



## Disproportionate loss of threatened terrestrial mammals along anthropogenic disturbance gradients



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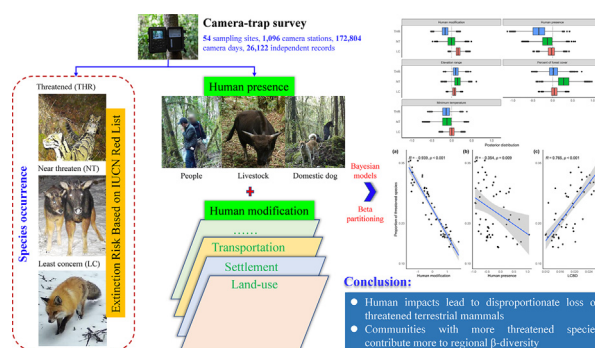
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### HIGHLIGHTS

- Human activities have opposing effects on richness patterns of total and threatened terrestrial mammals
- Threatened terrestrial mammals were more concentrated in areas less impacted by humans
- Human impacts can lead to disproportionate loss of threatened terrestrial mammals
- Communities with more threatened species contribute more to regional  $\beta$ -diversity

### GRAPHICAL ABSTRACT



### ARTICLE INFO

Editor: Rafael Mateo Soria

#### Keywords:

Anthropogenic activities  
Camera trap  
Conservation  
Human modification  
Occupancy  
Southwest China  
Species richness

### ABSTRACT

Tens of thousands of species are increasingly confronted with habitat degradation and threatened with local extirpation and global extinction as a result of human activities. Understanding the local processes that shape the regional distribution patterns of at-risk species is useful in safeguarding species against threats. However, there is only limited understanding of the processes that shape the regional distribution patterns of threatened species. We explored the drivers and patterns of species richness of threatened, non-threatened and total terrestrial mammals by employing multi-region multi-species occupancy models based on data from a broad camera trapping survey at 1096 stations stratified across different levels of human activities in 54 mountain forests in southwest China. We compared correlates between total and threatened species richness and examined relationships of human impact variables with the proportion of threatened species and the site's local contribution to  $\beta$  diversity (LCBD). We found that threatened species richness was negatively related to human modification and human presence. However, both non-threatened and total species richness increased as human modification increased. Predicted proportions of threatened species were strongly and positively related to LCBD but negatively related to human modification and human presence. Our results indicate that human impacts can lead to disproportionate loss of threatened terrestrial mammals and highlight the importance of considering threatened species diversity independently from total species richness for directing conservation

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resources. Our approach represents one of the highest-resolution analyses of different types of human impacts on regional diversity patterns of threatened terrestrial mammals available to inform conservation policy.

## 1. Introduction

It is well known that humans are escalating the global rate of biodiversity loss, leading to an extinction crisis (Ceballos et al., 2015, 2017; Jenkins, 2003) and tens of thousands of species are increasingly confronted with habitat degradation and threatened with local extirpation and global extinction as a result of human activities (Cowie et al., 2022; Howard et al., 2020; Tilman et al., 2017). Mammals are especially vulnerable to human-driven threats with 26 % of species globally threatened with extinction (IUCN, 2021). From a conservation planning perspective, identifying where hotspots of at-risk species occur and which variables shape their occurrence is essential for directing conservation resources and actions (Howard et al., 2019; Wilson et al., 2005). However, there is only limited understanding of the processes that shape the distribution patterns of threatened species (Howard et al., 2020).

Understanding why some areas support more or fewer threatened species than would be expected considering their richness is essential for identifying conservation priorities and also for guiding conservation actions (Howard et al., 2020; Newbold et al., 2018). Threatened species might be expected to be more likely to occur where threats are intense, or in refuges from those threats, or in areas of high overall species richness (Howard et al., 2019; Polaina et al., 2018). There are two alternative hypotheses proposed to explain correlates between threatened species distribution and threatening processes. The threat hypothesis proposes that threatened species are those that encounter more anthropogenic threats, so they are more likely to occur in heavily exploited areas than in less modified landscapes. It thus predicts a positive correlation between the level of threatening activities and the proportion of at-risk species (Howard et al., 2019; Polaina et al., 2018). In contrast, the shelter hypothesis proposes that, as susceptible species locally disappear in heavily exploited areas, remaining populations persist in areas with less human activity, where more habitat with higher integrity is retained (Polaina et al., 2018). Thus, the shelter hypothesis predicts a negative relationship between the intensity of threatening pressure and the proportion of threatened species (Polaina et al., 2018; Yang et al., 2021). Conservation strategies to protect threatened species under the threat hypothesis would require consideration of habitat fragmentation in highly modified landscapes and identify ecological corridors accordingly. On the other hand, conservation actions to retain threatened species under the shelter hypothesis may require strictly preventing human activities in these remaining shelters.

Species differ in their vulnerabilities to extinction (Chen et al., 2019; Wang et al., 2018; Polaina et al., 2019) and, as a result, anthropogenic gradients that drive total and nonthreatened species distribution may operate differently for threatened species (Howard et al., 2019; Moura et al., 2016). Although substantial studies have explored the determinants of spatial gradients in total species diversity (Nogués-Bravo et al., 2008; Stein et al., 2014), few studies have deciphered the drivers of spatial distribution patterns of threatened species and how they differ from those of non-threatened and total species diversity. The few studies that have often used broad spatial scales such as continental or global, and have linked the diversity of threatened species with coarse correlates of human impacts, measured in terms of economic activity (gross national product, GNP), human population density, or land use (Davies et al., 2006; Howard et al., 2020; Ives et al., 2016; Magle et al., 2021). For example, on a global scale, Kerr and Currie (1995) found the proportion of threatened bird species is strongly associated with human population density, whereas the number of threatened mammal species is more highly related to per capita GNP. At a near-continental scale, Howard et al. (2019) found the area of anthropogenic land use is positively related to threatened species richness

but is negatively associated with total species richness. Howard et al. (2020) also found the impact of human activities in driving threatened vertebrate species richness varied substantially between zoogeographic regions and was more explanatory at regional scales. Studies at global or biogeographic realm scale provide valuable insights into what is driving broad-scale occurrence patterns of threatened species, but are unable to account for the localized changes that underlie these patterns (Howard et al., 2019). In addition, broad-scale data on species occurrence and threat levels are prone to be variable in both precision and quality (Howard et al., 2020). In the end, effective conservation planning must be fulfilled at regional and local scales where the ultimate economic and political drivers of threatening processes occur (Howard et al., 2019). Unfortunately, the empirical understanding of regional distribution patterns of threatened species often remains poor. Shuai et al. (2021), however, considering extinction risk in China, found that higher Human Footprint Index analyzed at a fine-grained scale of 1 km square resolution was associated with a marginally higher extinction risk for Carnivora, but not for all species taken together or for Artiodactyla or Lagomorpha considered separately.

From a conservation planning perspective, it is important to identify the optimal measures for defining conservation objectives and goals (Brooks et al., 2006; Niskanen et al., 2017). Species richness is widely used as a proxy for identifying conservation priorities, as it accounts for biodiversity in its broadest sense (Myers et al., 2000). However, overall species richness, and even threatened species richness may be of limited use for conservation prioritization, due to poor correspondence between species richness hotspots and threats to biodiversity (Albuquerque and Beier, 2015; Lennon et al., 2011; Orme et al., 2005). The proportion of threatened species might be more useful than species richness for understanding the relative distribution of threatening activities (Yang et al., 2021). A less often used but potentially valuable diversity metric for defining conservation targets is a site's local contribution to  $\beta$ -diversity (LCBD; Niskanen et al., 2017). This metric quantifies the ecological uniqueness of a site, with high values indicating communities that have more unique species combinations that should be prioritized for conservation (Niskanen et al., 2017; Santos et al., 2021).

Here we use broad regional camera-trap data collected from the China Biodiversity Observation and Research Network for mammals (Sino-Bon Mammals) in a global biodiversity hotspot in the mountains of southwest China to explore the drivers and patterns of species richness and proportion of threatened mammals. Our main goal is to identify the spatial distribution of threatened species in relation to environmental gradients and different levels of human activities. We ask whether variation in at-risk species richness and proportion can be explained by spatial variation in environmental and anthropogenic factors. By comparing the drivers and patterns of total and threatened species richness, we attempt to provide more comprehensive knowledge on what shapes distribution of threatened species, independent of what determines the number of overall species at a broad regional scale. Furthermore, we compare species richness and proportion of threatened mammals with total species richness and LCBD to examine spatial congruence between diversity metrics. We propose the following two hypotheses: threatened species richness is expected to be positively related to overall species richness (Howard et al., 2020; Jokimäki et al., 2018) but negatively related to the level of anthropogenic activities (as predicted by the shelter hypothesis; Polaina et al., 2018); and proportion of threatened species at a site is expected to be positively related to its LCBD, as threatened species are more impacted by environmental differences and by disturbance and have higher turnover rates than non-threatened species (Monks and Burrows, 2014).

## 2. Materials and methods

### 2.1. Study area

The study was conducted at 54 sites in the Hengduan Mountains in southwest China (longitude varying from 93°49' to 101°28' E, latitude from 24°03'–29°50' N) (Fig. 1). This area belongs to one of the world's 36 biodiversity hotspots, and is the most botanically rich subtropical forest ecosystem in the world (CEPF (Critical Ecosystem Partnership Fund), 2002). The area includes the Three Parallel Rivers UNESCO World Heritage Site (Tang et al., 2006), where three major rivers, the Jinsha Jiang (Yangtze), Lancang Jiang (Mekong) and Nu Jiang (Salween), run roughly parallel, north to south, carving deep gorges through the region. Farther west are the gorges and mountains surrounding the Dulong Jiang (upper Ayeyarwady) and Yarlung Zangbo Jiang (upper Brahmaputra). The mountain ranges are characterized by significant vertical relief. Elevation changes of >6000 m between mountain summits and river valleys support a complete spectrum of vegetation types (CEPF (Critical Ecosystem Partnership Fund), 2002). Dominant vegetation types include evergreen

broad-leaved forest, oak forest, rhododendron forest, warm coniferous forest, dark conifer forest and dwarf shrubland. The hotspot is also home to several of the world's best-loved and most threatened mammals, such as Snow leopard *Panthera unica*, Red panda *Ailurus fulgens*, Yunnan snub-nosed monkey *Rhinopithecus bieti* and Takin *Budorcas taxicolor* (Li et al., 2022). The fauna in the Hengduan Mountains are poorly studied, diverse, and subject to multiple anthropogenic threats such as habitat modification and direct presence of humans in wildlife habitat (Li et al., 2022). The region also has a high concentration of ethnic minorities, with 25 officially recognized ethnic minority groups comprising 14 million people (Li et al., 2016b). Local ethnic minorities rely strongly on natural resources, and anthropogenic activities such as livestock grazing and non-timber forest resources collection are prevalent throughout the Hengduan Mountains (Li et al., 2022). Most of the natural forests in the Hengduan Mountains are under some kinds of protection, as community managed sacred sites, state-owned forest, provincial or national nature reserves. Thirty-seven of our sites belong to national nature reserves, 10 sites are state-owned forests, 4 sites are national parks, and 3 sites are provincial nature reserves (Supporting Information Table S1).

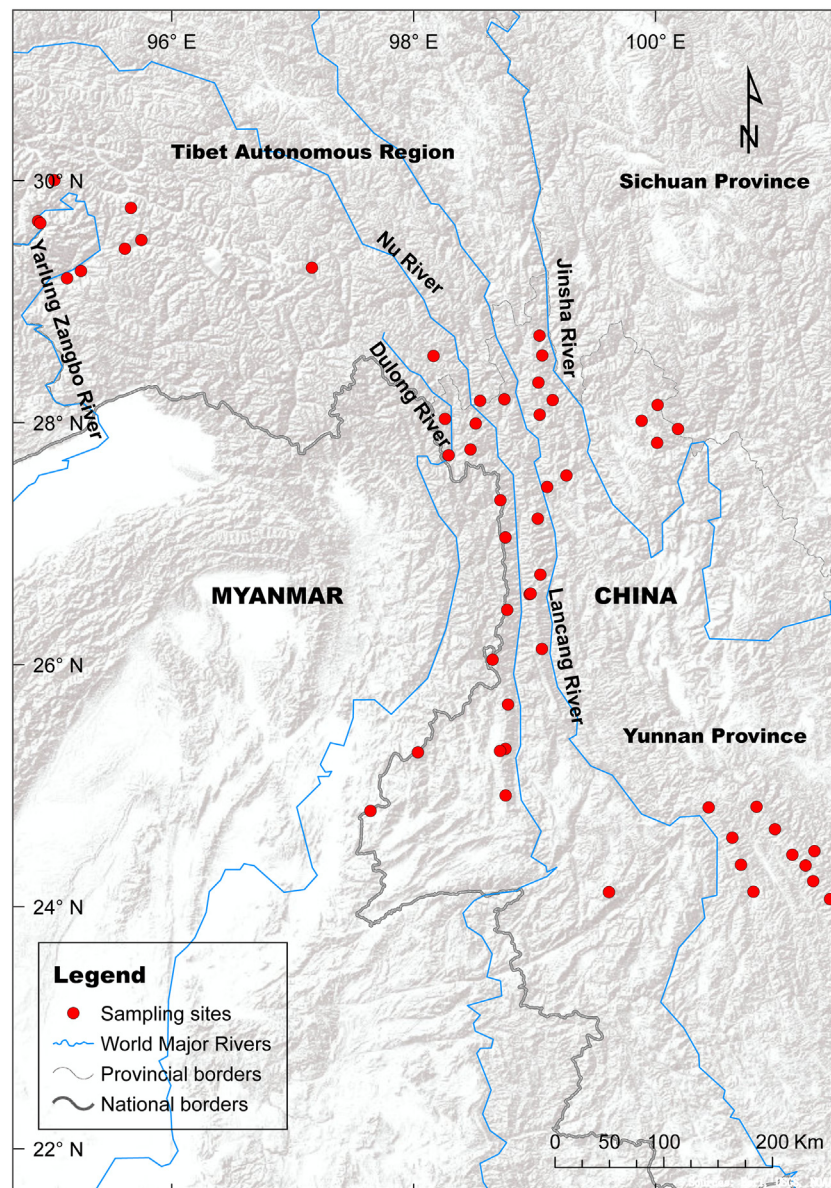


Fig. 1. Camera-trap survey sites in the mountains of southwest China.

## 2.2. Camera trap survey

Our camera trap survey was initiated by the China Biodiversity Observation and Research Network for Mammals (Sino-Bon Mammals) in the mountains of southwest China. We investigated the mammal community using non-invasive camera-trap surveys during the dry season (November–May) from 2020 to 2021. Our survey period was therefore representative of the dry and cold season in the mountains of southwest China. We surveyed 54 forest sites spaced at a minimum of 20 km apart and we considered each site to be an independent community (Fig. 1). The sampling design at each site consisted of 20–33 camera stations spaced apart by a minimum of 800 m and not baited. Three brands of cameras were used (Canglu S1, EREAGLE© E1B and Yianws L720). We set camera traps following the protocol described by Li et al. (2022). We identified mammals to species when possible. We found it is difficult to identify muntjac to species based on camera-trap images, especially at night. Thus, we pooled all detections of the genus and classified them as “*Muntjac* spp.”. We scored direct human presence (records of dogs, livestock or people) in each camera during the sampling period. All images of the same species or direct human presence were considered independent detections when at least 1 h passed between consecutive photographs (Li et al., 2021). The mean sampling effort for each forest site was 3200 camera days (Supporting Information Table S1). The total realized sampling effort was 172,804 camera days from 1096 camera traps that effectively operated, which yielded 26,122 independent detections of 56 medium- and large-bodied mammal species (body mass  $\geq 500$  g) and 5382 independent records of co-occurring human activities (Table S2).

## 2.3. Anthropogenic and environmental covariates

We derived two types of anthropogenic impacts: long-term human modification (e.g., night-time lights, settlement, transportation, etc.) and short-term human presence (occurrence of domestic animals and people as observed with camera traps), and examined their effects on threatened and non-threatened mammal communities separately. We quantified the level of human modification based on the Human Modification (HM) map metric (Kennedy et al., 2019), which is based on 13 anthropogenic impacts caused by five major human activities (agriculture, electrical infrastructure, energy production, human settlement, mining and transportation). The HM dataset thus provides a cumulative estimate of human modification of terrestrial ecosystems at a resolution of 1 km (Kennedy et al., 2019). We quantified the intensities of directly recorded human presence at a camera-trap station by calculating the total number of independent events of people or domestic animals per 100 camera trapping days during the study period.

We compiled a set of natural habitat covariates presumed to impact terrestrial mammal diversity and distribution: (1) elevation range, reflecting terrain condition and habitat heterogeneity within a study site (Rovero et al., 2020); (2) minimum temperature of coldest month, which plays a key role in the distribution of many species in the cold season (Schneider et al., 2021); (3) mean annual precipitation which relates to primary productivity (Ye et al., 2018); and (4) percent of forest cover, which supports food resources, escape shelter and thermal cover (Long et al., 2005). We used the field recorded elevation occupied by all camera-trap stations in a sampling site to measure the elevation range of the study site. The two climatic variables were downloaded from the WorldClim database (<http://www.worldclim.org/bioclimate>). Percent of forest cover was derived from the 250 m Moderate Resolution Imaging Spectroradiometer (MODIS) imagery (MOD44B Vegetation Continuous Fields (VCF) yearly product) of the study area for the period between 2020 and 03-05 and 2021-03-06. We tested for collinearity among covariates using a threshold value of  $|r| = 0.7$  (Dormann et al., 2013) and dropped the annual mean precipitation as it was highly correlated to annual minimum temperature ( $r = 0.77$ ). Previous studies had found that annual minimum temperature was one of the most important factors in shaping the distribution of many mammal species in mountain habitats (Badgley and Fox, 2000). We centered and standardized all covariates prior to analysis.

## 2.4. Data analysis

We divided the detected mammals into three categories: threatened species (listed as critically endangered, endangered, or vulnerable species), near-threatened species (listed as near-threatened species) and non-threatened species (listed as least concern species) based on IUCN Red List of Threatened Species ([iucnredlist.org](http://iucnredlist.org)) and, separately, the China Biodiversity Red List (Jiang, 2021). Since results were similar, only the results from the IUCN Red List are presented here (see Supporting information Table S2, Fig. S1 and S2). For each station, we divided the total sampling period into 5-day intervals (sampling occasions) and scored detection/non-detection matrices for 56 mammals  $>0.5$  kg. We adopted a hierarchical multi-region occupancy framework that allowed us to separately estimate species richness and proportions of threatened and non-threatened species while accounting for imperfect detection (Sutherland et al., 2016; Tenan et al., 2017). The modeling approach assumed that each species  $i = 1, 2, \dots, n_r$  detected at sampling site  $r$  can be assigned a unique threatened category (threatened, near-threatened and non-threatened), with category membership indicated by  $g_{ir}$ . Variation in site- and category-specific richness ( $N_{gr}$ ) is assumed to be a Poisson process,  $N_{gr} \sim \text{Poisson}(\lambda_{gr})$ , where  $\lambda_{gr}$  is the expected category- and site-specific richness modelled as a function of anthropogenic disturbances (human modification (HM) and directly recorded human presence (HP)) and environmental covariates (elevation range (ER), minimum temperature of the coldest month (MT) and percent forest cover (FC)).

$$\log(\lambda_{gr}) = \beta_{0g} + \beta_{1g}HM_r + \beta_{2g}HP_r + \beta_{3g}ER_r + \beta_{4g}MT_r + \beta_{5g}FC_r$$

We decided to fit only linear models after visually inspecting the residual vs. fitted plot of the linear model, which indicated that the spread of residuals tended to be normally distributed around the residual = 0 line (Fig. S3).

The category indicator variable  $g_{ir}$  has a categorical distribution:  $g_{ir} \sim \text{Cat}(\pi_r)$ , with probabilities  $\pi_r = (\pi_{1r}, \dots, \pi_{Cr})$  and  $\pi_{gr} = \lambda_{gr} / \sum_g \lambda_{gr}$ . Parameter  $\pi_{gr}$  is the probability that a randomly chosen species from community  $r$  belongs to category  $g$ .

The true occupancy states of species  $i$  in camera trapping station  $j$  of sampling site  $r$  are denoted as:  $z_{ijr} \sim \text{Bern}(\psi_{ijr}w_{ir})$ , where  $\psi_{ijr}$  is the species-specific occurrence probability for each camera trapping station in each sampling site and  $w_{ir}$  indicates whether species  $i$  exists in site  $r$  ( $w_{ir} = 1$ ) or whether it is structural zero ( $w_{ir} = 0$ ). We found no significant effects of trap-level covariates on  $\psi_{ijr}$ , thus the occupancy sub-model was modelled using species- and site-specific random intercepts,  $\text{logit}(\psi_{ijr}) = \alpha_{0ir}$ , with  $\alpha_{0ir} \sim N(\mu_{ar}, \sigma_{ar}^2)$ , where  $\mu_{ar}$  is the site-specific mean occupancy on logit scale (see Supplementary Code Script S1).

Following the approach of Tenan et al. (2017), we used data augmentation to estimate site-level overall and category species richness while accounting for the number of unobserved species that were present at the site but never detected. To do this, we augmented the detection and category data for all sampling sites such that the total number of potential species in the community was  $M = 100$ . The choice of  $M$  is somewhat arbitrary and is only required to be much larger than the total species in the richest community (Sutherland et al., 2016). For species that were actually observed during the study in a site,  $w_{ir}$  is constantly equal to 1. If a species was not observed in a site,  $w_{ir}$  is governed by the hyperparameter  $\Omega_r$  such that  $w_{ir} \sim \text{Bern}(\Omega_r)$ , where  $\Omega_r$  is used to estimate the number of  $M - n_r$  ‘all-zero’ encounter histories that represent unobserved species that were present at the site but were never detected. Thus, we specified  $\Omega_r = (\sum_g \lambda_{gr}) / M$ . We modelled observed detection frequencies as  $y_{ijr} \sim \text{Bin}(K_{jr}, p_{ijr}z_{ijr})$ , where  $p_{ijr}$  is the detection probability of species  $i$  at camera-trap station  $j$  in site  $r$ , which was modelled as a function of human presence ( $hp_{jr}$ ):  $\text{logit}(p_{ijr}) = \delta_{0ir} + \delta_{1i}hp_{jr}$ , with  $\delta_{0ir} \sim N(\mu_{\delta r}, \sigma_{\delta r}^2)$ , where  $\mu_{\delta r}$  is the site-specific mean detection probability on logit scale (see Supplementary Code Script S1).  $K_{jr}$  is the number of distinct sampling occasions at camera-trap station  $j$  in site  $r$ . Further details on the model formulation

for occupancy and detection probability are described in Supporting Information Script S1.

We fitted models using a Bayesian approach and Markov chain Monte Carlo in JAGS version 3.4.0 (Plummer, 2003) via the package R2Jags (Su and Yajima, 2015) to interface with software R. We made parameter estimates from 30,000 samples of the posterior distribution (3 chains, burn-in of 30,000, and thinning of 10; see Supporting Information Script S1 for model code).

We calculated species occupancy for each sampling site (community) using the species occupancy sub models in the hierarchical multi-region multi-species occupancy models (Supporting Information Script S1). Based on these species metrics, we calculated LCBF values for each site following the approach proposed by Legendre and De Cáceres (2013). We standardized the occupancy-based species-by-site community matrix by Hellinger transformation and calculated LCBF indices using the beta.div function available from the 'adespatial' package in R (Dray et al., 2018).

All inferences are based on posterior means and 95 % Bayesian credible intervals. We used Pearson correlation tests to assess the relationships between LCBF and the model derived parameters of category proportion ( $\tau_r$ ) at each site. We used the traditional threshold of  $p < 0.05$  for statistical significance for  $t$ -tests.

### 3. Results

In 172,804 camera days, we obtained 26,122 independent records of 56 terrestrial mammals across all 54 sampling sites. Eighteen species were categorized by IUCN as globally threatened (2 species critically endangered, 8 endangered, and 8 vulnerable), 9 species as near threatened, and 29 species as least concern. We documented several species of conservation concern, including Chinese pangolin (*Manis pentadactyla*), Myanmar snub-nosed monkey (*Rhinopithecus strykeri*) and red panda (*Ailurus fulgens*) (Table S2).

The hierarchical community model predicting threatened species richness revealed a significant and negative association with human modification, with 95 % Bayesian credible interval for the beta coefficient not overlapping zero ( $\beta = -0.167$ , SD = 0.104, 95 % BCI:  $-0.328$  to  $-0.008$ ; Fig. 2, Table S3). In contrast, human modification had a significant and positive relationship with non-threatened species richness ( $\beta = 0.153$ , SD = 0.074, 95 % BCI: 0.006 to 0.304; Fig. 2, Table S3). Human presence had the highest negative, although nonsignificant, relationship to threatened species richness among the three IUCN

categories ( $\beta = -0.350$ , SD = 0.218, 95 % BCI:  $-0.771$  to 0.077; Fig. 2, Table S3). None of the natural environmental variables had significant effect on species richness of the three categories (Fig. 2, Table S3).

We found no significant relationship between model predicted total and threatened species richness ( $t = 1.683$ ,  $df = 52$ ,  $p = 0.098$ ). Predicted threatened species richness was negatively related to human modification ( $t = -6.817$ ,  $df = 52$ ,  $p < 0.001$ ) and human presence ( $t = -3.279$ ,  $df = 52$ ,  $p = 0.002$ ). Notably, predictions of both total and non-threatened species richness increased as human modification increased (Fig. 3).

Model predicted threatened species proportions were strongly and negatively related to human modification ( $t = -19.639$ ,  $df = 52$ ,  $p < 0.001$ ) and human presence ( $t = -6.422$ ,  $df = 52$ ,  $p < 0.001$ , Fig. 4). LCBF values increased as the proportion of threatened species increased (Fig. 4).

### 4. Discussion

Based on broad regional scale standardized camera trap monitoring data and a multiregional occupancy model, our results demonstrated that threatened terrestrial mammals were more concentrated in areas less impacted by humans, confirming our shelter hypothesis and indicating that vulnerable species have already disappeared locally from heavily modified habitats. Contrary to our expectations, our model also shows that the richness patterns and drivers for threatened species differ dramatically from those for richness overall. Although total species richness increased with human modification, both threatened species richness and proportion decreased with both human impact variables. As predicted, there was a congruence between threatened species proportion and the LCBF metric. We discuss our results in regard to the processes shaping distribution patterns of threatened species and consider the utility of our findings for conservation practitioners.

Our findings suggest that human modification was the primary driver of the regional spatial distribution patterns of numbers of threatened terrestrial mammal species, followed by human presence, with natural environmental factors playing a more minor role. The apparently incongruent patterns of human modification's impacts comparing total and threatened species richness could be attributed to its contrasting effects on threatened and non-threatened species. Human activities and related landscape changes often lead to habitat degradation and increasing effects of fear to

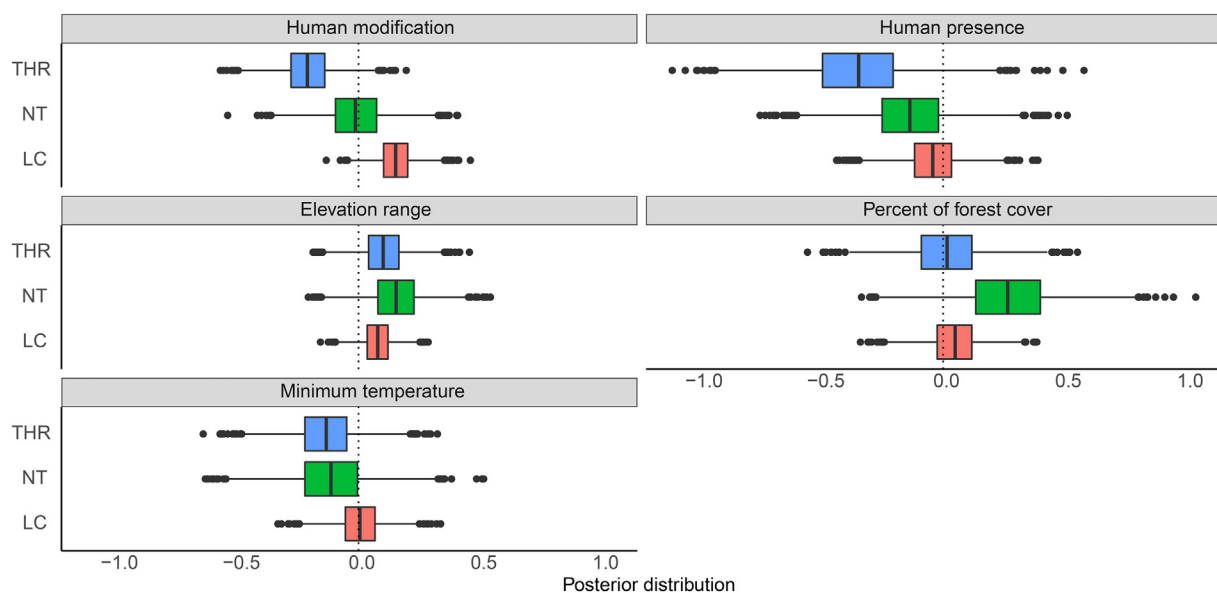


Fig. 2. Influence of anthropogenic and natural environmental variables on species richness of threatened (THR), near-threatened (NT) and non-threatened (LC) terrestrial mammals (Distribution of posterior predicted beta coefficients).

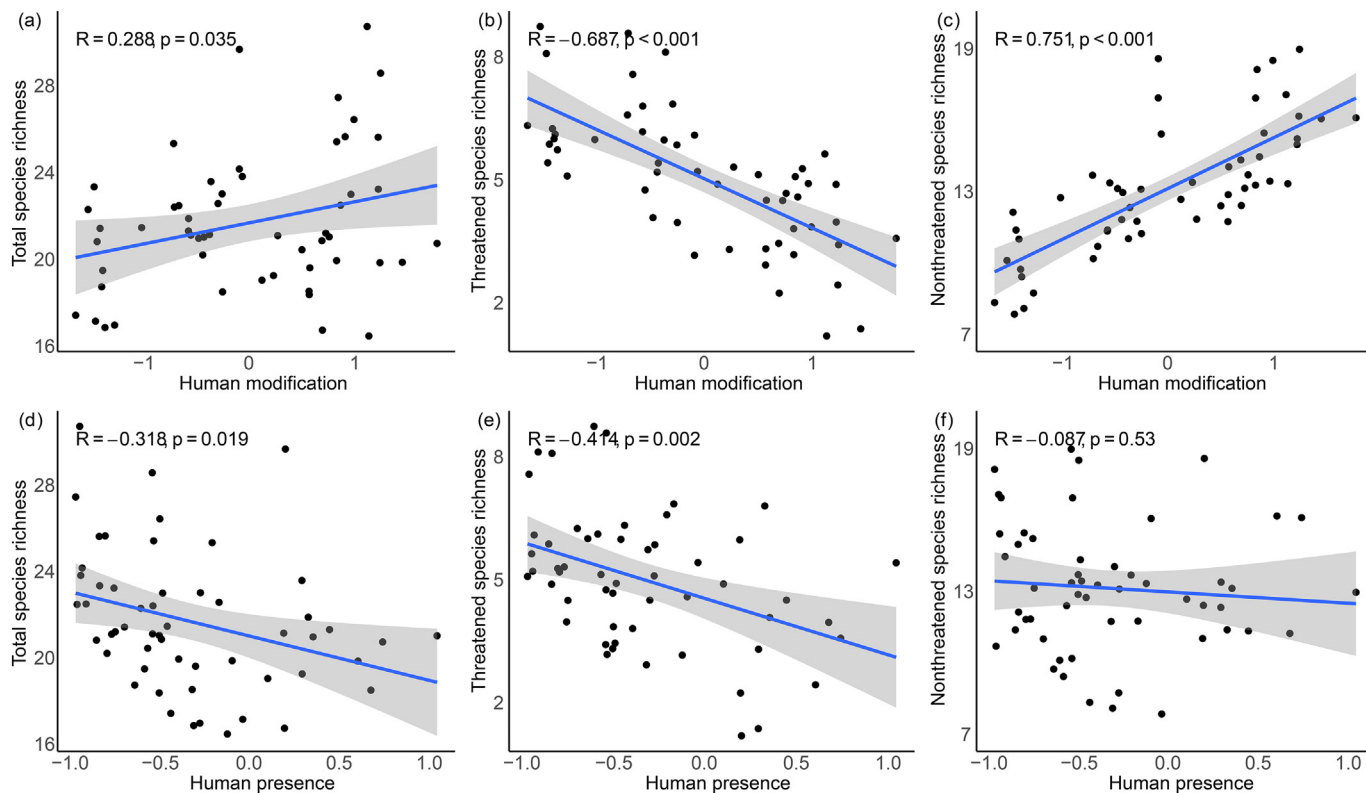


Fig. 3. Relationship between human modification and human presence and the total species richness (a, d), threatened species richness (b, e) and non-threatened species richness (c, f).

which species are exposed (Mendes et al., 2020), relegating more sensitive or less adaptable species to less impacted areas (Li et al., 2021). However, anthropogenic activities are not random in their positive and negative effects on wildlife. While some vulnerable species decline as a result of human impacts (“losers”), some common species apparently benefit and thrive in human modified environments (“winners,” McKinney and

Lockwood, 1999; Newbold et al., 2018; Valdez et al., 2021). The apparently beneficial effect of human modification on non-threatened species richness may reflect the anthropogenic creation of disturbed habitats that are preferred by certain “weedy” non-threatened species, but apparently not by many threatened species. In contrast, the mere presence of humans may not ensure creation of these habitats, and so has no beneficial effect

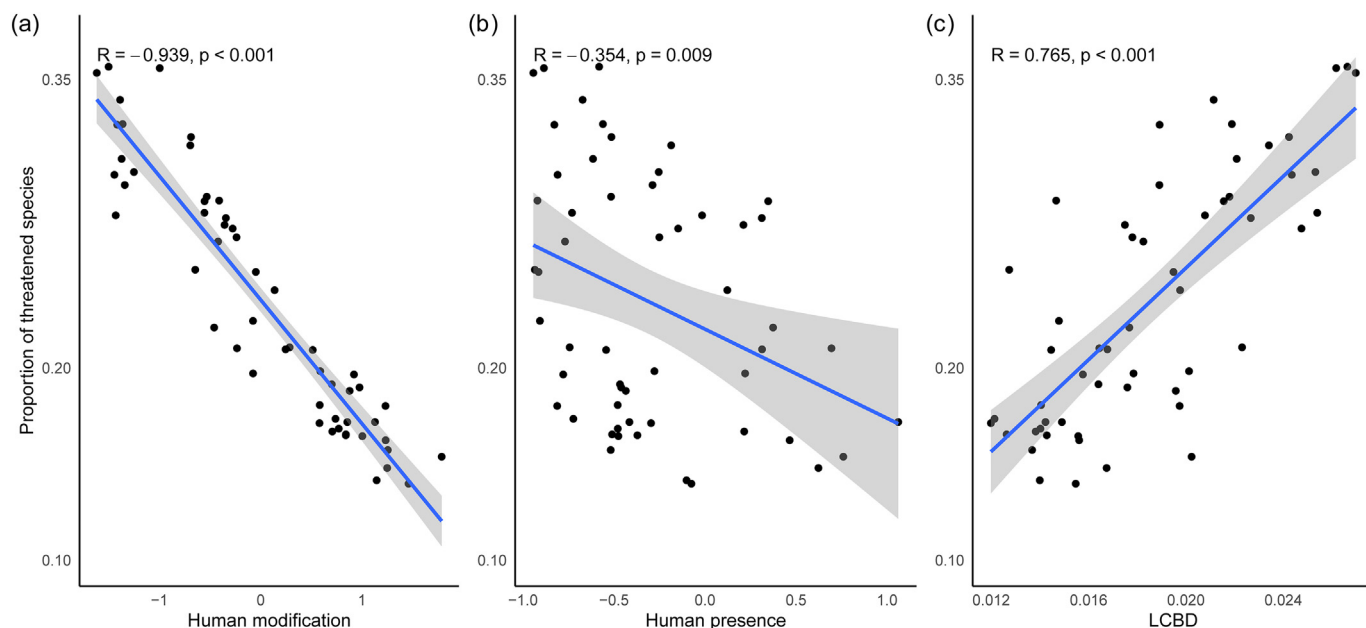


Fig. 4. Relationship between the estimated proportion of threatened species and human modification (a), human presence (b) and local contribution to beta diversity (LCBD; c).

on species richness. Our results show that the mean effects of human presence on categorical species richness increased as extinction risk increased, with threatened species the most affected, followed by near-threatened species and then non-threatened species. These findings highlight the importance of considering threatened species diversity independently from total and non-threatened species diversity for directing conservation resources. Conservation planning aimed at preserving higher total species richness will not guarantee that more threatened species will be preserved along with it.

Our results showed a negative relationship of diversity and proportion of threatened species with levels of human activities. These findings agree with predictions from the shelter hypothesis and highlight the importance of habitats where high concentrations of threatened species occur in less impacted regions. On the contrary, a previous global scale study revealed a positive relationship between richness of threatened mammals and human-dominated land uses (Howard et al., 2020). The differences between the results of our regional model and that of the global analyses imply that the processes driving at-risk species diversity are strongly scale-dependent (Keil et al., 2018). Thus, it is important to identify the optimal scale for studying extinction risk. Although global scale studies of extinction risk can offer important information on what is driving large-scale concentrations of threatened species, their spatial grain is too coarse to detect local heterogeneity in species occurrence (e.g., local disappearance of at-risk species) and threats (e.g., human presence), which are critical information for informing landscape conservation and management to promote threatened species persistence (Howard et al., 2019). In contrast, detailed local analyses can identify the drivers of changes at high-resolution, but conclusions drawn from such fine-grained studies may lack broad conservation application (Bonnot et al., 2013). Our regional scale model provides a compromise between understanding the fine-grain processes driving extinction risk and deriving generalizable conservation implications (Howard et al., 2019).

Low proportion of threatened species in human dominated regions may represent past extinction of sensitive species (Polaina et al., 2018). Our estimates of contemporary human activities do not incorporate legacies of historical human impacts, which are known to play important roles in shaping current threatened species distributions (Dullinger et al., 2013; Li et al., 2016a; Yang et al., 2021). Our objective in the present study was to identify the relationship between observed human impacts and distributions of threatened terrestrial mammals across a range of environmental gradients. However, we note that accurately predicting future distribution patterns of threatened mammals should integrate both historical and contemporary threats related to extinction processes. Further detailed studies need to be done to explicitly disentangle historical and recent drivers shaping regional distribution patterns of threatened species. Nevertheless, based on large spatial scale camera trap data, our approach represents one of the highest-resolution analyses of contemporary human impacts on regional diversity patterns of threatened terrestrial mammals currently available to inform conservation policy.

As we expected, variation in community uniqueness (LCBD) is related to changes in proportion of threatened species, such that high LCBD values are associated with high proportion of threatened species. These relationships indicate that communities with more threatened species contribute more to regional  $\beta$ -diversity. Our findings imply that the proportion of threatened species not only quantify the regional concentration of at-risk species of conservation concern, but also may represent a large degree of the uniqueness of a site in terms of species combinations (García-Navas et al., 2022). Previous studies have reported a negative relationship between total species richness and LCBD values on some occasions for different taxonomic groups (da Silva et al., 2018; García-Navas et al., 2022; Heino and Grönroos, 2017; Santos et al., 2021), indicating that species-rich sites are more likely to share common species with other sites and thus have lower LCBD (Niskanen et al., 2017). This relationship seems to hold for common species, but the relationship is positive if considering only rare or threatened species (Qiao et al., 2015). Rare and threatened species could be locally lost or replaced by common species due to their limited geographic

ranges, small population size and vulnerability to external factors, such as habitat modification and climate change (Zhang et al., 2015). From a practical conservation perspective, high LCBD values may indicate that sites have either unique species composition of high conservation value or degraded species-poor conditions that make them priorities for habitat restoration (Santos et al., 2021). The congruent patterns between LCBD and threatened species proportion could improve the use of the LCBD metric in guiding conservation actions and assessing the consequences of human impacts on local species combinations.

Understanding where threatened species are distributed is critical to setting conservation priorities. By assessing the patterns and drivers of threatened species distribution at a regional scale, our study provides a framework for estimating the filtering effect of anthropogenic activities on terrestrial mammal communities, helping to inform a comprehensive strategy for conservation prioritization and evaluation. Our results confirm that, as human modification and human presence increase, terrestrial mammal community composition shifts towards common species with low extinction risk. The disproportionate loss of threatened terrestrial mammals in human modified habitats is of significant concern for regional biodiversity conservation and ecosystem functioning, given that these animals tend to be at the highest risk of extinction and may play unique and important ecological roles. Continued habitat modification and increased human presence in remaining natural areas portend more local defaunation of threatened species in human-dominated landscapes. The impacts of human presence and modification on threatened wildlife should be carefully considered in planning for land-use and for management of protected areas, the last refuges of many of these threatened species. Policies and budgets for biodiversity conservation should provide continuous support for activities such as monitoring, social and behavior change communications, checkpoints at major access points, patrolling into remote areas and enforcement to control the impacts of human access and exploitation.

## 5. Conclusion

Our approach represents one of the highest-resolution analyses available of different types of human impacts on regional diversity patterns of threatened terrestrial mammals which can inform conservation policy. Our findings demonstrate that human impacts can lead to disproportionate loss of threatened terrestrial mammals and indicate that conservation efforts based solely on overall species richness may fail to provide adequate protection for many threatened species. Identifying priority areas for conservation by targeting clusters of threatened species and unique communities is a first step towards effective biodiversity management and conservation. For example, for purposes of comparing value of investment in protecting different sites in the region, the occurrence of threatened mammals derived from the model could be weighted to produce a relative score for each site, accounting for site area relative to overall area of remaining habitat for each species and differentially weighting near threatened, vulnerable, endangered and critically endangered species, analogous to the Species Threat Abatement and Recovery metric (Mair et al., 2021). To stem extinction, conservation actions must integrate regional scale strategy alongside fine-scale specie-specific strategies in remaining shelter areas that currently support threatened species (Howard et al., 2019). Standardized and long-term monitoring of threatened species within specific regional landscapes will provide a more comprehensive understanding of what determines regional threat processes and better prioritizations of interventions to save species.

## CRediT authorship contribution statement

**Xuelong Jiang:** Conceptualization, Funding acquisition, Project administration. **Xueyou Li:** Conceptualization, Funding acquisition, Methodology, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Wenqiang Hu:** Investigation, Data curation. **William V. Bleisch:** Writing – review & editing. **Quan Li & Hongjiao Wang:**

Investigation, Data curation. **Zhongyi Qin, Jun Sun, Fuyou Zhang & Bu Ti:** Investigation.

## Data availability

Data will be made available on request.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

We thank the Yunnan Forestry and Grassland Department and the Tibet Forestry and Grassland Department for their logistic support and authorities for permitting the study. We thank Minjing Pu, Kang Luo, Changzhe Pu and other collaborators that helped collect data. The study was Supported by the Second Tibetan Plateau Scientific Expedition and Research Program (STEP, #2019 QZKK0501), the Key Program for Basic Research of Yunnan Province (#2018FA052), the National Natural Science Foundation of China (#31601874), and the China Biodiversity Monitoring and Research Network (Sino Bon).

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.158038>.

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