



# Socio-ecological gap analysis to forecast species range contractions for conservation

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Conservation requires both a needs assessment and prioritization scheme for planning and implementation. Range maps are critical for understanding and conserving biodiversity, but current range maps often omit content, negating important metrics of variation in populations and places. Here, we integrate a myriad of conditions that are spatially explicit across distributions of carnivores to identify gaps in capacity necessary for their conservation. Expanding on traditional gap analyses that focus almost exclusively on quantifying discordance in protected area coverage across a species' range, our work aggregates threat layers (e.g., drought, human pressures) with resources layers (e.g., protected areas, cultural diversity) to identify gaps in available conservation capacity (ACC) across ranges for 91 African carnivores. Our model indicated that all species have some portion of their range at risk of contraction, with an average of 15 percentage range loss. We found that the ACC differed based on body size and taxonomy. Results deviated from current perceptions of extinction risks for species with an International Union for Conservation of Nature (IUCN) threat status of Least Concern and yielded insights for species categorized as Data Deficient. Our socio-ecological gap analysis presents a geospatial approach to inform decision-making and resource allocation in conservation. Ultimately, our work advances forecasting dynamics of species' ranges that are increasingly vital in an era of great socio-ecological change to mitigate human-wildlife conflict and promote inclusive carnivore conservation across geographies.

geospatial | Africa | carnivore | human pressure | protected area

Present species ranges reflect historic conditions and extant pressures coupled with biology and resource availability (1, 2). Despite an exhaustive focus on climate change inducing range shifts, the heterogeneity of conditions within a species' range is complex and extends beyond environmental properties to delimit distributions and alter ecology (3, 4). Now, in an era of immense anthropogenic influence, social factors stemming from human values, interactions with nature, and land use are increasingly governing range dynamics and threatening the persistence of species (5, 6). Implicit in conservation efforts to preserve biodiversity is the maintenance of individual and overlapping species ranges. The fluidity of spatial patterns of biodiversity results from those environmental, ecological, macroevolutionary, and social processes causing species' ranges to shift with specific concern for contraction at varying temporal scales (7). Thus, building approaches and tools that aid in forecasting range dynamics remains a fundamental tenet of conservation biogeography research, necessitating the amalgamation of vast amounts of data for mapping (Fig. 1).

Geospatial analytical approaches are now integral to conservation planning and decision-making (8). Applied applications of mapping have extended beyond species presence to identify areas critical for natural processes, research, and conservation investment (9–11). Areas classified as highly vulnerable or “gaps” in protection help prioritize resource allocation. Traditional gap analysis at the species level overlay the distribution of protected areas with the distribution of a species range or their available habitat to quantify spatial discordance in coverage (12, 13). Such gap analysis approaches have been applied to a range of species and varying ecosystems to guide conservation efforts, e.g. seahorses (14), cacti (15), and rivers (16). Species or ecosystem representation and human pressures within existing protected areas provide another lens for conservation assessments (17–19). Coad et al. (20) reported that only 4 to 9% of terrestrial vertebrates are adequately represented within existing global protected areas. Ahmadi et al. (21) coupled gap analysis with network analysis using graph theory to consider the spatial configuration of conservation areas for large felids in Iran. These approaches still largely omit considering how the distribution of threats affect the vulnerability of species to extirpation and range contraction, although a gap analysis for giant panda (*Ailuropoda melanoleuca*) extended beyond only protected area coverage to

## Significance

Geospatial approaches are increasingly vital for conservation with applications of gap analysis informing decision-making and resource allocation. We extend traditional assessments by incorporating both the spatial distribution of threats and resources to build an index of available conservation capacity across a species' range. Using 91 African carnivores, we identified locations within each species' range at risk of contraction due to a deficit of resources available to potentially thwart present threats. Our results raise new concerns for African carnivores, particularly small-bodied species, contrary to current perceptions of their extinction risks.

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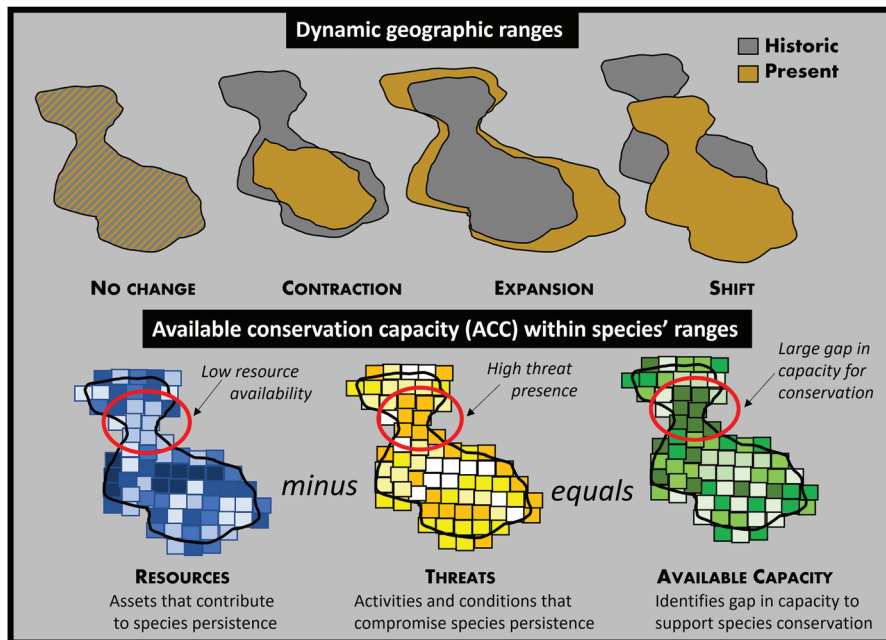
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**Fig. 1.** Species ranges vary in space, time, and in various characteristics. Temporal dynamics highlight potential changes in the amount and location occupied. Ranges may remain stable (no change), contract, expand, or shift. Regardless of the range outcome, the heterogeneous distribution of resources and threats contribute and compromise respectively to influence the available conservation capacity (ACC) of a species.

disparities in management considering timber extraction and other human disturbances in China (22).

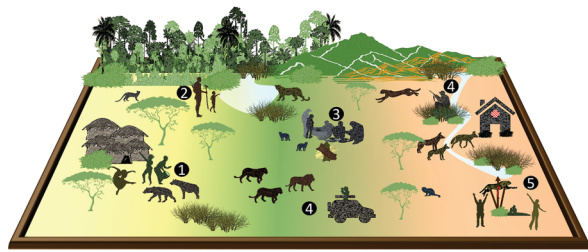
Land-use changes, including the expansion of urbanization and agricultural production, have and will continue to alter the ecology, evolution, behavior, and distribution of species (23, 24). Consequently, understanding the occurrence of these threats across a species' range could facilitate forecasting which populations may be vulnerable to habitat loss and where conflicts will emerge between conservation and development agendas. For example, Strona et al. (25) considered projected oil palm expansion to assess range loss of primates across Africa. As captured in the human footprint index (HFI), threats are not perturbing species in isolation but instead can operate synergistically across scales (26, 27). Mapping HFI or other threats is particularly promising for species of conservation concern to understand current and future risks (28, 29). As pressures mount, anticipating where contractions occur in species' ranges via population extirpations can aid in devising effective mitigation strategies. However, the singular focus on the distribution of threats, or alternatively protected areas for gap analysis, is insufficient and misrepresents actual conservation needs. Such approaches exclude how various resources available throughout a species' range can influence their probability of persistence. Areas rich in biodiversity often have improved ecosystem function and possess certain safeguards to prevent collapse (30). Recent work also highlights the contribution of indigenous land management to habitat and species conservation through their stewardship practices (e.g., ref. 31). Wildlife provide recreation services, provision food and materials, and generate revenue that contributes to national economies that motivate their conservation (32, 33). Despite the pervasive narrative of degradative anthropic factors, humans are also (though not equally) contributing to conservation efforts, and considering geographies with higher cultural diversity may enhance the capacity for conservation. For example, customary laws and traditional ceremonies of the Nharira community in central Zimbabwe include biodiversity protection (34). Thus, the blanket inclusion of human density as inherently and exclusively an environmental

stressor is not accurate. This is especially true given that the effectiveness of biodiversity conservation projects is directly contingent upon local and regional sociopolitical dimensions including governance (35). Therefore, conservation strategies in response to socio-ecological changes must then adequately incorporate these socio-ecological dimensions.

Many carnivores face global uncertainty and operate in dynamic socio-ecological processes that underscore their importance (36, 37). Carnivores connect systems through a myriad of pathways including their regulatory capacity in shaping ecosystems, charisma that contributes to gross domestic product through tourism, and complex direct and indirect human interactions (38). These species also often have wide distributions that intersect varying land management regimes that increase encounters with people and our domesticates. Africa contains a third of the world's carnivore species that persist in an environment fraught with anthropogenic pressures and rich biocultural diversity (39). Africans have coexisted with carnivores for millennia and exhibit intricate relationships with carnivores, as evident from the ubiquitous inclusion of carnivores in oral traditions and folktales (Box 1). For example, Africa's iconic lions (*Panthera leo*) serve as tokens of power, strength, and fierceness. As such, body parts of lions are used by tribal traditional healers for various spiritual and bodily ailments. The Xhosa of South Africa, Zimbabweans, the Samburu of Kenya, and the Gogo of Tanzania all use lion fat as a potion to ward off wicked spirits, exorcize evil spirits, repel creditors from debtors, and give courage, respectively (40). As such, advancing any conservation agenda for African carnivores requires knowing and engaging Africa's indigenous communities as key partners across the species' range. Here, we propose an innovative socio-ecological gap analysis that includes both threat and resource components to determine if existing capacities are sufficient to promote stable geographic ranges for African carnivores (Fig. 1).

Our model incorporates the distribution of habitat, biodiversity, and protected area along with cultural diversity as resources that inform conservation capacity across the geographic ranges of 91 African carnivores. African species in the order Carnivora

### Box 1.



1 Cultural maintenance of rituals, customs, and spiritual beliefs 2 Social cohesion of family bonding and community structure 3 Provisioning services of clothing, and materials such as bones for weaponry 4 Economic benefits from tourism 5 Substance of meat;

Africa's rich biocultural diversity induces complex interactions between nature and local people. In Ethiopia, communities vary in their relationship with spotted hyenas (*C. crocuta*), with some viewing them as abnormal and perceived agents of evil while others have a spiritual connection (65). Carnivore pelts provide resources to support ornamentation for rituals and medicinal practices for African communities. Traditional cultures in Nigeria use leopard skin to treat snake bites and convulsion and believe the skin, teeth, and hair of the spotted hyena can combat adultery and promiscuity (66). In Tanzania, otters' parts are believed to have medicinal and witchcraft properties, while some west and central African communities believe carrying otter fur renders them invisible to their enemies (67). The Mbuti people of Democratic Republic of Congo use skins of civets and genets for ornamental and medicinal purposes (68). Similar traditional cultural uses have also been reported in local communities in Cameroon, where skins are sold in the markets as love charms and have decorative, spiritual, and medicinal uses (69). Overall, as market value increases for pelts and use shifts from small-scale village level to more commercial purposes, concerns of overexploitation mount for carnivore species in these regions.

range in body size from ~250 g (dwarf mongoose) to over 200 kg (African lion). African carnivores also vary across ecological attributes including sociality, arboreality, nocturnality, and dietary breadth that influence their extinction risks. Geographic ranges for these species are wide, small, contracting, and fragmented. Such diversity of species characteristics makes African carnivores a useful model to build and test the conceptual framework of a capacity gap analysis in conservation planning. Conceptually, species with ranges composed of smaller capacity gaps (i.e., more available conservation capacity, ACC) should be less threatened with extinction. For carnivore conservation to be effective in an era of extreme environmental changes resources must be pooled across disciplines that enhance traditional gap analysis. We use the availability of these resources compared to the distribution of threats including hunting pressure, human modification, and drought to determine capacity scenarios that enable forecasting locations within a species' range at risk of contraction (figure S1 in ref. 41). Simply put, areas across a species' distribution where threats outweigh resources are at immediate risk of contraction. We argue that only when both the distribution of threats and the distribution of resources are simultaneously considered can one identify where there are gaps in capacity for mitigation. Ultimately, assessing the ACC across a species' range is necessary to both combat threats and anticipate range dynamics.

## Results

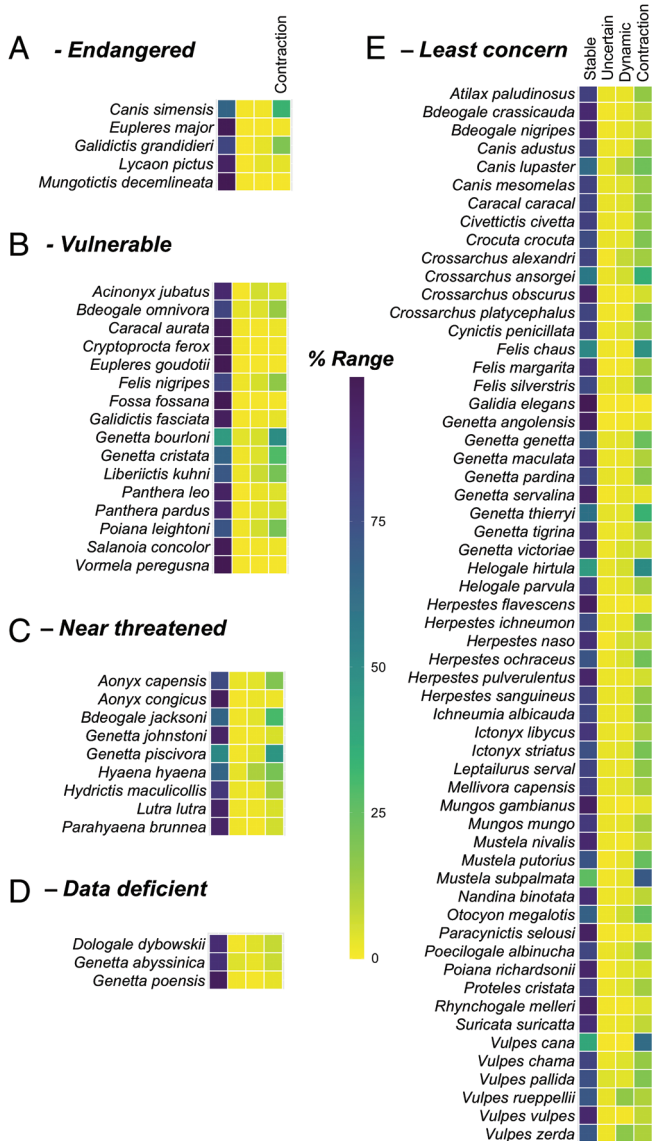
We assessed the ACC for 91 African carnivore species across eight families based on the coupled distribution of threats and

resources that reflect social, environmental, and ecological factors at two scales, individual grid cells within the range ( $ACC_i$ ) and the entire range ( $ACC_r$ ) for a species (see Eq. 1). All maps are presented in the supplementary materials (41). Our final list of African carnivores with available range maps from the International Union for Conservation of Nature (IUCN) included 91 species with only extant ranges used for analyses (table S1 in ref. 41). Range sizes (mean = 748,920 km<sup>2</sup>, SE = 101,645) and body sizes (mean = 7.95 kg; SE = 1.99) varied as well as current IUCN threat status among these carnivores with 21 species classified as Endangered (EN) or Vulnerable (VU). While the majority ( $n = 58$ , 64%) of African carnivores are classified as Least Concern (LC), range shifts are still plausible for these species in future.

The distribution of threats and available resources that contribute to species persistence were highly variable among African carnivores and throughout their ranges (table S2 and figure S2 in ref. 41). We aggregated five geospatial layers of human modifications as well as drought and hunting pressures to investigate these threats across carnivore distributions throughout Africa (table S3 in ref. 41). We found risks from drought and hunting pressure were the most prevalent threat, as their normalized mean values (mean<sub>NV</sub>) were the highest across carnivore ranges on average. The different modifications induced from human land use were more limited across the distribution of African carnivores. For 8% of carnivores including the endangered Ethiopian wolf *Canis simensis*, agriculture was a widespread threat across their distributions with mean<sub>NV</sub> ranging from 0.483 to 0.782. However, we also found that metrics of biocultural diversity, such as mammal, bird, and amphibian diversity (B\_DIV) and ethnic diversity (C\_DIV), were widespread resources across carnivore ranges. Specifically, C\_DIV comprised the highest mean<sub>NV</sub> compared to other resources for 12% of African carnivores including two EN species (*Eupleres major* and *Mungotictis decemlineata*). For 11% of the species in our analysis, habitat was also a widely distributed resource that contributed to portions of carnivore ranges being stable.

Our capacity gap analysis revealed several potential outcomes with varying implications for conservation of African carnivores (figure S1 in ref. 41). On average, 81% of carnivore ranges were stable due to the surplus of resources compared to threats across ranges compared to 15% of carnivore ranges having a deficiency that could lead to contractions across IUCN threat categories based on their  $ACC_i$  value. We also found proportions of African carnivore ranges where threats and resources were comparably low (mean = 3% of ranges; range: 0 to 16%), subject to rapid transitions that could induce range contractions. Interestingly, a small proportion of African carnivore ranges were classified as uncertain due to comparably high amounts of threats and resources in specific areas of their distribution (mean = 1.3% of ranges; range: 0 to 4%). As such, cooperation between natural and social agendas becomes essential in these locations across a species' range. Ultimately, forecasting range dynamics informs expectations of spatial patterns in biodiversity as well as conservation prioritization and strategies at the individual species level.

Perceptions of extinction risks guide conservation efforts. Our approach considers the heterogeneity of threats and resources throughout a species' range to forecast range dynamics. Species varied widely in the  $ACC_i$  across their ranges (Fig. 2). Additionally, our results represent an independent validation of current knowledge on the conservation status of African carnivores (Fig. 3). Three carnivores in our dataset were Data Deficient under the IUCN classification: *Dologale dybowskii*, *Genetta abyssinica*, and



**Fig. 2.** Percentage of a species' range classified by ACC outcomes: stable, uncertain, dynamic, or contraction (left to right) for African carnivores across IUCN threat categories.

*Genetta poensis*. All three of these species are small-bodied with relatively small geographic ranges (78,960 km<sup>2</sup>, 83,225 km<sup>2</sup>, and 21,070 km<sup>2</sup>, respectively). Our results indicated which threats were persistent across their ranges: drought and agricultural modification for *D. dybowskii*, drought and hunting pressure for *G. abyssinica*, and only hunting pressure for *G. poensis*. While immediate concerns may not exist for *G. poensis* based on the ACC<sub>j</sub> index, our results raise some concern for the other two Data Deficient African carnivores, as 7% of both ranges are at risk of contraction. A range loss of 7% for a species with a small, isolated geographic range could have major consequences for their future persistence as well as major socio-ecological ramifications.

Most concerning are species with high-capacity gaps (i.e., negative ACC<sub>i</sub>) throughout considerable portions of their range (Fig. 2). In some cases, these species are currently classified accordingly with IUCN threat classification of Endangered. For example, Grandidier's vontsira (*Galidictis grandidieri*) and the Ethiopian wolf have small, restricted ranges occupying a single country with 19% and 33% of their ranges, respectively, at risk of contraction. However, the LC bat-eared fox (*Otocyon*

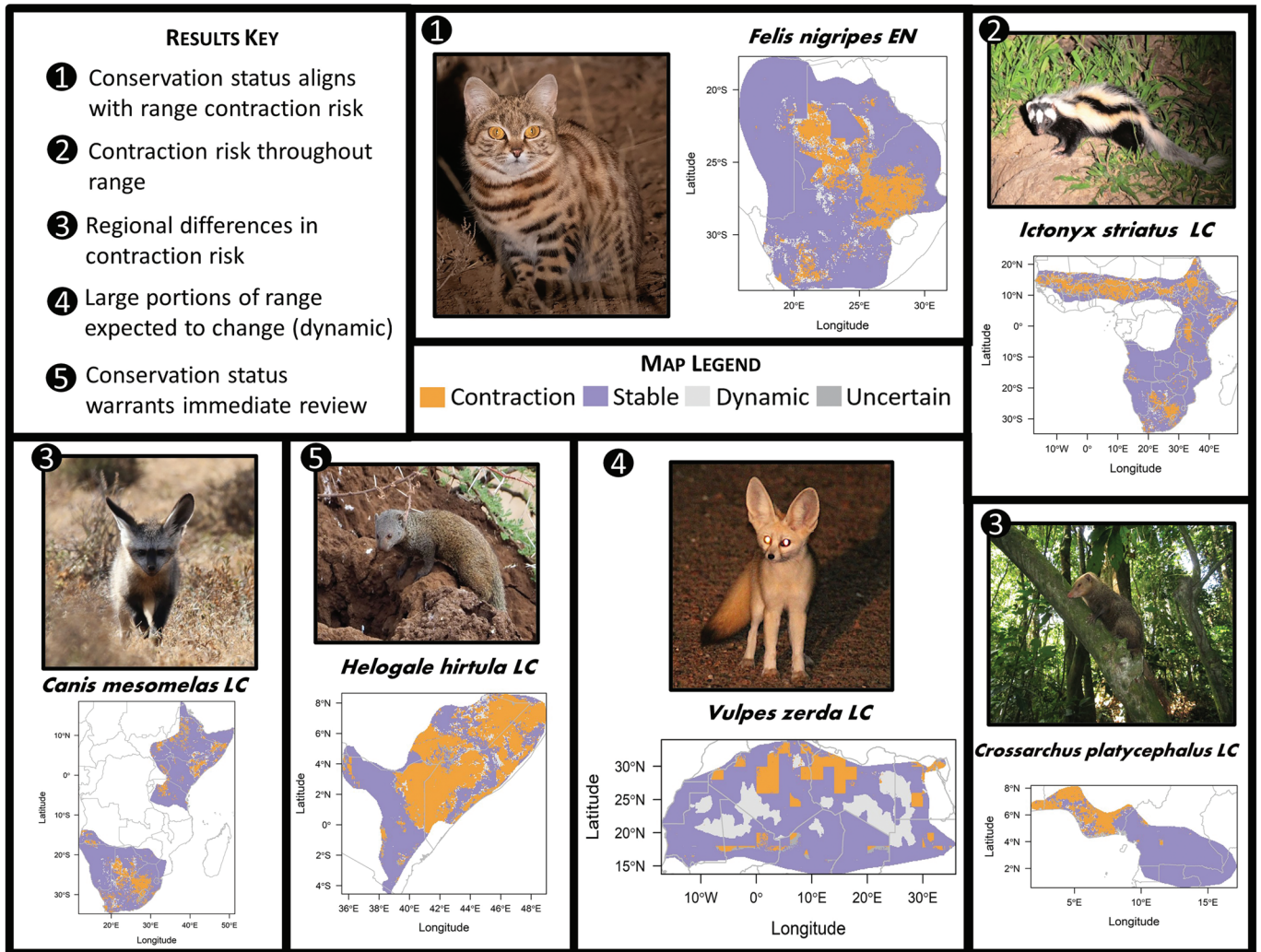
*megalotis*) currently exists within two disjoint ranges, one in eastern Africa (Kenya and Tanzania) and one in southern Africa (Namibia, Botswana, South Africa), and has 25% of its current distribution at-risk of contraction. Overall, we found the majority of Least Concern species (98%) had portions of their range vulnerable to contraction with six species having over one-third of their distributions in Africa at risk.

We further investigated whether species characteristics affected the ACC<sub>j</sub> index value for species using structural equation modeling. Specifically, we included body size, range size, IUCN threat status, and population trend as well as carnivore family. We found a significant positive relationship for body size (standardized  $\beta = 0.22$ ;  $P = 0.0274$ ), indicating that larger carnivores have more conservation capacity. We also found a taxonomic signature with varied relationships among carnivore families with a positive effect of Eupleridae, the Malagasy carnivore guild (standardized  $\beta = 0.57$ ;  $P < 0.001$ ), on ACC<sub>j</sub>. Interestingly, Malagasy carnivores also had significant positive and negative indirect paths to IUCN threat status and population trend, respectively. Contrary to expectations though, ACC<sub>j</sub> was not significantly influenced by the current threat status or population trends (figure S3 in ref. 41).

## Discussion

Despite advancements in geospatial analysis for conservation, we developed a socio-ecological gap analysis that enhances traditional approaches to anticipate how ranges of African carnivores may change in the future due to the distribution of ACC. We explicitly incorporate resources (e.g., protected areas) and threats (e.g., drought pressure) to better understand how extirpation risk might vary spatially and temporally across the geographic ranges of 91 African carnivores. We found that the most common threats across species were drought and hunting pressures, while the biocultural diversity metric was a valuable resource for many species. Although an average of 81% of a species' geographic range was classified as stable due to a surplus of resources compared to threats, we found that, on average, 15% of a species' range was at risk of contraction due to burgeoning threats. In addition, we found that many species that are classified as Least Concern under the IUCN threat schema had the highest percentages of their range at risk of contraction. Our conceptual framework expanded approaches to assess conservation status and anticipate range dynamics based on an ACC index. Additionally, species with higher ACC may serve as an umbrella, broadening effects of single-species conservation efforts.

The IUCN Red List (42) remains the premier source of information of conservation status along with the Living Planet Index with time-series abundance data to guide prioritization efforts (43). However, we did not find strong evidence of alignment between ACC and IUCN conservation status, specifically in that carnivore species categorized as Least Concern did not have low risk of range contractions and those categorized as Endangered did not have the highest ACC. While most African carnivores are classified as Least Concern, they occur in regions undergoing rapid environmental and social change that may threaten the persistence for specific populations. Notably, these results highlight that our current prioritization of species status may be masked by conspicuous local abundance of species that are still vulnerable to extirpation. Additionally, prior investigations of range dynamics highlighted concerns of range contractions among large carnivores (44). Despite several iconic large carnivores of Africa including the African lion and spotted



**Fig. 3.** Exemplar results for African species with the distribution of ACC outcomes to forecast range dynamics. EN and LC denotes Endangered and Least Concern species according to the IUCN Redlist, respectively. (Photo source: iNaturalist; photo credit: *Felis nigripes* – South Africa, Niall Perrins; *Ictonyx striatus* – Malawi, markusgmeiner; *Crossarchus platycephalus* – Central African Republic, Rod Cassidy; *Vulpes zerda* – Western Sahara, Martina Milanese; *Helogale purvula* – Kenya, Zarek Cockar; *Canis mesomelas* – South Africa, jandutoit).

hyena (*Crocuta crocuta*), the carnivore community of Africa is composed mainly of a diverse assortment of small carnivores. We found that smaller carnivores had less ACC. These small carnivores perform vital ecosystem services, support local communities, and disproportionately receive less funding and conservation attention compared to large carnivores (45).

Traditional range maps limit decision-making for conservation because of omitted information (3). However, knowing a place requires knowing its inhabitants and their interactions; cultural diversity and linguistic diversity is often coupled with biodiversity (46, 47). Culturally relevant maps that incorporate people's activities and values in places can also enhance collaboration and effectiveness of conservation efforts. For example, some carnivore species serve as totems of reverence and power within many African communities, which governs their behavior and level of exploitation (Box 1). Though extractive practices are viewed by Western, European-centric values as challenges for conservation, a more inclusive ideology would recognize such use indicates values and opportunities for cooperative management. This is especially true when sustainability is embedded within practices, as evident by Daasanach elders in Kenya reporting reuse of carnivore skins in successive cultural ceremonies so as to not harm

leopard (*Panthera pardus*) and cheetah (*Acinonyx jubatus*) populations (48); according to results of our model these populations are not at risk of extirpation. The distribution of African cultures explicitly represents opportunities for enhanced capacity, a type of social capital, that could contribute to conservation. Historically, designated government protected areas and national parks have been an extension of Eurocentric values and colonial conservation practices, representing a barrier to traditional ecological knowledge and practice (49). Additionally, positioning the nations of Africa as assets may help reduce potentially exacerbating environmental injustices and social inequities resulting from traditionally exclusionary conservation interventions.

Geography remains critically important to conservation planning with continued advancement of quantitative and modeling approaches (50). However, we first acknowledge that results of any analysis reliant on range maps requires validation before local-level interventions can occur for species conservation. Our work relied exclusively on IUCN range maps to assess conservation capacity in our socio-ecological gap analysis, but we recognize these maps are fraught with inconsistencies and errors such as occurrence records far beyond the species' actual range or omission of known

occurrence points (51). Another persistent challenge in our analysis is reconciling the scale of divergent socio-ecological data layers. In our case, relevant information both in relation to spatially explicit threats and resources were omitted because of scale. On one end, the Environmental Justice Atlas (<https://ejatlas.org/>) provides a global representation of environmental activities that are often extractive and interact with human well-being that cause social conflict. These point data are not presented at a scale that reflects the geographic footprint of activities and reporting varies, causing discrepancies in interpretation, despite shared consequences for wildlife that would inform vulnerability risks for African carnivores. However, some of the oil and gas mining coverage is captured within the human modification dataset we used in our analysis. We also attest to not presenting a comprehensive model of all pressures on the continent of Africa threatening species, which could be expanded in subsequent analysis to enhance forecasting range dynamics. On the other end, much relevant resource information such as conservation spending or environmental governance that could inform capacity requires finer spatial scale datasets instead of being constrained to the country level (52, 53). Additionally, distinct from government protected areas, the recognition of indigenous lands in conservation efforts underscores an immediate need to develop this geospatial layer across scales (31).

Another limitation in our approach involves excluding the temporal patterns in resources or threats that would alter the spatial distribution of conservation capacity. Conservation maps are often static representations of dynamic, interacting processes (54). We did not project changes in ACC and instead focused on building the conceptual framework to categorize current contributions across ranges. Our approach also explicitly identifies locations of spatial refugia across a species' range. Populations in these locations are more likely to be stable and potentially serve as source populations in the maintenance of genetic and phenotypic diversity. However, the ACC index we developed could be used for back-casting and forecasting historic and future ranges, respectively. For example, examining historic ranges could inform whether contractions could have been predicted by applying the ACC index at distinct time periods in the past. Results from our model yielded insights into anticipating where ranges may contract to target interventions and identify partners necessary to promote extirpation avoidance.

## Conclusion

Overall, incorporating the “texture” in the form of ACC across a species' range highlighted the spatial consequences of heterogeneity in the distribution and intensity of threats as well as the distribution and availability of resources. Because species' ranges and the conditions encompassed within them are dynamic, an effective strategy must devise spatially explicit and temporally relevant actions that incorporate various knowledge systems and information types. We demonstrated the importance of threats being contrasted with resources to assess capacity and conclude the extent of risks to prioritize interventions. Our approach presents an elegantly simple strategy to forecast future range dynamics. Using African carnivores as the model system, we further demonstrated the complexity of ecological, environmental, and social factors that challenge the persistence of biodiversity in Africa. Conservation planning must acknowledge the interconnectedness of human and natural systems as well as stress the necessity of social-ecological approaches in conservation practice (55). We employed an interdisciplinary approach by including people not

simply through a single disruptive lens of anthropogenic pressures but rather acknowledging that cultural value and heritage of African peoples can fundamentally contribute to species conservation amid extractive customs. As such, by seeking, incorporating, and respecting the traditional ecological knowledge of people in places, conservation can progress to a more inclusive practice and protect species' ranges under varying global change scenarios.

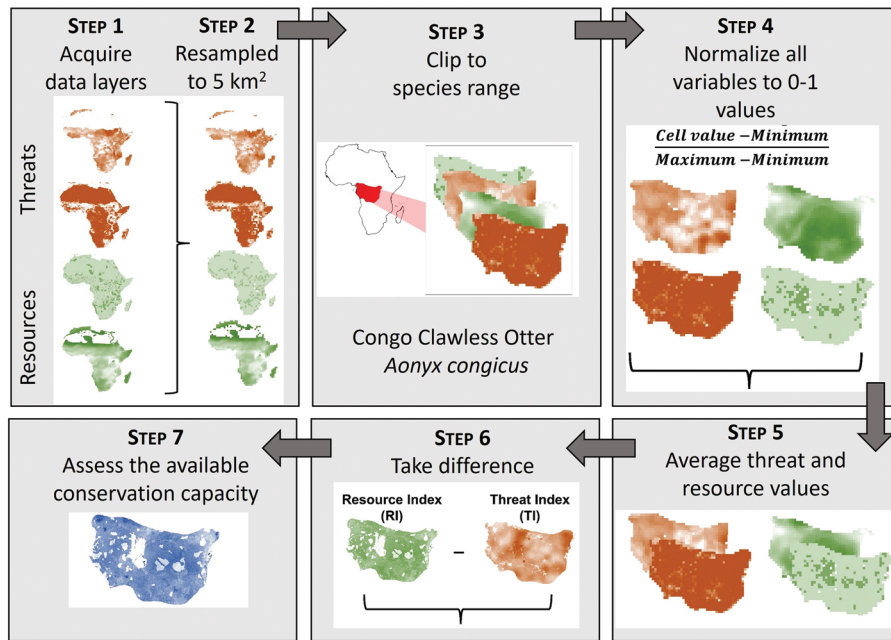
## Materials and Methods

**Datasets.** We obtained a species list from the IUCN Red List of extant terrestrial African carnivores excluding Otariidae and Phocidae species. Our query originally yielded 105 species that were then verified through a literature search and occurrence records in the Global Biodiversity Information Facility (GBIF) database. We removed *Canis lupus* and *Canis aureus* because of limited potential range in Africa and unresolved taxonomy of African wolves in North Africa (56). We also excluded *Viverricula indica* as no range map was available through IUCN. Our final list of carnivores with available IUCN range maps included 91 species across eight families with only extant ranges used for analyses. The dataset comprised 21 species with higher risk of extirpation or extinction based on current assessments that warranted classifications of Endangered (EN) or Vulnerable (VU). See table S1 in ref. 41 for the full species list with associated traits.

All spatial data were downloaded and compiled from open-access platforms, publications, and government geospatial data repositories (table S3 in ref. 41). Threat layers included human modification, drought, and hunting pressure. The drought data were reported as a Standardized Evapotranspiration Index with values ranging from  $-2$  to  $2$ . Human modification to terrestrial ecosystems included spatially explicit datasets on five major anthropogenic stressors: urban/built-up infrastructure; agricultural production and timber harvest; energy production and mining; transportation and service corridors; and human intrusion, natural system modification, and pollution. These data were extracted for each stressor group for Africa from 2017 global datasets at 1,000-m resolution (57). Given the vast uncertainty in climate projection models for Africa, we did not include climate change per se as a threat variable. Instead, we used a standardized precipitation evapotranspiration index as a metric of drought for Africa in 2016 at 1-mo temporal resolution and 5-km spatial resolution (58). From Zhu et al. (59) global model of hunting-gathering populations of present-day climate, we extracted hunting time as an index of hunting pressure across Africa at spatial resolution of  $2^\circ$  latitude. The estimate of hunting time was calculated in part from information on population density, animal biomass availability, daily dry matter intake of meat, and energy reserves based on consumption the previous day. However, the model omits considerations of small animals such as birds, reptiles, insects, and small mammals that would underestimate food availability and estimates of meat in the diet.

Resource layers included habitat, protected area, biodiversity, and cultural diversity (table S3 in ref. 41). Habitat was derived from the European Space Agency CCI Land cover 2020 classification at 300-m resolution. To capture the breadth of habitat requirements and conditions suitable for generalist carnivore species, we identified all land-cover types that could represent suitable habitat for these species. We then combined these land-cover types into six broader categories: forest, grassland, shrub, mixed, sparse, and flooded vegetation all as habitat with individual values of 1 (table S4 in ref. 41). Protected Area (PA) coverage was obtained from the World Database of Protected Areas as polygons for protected areas and community managed areas (version February 2022). Biological diversity (B\_DIV) was calculated as species richness for mammals, birds excluding seabirds, and amphibians at 10-km resolution from 2018 using IUCN and Birdlife International range maps (<https://biodiversitymapping.org/>). Cultural and ethnic diversity (C\_DIV) was calculated as ethnic group richness throughout Africa (60). Individual polygons from this dataset could represent up to three ethnic groups and data occur at 7.5-km resolution. While these data were compiled originally for application in understanding and anticipating civil conflict, we repurpose for a positive application as cultural beliefs can aid in conservation efforts (55). Therefore, capturing the representation of different ethnicities could reflect opportunities that enhance capacity.

**Geoprocessing Spatial Data.** Because the spatial data obtained for threat and resource variables varied widely in format, resolution, and spatial projection, we



**Fig. 4.** Workflow diagram of geoprocessing for spatial threat and resource layers to create the ACC across a species' range.

completed several preprocessing steps prior to analysis that depended on the format of the data (Fig. 4). Data stored as polygons (e.g., PA) were processed to be represented in a numerical raster format, specifying the cell size of the output to be 5 km<sup>2</sup>. Data on the location and settlement patterns of C\_DIV were also stored in polygon vector format and therefore converted into raster files with the number of distinct ethnic groups whose settlements overlap the output cell ranging 0 to 5. Habitat data were processed similarly to C\_DIV in that the output raster displayed the number of suitable habitats (i.e., forest, grassland, shrub, mixed, sparse and flooded vegetation; table S4 in ref. 41). We did not create separate land-cover variables for each classification for a binary classification of each habitat type to avoid zero inflation and instead aggregated for each 5-km<sup>2</sup> cell ranging from 0 to 6.

The remaining data resources and threats were contained in numerical raster files at varying spatial resolutions. All raster files containing continuous data were resampled to a spatial resolution of 5 km<sup>2</sup> through bilinear interpolation of cells. Raster files containing discrete numerical data were resampled to the same spatial resolution (5 km<sup>2</sup>) using the nearest-neighbor method. Bilinear interpolation is the preferred method for resampling raster files of continuous data, as it mitigates the "staircase effect" and blockiness that results from using the nearest-neighbor method when resampling continuous data. On the other hand, the nearest-neighbor method is more appropriate for discrete and categorical raster data (61). We chose the 5-km<sup>2</sup> resolution to align with the finest-scale environmental dataset in our analysis (i.e., drought). This scale also serves as an intermediate resolution with other layers in our dataset and has biological relevance for carnivore home-range and movement patterns, though we still must caution in making specific local decisions from our analysis without additional validation steps. All preprocessing procedures were performed in ArcGIS Pro version 2.8.0.

**ACC.** The dataset of threat and resource variables had a wide range of values including continuous and binary classification. To facilitate comparison and calculation of the ACC index, all variables were normalized to scale from 0 to 1. To achieve this, we clipped each resource and threat raster file to the extent and geometry of each species range and then normalized the values of each variable at the clipped extent rather than at the continental scale to better capture the localized variability in resource and threat values occurring at the scale relevant to the species in question. The ACC index represents the difference between the resources available and threats occurring in a spatially explicit manner. For each species, the ACC was calculated for each grid cell within a species' geographic range as well as at global level as an aggregated total (Eq. 1). We assigned equal weight to each

variable, although future analysis could scale particular variables based on their ecological importance for a given species or group of species, if this information is known.

$$ACC_j = \frac{S_j}{n_j} \quad [1]$$

$$S_j = \left( \sum_{i=1}^{n_j} \left( \frac{\sum R_{ij}}{x_{ij}} \right) - \left( \frac{\sum T_{ij}}{y_{ij}} \right) \right) * 100$$

ACC<sub>j</sub> represents the global level as the total capacity gap for species *j* where *R* is the sum of normalized resources values and *T* is the sum of normalized threat values across *n* locations of a species' geographic range. Because all resource and threat variables may not be present at each location and to make all variables that were present weighted equally, we divided *R* and *T* by *x<sub>ij</sub>* and *y<sub>ij</sub>* representing the number of resources and threats included, respectively. ACC<sub>i</sub> were mapped for each 5-km<sup>2</sup> grid cell across the species range. Positive values indicate a surplus of available resources that presumably can combat threats across landscapes, while negative values signal a deficit of resources and raise concerns for the local persistence of species. ACC<sub>i</sub> values that resulted in differences between resources and threats of <|0.01| were deemed negligible and assigned 0 as the functional value. In summary, the mean difference of averaged normalized resources and threats values were calculated to derive the ACC at the global scale as a single value (ACC<sub>j</sub>) and for each individual cell within a species range (ACC<sub>i</sub>).

Several scenarios can emerge from ACC<sub>i</sub> calculations across a species' range where outcomes affect the persistence of species (Fig. 1). When *R* exceeds *T* (*R*<sub>HIGH</sub> - *T*<sub>LOW</sub>) there is perhaps enough capacity to mitigate threat and expect species' populations in that location to be largely unchanged, resulting in stable ranges. In contrast, when *T* exceeds *R* (*R*<sub>LOW</sub> - *T*<sub>HIGH</sub>) species' populations are at risk for extirpation that could result in range contractions. However, resources derived from natural sources are likely more sensitive to changes, particularly depletion, while the spatial coverage of threats would expand. Therefore, in addition to considering proportions of ranges that are likely stable and those vulnerable to contraction we also identified two additional categories when resources and threats are comparable (*R* ≈ *T*). These have two emergent scenarios when ACC<sub>i</sub> ≈ 0. In the high scenario (*R*<sub>HIGH</sub> ≈ *T*<sub>HIGH</sub>) when the *R* and *T* values are above the median of the distribution, there is much uncertainty and high potential human-carnivore conflict at locations within a species' range. This scenario requires a heavy investment in consultation and collaboration to ensure shared positive outcomes across socio-environmental agendas. In the low scenario (*R*<sub>LOW</sub> ≈ *T*<sub>LOW</sub>) when the *R* and *T* values are below the median of the

distribution, close monitoring is required as  $T$  are likely to emerge more rapidly than  $R$ , which can result in a quick transition to the at-risk scenario. As such, both scenarios that result in  $ACC_i \approx 0$  are highly volatile requiring close monitoring.

**Analysis.** We assessed the relative contribution of a species' IUCN threat status on  $ACC_i$  compared to other explanatory variables including range size, taxonomic family, body size, and IUCN population trends using structure equation models (SEM) in the `piecewiseSEM` package (62). SEMs unite multiple predictor and response variables into a causal network, often visualized through path diagrams. Geographic range size was estimated as the number of cells in the species geographic range layer taken from IUCN and average body weight derived from Myhrvold et al. (63). Range, average body size, and  $ACC$  were all continuous variables. IUCN status of Least Concern (1), Data Deficient (2), Near Threatened (3), Vulnerable (4), and Endangered (5) as well as population trends of Decreasing (1), Unknown (2), Stable (3), and Increasing (4) were ordered categorical variables. We found no indication of multicollinearity using the variance

inflation factor among variables in our analysis using the `car` package (64). We assessed the model goodness-of-fit using Shipley's test of d-separation through Fisher's  $C$  statistic (adequate separation with  $P > 0.05$ ). We expected that if conservation status reflects extirpation risks, then conservation status will be a significant predictor of the  $ACC$  index.

**Data, Materials, and Software Availability.** All data sources and products from analyses are available in the supporting information including individual species  $ACC$  maps that have been deposited in Dryad (<https://datadryad.org/stash/share/ZamtKCx8Q7XsrlsFBo21yvGAddTUKOQaco46QwjmxBM>) (41).

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1. J. Bridle, A. Hoffmann, Understanding the biology of species' ranges: When and how does evolution change the rules of ecological engagement? *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **377**, 20210027 (2022).
2. E. Polaina, M. González-Suárez, E. Revilla, The legacy of past human land use in current patterns of mammal distribution. *Ecography* **42**, 1623–1635 (2019).
3. N. C. Harris, S. Gámez, G. I. Gadsden, R. Malhotra, Textured species range maps enhance interdisciplinary science capacity across scales. *Front. Ecol. Environ.* **20**, 319–326 (2022).
4. A. Johnston et al., Comparing abundance distributions and range maps in spatial conservation planning for migratory species. *Ecol. Appl.* **30**, e02058 (2020).
5. M. Di Marco, L. Santini, Human pressures predict species' geographic range size better than biological traits. *Glob. Change Biol.* **21**, 2169–2178 (2015).
6. A. M. C. Santos et al., Current climate, but also long-term climate changes and human impacts, determine the geographic distribution of European mammal diversity. *Glob. Ecol. Biogeogr.* **29**, 1758–1769 (2020).
7. M. Pacifici et al., Global correlates of range contractions and expansions in terrestrial mammals. *Nat. Commun.* **11**, 2840 (2020).
8. D. Zurell et al., Spatially explicit models for decision-making in animal conservation and restoration. *Ecography* **41**, 1–16 (2021).
9. N. Loiseau et al., Global distribution and conservation status of ecologically rare mammal and bird species. *Nat. Commun.* **11**, 5071 (2020).
10. A. Zizka, C. D. Barratt, C. D. Ritter, T. Joergers-Hickfang, V. M. A. Zizka, Existing approaches and future directions to link macroecology, macroevolution and conservation prioritization. *Ecography*.
11. S. Andréfouët, O. Bionaz, Lessons from a global remote sensing mapping project. A review of the impact of the Millennium Coral Reef Mapping Project for science and management. *Sci. Total Environ.* **776**, 145987 (2021).
12. A. S. L. Rodrigues et al., Global gap analysis: Priority regions for expanding the global protected-area network. *Bioscience* **54**, 1092–1100 (2004).
13. O. Venter et al., Targeting global protected area expansion for imperiled biodiversity. *PLoS Biol.* **12**, e1001891 (2014).
14. X. Zhang, A. C. J. Vincent, Conservation prioritization for seahorses (*Hippocampus* spp.) at broad spatial scales considering socioeconomic costs. *Biol. Conserv.* **235**, 79–88 (2019).
15. B. Goetsch, A. P. Durán, K. J. Gaston, Global gap analysis of cactus species and priority sites for their conservation. *Conserv. Biol.* **33**, 369–376 (2019).
16. J. Major, D. Perry, C. Aslan, R. McManamay, Identifying gaps in protected areas to expand integrated riverine ecosystem conservation. *Conserv. Sci. Pract.* **3**, e470 (2021).
17. S. H. M. Butchart et al., Shortfalls and solutions for meeting national and global conservation area targets. *Conserv. Lett.* **8**, 329–337 (2015).
18. K. R. Jones et al., One-third of global protected land is under intense human pressure. *Science* **360**, 788–791 (2018).
19. N. Politi, L. Rivera, S. Martinuzzi, V. C. Radeloff, A. M. Pidgeon, Conservation prioritization when species distribution data are scarce. *Landsc. Urban Plan.* **210**, 104067 (2021).
20. L. Coad et al., Widespread shortfalls in protected area resourcing undermine efforts to conserve biodiversity. *Front. Ecol. Environ.* **17**, 259–264 (2019).
21. M. Ahmadi et al., Species and space: A combined gap analysis to guide management planning of conservation areas. *Landsc. Ecol.* **35**, 1505–1517 (2020).
22. B. Yang et al., Gap analysis of giant panda conservation as an example for planning china's national park system. *Curr. Biol.* **30**, 1287–1291.e2 (2020).
23. R. P. Powers, W. Jetz, Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nat. Clim. Chang.* **9**, 323–329 (2019).
24. E. C. Ellis et al., People have shaped most of terrestrial nature for at least 12,000 years. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2023483118 (2021).
25. G. Strona et al., Small room for compromise between oil palm cultivation and primate conservation in Africa. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 8811–8816 (2018).
26. O. Venter et al., Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat. Commun.* **7**, 12558 (2016).
27. K. Kimmel, M. Clark, D. Tilman, Impact of multiple small and persistent threats on extinction risk. *Conserv. Biol.* **10.1111/cobi.13901** (2022).
28. V. J. Tulloch et al., Why do we map threats? Linking threat mapping with actions to make better conservation decisions. *Front. Ecol. Environ.* **13**, 91–99 (2015).
29. 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).
30. T. H. Oliver et al., Biodiversity and resilience of ecosystem functions. *Trends Ecol. Evol.* **30**, 673–684 (2015).
31. C. J. O'Bryan et al., The importance of Indigenous Peoples' lands for the conservation of terrestrial mammals. *Conserv. Biol.* **35**, 1002–1008 (2021).
32. G. M. Mace, K. Norris, A. H. Fitter, Biodiversity and ecosystem services: A multilayered relationship. *Trends Ecol. Evol.* **27**, 19–26 (2012).
33. F. Isbell et al., Linking the influence and dependence of people on biodiversity across scales. *Nature* **546**, 65–72 (2017).
34. E. Mavhura, S. Mushure, Forest and wildlife resource-conservation efforts based on indigenous knowledge: The case of Nharira community in Chikomba district, Zimbabwe. *For. Policy Econ.* **105**, 83–90 (2019).
35. D. R. Magness et al., Management foundations for navigating ecological transformation by resisting, accepting, or directing social-ecological change. *Bioscience* **72**, 30–44 (2022).
36. W. J. Ripple et al., Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484 (2014).
37. J. T. Bruskotter et al., Modernization, risk, and conservation of the world's largest carnivores. *Bioscience* **67**, 646–655 (2017).
38. J. Lozano et al., Human-carnivore relations: A systematic review. *Biol. Conserv.* **237**, 480–492 (2019).
39. IUCN, The IUCN Red List of Threatened Species, Version 2021-3. <https://www.iucnredlist.org> Accessed 16 January 2022.
40. N. Sifuna, The future of traditional customary uses of wildlife in modern Africa: A case study of Kenya and Botswana. *Adv. Anthropol.* **2**, 31–38 (2012).
41. N. C. Harris et al., Textured range maps based on available conservation capacity (ACC) for 91 African carnivores. Dryad. <https://datadryad.org/stash/share/ZamtKCx8Q7XsrlsFBo21yvGAddTUKOQaco46QwjmxBM>. Deposited May 31, 2022.
42. A. S. L. Rodrigues, J. D. Pilgrim, J. F. Lamoreux, M. Hoffmann, T. M. Brooks, The value of the IUCN Red List for conservation. *Trends Ecol. Evol.* **21**, 71–76 (2006).
43. J. Loh et al., The Living Planet Index: Using species population time series to track trends in biodiversity. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **360**, 289–295 (2005).
44. C. Wolf, W. J. Ripple, Range contractions of the world's large carnivores. *R. Soc. Open Sci.* **4**, 170052 (2017).
45. C. Marneweck et al., Shining the spotlight on small mammalian carnivores: Global status and threats. *Biol. Conserv.* **255**, 109005 (2021).
46. L. J. Gorenflo, S. Romaine, R. A. Mittermeier, K. Walker-Painemilla, Co-occurrence of linguistic and biological diversity in biodiversity hotspots and high biodiversity wilderness areas. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 8032–8037 (2012).
47. B. R. Tershy, K.-W. Shen, K. M. Newton, N. D. Holmes, D. A. Croll, The importance of islands for the protection of biological and linguistic diversity. *Bioscience* **65**, 592–597 (2015).
48. D. M. Mwamidi et al., Contemporary pastoral commons in East Africa as OECMs: A case study from the Daasanach community. *Parks* **24**, 79–88 (2018).
49. P. Kashwan, R. V. Duffy, F. Massé, A. P. Asiyambi, E. Marijnen, From racialized neocolonial global conservation to an inclusive and regenerative conservation. *Environment* **63**, 4–19 (2021).
50. E. Di Minin, R. A. Correia, T. Toivonen, Quantitative conservation geography. *Trends Ecol. Evol.* **37**, 42–52 (2022).
51. C. J. Marsh et al., Expert range maps of global mammal distributions armonized to three taxonomic authorities. *J. Biogeogr.* **49**, 979–992 (2022).
52. A. Waldron et al., Reductions in global biodiversity loss predicted from conservation spending. *Nature* **551**, 364–367 (2017).
53. M. A. Titley, S. H. M. Butchart, V. R. Jones, M. J. Whittingham, S. G. Willis, Global inequities and political borders challenge nature conservation under climate change. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2011204118 (2021).
54. W. L. Geary et al., Threat webs: Reframing the co-occurrence and interactions of threats to biodiversity. *J. Appl. Ecol.* **10.1111/1365-2664.13427** (2019).
55. R. M. Niemiec et al., Integrating social science into conservation planning. *Biol. Conserv.* **262**, 109298 (2021).
56. M. Krofel et al., Towards resolving taxonomic uncertainties in wolf, dog and jackal lineages of Africa, Eurasia and Australasia. *J. Zool.* **10.1111/jzo.12946** (2021).
57. C. M. Kennedy, J. R. Oakleaf, D. M. Theobald, S. Baruch-Mordo, J. Kiesecker, Managing the middle: A shift in conservation priorities based on the global human modification gradient. *Glob. Change Biol.* **25**, 811–826 (2019).
58. J. Peng et al., A pan-African high-resolution drought index dataset. *Earth Syst. Sci. Data* **12**, 753–769 (2020).
59. D. Zhu, E. D. Galbraith, V. Reyes-García, P. Ciais, Global hunter-gatherer population densities constrained by influence of seasonality on diet composition. *Nat. Ecol. Evol.* **5**, 1536–1545 (2021).
60. N. B. Weidmann, J. K. Rod, L.-E. Cederman, Representing ethnic groups in space: A new dataset. *J. Peace Res.* **47**, 491–499 (2010).
61. A. C. Bovik, *The Essential Guide to Image Processing* (Academic Press, 2009).
62. J. S. Lefcheck, `piecewiseSEM`: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* **7**, 573–579 (2016).



63. N. P. Myhrvold *et al.*, An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology* **96**, 3109–3109 (2015).
64. J. Fox, S. Weisberg, *An R Companion to Applied Regression* (SAGE Publications, 2018).
65. J. K. Young, D. L. Coppock, J. A. Baggio, K. A. Rood, G. Virga, Linking human perceptions and spotted hyena behavior in urban areas of Ethiopia. *Animals (Basel)* **10**, 2400 (2020).
66. S. K. Timothy, D. U. Habib, A. E. Ayodeji, Survey of zoological materials used in traditional medicine in Sabon Gari and Zaria local government areas, Kaduna state, Nigeria. *J. Complement. Med. Res.* **8**, 32–39 (2018).
67. D. W. De Luca, N. E. Mpunga, *Small Carnivores of the Mt Rungwe-Kitulo Landscape, Southwest Tanzania: Presence, Distributions and Threats* (Small Carnivore Conservation, 2013), pp. 67–82.
68. F. Maisels, E. Keming, M. Kemei, C. Toh, The extirpation of large mammals and implications for montane forest conservation: The case of the Kilum-Ijim Forest, North-west Province, Cameroon. *Oryx* **35**, 322–331 (2001).
69. K. S. Bobo, F. F. M. Aghomo, B. C. Ntumwel, Wildlife use and the role of taboos in the conservation of wildlife around the Nkwende Hills Forest Reserve, South-west Cameroon. *J. Ethnobiol. Ethnomed.* **11**, 2 (2015).