

Human disturbance increases spatiotemporal associations among mountain forest terrestrial mammal species



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Xueyou Li , William V. Bleisch, Wenqiang Hu, Quan Li, Hongjiao Wang, Zhongzheng Chen, Ru Bai, Xuelong Jiang 

State Key Laboratory of Genetic Resources and Evolution & Yunnan key laboratory of biodiversity and ecological conservation of Gaoligong Mountain, Kunming Institute of Zoology, Chinese Academy of Sciences • China Exploration and Research Society, 2707-08 SouthMark, Wong Chuk Hang, Hong Kong, China • Anhui Provincial Key Laboratory of the Conservation and Exploitation of Biological Resources, College of Life Sciences, Anhui Normal University, Wuhu, China

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Abstract

Spatial and temporal associations between sympatric species underpin biotic interactions, structure ecological assemblages, and sustain ecosystem functioning and stability. However, the resilience of interspecific spatiotemporal associations to human activity remains poorly understood, particularly in mountain forests where anthropogenic impacts are often pervasive. Here we applied context-dependent Joint Species Distribution Models to a systematic camera-trap survey dataset from a global biodiversity hotspot in eastern Himalaya to understand how prominent human activities in mountain forests influence species associations within terrestrial mammal communities. We obtained 10,388 independent detections of 17 focal species (12 carnivores and five ungulates) from 322 stations over 43,163 camera days of effort. We identified a higher incidence of positive associations in habitats with higher levels of human modification (87 %) and human presence (83 %) compared to those located in habitats with lower human modification (64 %) and human presence (65 %) levels. We also detected a significant reduction of pairwise encounter time at increasing levels of human disturbance, corresponding to more frequent encounters between pairs of species. Our findings indicate that human activities can push mammals together into more frequent encounters and associations, which likely influences the coexistence and persistence of wildlife, with potential far-ranging ecological consequences.

eLife assessment

In this study, camera trapping and species distribution models are used to show that human disturbance in mountain forests in the eastern Himalayas pushes medium-sized and large mammal species into narrower habitat space, thus increasing their co-occurrence. While the collected data provide a **useful** basis for further work, the study presents **incomplete** evidence to support the claim that increased co-occurrence may indicate positive interactions between species.

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Introduction

Pervasive human activities can disrupt invisible facets of biodiversity such as species associations, with potential cascading ecosystem effects (Naeem et al., 1994 [↗](#); Parsons et al., 2022 [↗](#)). Human encroachment into natural ecosystems squeezes the spatiotemporal niches of wildlife species (Gilbert et al., 2022 [↗](#)), altering the number and magnitude of associations in a community (Burkle et al., 2013 [↗](#)), and accelerating species decline and loss (Jones et al., 2018 [↗](#)). Humans play a role as ‘super predators’ in shaping the co-occurrence of other species with complicated indirect modifications to multiple interactions between organisms (Gilbert et al., 2022 [↗](#); Moll et al., 2021 [↗](#)). Human disturbance, such as chronic landscape modification and acute direct human presence, may significantly alter spatiotemporal distribution of species and fundamentally change the way that species interact (Li et al., 2022a [↗](#); Sévêque et al., 2020 [↗](#)). For example, expanding human footprints have compressed the space and time available for mammals to share by restricting animal movements (Tucker et al., 2018 [↗](#)) and increasing wildlife nocturnality (Gaynor et al., 2018 [↗](#)). As human and animal activities increasingly overlap in time and space, it is important to assess and quantify the potential for human-induced changes in species association to ecosystem structure and function (Penjor et al., 2022 [↗](#)).

Species are not distributed independently of each other; rather, they co-occur in time and space and interact (Tilman, 1994 [↗](#); Wisz et al., 2013 [↗](#)). The spatiotemporal co-occurrence of species, termed interspecific associations, provides unique ecological information and has important consequence for ecosystem integrity (Gorczynski et al., 2022 [↗](#); Keil et al., 2021 [↗](#)). However, segregated species co-occurrence could be generated by processes such as negative interspecific interaction, distinct environment requirements, and dispersal limitations; similarly, aggregated species pairs may reflect positive interspecific interaction but could also reflect shared environmental preferences (Lyons et al., 2016 [↗](#); Song et al., 2020 [↗](#)). Although interspecific co-occurrence or avoidance cannot be used to directly estimate species interactions (Blanchet et al., 2020 [↗](#)), animals cannot interact if their spatiotemporal niches do not overlap (Gilbert et al., 2022 [↗](#)) and strong interactions should be expected to lead to significant associations. Thus, interspecific associations convey key information about interactions between sympatric species (Boron et al., 2023 [↗](#)).

Disruptions to the spatiotemporal relationships of species can result in serious ecological consequences including alteration of community structure (Tulloch et al., 2018 [↗](#)), upsetting the competitive balance between species (Boron et al., 2023 [↗](#)), increasing disease transmission (Hassell et al., 2017 [↗](#)), and accelerating local extinction (Fidino et al., 2019 [↗](#)). This can significantly distort the distribution of ecological functions that species provide, ultimately influencing ecosystem dynamics (Gardner et al., 2019 [↗](#)). Taken as a whole, interactions between sympatric species play a fundamental role in community assembly and are intricately related to

ecosystem stability and resilience (Boron et al., 2023). Thus, understanding how interspecific spatiotemporal associations change across human disturbance gradients provides valuable insight into the long-term implications of human impacts on ecosystem function and recovery relevant to biodiversity conservation in the Anthropocene.

Species interactions are known to be context-dependent such that they can vary across space and time, for example along environmental gradients (Chamberlain et al., 2014; Davis et al., 2018; Pellissier et al., 2018; Perrin et al., 2022). For example, gradients in stress are associated with variation in the outcomes of pairwise species interactions (Chamberlain et al., 2014). A key challenge in community ecology is to identify the conditions under which negative and positive species interactions are more likely to occur. For example, the controversial stress-gradient hypothesis predicts that positive interactions should increase as environmental conditions become more severe. Alpine bird communities have been shown to have a higher frequency of positive associations in grasslands with low productivity compared with in forests with high productivity (García-Navas et al., 2021) and savannah ungulates are more likely to form mixed-species groups in areas where there is predation risk (Beaudrot et al., 2020). Increasingly, major stresses on wild communities derive from human activity, and understanding how species interactions vary in response to human disturbance is pivotal in making robust ecological predictions about biodiversity responses to changing environmental conditions (Dangles et al., 2018; Perrin et al., 2022). However, a review of the literature indicates that the impact of human activity on interspecific interactions of terrestrial mammals remains poorly understood (Boron et al., 2023), particularly in mountain forests where anthropogenic impacts are often pervasive and increasing.

Medium and large-sized terrestrial mammals are a key components of mountain forest communities. They play crucial roles in maintaining biodiversity and ecosystem functions (Lacher et al., 2019), and are especially vulnerable to anthropogenic activities (Li et al., 2022b). Here, we set out to investigate the spatial and temporal patterns of occurrence and the interspecific associations within a terrestrial mammalian community along human disturbance gradients. We executed a systematic camera trapping survey spanning 4,100 km² of the Yarlung Zangbo Grand Canyon National Nature Reserve in the eastern Himalayas at a total of 322 camera trapping stations, obtaining detections of both wildlife and humans. We classified human disturbances into two groups: human modification (i.e. relating to habitat modifications by humans) or human presence (i.e. referring to the direct presence of humans) disturbances. We employed a context-dependent joint species distribution model (JSDM; Tikhonov et al., 2017) to infer pairwise species associations along human disturbance gradients. We used kernel density distributions of animal diel activity and time between detections of species pairs (time-to-encounter) to compare temporal associations at low and high human disturbances. We consider two hypotheses regarding temporal and spatial interspecific associations. The spatial compress hypothesis posits that human modification on habitats would suppress space available for animals to share (Tilman et al., 2017), resulting in increased positive spatial associations between species. The temporal compress hypothesis postulates that fear of direct human presence would compress diurnal activity in animals (Gaynor et al., 2018), resulting in reduced encounter time (or increased encounter rate) between species (Figure 1). Our study incorporates two different types of human disturbances in the analysis to elucidate the effects of humans on multidimensional (i.e., space and time) species associations. We then consider implications for conservation.

Results

Our camera traps obtained 10,388 independent detections of 17 focal species (12 carnivores and five ungulates) from 322 stations over 43,163 camera days of effort (Table 1). We documented a number of species and subspecies of conservation concern, including Bengal tiger *Panthera tigris*

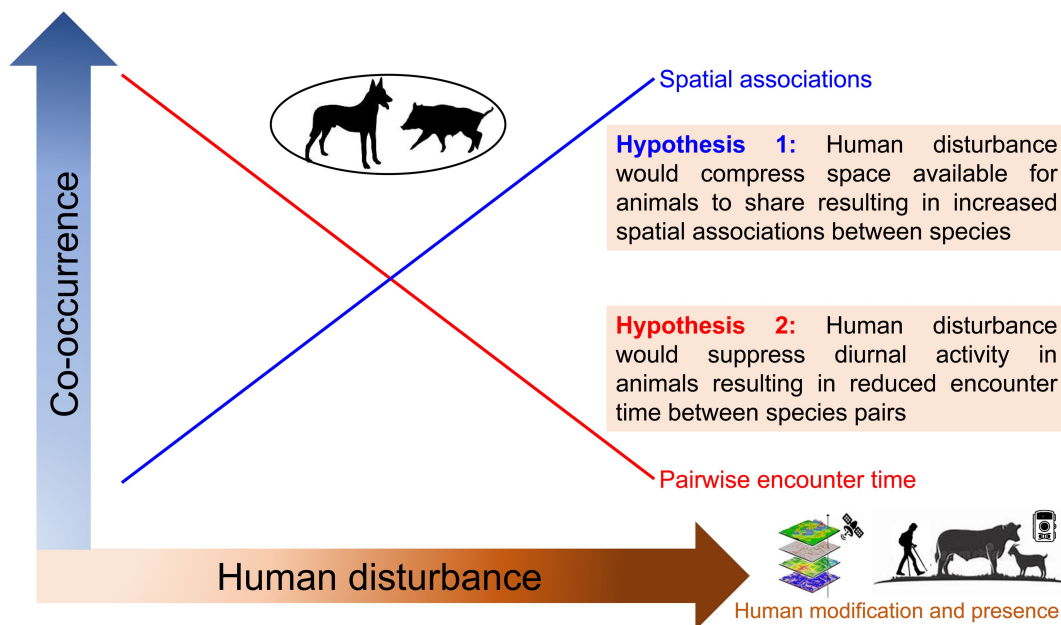


Figure 1

Conceptual framework illustrating the community-level effects of human disturbance on spatiotemporal associations among mountain forest terrestrial mammal species.

trigris, clouded leopard *Neofelis nebulosa* and dhole *Cuon alpinus*. We also captured 2,224 independent detections of humans during the survey period.

Species-specific response to habitat covariates

Species varied in their responses to habitat covariates. Nine out of 17 species showed strong positive response to forest cover (**Figure 2** [↗](#), Figure 2—source data 1). Human presence had apparent negative effects on the occurrence of clouded leopard (mean = -0.967, 95% CI = -2.35 to -0.025), takin *Budorcas taxicolor* (mean = -0.449, 95% CI = -0.935 to -0.071) and red goral *Naemorhedus baileyi* (mean = -0.806, 95% CI = -0.935 to -0.071), but was apparently positively associated with the occurrence of wild boar *Sus scrofa* (mean = 0.521, 95% CI = 0.045 to 1.093) and golden cat *Catopuma temminckii* (mean = 0.427, 95% CI = 0.165 to 0.804; Figure 2—source data 1). Human modification was apparently negatively associated with the occurrence of dhole (mean = -0.24, 95% CI = -0.493 to -0.027), red fox *Vulpes vulpes* (mean = -1.588, 95% CI = -2.656 to -0.769), Asiatic black bear *Ursus thibetanus* (mean = -0.234, 95% CI = -0.42 to -0.056), red goral (mean = -0.665, 95% CI = -1.129 to -0.238) and Mainland serow *Capricornis sumatraensis* (mean = -0.477, 95% CI = -0.697 to -0.26), but was positively apparently associated with muntjac *Muntjac* spp. (mean = 3.632, 95% CI = 0.946 to 9.999), masked palm civet *Paguma larvata* (mean = 2.076, 95% CI = 1.26 to 3.145), large Indian civet *Viverra zibetha* (mean = 0.782, 95% CI = 0.175 to 1.558) and marbled cat *Pardofelis marmorata* (mean = 0.689, 95% CI = 0.232 to 1.236; **Figure 2** [↗](#), Figure 2—source data 1).

Effects of human disturbances on spatial co-occurrence

Out of the 136 estimated pairwise residual correlation coefficients in occupancy, 87 (64 %) were positive at lower human modifications (**Figure 3a** [↗](#)). At the moderate and higher modifications, the species pairs with positive associations increased to 107 (79 %) and 118 (87%) respectively (**Figure 3b,c** [↗](#)). At lower modifications, correlation coefficients for 18 species pairs were positive and had a 95 % CI that did not overlap zero (Figure 3—figure supplement 1), and the number increased to 65 in moderate modifications (Figure 3—figure supplement 2) but dropped to 29 at higher modifications (Figure 3—figure supplement 3).

Along human presence gradients, 88 pairwise residual correlation coefficients (65 %) at lower human presence habitats were positive or close to neutral (**Figure 4a** [↗](#)). At the moderate and higher human presence habitats, the species pairs with positive associations increased to 115 (85 %) and 113 (83%) respectively (**Figure 4b,c** [↗](#)). The significant positive associations at low, moderate and higher human presence habitats were 6 (4%, Figure 4—figure supplement 1), 76 (56 %, Figure 4—figure supplement 2), and 44 (32%, Figure 4—figure supplement 3) respectively.

Effects of human disturbances on temporal co-occurrence

Human presence was associated with significantly increased nocturnality of carnivores (mean = 0.163, 95% CI = 0.089 to 0.236, **Figure 5a** [↗](#)), but showed no significant effects on ungulates (mean = -0.004, 95% CI = -0.031 to 0.023, **Figure 5b** [↗](#)) and combination of guilds (mean = -0.001, 95% CI = -0.028 to 0.026; **Figure 5c** [↗](#)). Human modification had no strong effects on nocturnality of any guilds and combination of guilds (i.e. 95 % CIs include zero, Figure 5—figure supplement 1).

Both human modification and human presence were associated with significantly reduced time between detections of pairs (human modification: mean = -1.07, 95% CI = -1.39 to -0.73; human presence: mean = -0.69, 95% CI = -0.92 to -0.46; **Figure 6** [↗](#)).

Table 1

Independent detection of ground-dwelling medium- and large-bodied mammal species based on camera trapping survey in the Yarlung Zangbo Grand Canyon, southeast Tibet

Order	Family	Genus	Species	Independent detections	IUCN Category
Cetartiodactyla	Bovidae	<i>Budorcas</i>	<i>Budorcas taxicolor</i>	92	VU
Cetartiodactyla	Bovidae	<i>Capreolus</i>	<i>Capreolus milneedwardsi</i>	2992	NT
Carnivora	Felidae	<i>Canis</i>	<i>Canis temminckii</i>	232	NT
Carnivora	Canidae	<i>Civus</i>	<i>Civus alpinus</i>	256	EN
Carnivora	Mastellidae	<i>Martes</i>	<i>Martes flavigula</i>	409	LC
Cetartiodactyla	Cervidae	<i>Moschus</i>	<i>Moschus moschifer</i>	4696	LC
Cetartiodactyla	Bovidae	<i>Naemorhedus</i>	<i>Naemorhedus baileyi</i>	254	VU
Carnivora	Felidae	<i>Neofelis</i>	<i>Neofelis nebulosa</i>	45	VU
Carnivora	Viverridae	<i>Paguma</i>	<i>Paguma larvata</i>	223	LC
Carnivora	Felidae	<i>Panthera</i>	<i>Panthera tigris</i>	26	EN
Carnivora	Felidae	<i>Pardofelis</i>	<i>Pardofelis marmorata</i>	54	NT
Carnivora	Felidae	<i>Prionailurus</i>	<i>Prionailurus bengalensis</i>	164	LC
Carnivora	Prionodontidae	<i>Prionodon</i>	<i>Prionodon pardicolor</i>	28	LC
Cetartiodactyla	Suidae	<i>Sus</i>	<i>Sus scrofa</i>	269	LC
Carnivora	Ursidae	<i>Ursus</i>	<i>Ursus thibetanus</i>	463	VU
Carnivora	Viverridae	<i>Viverra</i>	<i>Viverra zibetha</i>	37	LC
Carnivora	Canidae	<i>Vulpes</i>	<i>Vulpes vulpes</i>	88	LC

Figure 2

The effects of environmental and anthropogenic variables on terrestrial mammals in the Yarlung Zangbo Grand Canyon.

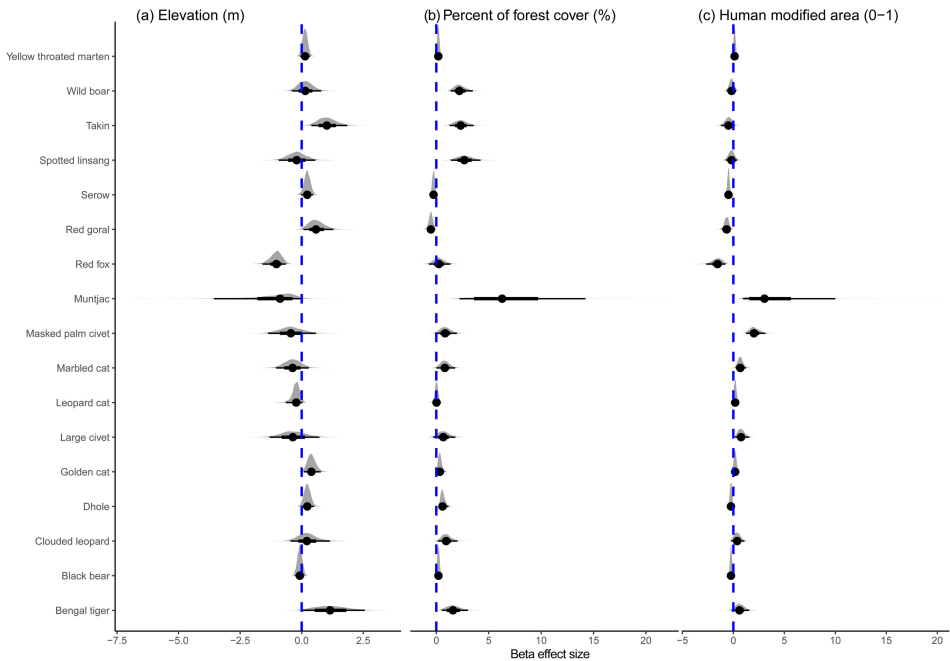


Figure 3

Estimates of associations between 17 terrestrial mammals across camera trapping stations with different human modification in the Yarlung Zangbo Grand Canyon. Associations are shown for the region's (a) minimum (Lower), (b) mean (Moderate) and (c) maximum (Higher) human modifications.

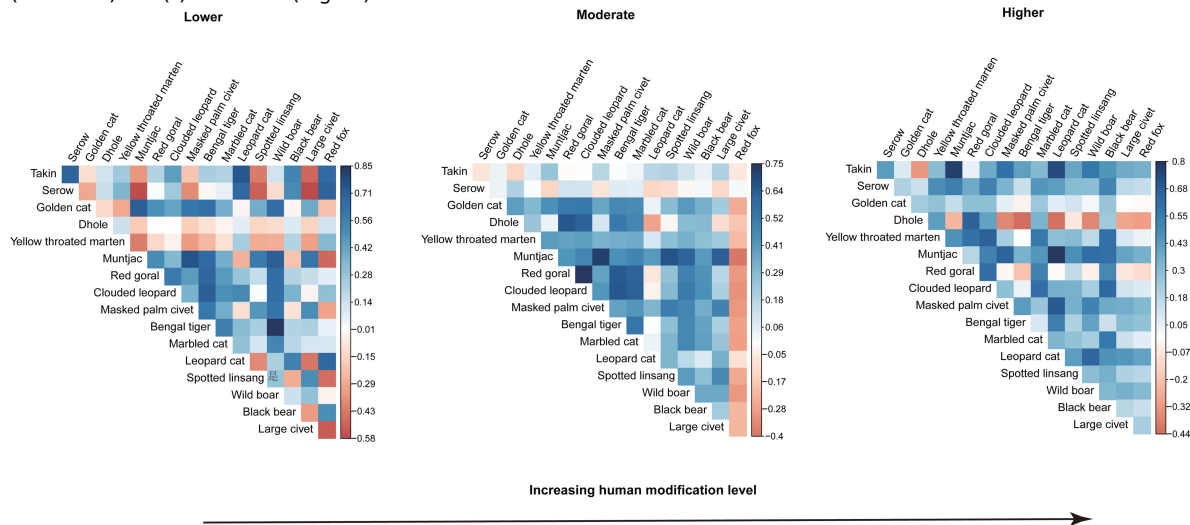


Figure 4

Estimates of associations between 17 terrestrial mammals across camera trapping stations with different human presence in the Yarlung Zangbo Grand Canyon. Associations are shown for the region's (a) minimum (Lower), (b) mean (Moderate) and (c) maximum (Higher) human presence.

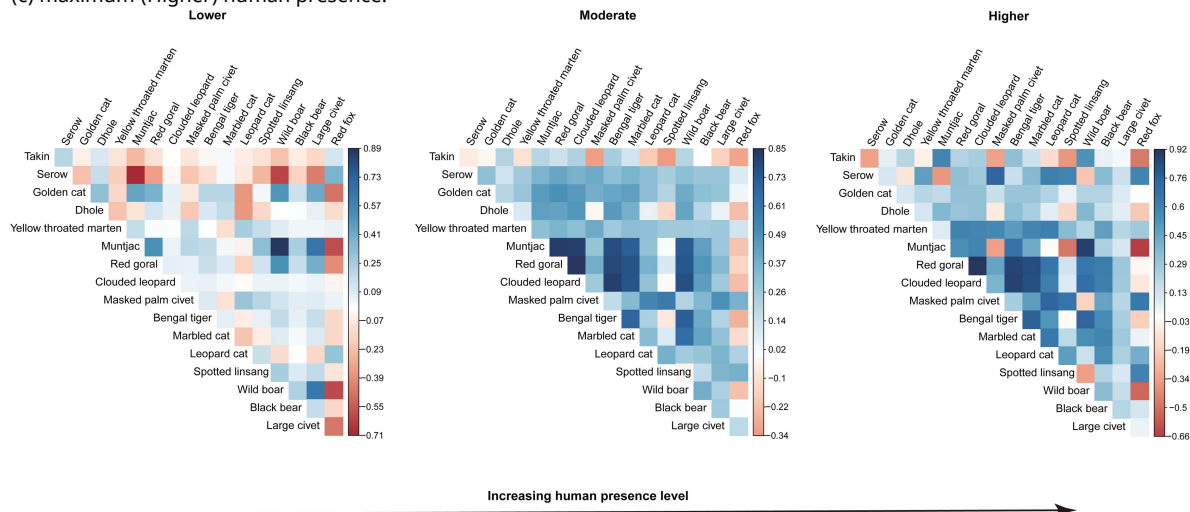
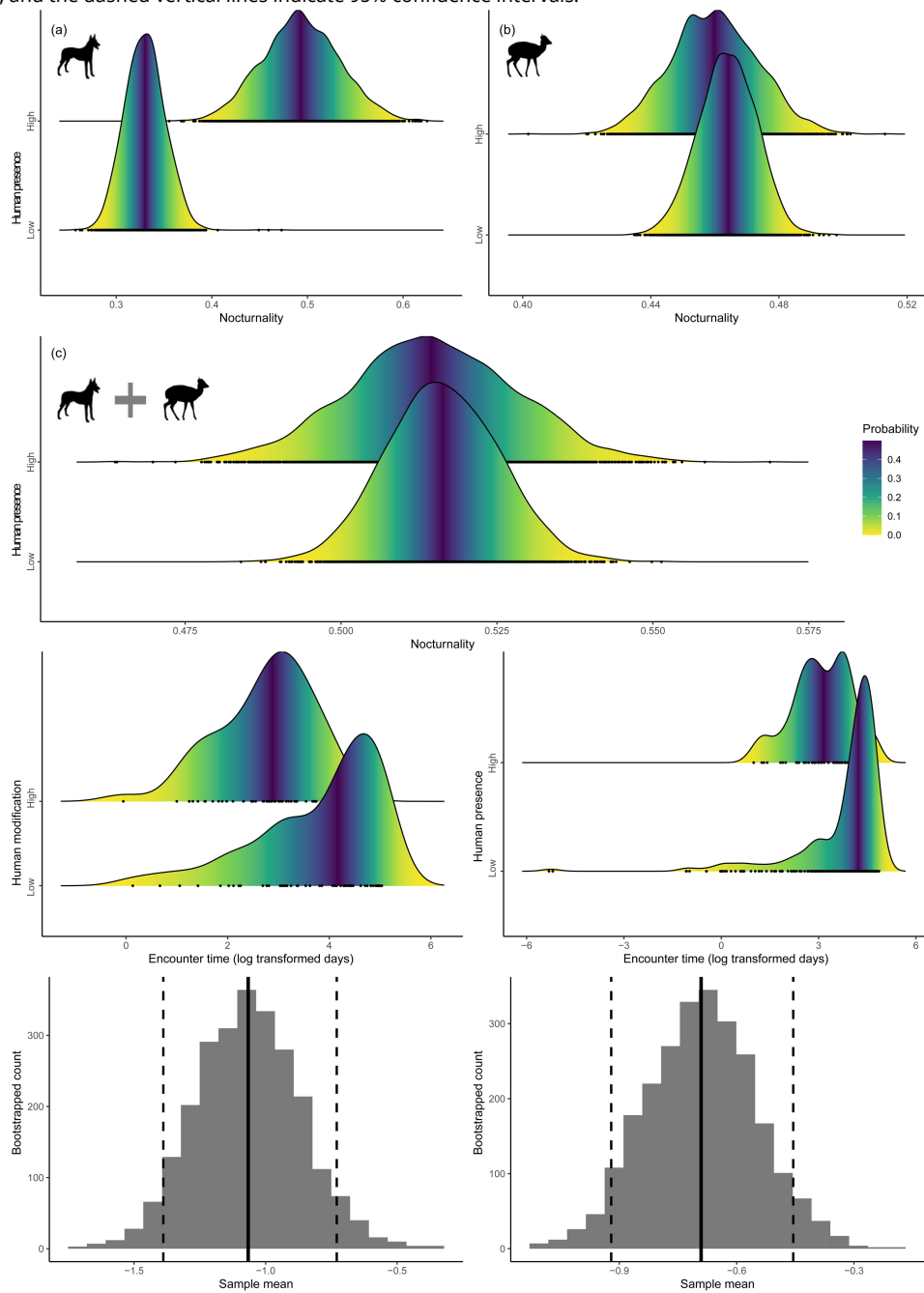


Figure 5

Density distributions of encounter time between successive detections of species pairs (in log-transformed days) in low- and high-human modification (a) and human presence (b) habitats, and differences in time-to-encounter between species pairs in low- and high-human modification (c) and human presence (d) habitats. The solid vertical lines in (c) and (d) represent mean differences, and the dashed vertical lines indicate 95% confidence intervals.



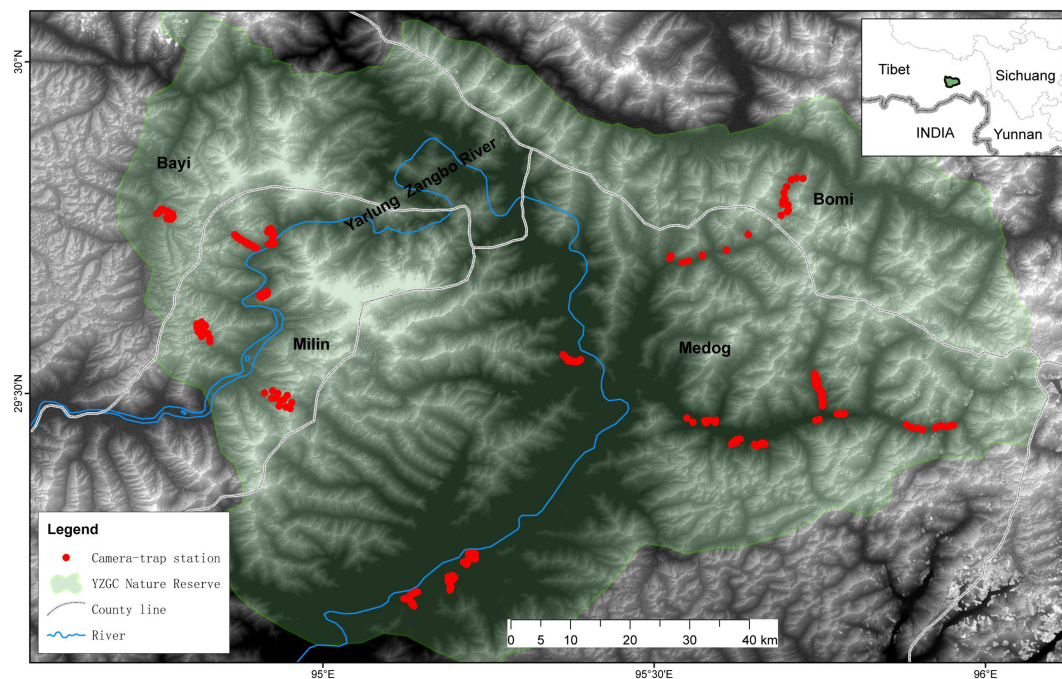


Figure 6

Location of study area in the Yarlung Zangbo Grand Canyon National Nature Reserve in the southeast of Tibetan Autonomous Region of China.

Discussion

Despite accumulating evidence of widespread impacts of humans on wildlife distribution and activity patterns, our understanding of how different types of anthropogenic pressures reshape species associations remains limited (Van Scoyoc et al., 2023 [↗](#)). Here, we compared the impacts of human modification (spatial compress effects) and human presence (temporal compress effects) on spatiotemporal associations among threatened terrestrial mammals based on systematic camera-trapping data in an understudied Himalayan landscape. Our results show a strong influence of humans on species co-occurrence patterns. The overall results of the spatiotemporal associations across levels of human modification and human presence suggest that humans are associated with increasing positive spatiotemporal associations among species. Specifically, we detected a higher incidence of positive associations in habitats with moderate and higher levels of human modification and human presence compared to those located in habitats with lower disturbance levels (**Figure 3** [↗](#), **4** [↗](#)). On the temporal axis, we detected a significant reduction of pairwise encounter time at increasing levels of human disturbance (**Figure 5** [↗](#)). Our results are therefore demonstrate that human disturbance can upset interspecific associations both on spatial and temporal niche dimensions.

Interspecific spatial associations can arise from species interaction, response to environmental covariates and common dispersal barriers (Blanchet et al., 2020 [↗](#); de Jonge et al., 2021 [↗](#); Poggiato et al., 2021 [↗](#)). Our context-dependent JSDM, which accounts for similarities and disparities in species-specific response to habitat covariates considered relevant to medium- and large-bodied mammal species, detected a higher prevalence of interspecific spatial associations in human disturbed habitats. Humans can have “bottom-up” impacts on animal distribution and associations by land use change and habitat modification (Riggio et al., 2020 [↗](#); Tucker et al., 2018 [↗](#)). Human activities can also have top-down impacts on spatiotemporal associations among animals by directly or indirectly changing the landscape of fear (Palmer et al., 2022 [↗](#); Suraci et al., 2019 [↗](#)). Previous studies suggest that human disturbance may compress the space and time available for communities to use, resulting in increased frequency of positive associations (Gilbert et al., 2022 [↗](#); Sévêque et al., 2022 [↗](#)). We interpret our results to mean that anthropogenic presence and disturbance reduce available habitats for wildlife, causing a greater predominance of positive associations in anthropogenic landscapes. On the one hand, human presence, such as while grazing livestock and gathering resource, generates landscapes of fear for wildlife (Gaynor et al., 2019 [↗](#); Palmer et al., 2022 [↗](#); Suraci et al., 2019 [↗](#)) and may downgrade habitat quality by overexploitation (Filazzola et al., 2020 [↗](#)). On the other hand, human modification such as land-use change often constrains the realized niche space of wildlife, restricting animal movement (Smith et al., 2018 [↗](#); Tucker et al., 2018 [↗](#)). Overall, our study provides one of the first tests of whether positive spatiotemporal associations between terrestrial mammals increase along gradients of different types of anthropogenic pressures. Our results add to the growing body of evidence that suggests anthropogenic activities reduce available niche space for animals, causing observed positive spatial associations among species (Gilbert et al., 2022 [↗](#); Gorczynski et al., 2022 [↗](#); Murphy et al., 2021 [↗](#)).

Identifying thresholds of anthropogenic activity that shift species behavior and co-occurrence will be key to drawing useful inference from human impact studies and improving our knowledge on when altered associations may lead to reverberating impacts on ecosystems (Van Scoyoc et al., 2023 [↗](#); Wilson et al., 2020 [↗](#)). We note that the number of species pairs with significant positive associations rapidly increased from lower to moderate levels of human disturbance, but dropped from mean to higher level of human disturbance (Figure 3—figure supplement 1-3 and Figure 4—figure supplement 1-3). Such patterns are consistent across human modification and human presence levels, indicating a threshold after which the positive effects of human disturbance on species associations were dampened. Human disturbance is an important factor in shaping species

distributions (Jones et al., 2018 [↗](#); Samia et al., 2015 [↗](#)). Wildlife often has a limited tolerance threshold to human activity (Polaina et al., 2018 [↗](#); Samia et al., 2015 [↗](#); Smith et al., 2019 [↗](#)). When human pressures reach levels that preclude a species occurring at a site (Polaina et al., 2018 [↗](#)), prediction of species associations in an anthropogenic context may become uninformative. More work needs to be done to further clarify the mechanisms driving the observed co-occurrence patterns.

Anthropogenic activities can also shift temporal niche of animals (Gaynor et al., 2018 [↗](#); Li et al., 2022a [↗](#)), possibly altering encounter rates among species and trophic dynamics that structure communities (Gilbert et al., 2022 [↗](#); Karanth et al., 2017 [↗](#); Mills and Harris, 2020 [↗](#)). Congruent with our hypothesis, we observed significant reduction of pairwise encounter time at increasing levels of human disturbance, corresponding to more frequent encounters between the pairs (Gilbert et al., 2022 [↗](#)). Although we did not find a significant shift in nocturnality at community level, we detected a significant shift to nocturnal activity of carnivores, indicating different sensitivities to human presence among the carnivores and ungulates in our study system. Fear of humans may explain the temporal response of wildlife to human presence. Numerous studies have shown that fear of humans as “super predators” can have suppressive effects on wildlife activity, which may contribute to increased temporal overlap among species (e.g., Sévêque et al., 2022 [↗](#); Suraci et al., 2019 [↗](#)).

All in all, our results indicate that both human modification and human presence may rewire species interactions by increasing spatial and temporal co-occurrence. Studies on the impacts of humans on wildlife communities should explicitly account for different types of co-occurring disturbances (Li et al., 2022a [↗](#)). Our camera trapping survey observed that human presence is pervasive even inside this remote protected area in the Tibetan Autonomous Region, indicating that wildlife and their habitats are exposed to frequent human disturbance. Humans exploit resources in protected areas in many ways, including through livestock herding, resource gathering, illegal hunting, and recreation, all of which impact wildlife and their habitats to varying degrees (Harris et al., 2019 [↗](#); Mills and Harris, 2020 [↗](#)). Our results demonstrate prevalent disruptions to species co-occurrence patterns from humans. If we are to preserve biodiversity in protected area, we must work to understand the negative effects on multiple facets of biodiversity from co-occurring anthropogenic pressures. Only then can we design effective mitigation measures.

Although interspecific associations should not be directly interpreted as a signal of biotic interactions between pairs of species (Blanchet et al., 2020 [↗](#); Poggiato et al., 2021 [↗](#)), it describes a unique facet of biodiversity, and can provide important insights into the coexistence and persistence of wildlife as well as ecosystem function in settings with anthropogenic activity (Keil et al., 2021 [↗](#); Lai et al., 2020 [↗](#); Van Scoyoc et al., 2023 [↗](#)). Since interspecific associations often increase with the ecological similarity of species involved (Gorczynski et al., 2022 [↗](#)), the tendency of many species towards positive associations with increase in anthropogenic pressures indicates a trend towards homogenization of terrestrial mammal communities. Such human-mediated changes in species co-occurrence patterns can have serious ecological consequences at multiple scales (Gilbert et al., 2022 [↗](#); Gorczynski et al., 2022 [↗](#)). For individual species, increased positive associations may affect fitness and population dynamics, increasing local extinction rates (Kuussaari et al., 2009 [↗](#); Parsons et al., 2022 [↗](#)). Increase in spatial aggregation among functionally similar species may be indicative of a hidden extinction debt (Kuussaari et al., 2009 [↗](#)). At the community level, increased positive associations may depress co-occurrence network complexity and stability, amplify interactions such as predation, and simplify communities with similar traits or co-occurrence patterns (Manlick and Pauli, 2020 [↗](#); Mills and Harris, 2020 [↗](#)). Also increased encounter rates between species may expand disease transmission across communities (Hassell et al., 2017 [↗](#)). In addition, wildlife can host a variety of zoonotic disease (Wicker et al., 2017 [↗](#)) and populations unnaturally associated with humans are more likely to transmit pathogens (Jones et al., 2013 [↗](#)). We observed that several species such as

masked palm civet and wild boar are positively associated with humans in our study area, indicating a substantial overlap between their habitats and human activity. Ongoing habitat modification, livestock grazing and resource gathering in this region may increase probability of pathogen exchange.

The effects of human disturbance on species associations might be scale-dependent (Gilbert et al., 2022 [↗](#)). At present, our sampling design only considers the effects of cumulative human modification and instantaneous local human presence on spatial associations and temporal encounter time at each camera trapping station. We are not able to compare the effects of human disturbance at broader scales (e.g., landscape scale) as such an analysis requires adequate data from hierarchical samplings. Estimating the effects of human disturbance at different spatial scale on species associations is a promising approach. Thus, we encourage future work to further clarify the multiscale ecological effects of human disturbance on species associations.

In conclusion, our study demonstrated that anthropogenic pressures increase spatiotemporal associations of terrestrial mammals from low to mean levels of human disturbances, but the frequency of positive spatial associations dropped from mean to higher level of human disturbances. Such variations in species associations likely influence the coexistence and persistence of wildlife, with potentially far-ranging ecological consequences. Because terrestrial mammals like carnivores and ungulates play fundamental roles in regulating montane forest ecosystems, the prevalent disruptions to their associations may precipitate biodiversity loss and impair ecosystem function. With increasing human presence and human modification of areas throughout the world, identifying thresholds of anthropogenic activity that shift species relationships, limiting human activity and increasing landscape connectivity across protected areas may be imperative to maintain interspecific spatiotemporal associations that underpin ecosystem resilience. Moreover, the methods we applied highlight the utility of camera trapping surveys in studying the spatiotemporal relationships among elusive species in settings with anthropogenic activities.

Materials and methods

Study area

The study was carried out inside the Yarlung Zangbo Grand Canyon National Nature Reserve (29°05'–30°02' N, 94°39'–96°6' E) in Nyingchi City in the southeast Tibet Autonomous Region of China (Figure 7). This area is situated within the Eastern Himalaya Biodiversity Hotspot, a globally important region for biodiversity conservation (Li et al., 2021 [↗](#)). The Yarlung Zangbo Grand Canyon is the deepest in the world, with an elevation drop of more than 7000 m, and has the reputation of “Gene Bank of Mountain Biological Resources” and “Natural Vegetation Museum” (Duan et al., 2022 [↗](#)). This region is characterized by dramatic vertical zonation of vegetation. From the valley bottom to the mountain peak, the main vegetation types consist of low mountain tropical monsoon rain forest, subtropical mountain evergreen broad-leaved forest, mid-mountain warm coniferous forest, sub-alpine cold coniferous forest, alpine subfrigid shrub meadow, and periglacial alpine vegetation (Deng et al., 2011 [↗](#)). The complete landscapes in the region harbors endangered species such as Bengal tiger *Panthera tigris tigris* (Li et al., 2023 [↗](#)). Human activities such as decentralized residential settlements and free-ranging livestock grazing is prevalent in the region, even within the protected area (Li et al., 2021 [↗](#)).

Camera trap sampling

Camera trap detections of terrestrial mammals were collected during the dry season between November 2020 and April 2021 and November 2021 and April 2022 to avoid the heavy rainy seasons in the region. The mean trapping efforts were 134 days (89 to 147 days range). We used Yianws L720 camera traps to conduct the survey. To determine how anthropogenic factors shape

spatiotemporal associations among terrestrial mammals, we set up camera trapping stations within the nature reserve based on intensity of human activities and distance to nearest human settlement. We deployed 350 camera stations in the reserve with different degrees of anthropogenic disturbance, maintaining at least 800 m between them (range 886 to 2233 m, median 1219). This distance may not satisfy the assumption of population closure and there may be some degree of pseudo-replication as observations of wide-ranging animals may not be independent. For these species, the occupancy estimate can be thought of as an estimate of the probability that the species used the area where the camera trapping station was located, rather than true occupancy (Li et al., 2018 [DOI](#)). Our camera trapping stations spanned a gradient of forest areas with varying levels of human activities and habitat modifications in the surrounding area. We affixed camera traps to trees between 80 and 100 cm off the ground, and they were not baited. Camera sensitivity was set to “low” to reduce false detections triggered by nonanimal movements. We set cameras to take three photos per detection event, with 3 s delay between subsequent detections. Camera trap photos were later identified to species when possible. We combined all human presence photos into a single “Human” categorization representing a variety of human activities detected around a camera station (e.g. resource gathering, livestock grazing, recreation etc.). All photos of the same species (including humans) at the same camera station were considered independent detections if separated by at least 1 h (Li et al., 2021 [DOI](#)). Several camera stations were invalid due to camera malfunctions or lost camera. The total valid sampling effort was 43,163 camera days from 322 camera stations that operated effectively. The target species consisted of ground-dwelling mammal species observed in more than 10 camera stations and weighing more than 1 kg. Thus, the occurrence dataset consists of presence-absence information on 17 mammal species at 322 camera stations.

Anthropogenic and habitat covariates

We derived two different types of human impacts: chronic human modification (e.g., settlement, transportation night-time lights etc.) and acute direct human presence (occurrence of people and domestic animals detected by camera traps) to address our hypotheses. We explored the degree of habitat modification based on the Human modification (HM) map metric (Kennedy et al., 2019 [DOI](#)). The HM metric provides a cumulative estimate of artificial modification of terrestrial landscapes based on 13 anthropogenic stressors caused by five human activities (human settlement, agriculture, transportation, energy production and electrical infrastructure) at a resolution of 1km (Kennedy et al., 2019 [DOI](#)). The metric is based on both the intensity and extent of impact of each anthropogenic stressor and ranges from 0 (no human disturbance) to 1 (highest human disturbance). Our sampling stations represent a varied gradient of human modification from 0.04 in minimum to 0.28 in maximum, with a mean value of 0.12 (sd = 0.05). We quantified the level of acute direct human presence around each camera trapping station by calculating the independent detections of human-related activities (e.g., livestock grazing, forest resource collection and tourism) per 100 camera-trap days. The range of human presence recorded by our camera trapping survey was 0 to 46.81, with a mean value of 6.42 (sd = 8.61). We also chose a set of two environmental covariates known to impact spatiotemporal distribution of mammals (Li et al., 2018 [DOI](#)) and presumed to affect interspecific associations: (1) elevation, which plays a key role in shaping spatial distribution of many species in mountain forests (He et al., 2019 [DOI](#); Li et al., 2018 [DOI](#)), and (2) percent of forest cover, which provides food resources, thermal cover and escape shelter for animals (Long et al., 2005 [DOI](#)). We derived percent of forest cover for each camera station based on the 250 m Moderate Resolution Imaging Spectroradiometer (MODIS) imagery (MOD44B Vegetation Continuous Fields (VCF) yearly product) of the study area for the period of 2021. For each camera trapping station, we derived human modification and percent of forest cover with a buffer radius of 500 m. This spatial scale should capture the environment that influences both resident animals with small home ranges and transient animals moving through the area. Prior to analysis, we log-transformed [$\log(x + 0.1)$] human presence data to account for its highly skewed distribution. We also standardized human modification and other environmental covariates by scaling to have mean of zero and unit variance.

Spatial co-occurrence analysis

We employed a context-dependent joint species distribution model (JSDM; Tikhonov et al., 2017) to characterize interspecific spatial associations of sympatric species. JSDMs are able to separate spatial associations between species into shared environmental preferences and residual correlations that cannot be explained by the environmental factors (Pollock et al., 2014). The context-dependent JSDM approach allow residual correlations to vary across the environment by incorporating species- and site-specific latent variables in the model (Tikhonov et al., 2017). We followed this approach and constructed a context-dependent model by utilizing a latent variable structure, where the factor loadings are modelled as a linear regression of covariates, allowing species associations to covary with human disturbance covariates. For our camera trap detections, we modelled the presence-absences of species j at camera station i as:

$$y_{ij} \sim \text{Bern}(\Psi_{ij})$$

with $\Psi_{ij} = \phi^{-1}(\eta_{ij})$, where Ψ_{ij} is the species-specific occurrence probability for each camera trapping station, and ϕ^{-1} is the inverse of a probit link-function. We modelled η_{ij} as:

$$\eta_{ij} = \sum_{k=1}^{n_c} x_{ik} \beta_{jk} + \varepsilon_{ij}$$

where n_c denotes the number of fixed covariates (i.e., elevation, percent of forest cover, human modification, and human presence) plus intercept, β_{jk} denotes the effect of environmental covariate k on species j , x_{ik} denotes the measured covariates $k = 1 \dots n_c$ in the sampling unit i . The intercept of the model is included by setting $x_{i1} = 1$ for all sampling units, so that the number of measured environmental covariates is $n_c - 1$. The species associations are modelled through the term ε_{ij} , which is defined by a latent factor model:

$$\varepsilon_{ij} = \sum_{h=1}^{n_f} z_{ih} \lambda_{jh}(x_{i\cdot}^*)$$

where z_{ih} denotes the value of latent factor $h = 1 \dots n_f$ at the sampling unit i , $\lambda_{jh}(x_{i\cdot}^*)$ denotes the response (factor loading) of species j to latent factor h , given a vector of predictors $x_{i\cdot}^*$. The predictors $x_{i\cdot}^* = (x_{i1}^*, \dots, x_{in_c}^*)$ on which the species associations are assumed to depend can be arbitrary, usually a subset of environmental predictors (Tikhonov et al., 2017). Here we model the factor loadings of species as a function of the two types of human disturbances (i.e., human modification and human presence):

$$\lambda_{jh}(x_{i\cdot}^*) = \sum_{k=1}^{n_c^*} x_{ik}^* \lambda_{jhk}$$

where n_c^* denotes the number of covariates assumed to impact residual correlations plus intercept. The intercept is included to the regression part by setting $x_{i1}^* = 1$ for all sampling units. In this study, assume $n_f = 3$, as our Deviance information criteria did not improve notably with the addition of more latent variables. We defined the covariance matrix of species factor loading as a function of human disturbances as $\varepsilon_i \sim N(0, \Omega(x_i^*))$, where $\Omega(x_i^*) = \Lambda(x_i^*) \Lambda(x_i^*)^T$, and $\Lambda(x_i^*)$ is the matrix of factor loadings, which depends on the human disturbances. We then scale this covariance matrix Ω to interspecific correlation matrices R by defining $R_{j_1 j_2} = \Omega_{j_1 j_2} / \sqrt{\Omega_{j_1 j_1} \Omega_{j_2 j_2}}$ for each pair of species, which represents disturbance-dependent associations between species that are not explained by fixed species-specific effects of environmental predictors. These resulted in values between -1 and 1, with negative values representing negative association between species, and positive values implying the opposite.

We estimated changes in species associations over continuous gradients of human modification (range: 0.04 to 0.28) and human presence gradients (range: 0.00 to 46.81). After fitting the model to data, we used the parameterized model to infer how species associations depend on human presence and human modification and generated predictions at minimum (lower), mean (moderate) and maximum (higher) conditions of the two variables separately.

We fitted the model based on a Bayesian approach using the greta R-package (Golding, 2019 [↗](#)) as described by Perrin et al. (2022) [↗](#). We specified uninformative normally-distributed priors for all parameters. We made inference from 3000 samples on three chains after a burn-in of 2000 samples.

Temporal co-occurrence analysis

For temporal co-occurrence analysis, we defined “Low” and “High” categories of human presence and human modification. We ranked camera trapping stations based on human presence and human modification separately, and filtered detections from the 25% most- (“High” category) and least- (“Low” category) disturbed camera trap stations and pooled detections within each category. We used kernel density distributions of animal diel activity and time between detections of species pairs (time-to-encounter) to compare temporal associations at lower and higher human disturbances. To examine if changes in species diel activity patterns were a mechanism behind anthropogenic impacts, we computed the nocturnal probability and time between consecutive detections of species pairs from lower- and higher-disturbance habitats. We transformed the detection time stamp to “solar time” to eliminate the impacts of day-length variation in day length (Nouvellet et al., 2012 [↗](#)). We retained only those species that had at least 30 independent detections in the low- and high-disturbance categories. For nocturnality analysis, we excluded detections within the hour around sunrise and sunset to avoid the effects of crepuscular activities on nocturnal probability. Thus, we defined nocturnal records as detections 1 h after sunset up to 1 h before sunrise. We conducted a binomial t-test to evaluate shifts in species nocturnality in the low- and high-disturbance categories.

To calculate time between detections of species pairs, we filtered camera stations to only those that detected at least two species for each disturbance category. We then calculated the time (in days) between successive detections across species pairs at each camera station. For analysis, we log transformed the time-to-encounter values to account for their markedly skewed distribution. We used 10,000 bootstrapped samples to evaluate 95% confidence interval (CI) shifts in time-to-encounter of species pairs from camera stations in the low- and high-disturbance categories. Results were considered to be significant if the key values fell outside of the 95% Confidence Interval.

Data availability

The authors declare that the data supporting the findings of this study are available within the article and its supplementary materials. Occupancy model data (independent detections of wildlife species and human activities histories and model covariates) are openly available in Science Data Bank: <https://doi.org/10.57760/sciencedb.11804> [↗](#).

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with data management.

Supplementary

Figure 2—source data 1 Standardized beta coefficients, and 95 % credible intervals, for the influence of anthropogenic and environmental covariates on the probability a species used an area during our camera-trap survey in Medog region. * denotes significant positive and negative effects based on 95 % CIs.

Figure 3—figure supplement 1 95 % confidence intervals of residual associations between species pairs at lower human modification level. * denotes significant associations (i.e., $p < 0.01$).

Figure 3—figure supplement 2 95 % confidence intervals of residual associations between species pairs at moderate modification level. * denotes significant associations (i.e., $p < 0.01$).

Figure 3—figure supplement 3 95 % confidence intervals of residual associations between species pairs at higher modification level. * denotes significant associations (i.e., $p < 0.01$).

Figure 4—figure supplement 1 95 % confidence intervals of residual associations between species pairs at lower human presence level. * denotes significant associations (i.e., $p < 0.01$).

Figure 4—figure supplement 2 95 % confidence intervals of residual associations between species pairs at moderate human presence level. * denotes significant associations (i.e., $p < 0.01$).

Figure 4—figure supplement 3 95 % confidence intervals of residual associations between species pairs at higher presence level. * denotes significant associations (i.e., $p < 0.01$).

Figure 5—figure supplement 1 Shifts in nocturnality of carnivores (a), ungulates (b) and combination of carnivores and ungulates (c) in the lower- and higher-human modification habitats.

References

- Beaudrot L, Palmer MS, Anderson TM, Packer C (2020) **Mixed-species groups of Serengeti grazers: a test of the stress gradient hypothesis** *Ecology* **101**
- Blanchet FG, Cazelles K, Gravel D (2020) **Co-occurrence is not evidence of ecological interactions** *Ecology Letters* **23**:1050–1063
- Boron V, Deere NJ, Hyde M, Bardales R, Stasiukynas D, Payán E (2023) **Habitat modification destabilizes spatial associations and persistence of Neotropical carnivores** *Current Biology*
- Burkle LA, Marlin JC, Knight TM (2013) **Plant-Pollinator Interactions over 120 Years: Loss of Species, Co-Occurrence, and Function** *Science* **339**:1611–1615 <https://doi.org/10.1126/science.1232728>
- Chamberlain SA, Bronstein JL, Rudgers JA (2014) **How context dependent are species interactions?** *Ecology Letters* **17**:881–890 <https://doi.org/10.1111/ele.12279>

- Dangles O, Herrera M, Carpio C, Lortie CJ (2018) **Facilitation costs and benefits function simultaneously on stress gradients for animals** *Proceedings of the Royal Society B: Biological Sciences* **285** <https://doi.org/10.1098/rspb.2018.0983>
- Davis CL *et al.* (2018) **Ecological correlates of the spatial co-occurrence of sympatric mammalian carnivores worldwide** *Ecology Letters* **21**:1401–1412
- de Jonge MMJ, Benítez-López A, Hennekens S, Santini L, Huijbregts MAJ, Schipper AM. (2021) **Conditional love? Co-occurrence patterns of drought-sensitive species in European grasslands are consistent with the stress-gradient hypothesis** *Global Ecology and Biogeography* **30**:1609–1620
- Deng L, Chen D, Deng L (2011) **Ecological evaluation of Yarlung Zangbo Grand Canyon National Nature Reserve in Tibet** *Scientia Silvae Sinicae* **47**:1–6
- Duan S, Han F, Li F, Yang Z (2022) **Spatial evaluation of the ecological value importance of national park in Yarlung Tsangpo Grand Canyon** *Journal of Environmental Management* **320**
- Fidino M, Simonis JL, Magle SB (2019) **A multistate dynamic occupancy model to estimate local colonization–extinction rates and patterns of co-occurrence between two or more interacting species** *Methods in Ecology and Evolution* **10**:233–244
- Filazzola A, Brown C, Dettlaff MA, Batbaatar A, Grenke J, Bao T, Peetoom Heida I, Cahill Jr JF (2020) **The effects of livestock grazing on biodiversity are multi-trophic: a meta-analysis** *Ecology Letters* **23**:1298–1309
- García-Navas V, Sattler T, Schmid H, Ozgul A (2021) **Bird species co-occurrence patterns in an alpine environment supports the stress-gradient hypothesis** *Oikos* **130**:1905–1918
- Gardner CJ, Bicknell JE, Baldwin-Cantello W, Struebig MJ, Davies ZG (2019) **Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis** *Nature Communications* **10** <https://doi.org/10.1038/s41467-019-12539-1>
- Gaynor KM, Brown JS, Middleton AD, Power ME, Brashares JS (2019) **Landscapes of Fear: Spatial Patterns of Risk Perception and Response** *Trends in Ecology & Evolution* **34**:355–368
- Gaynor KM, Hojnowski CE, Carter NH, Brashares JS (2018) **The influence of human disturbance on wildlife nocturnality** *Science* **360**:1232–1235
- Gilbert NA, Stenglein JL, Pauli JN, Zuckerberg B (2022) **Human disturbance compresses the spatiotemporal niche** *Proceedings of the National Academy of Sciences* **119**
- Golding N (2019) **greta: simple and scalable statistical modelling in R** *Journal of Open Source Software* **4** <https://doi.org/10.21105/joss.01601>
- Gorczynski D *et al.* (2022) **Human density modulates spatial associations among tropical forest terrestrial mammal species** *Global Change Biology* **28**:7205–7216
- Harris NC, Mills KL, Harissou Y, Hema EM, Gnoumou IT, VanZoeren J, Abdel-Nasser YI, 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**

- Hassell JM, Begon M, Ward MJ, Fèvre EM (2017) **Urbanization and Disease Emergence: Dynamics at the Wildlife–Livestock–Human Interface** *Trends in Ecology & Evolution* **32**:55–67
- He J, Zhao W, Li A, Wen F, Yu D (2019) **The impact of the terrain effect on land surface temperature variation based on Landsat-8 observations in mountainous areas** *International Journal of Remote Sensing* **40**:1808–1827
- Jones BA *et al.* (2013) **Zoonosis emergence linked to agricultural intensification and environmental change** *Proceedings of the National Academy of Sciences* **110**:8399–8404
- Jones KR, Venter O, Fuller RA, Allan JR, Maxwell SL, Negret PJ, Watson JEM (2018) **One-third of global protected land is under intense human pressure** *Science* **360**:788–791
- Karanth KU, Srivathsa A, Vasudev D, Puri M, Parameshwaran R, Kumar NS (2017) **Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient** *Proceedings of the Royal Society B: Biological Sciences* **284**
- Kathleen Lyons S *et al.* (2016) **Holocene shifts in the assembly of plant and animal communities implicate human impacts** *Nature* **529**:80–83 <https://doi.org/10.1038/nature16447>
- Keil P, Wiegand T, Tóth AB, McGlinn DJ, Chase JM (2021) **Measurement and analysis of interspecific spatial associations as a facet of biodiversity** *Ecological Monographs* **91**
- Kennedy CM, Oakleaf JR, Theobald DM, 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
- Kuussaari M *et al.* (2009) **Extinction debt: a challenge for biodiversity conservation** *Trends in Ecology & Evolution* **24**:564–571
- Lacher TE, Davidson AD, Fleming TH, Gómez-Ruiz EP, McCracken GF, Owen-Smith N, Peres CA, Vander Wall SB (2019) **The functional roles of mammals in ecosystems** *Journal of Mammalogy* **100**:942–964 <https://doi.org/10.1093/jmammal/gyy183>
- Lai XL, Zhou WL, Gao HL, Wang M, Gao K, Zhang BW, Wei FW, Nie YG (2020) **Impact of sympatric carnivores on den selection of wild giant pandas** *Zoological Research* **41**
- Li X, Bleisch W., 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, Bleisch WV, Li Q, Wang H, Lu W, Sun J, Zhang F, Ti B, Jiang X (2022) **Functional diversity loss and change in nocturnal behavior of mammals under anthropogenic disturbance** *Conservation Biology* **36**
- Li X, Hu W, Bleisch WV, Li Q, Wang H, Ti B, Qin Z, Sun J, Zhang F, Jiang X (2022) **Disproportionate loss of threatened terrestrial mammals along anthropogenic disturbance gradients** *Science of The Total Environment* **850**
- Li XY, Bleisch WV, Liu XW, Hu WQ, Jiang XL (2021) **Human disturbance and prey occupancy as predictors of carnivore richness and biomass in a Himalayan hotspot** *Animal Conservation* **24**:64–72

- Li XY, Hu WQ, Wang HJ, Jiang XL (2023) **Tiger reappearance in Medog highlights the conservation values of the region for this apex predator** *Zoological Research* **44**:747–749
- Long ES, Diefenbach DR, Rosenberry CS, Wallingford BD, Grund MD (2005) **Forest Cover Influences Dispersal Distance of White-Tailed Deer** *Journal of Mammalogy* **86**:623–629 [https://doi.org/10.1644/1545-1542\(2005\)86\[623:FCIDDO\]2.0.CO;2](https://doi.org/10.1644/1545-1542(2005)86[623:FCIDDO]2.0.CO;2)
- Manlick PJ, Pauli JN (2020) **Human disturbance increases trophic niche overlap in terrestrial carnivore communities** *Proceedings of the National Academy of Sciences* **117**:26842–26848
- Mills KL, Harris NC (2020) **Humans disrupt access to prey for large African carnivores** *eLife* **9** <https://doi.org/10.7554/eLife.60690>
- Moll RJ, Killion AK, Hayward MW, Montgomery RA (2021) **A Framework for the Eltonian Niche of Humans** *BioScience* **71**:928–941 <https://doi.org/10.1093/biosci/biab055>
- Murphy A, Diefenbach DR, Ternent M, Lovallo M, Miller D (2021) **Threading the needle: How humans influence predator–prey spatiotemporal interactions in a multiple-predator system** *Journal of Animal Ecology* **90**:2377–2390
- Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1994) **Declining biodiversity can alter the performance of ecosystems** *Nature* **368**:734–737 <https://doi.org/10.1038/368734a0>
- Nouvellet P, Rasmussen GSA, Macdonald DW, Courchamp F (2012) **Noisy clocks and silent sunrises: measurement methods of daily activity pattern** *Journal of Zoology* **286**:179–184
- Palmer MS, Gaynor KM, Becker JA, Abraham JO, Mumma MA, Pringle RM (2022) **Dynamic landscapes of fear: understanding spatiotemporal risk** *Trends in Ecology & Evolution* **37**:911–925
- Parsons AW, Kellner KF, Rota CT, Schuttler SG, Millspaugh JJ, Kays RW (2022) **The effect of urbanization on spatiotemporal interactions between gray foxes and coyotes** *Ecosphere* **13**
- Pellissier L *et al.* (2018) **Comparing species interaction networks along environmental gradients** *Biological Reviews* **93**:785–800 <https://doi.org/10.1111/brv.12366>
- Penjor U, Astaras C, Cushman SA, Kaszta Ź, Macdonald DW (2022) **Contrasting effects of human settlement on the interaction among sympatric apex carnivores** *Proceedings of the Royal Society B: Biological Sciences* **289**
- Perrin SW, van der Veen B, Golding N, Finstad AG. (2022) **Modelling temperature-driven changes in species associations across freshwater communities** *Global Change Biology* **28**:86–97
- Poggiato G, Münkemüller T, Bystrova D, Arbel J, Clark JS, Thuiller W (2021) **On the Interpretations of Joint Modeling in Community Ecology** *Trends in Ecology & Evolution* **36**:391–401
- Polaina E, González-Suárez M, Kuemmerle T, Kehoe L, Revilla E (2018) **From tropical shelters to temperate defaunation: The relationship between agricultural transition stage and the distribution of threatened mammals** *Global Ecology and Biogeography* **27**:647–657

Pollock LJ, Tingley R, Morris WK, Golding N, O'Hara RB, Parris KM, Vesk PA, McCarthy MA (2014) **Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM)** *Methods in Ecology and Evolution* **5**:397–406

Riggio J *et al.* (2020) **Global human influence maps reveal clear opportunities in conserving Earth's remaining intact terrestrial ecosystems** *Global Change Biology* **26**:4344–4356

Samia DSM, Nakagawa S, Nomura F, Rangel TF, Blumstein DT (2015) **Increased tolerance to humans among disturbed wildlife** *Nature Communications* **6** <https://doi.org/10.1038/ncomms9877>

Sévêque A, Gentle LK, López-Bao JV, Yarnell RW, Uzal A (2020) **Human disturbance has contrasting effects on niche partitioning within carnivore communities** *Biological Reviews* **95**:1689–1705

Sévêque A, Gentle LK, Vicente López-Bao J, Yarnell RW, Uzal A (2022) **Impact of human disturbance on temporal partitioning within carnivore communities** *Mammal Review* **52**:67–81 <https://doi.org/10.1111/mam.12265>

Smith JA, Duane TP, Wilmsers CC (2019) **Moving through the matrix: Promoting permeability for large carnivores in a human-dominated landscape** *Landscape and Urban Planning* **183**:50–58

Smith JA, Thomas AC, Levi T, Wang Y, Wilmsers CC (2018) **Human activity reduces niche partitioning among three widespread mesocarnivores** *Oikos* **127**:890–901

Song WY., Li XY., Chen ZZ., Li Q, Onditi KO., He SW, Jiang XL (2020) **Isolated alpine habitats reveal disparate ecological drivers of taxonomic and functional beta-diversity of small mammal assemblages** *Zoological Research* **41**:670–683

Suraci JP, Clinchy M, Zanette LY, Wilmsers CC (2019) **Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice** *Ecology Letters* **22**:1578–1586

Tikhonov G, Abrego N, Dunson D, Ovaskainen O (2017) **Using joint species distribution models for evaluating how species-to-species associations depend on the environmental context** *Methods in Ecology and Evolution* **8**:443–452

Tilman D (1994) **Competition and Biodiversity in Spatially Structured Habitats** *Ecology* **75**:2–16

Tilman D, Clark M, Williams DR, Kimmel K, Polasky S, Packer C (2017) **Future threats to biodiversity and pathways to their prevention** *Nature* **546**:73–81 <https://doi.org/10.1038/nature22900>

Tucker MA *et al.* (2018) **Moving in the Anthropocene: Global reductions in terrestrial mammalian movements** *Science* **359**:466–469

Tulloch AIT, Chadès I, Lindenmayer DB (2018) **Species co-occurrence analysis predicts management outcomes for multiple threats** *Nature Ecology & Evolution* **2**:465–474 <https://doi.org/10.1038/s41559-017-0457-3>

Van Scoyoc A, Smith JA, Gaynor KM, Barker K, Brashares JS. (2023) **The influence of human activity on predator-prey spatiotemporal overlap** *Journal of Animal Ecology* **92**:1124–1134

Wicker LV, Canfield PJ, Higgins DP (2017) **Potential Pathogens Reported in Species of the Family Viverridae and Their Implications for Human and Animal Health** *Zoonoses and Public Health* **64**:75–93

Wilson MW, Ridlon AD, Gaynor KM, Gaines SD, Stier AC, Halpern BS (2020) **Ecological impacts of human-induced animal behaviour change** *Ecology Letters* **23**:1522–1536 <https://doi.org/10.1111/ele.13571>

Wisz MS *et al.* (2013) **The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling** *Biological Reviews* **88**:15–30 <https://doi.org/10.1111/j.1469-185X.2012.00235.x>

Editors

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Reviewer #1 (Public Review):

Summary:

This study examines the spatial and temporal patterns of occurrence and the interspecific associations within a terrestrial mammalian community along human disturbance gradients. They conclude that human activity leads to a higher incidence of positive associations.

Strengths:

The theoretical framework of the study is brilliantly introduced. Solid data and sound methodology. This study is based on an extensive series of camera trap data. Good review of the literature on this topic.

Weaknesses:

The authors do not delve into the different types of association found in the study. A more ecological perspective explaining why certain species tend to exhibit negative associations and why others show the opposite pattern (and thus, can be used as indicator species) is missing. Also, the authors do not clearly distinguish between significant (true) non-random associations and random associations.

Anthropogenic pressures can shape species associations by increasing spatial and temporal co-occurrence, but above a certain threshold, the positive influence of human activity in terms of species associations could be reverted. This study can stimulate further work in this direction.

<https://doi.org/10.7554/eLife.92457.2.sa1>

Reviewer #2 (Public Review):

Summary:

This study analyses camera trapping information on the occurrence of forest mammals along a gradient of human modification of the environment. The key hypotheses are that human disturbance squeezes wildlife into a smaller area or their activity into only part of the day, leading to increased co-occurrence under modification. The method used is joint species distribution modelling (JSDM).

Strengths:

The data source seems to be very nice, although since very little information is presented, this is hard to be sure of. Also, the JSDM approach is, in principle, a nice way of simultaneously analysing the data.

Weaknesses:

The manuscript suffers from a mismatch of hypotheses and methods at two different levels.

(1) At the lower level, we would need to better understand what the individual species do and "like" (their environmental niche).

(2) The hypothesis clearly asks for an analysis of the statistical interaction between human disturbance and co-occurrence. Yet, the study is not set up in a way to test this directly.

The hypotheses point towards presenting the spatial and the temporal niche, and how it changes, species for species, under human disturbance. To this, one could then add the layer of interspecific associations.

The change in activity and space use could be analysed by looking at the activity times and spatial distribution directly. If biotic interactions change along the disturbance gradient, then observed data are already the outcome of such changed interactions. We thus cannot use the data to infer them! But we can show, for each species, that the habitat preferences change along the disturbance gradient - or not, as the case may be.

The per-species models are simplistic: the predictors are only linear, and there are no statistical interactions. It is unclear how spatial autocorrelations of residuals were treated, although they form the basis for the association analysis. Why are times of day and day of the year not included as predictors IN INTERACTION with niche predictors and human disturbance, since they represent the temporal dimension on which niches are hypothesised to change?

The discussion has little to add to the results. The complexity of the challenge (understanding a community-level response after accounting for species-level responses) is not met, and instead substantial room is given to general statements of how important this line of research is. What is the advance in ecological understanding at the community level?

<https://doi.org/10.7554/eLife.92457.2.sa0>

Author response:

The following is the authors' response to the original reviews.

Reviewer #1 (Public Review):

Summary:

This study examines the spatial and temporal patterns of occurrence and the interspecific associations within a terrestrial mammalian community along human

disturbance gradients. They conclude that human activity leads to a higher incidence of positive associations.

Strengths:

The theoretical framework of the study is brilliantly introduced. Solid data and sound methodology. This study is based on an extensive series of camera trap data. Good review of the literature on this topic.

Weaknesses:

The authors use the terms associations and interactions interchangeably.

This is not the case. In fact, we state specifically that "... interspecific associations should not be directly interpreted as a signal of biotic interactions between pairs of species..." However, co-occurrence can be an important predictor of likely interactions, such as competition and predation. We stand by our original text.

It is not clear what the authors mean by "associations". A brief clarification would be helpful.

Our specific definition of what is meant here by spatial association can be found in the Methods section. To clarify, the calculation of the index of associations is based on the covariance for the two species of the residuals (epsilon) after consideration of all species-specific response to known environmental covariates. These covariances are modelled to allow them to vary with the level of human disturbance, measured as human presence and human modification. After normalization, the final index of association is a correlation value that varies between -1 (complete disassociation) and +1 (complete positive association).

Also, the authors do not delve into the different types of association found in the study. A more ecological perspective explaining why certain species tend to exhibit negative associations and why others show the opposite pattern (and thus, can be used as indicator species) is missing.

Suggesting the ecological underpinnings of the associations observed here would mainly be speculation at this point, but the associations demonstrated in this analysis do suggest promising areas for the more detailed research suggested.

Also, the authors do not distinguish between significant (true) non-random associations and random associations. In my opinion, associations are those in which two species co-occur more or less than expected by chance. This is not well addressed in the present version of the manuscript.

Results were considered to be non-random if correlation coefficients (for spatial association) or overlap (for temporal association) fell outside of 95% Confidence Intervals. This is now stated clearly in the Methods section. In Figure 3—figure supplement 1-3 and Figure 4—figure supplement 1-3, $p < 0.01$ levels are also presented.

The obtained results support the conclusions of the study.

Anthropogenic pressures can shape species associations by increasing spatial and temporal co-occurrence, but above a certain threshold, the positive influence of human activity in terms of species associations could be reverted. This study can stimulate further work in this direction.

Reviewer #2 (Public Review):

Summary:

This study analyses camera trapping information on the occurrence of forest mammals along a gradient of human modification of the environment. The key hypotheses are that human disturbance squeezes wildlife into a smaller area or their activity into only part of the day, leading to increased co-occurrence under modification. The method used is joint species distribution modelling (JSDM).

Strengths:

The data source seems to be very nice, although since very little information is presented, this is hard to be sure of. Also, the JSDM approach is, in principle, a nice way of simultaneously analysing the data.

Weaknesses:

The manuscript suffers from a mismatch of hypotheses and methods at two different levels.

(1) At the lower level, we first need to understand what the individual species do and "like" (their environmental niche). That information is not presented, and the methods suggest that the representation of each species in the JSDM is likely to be extremely poor.

The response of each species to the environmental covariates provides a window into their environmental niche, encapsulated in the beta coefficients for each environmental covariate. This information is presented in Figure 2.

(2) The hypothesis clearly asks for an analysis of the statistical interaction between human disturbance and co-occurrence. Yet, the model is not set up this way, and the authors thus do a lot of indirect exploration, rather than direct hypothesis testing.

Our JSDM model is set up specifically to examine the effect of human disturbance on co-occurrence, after controlling for shared responses to environmental variables. It directly tests the first hypothesis, since, if increase in indices of human disturbance had not tended to increase the measured spatial correlations between species as detected by the model, we would have rejected our stated hypothesis that human modification of habitats results in increased positive spatial associations between species.

Even when the focus is not the individual species, but rather their association, we need to formulate what the expectation is. The hypotheses point towards presenting the spatial and the temporal niche, and how it changes, species for species, under human disturbance. To this, one can then add the layer of interspecific associations.

Examining each species one by one and how each one responds to human disturbance would miss the effects of any meaningful interactions between species. The analysis presented provides a means to highlight associations that would have been overlooked. Future research could go on to analyze the strongest associations in the community and the strongest effects of human disturbance so as to uncover the underlying interactions that give rise to them and the mechanisms of human impact. We believe that this will prove to be a much more productive approach than trying to tackle this problem species by species and pair by pair.

The change in activity and space use can be analysed much simpler, by looking at the activity times and spatial distribution directly. It remains unclear what the contribution

of the JSJM is, unless it is able to represent this activity and spatial information, and put it in a testable interaction with human disturbance.

The topic is actually rather complicated. If biotic interactions change along the disturbance gradient, then observed data are already the outcome of such changed interactions. We thus cannot use the data to infer them! But we can show, for each species, that the habitat preferences change along the disturbance gradient - or not, as the case may be.

Then, in the next step, one would have to formulate specific hypotheses about which species are likely to change their associations more, and which less (based e.g. on predator-prey or competitive interactions). The data and analyses presented do not answer any of these issues.

We suggest that the so-called “simpler” approach described above is anything but simple, and this is precisely what the Joint Species Distribution Model improves upon. As pointed out in the Introduction, simply examining spatial overlap is not enough to detect a signal of meaningful biotic interaction, since overlap could be the result of similar responses to environmental variables. With the JSJM approach, this would not be considered a positive association and would then not imply the possible existence of meaningful interaction.

Another more substantial point is that, according to my understanding of the methods, the per-species models are very inappropriate: the predictors are only linear, and there are no statistical interactions (L374). There is no conceivable species in the world whose niche would be described by such an oversimplified model.

While interaction terms can be included in the JSJM, this would considerably increase the complexity of the models. In previous work, we have found no strong evidence for the importance of interaction terms and they do not improve the performance of the models.

We have no idea of even the most basic characteristics of the per-species models: prevalences, coefficient estimates, D2 of the model, and analysis of the temporal and spatial autocorrelation of the residuals, although they form the basis for the association analysis!

The coefficient estimates for response to environmental variables used in the JSJM are provided in Figure 2 and Figure 2—source data 1.

Why are times of day and day of the year not included as predictors IN INTERACTION with niche predictors and human disturbance, since they represent the temporal dimension on which niches are hypothesised to change?

Also, all correlations among species should be shown for the raw data and for the model residuals: how much does that actually change and can thus be explained by the niche models?

The discussion has little to add to the results. The complexity of the challenge (understanding a community-level response after accounting for species-level responses) is not met, and instead substantial room is given to general statements of how important this line of research is. I failed to see any advance in ecological understanding at the community level.

We agree that the community-level response to human disturbance is a complex topic, and we believe it is also a very important one. This research and its support of the spatial compression hypothesis, while not providing definitive answers to detailed mechanisms,

opens up new lines of inquiry that makes it an important advance. For example, the strong effects of human disturbance on certain associations that were detected here could now be examined with the kind of detailed species by species and pair by pair analysis that this reviewer appears to demand.

Reviewer #1 (Recommendations For The Authors):

L27 indicates instead of "idicates".

We thank the reviewer for catching that error.

L64 I would refer to potential interactions or just associations. It is always hard to provide evidence for the existence of true interactions.

We have revised to “potential interactions” to qualify this statement.

L69 Suggestion: distort instead of upset.

We thank the reviewer for catching that error.

L70-71 Here, authors use the term associations. Please, be consistent with the terminology throughout the manuscript.

We thank the reviewer for raising this important point. The term “co-occurrence” appears to be used inconsistently in the literature, so we have tried to refer to it only when referencing the work of us. For us, co-occurrence means “spatial overlap” without qualification as to whether it is caused by interaction or simply by similar responses to environmental factors (see Blanchet et al. 2020, Argument 1). In our view, interactions refer to biotic effects like predation, competition, commensalism, etc., while associations are the statistical footprint of these processes. In keeping with this understanding, in Line 73, we changed "association" to the stronger word "interaction," but in Line 76, we keep the words "spatiotemporal association", which is presumed to be the result of those interactions. In Line 91, we have changed “interactions” to “associations,” as we do not believe interactions were demonstrated in that study.

L76 "Species associations are not necessarily fixed as positive or negative..." This sentence is misleading. I would say that species associations can vary across time and space, for instance along an environmental gradient.

We thank the reviewer for pointing out the potential for confusion. In Line 79, we have changed as suggested.

L78 "Associations between free-ranging species are especially context-dependent" Loose sentence. Please, explain a bit further.

We have changed the sentence to be more specific; “Interactions are known to be context-dependent; for example, gradients in stress are associated with variation in the outcomes of pairwise species interactions.”

L83-85 This would be a good place to introduce the 'stress gradient' hypothesis, which has also been applied to faunal communities in a few studies. According to this hypothesis, the incidence of positive associations should increase as environmental conditions harden.

In our review of the literature, we find that the stress gradient hypothesis is somewhat controversial and does not receive strong support in vertebrates. We have added the phrase “...the controversial stress-gradient hypothesis predicts that positive associations should increase as environmental conditions become more severe...”

L86-88 Well, overall, the number of studies examining spatiotemporal associations in vertebrates is relatively small. That is, bird associations have not received much more attention than those of mammals. I find this introductory/appealing paragraph a bit rough. I think the authors can do better and find a better justification for their work.

We thank the reviewer for the comments. We have rewritten the paragraph extensively to make it clearer and to provide a stronger justification for the study.

L106 "[...] resulting in increased positive spatial associations between species" I'd say that habitat shrinking would increase the level of species clustering or co-occurrence, but in my opinion, not necessarily the incidence of positive associations. It is not clear to me if the authors use positive associations as a term analogous to co-occurrence.

We thank the reviewer for raising this very important distinction. Habitat shrinking would increase levels of species co-occurrence, but this is not particularly interesting. We wanted to test whether there were effects on species interactions, as revealed by associations. We find that the terms association and co-occurrence are used somewhat loosely in the literature and so have made some new effort to clarify and systematize this in the manuscript. For example, there appear to be differences in the way “co-occurrence” is used in Boron 2023 and in Blanchet 2020. We do not use the term “positive spatial association” as analogous to “spatial co-occurrence.”. Spatial co-occurrence, which for us has the meaning of spatial overlap, could simply be the result of similar reactions to environmental co-variables, not reflecting any biotic interaction. Joint Species Distribution Models enable the partitioning of spatial overlap and segregation into that which can be explained by responses to known environmental factors, and that which cannot be explained and thus might be the result of biotic interactions. It is only the latter that we are calling spatial association, which can be positive or negative. These associations may be the statistical footprint of biotic interactions.

Results:

Difference between random and non-random association patterns. It is not clear to me if the reported associations are significant or not. The authors only report the sign of the association (either positive or negative) but do not clarify if these associations indicate that two species coexist more or less than expected by chance. In my opinion, that is the difference between true ecological associations (e.g., via facilitation or competition effects) and random co-existence patterns. This is paramount and should be addressed in a new version of the manuscript.

This information is provided in Figure 3—figure supplement 1,2,3 and Figure 4—figure supplement 1,2,3. This is referenced in the text as follows, “... correlation coefficients for 18 species pairs were positive and had a 95 % CI that did not overlap zero, and the number increased to 65 in moderate modifications but dropped to 29 at higher modifications” and so on. This criterion for significance (ie., greater than expected by chance) is now stated at the end of the Materials and methods. In Figure 3—figure supplement 1,2,3 and Figure 4—figure supplement 1,2,3, those correlations that were significant at $p < 0.01$ are also shown.

I am also missing a more ecological explanation for the observed findings. For instance, the top-ranked species in terms of negative associations is the red fox, whereas the muntjac seems to be the species whose presence can be used as an indicator for that of

other species. What are the mechanisms underlying these patterns? Do red foxes compete for food with other species? Do the species that show positive associations (red goral, muntjac) have traits or a diet that are more different from those of other species? More discussion on these aspects (role of traits and the trophic niche) would be necessary to better understand the obtained results.

The purpose of this paper was to test the compression hypotheses, and we have tried to keep that as the focus. However, the analysis does open up interesting lines of inquiry for future research to decipher the details of the interactions between species and the mechanisms by which human disturbance facilitates or disrupts these interactions. The reviewer raises some interesting possibilities, but at this point, any discussion along these lines would be largely speculation and could lengthen the paper without great benefit.

Reviewer #2 (Recommendations For The Authors):

The manuscript should be accompanied by all data and code of analysis.

All data and RScripts have been made available in Science Data Bank: <https://doi.org/10.57760/sciencedb.11804>.

The sentence "not much is known" is weak: it suggests the authors did not bother to quantify what IS known, and simply waved any previous knowledge aside. Surely we have some ideas about who preys on whom, and which species have overlapping resource requirements (e.g., due to jaw width). For those, we would expect a particularly strong signal, if the association is indeed indicative of interactions.

We believe that the reviewer is referring to the statement in Line 90-92 about the lack of understanding of the resilience of terrestrial mammal associations to human disturbance. We have added a reference to one very recent publication that addresses the issue (Boron et al., 2023), but otherwise we stand by our statement. We have, however, added a qualifier to make it clear that we did indeed look for previous knowledge; "However, a review of the literature indicates that"

Figures:

Fig. 1. This reviewer considers that this is too trivial and should be deleted.

This is a graphical statement of the hypotheses and may be helpful to some readers.

Fig. 2. Using points with error bars hides any potential information.

Done as suggested.

That only 4 predictors are presented is unacceptably oversimplified.

Only 4 predictors are included because, in previous work, we found that adding additional predictors or interactions did little to improve the model's performance (Li et al. 2018, 2021 and 2022) and could lead to over-fitting.

Fig. 5. and 6. aggregate extremely strongly over species; it remains unclear which species contribute to the signal, and I guess most do not.

The number of detection events presented in Table 1 should help to clarify the relative contribution of each species to the data presented in Figures 5 and 6.

L55: can you give any such "unique ecological information"

L60: Lyons et al. (Kathleen is the first name) has been challenged by Telford et al. (2016 Nature) as methodologically flawed.

The first name has been deleted. The methodological flaw has to do with interpretation of the fossil record and choice of samples, not with the need to partition shared environmental preferences and interactions.

L61 contradicts line 64: Blanchet et al. (2022, specifying some arguments from Dormann et al. 2018 GEB) correctly point out that logically one cannot infer the existence or strength from co-occurrence data. It is thus wrong to then claim (citing Boron et al.) that such data "convey key information about interactions". The latter statement is incorrect. A tree and a beetle can have extremely high association and nothing to do with each other. Association does not mean anything in itself. When two species are spatially and temporally non-overlapping, they can exhibit perfect "anti-association", yet, by the authors' own definition, cannot interact.

We believe that the reviewer's concerns arise from a misunderstanding of how we use the term association. In our usage, an association is not the same as co-occurrence or overlap, which may simply be the result of shared responses to environmental variables. The co-occurring tree and beetle would not be found to have any association in our analysis, only shared environmental sensitivities. In contrast, associations can be the statistical footprint of interactions, and would be overlaid onto any overlap due to similar responses to the environment. In the case of negative associations, such as might be the result of competitive exclusion or avoidance of predators, the two species would share environmental responses but show lower than expected spatial overlap. Even though they might be only rarely found in the same vicinity, they would indeed be interacting when they were together.

Joint Species Distribution Models "allow the partitioning of the observed correlation into that which can be explained by species responses to environmental factors... and that which remains unexplained after controlling for environmental effects and which may reflect biotic interactions." (Garcia Navas et al. 2021). It is the latter that we are calling "associations."

L63: Gilbert reference: Good to have a reference for this statement.

This point is important, but the reviewer's comments below have made it clear that it is even more important to point out that strong interactions should be expected to lead to significant associations. We have added a statement to clarify this.

L70-72: Incorrect, interactions play a role, not associations (which are merely statistical).

In this, we agree, and we have revised the statement to refer to interactions, not associations. In our view, an interaction is a biological phenomenon, while an association is the resulting statistical signal that we can detect.

L75: Associations tell us nothing, only interactions do. Since these can not be reliably inferred, this statement and this claim are wrong.

We thank the reviewer for raising this point, but we beg to disagree. Strong interactions should be expected to lead to significant associations that can be detected in the data. Associations, which can be measured reliably, are the evidence of potential interactions, and hence associations can tell us a great deal. We have added a note to this effect after the Gilbert reference above to clarify this point.

However, we do accept that associations must be interpreted with caution. As Blanchet et al. 2020 explain, " ...the co-occurrence signals (e.g. a significant positive or negative correlation value) estimated from these models could originate from any abiotic factors that impact species differently. Therefore, this correlation cannot be systematically interpreted as a signal of biotic interactions, as it could instead express potential non-measured environmental drivers (or combinations of them) that influence species distribution and co-distribution." Or alternatively an association could be the result of interaction with a 3rd species.

L87: Regarding your claim, how would you know you DO understand? For that, you need to formulate an expectation before looking at the data and then show you cannot show what you actually measure. (Jaynes called this the "mind-projection fallacy".)

We are not sure if the reviewer is criticizing our paper or the entire field of community ecology. Perhaps it is the statement that "...resilience of interspecific spatiotemporal associations of terrestrial mammals to human activity remains poorly understood...." Since we are confident that the reviewer believes that mammals do interact, we guess that it is the term "association" that is questioned. We have revised this to "...the impacts of human activity on interspecific interactions of terrestrial mammals remains poorly understood..."

In this particular case, we did formulate an expectation before looking at the data, in the form of the two formal hypotheses that are clearly stated in the Introduction and illustrated in Figure 1. If the hypotheses had not been supported, then we would have accepted that we do not understand. But as the data are consistent with the hypotheses, we submit that we do understand a bit more now.

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