaps in spatial conservation planning. Currently, the extent of terrestrial carnivore overlap with conservation lands and human pressures has not been comprehensively assessed at a global scale, or has been limited to a small number of species (*27*, *35*–*38*). This has hampered our understanding of which terrestrial carnivore species or taxonomic groups are most at risk of ongoing decline due to human pressures, as well as which conservation lands are best positioned to be managed for terrestrial carnivore protection.

We conducted a comprehensive global assessment to investigate the overlap between IPLs (*33*), PAs (*39*), and WAs (*34*) within the distribution ranges of terrestrial carnivore species worldwide. We also analyzed the combined extent of these three conservation land layers (i.e., IPLs, PAs, and WAs, hereafter referred to as "combined protected areas") within the distribution ranges of all extant terrestrial carnivore species. This overlap may highlight areas of particular importance for regional conservation and/or serve as larger core habitats for carnivore species. This assessment used data from the recently published database on the distribution ranges of 257 terrestrial carnivore species (*40*). In addition, we examined the composition of carnivore communities under different intensities of anthropogenic pressure, i.e., from low (coolspots) to high (hotspots) intensity of human impacts, by using the recently updated Human Footprint dataset (*41*). This layer integrates eight distinct types of human pressures, making it the most comprehensive and highest-resolution globally consistent dataset of anthropogenic threats (*41*), and serves as a valuable tool for monitoring environmental and biodiversity changes. This can offer important insights into macroecological patterns to guide conservation efforts (*42*). Thus, the Human Footprint encompasses many of the primary drivers of population decline and extinction risk within the ranges of species that are particularly vulnerable to collapse when their habitat is reduced or fragmented (*14*, *27*, *37*, *43*).

MATERIALS AND METHODS

Species distribution data

We collected data on the geographical range of all extant carnivore species from the IUCN Red List (http://iucnredlist.org, accessed June 2024), encompassing 297 carnivore taxa (*40*). These species are classified into 16 families within the Carnivora order: Mustelidae (64 species), Felidae (39), Canidae (38), Herpestidae (35), Viverridae (33), Phocidae (19), Otariidae (16), Procyonidae (14), Mephitidae (12), Eupleridae (10), Ursidae (8), Hyaenidae (4), Prionodontidae (2), Ailuridae (1), Nandiniidae (1), and Odobenidae (1). Each species was categorized based on the "Red List" classification system (if applicable): Not Evaluated, Data Deficient (DD), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the Wild, and Extinct (EX) (*40*). Information on population trends (i.e., declining, stable, increasing, or unknown) was also compiled from the IUCN (*40*). Our analyses excluded EX species and the marine pinniped families of Phocidae, Otariidae, and Odobenidae, resulting in a dataset relevant to 257 terrestrial carnivore taxa.

Global Human Footprint dataset

We acquired spatial data on human pressures from the recently updated global human footprint maps by Mu *et al.* (*41*). This layer captures the annual dynamics of the global Human Footprint, using eight variables to comprehensively cover various aspects of human pressures on the natural environment at a 1-km^2 resolution worldwide. These eight variables serve as proxies of diverse human pressures on nature for the year 2018, the most recent year available, each of them contributing insight from different aspects: (a) built environments, (b) human population density, (c) electric infrastructure, (d) croplands, (e) pasture lands, (f) roads, (g) railways, and (h) navigable waterways. Each footprint layer is scaled between 1 and 10 based on its estimated impact on the environment, where these scores are accumulated in each pixel to provide a total score out of 50 (*41*). Consequently, this layer currently stands as the most comprehensive global human pressure dataset available, capturing the greatest number of human modification indices, which may drive population decline in species and explain extinction risk in biodiversity (*44*, *45*).

Analyzing human pressure in species distributions

We overlaid the ranges of each species onto the Human Footprint map for 2018, using an equal area World Mollweide projection in ArcGIS 10.1 (*46*). This overlapping approach generated a dataset where each species had an area of its range composed of individual Human Footprint index values [ranging from low (coolspots) to high (hotspots) pressures, as described below]. Therefore, following Di Marco *et al.* (*47*) and Watson *et al.* (*34*), we established a threshold criterion by setting the human footprint score ≥ 4 to identify areas under intense human pressure, whereas a threshold of <4 identified low human pressure across ecosystems and biodiversity (*25*, *48*, *49*). A score ≥ 4 implies a substantial intensity of human activity in the ecosystems, rendering it no longer considered a natural environment (*25*, *34*, *47*). Recent analyses have reported that beyond this ≥ 4 threshold, animal species are critically threatened by habitat loss or fragmentation and are at a high risk of extinction (*49*).

We also considered five disturbance levels to determine the varying degrees of threat to carnivore ranges, classified according to the human footprint values (*42*). This classification method is as follows: a "no human disturbance" area has a human footprint of 0; a "low disturbance" area has a human footprint of 1 to 2; a "moderate disturbance" area has a human footprint of 3 to 5; a "high disturbance" area has a human footprint of 6 to 11; and a "very high disturbance" area has a human footprint of 12 to 50 (*42*). Therefore, a higher level of human footprint intensity indicates more intense human activities, implying that carnivore ranges will be more affected by human activities; "low" signifies a low intensity of the human footprint, where only negligible human activities can be observed. A region with a moderate-intensity human footprint is often considered an area where more adaptable carnivores can thrive within human-modified landscapes (*14*, *27*). The human footprint at this level mostly includes scattered rural settlements, pastures, cultivated land, and a moderate density of transportation facilities.

Analyzing conservation lands overlap with species distributions

The importance of PAs, IPLs, and WAs as a potential refuge habitat was evaluated. These three types of conservation lands have been considered of crucial importance in safeguarding biodiversity and maintaining natural ecological and biological processes within a landscape as they may contribute to defining biodiversity-related patterns and processes, such as preventing species population declines and the overarching extinction crisis (*14*, *27*, *33*, *36*, *38*, *43*). The three major spatial layers considered were as follows:

1) PAs: These are lands formally protected and designated for their natural, ecological, and associated cultural values, as defined by the IUCN (*39*). We included all 10 distinct PA categories (*39*): Ia—Strict Nature Reserve: Areas strictly designated to protect biodiversity and ecosystems, often with minimal human intervention, primarily for scientific research and monitoring; Ib—Wilderness Area: Areas that are mostly unmodified by human activity, aiming to protect their long-term ecological integrity and maintain their natural condition. They allow for low-impact recreation: II—National Park: Areas that prioritize conservation while allowing for substantial human recreation, such as tourism, provided it does not compromise ecological values; III—Natural Monument or Feature: Areas focused on protecting specific natural features or monuments, which may be landforms, sea mounts, geological features, or living features; IV—Habitat/Species Management Area: Areas where active management is required to protect particular species or habitats, often involving direct intervention or habitat manipulation; V—Protected Landscape/Seascape: Areas where the interaction between people and nature has shaped the landscape or seascape, emphasizing the integration of sustainable human practices to maintain the area's character and ecological value; VI—Protected Area with Sustainable Use of Natural Resources: Areas that emphasize the sustainable use of natural resources while also aiming to conserve ecosystems and habitats. Human activities are allowed, provided they do not degrade the natural environment and, last, Not Applicable, Not Reported, and Not Assigned: Categories used when specific IUCN management objectives are not available or defined for a particular protected area.

2) IPLs: This category includes terrestrial lands and spatial territories managed or owned by Indigenous nations or peoples. IPLs constitute an important portion of recognized terrestrial conservation land, habitat protection, and ecologically intact landscapes worldwide (*33*).

3) WAs: This layer identifies pristine areas where natural ecological and biological processes operate with minimal anthropogenic pressures and disturbances, such as large-scale landscape transformation, industrial activity, or infrastructure development (*34*). The latter differs from the "Ib—Wilderness Area-IUCN" classification, as "WAs" are based on recent human footprint data rather than formal designations (*34*, *41*). Each of these three conservation categories—IPLs, PAs, and WAs—has specific guidelines and objectives tailored to their level of protection and the type of human interaction allowed within the area (*33*, *34*, *39*).

To assess the effectiveness of conservation lands in protecting species, we calculated the spatial overlap between each carnivore species' distribution and each type of conservation land globally. All spatial data were analyzed using a Mollweide equal area projection in ArcGIS 10.1 (*46*). Specifically, we used a one-way analysis of variance to test for significant differences between the range sizes of species protected (i.e., inside) and those not protected (i.e., outside) by each type of conservation lands (i.e., IPLs, PAs, and WAs), and also tested for both human pressure categories [i.e., low (coolspots) to high (hotspots)].

RESULTS

Global hotspots and coolspots of human impacts on carnivore species

Hotspots of human impact on threatened and near-threatened carnivore species reveal critical regions predominantly in Southeastern Asia, the Sahel, portions of Eastern Africa, Northern India, and Southeastern South America (Fig. 1A). Families such as Canidae, Eupleridae, Felidae,

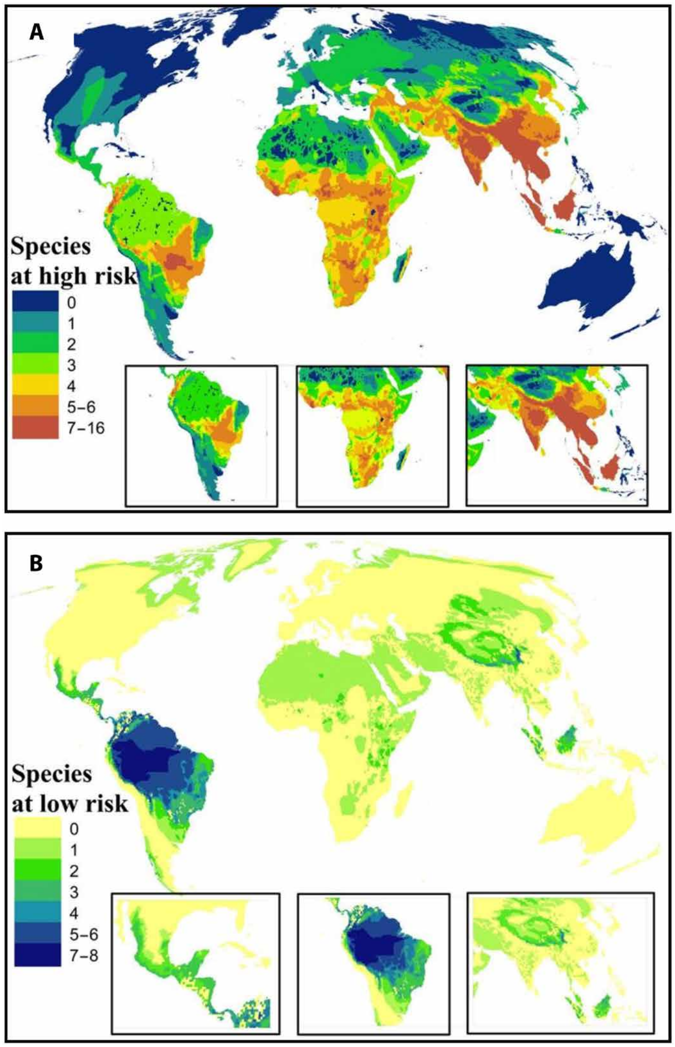

Fig. 1. Characteristics and distribution of the global carnivore hotspots and coolspots. (**A**) Global hotspots of high-risk human impact on threatened and near-threatened carnivore species. (**B**) Global coolspots of low-risk human impact on threatened and near-threatened carnivore species. Color ranges indicate the number of species in a grid cell affected by low to high human impacts on average range size ≥40%. Maps use a 50 km–by–50 km grid and a Mollweide equal area projection.

Herpestidae, Mustelidae, and Viverridae exhibited high vulnerability to human impact, underscoring their varying range sizes and sensitivities to threatening processes, despite co-inhabiting the same locations (Fig. 2). There is notable spatial heterogeneity in the intensity of threats for these families, particularly among the Neotropical, Afrotropical, and Indo-Malay regions (Fig. 2).

Coolspots, characterized by carnivore populations under lower human pressure, are mostly narrowly distributed, often encompassing areas with high topographic relief such as mountain ranges in México (i.e., the Sierra Madre Oriental and Occidental), parts of the Andes, the Amazon basin, parts of Eastern Africa, and parts of southeast and central Asia, including the Tibetan plateau, the Himalayas, and surrounding mountain ranges (referred to as High Asia) (Fig. 1B). These regions stand out as globally dominant with low human risk, with the Amazon rainforest emerging as the overwhelmingly predominant global coolspot, despite its ongoing habitat loss and fragmentation [e.g., (*50*)]. In addition, our findings highlight that, depending on the different sensitivities of carnivore species to human threats, coolspots for some species can also be risky hotspots for others. An example of this situation is represented by the Tibetan plateau, the Himalayas, Borneo, and Sumatra. These Asian regions, even if characterized by high species richness, also represent risky hotspots for those species more sensitive to anthropogenic threats. That is, while some carnivore species will be considerably affected by human presence and activities in certain regions, other sympatric species may be less affected.

Species distribution of carnivore species within global conservation lands

We found that within the global carnivore range of approximately 1575 million km^2, IPLs cover 26%, while PAs and WAs cover 10 and 16%, respectively. Overall, 35% of the global carnivore range overlaps

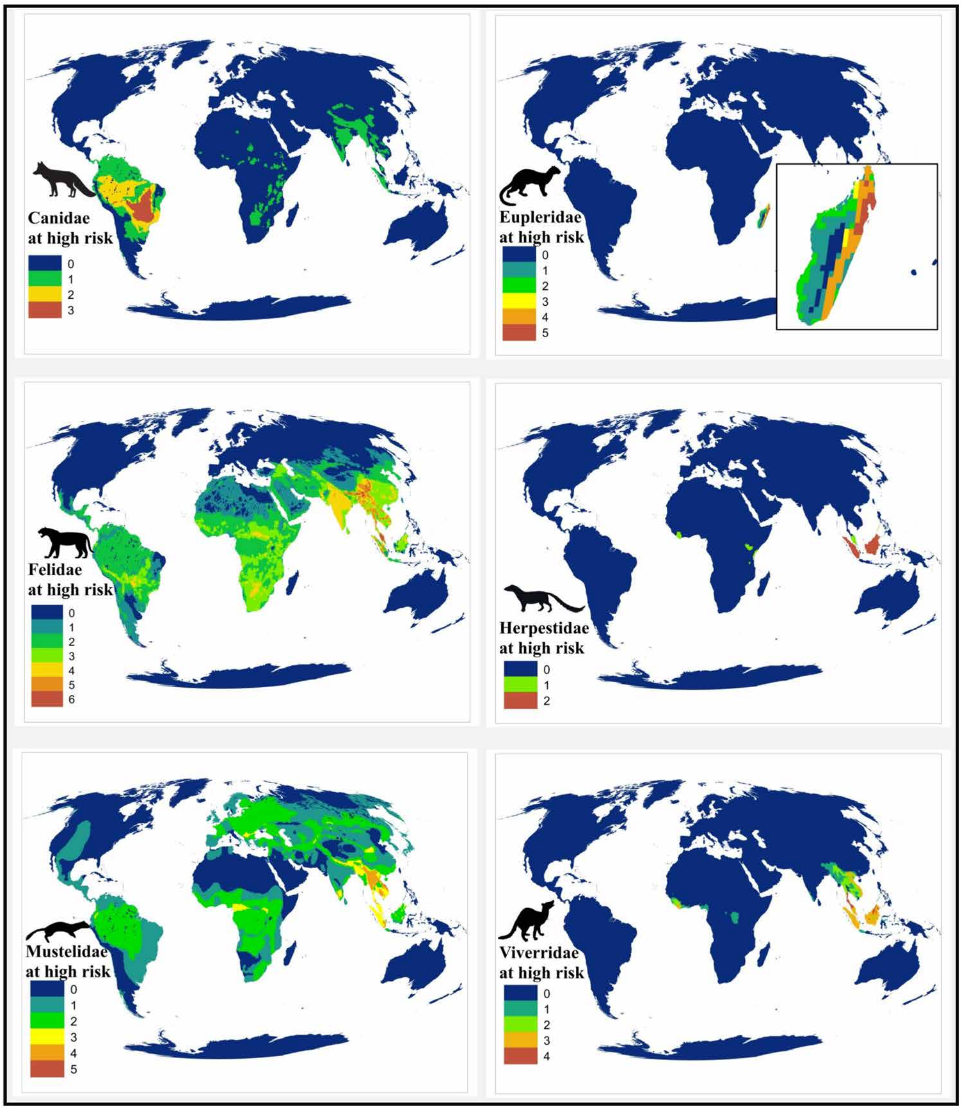

Fig. 2. Distribution of the global carnivore hotspots by families. Global hotspots of human impacts for threatened and near-threatened species within families such as Canidae, Eupleridae, Felidae, Herpestidae, Mustelidae, and Viverridae. Color ranges indicate the number of species in a grid cell affected by high human impact on total range size. Maps use a 50 km–by–50 km grid and a Mollweide equal area projection.

with a combination of all three conservation lands (i.e., combined protected areas: IPLs, PAs, and WAs). We found that 77 species (30% of all carnivores) had a minimal overlap (<20%) of their range situated on IPLs (Fig. 3A). We also found that 206 species (80%) exhibited minimal overlap (<20%) within PAs, while 113 species (44%) demonstrated minimal overlap (<20%) in WAs. Our findings also indicate that only 16 species (6%) exhibit substantial overlap (i.e., 60 to 80%) within IPLs. Similarly, two species (1%) show this level of overlap (i.e., 60 to 80%) with PAs, while four species (2%) overlap (i.e., 60 to 80%) with WAs (Fig. 3A). For instance, the Bornean ferret badger (*Melogale everetti*), classified as Endangered by the IUCN, is the sole species that completely overlaps (100% range) with IPLs. The Hose's civet (*Diplogale hosei*), classified as VU, overlaps with 97% within IPLs; the Tonkin weasel (*Mustela tonkinensis*), classified as DD, shares 95% overlap within IPLs; and the Borneo bay cat (*Catopuma badia*), classified as Endangered, overlaps by 91% within IPLs. Furthermore, Grandidier's vontsira (*Galidictis grandidieri*), also classified as Endangered, exhibits a 78% overlap within PAs. The African wild dog (*Lycaon pictus*), also Endangered, shows a 62% overlap within PAs. In addition, both the Tonkin weasel and the eastern mountain coati (*Nasuella meridensis*), also classified as Endangered, share a 60% overlap within PAs (see Fig. 3A). Overall, our results indicate significant differences (analysis of variance, $P < 0.05$) in the distribution range sizes of carnivore species across the three global conservation lands (IPLs, PAs, and WAs), depending on whether the ranges were protected (inside) or nonprotected (outside). Specifically, species exhibited a larger proportion of their geographical ranges outside of conservation lands.

Our analysis also revealed distinct range overlap patterns among the carnivore families. Specifically, the following families exhibited a substantial overlap (20 to 40%) within IPLs: Canidae with 11 species (31%), Felidae with 18 species (46%), Herpestidae with 16 species (44%), and Mustelidae with 23 species (37%) (Fig. 3B). On the other hand, we observed that most species have low overlap with PAs and WAs. Specifically, Herpestidae (30 species, 86%), Mustelidae (53 species, 84%), Canidae (30 species, 83%), Felidae (30 species, 77%), and Viverridae (28 species, 85%) each showed <20% of range overlap with PAs (Fig. 3C). As for WAs, Canidae with 17 species (47%), Felidae with 24 species (62%), Herpestidae with 14 species (40%), and Mustelidae with 31 species (49%) all exhibited <20% average range overlap (Fig. 3D).

Distribution of carnivore species from low to high human pressures

We found that 64% of carnivore species are associated with regions experiencing high human pressure, while 36% exhibit range overlaps with areas characterized by low human pressure (Fig. 4A). According to the classification of the IUCN Red List, both threatened (i.e., VU, Endangered, and CR) and nonthreatened (i.e., LC and NT) species have a similar proportion of their distribution ranges exposed to high human pressure (Fig. 4B). All carnivore families classified as threatened or near-threatened, such as Canidae, Eupleridae, Felidae, Mustelidae, and Viverridae, are exposed to elevated anthropogenic pressures, which are particularly intense for these groups (Fig. 4C). When categorizing the carnivore species by their population trend (i.e., unknown, increasing, stable, and decreasing), all

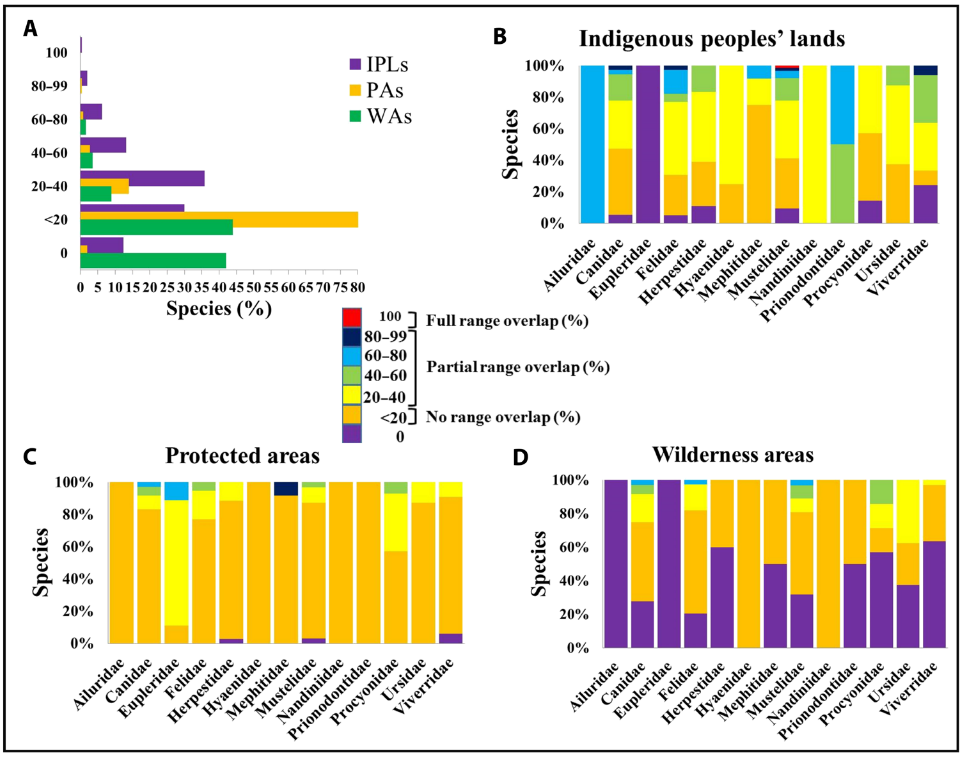

Fig. 3. Overview of range overlaps between conservation lands and carnivore species. (**A**) Overlap percentages between carnivore species distribution ranges and each of the three categories of conservation lands: IPLs, PAs, and WAs. Overlap percentages between carnivore species families within (**B**) IPLs, (**C**) PAs, and (**D**) WAs.

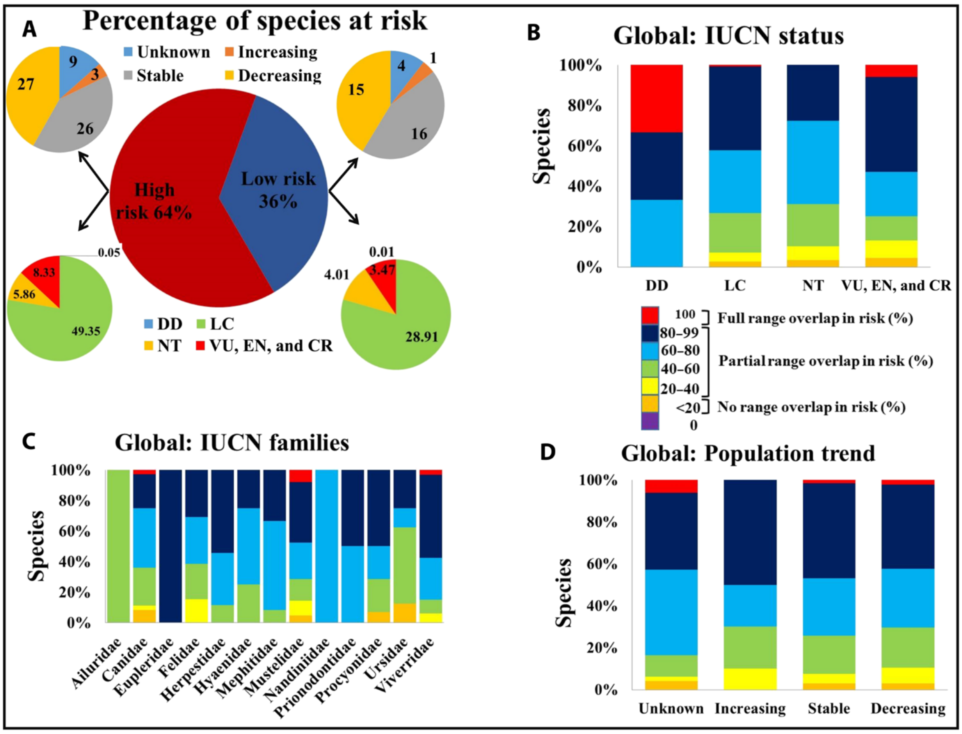

Fig. 4. Overview of range overlaps between human pressures and carnivore species. (**A**) The percent area of worldwide carnivore species distribution ranges that overlap with low to high human footprint, as well as the percentage of species whose range overlaps with their IUCN conservation category and their IUCN population trend. (**B**) Percent of carnivore species, grouped following their IUCN conservation categories (DD = Data Deficient, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, and CR = Critically Endangered), whose ranges overlap with different percentages of human impact. (**C**) Percent of carnivore species families ranges overlap with different percentages of human impact. (**D**) Percent of carnivore species, grouped following their IUCN population trend (Unknown, Increasing, Stable, and Decreasing) whose ranges overlap with different percentages of human impact. Source of IUCN data IUCN Red List (https://iucnredlist.org/).

categories have relatively similar overlap with areas characterized by partial to complete high human pressure. The highest risk is associated with populations categorized as decreasing, followed by populations showing stable, unknown, and increasing trends (Fig. 4D). Overall, our analysis at a global scale showed significant differences (analysis of variance, $P < 0.05$) in the geographic range sizes between low-impact (coolspots) and high-impact (hotspots) areas. Specifically, carnivore species inhabiting high-impact lands exhibited a larger proportion of overlap in their geographical ranges compared to those in low-impact areas.

Last, when considering the five disturbance levels of human footprint, our results reveal consistent patterns among carnivore species globally, as well as those grouped according to their IUCN population trend and IUCN conservation categories (DD, LC, NT, VU, EN, and CR), and grouped by families (Fig. 5, A to D). Specifically, the cumulative distribution of human footprint values within species' geographic ranges indicates that beyond the threshold of human footprint of ≥4, terrestrial carnivore species tend to have a wider range and are considerably more vulnerable, thus increasing the risk of extinction (Fig. 5, A to D).

Geographical distribution of conservation lands worldwide

Our results indicate that global conservation lands (i.e., IPLs, PAs, and WAs, collectively referred to as combined protected areas) cover approximately 60 million km^2. Of this, approximately 38 million km^2 corresponds to IPLs, 16 million km^2 to PAs, and 30 million km^2 to WAs. The East Palearctic and Nearctic regions contain the largest conservation land areas, each covering approximately 12 million km^2 (including IPLs, PAs, and WAs), followed by the Afrotropic and West Palearctic regions, with approximately 11 and 8 million km^2, respectively. The Neotropic and Australasia regions have similar coverage, with about 7.5 and 6 million km^2, while the Indo-Malay region accounts for only 3 million km^2 (see Table 1 and Fig. 6). In contrast, we found that the overlap between PAs and WAs is minimal in the Indo-Malay region, covering only 0.2% of the area, while the highest overlap occurs in the Neotropic region at 7%. A similar pattern was observed for PAs and IPLs, with only 0.4% overlap in the Afrotropic and Nearctic regions, whereas the Neotropic region has 8.5% of its area shared between these conservation land types. The highest percentage of overlap between WAs and IPLs was found in the East Palearctic (27.5%) and Australasia (17%) regions (see Table 1 and Fig. 6).

DISCUSSION

Our findings provide a comprehensive global-scale assessment of the worldwide spatial juxtaposition among terrestrial carnivores, conservation areas, and anthropogenic pressures. This evaluation holds particular significance given the precedence of vertebrate studies emphasizing the pivotal role of conservation lands in biodiversity preservation (*27*, *35*–*37*, *43*, *48*). Our findings provide valuable insights into landscape conservation planning for species with

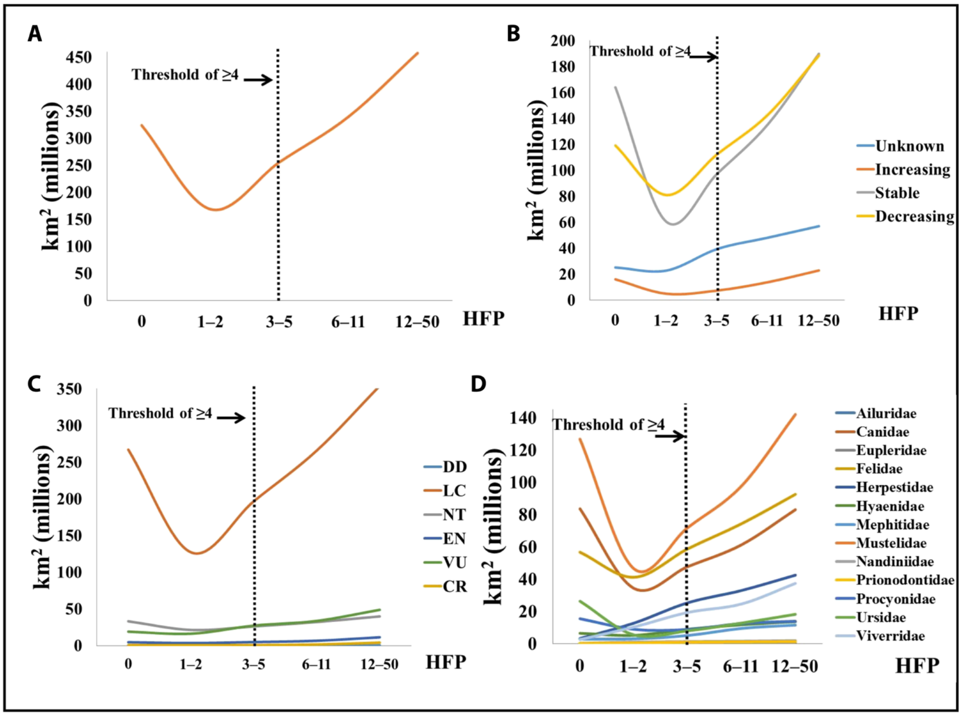

Fig. 5. Dispersal plot displaying the distribution range of global carnivore species across the human footprint gradient. (**A**) Cumulative extent of human footprint values within 257 carnivore species ranges. (**B**) Carnivore species grouped according to their IUCN population trend (Unknown, Increasing, Stable, and Decreasing). (**C**) Carnivore species grouped according to their IUCN conservation categories (DD = Data Deficient, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, and CR = Critically Endangered). (**D**) Carnivore species families whose ranges overlap with different intensities of human impact indices. The lines represent the average change in the overlap between carnivore species ranges in million square kilometers and human footprint values. Please note that the dashed line represents the threshold criterion by setting the human footprint score ≥ 4 to identify areas under intense human pressure, whereas a threshold of <4 identifies low human pressure across carnivore ranges.

Table 1. Global estimates of conservation land area coverage and terrestrial lands. Estimated distributional coverage (in million square kilometers) for each conservation land type, i.e., IPLs, PAs, and WAs, across biogeographical regions. Note: The intersection (∩) represents the area shared between two conservation land types (e.g., PAs ∩ WAs). Percentages (%) indicate the proportion of each region covered by conservation lands and the extent of overlap. Values may be approximate due to contested boundaries between conservation areas and terrestrial lands.

Regions	Land	PAs	WAs	IPLs	PAs ∩ WAs	PAs ∩ IPLs	WAs ∩ IPLs	PAs, WAs, and IPLs pooled
Afrotropic	25	3 (12%)	3 (12%)	8.5 (34%)	0.26 (1%)	0.1 (0.4%)	1.7 (6.8%)	11.1 (44.4%)
Australasia	9.3	2 (21.5%)	2 (21.5%)	4.4 (47.3%)	0.35 (3.7%)	0.55 (5.9%)	1.6 (17.2%)	6.1 (65.5%)
Indo-Malay	8.5	1 (11.7%)	0.1 (1.1%)	3 (35.2%)	0.02 (0.2%)	0.25 (2.9%)	0.07 (0.8%)	3.16 (37.1%)
Nearctic	23	3 (13%)	9.3 (40.4%)	3.4 (14.7%)	1.17 (5%)	0.1 (0.4%)	1.15 (5%)	12.11 (52.6%)
Neotropic	20	4.3 (21.5%)	3 (15%)	4 (20%)	1.4 (7%)	1.7 (8.5%)	1.29 (6.4%)	7.5 (37.5%)
East Palearctic	20.4	1 (4.9%)	7.3 (35.7%)	10 (49%)	0.13 (0.6%)	0.16 (0.7%)	5.6 (27.4%)	12.1 (59.3%)
West Palearctic	30.1	2 (6.6%)	4.4 (14.6%)	4.8 (15.9%)	1.18 (3.9%)	0.31 (1%)	2.16 (7.1%)	8.2 (27.2%)

extensive spatial requirements as well as for carnivores with small home ranges. This necessitates political and financial commitments for ambitious conservation strategies spanning local, regional, and continental scales, as well as connectivity strategies across the planet (*29*, *51*, *52*). Notably, areas designated as protected or with conservation status have proven instrumental for iconic species and other large mammals (*14*, *27*, *36*, *51*). Our study underscores the pivotal role of these designated lands in global biodiversity conservation. IPLs, PAs, and WAs emerge as arguably the most critical components of global conservation planning efforts, especially for carnivore populations and other vertebrates worldwide (*37*, *43*, *53*).

Conservation lands collectively cover crucial regions for safeguarding biodiversity worldwide (*14*, *34*, *36*, *54*). The significance of protected habitats in buffering animal populations against anthropogenic pressures is well documented, providing essential resources such as food, suitable resting/sleeping locations, and breeding

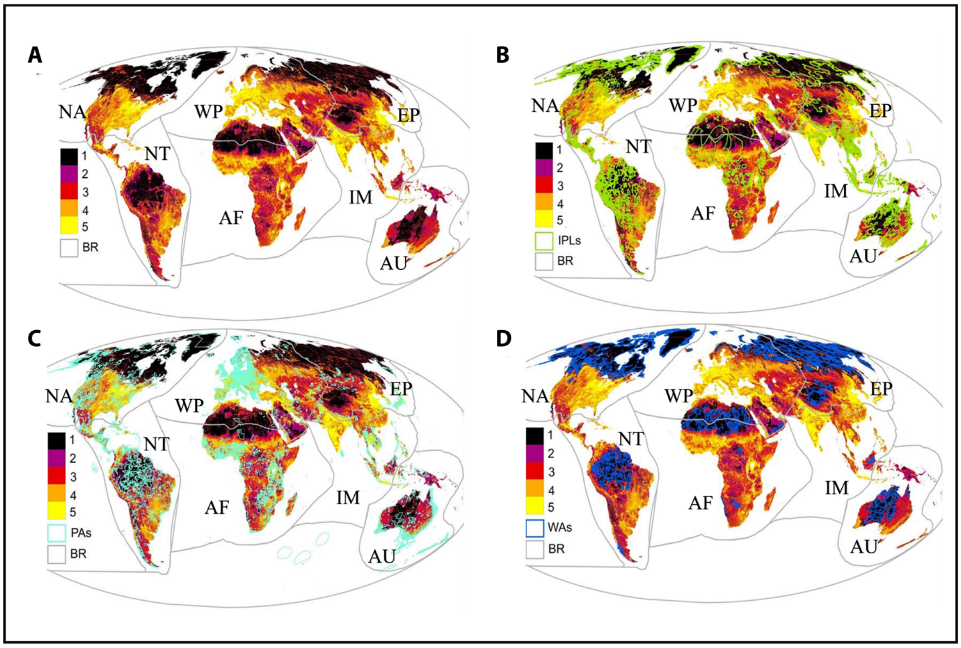

Fig. 6. Global biogeographical regions (BR) overlap with human footprint distributions, IPLs, PAs, and WAs. (**A**) Map showing the distribution of human disturbance levels worldwide, where levels are categorized as follows: (1) no human disturbance, (2) low human disturbance, (3) moderate human disturbance, (4) high human disturbance, and (5) very high human disturbance, according to Venter *et al.* (*42*). (**B**) Map of the distribution of human disturbance levels alongside IPLs. (**C**) Map of the distribution of human disturbance levels in relation to PAs. (**D**) Map of the distribution of human disturbance levels along with WAs. For this spatial analysis, PAs were not divided into their different categories; instead, all categories from I to VI, as well as those marked as not applicable, not assigned, or not reported, were considered as a single group. Note that the resolution may be approximate due to contested boundaries between IPLs, PAs, and WAs. The abbreviations for biogeographical regions are as follows: Afrotropical (AT), Australasian (AU), Nearctic (NA), Neotropical (NT), Indo-Malayan (IM), West Palearctic (WP), and East Palearctic (EP).

opportunities (*35*, *36*, *38*, *43*, *48*). For instance, global primate species research, distributed across 91 countries primarily in the Neotropic, Afrotropic, and Indo-Malayan realms, revealed that IPLs contribute to 30% of the primate range, hosting 71% of primate species (*36*). Similarly, O'Bryan *et al.* (*35*) emphasized the substantial impact of IPLs on terrestrial mammals, reporting that 473 (47%) threatened species occurred on IPLs, with 26% having more than 50% of their habitat on these lands. Consistent with these findings, Torres-Romero *et al.* (*38*) highlighted the critical role of PAs and IPLs, constituting 30% of essential landscapes for jaguars (*Panthera onca*) across their range.

Our results reveal that IPLs (26%), PAs (10%), and WAs (16%) cover equal to or less than a quarter of the potential habitats of the world's carnivores. Despite this, all three types of conservation land collectively account for 35% of carnivore ranges, playing a vital role in maintaining relatively intact landscapes for these species. However, in recent decades, anthropogenic pressure on global conservation lands and otherwise intact forest habitats has accelerated (*18*, *25*, *55*). The year 2019, for instance, witnessed devastating bushfires, affecting approximately 308,048 km^2 of the Amazon Basin, nearly 70% more than the previous year and affecting large portions of Brazil, Venezuela, Bolivia, and Colombia (*56*). Likewise, the 2019/2020 megafires in Australia burnt approximately 97,000 km^2 of vegetation across southern and eastern Australia, of which a large proportion was forests and woodlands (*28*). This is in addition to heightened pressures linked to both local and global economic demands, driving the expansion of agricultural and livestock activities, also inside PAs, and leading to deforestation and substantial biodiversity loss (*57*–*60*). Global forest loss is attributed mostly to deforestation through permanent land use change for commodity production, followed by forestry and shifting agriculture (*61*). There is an urgent need for comprehensive conservation strategies to address the escalating threat of the ongoing mass extinction. Projections of population growth suggest that Asia will remain one of the most densely populated continents until the mid–21st century, with African countries surpassing Asian populations by the end of the century (*62*). The adverse impacts of human population growth are magnified by concurrent infrastructure development, especially the expansion of roadways and the subsequent increase in traffic volume, which can result in both direct mortality and limit species movement (*63*, *64*). This demographic shift accentuates the increasing significance of understanding and mitigating human impacts on carnivore species, particularly those with small and restricted ranges or population sizes <1000 individuals, which are inherently more vulnerable and facing imminent extinction (*65*).

While our findings raise notable concerns, a glimmer of hope remains [see (*66*)]. The threats identified are not insurmountable, and the potential for mitigation exists through in situ conservation actions [e.g., (*67*–*69*)]. Addressing these challenges mandates the expansion of conservation lands, emphasizing the urgent need for a decree to allocate additional territories for conservation purposes (*70*), alongside supporting the mainstream adoption of area-based conservation to achieve the 30 × 30 target of conserving at least 30% of Earth's surface by 2030, thereby helping to mitigate the unprecedented rate of biodiversity loss threatening ecosystem function and the vital contributions of nature to human life (*71*). Furthermore, recognizing and promoting effective management practices within diverse societies over their territories is pivotal (*72*). One promising strategy involves advocating for the establishment of voluntary conservation areas, even within partially anthropized systems, as demonstrated by designated conservation areas in México (*73*). In light of these considerations, comprehensive continental, regional, and local carnivore conservation planning becomes essential. This planning should integrate the diverse human biomes used by these species to facilitate dispersal and connectivity between protected and nonprotected areas to sustain the permanent presence of carnivores within the human-modified matrix (*27*, *38*, *50*, *74*).

Focusing conservation efforts on the identified hotspots and coolspots of human pressure can lead to a tailored approach toward conserving areas with exceptionally high threatened carnivore species richness characterized by species-specific threats. Proactively securing coolspots as refugia and preventing initial human impacts in these areas can considerably enhance conservation outcomes (*75*, *76*). This strategic approach not only may benefit the targeted species but also could contribute to the overall long-term persistence of many other animal and plant species—an imperative need in the face of the rapidly accelerating human-driven extinction crisis. Therefore, as we navigate this era of heightened extinction risk, safeguarding areas free from threatening processes, even those extensively transformed by anthropogenic activities, and understanding interspecific interactions hold substantial value for the persistence of carnivore populations in the 21st century. This is particularly true if coexistence frameworks are adopted or implemented (*26*, *27*, *72*).

A crucial consideration in interpreting our findings is the limitation inherent in the human footprint data because such data do not encompass all direct pressures affecting biodiversity, such as climate change, pollution, infectious diseases, overexploitation, invasive species, hunting, trapping, and illegal killings (*25*). This renders our assessment a conservative estimate of the true pressure faced by carnivore species, implying that the actual impact on many species may be more severe than depicted in our maps (Figs. 1 and 2). Nevertheless, certain indirect pressures, including overexploitation through hunting, poaching, pollution, human disturbance, utility lines, and invasive species, are indirectly captured through proxies like human population density and accessibility created by roads and navigable river networks within the Human Footprint dataset (*76*–*79*).

While acknowledging the conservative nature of our results, it is noteworthy that several carnivore species exhibit resilience within anthropogenic landscapes, such as agricultural and managed forestry lands, provided it does not detrimentally affect their prey populations or result in intense persecution of carnivores [e.g., (*14*, *24*, *27*)]. Large carnivore persistence in human-modified landscapes, such as those that currently characterize Europe, illustrates that carnivores may even thrive outside protected areas, but they may largely depend on connectivity between areas with low human pressure and intact wilderness zones (*80*). For example, brown bears (*Ursus arctos*) in Norway rely on females traveling from wilderness areas in Sweden (*81*), and the distribution of the Eurasian lynx (*Lynx lynx*) is closely associated with protected areas in central Europe (*82*). Furthermore, effectively preventing human-carnivore conflicts is crucial for the persistence of large carnivores (*83*) and can support their recovery even in human-modified landscapes (*84*). At a global scale, the abundance and distribution of large carnivores are positively correlated with the presence of protected areas (*85*), though their surroundings often act as population sinks (*86*). This phenomenon is likely due to habitat degradation, disturbance, lower prey availability, or higher poaching rates outside protected areas (*82*).

Conserving large carnivores within protected areas is not an easy task (*87*). In northern Sweden, for instance, where the main prey of large carnivores is semi-domestic reindeer (*Rangifer tarandus*) owned by the Indigenous Sámi community, illegal poaching of brown bears, Eurasian lynx, and wolverines (*Gulo gulo*) was higher inside the national parks than in surrounding, unprotected areas (*88*). This case illustrates that some PAs have diminished conservation value, even becoming "paper parks" (*53*). Aside from large carnivores, a considerable portion of the world's threatened or NT carnivore species are smaller bodied and often encounter distinct challenges. These challenges include negative top-down impacts of larger carnivores, which can sometimes exceed carrying capacity, especially in smaller fenced reserves (*89*).

Among the most threatened small carnivores are the Eupleridae of Madagascar, which also represent one of the least studied carnivore families worldwide (*14*, *90*). Euplerids exhibit the highest range overlap between species ranges and protected areas among all carnivore families. However, management efforts to protect biodiversity within PAs in Madagascar are highly variable, despite their critical importance for effective long-term species conservation (*91*, *92*). Like most carnivores, euplerids are adversely affected by habitat degradation and fragmentation, the presence of nonnative/exotic carnivores (e.g., feral dogs and cats), disease, hunting, and retaliatory killings, even within PAs (*93*). Their populations have been observed to decline rapidly as human encroachment drives the colonization of exotic carnivores (*94*).

We observed variations in the exposure of carnivore ranges to different proportions of intense human-modified land-use types (Figs. 3 to 5). This aligns with a growing body of evidence suggesting that some large carnivores strategically select sites with higher prey biomass, potentially intensifying human-carnivore conflicts due to depredations on livestock and pets, especially in the absence of natural prey and suitable habitat (*95*–*97*). It is important to recognize that species residing in more human-modified habitats may experience lower population density, smaller home ranges, altered reproductive rates, and substantial behavioral changes compared to their counterparts in more natural habitats (*12*, *98*). Furthermore, the illegal killing of large carnivores is a major issue both inside and outside of protected areas, often stemming from inadequate law enforcement (*82*, *88*). Reducing human-caused mortality, which affects many large carnivores globally (*27*, *86*), is therefore an essential conservation strategy. Effective law enforcement supports the expansion of large carnivore conservation efforts even in areas with high human densities (*99*). Other strategies focus on spatial and/or temporal separation of carnivores from humans and their property (e.g., livestock) to prevent conflicts [see (*100*)]. Zoning areas for specific purposes can help prevent conflicts and support conservation (*101*, *102*), though this approach may not always be feasible or affordable (*103*). In some areas, implementing livestock depredation compensation systems may be a more effective conservation measure (*104*). Ultimately, the feasibility and implementation of various actions must be tailored to different ecosystems, species, and social contexts (*100*).

Involving local human communities in the conservation and management of carnivores is highly desirable. This seems particularly relevant in IPLs, where a notable overlap with carnivore occurrences has been observed. In some areas, Indigenous communities contribute to monitoring large carnivores. For instance, in Kenya, Maasai warriors assist in counting African lions (*Panthera leo*), help prevent livestock depredation, and discourage local lion killings, which benefits both lion conservation and community engagement (*105*). Similarly, in Sweden, cooperation between scientists and Sami reindeer herders has facilitated the assessment of the economic feasibility of various measures to prevent or compensate for carnivore depredation on reindeer (*103*). These examples demonstrate that combining scientific approaches with Indigenous knowledge can be effective for biodiversity conservation (*106*).

We acknowledge that other important factors, beyond the percentage of protected land, are crucial for the conservation of some carnivore species [see (*107*, *108*)]. These factors include the level of land protection, habitat quality, its specific characteristics, the species' natural history traits (e.g., generalist or specialist), and interspecific intraguild relationships and their dynamics. Such factors can meaningfully affect species occurrence, population size, and the effectiveness of conservation efforts (*90*, *109*–*111*). For example, the savanna tiger cat (*Leopardus tigrinus*) exemplifies this issue. Its populations are declining due to rapid habitat loss and fragmentation from agricultural expansion within the core of its range, compounded by disease transmission from domestic and feral carnivores. This species consistently shows very low population densities, particularly within protected areas, owing to the prevalent negative impacts within these areas. Consequently, the species' protection often extends beyond protected areas, into regions where wilderness areas or wildlands no longer exist. Combined with its habitat-specific needs and low autosomal heterozygosity, this places the species in a highly vulnerable position (*109*, *111*) and necessitates targeted conservation efforts.

For species affected by dominant interspecific predators, such as the ocelot (*Leopardus pardalis*), a felid of the Neotropics that typically does not attain viable populations inside protected areas, conservation efforts should largely focus on nonprotected areas (*110*, *112*). Effective conservation of small- to medium-sized cats on nonprotected private lands is therefore crucial. For example, the savanna tiger-cat's range is predominantly located in Brazil, with its core habitats situated within the rapidly diminishing savanna formations of the country's agricultural frontier. Consequently, conservation planning for this species requires specific planning. This includes public policy that mandates landowners to designate 35% of each property as untouched, integrating these areas into protected land and wilderness areas. Such measures would enhance connectivity among remaining areas in both forested and nonforested environments. The implementation of Brazil's "Rural Environmental Registry" will be pivotal in this endeavor (*111*).

Last, it is important to note that datasets such as the IUCN Red List, PAs, IPLs, and WAs, along with human footprint data, are continually evolving and being refined as additional information about species and human impacts becomes available (*32*–*34*, *41*–*43*, *113*, *114*). Furthermore, the data on IPLs in this study is known to not fully reflect the most accurate information regarding Indigenous self-determination in conservation (*115*). Addressing those inaccuracies in the data is important for future research on this topic. Enhancing the degree to which Indigenous peoples exercise self-determination in conservation can lead to more durable strategies for conserving carnivores and other wildlife. Overall, empirical tests have generally demonstrated reasonable concordance with some errors [e.g., (*41*, *113*, *116*)]. While unidirectional errors could potentially introduce bias, specific reasons for such bias have not been identified, nor have they been noted in the literature. Over the past several decades, IUCN data, along with global anthropogenic and landscape data, have been instrumental in establishing conservation and sustainable development standards. The ongoing refinement and updating of IUCN and other datasets will therefore make this type of work even more powerful and impactful.

The global distribution patterns of carnivore species across conservation lands reveal varying proportions, with IPLs being custodians of 26% of their range, PAs accounting for 10%, and WAs encompassing 16%, while these three types collectively safeguard 35% of the world's carnivore range. Although our results did not show a clear connection between species' conservation status and the proportion of their ranges within these conservation lands, these lands will play a pivotal role in the future global conservation of carnivore species. For example, they may serve as sources for carnivores expanding into less-protected areas (*27*, *80*). Urgent and enhanced support for conservation lands is still imperative to sustain carnivore populations, ensuring the persistence of habitats and species on a global scale (*14*, *27*, *72*, *117*). Current trends in the loss of natural habitats pose a serious threat to these species, risking local, regional, or even global extinction, particularly when conservation lands contain only a small proportion of their protected populations (*22*, *33*, *34*). Given the escalating human influence on the planet, time and space are rapidly diminishing for carnivore species, necessitating prioritized actions against intense human pressures. Our analyses suggest that 36% of global carnivore species overlap with areas characterized by low human pressure, while 64% are linked to regions experiencing high human pressure. Among these high-pressure regions, species classified as threatened or near-threatened by the IUCN—particularly within the families Canidae, Eupleridae, Felidae, Herpestidae, Mustelidae, and Viverridae—exhibit high vulnerability to human impact. This vulnerability is largely determined by the proportion of their habitat exposed to increasing human pressures, which elevates their extinction risk worldwide. Our analytical framework enables the mapping of diverse intensities of human impacts, presenting an original approach for delineating various levels of human influence in conjunction with conservation areas on species distributions at a global scale. This conceptual advancement in cumulative pressure mapping on world carnivore species can apply to any scale or taxa. Looking forward, the long-term survival of more than half of Earth's carnivore diversity demands a coordinated approach that encompasses efforts to protect biodiversity beyond conservation lands. An ambitious and strategic program is essential for establishing and managing an expanded protected-area system, enhancing the number and connectivity between protected and unprotected areas. Such initiatives should aim to facilitate the movement of carnivore species while concurrently safeguarding other endangered species and enriching the functioning of extensive ecological communities or entire ecosystems, where large carnivores can serve as apex predators, keystone species, and connectivity umbrellas [e.g., (*21*, *27*, *118*)]. This integrated strategy is crucial for securing the enduring existence of Earth's diverse carnivore populations in the face of unprecedented human pressures.

REFERENCES AND NOTES

1. R. Dirzo, H. S. Young, M. Galetti, G. Ceballos, N. J. Isaac, B. Collen, Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
2. R. H. Cowie, P. Bouchet, B. Fontaine, The sixth mass extinction: Fact, fiction or speculation? *Biol. Rev.* **97**, 640–663 (2022).
3. G. Ceballos, P. R. Ehrlich, A. D. Barnosky, A. García, R. M. Pringle, T. M. Palmer, Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Sci. Adv.* **1**, e1400253 (2015).

4. J. M. De Vos, L. N. Joppa, J. L. Gittleman, P. R. Stephens, S. L. Pimm, Estimating the normal background rate of species extinction. *Conserv. Biol.* **29**, 452–462 (2015).
5. G. Ceballos, P. R. Ehrlich, Mutilation of the tree of life via mass extinction of animal genera. *Proc. Natl. Acad. Sci. U.S.A.* **120**, e2306987120 (2023).
6. W. J. Ripple, C. Wolf, T. M. Newsome, M. Galetti, M. Alamgir, E. Crist, M. I. Mahmoud, W. F. Laurance, 15,364 scientist signatories from 184 countries, World scientists' warning to humanity: A second notice. *BioScience* **67**, 1026–1028 (2017).
7. R. Dirzo, G. Ceballos, P. R. Ehrlich, Circling the drain: The extinction crisis and the future of humanity. *Phil. Trans. R. Soc. B* **377**, 20210378 (2022).
8. C. Hilton-Taylor, D. Brackett, The IUCN Red List of Threatened Species (2000), p. 6.
9. E. Eizirik, W. Murphy, K. Koepfli, W. Johnson, J. Dragoo, R. Wayne, S. O'Brien, Pattern and timing of diversification of the mammalian order Carnivora inferred from multiple nuclear gene sequences. *Mol. Phylogenet. Evol.* **56**, 49–63 (2010).
10. D. Wilson, R. Mittermeier, J. Hoyo, P. Cavallini, T. Llobet, *Handbook of the Mammals of the World: Carnivores* (Lynx, ed. 1, 2009), vol. 1.
11. L. Hunter, P. Barrett, *Carnivores of the World* (Princeton Univ. Press, ed. 2, 2019).
12. W. J. Ripple, J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, A. J. Wirsing, Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484 (2014).
13. J. Terborgh, L. Lopez, P. Nuñez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, L. Balbas, Ecological meltdown in predator-free forest fragments. *Science* **294**, 1923–1926 (2001).
14. E. J. Torres-Romero, A. J. Giordano, Impact of the Anthropocene on the status of the world's small carnivores: A global macroecological perspective. *J. Biogeogr.* **49**, 916–929 (2022).
15. T. M. Williams, J. A. Estes, D. F. Doak, A. M. Springer, Killer appetites: Assessing the role of predators in ecological communities. *Ecology* **85**, 3373–3384 (2004).
16. C. Marneweck, A. R. Butler, L. C. Gigliotti, S. N. Harris, A. J. Jensen, M. Muthersbaugh, B. A. Newman, E. A. Saldo, K. Shute, K. L. Titus, S. W. Yu, D. S. Jachowski, Shining the spotlight on small mammalian carnivores: Global status and threats. *Biol. Conserv.* **255**, 109005 (2021).
17. A. Helman, A. Zarzo-Arias, V. Penteriani, Understanding potential responses of large carnivore to climate change. *Hystrix* **33**, 126–133 (2022).
18. R. Dobrovolski, R. D. Loyola, F. Guilhaumon, S. F. Gouveia, J. A. F. Diniz-Filho, Global agricultural expansion and carnivore conservation biogeography. *Biol. Conserv.* **165**, 162–170 (2013).
19. Z. J. Farris, C. D. Golden, S. Karpanty, A. Murphy, D. Stauffer, F. Ratelolahy, V. Andrianjakarivelo, C. M. Holmes, M. J. Kelly, Hunting, exotic carnivores, and habitat loss: Anthropogenic effects on a native carnivore community, Madagascar. *PLOS ONE* **10**, e0136456 (2015).
20. A. P. Jennings, M. Naim, A. D. Advento, A. A. K. Aryawan, S. Ps, J. P. Caliman, A. Verwilghen, G. Veron, Diversity and occupancy of small carnivores within oil palm plantations in Central Sumatra, Indonesia. *Mammal Res.* **60**, 181–188 (2015).
21. A. Ordiz, R. Bischof, J. E. Swenson, Saving large carnivores, but losing the apex predator? *Biol. Conserv.* **168**, 128–133 (2013).
22. P. Strampelli, P. Henschel, C. E. Searle, D. W. Macdonald, A. J. Dickman, Habitat use of and threats to African large carnivores in a mixed-use landscape. *Conserv. Biol.* **36**, e13943 (2022).
23. A. C. Burton, C. Beirne, K. M. Gaynor, C. Sun, A. Granados, M. L. Allen, J. M. Alston, G. C. Alvarenga, F. S. Álvarez Calderón, Z. Amir, C. Anhalt-Depies, C. Appel, S. Arroyo-Arce, G. Balme, A. Bar-Massada, D. Barcelos, E. Barr, E. L. Barthelmess, C. Baruzzi, S. M. Basak, N. Beenaerts, J. Belmaker, O. Belova, B. Bezarević, T. Bird, D. A. Bogan, N. Bogdanović, A. Boyce, M. Boyce, L. Brandt, J. F. Brodie, J. Brooke, J. W. Bubnicki, F. Cagnacci, B. S. Carr, J. Carvalho, J. Casaer, R. Černe, R. Chen, E. Chow, M. Churski, C. Cincotta, D. Ćirović, T. D. Coates, J. Compton, C. Coon, M. V. Cove, A. P. Crupi, S. D. Farra, A. K. Darracq, M. Davis, K. Dawe, V. De Waele, E. Descalzo, T. A. Diserens, J. Drimaj, M. Duľa, S. Ellis-Felege, C. Ellison, A. Ertürk, J. Fantle-Lepczyk, J. Favreau, M. Fennell, P. Ferreras, F. Ferretti, C. Fiderer, L. Finnegan, J. T. Fisher, M. C. Fisher-Reid, E. A. Flaherty, U. Fležar, J. Flousek, J. M. Foca, A. Ford, B. Franzetti, S. Frey, S. Fritts, Š. Frýbová, B. Furnas, B. Gerber, H. M. Geyle, D. G. Giménez, A. J. Giordano, T. Gomercic, M. E. Gompper, D. M. Gräbin, M. Gray, A. Green, R. Hagen, R. Hagen, S. Hammerich, C. Hanekom, C. Hansen, S. Hasstedt, M. Hebblewhite, M. Heurich, T. R. Hofmeester, T. Hubbard, D. Jachowski, P. A. Jansen, K. J. Jaspers, A. Jensen, M. Jordan, M. C. Kaizer, M. J. Kelly, M. T. Kohl, S. Kramer-Schadt, M. Krofel, A. Krug, K. M. Kuhn, D. P. J. Kuijper, E. K. Kuprewicz, J. Kusak, M. Kutal, D. J. R. Lafferty, S. LaRose, M. Lashley, R. Lathrop, T. E. Lee Jr., C. Lepczyk, D. B. Lesmeister, A. Licoppe, M. Linnell, J. Loch, R. Long, R. C. Lonsinger, J. Louvrier, M. S. Luskin, P. MacKay, S. Maher, B. Manet, G. K. H. Mann, A. J. Marshall, D. Mason, Z. McDonald, T. McKay, W. J. McShea, M. Mechler, C. Miaud, J. J. Millspaugh, C. M. Monteza-Moreno, D. Moreira-Arce, K. Mullen, C. Nagy, R. Naidoo, I. Namir, C. Nelson, B. O'Neill, M. T. O'Mara, V. Oberosler, C. Osorio, F. Ossi, P. Palencia, K. Pearson, L. Pedrotti, C. E. Pekins, M. Pendergast, F. F. Pinho, R. Plhal, X. Pocasangre-Orellana, M. Price, M. Procko, M. D. Proctor, E. E. Ramalho, N. Ranc, S. Reljic, K. Remine, M. Rentz, R. Revord, R. Reyna-Hurtado, D. Risch, E. G. Ritchie, A. Romero, C. Rota, F. Rovero, H. Rowe, C. Rutz, M. Salvatori, D. Sandow, C. M. Schalk, J. Scherger, J. Schipper, D. G. Scognamillo, C. H. Şekercioğlu, P. Semenzato, J. Sevin, H. Shamon, C. Shier, E. A. Silva-Rodríguez, M. Sindicic, L. K. Smyth, A. Soyumert, T. Sprague, C. C. St. Clair, J. Stenglein, P. A. Stephens, K. M. Stępniak, M. Stevens, C. Stevenson, B. Ternyik, I. Thomson, R. T. Torres, J. Tremblay, T. Urrutia, J.-P. Vacher, D. Visscher, S. L. Webb, J. Weber, K. C. B. Weiss, L. S. Whipple, C. A. Whittier, J. Whittington, I. Wierzbowska, M. Wikelski, J. Williamson, C. C. Wilmers, T. Windle, H. U. Wittmer, Y. Zharikov, A. Zorn, R. Kays, Mammal responses to global changes in human activity vary by trophic group and landscape. *Nat. Ecol. Evol.* **8**, 924–935 (2024).
24. P. W. Bateman, P. A. Fleming, Big city life: Carnivores in urban environments. *J. Zool.* **287**, 1–23 (2012).
25. K. R. Jones, O. Venter, R. A. Fuller, J. R. Allan, S. L. Maxwell, P. J. Negret, J. E. M. Watson, One-third of global protected land is under intense human pressure. *Science* **360**, 788–791 (2018).
26. J. V. López-Bao, J. Bruskotter, G. Chapron, Finding space for large carnivores. *Nat. Ecol. Evol.* **1**, 0140 (2017).
27. E. J. Torres-Romero, A. J. Giordano, G. Ceballos, J. V. López-Bao, Reducing the sixth mass extinction: Understanding the value of human-altered landscapes to the conservation of the world's largest terrestrial mammals. *Biol. Conserv.* **249**, 108706 (2020).
28. M. Ward, A. I. Tulloch, J. Q. Radford, B. A. Williams, A. E. Reside, S. L. Macdonald, H. J. Mayfield, M. Maron, H. P. Possingham, S. J. Vine, J. L. O'Connor, E. J. Massingham, A. C. Greenville, J. C. Z. Woinarski, S. T. Garnett, M. Lintermans, B. C. Scheele, J. Carwardine, D. G. Nimmo, D. B. Lindenmayer, R. M. Kooyman, J. S. Simmonds, L. J. Sonter, J. E. M. Watson, Impact of 2019–2020 mega-fires on Australian fauna habitat. *Nat. Ecol. Evol.* **4**, 1321–1326 (2020).
29. D. R. Williams, C. Rondinini, D. Tilman, Global protected areas seem insufficient to safeguard half of the world's mammals from human-induced extinction. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2200118119 (2022).
30. T. Newbold, L. N. Hudson, S. L. L. Hill, S. Contu, I. Lysenko, R. A. Senior, L. Börger, D. J. Bennett, A. Choimes, B. Collen, J. Day, A. De Palma, S. Díaz, S. Echeverria-Londoño, M. J. Edgar, A. Feldman, M. Garon, M. L. K. Harrison, T. Alhusseini, D. J. Ingram, Y. Itescu, J. Kattge, V. Kemp, L. Kirkpatrick, M. Kleyer, D. L. P. Correia, C. D. Martin, S. Meiri, M. Novosolov, Y. Pan, H. R. P. Phillips, D. W. Purves, A. Robinson, J. Simpson, S. L. Tuck, E. Weiher, H. J. White, R. M. Ewers, G. M. Mace, J. P. W. Scharlemann, A. Purvis, Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45–50 (2015).
31. J. Terraube, J. Van Doninck, P. Helle, M. Cabeza, Assessing the effectiveness of a national protected area network for carnivore conservation. *Nat. Commun.* **11**, 2957 (2020).
32. UNEP-WCMC and IUCN, *UNEP-WCMC and IUCN Protected Planet Report 2020* (UNEP-WCMC and IUCN, 2020).
33. S. T. Garnett, N. D. Burgess, J. E. Fa, Á. Fernández-Llamazares, Z. Molnár, C. J. Robinson, J. E. M. Watson, K. K. Zander, B. Austin, E. S. Brondizio, N. F. Collier, T. Duncan, E. Ellis, H. Geyle, M. V. Jackson, H. Jonas, P. Malmer, B. McGowan, A. Sivongxay, I. Leiper, A spatial overview of the global importance of Indigenous lands for conservation. *Nat. Sustain.* **1**, 369–374 (2018).
34. J. E. M. Watson, D. F. Shanahan, M. Di Marco, J. Allan, W. F. Laurance, E. W. Sanderson, B. Mackey, O. Venter, Catastrophic declines in wilderness areas undermine global environment targets. *Curr. Biol.* **26**, 2929–2934 (2016).
35. C. J. O'Bryan, S. T. Garnett, J. E. Fa, I. Leiper, J. A. Rehbein, Á. Fernández-Llamazares, M. V. Jackson, H. D. Jonas, E. S. Brondizio, N. D. Burgess, C. J. Robinson, K. K. Zander, Z. Molnár, O. Venter, J. E. M. Watson, The importance of indigenous peoples' lands for the conservation of terrestrial mammals. *Conserv. Biol.* **35**, 1002–1008 (2021).
36. A. Estrada, P. A. Garber, S. Gouveia, Á. Fernández-Llamazares, F. Ascensão, A. Fuentes, S. T. Garnett, C. Shaffer, J. Bicca-Marques, J. E. Fa, K. Hockings, S. Shanee, S. Johnson, G. H. Shepard, N. Shanee, C. D. Golden, A. Cárdenas-Navarrete, D. R. Levey, R. Boonratana, R. Dobrovolski, A. Chaudhary, J. Ratsimbazafy, J. Supriatna, I. Kone, S. Volampeno, Global importance of Indigenous peoples, their lands, and knowledge systems for saving the world's primates from extinction. *Sci. Adv.* **8**, eabn2927 (2022).
37. E. J. Torres-Romero, V. Nijman, D. Fernández, T. M. Eppley, Human-modified landscapes driving the global primate extinction crisis. *Glob. Change Biol.* **29**, 5775–5787 (2023).
38. E. J. Torres-Romero, G. Ceballos, F. Botello, J. I. G. Rojas, A. J. Giordano, J. V. López-Bao, Jaguar conservation in the American continent: The role of protected landscape and human-impacted biomes: Conservación del jaguar en el continente americano: Papel de las áreas protegidas y biomas con intervención humana. *Rev. Biol. Trop.* **71**, e50507 (2023).
39. UNEP-WCMC and IUCN, *UNEP-WCMC and IUCN Protected Planet Report 2024* (UNEP-WCMC and IUCN, 2024).
40. IUCN, The IUCN Red List of Threatened Species (2024). https://iucnredlist.org.
41. H. Mu, X. Li, Y. Wen, J. Huang, P. Du, W. Su, S. Miao, M. Geng, A global record of annual terrestrial human footprint dataset from 2000 to 2018. *Sci. Data* **9**, 176 (2022).

42. O. Venter, E. W. Sanderson, A. Magrach, J. R. Allan, J. Beher, K. R. Jones, H. P. Possingham, W. F. Laurance, P. Wood, B. M. Fekete, M. A. Levy, J. E. M. Watson, Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat. Commun.* **7**, 12558 (2016).
43. E. J. Torres-Romero, J. T. Fisher, V. Nijman, F. He, T. M. Eppley, Accelerated human-induced extinction crisis in the world's freshwater mammals. *Glob. Environ. Change Adv.* **2**, 100006 (2024).
44. J. Riggio, J. E. Baillie, S. Brumby, E. Ellis, C. M. Kennedy, J. R. Oakleaf, A. Tait, T. Tepe, D. M. Theobald, O. Venter, J. E. M. Watson, A. P. Jacobson, Global human influence maps reveal clear opportunities in conserving Earth's remaining intact terrestrial ecosystems. *Glob. Change Biol.* **26**, 4344–4356 (2020).
45. R. Yang, X. Dong, S. Xu, K. Wang, X. Li, W. Xiao, Y. Ye, Fragmentation of key biodiversity areas highlights attention to human disturbance patterns. *Biol. Conserv.* **290**, 110428 (2024).
46. ESRI, *ArcGIS Desktop: Release 10.1* (Environmental Systems Research Institute, 2011).
47. M. Di Marco, C. Rondinini, L. Boitani, K. A. Murray, Comparing multiple species distribution proxies and different quantifications of the human footprint map, implications for conservation. *Biol. Conserv.* **165**, 203–211 (2013).
48. C. J. O'Bryan, J. R. Allan, M. Holden, C. Sanderson, O. Venter, M. Di Marco, E. McDonald-Madden, J. E. M. Watson, Intense human pressure is widespread across terrestrial vertebrate ranges. *Glob. Ecol. Conserv.* **21**, e00882 (2020).
49. M. Di Marco, O. Venter, H. P. Possingham, J. E. M. Watson, Changes in human footprint drive changes in species extinction risk. *Nat. Commun.* **9**, 4621 (2018).
50. K. R. Crooks, C. L. Burdett, D. M. Theobald, C. Rondinini, L. Boitani, Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **366**, 2642–2651 (2011).
51. R. M. Pringle, Upgrading protected areas to conserve wild biodiversity. *Nature* **546**, 91–99 (2017).
52. S. Saura, B. Bertzky, L. Bastin, L. Battistella, A. Mandrici, G. Dubois, Global trends in protected area connectivity from 2010 to 2018. *Biol. Conserv.* **238**, 108183 (2019).
53. E. Di Minin, T. Toivonen, Global protected area expansion: Creating more than paper parks. *BioScience* **65**, 637–638 (2015).
54. J. E. Fa, J. E. M. Watson, I. Leiper, P. Potapov, T. D. Evans, N. D. Burgess, Z. Molnár, Á. Fernández-Llamazares, T. Duncan, S. Wang, B. J. Austin, H. Jonas, C. J. Robinson, P. Malmer, K. K. Zander, M. V. Jackson, E. Ellis, E. S. Brondizio, S. T. Garnett, Importance of Indigenous peoples' lands for the conservation of Intact Forest Landscapes. *Front. Ecol. Environ.* **18**, 135–140 (2020).
55. S. Qin, R. E. Golden Kroner, C. Cook, A. T. Tesfaw, R. Braybrook, C. M. Rodriguez, C. Poelking, M. B. Mascia, Protected area downgrading, downsizing, and degazettement as a threat to iconic protected areas. *Conserv. Biol.* **33**, 1275–1285 (2019).
56. J. Lizundia-Loiola, M. L. Pettinari, E. Chuvieco, Temporal anomalies in burned area trends: Satellite estimations of the Amazonian 2019 fire crisis. *Remote Sens.* **12**, 151 (2020).
57. X. P. Song, M. C. Hansen, P. Potapov, B. Adusei, J. Pickering, M. Adami, A. Lima, V. Zalles, S. V. Stehman, C. M. Di Bella, M. C. Conde, E. J. Copati, L. B. Fernandes, A. Hernandez-Serna, S. M. Jantz, A. H. Pickens, S. Turubanova, A. Tyukavina, Massive soybean expansion in South America since 2000 and implications for conservation. *Nat. Sustain.* **4**, 784–792 (2021).
58. C. A. Boulton, T. M. Lenton, N. Boers, Pronounced loss of Amazon rainforest resilience since the early 2000s. *Nat. Clim. Change* **12**, 271–278 (2022).
59. C. A. Nunes, E. Berenguer, F. França, J. Ferreira, A. C. Lees, J. Louzada, E. J. Sayer, R. Solar, C. C. Smith, L. E. O. C. Aragão, D. de Lima Braga, P. Barbosa de Camargo, C. E. P. Cerri, R. C. de Oliveira Jr., M. Durigan, N. Moura, V. H. F. Oliveira, C. Ribas, F. Vaz-de-Mello, I. Vieira, R. Zanetti, J. Barlow, Linking land-use and land-cover transitions to their ecological impact in the Amazon. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2202310119 (2022).
60. J. S. Albert, A. C. Carnaval, S. G. Flantua, L. G. Lohmann, C. C. Ribas, D. Riff, J. D. Carrillo, Y. Fan, J. J. P. Figueiredo, J. M. Guayasamin, C. Hoorn, G. H. De Melo, N. Nascimento, C. A. Quesada, C. Ulloa Ulloa, P. Val, J. Arieira, A. C. Encalda, C. A. Nobre, Human impacts outpace natural processes in the Amazon. *Science* **379**, eabo5003 (2023).
61. P. G. Curtis, C. M. Slay, N. L. Harris, A. Tyukavina, M. C. Hansen, Classifying drivers of global forest loss. *Science* **361**, 1108–1111 (2018).
62. P. Gerland, A. E. Raftery, H. Ševčíková, N. Li, D. Gu, T. Spoorenberg, L. Alkema, B. K. Fosdick, J. Chunn, N. Lalic, G. Bay, T. Buettner, G. K. Heilig, J. Wilmoth, World population stabilization unlikely this century. *Science* **346**, 234–237 (2014).
63. A. Torres, J. A. G. Jaeger, J. C. Alonso, Assessing large-scale wildlife responses to human infrastructure development. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 8472–8477 (2016).
64. A. Ceia-Hasse, L. Borda-de-Água, C. Grilo, H. M. Pereira, Global exposure of carnivores to roads. *Glob. Ecol. Biogeogr.* **26**, 592–600 (2017).
65. G. Ceballos, P. R. Ehrlich, P. H. Raven, Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 13596–13602 (2020).
66. K. E. Ingeman, L. Z. Zhao, C. Wolf, D. R. Williams, A. L. Ritger, W. J. Ripple, K. L. Kopecky, E. M. Dillon, B. P. DiFiore, J. S. Curtis, S. R. Csik, A. Bui, A. C. Stier, Glimmers of hope in large carnivore recoveries. *Sci. Rep.* **12**, 10005 (2022).
67. W. F. Laurance, G. R. Clements, S. Sloan, C. S. O'Connell, N. D. Mueller, M. Goosem, O. Venter, D. P. Edwards, B. Phalan, A. Balmford, R. Van Der Ree, I. B. Arrea, A global strategy for road building. *Nature* **513**, 229–232 (2014).
68. L. L. Lichtenfeld, C. Trout, E. L. Kisimir, Evidence-based conservation: Predator-proof bomas protect livestock and lions. *Biodivers. Conserv.* **24**, 483–491 (2015).
69. J. S. McManus, A. J. Dickman, D. Gaynor, B. H. Smuts, D. W. Macdonald, Dead or alive? Comparing costs and benefits of lethal and non-lethal human-wildlife conflict mitigation on livestock farms. *Oryx* **49**, 687–695 (2015).
70. K. U. Karanth, R. Chellam, Carnivore conservation at the crossroads. *Oryx* **43**, 1–2 (2009).
71. E. Dinerstein, C. Vynne, E. Sala, A. R. Joshi, S. Fernando, T. E. L. J. Mayorga, D. Olson, G. P. Asner, J. E. M. Baillie, N. D. Burgess, K. Burkart, R. F. Noss, Y. P. Zhang, A. Baccini, T. Birch, N. Hahn, L. N. Joppa, E. Wikramanayake, A global deal for nature: Guiding principles, milestones, and targets. *Sci. Adv.* **5**, eaaw2869 (2019).
72. A. Trouwborst, Global large carnivore conservation and international law. *Biodivers. Conserv.* **24**, 1567–1588 (2015).
73. R. Gutiérrez-Hernández, F. J. Sahagún-Sánchez, P. Delgado- Sánchez, P. Castillo-Lara, J. Fortanelli-Martínez, H. Reyes-Hernández, J. A. De-Nova, Reevaluación de los bosques tropicales estacionalmente secos de la Reserva de la Biosfera Sierra del Abra Tanchipa y áreas con potencial para su conservación. *Bot. Sci.* **99**, 735–751 (2021).
74. E. W. Sanderson, J. Moy, C. Rose, K. Fisher, B. Jones, D. Balk, P. Clyne, D. Miquelle, J. Walston, Implications of the shared socioeconomic pathways for tiger (*Panthera tigris*) conservation. *Biol. Conserv.* **231**, 13–23 (2019).
75. M. G. Betts, C. Wolf, W. J. Ripple, B. Phalan, K. A. Millers, A. Duarte, S. H. M. Butchart, T. Levi, Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature* **547**, 441–444 (2017).
76. J. R. Allan, J. E. M. Watson, M. Di Marco, C. J. O'Bryan, H. P. Possingham, S. C. Atkinson, O. Venter, Hotspots of human impact on threatened terrestrial vertebrates. *PLOS Biol.* **17**, e3000158 (2019).
77. D. Spear, L. C. Foxcroft, H. Bezuidenhout, M. A. McGeoch, Human population density explains alien species richness in protected areas. *Biol. Conserv.* **159**, 137–147 (2013).
78. N. Levin, S. Kark, D. Crandall, Where have all the people gone? Enhancing global conservation using night lights and social media. *Ecol. Appl.* **25**, 2153–2167 (2015).
79. W. S. Symes, D. P. Edwards, J. Miettinen, F. E. Rheindt, R. Carrasco, Combined impacts of deforestation and wildlife trade on tropical biodiversity are severely underestimated. *Nat. Commun.* **9**, 4052 (2018).
80. J. J. Gilroy, A. Ordiz, R. Bischof, Carnivore coexistence: Value the wilderness. *Science* **347**, 382–382 (2015).
81. R. Bischof, J. E. Swenson, Linking noninvasive genetic sampling and traditional monitoring to aid management of a trans-border carnivore population. *Ecol. Appl.* **22**, 361–373 (2012).
82. J. Müller, M. Wölfl, S. Wölfl, D. W. Müller, T. Hothorn, M. Heurich, Protected areas shape the spatial distribution of a European lynx population more than 20 years after reintroduction. *Biol. Conserv.* **177**, 210–217 (2014).
83. L. M. van Eeden, A. Eklund, J. R. B. Miller, J. V. López-Bao, G. Chapron, M. R. Cejtin, M. S. Crowther, C. R. Dickman, J. Frank, M. Krofel, D. W. Macdonald, J. McManus, T. K. Meyer, A. D. Middleton, T. M. Newsome, W. J. Ripple, E. G. Ritchie, O. J. Schmitz, K. J. Stoner, M. Tourani, A. Treves, Carnivore conservation needs evidence-based livestock protection. *PLOS Biol.* **16**, e2005577 (2018).
84. G. Chapron, P. Kaczensky, J. D. C. Linnell, M. von Arx, D. Huber, H. Andrén, J. V. López-Bao, M. Adamec, F. Álvares, O. Anders, L. Balčiauskas, V. Balys, P. Bedő, F. Bego, J. C. Blanco, U. Breitenmoser, H. Brøseth, L. Bufka, R. Bunikyte, P. Ciucci, A. Dutsov, T. Engleder, C. Fuxjäger, C. Groff, K. Holmala, B. Hoxha, Y. Iliopoulos, O. Ionescu, J. Jeremić, K. Jerina, G. Kluth, F. Knauer, I. Kojola, I. Kos, M. Krofel, J. Kubala, S. Kunovac, J. Kusak, M. Kutal, O. Liberg, A. Majić, P. Männil, R. Manz, E. Marboutin, F. Marucco, D. Melovski, K. Mersini, Y. Mertzanis, R. W. Mysłajek, S. Nowak, J. Odden, J. Ozolins, G. Palomero, M. Paunović, J. Persson, H. Potočnik, P.-Y. Quenette, G. Rauer, I. Reinhardt, R. Rigg, A. Ryser, V. Salvatori, T. Skrbinšek, A. Stojanov, J. E. Swenson, L. Szemethy, A. Trajçe, E. Tsingarska-Sedefcheva, M. Váňa, R. Veeroja, P. Wabakken, M. Wölfl, S. Wölfl, F. Zimmermann, D. Zlatanova, L. Boitani, Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* **346**, 1517–1519 (2014).
85. R. Woodroffe, "Strategies for carnivore conservation: Lessons from contemporary extinctions," in *Carnivore Conservation*, J. L. Gittleman, S. M. Funk, D. W. MacDonald, R. K. Wayne, Eds. (Cambridge Univ. Press, 2001), pp. 61–92.
86. R. Woodroffe, J. R. Ginsberg, Edge effects and the extinction of populations inside protected areas. *Science* **280**, 2126–2128 (1998).
87. S. P. Finnegan, L. Galvez-Bravo, L. Silveira, N. M. Tôrres, A. A. Jácomo, G. B. Alves, F. Dalerum, Reserve size, dispersal and population viability in wide-ranging carnivores: The case of jaguars in Emas National Park, Brazil. *Anim. Conserv.* **24**, 3–14 (2021).
88. G. R. Rauset, H. Andren, J. E. Swenson, G. Samelius, P. Segerström, A. Zedrosser, J. Persson, National parks in northern Sweden as refuges for illegal killing of large carnivores. *Conserv. Lett.* **9**, 334–341 (2016).

89. M. W. Hayward, J. O'Brien, G. I. Kerley, Carrying capacity of large African predators: Predictions and tests. *Biol. Conserv.* **139**, 219–229 (2007).
90. Z. M. Brooke, J. Bielby, K. Nambiar, C. Carbone, Correlates of research effort in carnivores: Body size, range size, and diet matter. *PLOS ONE* **9**, e93195 (2014).
91. Z. J. Farris, B. D. Gerber, K. Valenta, R. Rafaliarison, J. C. Razafimahaimodison, E. Larney, T. Rajaonarivelo, Z. Randriana, P. C. Wright, C. A. Chapman, Threats to a rainforest carnivore community: A multi-year assessment of occupancy and co-occurrence in Madagascar. *Biol. Conserv.* **210**, 116–124 (2017).
92. A. Pyhälä, J. Eklund, M. F. McBride, M. A. Rakotoarijaona, M. Cabeza, Managers' perceptions of protected area outcomes in Madagascar highlight the need for species monitoring and knowledge transfer. *Conserv. Sci. Pract.* **1**, e6 (2019).
93. E. M. Wampole, Z. J. Farris, B. D. Gerber, A synthesis of life-history traits, functional traits, and consequences of anthropogenic pressures on Madagascar's threatened carnivorans, Eupleridae. *Mammal Rev.* **51**, 402–419 (2021).
94. Z. J. Farris, M. J. Kelly, S. Karpanty, A. Murphy, F. Ratelolahy, V. Andrianjakarivelo, C. Holmes, The times they are a-changin': Multi-year surveys reveal exotics replace native carnivores at a Madagascar rainforest site. *Biol. Conserv.* **206**, 320–328 (2017).
95. V. Athreya, M. Odden, J. D. Linnell, J. Krishnaswamy, K. U. Karanth, A cat among the dogs: Leopard *Panthera pardus* diet in a human-dominated landscape in western Maharashtra, India. *Oryx* **50**, 156–162 (2016).
96. I. Majgaonkar, S. Vaidyanathan, A. Srivathsa, S. Shivakumar, S. Limaye, V. Athreya, Land-sharing potential of large carnivores in human-modified landscapes of western India. *Conserv. Sci. Pract.* **1**, e34 (2019).
97. E. W. Sanderson, D. G. Miquelle, K. Fisher, A. Harihar, C. Clark, J. Moy, P. Potapov, N. Robinson, L. Royte, D. Sampson, J. Sanderlin, C. B. Yackulic, M. Belecky, U. Breitenmoser, C. Breitenmoser-Würtsen, P. Chanchani, S. Chapman, A. Deomurari, S. Duangchantrasiri, E. Facchini, T. N. E. Gray, J. Goodrich, L. Hunter, M. Linkie, W. Marthy, A. Rasphone, S. Roy, D. Sittibal, T. Tempa, M. Umponjan, K. Wood, Range-wide trends in tiger conservation landscapes, 2001-2020. *Front. Conserv. Sci.* **4**, 1191280 (2023).
98. A. Ordiz, O. G. Støen, M. Delibes, J. E. Swenson, Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia* **166**, 59–67 (2011).
99. J. D. C. Linnell, J. E. Swenson, R. Anderson, Predators and people: Conservation of large carnivores is possible at high human densities if management policy is favourable. *Anim. Conserv.* **4**, 345–349 (2001).
100. A. Ordiz, M. Aronsson, J. Persson, O. G. Støen, J. E. Swenson, J. Kindberg, Effects of human disturbance on terrestrial apex predators. *Diversity* **13**, 68 (2021).
101. A. Johnson, C. Vongkhamheng, M. Hedemark, T. Saithongdam, Effects of human–carnivore conflict on tiger (*Panthera tigris*) and prey populations in Lao PDR. *Anim. Conserv.* **9**, 421–430 (2006).
102. A. Ordiz, S. Sæbø, J. Kindberg, J. E. Swenson, O. G. Støen, Seasonality and human disturbance alter brown bear activity patterns: Implications for circumpolar carnivore conservation? *Anim. Conserv.* **20**, 51–60 (2017).
103. A. Tallian, O.-G. Støen, B. Immerzeel, J. Kindberg, A. Ordiz, L. T. Persson, P. Segerström, A. Skarin, R. Stokke, T. Tveraa, B. Åhman, J. Frank, Large carnivore conservation and traditional pastoralism: A case study on bear–reindeer predation mitigation measures. *Ecosphere* **14**, e4564 (2023).
104. J. Persson, G. R. Rauset, G. Chapron, Paying for an endangered predator leads to population recovery. *Conserv. Lett.* **8**, 345–350 (2015).
105. S. Dolrenry, L. Hazzah, L. G. Frank, Conservation and monitoring of a persecuted African lion population by Maasai warriors. *Conserv. Biol.* **30**, 467–475 (2016).
106. M. Torrents-Ticó, Á. Fernández-Llamazares, D. Burgas, M. Cabeza, Convergences and divergences between scientific and Indigenous and Local Knowledge contribute to inform carnivore conservation. *Ambio* **50**, 990–1002 (2021).
107. W. J. Ripple, K. Abernethy, M. G. Betts, G. Chapron, R. Dirzo, M. Galetti, T. Levi, P. A. Lindsey, D. W. Macdonald, B. Machovina, T. M. Newsome, C. A. Peres, A. D. Wallach, C. Wolf, H. Young, Bushmeat hunting and extinction risk to the world's mammals. *R. Soc. Open Sci.* **3**, 160498 (2016).
108. C. Wolf, W. J. Ripple, Prey depletion as a threat to the world's large carnivores. *R. Soc. Open Sci.* **3**, 160252 (2016).
109. T. G. de Oliveira, B. C. Lima, L. Fox-Rosales, R. S. Pereira, E. Pontes-Araujo, A. L. de Sousa, A refined population and conservation assessment of the elusive and endangered northern tiger cat (*Leopardus tigrinus*) in its key worldwide conservation area in Brazil. *Glob. Ecol. Conserv.* **22**, e00927 (2020).
110. T. G. de Oliveira, L. A. Fox-Rosales, E. A. D. Paemelaere, K. M. P. M. de Barros Ferraz, The dominant mesopredator and savanna formations shape the distribution of the threatened northern tiger cat (*Leopardus tigrinus*) in the Amazon. *Sci. Rep.* **12**, 18697 (2022).
111. T. G. de Oliveira, L. A. Fox-Rosales, J. D. Ramírez-Fernández, J. C. Cepeda-Duque, R. Zug, C. Sanchez-Lalinde, M. J. R. Oliveira, P. H. D. Marinho, A. Bonilla-Sánchez, M. C. Marques, K. Cassaro, R. Moreno, D. Rumiz, F. B. Peters, J. Ortega, G. Cavalcanti, M. S. Mooring, S. R. Blankenship, E. Brenes-Mora, D. Dias, F. D. Mazim, E. Eizirik, J. L. Diehl, R. V. Marques, A. C. C. Ribeiro, R. A. Cruz, E. Pasa, L. P. C. Meira, A. Pereira, G. B. Ferreira, F. F. de Pinho, L. M. M. Sena, V. R. de Morais, M. R. Luiz, V. E. C. Moura, M. O. Favarini, K. P. G. Leal, P. G. C. Wagner, M. C. dos Santos, J. Sanderson, E. P. Araújo, F. H. G. Rodrigues, Ecological modeling, biogeography, and phenotypic analyses setting the tiger cats' hyperdimensional niches reveal a new species. *Sci. Rep.* **14**, 2395 (2024).
112. T. G. de Oliveira, M. A. Tortato, L. Silveira, C. B. Kasper, F. D. Mazim, M. Lucherini, A. T. A. Jácomo, J. B. G. Soares, R. V. Marques, M. Sunquist, "Ocelot ecology and its effect on the small- felid guild in the lowland neotropics," in *Biology and Conservation of Wild Felids*, D. W. Macdonald, A. J. Loveridge, Eds. (Oxford Univ. Press, ed. 1, 2010), pp. 559–580.
113. C. Chen, J. F. Brodie, R. Kays, T. J. Davies, R. Liu, J. T. Fisher, J. Ahumada, W. McShea, D. Sheil, B. Agwanda, M. H. Andrianarisoa, R. D. Appleton, R. Bitariho, S. Espinosa, M. M. Grigione, K. M. Helgen, A. Hubbard, C. M. Hurtado, P. A. Jansen, X. Jiang, A. Jones, E. L. Kalies, C. Kiebou-Opepa, X. Li, M. G. M. Lima, E. Meyer, A. B. Miller, T. Murphy, R. Piana, R.-C. Quan, C. T. Rota, F. Rovero, F. Santos, S. Schuttler, A. Uduman, J. K. van Bommel, H. Young, A. C. Burton, Global camera trap synthesis highlights the importance of protected areas in maintaining mammal diversity. *Conserv. Lett.* **15**, e12865 (2022).
114. C. Schmidt, S. Hoban, M. Hunter, I. Paz-Vinas, C. J. Garroway, Genetic diversity and IUCN red list status. *Conserv. Biol.* **37**, e14064 (2023).
115. E. S. Brondízio, Y. Aumeeruddy-Thomas, P. Bater, J. Carino, A. Fernández-Llamazares, M. F. Ferrari, K. Galvin, V. Reyes-García, P. McElwee, Z. Molnár, A. Samakov, U. B. Shrestha, Locally based, regionally manifested, and globally relevant: Indigenous and local knowledge, values, and practices for nature. *Annu. Rev. Env. Resour.* **46**, 481–509 (2021).
116. M. J. E. Broekman, J. P. Hilbers, M. A. J. Huijbregts, T. Mueller, A. H. Ali, H. Andrén, J. Altmann, M. Aronsson, N. Attias, H. L. A. Bartlam-Brooks, F. M. van Beest, J. L. Belant, D. E. Beyer, L. Bidner, N. Blaum, R. B. Boone, M. S. Boyce, M. B. Brown, F. Cagnacci, R. Černe, S. Chamaillé-Jammes, N. Dejid, J. Dekker, A. L. J. Desbiez, S. L. Díaz-Muñoz, J. Fennessy, C. Fichtel, C. Fischer, J. T. Fisher, I. Fischhoff, A. T. Ford, J. M. Fryxell, B. Gehr, J. R. Goheen, M. Hauptfleisch, A. J. M. Hewison, R. Hering, M. Heurich, L. A. Isbell, R. Janssen, F. Jeltsch, P. Kaczensky, P. M. Kappeler, M. Krofel, S. LaPoint, A. D. M. Latham, J. D. C. Linnell, A. C. Markham, J. Mattisson, E. P. Medici, G. de Miranda Mourão, B. Van Moorter, R. G. Morato, N. Morellet, A. Mysterud, S. Mwiu, J. Odden, K. A. Olson, A. Orniсāns, N. Pagon, M. Panzacchi, J. Persson, T. Petroelje, C. M. Rolandsen, D. Roshier, D. I. Rubenstein, S. Saïd, A. R. Salemgareyev, H. Sawyer, N. M. Schmidt, N. Selva, A. Sergiel, J. Stabach, J. Stacy-Dawes, F. E. C. Stewart, J. Stiegler, O. Strand, S. Sundaresan, N. J. Svoboda, W. Ullmann, U. Voigt, J. Wall, M. Wikelski, C. C. Wilmers, F. Zięba, T. Zwijacz-Kozica, A. M. Schipper, M. A. Tucker, Evaluating expert-based habitat suitability information of terrestrial mammals with GPS-tracking data. *Glob. Ecol. Biogeogr.* **31**, 1526–1541 (2022).
117. E. Di Minin, R. Slotow, L. T. Hunter, F. Montesino Pouzols, T. Toivonen, P. H. Verburg, N. Leader-Williams, L. Petracca, A. Moilanen, Global priorities for national carnivore conservation under land use change. *Sci. Rep.* **6**, 23814 (2016).
118. T. Dutta, M. De Barba, N. Selva, A. C. Fedorca, L. Maiorano, W. Thuiller, A. Zedrosser, J. Signer, F. Pflüger, S. Frank, P. M. Lucas, N. Balkenhol, An objective approach to select surrogate species for connectivity conservation. *Front. Ecol. Evol.* **11**, 1078649 (2023).

Acknowledgments: We are grateful to E. W. Sanderson, L. Hunter, and D. Valenzuela Galvan for useful suggestions on an earlier version of the manuscript. We also thank S. Garnett for providing the GIS layer for IPLs and the reviewers. We acknowledge that this study includes spatial analyses involving IPLs as mapped in Garnett *et al.* (*33*). No direct engagement with Indigenous communities occurred, and the data were used solely for spatial assessment purposes. We recognize the importance of Indigenous data sovereignty and transparency in the use of such data. **Funding:** This work was supported by Secretaría de Ciencia, Humanidades, Tecnología e Innovación (SECIHTI-México), fellowship 5943610 (E.J.T.-R.); Slovenian Research and Innovation Agency, grants J1-50013 and P4-0059 (M.K.); I + D + i Project PID2020-114181GB-I00 funded by MCIN/AEI/10.13039/501100011033; and the European Union (V.P. and A.O). **Author contributions:** Conceptualization: E.J.T.-R. Methodology: E.J.T.-R. Investigation: E.J.T.-R. Visualization: E.J.T.-R., T.M.E., W.J.R., N.H.C., A.O., and V.P. Supervision: E.J.T.-R. Writing—original draft: E.J.T.-R. and T.M.E. Writing—review and editing: E.J.T.-R., T.M.E., W.J.R., T.M.N., M.K., N.H.C., T.G.d.O., A.O., N.S., and V.P. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All the shapefiles used in this article are freely accessible through the IUCN Red List data (www.iucnredlist.org, refer to Section Materials; https://iucnredlist.org/resources/spatial-data-download). All data needed to evaluate the conclusions in the paper are present in the paper.

Submitted 6 May 2024
Accepted 11 June 2025
Published 16 July 2025
10.1126/sciadv.adq2853