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Functional diversity loss and change in nocturnal behavior of mammals under anthropogenic disturbance

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Article impact statement
Concurrent effects of different types of human disturbance on wildlife communities need to be considered in conservation planning.

Abstract

In the Anthropocene, understanding the impacts of anthropogenic influence on biodiversity and behavior of vulnerable wildlife communities is increasingly relevant to effective conservation. However, comparative studies aimed at disentangling the concurrent effect of different types of human disturbance on multifaceted biodiversity and on activity patterns of mammals are surprisingly rare. We applied a multiregion community model to separately estimate the effects of cumulative human modification (e.g., settlement, agriculture, and transportation) and human presence (aggregated presence of dogs, people, and livestock) on species richness and functional composition of medium- and large-bodied mammals based on camera trap data collected across 45 subtropical montane forests. We divided the detected mammal species into three trophic guilds–carnivores, herbivores, and omnivores–and assessed the nocturnal shifts of each guild in response to anthropogenic activities. Overall, species richness tended to increase (β coefficient = 0.954) as human modification increased but richness decreased as human presence increased (β = –1.054). Human modification was associated with significantly lower functional diversity (mean nearest taxon distance [MNTD], β = –0.134; standardized effect sizes of MNTD, β = –0.397), community average body mass (β = –0.240), and proportion of carnivores (β = –0.580). Human presence was associated with a strongly reduced proportion of herbivores (β = –0.522), whereas proportion of omnivores significantly increased as human presence (β = 0.378) and habitat modification (β = 0.419) increased. In terms of activity patterns, omnivores (β = 12.103) and carnivores (β = 9.368) became more nocturnal in response to human modification. Our results suggest that human modification and human presence have differing effects on mammals and demonstrate that anthropogenic disturbances can lead to drastic loss of functional diversity and result in a shift to nocturnal behavior of mammals. Conservation planning should consider concurrent effects of different types of human disturbance on species richness, functional diversity, and behavior of wildlife communities.

KEYWORDS
camera trap, community occupancy, functional traits, human disturbance, southwest China, trophic guild, wildlife nocturnality

Pérdidas en la Diversidad Funcional y Cambios en el Comportamiento Nocturno de los Mamíferos bajo la Perturbación Antropogénica
Resumen: En el Antropoceno, el conocimiento sobre la influencia antropogénica sobre la biodiversidad y el comportamiento de las comunidades vulnerables de fauna es cada vez

más relevante para la conservación efectiva. Sin embargo, sorprende que los estudios comparativos dirigidos a desentrañar el efecto concurrente de los diferentes tipos de perturbación humana sobre la biodiversidad multifacética y sobre los patrones de actividad de los mamíferos son escasos. Aplicamos un modelo de comunidad multirregional para estimar de manera separada los efectos de la modificación humana (p. ej.: establecimientos, agricultura, transporte) y la presencia humana (presencia agregada de perros, gente y ganado) acumuladas sobre la riqueza de especies y la composición funcional de los mamíferos de tamaño mediano y grande con base en datos de fototrampas recolectados en 45 bosques montanos subtropicales. Dividimos las especies de mamíferos detectadas en tres gremios tróficos: carnívoros, herbívoros y omnívoros, y analizamos los cambios nocturnos de cada gremio como respuesta a las actividades antropogénicas. En general, la riqueza de especies tuvo una tendencia al incremento (coeficiente $\beta = 0.954$) conforme aumentaron las modificaciones humanas, pero la riqueza disminuyó conforme incrementó la presencia humana ($\beta = -1.054$). Las modificaciones humanas estuvieron asociadas con una diversidad funcional (distancia promedio al taxón más cercano [DPTC], $\beta = -0.134$; tamaños del efecto estandarizado de la DPTC, $\beta = -0.397$), masa corporal promedio de la comunidad ($\beta = -0.240$) y proporción de carnívoros ($\beta = -0.580$) significativamente más bajas. La presencia humana estuvo asociada con una proporción gravemente reducida de herbívoros ($\beta = -0.522$), mientras que la proporción de omnívoros incrementó significativamente conforme aumentaron la presencia humana ($\beta = 0.378$) y la modificación del hábitat ($\beta = 0.419$). En cuanto a los patrones de actividad, los omnívoros ($\beta = 12.103$) y los carnívoros ($\beta = 9.368$) se volvieron más nocturnos como respuesta a las modificaciones humanas. Nuestros resultados sugieren que las modificaciones humanas y la presencia de personas tienen efectos diferentes sobre los mamíferos y demuestran que las perturbaciones antropogénicas pueden llevar a pérdidas drásticas de la diversidad funcional y resultar en un cambio hacia el comportamiento nocturno en los mamíferos. La planeación de la conservación debería considerar los efectos concurrentes de los diferentes tipos de perturbaciones humanas sobre la riqueza de especies, la diversidad funcional y el comportamiento de las comunidades faunísticas.

PALABRAS CLAVE
fototrampas, gremio trófico, hábitos nocturnos de la fauna, ocupación comunitaria, perturbación humana, rasgos funcionales, suroeste de China

【摘要】
在人类世, 理解人类活动对受胁野生动物群落结构及行为的影响与生物多样性的有效保护密切相关, 然而鲜有研究对比分析不同类型人类活动对哺乳动物物种和功能多样性的影响。本研究基于亚热带山地森林 45 个调查样地的红外相机监测数据, 采用多区域群落模型分析长期累积的人类改造 (居民点、农业和交通运输等) 和实时人类活动 (红外相机记录到的狗、人和牲畜) 对大中型哺乳动物物种多样性及功能组成的影响。研究将红外相机探测到的哺乳动物按食性 (功能) 分为食肉类、食草类和杂食类, 并分析人类活动对各类群夜行性变化的影响。结果表明: 整体物种多样性随人类改造的增加而上升 ($\beta = 0.954$), 但随实时人类活动的增加而下降 ($\beta = -1.054$); 群落功能多样性 (MNTD, $\beta = -0.134$; ses.MNTD, $\beta = -0.397$)、平均体重 ($\beta = -0.240$) 和食肉类占比 ($\beta = -0.580$) 均随人类改造的增加而显著下降;食草类占比随实时人类活动的增强而显著减少 ($\beta = -0.522$); 杂食类占比则随人类改造 ($\beta = 0.378$) 和实时人类活动 ($\beta = 0.419$) 的增加而显著增加; 行为节律分析结果表明, 人类改造显著增加杂食类 ($\beta = 12.103$) 和食肉类 ($\beta = 9.368$) 夜行性水平。研究证实, 人类改造和实时人类活动对哺乳动物群落结构及功能的影响存在差别; 人类活动会导致哺乳动物功能多样性急剧减少和夜行性行为显著改变。因此, 制定保护计划时应该综合考虑不同类型人类活动对野生动物物种多样性、功能多样性和行为的共同影响。

关键词: 红外相机, 群落占域, 率功能性状, 人为干扰, 中国西南, 生态类群, 野生动物夜行性

INTRODUCTION

Human impacts on natural ecosystems have become pervasive, with 95% of land having at least some degree of anthropogenic modification (Kennedy et al., 2019). Humans have dramatically altered natural habitats (Kennedy et al., 2019), jeopardized global biodiversity (Dirzo et al., 2014; Martínez-Ramos et al., 2016), and disrupted ecosystem processes and functioning (Ellis & Ramankutty, 2008; Steffen et al., 2015). As anthropogenic activities expand in natural areas, wildlife habitats face growing fragmentation, degradation, and loss (Côté et al., 2016; Wittische et al., 2021), which negatively affect species distribution, diel activity, reproduction, and survival (Frid & Dill, 2002; Newbold et al., 2015). Understanding patterns in multifaceted diversity and activity patterns of vulnerable wildlife communities and their responses to anthropogenic threats is increasingly relevant to effective conservation (Laméris et al., 2020; Rovero et al., 2020). Although a growing body of research points to the negative effects of anthropogenic activities on wildlife species richness and abundance (Dirzo et al., 2014; Gaynor et al., 2019), comparative studies aimed at disentangling the concurrent effect of different types of human disturbance on multifaceted biodiversity and activity patterns are surprisingly rare (but see Boron et al., 2019; Mendes et al., 2020; Wright et al., 2020).

Wild animals tend to respond to anthropogenic activities by transforming their habitat use or shifting activity patterns to avoid humans spatially or temporally (Gaynor et al., 2018; Laméris et al., 2020). They appear to associate human presence with risk of predation (Darimont et al., 2015; Frid & Dill, 2002). Indeed, human-induced changes in habitat use and activity patterns have been reported extensively (e.g., Gaynor et al., 2018; Harris et al., 2019; Watabe & Saito, 2021). For example, human-modified agricultural landscapes display lower mammal species richness than natural areas (Boron et al., 2019). Few intact refuges remain for wildlife to escape to (Gaynor et al., 2018). In anthropogenic landscapes, wildlife may overlap in space with humans and adjust their activity patterns to avoid human contact (Gaynor et al., 2018; Watabe & Saito, 2021). A global study on temporal dynamics of mammals suggests that, irrespective of ecosystem type and taxa, many species become markedly more nocturnal in response to human disturbance (Gaynor et al., 2018).

The effects of anthropogenic disturbance on wildlife depend on the type, intensity, and extent of disturbance and generally vary among species (Gaynor et al., 2018; Nickel et al., 2020 Tucker et al., 2018). For example, large predators exhibit lower occurrence, where the human footprint is high but avoid high human presence temporally rather than spatially (Nickel et al., 2020). In contrast, small carnivores prefer modified habitats but are less active where human presence is high (Nickel et al., 2020). According to predator–prey theory, chronic and spatially uniform anthropogenic stressors (e.g., human settlement, agriculture, and energy production) should result in outright changes in wildlife space use (Frid & Dill, 2002; Tucker et al.,

2018). Alternatively, short-term and temporally regular predation risk (e.g., presence of people and domestic animals) may prompt shifts in species temporal activity, such that wildlife avoid humans by decreasing activity at times of day when people are active (Nickel et al., 2020).

Although species richness represents the most direct and commonly used measure of biodiversity, it does not illuminate the resource use strategies and functional roles of species (Laméris et al., 2020; Oberosler et al., 2020). Functional diversity illuminates similarities or dissimilarities between species in an assemblage and offers a mechanistic link between species and their contribution to ecological processes (Weideman et al., 2020). Changes in functional composition and diversity of a community can alter or impair key ecosystem functions (Tilman et al., 1997). Hence, measures of functional diversity provide insights into ecological processes and inform effective conservation (Gorczynski et al., 2021). Body size, trophic guild (i.e., diet), and diel activity appear to be key functional traits closely correlated with anthropogenic disturbances (Gaynor et al., 2018; Mazel et al., 2017; Weideman et al., 2020). For example, mean body mass of mammal and bird assemblages is lower in disturbed or fragmented habitats than in natural areas (Lhoest et al., 2020; Rovero et al., 2020). Previous studies on functional responses of arthropod and bird assemblages to human modification (HM) suggest that human-induced land-cover changes filter for species that are more functionally similar, thus homogenizing functional diversity (Gámez-Virués et al., 2015; Weideman et al., 2020). However, examination of functional traits in research on response of mammals to human influences is relatively rare (but see Gorczynski et al., 2021; Laméris et al., 2020). This is unfortunate because mammals tend to be more sensitive to humans than other taxa and fulfil a variety of indispensable ecosystem functions, including seed dispersal, trophic regulation, nutrient cycling, and carbon storage, which in turn have direct and indirect effects on forest structure and ecosystem services (Rovero et al., 2020).

We evaluated the impacts of anthropogenic disturbances on the taxonomic and functional diversity of mammal communities in the Hengduan Mountains, a renowned hotspot of biodiversity in the mountains of southwestern China (Tang et al., 2006). We modeled regional differences in ecological metrics of interest (e.g., body mass and species richness) as a function of region-level covariates while accounting for imperfect detection and rarity of some species (Tenan et al., 2017). We examined body mass, trophic guild, and activity pattern as the functional attributes of target species because they closely relate to resource extraction and anthropogenic disturbances (Mazel et al., 2017; Rovero et al., 2020; Safi et al., 2011). We distinguished two types of anthropogenic disturbances–chronic HM and co-occurring human activities–and assessed their effects on mammal communities separately. In addition, we evaluated the impact of these disturbances on species activity patterns. We examined whether the two anthropogenic disturbances have similar effects on mammal communities. We addressed the following hypotheses: HM of landscapes facilitates human access

(Fischer & Lindenmayer, 2007) and thus HM is positively correlated with human presence at the landscape scale; human disturbance relegates more sensitive or imperiled species (i.e., large-sized mammals) to less modified areas (Mendes et al., 2020), resulting in a negative relationship between human disturbance and diversity of wildlife at the taxonomic and functional levels; community body mass is negatively associated with human disturbance; and mammals tend to respond to human disturbances by shifting their activity patterns (i.e., nocturnality of species increases along human disturbance gradients) (Gaynor et al., 2018). We sought to inform design of strategies to reconcile human disturbance and mammal conservation, including through protected area management and ecological impact assessment.

METHODS

Study area

We conducted the study at 45 sites in the Hengduan Mountains in southwestern China (93.84–102.36° E, 22.51–29.82° N) (Figure 1), which is the most botanically rich subtropical forest ecosystem in the world (CEPF, 2002). It is one of the world's 36 biodiversity hotspots and includes the Three Parallel Rivers UNESCO World Heritage Site (Tang et al., 2006). The Jinsha, Lancang, and Nu Rivers run approximately parallel from north to south through the entire region, passing between high mountains and ridges, such as Gaoligong, Biluo Snow, and Yunling Mountains. Elevation changes of more than 6000 m between mountain summits and river valleys support a complete spectrum of vegetation types (CEPF, 2002). The hotspot is also home to several of the world's most threatened mammals, such as Bengal tiger (*Panthera tigris tigris*), clouded leopard (*Neofelis nebulosa*), dhole (*Cuon alpinus*), and takin (*Budorcas taxicolor*) (Li et al., 2020). Most remaining natural forest in the Hengduan Mountains is under protection, as provincial or national nature reserves, national parks, state-owned forests, or community managed sacred sites. Twenty-six of our sites were in national nature reserves, eight in state-owned forests, seven in provincial nature reserves, and four in national parks. Elevational gradient of sites ranged from 178 to over 4310 m asl. Dominant vegetation types included evergreen broad-leaved forest, warm coniferous forest, oak forest, rhododendron forest, dark conifer forest, and dwarf shrubland (Appendix S1).

Camera trap survey

We investigated the mammal community with noninvasive camera-trap surveys conducted during the dry season (November–May) from 2018 to 2020. Our sampling period was, therefore, representative of the cold and dry season in the mountains of southwestern China. We sampled 45 forest sites spaced at a minimum of 20 km apart and considered each site a community (Figure 1). Our sampling sites spanned a gradient of forest areas with varying levels of human activities and distances from villages. We deployed 20–33 camera stations at each sampling site, depending on the elevational range, forest area, habitat heterogeneity, and accessibility. Camera stations were spaced a minimum of 800 m apart and were not baited. Three brands of cameras were used (EREAGLE E1B, Yianws L720, and Canglu S1). We set camera traps approximately 1 m off the ground and away from trails apparently used by humans to avoid vandalism. We set camera sensitivity to low to reduce false detections triggered by nonanimal movements. We programed cameras to take three photos per detection event. The minimum delay between subsequent detections was 3 s. After collection, we identified mammals to species when possible. Because it is difficult to identify muntjac to species based on camera-trap photographs, we pooled all photographs of the genus and classified them as *Muntjac* spp. (Appendix S2). We also scored cooccurring human presence (records of people, livestock, and dogs) in each camera during the sampling period. All images of the same species (including humans) on the same camera were considered independent records if separated by at least 1 h (Li et al., 2021). Several camera stations had no data due to camera malfunctions or were lost. The total realized sampling effort was 139,492 camera days from 893 camera traps that operated effectively. The mean sampling effort for each camera station and forest site was 166 and 3099 camera days (Appendix S1).

Species trait data

We used mean adult body mass, trophic guild, and activity patterns as functional traits for all inventoried species (Mazel et al., 2017) and collected information on these factors and International Union for the Conservation of Nature (IUCN) status from existing databases. We sourced the EltonTraits database (Wilman et al., 2014) for body size, diet composition, and diel activity data. For the species not included in the EltonTraits database, we obtained trait metrics by examining the specimen records at the Kunming Institute of Zoology, Chinese Academy of Sciences. We restricted our analyses to medium- and large-bodied terrestrial mammals for which body mass was >500 g because of their large space and dietary requirements, sensitivity to human activities, and high levels of behavioral plasticity (Gaynor et al., 2018). Body mass ranged from 501 g to 1212 kg (5476 g). We excluded strictly arboreal mammalian species from analysis (Tobler et al., 2008). For analysis, we log transformed body mass data to account for its markedly skewed distribution. We aggregated species to compare human pressure across trophic guilds: carnivores, herbivores, and omnivores. We used the criteria in Atwood et al. (2020) to assign trophic guilds. Thus, species consuming ≥90% animal-based diet were categorized as carnivores, ≥90% plant-based diet as herbivores, and <90% animal- or plant-based diet as omnivores (Appendix S2). Based on the EltonTraits database, we assigned each species to one of four activity patterns: diurnal, nocturnal, crepuscular, and cathemeral (Appendix S2).
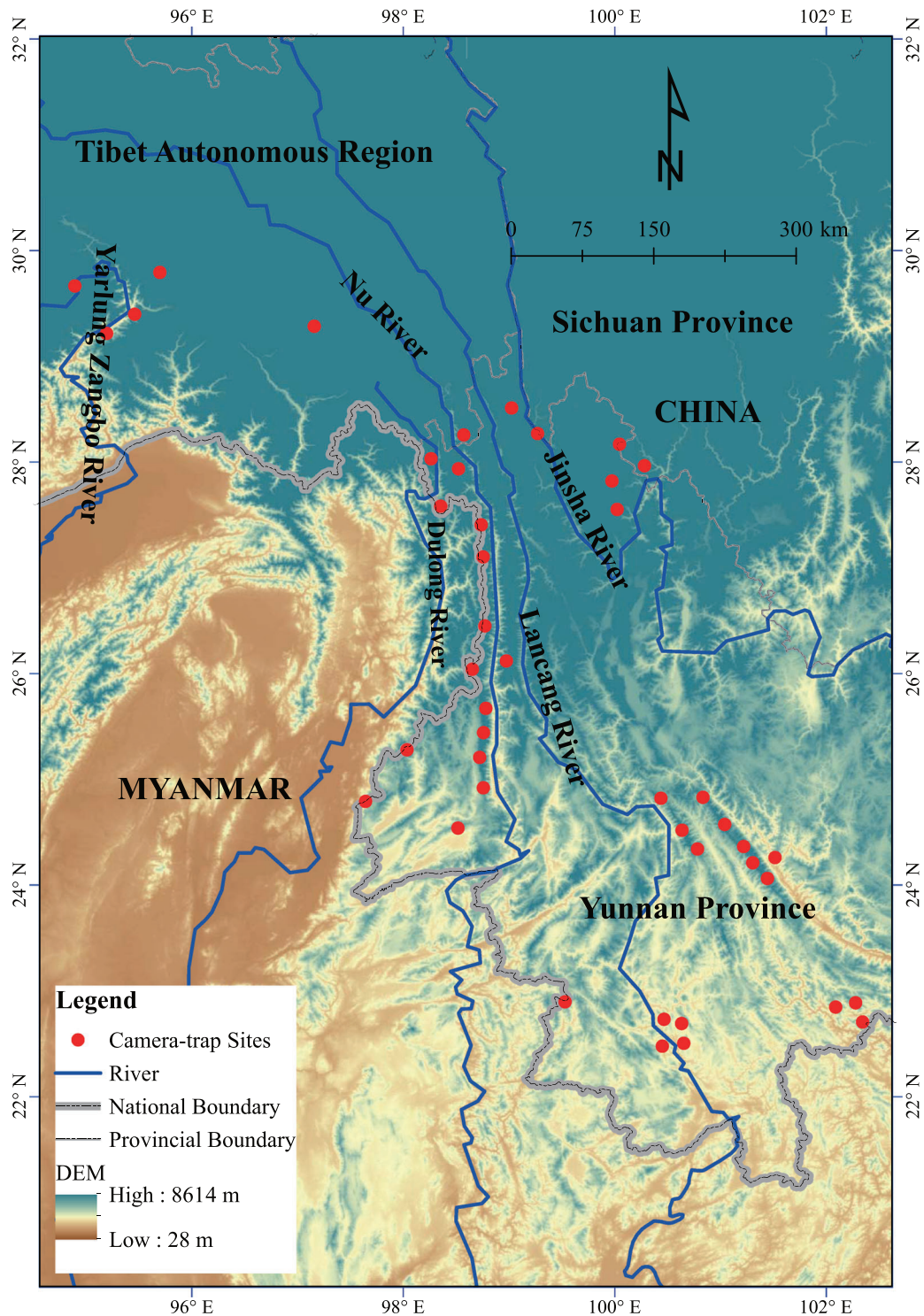
FIGURE 1 Camera-trap survey sites in subtropical montane forests southwestern China

Anthropogenic and habitat covariates

The HM map shows cumulative human pressures across global terrestrial lands (Kennedy et al., 2019). The HM data set provides a cumulative estimate of HM of terrestrial ecosystems based on 13 anthropogenic stressors caused by five major

human activities (human settlement, agriculture, transportation, mining and energy production, and electrical infrastructure) (median year of 2016). The spatially explicit global data set shows the proportion of each grid cell covered by the anthropogenic stressors and their estimated intensities of impacts and a continuous 0−1 metric of the ecological condition of land

at a resolution of 1 km. For each camera station, we used HM indices derived from the HM map as proxy of chronic and cumulative anthropogenic disturbance level around the camera trapping station. We measured the relative abundance indices (RAI) of co-occurring human presence at each camera trapping station (independent detections per 100 camera-trap days) by aggregating the detections of dogs, people, and livestock because the dog metric was correlated significantly with people and the RAI of livestock and combined index of dogs and people showed consistent effects on trophic guild richness and proportions (Appendix S3). For each station, we measured habitat covariates that potentially affect wildlife distribution: percent forest cover, which provides food resources, thermal cover, and escape shelter (Gibson et al., 2011); annual minimum temperature, which plays a key role in the distribution of many species in the cold season (Schneider et al., 2021); mean annual precipitation, which correlates with primary productivity (Ye et al., 2018); and elevation. Percent forest cover was derived from 250-m Moderate Resolution Imaging Spectroradiometer (MODIS) imagery (MOD44B Vegetation Continuous Fields product) of the study area for 2019. Annual minimum temperature and mean precipitation were downloaded from the WorldClim database (http://www.worldclim.org/bioclim). We calculated the mean values of each covariate for all camera stations in the same site to represent the site-level covariate. We also measured elevation range of camera traps for each sampling site because it reflects terrain condition and habitat heterogeneity (Rovero et al., 2020). We tested for collinearity among covariates with a threshold value of $|r| = 0.7$ (Dormann et al., 2013) and dropped mean elevation and precipitation because they were highly correlated to annual minimum temperature (Appendix S3). Prior to analysis, we log transformed [log $(x + 0.1)$] human presence data to account for its markedly skewed distribution. We standardized other variables to have mean of zero and unit variance.

Data analyses

We ran Pearson correlation tests to examine the association between HM indices and co-occurring human presence intensities at the camera-station and sampling-site scales. We used three functional traits (body mass as a continuous variable and trophic category and activity patterns as categorical) to estimate functional diversity for each sampling site based on actual camera trapping captures. We calculated Gower distance, which can be used to produce a distance matrix with mixed trait variables (Laliberté & Legendre, 2010), and used it to calculate functional diversity for each community (sampling site). We then estimated functional diversity as the mean nearest taxon distance (MNTD), a mean of the minimum phenotypic distances among species (Kembel et al., 2010), which provides helpful ecological information for understanding the underlying drivers structuring the functional composition of communities (Webb et al., 2002). Additionally, we calculated standardized effect size of MNTD (SES MNTD) with the functional distance. A negative value of SES MNTD would indicate the mammal community

had a tendency to be more functionally clustered than would be expected by chance. We examined the relationship between each functional diversity metric (MNTD and SES MNTD) and human disturbance values with Pearson correlation tests.

We extracted the date and time stamped on each independent event triggered by wildlife to analyze temporal dynamics. We transformed the original observation of clock time for each detection to a relative solar time to eliminate the impacts of day-length variation over the sampling site and period (Nouvellet et al., 2012). Once sunrise and sunset times were synchronized, we pooled all observations for each trophic guild and humans within each sampling site. We assessed the daily activity patterns of each guild and humans by fitting circular kernel density functions and estimated the coefficients of overlap (Dhat4) between humans and wildlife. A high coefficient of overlap indicated that activity patterns between the guild and humans were similar. For nocturnality analyses, we classified the guild-specific detections across sampling sites in two categories based on the time of sunrise and sunset. We eliminated detections within the hour around sunrise and sunset in the nocturnality analysis to avoid the effects of crepuscular activities on nocturnal probability. Thus, detections 1 h after sunset up to 1 h before sunrise were considered night records (assigned a value of 1), whereas detections 1 h after sunrise up to 1 h before sunset were considered day records (0). We used generalized linear models (family = binomial) to compare the effects of HM and human presence on each trophic guilds' nocturnality.

For each sampled site, we used species accumulation curves to visually determine whether species richness was adequately observed (Boron et al., 2019). Rarefaction curves were produced using the rarefaction method with 1000 randomizations (Gotelli & Colwell, 2001). For each station, we grouped every 5 days of camera-trap occurrence data into one sampling occasion to reduce zero inflation (Tobler et al., 2015). We implemented a recently developed multiregion community model to estimate variation in species richness and community functional composition among sampling sites. The underlying model assumptions were that each species $i = 1, 2, \ldots, n_r$ in the mammal community at sampling site r can be assigned a unique trophic guild (carnivore, herbivore, or omnivore) and that guild membership is indicated by g_{ir}. Variation in site- and guild-specific richness (N_{gr}) is assumed to be a Poisson process, $N_{gr} \sim Poisson(\lambda_{gr})$, where λ_{gr} is the expected guild- and site-specific richness modeled as a function of anthropogenic disturbances (HM and human presence), habitat covariates (elevation range, percent forest cover, and annual minimum temperature), and survey effort (log-transformed camera trapping days at each site):

$$log(\lambda_{gr}) = \beta_{0g} + \sum_{i=1}^{6} \beta_{ig} cov_{ir}. \tag{1}$$

The guild indicator variable g_{ir} has a categorical distribution: $g_{ir} \sim cat(\pi_r)$, with π_{gr} elements of g-length vector π_r and $\pi_{gr} = \frac{\lambda_{gr}}{\sum_g \lambda_{gr}}$. Parameter π_{gr} is the probability that a randomly chosen species i in community r belongs to guild g.

We assumed species-specific body mass (m_{ir}) is generated from a normal distribution: $m_{ir} \sim N(\mu m_r, \sigma^2_{mr})$, where μm_r and σ^2_{mr} are, respectively, the site-specific mean and variance of body mass. In addition, site-specific mean body mass, μm_r, was modeled as a function of anthropogenic disturbances (HM and human presence) and habitat covariates (elevation range, percent forest cover, and annual minimum temperature):

$$\mu m_r = mass_0 + \sum_{i=1}^{5} \beta_{mg} cov_{ir}. \tag{2}$$

We used data augmentation to estimate site-level species richness while accounting for the number of unobserved species (Dorazio & Royle, 2005). The approach of data augmentation assumes a uniform $(0, M_r)$ prior for N_r, the true number of species present in each sampled site (Sutherland et al., 2016). Within the data augmentation framework, the regional-specific species pool is assumed to be independent across sites and is controlled by the site-specific parameter Ω_r, representing the proportion of the total species that exist in site r, including those that were not detected (Sutherland et al., 2016). The site-specific species indicator w_{ir}, which is governed by the hyperparameter Ω_r (i.e., $w_{ir} \sim Bern[\Omega_r]$), denotes whether species i was present in the site r ($w_{ir} = 1$) or whether it is a structural zero ($w_{ir} = 0$). For species that were actually observed during the study in a site, w_{ir} is constantly equal to 1. The true number of species in each sampled site is estimated as N_r, the sum of species predicted within site r

$$N_r = \sum_{i=1}^{M} w_{ir} \tag{3}$$

For estimates of Ω_r to be comparable among sites, we used the same augmentation prior ($M_r = M = 100$) for N_r, where the choice of M is arbitrary and is only required to be larger than the true total of species in the richest community (Sutherland et al., 2016).

The occupancy states of species i in camera-trap station j of sampling site r are described as $z_{ijr} \sim Bern(\psi_{ijr} w_{ir})$, where ψ_{ijr} is the species-specific occurrence probability for each camera-trap station in each sampling site. We modeled observed detection frequencies as $y_{ijr} \sim bin(K_{jr} p_{ijr} z_{ijr})$, where K_{jr} is the number of sampling occasions at camera-trap station j in site r and p_{ijr} is the detectability of species i at camera-trap station j in site r. We modeled detectability as a function of human presence and body mass. We fitted models using a Bayesian formulation and Markov chain Monte Carlo in JAGS v3.4.0 (Plummer, 2003) via the package R2Jags (Su & Yajima, 2015) to interface with software R. We present the beta coefficients for each covariate as mean values of the posterior distribution, accompanied by 95% Bayesian credible intervals (BCI) to express uncertainty. We considered an effect significant if the 95% BCI did not overlap zero. We made inference from 30,000 samples of posterior distribution (three chains, thinning of 10, and burn-in of 30,000 [model code in Appendix S4]). We used linear regression models to estimate the effects of HM and human presence on species richness (N_r) and functional diversity (MNTD and SES MNTD) and controlled for effects of other environmental covariates. We used Pearson correlation tests to assess the relationships between anthropogenic covariates and the model-derived parameters of guild proportion (π_r) at each site. We used the traditional significant level of $p < 0.05$ for statistical significance of t tests.

RESULTS

In 139,492 camera days, we obtained 20,614 independent detections of 61 medium- and large-bodied mammal species (body mass ≥ 500 g) and 5975 independent records of co-occurring human activities (Appendix S1). Twenty species were categorized by IUCN as globally threatened (one species critically endangered, 10 endangered, and nine vulnerable) and 10 species as near threatened. We documented several species and subspecies of conservation concern, including Bengal tiger, dhole, and red panda (*Ailurus fulgens*) (Appendix S2). Species accumulation curves indicated that we likely recorded most remaining species in all sampling sites (Appendix S3).

We found a robust negative effect of body mass on community-level detection probability (-0.069, 95% BCI -0.096 to -0.038). The association between HM and the average body mass was negative across sampling sites (-0.240, 95% BCI -0.445 to -0.030) (Appendix S3). Human modification and concurrent human presence were not correlated across camera stations ($t = 0.51$, df $= 891$, $p = 0.701$) or sampling sites ($t = 0.371$, df $= 43$, $p = 0.712$). Human modification and co-occurring human presence were also not equivalent in their effects on taxonomic and functional diversity of the mammal communities. Human modification had strongly negative effects on the two metrics of functional diversity (MNTD: β coefficient $= -0.134$, $t = -2.491$, $p = 0.017$; SES MNTD: $\beta = -0.397$, $t = -3.103$, $p = 0.003$) (Figure 2). Although co-occurring human presence had a strong negative effect on overall species richness ($\beta = -1.054$, $t = -3.005$, $p = 0.004$) (Figure 2 & Appendix S3), overall species richness tended to increase with HM ($\beta = 0.954$, $t = 1.800$, $p = 0.079$) (Figure 2 & Appendix S3).

At the trophic-guild level, effects of forest cover on the species richness of carnivores ($\beta = 0.201$, 95% BCI 0.001–0.406) and herbivores ($\beta = 0.179$, 95% BCI 0.014–0.371) (Appendix S3) were significantly positive. Although not significant, HM tended to have a positive association with species richness of herbivores ($\beta = 0.128$, 95% BCI -0.063 to 0.318), whereas human presence tended to have a negative impact ($\beta = -0.089$, 95% BCI -0.176 to 0.004).

Human modification showed a strong negative correlation with the estimated proportion of carnivores ($t = -4.669$, df $= 43$, $p < 0.001$) and a positive correlation with the estimated proportion of omnivores ($t = 3.002$, df $= 43$, $p = 0.004$) (Figure 3). Human presence was significantly and negatively correlated with estimated proportion of herbivores
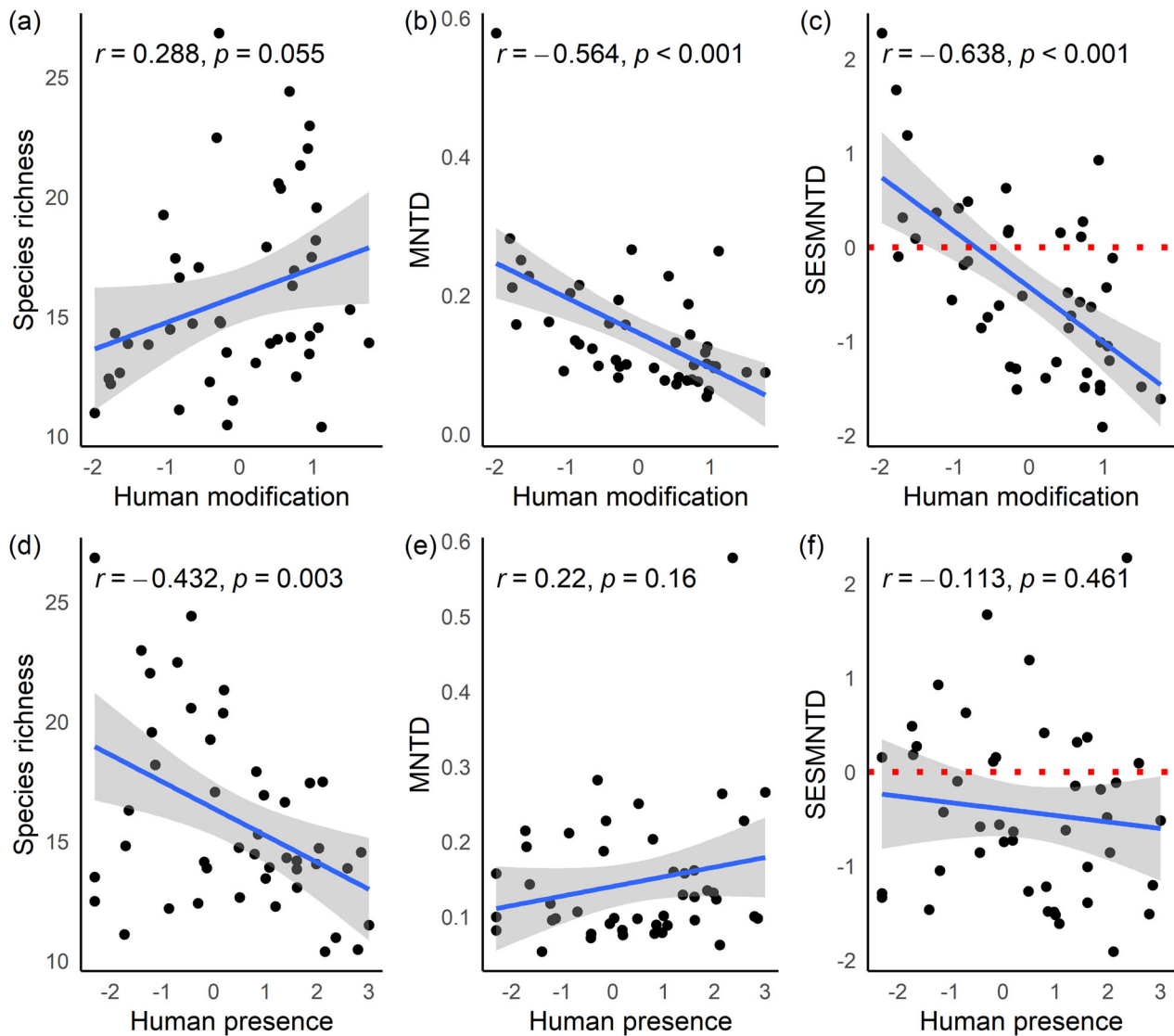
FIGURE 2 Relationships between anthropogenic covariates and (a, d) species richness and (b, c, e, f) functional diversity (red dash lines, 0; negative values of SES MNTD, mammal communities tendency to be more functionally clustered than expected by chance). Functional diversity is represented by the mean nearest taxon distance (MNTD) and the standardized effect size of MNTD (SES MNTD)

($t = -4.018$, df = 43, $p < 0.001$) and positively correlated with proportion of omnivores ($t = 2.678$, df = 43, $p = 0.01$) (Figure 3).

Omnivores had the highest temporal overlap coefficient with humans (Dhat4 = 0.72), followed by herbivores (Dhat4 = 0.56), and then carnivores (Dhat4 = 0.33). Human presence had significantly positive effects on the nocturnality of omnivores ($\beta = 0.616$, 95% BCI 0.55–0.678) but not on herbivores ($\beta = 0.024$, 95% BCI −0.003 to 0.05) and carnivores ($\beta = 0.064$, 95% BCI −0.397 to 0.169). Human modification had significantly positive effects on the nocturnality of omnivores ($\beta = 12.103$, 95% BCI 10.889–13.314) and carnivores ($\beta = 9.368$, 95% BCI 6.777–11.894), but not herbivores ($\beta = 0.399$, 95% BCI −0.093 to 0.883).

DISCUSSION

We applied hierarchical multiregion community modeling with data augmentation to evaluate species richness and functional composition while accounting for species that were possibly missed by camera traps. A multiregion model incorporates all species observed during sampling, regardless of sample location or occasion, and allows for hypothesis testing on guild-specific species richness (Sutherland et al., 2016; Tennan et al., 2017). The hierarchical occupancy model we used to estimate species richness accounts for imperfect detection and low occurrence of rare species (Dorazio & Royle, 2005).

The lack of evidence of correlation between HM and human presence contrasted with our expectation and hypothesis. As a
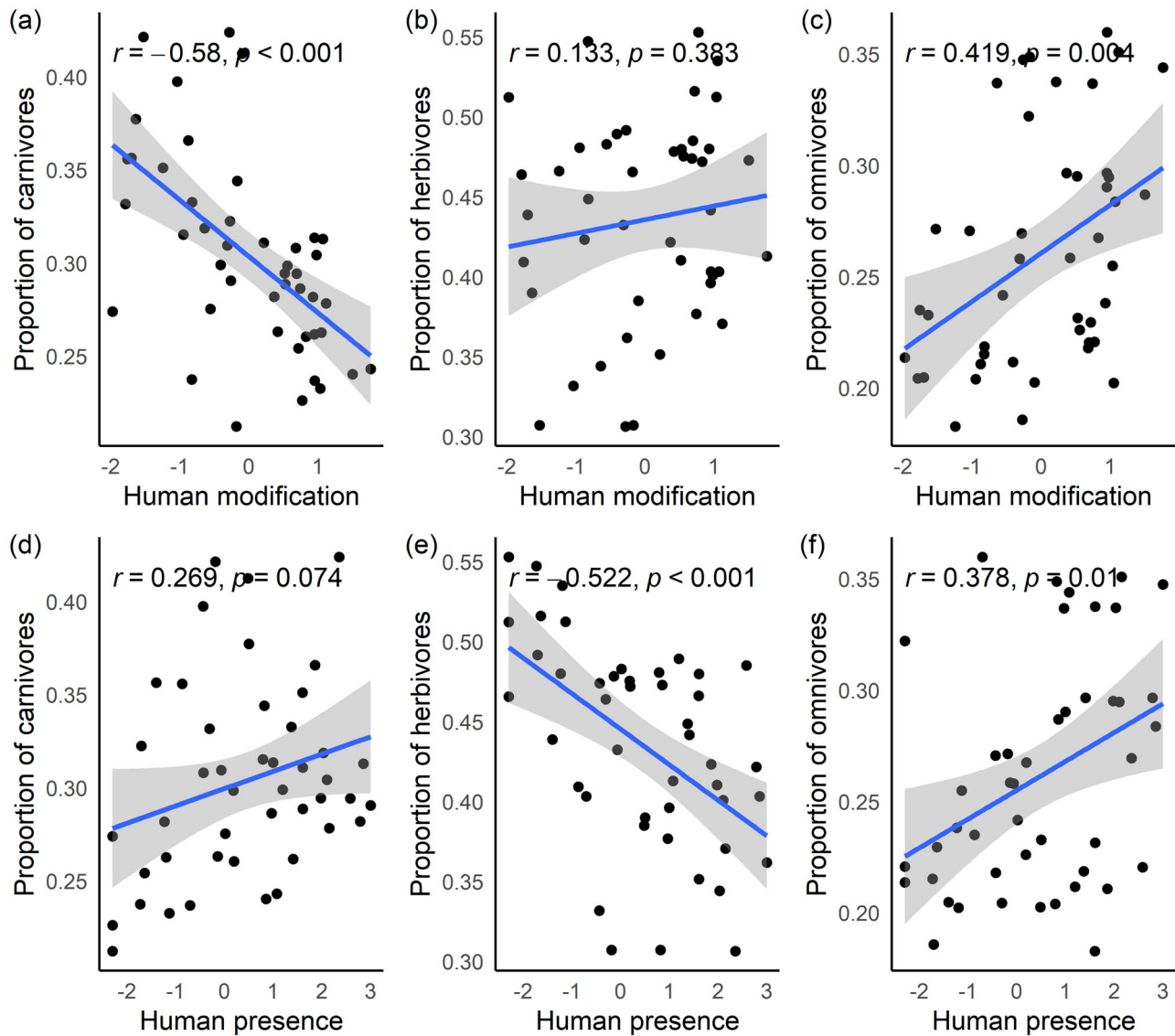
FIGURE 3 Correlations between human modification and human presence with the estimated proportion of (a, d) carnivores, (b, e) herbivores, and (c, f) omnivores

type of HM, human settlements in our study areas were scattered with typically fewer than 30 households. Agriculture in the region is limited to small-scale crop fields due to steep terrain and inconvenient transportation. However, local minority nationalities rely heavily on natural resources, and livestock grazing and nontimber forest resource collection are common throughout the Hengduan Mountains (Li et al., 2016; Li et al., 2018). Thus, co-occurring human activities can be extensive even in montane forests with very low HM. Indeed, our camera-trap survey documented substantial human activity across all sampling sites (Appendix S1). Although HM generally entails habitat alteration or destruction, impacts of human presence could include direct predation or depletion of key resources or could be related to animals avoiding the sight, sound, or scent of humans. Our results highlight the fact that human presence and its related impacts on mammal diversity and activity patterns are not necessarily spatially linked to HM, demonstrating the importance of considering concurrent effects of different types of human disturbance on wildlife communities when formulating conservation plans.

We expected predominantly negative effects of human activities on taxonomic and functional diversity of mammal communities. However, effects of HM and human presence on mammals were diverse (Figure 2). Overall species richness of the mammal communities was negatively correlated with human presence, and herbivores were the most sensitive guild influenced by human presence (Figure 3). We attribute this greater sensitivity of wild herbivores to human presence to pervasive livestock grazing, resulting in competitive exclusion (Harris et al., 2019). This would appear to be broadly consistent with the findings of a coarser global analysis that indicated that mammal community intactness is weakly and negatively correlated

with human footprint (Belote et al., 2020). That analysis, however, relied on the global human footprint map, which combines measures of human presence and habitat alteration in one index. We separated the two components of human presence and HM and found that human presence appears to have a large negative impact on species richness, whereas high levels of HM tended to be associated with more species richness (Figure 2). The congruence between overall species richness and HM may seem counterintuitive given that many human-modified habitats seem unsuitable and land-cover modifications have negative consequences for many wildlife species (Kennedy et al., 2019). However, positive effects of HM on taxonomic species richness of mammals is a widespread phenomenon in many regions, for example, Africa (Balmford et al., 2001), Europe (Araújo, 2003; Santos et al., 2020), and South America (de Lima et al., 2021).

The mechanisms underlying the correlations are not yet clear. One possible explanation for the tendency is the intermediate disturbance hypothesis, which postulates that species richness is highest at intermediate levels of disturbance (Araújo, 2003). Because our sampling sites were restricted to reserves receiving some level of management, HMs were limited to relatively lower habitat disturbance and small-scale agricultural plots. Such moderate HM can increase spatial heterogeneity, which will allow preadapted species to spread and thrive (Araújo, 2003; Boron et al., 2019; Santos et al., 2020). For example, previous studies suggest that some omnivorous species prefer to use human-modified habitats due to the accessibility of anthropogenic food resources (Fedriani et al., 2001) and the "human shield effect," which reduces predation risk (Berger, 2007).

Human modification was positively associated with the estimated proportion of omnivores but negatively associated with the proportion of carnivores, indicating a differing response of trophic guilds to humans. We found no significant effects of HM on the proportion of herbivores, which implies relatively high tolerance of herbivores to HM. Some large herbivores, such as muntjacs, are generalists in terms of diet and habitat, which is consistent with their adaptability to intermediate habitat modification (Li et al., 2021). There is also evidence that some herbivores may select habitat close to human settlements as protection against predators or because of preference for more productive disturbed habitats (Berger, 2007). Thus, in human-modified landscapes, some species can adapt and thrive, whereas some others are restricted to less disturbed habitats (Tucker et al., 2021).

Although HM may have increased overall species richness, it apparently had the opposite effect on functional diversity (Figure 2). The contrasting responses of taxonomic and functional diversity to human impacts indicate that a sole focus on one biodiversity metric may lead to erroneous conclusions regarding the effects of human disturbance on wildlife. Our results suggest that HM in subtropical montane forests is filtering for mammals with specific traits and thus homogenizing functional diversity, as evidenced by strong negative correlations of HM with the community average body mass and the proportion of carnivores. Declines in functional diversity may, in turn, lead to a loss of certain ecosystem functions (Gorczynski et al., 2021; Weideman et al., 2020).

Activity shifts toward nocturnality as a response to increasing anthropogenic activities has been demonstrated for many wildlife species and trophic guilds globally (Gaynor et al., 2018). Our results suggest that carnivores, omnivores, and herbivores had mixed responses to humans in diel activity. Omnivores shifted their activity patterns toward nocturnality in response to HM and human presence; carnivores became more nocturnal in landscapes with higher HM, whereas herbivores exhibited no statistically significant shift in response to humans. In human disturbed landscapes, wildlife species are subject to a "landscape of fear" associated with mortality and nuisance disturbance (Frid & Dill, 2002; Smith et al., 2017; Suraci et al., 2019). Thus, activity shifts of carnivores and omnivores in response to HM should be expected.

Our results demonstrated marked plasticity in omnivores' diel activity patterns in response to anthropogenic activities. Given the extensive activity overlap between omnivores and co-occurring human presence, significant activity shifts in response to human presence should be expected for omnivores, and shifts in the temporal partitioning of omnivores as a response to anthropogenic activities may facilitate human–wildlife coexistence (Bonnot et al., 2020 Gaynor et al., 2018). However, marked activity shifts in response to human pressure may result in behaviorally mediated trophic cascades with consequences for fitness and community interactions (Gaynor et al., 2018). The absence of nocturnality shifts in herbivores does not necessarily indicate an absence of human impact. Differences in body size and evolutionary processes may shape responses and mask shifts in activity patterns at the trophic level. Animals living alongside humans in modified habitats may have reduced activity range and foraging efficiency and higher metabolic costs, which can compromise species interactions and survival (Gaynor et al., 2018).

We were unable to tease apart the effects of species interactions on community structure and trophic guild activity patterns, since such an analysis would require adequate data on potential interacting species pairs. However, species interaction could affect community structure, which in turn would affect spatiotemporal distribution (Veech, 2006). Further studies should distinguish effects of human disturbance and species interaction on community structure and activity behavior of mammals. In addition, problems of low precision and poor coverage might have emerged because of unequal sampling of different habitats, such that certain rare types of land cover were not represented in the sampling. Low numbers of sampling stations at some sites might have led to some estimates with credible intervals that did not include the true values. Future surveys could adopt a stratified sampling approach to improve precision and coverage.

We found no strong correlation between elevational range and the species richness of any guilds (Appendix S3). The "area-heterogeneity trade-off" hypothesis suggests that increasing environmental heterogeneity may decrease species richness by reducing the availability of habitat for individual species (Allouche et al., 2012). The Hengduan Mountains are characterized by steep terrain with diverse vegetation types; however,

rapid increase in elevation range within a fixed space must lead to a reduction in the amount of high-quality habitat available for individual trophic guilds. We found a strong relationship between percent forest cover and overall species richness, as well as with richness of carnivores and herbivores (Appendix S3), highlighting the importance of retaining structurally intact forests for mammal conservation (Betts et al., 2017 Gibson et al., 2011).

Our results demonstrated that the nature of the effect of humans on mammal communities depended on the types and intensity of disturbance. Human presence and its related impacts on mammal diversity and activity patterns are not necessarily spatially linked to anthropogenic habitat modification. Our results suggested that wildlife may avoid human disturbance by adjusting both their use of space and time. Anthropogenic influences go far beyond altering mammal species richness and shifting behavior of mammals because disturbance can also lead to drastic loss of functional diversity, which may result in cascading consequence for community interactions and ecosystem functioning (Gorczynski et al., 2021 Weideman et al., 2020). As global human populations continue to expand into previously little visited habitats (Tucker et al., 2018), functional homogenization and activity shifts toward nocturnality are likely to happen on an increasingly broad scale. Conservation planning should consider concurrent effects of different types of human disturbance on wildlife communities and take into account species richness, functional diversity, and animal behavior. It is important to disentangle the exact impacts of human activities on wildlife behavior and diversity, the mechanisms of assembly of wildlife communities, and the ecological consequence of functional homogenization.

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LITERATURE CITED
Allouche, O., Kalyuzhny, M., Moreno-Rueda, G., Pizarro, M., & Kadmon, R. (2012). Area–heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the National Academy of Sciences*, 109, 17495–17500.

Araújo, M. B. (2003). The coincidence of people and biodiversity in Europe. *Global Ecology and Biogeography*, 12, 5–12.

Atwood, T. B., Valentine, S. A., Hammill, E., Mccauley, D. J., Madin, E. M. P., Beard, K. H., & Pearse, W. D. (2020). Herbivores at the highest risk of extinction among mammals, birds, and reptiles. *Science Advances*, 6, eabb8458.

Balmford, A., Moore, J. L., Brooks, T., Burgess, N., Hansen, L. A., Williams, P., & Rahbek, C. (2001). Conservation conflicts across Africa. *Science*, 291, 2616–2619.

Belote, R. T., Faurby, S., Brennan, A., Carter, N. H., Dietz, M. S., Hahn, B., Mcshea, W. J., & Gage, J. (2020). Mammal species composition reveals new insights into Earth's remaining wilderness. *Frontiers in Ecology and the Environment*, 18, 376–383.

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, 3, 620–623.

Betts, M. G., Wolf, C., Ripple, W. J., Phalan, B., Millers, K. A., Duarte, A., Butchart, S. H. M., & Levi, T. (2017). Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature*, 547, 441–444.

Bonnot, N. C., Couriot, O., Berger, A., Cagnacci, F., Ciuti, S., De Groeve, J. E., Gehr, B., Heurich, M., Kjellander, P., Kröschel, M., Morellet, N., Sönnichsen, L., & Hewison, A. J. M. (2020). Fear of the dark? Contrasting impacts of humans versus lynx on diel activity of roe deer across Europe. *Journal of Animal Ecology*, 89, 132–145.

Boron, V., Deere, N. J., Xofis, P., Link, A., Quiñones-Guerrero, A., Payan, E., & Tzanopoulos, J. (2019). Richness, diversity, and factors influencing occupancy of mammal communities across human-modified landscapes in Colombia. *Biological Conservation*, 232, 108–116.

CEPF (Critical Ecosystem Partnership Fund). (2002). Ecosystem profile: Mountains of Southwest China. https://www.cepf.net/our-work/biodiversity-hotspots/mountains-southwest-china.

Côté, I. M., Darling, E. S., & Brown, C. J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20152592.

Darimont, C. T., Fox, C. H., Bryan, H. M., & Reimchen, T. E. (2015). The unique ecology of human predators. *Science*, 349, 858–860.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345, 401–406.

Dorazio, R. M., & Royle, J. A. (2005). Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association*, 100, 389–398.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., Mcclean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46.

Ellis, E. C., & Ramankutty, N. (2008). Putting people in the map: Anthropogenic biomes of the world. *Frontiers in Ecology and the Environment*, 6, 439–447.

Fedriani, J. M., Fuller, T. K., & Sauvajot, R. M. (2001). Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography*, 24, 325–331.

Fischer, J., & Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: A synthesis. *Global Ecology and Biogeography*, 16, 265–280.

Frid, A., & Dill, L. M. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, 6, 11.

Gámez-Virués, S., Perović, D. J., Gossner, M. M., Börschig, C., Blüthgen, N., De Jong, H., Simons, N. K., Klein, A. -. M., Krauss, J., Maier, G., Scherber, C., Steckel, J., Rothenwöhrer, C., Steffan-Dewenter, I., Weiner, C. N., Weisser, W., Werner, M., Tscharntke, T., & Westphal, C. (2015). Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications*, 6, 8568.

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of fear: Spatial patterns of risk perception and response. *Trends in Ecology & Evolution*, 34, 355–368.

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, 360, 1232–1235.

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E., & Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, *478*, 378–381.

Gorczynski, D., Hsieh, C., Luciano, J. T., Ahumada, J., Espinosa, S., Johnson, S., Rovero, F., Santos, F., Andrianarisoa, M. H., Astaiza, J. H., Jansen, P. A., Kayijamahe, C., Moreira Lima, M. G., Salvador, J., & Beaudrot, L. (2021). Tropical mammal functional diversity increases with productivity but decreases with anthropogenic disturbance. *Proceedings of the Royal Society B: Biological Sciences*, *288*, 20202098.

Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, *4*, 379–391.

Harris, N. C., Mills, K. L., Harissou, Y., Hema, E. M., Gnoumou, I. T., Vanzoeren, J., Abdel-Nasser, Y. I., & Doamba, B. (2019). First camera survey in Burkina Faso and Niger reveals human pressures on mammal communities within the largest protected area complex in West Africa. *Conservation Letters*, *12*, e12667.

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*, 1463–1464.

Kennedy, C. M., Oakleaf, J. R., Theobald, D. M., Baruch-Mordo, S., & Kiesecker, J. (2019). Managing the middle: A shift in conservation priorities based on the global human modification gradient. *Global Change Biology*, *25*, 811–826.

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*, 299–305.

Laméris, D. W., Tagg, N., Kuenbou, J. K., Sterck, E. H. M., & Willie, J. (2020). Drivers affecting mammal community structure and functional diversity under varied conservation efforts in a tropical rainforest in Cameroon. *Animal Conservation*, *23*, 182–191.

Lhoest, S., Fonteyn, D., Daïnou, K., Delbeke, L., Doucet, J. -. L., Dufrêne, M., Josso, J. -. F., Ligot, G., Oszwald, J., Rivault, E., Verheggen, F., Vermeulen, C., Biwolé, A., & Fayolle, A. (2020). Conservation value of tropical forests: Distance to human settlements matters more than management in Central Africa. *Biological Conservation*, *241*, 108351.

Li, X., Bleisch, W. V., & Jiang, X. (2016). Effects of ethnic settlements and land management status on species distribution patterns: A case study of endangered musk deer (*Moschus* spp.) in Northwest Yunnan, China. *PLoS One*, *11*, e0155042.

Li, X., Bleisch, W. V., & Jiang, X. (2018). Using large spatial scale camera trap data and hierarchical occupancy models to evaluate species richness and occupancy of rare and elusive wildlife communities in southwest China. *Diversity and Distributions*, *24*, 1560–1572.

Li, X., Hu, W., Pu, C., Li, Q., Yu, Q., Hu, Z., Bleisch, W. V., & Jiang, X. (2020). Camera-trapping monitoring platform for mammals and pheasants in the Longitudinal Range and Gorge Region of Southwest China: Protocol, progress and future outlook. *Biodiversity Science*, *28*, 1090–1096.

Li, X. Y., Bleisch, W. V., Liu, X. W., Hu, W. Q., & Jiang, X. L. (2021). Human disturbance and prey occupancy as predictors of carnivore richness and biomass in a Himalayan hotspot. *Animal Conservation*, *24*, 64–72.

de Lima, D. O., Banks-Leite, C., Lorini, M. L., Nicholson, E., & Vieira, M. V. (2021). Anthropogenic effects on the occurrence of medium-sized mammals on the Brazilian Pampa biome. *Animal Conservation*, *24*, 135–147.

Martínez-Ramos, M., Ortiz-Rodríguez, I. A., Piñero, D., Dirzo, R., & Sarukhán, J. (2016). Anthropogenic disturbances jeopardize biodiversity conservation within tropical rainforest reserves. *Proceedings of the National Academy of Sciences*, *113*, 5323–5328.

Mazel, F., Wüest, R. O., Gueguen, M., Renaud, J., Ficetola, G. F., Lavergne, S., & Thuiller, W. (2017). The geography of ecological niche evolution in mammals. *Current Biology*, *27*, 1369–1374.

Mendes, C. P., Carreira, D., Pedrosa, F., Beca, G., Lautenschlager, L., Akkawi, P., Bercê, W., Ferraz, K. M. P. M. B., & Galetti, M. (2020). Landscape of human fear in Neotropical rainforest mammals. *Biological Conservation*, *241*, 108257.

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M.,

Harrison, M. L. K., Alhusseini, T., Ingram, D. J., et al. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*, 45–50.

Nickel, B. A., Suraci, J. P., Allen, M. L., & Wilmers, C. C. (2020). Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biological Conservation*, *241*, 108383.

Nouvellet, P., Rasmussen, G. S. A., Macdonald, D. W., & Courchamp, F. (2012). Noisy clocks and silent sunrises: Measurement methods of daily activity pattern. *Journal of Zoology*, *286*, 179–184.

Oberosler, V., Tenan, S., Zipkin, E. F., & Rovero, F. (2020). Poor management in protected areas is associated with lowered tropical mammal diversity. *Animal Conservation*, *23*, 171–181.

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing.

Rovero, F., Ahumada, J., Jansen, P. A., Sheil, D., Alvarez, P., Boekee, K., Espinosa, S., Lima, M. G. M., Martin, E. H., O'brien, T. G., Salvador, J., Santos, F., Rosa, M., Zvoleff, A., Sutherland, C., & Tenan, S. (2020). A standardized assessment of forest mammal communities reveals consistent functional composition and vulnerability across the tropics. *Ecography*, *43*, 75–84.

Safi, K., Cianciaruso, M. V., Loyola, R. D., Brito, D., Armour-Marshall, K., & Diniz-Filho, J. A. F. (2011). Understanding global patterns of mammalian functional and phylogenetic diversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 2536–2544.

Santos, A. M. C., Cianciaruso, M. V., Barbosa, A. M., Bini, L. M., Diniz-Filho, J. A. F., Faleiro, F. V., Gouveia, S. F., Loyola, R., Medina, N. G., Rangel, T. F., Tessarolo, G., & Hortal, J. (2020). Current climate, but also long-term climate changes and human impacts, determine the geographic distribution of European mammal diversity. *Global Ecology and Biogeography*, *29*, 1758–1769.

Schneider, L., Comte, V., & Rebetez, M. (2021). Increasingly favourable winter temperature conditions for major crop and forest insect pest species in Switzerland. *Agricultural and Forest Meteorology*, *298-299*, 108315.

Smith, J. A., Suraci, J. P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L. Y., & Wilmers, C. C. (2017). Fear of the human 'super predator' reduces feeding time in large carnivores. *Proceedings of the Royal Society B-Biological Sciences*, *284*, 20170433.

Steffen, W., Richardson, K., Rockström, J., Cornell, S. E., Fetzer, I., Bennett, E. M., Biggs, R., Carpenter, S. R., De Vries, W., De Wit, C. A., Folke, C., Gerten, D., Heinke, J., Mace, G. M., Persson, L. M., Ramanathan, V., Reyers, B., & Sörlin, S. (2015). Planetary boundaries: Guiding human development on a changing planet. *Science*, *347*, 1259855.

Su, Y., & Yajima, M. (2015). R2jags: Using R to run 'JAGS'. R package version 0.5–7. Available from https://cran.r-project.org/web/packages/R2jags/R2jags.pdf.

Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*, *22*, 1578–1586.

Sutherland, C., Brambilla, M., Pedrini, P., & Tenan, S. (2016). A multiregion community model for inference about geographic variation in species richness. *Methods in Ecology and Evolution*, *7*, 783–791.

Tang, Z., Wang, Z., Zheng, C., & Fang, J. (2006). Biodiversity in China's mountains. *Frontiers in Ecology and the Environment*, *4*, 347–352.

Tenan, S., Brambilla, M., Pedrini, P., & Sutherland, C. (2017). Quantifying spatial variation in the size and structure of ecologically stratified communities. *Methods in Ecology and Evolution*, *8*, 976–984.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. (1997). The Influence of functional diversity and composition on ecosystem processes. *Science*, *277*(5330), 1300–1302. https://doi.org/10.1126/science.277.5330.1300

Tobler, M. W., Carrillo-Percastegui, S. E., Leite Pitman, R., Mares, R., & Powell, G. (2008). An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation*, *11*, 169–178.

Tobler, M. W., Zúñiga Hartley, A., Carrillo-Percastegui, S. E., & Powell, G. V. N. (2015). Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. *Journal of Applied Ecology*, *52*, 413–421.

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., Van Beest, F. M., Blake, S., Blaum, N., Bracis, C., et al. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. _Science_, _359_, 466–469.

Tucker, M. A., Santini, L., Carbone, C., & Mueller, T. (2021). Mammal population densities at a global scale are higher in human-modified areas. _Ecography_, _44_, 1–13.

Veech, J. A. (2006). A probability-based analysis of temporal and spatial co-occurrence in grassland birds. _Journal of Biogeography_, _33_, 2145–2153.

Watabe, R., & Saito, M. U. (2021). Effects of vehicle-passing frequency on forest roads on the activity patterns of carnivores. _Landscape and Ecological Engineering_, _17_, 225–231.

Webb, C. O., Ackerly, D. D., Mcpeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. _Annual Review of Ecology and Systematics_, _33_, 475–505.

Weideman, E. A., Slingsby, J. A., Thomson, R. L., & Coetzee, B. T. W. (2020). Land cover change homogenizes functional and phylogenetic diversity within and among African savanna bird assemblages. _Landscape Ecology_, _35_, 145–157.

Wilman, H., Belmaker, J., Simpson, J., De La Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. _Ecology_, _95_, 2027–2027.

Wittische, J., Heckbert, S., James, P. M. A., Burton, A. C., & Fisher, J. T. (2021). Community-level modelling of boreal forest mammal distribution in an oil sands landscape. _Science of the Total Environment_, _755_, 142500.

Wright, A. D., Grant, E. H. C., & Zipkin, E. F. (2020). A hierarchical analysis of habitat area, connectivity, and quality on amphibian diversity across spatial scales. _Landscape Ecology_, _35_, 529–544.

Ye, J. -. S., Pei, J. -. Y., & Fang, C. (2018). Under which climate and soil conditions the plant productivity–precipitation relationship is linear or nonlinear? _Science of the Total Environment_, _616-617_, 1174–1180.

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