Human disturbance increases spatiotemporal associations among mountain forest terrestrial mammal species

Xueyou Li[1], William V. Bleisch[2], Wenqiang Hu[1], Quan Li[1], Hongjiao Wang[1], Zhongzheng Chen[3], Ru Bai[1], Xuelong Jiang[1]

[1] 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; [2] China Exploration and Research Society, 2707-08 SouthMark, Wong Chuk Hang, Hong Kong, China; [3] Anhui Provincial Key Laboratory of the Conservation and Exploitation of Biological Resources, College of Life Sciences, Anhui Normal University, Wuhu, China

For correspondence: lixueyou@mail.kiz.ac.cn (XL); jiangxl@mail.kiz.ac.cn (XJ)

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.

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 savanah 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 km^2 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 trigris 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

138 modifications, the species pairs with positive associations increased to 107 (79 %) and 118
139 (87%) respectively (Figure 3b,c). At lower modifications, correlation coefficients for 18 species
140 pairs were positive and had a 95 % CI that did not overlap zero (Figure 3—figure supplement
141 1), and the number increased to 65 in moderate modifications (Figure 3—figure supplement 2)
142 but dropped to 29 at higher modifications (Figure 3—figure supplement 3).

143 Along human presence gradients, 88 pairwise residual correlation coefficients (65 %) at
144 lower human presence habitats were positive or close to neutral (Figure 4a). At the moderate
145 and higher human presence habitats, the species pairs with positive associations increased to
146 115 (85 %) and 113 (83%) respectively (Figure 4b,c). The significant positive associations at
147 low, moderate and higher human presence habitats were 6 (4%, Figure 4—figure supplement
148 1), 76 (56 %, Figure 4—figure supplement 2), and 44 (32%, Figure 4—figure supplement 3)
149 respectively.

150 **Effects of human disturbances on temporal co-occurrence**

151 Human presence was associated with significantly increased nocturnality of carnivores (mean
152 = 0.163, 95% CI = 0.089 to 0.236, Figure 5a), but showed no significant effects on ungulates
153 (mean = -0.004, 95% CI = -0.031 to 0.023, Figure 5b) and combination of guilds (mean = -
154 0.001, 95% CI = -0.028 to 0.026; Figure 5c). Human modification had no strong effects on
155 nocturnality of any guilds and combination of guilds (i.e. 95 % CIs include zero, Figure 5—
156 figure supplement 1).

157 Both human modification and human presence were associated with significantly reduced
158 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).

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

222 community level, we detected a significant shift to nocturnal activity of carnivores, indicating
223 different sensitivities to human presence among the carnivores and ungulates in our study
224 system. Fear of humans may explain the temporal response of wildlife to human presence.
225 Numerous studies have shown that fear of humans as "super predators" can have suppressive
226 effects on widlife activity, which may contribute to increased temporal overlap among speceis
227 (e.g., Sévêque et al., 2022; Suraci et al., 2019).

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

241 Although interspecific associations should not be directly interpreted as a signal of biotic
242 interactions between pairs of species (Blanchet et al., 2020; Poggiato et al., 2021), it describes

243 a unique facet of biodiversity, and can provide important insights into the coexistence and
244 persistence of wildlife as well as ecosystem function in settings with anthropogenic activity
245 (Keil et al., 2021; Lai et al., 2020; Van Scoyoc et al., 2023). Since interspecific associations
246 often increases with the ecological similarity of species involved (Gorczynski et al., 2022), the
247 tendency of many species towards positive associations with increase in anthropogenic
248 pressures indicates a trend towards homogenization of terrestrial mammal communities. Such
249 human-mediated changes in species co-occurrence patterns can have serious ecological
250 consequences at multiple scales (Gilbert et al., 2022; Gorczynski et al., 2022). For individual
251 species, increased positive associations may affect fitness and population dynamics, increasing
252 local extinction rates (Kuussaari et al., 2009; Parsons et al., 2022). Increase in spatial
253 aggregation among functionally similar species may be indicative of a hidden extinction debt
254 (Kuussaari et al., 2009). At the community level, increased positive associations may depress
255 co-occurrence network complexity and stability, amplify interactions such as predation, and
256 simplify communities with similar traits or co-occurrence patterns (Manlick and Pauli, 2020;
257 Mills and Harris, 2020). Also increased encounter rates between species may expand disease
258 transmission across communities (Hassell et al., 2017). In addition, wildlife can host a variety
259 of zoonotic disease (Wicker et al., 2017) and populations unnaturally associated with humans
260 are more likely to transmit pathogens (Jones et al., 2013). We observed that several species
261 such as masked palm civet and wild boar are positively associated with humans in our study
262 area, indicating a substantial overlap between their habitats and human activity. Ongoing
263 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

306 Camera trap detections of terrestrial mammals were collected during the dry season between
307 November 2020 and April 2021 and November 2021 and April 2022 to avoid the heavy rainy
308 seasons in the region. The mean trapping efforts were 134 days (89 to 147 days range). We
309 used Yianws L720 camera traps to conduct the survey. To determine how anthropogenic factors
310 shape spatiotemporal associations among terrestrial mammals, we set up camera trapping
311 stations within the nature reserve based on intensity of human activities and distance to nearest
312 human settlement. We deployed 350 camera stations in the reserve with different degrees of
313 anthropogenic disturbance, maintaining at least 800 m between them (range 886 to 2233 m,
314 median 1219). This distance may not satisfy the assumption of population closure and there
315 may be some degree of pseudo-replication as observations of wide-ranging animals may not be
316 independent. For these species, the occupancy estimate can be thought of as an estimate of the
317 probability that the species used the area where the camera trapping station was located, rather
318 than true occupancy (Li et al., 2018). Our camera trapping stations spanned a gradient of forest
319 areas with varying levels of human activities and habitat modifications in the surrounding area.
320 We affixed camera traps to trees between 80 and 100 cm off the ground, and they were not
321 baited. Camera sensitivity was set to "low" to reduce false detections triggered by nonanimal
322 movements. We set cameras to take three photos per detection event, with 3 s delay between
323 subsequent detections. Camera trap photos were later identified to species when possible. We
324 combined all human presence photos into a single "Human" categorization representing a
325 variety of human activities detected around a camera station (e.g. resource gathering, livestock
326 grazing, recreation etc.). All photos of the same species (including humans) at the same camera

327 station were considered independent detections if separated by at least 1 h (Li et al., 2021).
328 Several camera stations were invalid due to camera malfunctions or lost camera. The total valid
329 sampling effort was 43,163 camera days from 322 camera stations that operated effectively.
330 The target species consisted of ground-dwelling mammal species observed in more than 10
331 camera stations and weighing more than 1 kg. Thus, the occurrence dataset consists of presence-
332 absence information on 17 mammal species at 322 camera stations.

333 **Anthropogenic and habitat covariates**

334 We derived two different types of human impacts: chronic human modification (e.g., settlement,
335 transportation night-time lights etc.) and acute direct human presence (occurrence of people
336 and domestic animals detected by camera traps) to address our hypotheses. We explored the
337 degree of habitat modification based on the Human modification (HM) map metric (Kennedy
338 et al., 2019). The HM metric provides a cumulative estimate of artificial modification of
339 terrestrial landscapes based on 13 anthropogenic stressors caused by five human activities
340 (human settlement, agriculture, transportation, energy production and electrical infrastructure)
341 at a resolution of 1km (Kennedy et al., 2019). The metric is based on both the intensity and
342 extent of impact of each anthropogenic stressor and ranges from 0 (no human disturbance) to 1
343 (highest human disturbance). Our sampling stations represent a varied gradient of human
344 modification from 0.04 in minimum to 0.28 in maximum, with a mean value of 0.12 (sd = 0.05).
345 We quantified the level of acute direct human presence around each camera trapping station by
346 calculating the independent detections of human-related activities (e.g., livestock grazing,
347 forest resource collection and tourism) per 100 camera-trap days. The range of human presence

348 recorded by our camera trapping survey was 0 to 46.81, with a mean value of 6.42 (sd = 8.61).
349 We also chose a set of two environmental covariates known to impact spatiotemporal
350 distribution of mammals (Li et al., 2018) and presumed to affect interspecific associations: (1)
351 elevation, which plays a key role in shaping spatial distribution of many species in mountain
352 forests (He et al., 2019; Li et al., 2018), and (2) percent of forest cover, which provides food
353 resources, thermal cover and escape shelter for animals (Long et al., 2005). We derived percent
354 of forest cover for each camera station based on the 250 m Moderate Resolution Imaging
355 Spectroradiometer (MODIS) imagery (MOD44B Vegetation Continuous Fields (VCF) yearly
356 product) of the study area for the period of 2021. For each camera trapping station, we derived
357 human modification and percent of forest cover with a buffer radius of 500 m. This spatial scale
358 should capture the environment that influences both resident animals with small home ranges
359 and transient animals moving through the area. Prior to analysis, we log- transformed [log (x +
360 0.1)] human presence data to account for its highly skewed distribution. We also standardized
361 human modification and other environmental covariates by scaling to have mean of zero and
362 unit variance.

363 **Spatial co-occurrence analysis**

364 We employed a context-dependent joint species distribution model (JSDM; Tikhonov et al.,
365 2017) to characterize interspecific spatial associations of sympatric species. JSDMs are able to
366 separate spatial associations between species into shared environmental preferences and
367 residual correlations that cannot be explained by the environmental factors (Pollock et al., 2014).
368 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:

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

with $\Psi_{ij} = \varphi^{-1}(\eta_{ij})$, 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 $k = 1 \ldots n_c$ 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 $h = 1 \ldots n_f$ 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 $x_{i\cdot}^{*} = (x_{i1}^{*}, \ldots, x_{in_c^{*}}^{*})$ 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 $\varepsilon_{i\cdot} \sim N(0, \Omega(x_{i\cdot}^{*}))$, where $\Omega(x_{i\cdot}^{*}) = \Lambda(x_{i\cdot}^{*})\Lambda(x_{i\cdot}^{*})^{\mathrm{T}}$, and $\Lambda(x_{i\cdot}^{*})$ 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 $R_{j1j2} = \Omega_{j1j2}/\sqrt{\Omega_{j1j1}\Omega_{j2j2}}$ 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,

410 2019) as described by Perrin et al. (2022). We specified uninformative normally-distributed
411 priors for all parameters. We made inference from 3000 samples on three chains after a burn-
412 in of 2000 samples.

413 **Temporal co-occurrence analysis**

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

430 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.

Acknowledgements

We thank the Tibetan Autonomous Region Forestry and Grassland Department for their logistic support and their authorities for permitting the study. We thank Minjing Pu, Kang Luo, Changzhe Pu and other collaborators that helped collect data. We also thank Cheng Chen for his assistance with data management.

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**, e03163. https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecy.3163

Blanchet FG, Cazelles K, Gravel D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, **23**, 1050-1063. https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.13525

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* In press. DOI: https://www.sciencedirect.com/science/article/pii/S0960982223010369

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**, 20180983. https://doi.org/10.1098/rspb.2018.0983

Davis CL, Rich Lindsey N, Farris ZJ, Kelly MJ, Di Bitetti MS, Blanco YD, Albanesi S, Farhadinia Mohammad S, Gholikhani N, Hamel S, Harmsen BJ, Wultsch C, Kane MD, Martins Q, Murphy AJ, Steenweg R, Sunarto S, Taktehrani A, Thapa K, Tucker JM, Whittington J, Widodo FA, Yoccoz NG, Miller DAW. (2018). Ecological correlates of the

spatial co-occurrence of sympatric mammalian carnivores worldwide. *Ecology Letters*, **21**, 1401-1412. https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.13124

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. https://onlinelibrary.wiley.com/doi/abs/10.1111/geb.13323

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**, 115943. https://www.sciencedirect.com/science/article/pii/S030147972201516X

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. https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/2041-210X.13117

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. https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.13527

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. https://onlinelibrary.wiley.com/doi/abs/10.1111/oik.08588

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:** 4590. DOI: 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. https://www.sciencedirect.com/science/article/pii/S0169534719300199

Gaynor KM, Hojnowski CE, Carter NH, Brashares JS. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, **360**, 1232-1235. https://www.science.org/doi/10.1126/science.aar7121

Gilbert NA, Stenglein JL, Pauli JN, Zuckerberg B. (2022). Human disturbance compresses the spatiotemporal niche. *Proceedings of the National Academy of Sciences*, **119**, e2206339119. https://www.pnas.org/doi/abs/10.1073/pnas.2206339119

Golding N. (2019). greta: simple and scalable statistical modelling in R. *Journal of Open Source Software*, **4**, 1601. https://doi.org/10.21105/joss.01601

Gorczynski D, Hsieh C, Ahumada J, Akampurira E, Andrianarisoa MH, Espinosa S, Johnson S, Kayijamahe C, Lima MGM, Mugerwa B, Rovero F, Salvador J, Santos F, Sheil D, Uzabaho E, Beaudrot L. (2022). Human density modulates spatial associations among tropical forest terrestrial mammal species. *Global Change Biology*, **28**, 7205-7216. https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.16434

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**, e12667. https://conbio.onlinelibrary.wiley.com/doi/abs/10.1111/conl.12667

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. https://www.sciencedirect.com/science/article/pii/S0169534716301847

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, Grace D, Kock R, Alonso S, Rushton J, Said MY, McKeever D, Mutua F, Young J, McDermott J, Pfeiffer DU. (2013). Zoonosis emergence linked to agricultural intensification and environmental change. *Proceedings of the National Academy of Sciences*, **110**, 8399-8404. https://www.pnas.org/doi/abs/10.1073/pnas.1208059110

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. https://www.science.org/doi/abs/10.1126/science.aap9565

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**, 20161860.

https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2016.1860 %X

Kathleen Lyons S, Amatangelo KL, Behrensmeyer AK, Bercovici A, Blois JL, Davis M, DiMichele WA, Du A, Eronen JT, Tyler Faith J, Graves GR, Jud N, Labandeira C, Looy CV, McGill B, Miller JH, Patterson D, Pineda-Munoz S, Potts R, Riddle B, Terry R, Tóth A, Ulrich W, Villaseñor A, Wing S, Anderson H, Anderson J, Waller D, Gotelli NJ. (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**, e01452. https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecm.1452

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. https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.14549

Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Öckinger E, Pärtel M, Pino J, Rodà F, Stefanescu C, Teder T, Zobel M, Steffan-Dewenter I. (2009). Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology & Evolution*, **24**, 564-571. https://www.sciencedirect.com/science/article/pii/S0169534709001918

Lacher TE, Jr., 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**, 273. https://www.zoores.ac.cn/en/article/id/c8757c33-ea3b-4c8d-9d03-8ad4b96e40a6.

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. https://onlinelibrary.wiley.com/doi/abs/10.1111/ddi.12792.

Li X, Hu W, Bleisch WV, Li Q, Wang H, Lu W, Sun J, Zhang F, Ti B, Jiang X. (2022a). Functional diversity loss and change in nocturnal behavior of mammals under anthropogenic disturbance. *Conservation Biology*, **36**, e13839. https://conbio.onlinelibrary.wiley.com/doi/abs/10.1111/cobi.13839

Li X, Hu W, Bleisch WV, Li Q, Wang H, Ti B, Qin Z, Sun J, Zhang F, Jiang X. (2022b). Disproportionate loss of threatened terrestrial mammals along anthropogenic disturbance gradients. Science of The Total Environment, 850, 158038. https://www.sciencedirect.com/science/article/pii/S0048969722051373

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. https://zslpublications.onlinelibrary.wiley.com/doi/abs/10.1111/acv.12600

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. https://www.zoores.ac.cn/en/article/id/d938ea54-208f-4d79-b4ec-6dc92b57cb2a

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

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. https://www.pnas.org/doi/abs/10.1073/pnas.2012774117

Mills KL, Harris NC. (2020). Humans disrupt access to prey for large African carnivores. *eLife*, **9**, e60690. 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. https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2656.13548

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. https://zslpublications.onlinelibrary.wiley.com/doi/abs/10.1111/j.1469-

7998.2011.00864.x

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. https://www.sciencedirect.com/science/article/pii/S0169534722001409

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**, e3993. https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecs2.3993

Pellissier L, Albouy C, Bascompte J, Farwig N, Graham C, Loreau M, Maglianesi MA, Melián CJ, Pitteloud C, Roslin T, Rohr R, Saavedra S, Thuiller W, Woodward G, Zimmermann NE, Gravel D. (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 Ż, Macdonald DW. (2022). Contrasting effects of human settlement on the interaction among sympatric apex carnivores. *Proceedings of the Royal Society B: Biological Sciences*, **289**, 20212681. https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2021.2681

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. https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.15888

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. https://www.sciencedirect.com/science/article/pii/S0169534721000045

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. https://onlinelibrary.wiley.com/doi/abs/10.1111/geb.12725

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. https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/2041-210X.12180

Riggio J, Baillie JEM, Brumby S, Ellis E, Kennedy CM, Oakleaf JR, Tait A, Tepe T, Theobald DM, Venter O, Watson JEM, Jacobson AP. (2020). Global human influence maps reveal clear opportunities in conserving Earth's remaining intact terrestrial ecosystems. *Global Change Biology*, **26**, 4344-4356. https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.15109

Samia DSM, Nakagawa S, Nomura F, Rangel TF, Blumstein DT. (2015). Increased tolerance to humans among disturbed wildlife. *Nature Communications*, **6**, 8877. 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. https://onlinelibrary.wiley.com/doi/abs/10.1111/brv.12635

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, Wilmers CC. (2019). Moving through the matrix: Promoting permeability for large carnivores in a human-dominated landscape. *Landscape and Urban Planning*, **183**, 50-58. https://www.sciencedirect.com/science/article/pii/S0169204618312829

Smith JA, Thomas AC, Levi T, Wang Y, Wilmers CC. (2018). Human activity reduces niche partitioning among three widespread mesocarnivores. *Oikos*, **127**, 890-901. https://onlinelibrary.wiley.com/doi/abs/10.1111/oik.04592

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. https://www.zoores.ac.cn/article/doi/10.24272/j.issn.2095-8137.2020.085.

Suraci JP, Clinchy M, Zanette LY, Wilmers CC. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*, **22**, 1578-1586. https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.13344

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. https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/2041-210X.12723

Tilman D. (1994). Competition and Biodiversity in Spatially Structured Habitats. *Ecology*, **75**, 2-16. https://esajournals.onlinelibrary.wiley.com/doi/abs/10.2307/1939377

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, Böhning-Gaese K, Fagan WF, Fryxell JM, Van Moorter B, Alberts SC, Ali AH, Allen AM, Attias N, Avgar T, Bartlam-Brooks H, Bayarbaatar B, Belant JL, Bertassoni A, Beyer D, Bidner L, van Beest FM, Blake S, Blaum N, Bracis C, … Mueller T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, **359**, 466-469. https://science.sciencemag.org/content/sci/359/6374/466.full.pdf

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. https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2656.13892

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. https://onlinelibrary.wiley.com/doi/abs/10.1111/zph.12290

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, Pottier J, Kissling WD, Pellissier L, Lenoir J, Damgaard CF, Dormann CF, Forchhammer MC, Grytnes J-A, Guisan A, Heikkinen RK, Høye TT, Kühn I, Luoto M,

Maiorano L, Nilsson M-C, Normand S, Öckinger E, Schmidt NM, Termansen M, Timmermann A, Wardle DA, Aastrup P, Svenning J-C. (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

689 **Table and table legends**

690 **Table 1** Independent detection of ground-dwelling medium- and large-bodied mammal

691 species based on camera trapping survey in the Yarlung Zangbo Grand Canyon,

692 southeast Tibet

Order	Family	Genus	Species	Independent detections	IUCN Category
Cetartiodactyla	Bovidae	*Budorcas*	*Budorcas taxicolor*	92	VU
Cetartiodactyla	Bovidae	*Capricornis*	*Capricornis milneedwardsii*	2992	NT
Carnivora	Felidae	*Catopuma*	*Catopuma temminckii*	232	NT
Carnivora	Canidae	*Cuon*	*Cuon alpinus*	256	EN
Carnivora	Mustelidae	*Martes*	*Martes flavigula*	469	LC
Cetartiodactyla	Cervidae	*Muntiacus*	*Muntiacus muntjak*	4696	LC
Cetartiodactyla	Bovidae	*Naemorhedus*	*Naemorhedus baileyi*	254	VU
Carnivora	Felidae	*Neofelis*	*Neofelis nebulosa*	45	VU
Carnivora	Viverridae	*Paguma*	*Paguma larvata*	223	LC
Carnivora	Felidae	*Panthera*	*Panthera tigris*	26	EN
Carnivora	Felidae	*Pardofelis*	*Pardofelis marmorata*	54	NT
Carnivora	Felidae	*Prionailurus*	*Prionailurus bengalensis*	164	LC
Carnivora	Prionodontidae	*Prionodon*	*Prionodon pardicolor*	28	LC
Cetartiodactyla	Suidae	*Sus*	*Sus scrofa*	269	LC
Carnivora	Ursidae	*Ursus*	*Ursus thibetanus*	463	VU
Carnivora	Viverridae	*Viverra*	*Viverra zibetha*	37	LC
Carnivora	Canidae	*Vulpes*	*Vulpes vulpes*	88	LC

693

694 **Figure legends**

695 **Figure 1** Conceptual framework illustrating the community-level effects of human disturbance

696 on spatiotemporal associations among mountain forest terrestrial mammal species.

697 **Figure 2** The effects of environmental and anthropogenic variables on terrestrial mammals in

698 the Yarlung Zangbo Grand Canyon.

699 **Figure 2—source data 1** Standardized beta coefficients, and 95 % credible intervals, for the

700 influence of anthropogenic and environmental covariates on the probability a species used an

701 area during our camera-trap survey in Medog region. * denotes significant positive and negative

702 effects based on 95 % CIs.

703 **Figure 3** Estimates of associations between 17 terrestrial mammals across camera trapping

704 stations with different human modification in the Yarlung Zangbo Grand Canyon. Associations

705 are shown for the region's (a) minimum (Lower), (b) mean (Moderate) and (c) maximum

706 (Higher) human modifications.

707 **Figure 3—figure supplement 1** 95 % confidence intervals of residual associations between

708 species pairs at lower human modification level. * denotes significant associations (i.e., $p <$

709 0.01).

710 **Figure 3—figure supplement 2** 95 % confidence intervals of residual associations between

711 species pairs at moderate modification level. * denotes significant associations (i.e., $p < 0.01$).

712 **Figure 3—figure supplement 3** 95 % confidence intervals of residual associations between

713 species pairs at higher modification level. * denotes significant associations (i.e., $p < 0.01$).

714

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

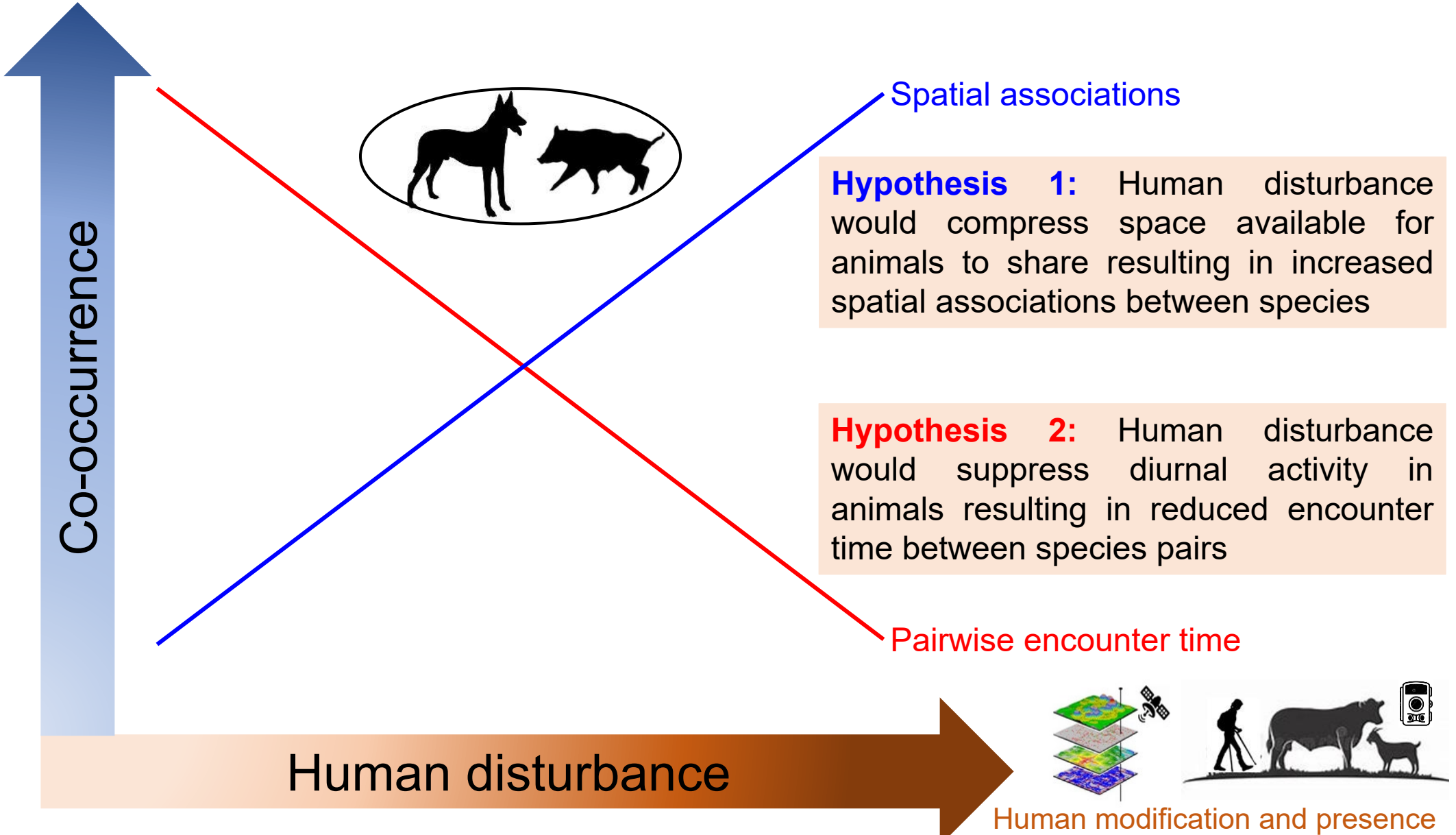
Figure 4—figure supplement 2 95 % confidence intervals of residual associations between species pairs at moderate human presence level. * denotes significant associations (i.e., $p < 0.01$).

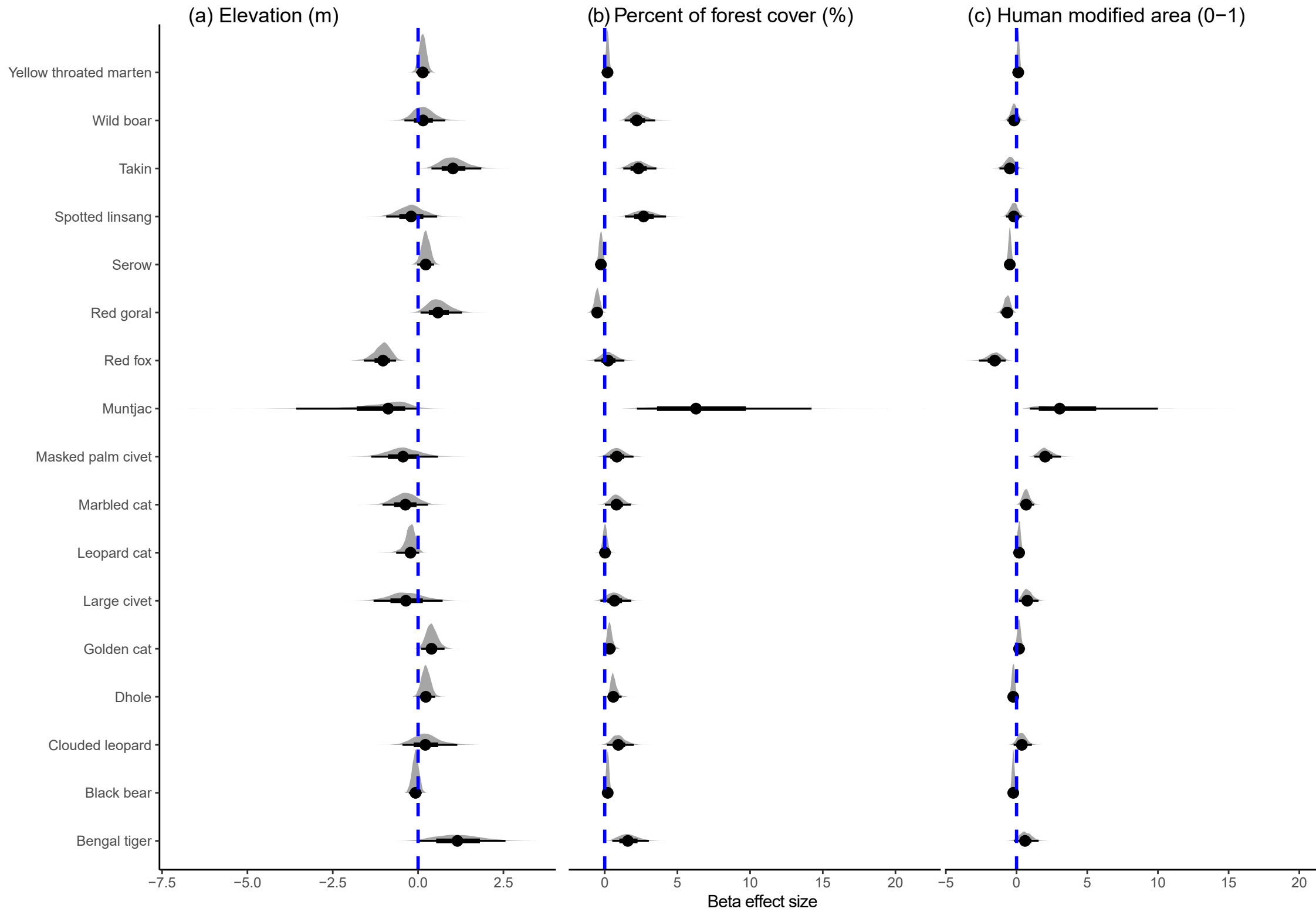
Figure 4—figure supplement 3 95 % confidence intervals of residual associations between species pairs at higher presence level. * denotes significant associations (i.e., $p < 0.01$).

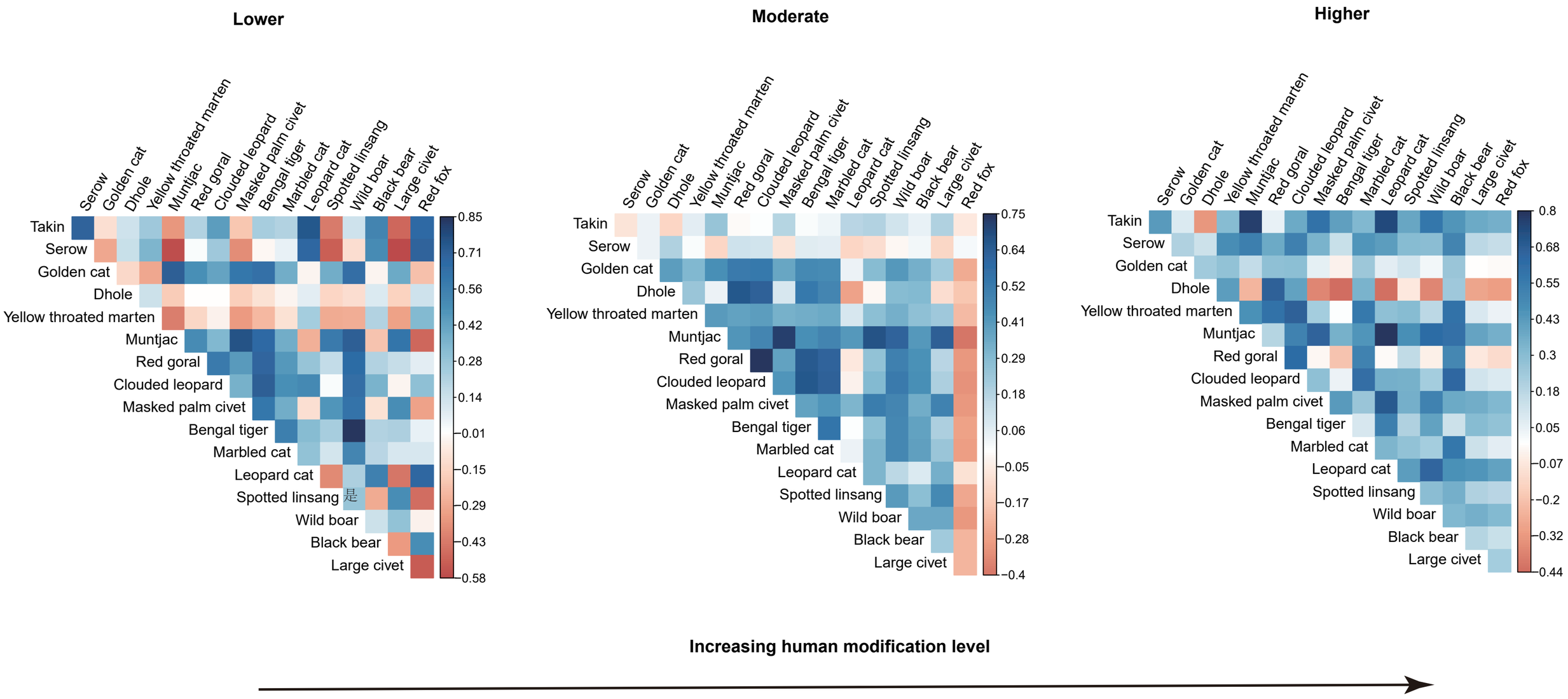
Figure 5 Density distributions of encounter time between successive detections of species pairs (in log-transformed days) in low- and high-human modification (a) and human presence (b) habitats, and differences in time-to-encounter between species pairs in low- and high-human modification (c) and human presence (d) habitats. The solid vertical lines in (c) and (d) represent mean differences, and the dashed vertical lines indicate 95% confidence intervals.

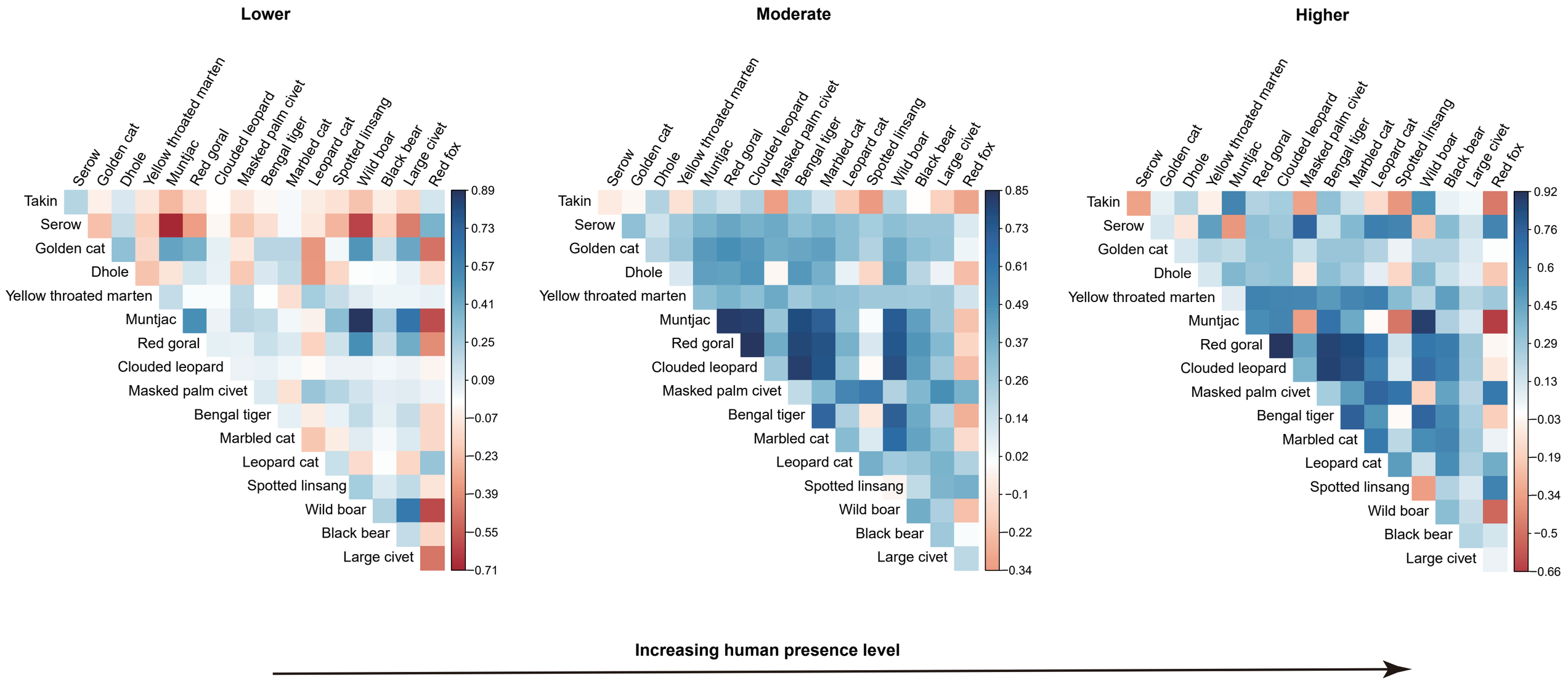
Figure 5—figure supplement 1 Shifts in nocturnality of carnivores (a), ungulates (b) and combination of carnivores and ungulates (c) in the lower- and higher-human modification habitats.

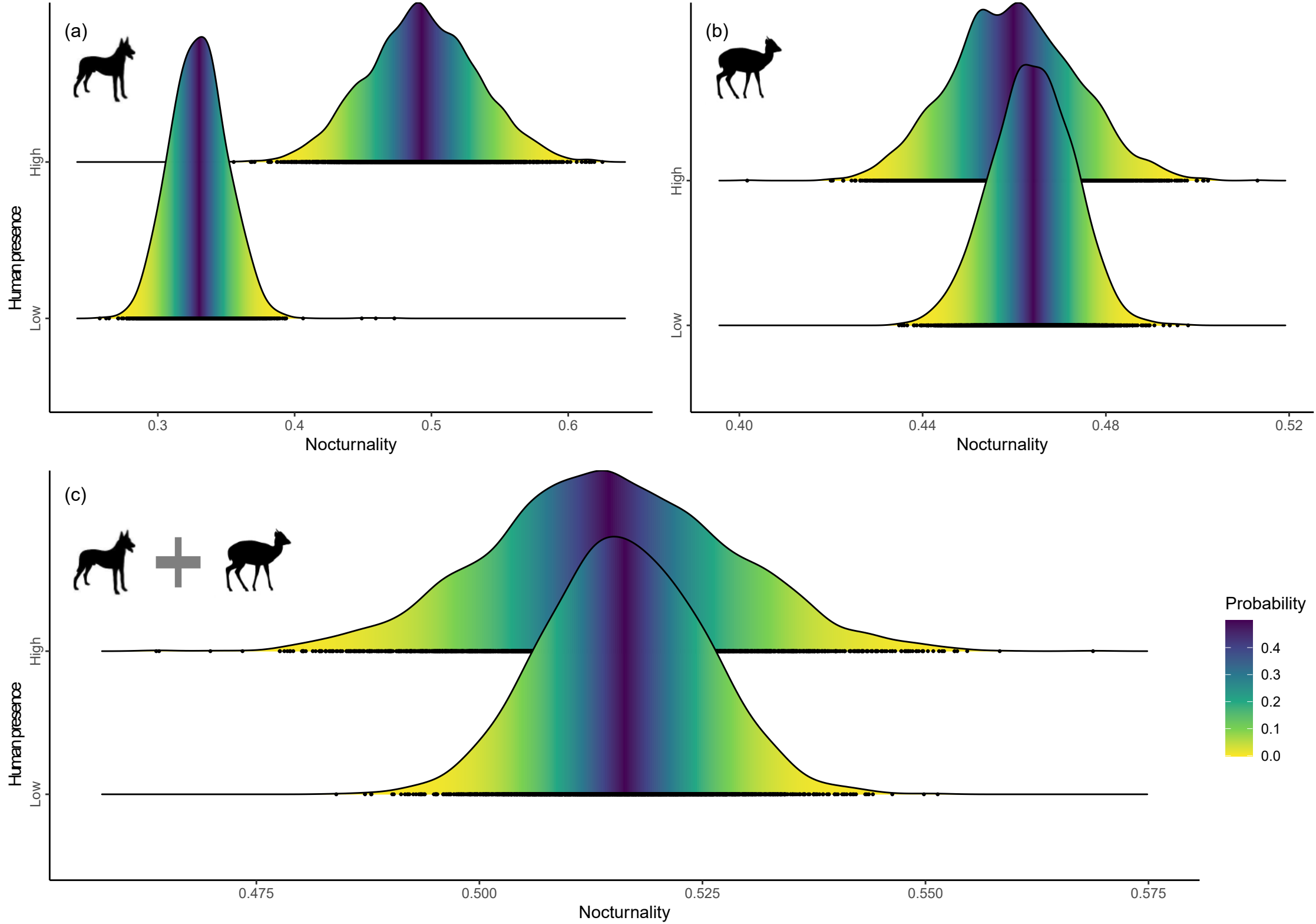
Figure 6 Location of study area in the Yarlung Zangbo Grand Canyon National Nature Reserve in the southeast of Tibetan Autonomous Region of China.

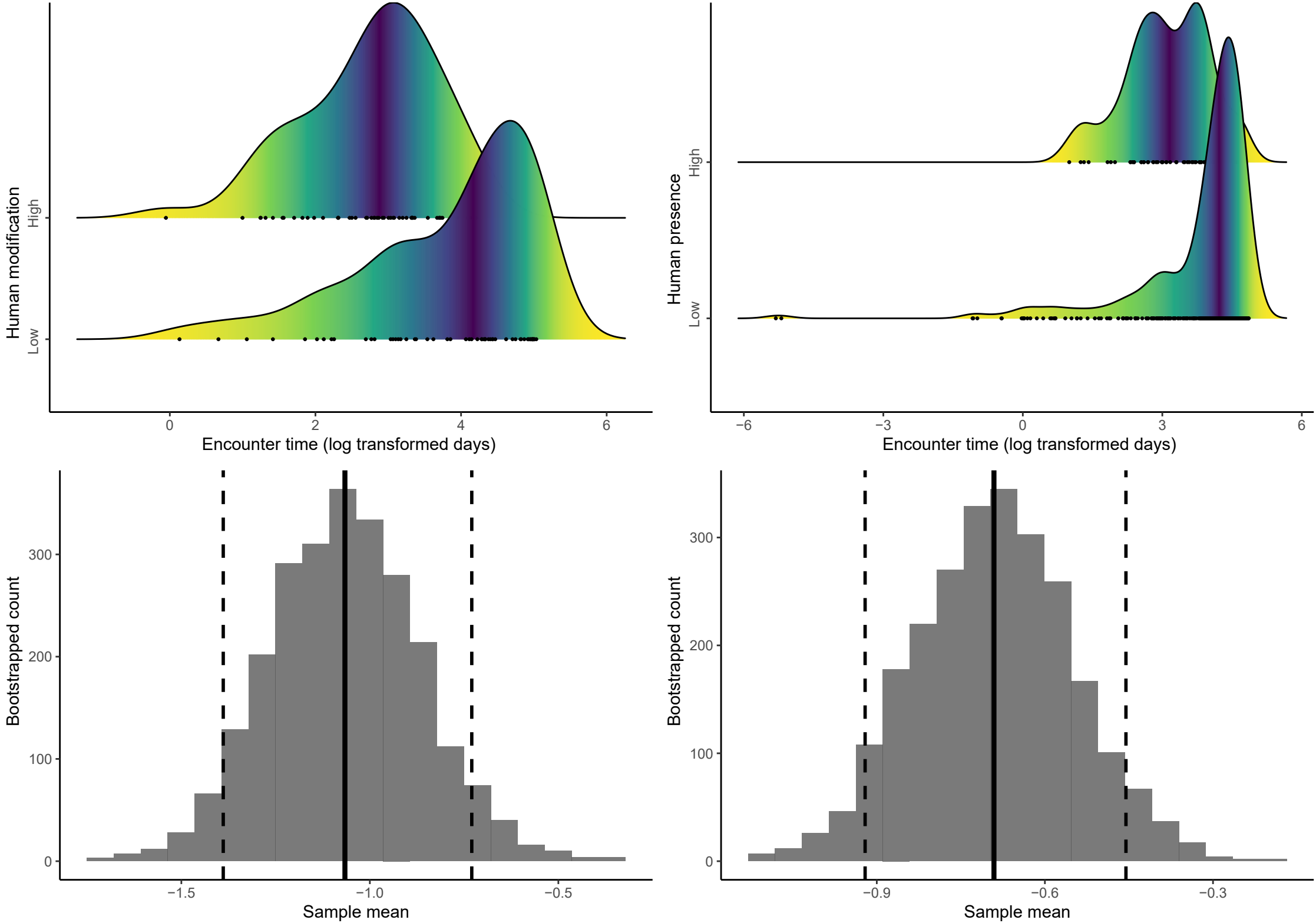

Co-occurrence
Spatial associations
Hypothesis 1: Human disturbance would compress space available for animals to share resulting in increased spatial associations between species
Hypothesis 2: Human disturbance would suppress diurnal activity in animals resulting in reduced encounter time between species pairs
Pairwise encounter time
Human disturbance
Human modification and presence

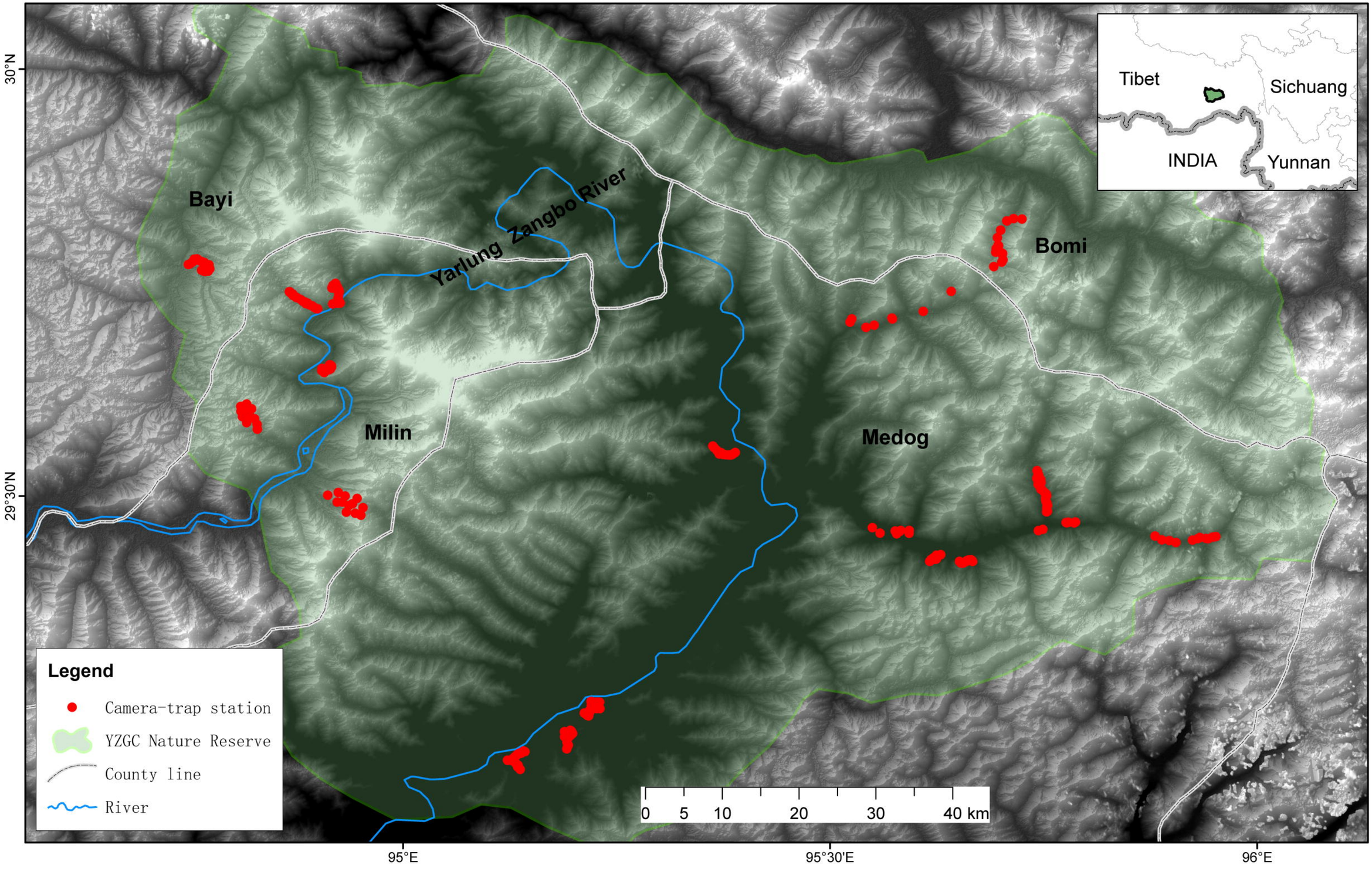

(a) Elevation (m)
(b) Percent of forest cover (%)
(c) Human modified area (0−1)
Yellow throated marten
Wild boar
Takin
Spotted linsang
Serow
Red goral
Red fox
Muntjac
Masked palm civet
Marbled cat
Leopard cat
Large civet
Golden cat
Dhole
Clouded leopard
Black bear
Bengal tiger
−7.5
−5.0
−2.5
0.0
2.5
0
5
10
15
20
−5
0
5
10
15
20
Beta effect size


Lower
Moderate
Higher
Serow
Golden cat
Dhole
Yellow throated marten
Muntjac
Red goral
Clouded leopard
Masked palm civet
Bengal tiger
Marbled cat
Leopard cat
Spotted linsang
Wild boar
Black bear
Large civet
Red fox
Takin
0.85
0.71
0.56
0.42
0.28
0.14
0.01
0.15
0.29
0.43
0.58
0.75
0.64
0.52
0.41
0.29
0.18
0.06
0.05
0.17
0.28
0.4
0.8
0.68
0.55
0.43
0.3
0.18
0.05
0.07
0.2
0.32
0.44
Increasing human modification level


Lower
Moderate
Higher
Serow
Golden cat
Dhole
Yellow throated marten
Muntjac
Red goral
Clouded leopard
Masked palm civet
Bengal tiger
Marbled cat
Leopard cat
Spotted linsang
Wild boar
Black bear
Large civet
Red fox
Takin
0.89
0.73
0.57
0.41
0.25
0.09
−0.07
−0.23
−0.39
−0.55
−0.71
0.85
0.73
0.61
0.49
0.37
0.26
0.14
0.02
−0.1
−0.22
−0.34
0.92
0.76
0.6
0.45
0.29
0.13
−0.03
−0.19
−0.34
−0.5
−0.66
Increasing human presence level


(a)
(b)
(c)
High
Low
Human presence
0.3
0.4
0.5
0.6
0.40
0.44
0.48
0.52
0.475
0.500
0.525
0.550
0.575
Nocturnality
Probability
0.4
0.3
0.2
0.1
0.0


Human modification
High
Low
0
2
4
6
Encounter time (log transformed days)
Human presence
High
Low
−6
−3
0
3
6
Encounter time (log transformed days)
Bootstrapped count
300
200
100
0
−1.5
−1.0
−0.5
Sample mean
Bootstrapped count
300
200
100
0
−0.9
−0.6
−0.3
Sample mean


30°N
29°30'N
95°E
95°30'E
96°E
Bayi
Milin
Medog
Bomi
Yarlung Zangbo River
Tibet
Sichuang
INDIA
Yunnan
Legend
Camera-trap station
YZGC Nature Reserve
County line
River
0 5 10 20 30 40 km