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# Widespread range contraction of carnivores in protected areas of China

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Protected areas (PAs) are cornerstones of biodiversity conservation, harbouring key mammal species such as apex predators that are important in maintaining trophic cascades and contribute to ecosystem resilience. However, whether PAs have preserved historical wildlife assemblages remains poorly quantified, mainly due to a lack of comparable data from historical and current periods. Here we used comprehensive data from historical investigations during the 1950s and 1970s, as well as current surveys based on 8,300 camera traps between 2008 and 2021 across 85 PAs in China, to assess range contractions of 82 large- and medium-bodied mammals. We found that carnivores disappeared from 59.4% of their historical sites, a rate much higher than that observed in ungulates (37.2%). Moreover, while 52.9% of PAs retained more than 70% of their ungulate species, over 70% of PAs lost over half of their carnivore species, with PAs in southern China being range contraction hotspots, particularly for carnivore species with larger body sizes and shorter generation lengths. Our findings reveal widespread range contraction of carnivores in China's PAs compared with historical periods, driven primarily by legacy effects of large-scale anthropogenic disturbances and human–wildlife conflict, necessitating initiatives to maintain and restore historical assemblages of carnivores alongside habitat protection.

Species range contraction, the shrinkage of a species' geographic distribution over time, is a critical issue in the biodiversity crisis[1,2]. Range contraction is particularly severe for large-bodied species: many large carnivore and herbivore species have lost over 90% and 80% of their historical ranges[2,3], and more than 70% of large terrestrial mammals have retreated from over 50% of their past range[4]. Consequently, less than 21% of Earth's land areas still support large mammal species (>20 kg) that were historically present[5], mainly in protected areas (PAs)[6]. To achieve the Kunming-Montreal Global Biodiversity Framework's target of reducing the extinction risk of threatened species, it is critical to identify high-risk species and regions that require immediate conservation efforts.

PAs are generally assumed to provide extensive natural habitats with limited human disturbances for numerous threatened species[7]. They play a key role in alleviating wildlife range contractions and preserving historical species assemblages[6,8], both of which are fundamental for maintaining community structure and ecosystem function within PAs[3]. Unfortunately, many PAs are still suffering from both historical and ongoing habitat degradation and overexploitation[9]. Current PAs are insufficient to support the long-term survival of half of terrestrial mammals[10], leading to wildlife retreat even within well-protected habitats[11], a phenomenon known as 'empty forests'[12]. Consequently, wildlife retreat within PAs, particularly the loss of large apex consumers, can trigger trophic downgrading[13], disrupt nutrient

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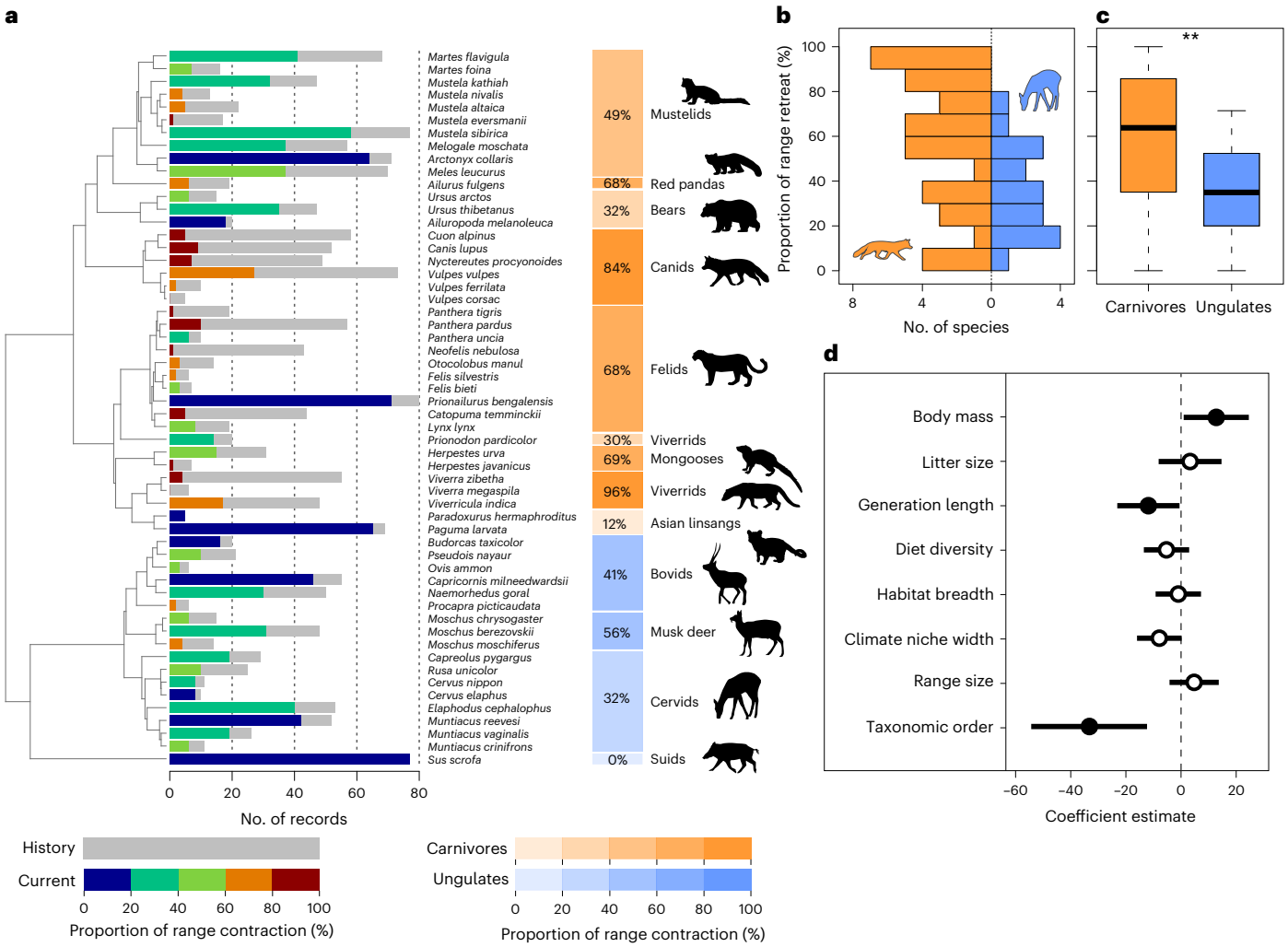


**Fig. 1 | Phylogenetic distribution of species range contraction in China's PAs.** **a**, The observed number of historical records (grey) and current records (colour) and the proportion of range contraction (gradient colours) are represented by bar lengths at branch tips of the phylogenies. $n = 56$ species (those with more than five historical records to ensure the accuracy of geographical range changes per species). This phylogeny was randomly drawn from 100 phylogenetic trees from Upham et al.[64]. **b**, Histogram showing the number of species in each proportion interval of range contraction. **c**, Box plots showing the distribution of observed species range contraction within carnivores and ungulates. The black line inside each box represents the median, the top and bottom of each box represent the 75th and 25th percentiles, respectively, and the whiskers extend to 1.5 times the interquartile range. Significant difference was evaluated using a two-sided Wilcoxon rank-sum test (**$P = 0.007$). **d**, Mean regression coefficients (points) and 95% CIs (error bars) for predicting the proportion of species range contraction in PGLS models. Filled dots indicate statistical significance determined by a two-sided $t$-test ($P < 0.05$). The $P$ values of predictor variables were 0.039 for body mass, 0.940 for litter size, 0.040 for generation length, 0.399 for diet diversity, 0.638 for habitat breadth, 0.052 for climate niche breadth, 0.352 for range size and 0.001 for taxonomic order. Multiple comparisons were not performed in data analyses. Credit: animal silhouettes in **a** and **b** from PhyloPic under a Creative Commons license CC0 1.0.

cycling[14] and ultimately reduce ecosystem resilience[15]. Yet, empirical evidence on whether PAs effectively preserve historical species assemblages remains scarce, primarily due to a lack of comparable data from historical and current periods[2].

China has a PA network including over 2,700 nature reserves, occupying approximately 15% of the country's land surface[16]. These PAs have conducted intensive surveys of wildlife species in the historical periods before and during the establishment of the PAs, mainly between the 1950s and 1970s. While these PAs are successful in forest recovery and ecosystem restoration[17], many species in these PAs have disappeared due to historical hunting and habitat degradation[18]. There is thus an urgent need to assess the extent to which current PAs effectively preserve historical wildlife assemblages[11]. For example, in Xishuangbanna's tropical forests, 17% (9 of 52) of large- and medium-bodied mammal species were extirpated from four PAs by the end of 2022[19]. Even within the distribution range of the giant panda, which has perhaps received the highest conservation priority, PAs have hardly prevented the population collapse of sympatric large carnivore species such as leopards and dholes[11]. Recently, China has set up a national-scale camera trapping monitoring network spanning hundreds of PAs[20], serving as a promising platform in biodiversity monitoring, particularly for large- and medium-bodied terrestrial mammals. Although some studies have assessed the range contraction of species in China on the basis of camera trap data[21,22], most of them are either case studies[23–25] or local and regional studies that cover specific ecosystem types[11,19]. The lack of a nationwide assessment limits our understanding of the patterns and drivers of species range contraction across China's PAs and hinders our ability to predict and reduce the risk of trophic downgrading or ecological marginalization.

To fill this gap, we compiled a dataset of 8,300 camera traps spanning over 1.8 million trap days in 85 PAs during 2008–2021 (current), and compared historical survey data collected mostly between the

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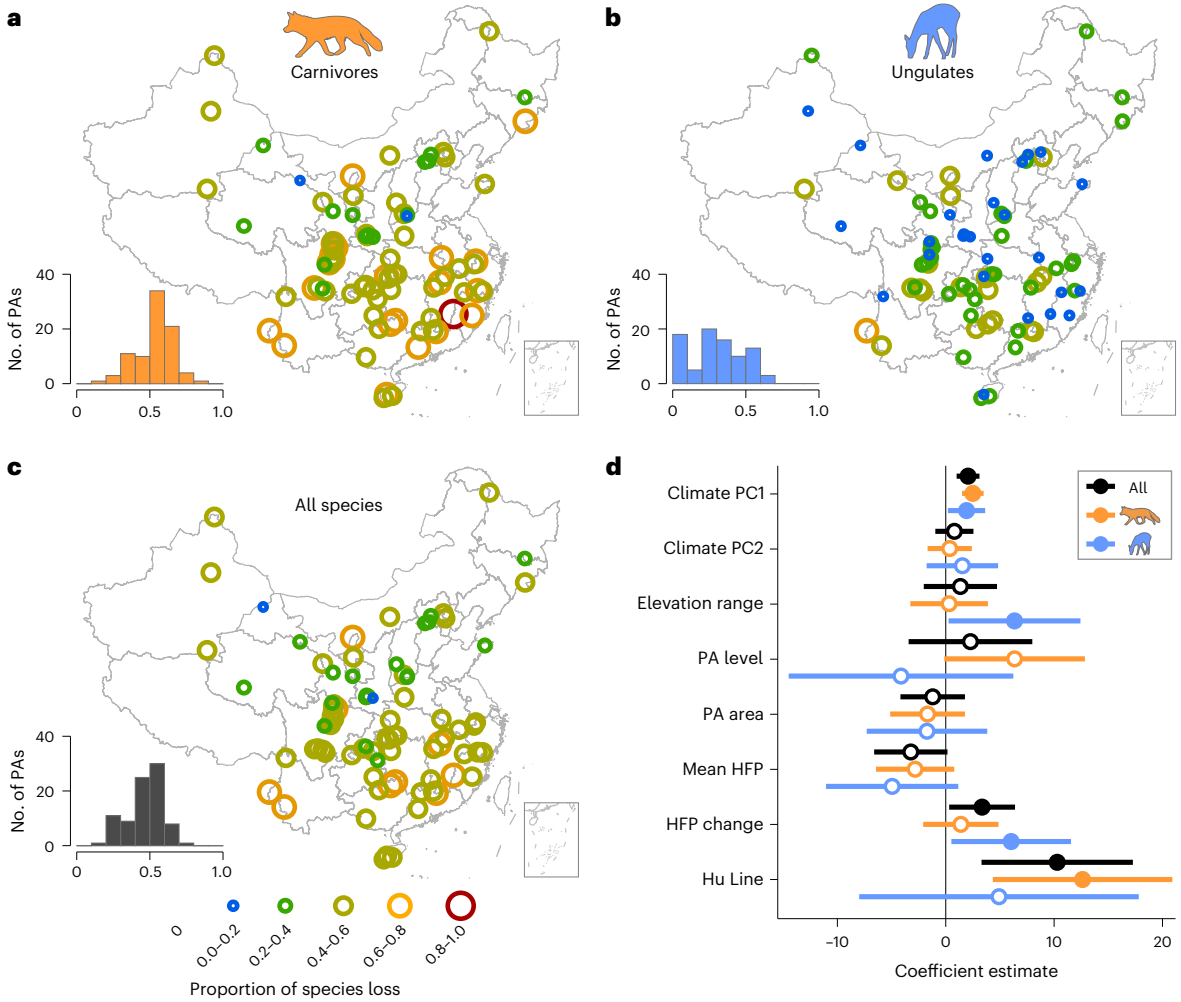


**Fig. 2 | Geographic patterns of species loss in PAs. a**–**c**, Maps showing the magnitude of species loss (one minus the ratio between the current and historical species richness) per PA ($n = 85$) for carnivores (**a**), ungulates (**b**) and all species (**c**). The histograms show the number of PAs within each interval of magnitude of species loss. **d**, Mean regression coefficients (points) and 95% CIs (error bars) for predicting the magnitude of species loss in LMMs. HFP, human footprint. Filled dots indicate statistical significance determined by a two-sided *t*-test ($P < 0.05$; see Supplementary Table 1 for specific *P* values). Multiple comparisons were not performed in data analyses. Basemaps in **a**–**c** from the Resource and Environment Science Data Center of the Chinese Academy of Sciences (http://www.resdc.cn)[71] (approval number GS(2019)1686). Credit: animal silhouettes in **a**, **b** and **d** from PhyloPic under a Creative Commons license CC0 1.0.

1950s and 1970s (historical) in the corresponding PAs, to assess the patterns and determinants of range contractions for carnivores and ungulates. We performed phylogenetic signal analyses and phylogenetic generalized least squares (PGLS) models to test whether range contractions were phylogenetically clustered and associated with species' life-history and ecological traits. Geographically, we fitted linear mixed-effects models (LMMs) to evaluate the potential drivers shaping the magnitude of range contractions per PA. We also projected the risk of range contraction per species using PGLS to identify the high-risk species and mapped hotspots of species with higher extirpation risk. By addressing these issues, this study presents an assessment of range contraction for large- and medium-bodied terrestrial mammals across China's PAs and provides valuable insights into the restoration of historical faunal assemblages.

## Results

### Overview of species range contraction

The mean proportion of range contraction per species across China's PAs was 52.3% compared with the historical surveys (±28.9% s.d.; lower quartile, 27.2%; upper quartile, 77.6%), suggesting that large- and medium-bodied mammal species disappeared from over half of their past ranges in less than a century (Fig. 1a). Carnivores showed a pronounced degree of range contraction, disappearing from 59.4% (±30.0% s.d.) of the PAs where they were historically recorded. Thirteen carnivore species lost ≥80% of their historical sites (Fig. 1a). Carnivore species such as the large-spotted civet (*Viverra megaspila*) and the Corsac fox (*Vulpes corsac*) were among the most extreme cases, with no current records in our camera trap dataset (Fig. 1a and Supplementary Figs. 1 and 2), followed by clouded leopard (*Neofelis nebulosa*, 97.7%), tiger (*Panthera tigris*, 94.7%), steppe polecat (*Mustela eversmanii*, 94.1%), large Indian civet (*Viverra zibetha*, 92.7%) and dhole (*Cuon alpinus*, 91.4%) (Supplementary Figs. 1–5). In contrast, ungulates disappeared from an average of 37.2% (±19.8% s.d.) of the PAs they previously inhabited (Fig. 1a and Supplementary Figs. 6–8), suggesting that the PA network was more efficient in conserving ungulates than carnivores (Wilcoxon rank-sum test, $P < 0.01$; Fig. 1b,c). For example, four ungulates, including Chinese serow (*Capricornis milneedwardsii*), Reeves' muntjac (*Muntiacus reevesi*), red deer (*Cervus elaphus*), and takin (*Budorcas taxicolor*), maintained at least 80% of the PAs they previously inhabited (Fig. 1a). The wild boar (*Sus scrofa*) was an exception; it did not experience any range contraction.

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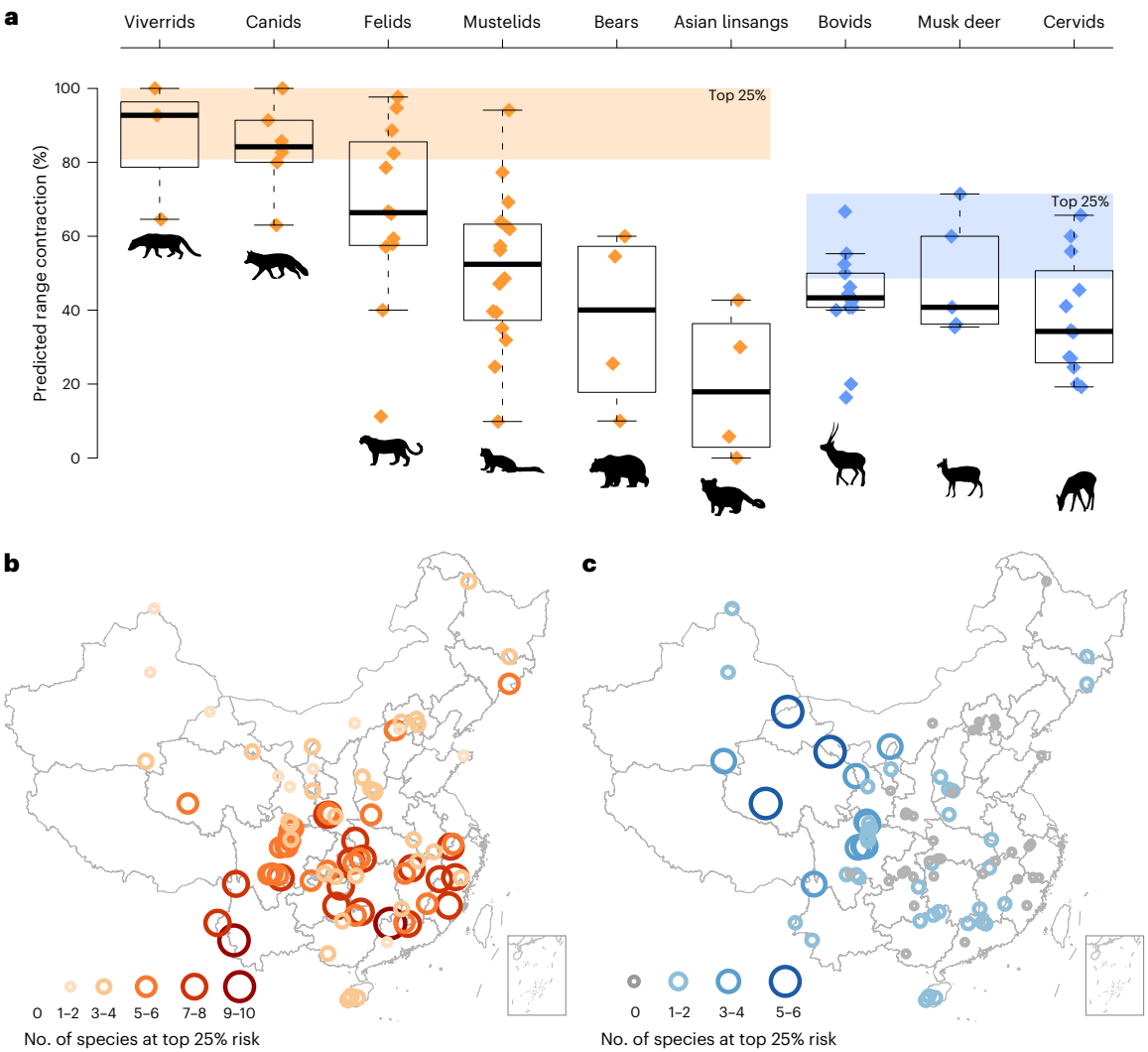


**Fig. 3 | Conservation priority in taxonomy and space. a**, Box plots showing the degree of range contraction in PAs per species within each family. The black line inside each box represents the median, the top and bottom of each box represent the 75th and 25th percentiles, respectively, and the whiskers extend to 1.5 times the interquartile range. The shaded areas show the range contraction of the top 25% of species at high risk for carnivores (orange) and ungulates (blue). **b**,**c**, Maps showing the number of top 25% high-risk species per PA for carnivores (**b**) and ungulates (**c**). Basemaps in **b** and **c** from the Resource and Environment Science Data Center of the Chinese Academy of Sciences (http://www.resdc.cn)[71] (approval number GS(2019)1686). Credit: animal silhouettes in **a** from PhyloPic under a Creative Commons license CC0 1.0.

Only 52.9% ($n$ = 46) of PAs retained more than half of their historical species richness (Supplementary Fig. 9a). The number of carnivore species historically recorded in each PA ranged from 7 to 29 species (mean 16 species per PA), but on average, less than half (47.8%; mean 7.5 species) of the carnivores remain in the present-day PAs. A total of 70.6% of PAs ($n$ = 60) have lost over half of their historical carnivore species, among which five PAs retained less than 30% (Supplementary Fig. 9b). In contrast, 17 PAs did not lose any ungulate species that were previously present, and 45 PAs (52.9%) retained more than 70% of their historical ungulate species (Supplementary Fig. 9c).

## Taxonomic variations in species range contraction

Our phylogenetic analysis revealed a strong and significant phylogenetic signal in range contraction among species (Pagel's $\lambda$ = 0.597, $P$ < 0.05; Fig. 1a), suggesting that the degree of range contraction is not randomly distributed across the phylogenetic tree. Instead, closely related species are likely to have experienced similar degrees of range contraction. For example, the viverrids, canids (for example, foxes, dholes and wolves) and felids (for example, tigers and leopards) on average had higher proportions of range contraction, whereas the Asian linsangs and bears persisted in most of the PAs where they were previously present (Fig. 1a).

After we corrected for phylogenetic effects, the extent of species range contraction was significantly associated with body mass ($\beta$ = 12.8; 95% confidence interval (CI), (1.0, 24.6)), generation length ($\beta$ = −11.8; 95% CI, (−23.1, −0.5)) and taxonomic order ($\beta$ = −33.2; 95% CI, (−54.3, −12.3); Fig. 1d). These results not only reconfirm the large variation in range contraction between carnivores and ungulates but also indicate that species with larger body size and shorter generation lengths have experienced more pronounced range contraction. On the basis of China's national key protected species lists, we found that range contractions were greater for Class I protected species than for unprotected species, but similar to those of Class II (Supplementary Fig. 10), suggesting that the species experiencing the greatest contractions are also those under the strictest legal protection.

## Geographic patterns of species range contraction

The magnitude of species loss per PA revealed that southern China exhibited a pronounced reduction in species range for both carnivores and ungulates (Fig. 2a–c), whereas the Tibetan Plateau and the

northwestern arid regions showed lower levels of range contraction (Fig. 2a–c). The LMMs identified climate principal component 1 (PC1) as a significant positive predictor for both carnivores ($\beta = 2.50$; 95% CI, (1.50, 3.50); $P < 0.001$) and ungulates ($\beta = 1.92$; 95% CI, (0.20, 3.64); $P = 0.029$; Fig. 2d and Supplementary Table 1), indicating that regions characterized by higher temperature and precipitation are associated with greater species losses. However, mean human footprint index, PA area and PA level did not show significant associations with species losses per PA ($P > 0.05$; Fig. 2d).

Some different patterns and drivers of species loss emerged between carnivores and ungulates (Fig. 2a,b). For carnivores, species loss was highly evident in southeastern China, while PAs in northwestern China, particularly in western Sichuan and the Hexi Corridor, displayed relatively low range contraction (Fig. 2a). The Hu Line ($\beta = 12.62$; 95% CI, (4.34, 20.91); $P = 0.003$), which divides China into distinct ecological zones, was identified as a significant predictor of carnivore species loss. For ungulates, the degree of species loss was significantly associated with elevation range ($\beta = 6.35$; 95% CI, (0.26, 12.43); $P < 0.05$) and human footprint change ($\beta = 6.04$; 95% CI, (0.52, 11.56); $P < 0.05$), but there were no strong geographic gradients (Fig. 2b). Such range contractions have left the PAs where carnivores persist increasingly isolated both in geographic space and in climate niches, a pattern not observed for ungulates (Supplementary Fig. 11). These results suggest that contractions in carnivore ranges were primarily driven by the legacy of large-scale anthropogenic disturbances (for example, those associated with the eastern side of the Hu Line), whereas ungulates were more susceptible to local-scale human disturbance (for example, increases in human footprint within PAs).

### Conservation priority across taxa and space

The identification of high-risk species and regions provides a biogeographical context for conservation prioritization in China. PGLS models based on tenfold blocked cross-validation yielded predictions of range contractions for 26 species that were not included in our training dataset due to few records in historical surveys. The combined dataset of observed ($n = 56$) and predicted ($n = 26$) values identified 12 carnivores and 9 ungulates as species at high risk of range contraction (Fig. 3a). The top 25% of high-risk carnivore species lost 91.3% of their historical sites on average, with viverrids, canids and felids exhibiting the most pronounced range contraction (Fig. 3a). By contrast, the ungulate species at high risk were scattered among families and lost 59.7% of their historical sites on average. When we translated these taxonomic priorities into a spatial context, we found that the number of high-risk species varied across China (Fig. 3b,c). PAs in southern China were home to a disproportionate share of high-risk carnivore species (Fig. 3b), and those in western China were shelters for high-risk ungulates such as the Tibetan gazelle (*Procapra picticaudata*) and white-lipped deer (*Przewalskium albirostris*; Fig. 3c).

## Discussion

By comparing comprehensive data from historical and current surveys, we documented widespread range contractions of large- and medium-bodied mammal species in China's PAs, with only half of PAs retaining more than 50% of their historical species richness in the past century. Carnivores have been disproportionately impacted, disappearing from nearly 60% of their historical ranges within PAs. In contrast to the widely accepted assumption that PAs effectively preserve historical wildlife communities[26], our study exposes critical gaps of PAs in protecting apex predators and highlights an urgent need to restore food webs.

Current PAs have partial success in preserving mammal assemblages, as ungulates still inhabit over 60% of PAs where they historically existed. Among these, 20% of PAs retain all of their previous ungulate species, and more than half of PAs still support over 70% of their historical ungulate communities, suggesting the effectiveness of PAs in preserving historical herbivore species. For example, the recovery of the Tibetan antelope (*Pantholops hodgsonii*) in Hoh Xil Nature Reserve is an iconic anti-poaching achievement of the PA system[27]. Similarly, the well-protected herbivore populations in the Serengeti (Tanzania) and Yellowstone (USA) demonstrate the crucial role of PAs in preserving wildlife owing to strict anti-poaching laws, community engagement and habitat restoration[28]. This is because ungulates, as generalist feeders, have a higher degree of adaptability to disturbances, and they can expand their range and increase dramatically in abundance in PAs due to the extirpation of apex predators.

However, carnivores have disappeared from nearly 60% of the PAs they once occupied. This finding reflects a global conservation paradox: despite PA expansions, current PA systems and conservation strategies are insufficient to protect carnivore species[9,10]. Even in the Giant Panda National Park, one of China's most famous and strict PAs, carnivores such as leopards and dholes have lost over 80% of their historical ranges[11]. Similarly, although well-managed PAs are crucial for animal conservation[29], rapid defaunation within PAs remains common in Africa[30]. This inter-continental evidence reveals a widespread retreat of carnivores in PAs[12]. Notably, some PAs in China have successfully restored populations of flagship species through intensive measures, including Amur tigers[31] and Amur leopards in northern China[32]. However, the success of such umbrella-species-focused conservation strategies does not necessarily translate into the protection of historical species assemblages[21,22], highlighting the critical gap between species-level recovery and ecosystem-level conservation.

Carnivores, as apex predators, need large PAs owing to their requirements for large habitats and abundant food resources[33], and they are particularly vulnerable to habitat loss and fragmentation[29]. For example, tigers (*Panthera tigris*) require extensive home ranges, from approximately 70–300 $km^2$ in tropical regions[34] to 400–780 $km^2$ in the Russian Far East[35]. Unfortunately, many PAs, especially those in southern China with dense human populations, are too small and fragmented to support the long-term survival of carnivore species[36]. In addition, large carnivores have a long history of conflicts with humans, which amplifies their extinction risks, and historical overexploitation is probably an important driver of carnivore retreat[37]. During the mid-twentieth century, China's campaigns against large carnivores precipitated population collapses that persist today due to the time-lagged effect of hunting and habitat loss[38], known as extinction debt. Moreover, the low population densities, lack of potential mates, and slow reproductive output further reduce population recovery from disturbances owing to Allee effects, resulting in local extirpations[39].

Unexpectedly, small carnivores with shorter generation lengths, such as viverrids and mongooses, also exhibited high range contractions. This finding contradicts the assumption that species with shorter generation times are more resilient to disturbance owing to rapid population recovery. This anomaly probably stems from historical policy gaps, as many large carnivore species have been listed as nationally key protected wildlife in China since 1989, and poaching of large mammals is now rare[40]. In contrast, many small carnivores receive inadequate legal protection, and they are still impacted by anthropogenic threats such as snares in PAs[41]. In addition, free-ranging dogs pose hidden threats to small carnivores in PAs by increasing the risk of local extinction through predation, competition and disease transmission[42]. These anthropogenic pressures contribute disproportionately to population declines and range contractions of small carnivores.

Although forest cover and plant diversity in China's PAs have recovered rapidly owing to National Forest Protection Programs implemented in 2000[17], the phenomenon of 'empty forests' is widely reported[43]. As a result, range contractions of carnivores have disrupted food webs, hampered nutrient cycling, reduced regional biodiversity and degraded ecosystem services[13–15]. For example, the local extinction of wolves resulted in hyperabundant ungulate populations that suppressed the growth and recruitment of aspens, which caused vegetation degradation and soil erosion in Yellowstone National Park[44].

In addition, the range contraction of carnivores can lead to ecological marginalization, a phenomenon where species retreat towards ecologically harsh areas at the edges of their historic niches[45]. For example, clouded leopards were widespread across southern China in history but now survive only in border regions between China and Southeast Asia, a region outside their ideal climate conditions[24]. Similarly, empirical evidence has supported the ecological marginalization of many of China's endangered species, such as the giant panda (*Ailuropoda melanoleuca*[46]) and the Asiatic golden cat (*Catopuma temminckii*[25]). This spatial mismatch between contemporary ranges and historic niche optima risks local extinctions owing to environmental fluctuations, demographic stochasticity and edge effects[45].

To achieve the Kunming-Montreal Global Biodiversity Framework's target of reducing the extinction risk of threatened species, conservation strategies should focus not only on vegetation cover but also on maintaining and restoring carnivores in their historical ranges[47]. Specifically, carnivore species conservation needs to tackle the long-standing challenge from human activities such as illegal hunting and wildlife trade[18], and hidden threats such as free-range dogs and snares[42]. Immediate funding and conservation efforts are also needed to connect the fragmented landscapes through wildlife corridors and to tightly conserve remnant populations in existing PAs. Europe's successful recovery of wolves, bears and lynx implies that beyond relying on isolated PAs, carnivores can be integrated into multifunctional landscapes through legal coexistence frameworks, compensation schemes for human–wildlife conflicts and greater social tolerance[48]. These actions can not only restore food webs and prevent empty-forest syndrome[12] but also reduce extinction risk from ecological marginalization. By aligning these efforts with policy innovations, we hope that China's PAs can evolve as dynamic, functional ecosystems rather than isolated biodiversity museums for safeguarding the long-term survival of large-bodied mammals.

We acknowledge several potential limitations in our analyses. First, we considered historical species occurrence in PAs as a baseline, yet some records of large-bodied carnivores (for example, tigers and leopards) were sourced from specimens, which might have already been extirpated long before the PA's establishment. Our results thus may underestimate the effectiveness of PAs in mitigating biodiversity loss. Second, camera trap surveys in China's PAs are predominantly conducted in forest ecosystems[49], with greater sampling effort in the southeastern parts of China and sparser coverage in the northwest (Supplementary Fig. 12). This spatial variation in sampling effort may increase the risk of false absences (that is, undetected presences) for species with naturally low detection probabilities (for example, clouded leopards and dholes) in under-sampled areas, potentially inflating the observed range contractions for these species. Furthermore, this could result in an underestimated evaluation of the magnitude of range contractions of arid and alpine species in northwestern China. Finally, our study focused on large- and medium-bodied mammals and did not include small-bodied species with low detectability. For example, certain otters[23] and pangolins[50] have experienced significant range contractions in China's PAs, but since they are more likely to be captured by trail-based or targeted camera trapping rather than the systematic grid-based designs typically used for biodiversity inventories[20], they were not included in our study. Future studies should enhance long-term wildlife monitoring by integrating environmental DNA, bioacoustics and unmanned aerial vehicles to better quantify how species distribution changes in response to anthropogenic pressures.

This study has demonstrated that large- and medium-bodied mammals have experienced widespread and substantial range contractions despite the establishment of extensive PAs across China in recent decades. While PAs have succeeded in preserving ungulate species, they are less effective in protecting carnivore species, particularly those with larger body sizes and shorter generation lengths. Therefore, even well-established PA networks such as those in China may inadequately protect and recover apex predators and their associated ecosystem functions. To avoid trophic downgrading and ecological marginalization, there is an urgent need to maintain and restore historical assemblages of carnivores alongside habitat protection.

## Methods

### Species records

To evaluate the magnitude of species range contraction, we compared presence–absence data from historical and current surveys in PAs. Historical species lists were extracted from survey reports created during the establishment of the PAs, representing the most baseline faunal composition typically dating back to the 1950s–1970s[11]. Historical survey data were integrated from multi-sourced evidence, including systematic faunal investigations, specimen collections, expert interviews and historical hunting records. We considered a species to be historically present in a PA if the species was included in historical species lists. Current survey data were collected during 2008–2021, primarily from national-scale camera trap biodiversity monitoring programmes[51]. Camera trapping provides the most reliable updates on species distributions in China, particularly for large- and medium-bodied mammals[20].

We systematically searched for publications on species checklists of PAs in China using the China National Knowledge Infrastructure (https://www.cnki.net/), Wanfang Data (https://www.wanfangdata.com.cn/) and the Weipu Chinese journals database (http://www.cqvip.com/) in October 2023. For historical surveys, we employed search terms including 'protected area', 'nature reserve', 'wildlife', 'fauna', 'mammal', 'vertebrate', 'inventory', 'survey' and 'China'. We also searched the Web of Science and Google Scholar using these keywords in English. To maximize the inclusion of historical data, we compiled species checklists from Chinese nature reserve investigation reports[52] and the China Nature Reserve Platform (http://www.zrbhq.cn/). For camera trap surveys, we used terms such as 'camera trap', 'infrared triggered camera', 'automatic camera', 'nature reserve', 'protected area', 'wildlife', 'mammal', 'vertebrate' and 'China'. We supplemented our database with species records from camera trap reviews in China[20,51] and our own fieldwork. We extracted species checklists from camera trap studies meeting the following criteria: (1) full checklists of species recorded during the surveys were reported, (2) data were sampled for at least 1,800 trap days (a minimum of 10 cameras for at least 180 days and nights) and (3) cameras were positioned 0.3–1 m off the ground to detect ground-dwelling species. To ensure valid comparisons, we excluded PAs that had species checklists available in only one temporal dataset, either historical records or camera trap surveys. This resulted in a national-scale dataset from over 8,300 camera traps in 85 PAs (covering approximately 9.11% of sites and 22.61% of the areas of China's PAs; Supplementary Table 2 and Supplementary Fig. 12), collectively sampling over 1.8 million camera-trap-days during 2008–2021 (Supplementary Fig. 13 and Supplementary Data 1).

We included only carnivores and ungulates in our analyses due to their large and medium body sizes (Supplementary Fig. 14), which allow for reliable detection and identification in historical surveys and camera trap surveys across China. We standardized species taxonomy using the most recent mammal species checklist of China[53]. Notably, some species recently recognized as distinct were historically considered subspecies of the same species. For example, a phylogenetic study differentiated takins into the Himalayan takin (*Budorcas taxicolor*) and the Chinese takin (*Budorcas taxicolor*) using a high-quality chromosome-level genome[54]. Similarly, red pandas were divided into the Himalayan (*Ailurus fulgens*) and the Chinese red pandas (*Ailurus styani*)[55]. To reconcile taxonomic differences, we merged some recently identified species into previously recognized species groups (Supplementary Table 3). We excluded Chinese river deer (*Hydropotes inermis*), Père David's deer (*Elaphurus davidianus*) and three otter species (*Lutra lutra*, *Aonyx cinerea* and *Lutrogale perspicillata*) as they

generally inhabit wetland environments and are scarcely detected in camera trap surveys. We also excluded 14 species with accidental occurrences owing to marginal distribution and/or suspicious historical records (for example, *Muntiacus gongshanensis*, *Melursus ursinus* and *Vulpes bengalensis*; Supplementary Table 4). The final dataset included 82 mammal species (48 carnivores and 34 ungulates).

### Species-level analyses

We used one minus the ratio of current records to historical records within PAs for each species to quantify species range contraction. This metric captures the actual proportion of species range contraction, although there may be biases for species in western China due to uneven spatial sampling (Supplementary Fig. 12). We excluded species with fewer than five historical records to ensure the accuracy of geographical range changes per species. This resulted in 56 mammal species for species-level analyses, including 38 carnivores (Supplementary Figs. 1–5) and 18 ungulates (Supplementary Figs. 6–8).

To assess whether closely related species exhibit similar degrees of distribution range contraction due to shared traits or evolutionary history, we calculated Pagel's $\lambda$ estimates of phylogenetic signal and tested for its significance using the phylosig function in the R package phytools (v.1.5.1)[56]. Pagel's $\lambda$ ranges from 0 to 1, with a $\lambda$ of 0 indicating no phylogenetic influence on species range contraction and a $\lambda$ of 1 indicating a strong influence of shared evolutionary history. For groups with a high phylogenetic signal, protecting one species might indirectly benefit its close relatives, while for groups with a lower signal, a more species-specific approach might be necessary. We also tested the difference in species range contraction between nationally protected species (Class I/II) and unprotected species on the basis of national key protected species lists of China (https://www.forestry.gov.cn/main/3457/20210205/122612568723707.html).

To explore the drivers of range contraction, we considered key life-history and ecological traits (that is, body mass, litter size, generation length, diet diversity, habitat breadth, climate niche breadth and range size) hypothesized to affect extinction risk in Chinese terrestrial mammals. Body mass for each mammal species was obtained from the PHYLACINE v.1.2 database[57]. Litter size and generation length for each species were derived from Etard et al.[58], with updates from other literature sources. For species lacking litter size information ($n = 7$), we used the mean litter size values of the genus as a surrogate. Diet diversity was calculated using the Shannon index on the proportions of ten diet categories extracted from the EltonTraits database[59], including invertebrates, vertebrates (endotherms, herpetofaunal species and/or fish), scavenged foods, fruits, nectar, seeds, other plant materials and unknown elements. Habitat breadth for each species was measured as the number of suitable habitats using the IUCN Habitat Classification Scheme and was obtained from Ding et al.[60]. Climate niche breadth was measured following the method proposed by Gómez-Rodríguez et al.[61]. Briefly, we quantified the range of climatic variables by overlaying the geographic distribution maps of different species with two variables: mean annual temperature (BIO1) and mean annual precipitation (BIO12). The climatic range for each species was normalized by comparing it to the range across all species in our dataset. For a specific species $i$ out of a total of $j$ species, the standardized range (StRg) was calculated by $StRg_i = [Rg_i - \min(Rg_i{:}Rg_j)]/[\max(Rg_i{:}Rg_j) - \min(Rg_i{:}Rg_j)]$. The climatic niche breadth for each species was derived by multiplying the standardized ranges of BIO1 and BIO12 (ref. 61), and thus this index varies from 0 to 1, with higher values indicating a broader climatic niche space. Range size was measured using the polygon-based geographic range from the IUCN Red List database (http://www.iucnredlist.org).

To disentangle the relative roles of species traits in triggering distribution range contraction, we performed PGLS models under a Brownian motion model of evolution using the R package caper (v.1.0.2)[62]. The predictor variables included body mass, litter size, generation length, diet diversity, habitat breadth, climate niche width, range size and subgroup (ungulate or carnivore). Body mass and range size were log-transformed, and all predictor variables were standardized (with a mean of 0 and an s.d. of 1) to allow comparisons between model coefficients. All continuous variables were checked for multicollinearity using pairwise Pearson correlation ($r$), and only one pair (body mass and generation length) was marginally above the commonly used threshold of $|r| = 0.7$ (Supplementary Fig. 15). We also assessed collinearity using variance inflation factors (VIFs) in the global models and found that all VIFs were lower than 4. In addition, we used an information-theoretic approach to determine the optimal models and predictors that were not affected by collinearity; thus, all of the predictors were included in the analyses. We checked for normality and homoscedasticity of residuals by visual inspection of the diagnostic plots (Supplementary Fig. 16) and did not find substantial deviations from the model assumptions.

For each analysis, we built a full model consisting of all predictor variables and used a multimodel approach based on the Akaike information criterion corrected for small sample sizes (AICc) in the R package MuMIn (v.1.47.5)[63]. We ran 255 models ($2^8 - 1$) for all possible combinations of eight predictors and subset the set of most likely models with $\Delta AICc < 4$. The statistical estimates of each variable were assessed by model averaging using the weights of the models that included the respective variables. To control for phylogenetic uncertainty, we extracted a set of 100 random phylogenetic trees from Upham et al.[64] and included each phylogeny in a PGLS model. The overall effect size estimates of each predictor variable were summarized across these 100 models. The significance of predictor variables was considered if the 95% CI for the coefficient did not overlap with zero.

### PA-level analyses

We considered several location-level factors that potentially affect the magnitude of species losses among different PAs, including climate (temperature and precipitation), topography (elevation and elevation range), protection status (area and level) and human impact (human footprint and human population distribution). Climate data, including 19 bioclimatic variables, were obtained from the WorldClim database[65]. Due to the high correlation among bioclimatic variables across China, we conducted a principal component analysis to reduce the dimensionality of the data and minimize collinearity. We included the first two ordination axes (that is, PC1 and PC2) as predictors because these two axes explained 82.0% of the variation (Supplementary Table 5). The elevation data were derived from the ETOPO Global Relief Model from the National Centres for Environmental Information (https://www.ngdc.noaa.gov/), and the elevation range was measured as the difference between the maximum and minimum elevations. The area and protection level of each PA were derived from the Nature Reserve Checklist of China (v.2017; https://www.mee.gov.cn/). Human footprint data were derived from Mu et al.[66] and were generated using human pressure variables including built environments, human population density, nighttime light, agricultural land uses and transportation infrastructure[66]. Due to negligible annual variations in human footprint per PA (Supplementary Fig. 17), we averaged the annual layers between 2000 and 2018 to represent the anthropogenic pressures experienced by each PA. Apart from the mean value reflecting the absolute level of human footprint, we also included changes in human footprint during 2000 and 2018 in each PA to capture the degree of human pressure changes. The Hu Line (also called the Heihe-Tengchong Line)—a northeast–southwest-oriented boundary dividing China into eastern and western parts on the basis of population density—was used as a binary predictor to explore the large-scale effect of human pressure on species loss. Each PA was assigned to either the eastern or western part of China on the basis of the midpoint of its latitudinal and longitudinal range.

To explore the potential drivers shaping the magnitude of species losses per PA, we fitted LMMs with a Gaussian error structure using the R package nlme (v.3.1-162)[67]. The response variable was measured as one

minus the ratio between the current and historical species richness of each PA. We included random intercepts for zoogeographical realm and for sampling efforts (that is, total camera-trap-days per PA). All other location-specific factors (that is, climate, area, level, elevation, elevation range, human footprint and the Hu Line) were treated as fixed predictors. We built separate models for carnivores, ungulates and both. Collinearity among continuous predictors was tested using pairwise Pearson correlation and VIFs. Given a high Pearson correlation between elevation and elevation range ($|r| = 0.76$; Supplementary Fig. 18) and the highest VIF for elevation (VIF = 9.9) in the full model, we excluded elevation to ensure that collinearity among variables was always low ($|r| \leq 0.7$ and VIFs $\leq 4$). To assess the residual diagnostics of the statistical models, we evaluated the relationship of residuals to theoretical quantiles and predicted values. These model diagnostics confirmed that the Gaussian distributional assumption for the response variable was appropriate (Supplementary Fig. 19).

To account for potential spatial autocorrelation, we incorporated the latitude and longitude of each PA into a correlation structure within our full LMMs. We fitted these models using four correlation structures in the nlme package[67]: spherical (corSpher), rational quadratic (corRatio), Gaussian (corGaus) and exponential (corExp). We used AICc scores to compare each LMM with and without a spatial correlation structure and selected the model with the lowest AICc value as the best-fit model. In all comparisons, the models with no structure consistently had the lowest AICc values (Supplementary Table 6), indicating that spatial autocorrelation did not significantly improve the model fit. The spatial correlation structure thus was not included in further analyses. For the LMMs, we used a model averaging approach to assess the statistical estimates of each variable. Model-averaging analysis was performed using the dredge and model.avg functions in the MuMIn package[63].

### Identifying conservation priority

We ranked the degree of distribution range contraction per species separately for carnivores and ungulates and identified conservation priorities by focusing on the top 25% of species with high-risk distribution range contraction. To estimate the degree of range contraction for species not included in the training database ($n = 26$; that is, species with fewer than five records in historical surveys), we used PGLS models based on a set of predictors selected by the best model with the lowest ΔAICc. To enhance the reliability of predictions, we used a tenfold blocking cross-validation approach that accounts for phylogenetic structure[68]. This method divides our species dataset into ten clusters on the basis of evolutionary relationships among species, ensuring that species within the same cluster are more closely related to each other than to those in other clusters. For each round of validation, we designated nine of these clusters as the training dataset to fit the PGLS models and extracted predicted values from the optimal models. By aggregating the results from all ten rounds across 100 random phylogenetic trees (that is, 1,000 repetitions), we obtained an overall measure of prediction and identified species in the top 25% of range contraction. Finally, we mapped the number of potential priority species (top 25% high-risk species) in each PA to highlight conservation priority areas.

### Reporting summary

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

## Data availability

The species records from historical and current surveys that support the findings of this study are available in Supplementary Data 1.

## Code availability

All the computational analyses were performed in R v.4.3.0 (ref. 69). The code to run the analyses is available via Figshare at https://doi.org/10.6084/m9.figshare.28694552 (ref. 70).

## References


1. Laliberte, A. S. & Ripple, W. J. Range contractions of North American carnivores and ungulates. *BioScience* **54**, 123–138 (2004).
2. Wolf, C. & Ripple, W. J. Range contractions of the world's large carnivores. *R. Soc. Open Sci.* **4**, 170052 (2017).
3. Ripple, W. J. et al. Collapse of the world's largest herbivores. *Sci. Adv.* **1**, e1400103 (2015).
4. Ceballos, G. & Ehrlich, P. R. Mammal population losses and the extinction crisis. *Science* **296**, 904–907 (2002).
5. Morrison, J. C., Sechrest, W., Dinerstein, E., Wilcove, D. S. & Lamoreux, J. F. Persistence of large mammal faunas as indicators of global human impacts. *J. Mammal.* **88**, 1363–1380 (2007).
6. Pacifici, M., Di Marco, M. & Watson, J. E. M. Protected areas are now the last strongholds for many imperiled mammal species. *Conserv. Lett.* **13**, e12748 (2020).
7. Gray, C. L. et al. Local biodiversity is higher inside than outside terrestrial protected areas worldwide. *Nat. Commun.* **7**, 12306 (2016).
8. Torres-Romero, E. J. et al. Global scale assessment of the human-induced extinction crisis of terrestrial carnivores. *Sci. Adv.* **11**, eadq2853 (2025).
9. Laurance, W. F. et al. Averting biodiversity collapse in tropical forest protected areas. *Nature* **489**, 290–294 (2012).
10. Williams, D. R., Rondinini, C. & Tilman, D. Global protected areas seem insufficient to safeguard half of the world's mammals from human-induced extinction. *Proc. Natl. Acad. Sci. USA* **119**, e2200118119 (2022).
11. Li, S. et al. Retreat of large carnivores across the giant panda distribution range. *Nat. Ecol. Evol.* **4**, 1327–1331 (2020).
12. Benítez-López, A., Santini, L., Schipper, A. M., Busana, M. & Huijbregts, M. A. J. Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics. *PLoS Biol.* **17**, e3000247 (2019).
13. Estes, J. A. et al. Trophic downgrading of planet Earth. *Science* **333**, 301–306 (2011).
14. Doughty, C. E., Wolf, A. & Malhi, Y. The legacy of the Pleistocene megafauna extinctions on nutrient availability in Amazonia. *Nat. Geosci.* **6**, 761–764 (2013).
15. Dirzo, R. et al. Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
16. Huang, Y., Fu, J., Wang, W. & Li, J. Development of China's nature reserves over the past 60 years: an overview. *Land Use Policy* **80**, 224–232 (2019).
17. Xu, Y. et al. Have China's national forest reserves designated since 1990 conserved forests effectively? *J. Environ. Manage.* **306**, 114485 (2022).
18. Lau, M. W.-N., Fellowes, J. R. & Chan, B. P. L. Carnivores (Mammalia: Carnivora) in South China: a status review with notes on the commercial trade. *Mamm. Rev.* **40**, 247–292 (2010).
19. Cao, H. et al. Assessment of changes in the composition and distribution of large and medium-sized mammals in Xishuangbanna, Southwest China. *Ecol. Evol.* **14**, e70432 (2024).
20. Xiao, Z. et al. Wildlife monitoring and research using camera-trapping technology across China: the current status and future issues. *Biodivers. Sci.* **30**, 22451 (2022).
21. Liu, J., Kang, Y., Jensen, A. J., Kays, R. & Jiang, A. Apex predator loss drives trophic downgrading in China's protected areas. *Curr. Biol.* **35**, 2872–2880 (2025).
22. Zhang, L. et al. Conservation effectiveness of Chinese protected areas on the completeness of medium- and large-bodied mammal community. *Biol. Conserv.* **306**, 111128 (2025).
23. Zhang, L. et al. The neglected otters in China: distribution change in the past 400 years and current conservation status. *Biol. Conserv.* **228**, 259–267 (2018).

24. Ma, Z. et al. An update on the current distribution and key habitats of the clouded leopard (*Neofelis nebulosa*) populations in China. *Biodivers. Sci.* **30**, 59–73 (2022).
25. Duan, F. et al. Distribution of the Asiatic golden cat (*Catopuma temminckii*) and variations in its coat morphology in China. *Ecol. Evol.* **14**, e10900 (2024).
26. Gaston, K. J., Jackson, S. F., Cantú-Salazar, L. & Cruz-Piñón, G. The ecological performance of protected areas. *Annu. Rev. Ecol. Evol. Syst.* **39**, 93–113 (2008).
27. Pei, J. et al. Recovered Tibetan antelope at risk again. *Science* **366**, 194 (2019).
28. Linnell, J. D. C. et al. The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. *Biol. Conserv.* **244**, 108500 (2020).
29. Magioli, M. et al. The role of protected and unprotected forest remnants for mammal conservation in a megadiverse Neotropical hotspot. *Biol. Conserv.* **259**, 109173 (2021).
30. Craigie, I. D. et al. Large mammal population declines in Africa's protected areas. *Biol. Conserv.* **143**, 2221–2228 (2010).
31. Qi, J. et al. Integrated assessments call for establishing a sustainable meta-population of Amur tigers in northeast Asia. *Biol. Conserv.* **261**, 109250 (2021).
32. Wang, T. et al. Amur tigers and leopards returning to China: direct evidence and a landscape conservation plan. *Landsc. Ecol.* **31**, 491–503 (2016).
33. Wolf, C. & Ripple, W. J. Prey depletion as a threat to the world's large carnivores. *R. Soc. Open Sci.* **3**, 160252 (2016).
34. Simcharoen, A. et al. Female tiger *Panthera tigris* home range size and prey abundance: important metrics for management. *Oryx* **48**, 370–377 (2014).
35. Hernandez-Blanco, J. A. et al. Social structure and space use of Amur tigers (*Panthera tigris altaica*) in Southern Russian Far East based on GPS telemetry data. *Integr. Zool.* **10**, 365–375 (2015).
36. Sun, W., Zhao, Y., Chen, W. & Bai, Y. Current national nature reserves are insufficient to safeguard the long-term survival of birds and mammals in China. *Commun. Earth Environ.* **5**, 304 (2024).
37. Ripple, W. J. et al. Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484 (2014).
38. Teng, S. N., Xu, C., Teng, L. & Svenning, J.-C. Long-term effects of cultural filtering on megafauna species distributions across China. *Proc. Natl. Acad. Sci. USA* **117**, 486–493 (2020).
39. Daskalova, G. N., Myers-Smith, I. H. & Godlee, J. L. Rare and common vertebrates span a wide spectrum of population trends. *Nat. Commun.* **11**, 4394 (2020).
40. Gong, S. et al. Integrating and updating wildlife conservation in China. *Curr. Biol.* **30**, R915–R919 (2020).
41. Li, Q. et al. Habitat accessibility and snares impact large cats and their prey in Northeast Tiger and Leopard National Park, China. *Biol. Conserv.* **289**, 110414 (2024).
42. Weng, Y. et al. The incursion of free-ranging dogs into protected areas: a spatio-temporal analysis in a network of giant panda reserves. *Biol. Conserv.* **265**, 109423 (2022).
43. Corlett, R. T. The impact of hunting on the mammalian fauna of tropical Asian forests. *Biotropica* **39**, 292–303 (2007).
44. Beschta, R. L. & Ripple, W. J. Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biol. Conserv.* **142**, 2401–2414 (2009).
45. Britnell, J. A., Zhu, Y., Kerley, G. I. H. & Shultz, S. Ecological marginalization is widespread and increases extinction risk in mammals. *Proc. Natl. Acad. Sci. USA* **120**, e2205315120 (2023).
46. Kerley, G. I. H., Te Beest, M., Cromsigt, J. P. G. M., Pauly, D. & Shultz, S. The Protected Area Paradox and refugee species: the giant panda and baselines shifted towards conserving species in marginal habitats. *Conserv. Sci. Pract.* **2**, e203 (2020).
47. Wolf, C. & Ripple, W. J. Rewilding the world's large carnivores. *R. Soc. Open Sci.* **5**, 172235 (2018).
48. Boitani, L. & Linnell, J. D. in *Rewilding European Landscapes* (eds Pereira, H. M. & Navarro, L. M.) 67–84 (Springer International, 2015).
49. Mugerwa, B. et al. Global disparity of camera trap research allocation and defaunation risk of terrestrial mammals. *Remote Sens. Ecol. Conserv.* **10**, 121–136 (2023).
50. Kong, Y. et al. Distribution records and conservation status of Chinese pangolin (*Manis pentadactyla*) in China during 2010–2020. *Biodivers. Sci.* **29**, 910–917 (2021).
51. Wan, Y., Li, J., Yang, X., Li, S. & Xu, H. Progress of the China mammal diversity observation network (China BON-Mammal) based on camera-trapping. *Biodivers. Sci.* **28**, 1115–1124 (2020).
52. He, J., Kreft, H., Gao, E., Wang, Z. & Jiang, H. Patterns and drivers of zoogeographical regions of terrestrial vertebrates in China. *J. Biogeogr.* **44**, 1172–1184 (2017).
53. Wei, F., Yang, Q., Wu, Y., Jiang, X. & Liu, S. *Taxonomy and Distribution of Mammals in China* (Science Press, 2022).
54. Yang, L. et al. Evolutionary conservation genomics reveals recent speciation and local adaptation in threatened takins. *Mol. Biol. Evol.* **39**, msac111 (2022).
55. Hu, Y. et al. Genomic evidence for two phylogenetic species and long-term population bottlenecks in red pandas. *Sci. Adv.* **6**, eaax5751 (2020).
56. Revell, L. J. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**, 217–223 (2012).
57. Faurby, S. et al. PHYLACINE 1.2: the phylogenetic atlas of mammal macroecology. *Ecology* **99**, 2626–2626 (2018).
58. Etard, A., Morrill, S. & Newbold, T. Global gaps in trait data for terrestrial vertebrates. *Glob. Ecol. Biogeogr.* **29**, 2143–2158 (2020).
59. Wilman, H. et al. EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* **95**, 2027–2027 (2014).
60. Ding, C. et al. A dataset on the morphological, life-history and ecological traits of the mammals in China. *Biodivers. Sci.* **30**, 21520 (2022).
61. Gómez-Rodríguez, C., Baselga, A. & Wiens, J. J. Is diversification rate related to climatic niche width? *Glob. Ecol. Biogeogr.* **24**, 383–395 (2015).
62. Orme, D. et al. caper: comparative analysis of phylogenetics and evolution in R. R package version 1.0.2 (2023).
63. Bartoń, K. MuMIn: Multi-model inference. R package version 1.47.5 (2023).
64. Upham, N. S., Esselstyn, J. A. & Jetz, W. Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biol.* **17**, e3000494 (2019).
65. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
66. Mu, H. et al. A global record of annual terrestrial Human Footprint dataset from 2000 to 2018. *Sci. Data* **9**, 176 (2022).
67. Pinheiro, J., Bates, D. & R Core Team. nlme: linear and nonlinear mixed effects models. R package version 3.1-162 (2023).
68. Roberts, D. R. et al. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography* **40**, 913–929 (2017).
69. R Development Core Team *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2021).
70. He, J. et al. Data from: Widespread range contraction of carnivores in protected areas of China. *Figshare* https://doi.org/10.6084/m9.figshare.28694552 (2026).
71. Xu, X. *Multi-Year Provincial Administrative Boundary Data in China* (Resource and Environment Science Data Center of the Chinese Academy of Sciences, 2023); https://www.resdc.cn/DOI/DOI.aspx?DOIid=122

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## Author contributions
J.H. and J.L. conceived the ideas and designed the study. J.H, L.Z. and J.Y. collected the data. J.H. and J.L. performed the analyses. J.H. and J.L. led the writing of the paper. J.H., F.W., Z.X. and J.L. contributed to the revisions of the paper. All authors reviewed the contents and approved the final paper.

## Competing interests
The authors declare no competing interests.

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