Liu et al. *Zool. Res. Divers. Conserv.* 2025, 2(1): 55−64
https://doi.org/10.24272/j.issn.2097-3772.2025.002
https://cstr.cn/32249.14.zrdc.2025.002

ZRDC Zoological Research: Diversity and Conservation

Article Open Access

Occupancy and coexistence patterns of sympatric felid species in human-disturbed tropical habitats of Xishuangbanna, southwestern China

Ying Liu[1,2,3,#], Ru-Chuan He[1,3,#], Lin Wang[1,3], Christos Mammides[1,3,4], Rui-Chang Quan[1,3,*]

[1] *Southeast Asia Biodiversity Research Institute*, *Chinese Academy of Sciences* & *Center for Integrative Conservation*, *Xishuangbanna Tropical Botanical Garden*, *Chinese Academy of Sciences*, *Mengla*, *Yunnan* 666303, *China*

[2] *University of Chinese Academy of Sciences*, *Beijing* 100049, *China*

[3] *Yunnan International Joint Laboratory of Southeast Asia Biodiversity Conservation* & *Yunnan Key Laboratory for Conservation of Tropical Rainforests and Asian Elephants*, *Menglun*, *Mengla*, *Yunnan* 666303, *China*

[4] *Yunnan International Joint Laboratory for the Conservation and Utilization of Tropical Timber Tree Species*, *Xishuangbanna Tropical Botanical Garden*, *Chinese Academy of Sciences*, *Mengla*, *Yunnan* 666303, *China*

ABSTRACT

Felid species hold critical ecological roles within tropical forest ecosystems and are particularly susceptible to human-induced disturbances. However, there is limited research on how sympatric felid species are distributed and coexist in human-dominated habitats. Using a long-term camera trap survey conducted in the disturbed tropical habitats of Xishuangbanna, southwestern China, we assessed the occupancy and spatio-temporal segregation among four sympatric felid species (Leopard cat *Prionailurus bengalensis*, Marbled cat *Pardofelis marmorata*, Asiatic golden cat *Catopuma temminckii*, and Clouded leopard *Neofelis nebulosa*), and explored how these patterns correlate with similarities in species traits. We found that the occupancy probabilities of leopard cats and clouded leopards were primarily influenced by anthropogenic disturbances rather than natural factors, with both species negatively affected by croplands. Similar species responses to croplands and livestock may facilitate the co-occurrence of leopard cats with clouded leopards in areas farther from croplands and with golden cats in regions with higher livestock abundance. The lack of significant spatial segregation among species is likely due to the observed segregation in daily activity patterns, which positively correlated with species trait similarities. Our study enhances our understanding of felid community assembly in the face of expanding human activity, offering valuable insights for future conservation in the Xishuangbanna region.

Keywords: Anthropogenic disturbance; Carnivores; Conservation; Spatio-temporal interaction; Species coexistence

INTRODUCTION

Human activities are the primary drivers of global biodiversity loss and local extinctions (Dirzo et al., 2014; Wan et al., 2019), exerting profound influences on numerous ecological processes, including niche segregation (Sévêque et al., 2020), ecological succession (MacDougall et al., 2013), and species adaptation (Doherty et al., 2021). Consequently, studying the impact of anthropogenic disturbances is crucial in ecological research in the Anthropocene era (Albuquerque et al., 2018). Furthermore, understanding how sympatric species respond to human disturbances and coexist in human-dominated landscapes is essential for advancing our knowledge of community ecology and supporting biodiversity conservation (He et al., 2024; Sévêque et al., 2020).

The selective pressures exerted by anthropogenic disturbances have emerged as pivotal drivers in influencing

Received: 14 January 2025; Accepted: 13 March 2025; Online: 14 March 2025

Foundation items: This research was funded by the National Natural Science Foundation of China (32371745); the Transboundary Cooperation on Biodiversity Research and Conservation in Gaoligong Mountains (E1ZK251); the 14th Five-Year Plan of the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (E3ZKFF7B, E3ZKFF9B); the Yunnan Revitalization Talent Support Program “Innovation Team” Project (202405AS350019); Yunnan International Joint Laboratory for the Conservation and Utilization of Tropical Timber Tree Species (202403AP140004); and the Postdoctoral Fellowship of Xishuangbanna Tropical Botanical Garden, CAS

[#]Authors contributed equally to this work

*Corresponding author, E-mail: quanrc@xtbg.ac.cn

the abundance and distribution of wildlife species (Dirzo et al., 2014). Moreover, these pressures act as significant habitat filters, reshaping the sympatric patterns of coexisting species and altering their coexistence dynamics—an effect particularly evident in carnivore guilds facing intense competition (Li et al., 2023). Anthropogenic disturbances can reshape sympatric patterns through the simultaneous exclusion of competing species or by eliciting divergent responses (attraction/avoidance) within such groups, thus variably influencing the risk of competitive exclusion and local extinction of subordinate species by their dominant counterparts (Lewis et al., 2015; Moll et al., 2018). Alterations in patterns of habitat overlap are instrumental in driving behavioral character displacement (e.g., spatial and temporal avoidance) among competing species, thereby promoting their coexistence (Karanth et al., 2017). In sympatric habitats, subordinate species might evade dominant species spatially by occupying alternative locations, thereby creating a "checkerboard" distribution pattern with their dominant counterparts (Stone & Roberts, 1990). Additionally, subordinate species may minimize temporal overlaps by adjusting their daily activity pattern, thus decreasing the simultaneous use of shared spaces with dominant species (Kronfeld-Schor & Dayan, 2003). The degree of these spatio-temporal segregations is associated with the strength of competition and the similarity of species traits, such as similarity in body size and diet.

Felid species, as flagship species with key ecological roles, have been a focal group for studying coexistence mechanisms due to their high similarity in morphological traits, ecological requirements, and strong territorial behavior, which suggest more intense intraguild competition (Santos et al., 2019). Yet their shared characteristics, such as low population density, stringent requirements for high-quality habitat, and large home range, made them susceptible to anthropogenic disturbance (Ripple et al., 2014). The expansion of human activities, such as urbanization and agricultural development, is converting natural habitats into human-modified landscapes, reducing habitat suitability and patch connectivity (Saunders et al., 1991), which in turn affects habitat use and population sizes of felid species (Zanin et al., 2015; Wearn et al., 2013). Furthermore, anthropogenic disturbances have the potential to induce displacement in sympatric felid populations, resulting in spatial compression into diminished habitats. This constriction likely exacerbates competitive exclusion among these species, consequently precipitating declines in their populations and increasing the risk of local extinctions. For example, residential development could increase the likelihood of encounters among wild felid species (Lewis et al., 2015). The increase in sympatry may force felid species to alleviate competition through spatial or temporal avoidance, according to niche theory (Karanth et al., 2017; Li et al., 2019). However, there are limited studies that have investigated how sympatric felid species coexist in human-dominated habitats (but see Li et al., 2019).

Xishuangbanna is part of the Indo-Burma global biodiversity hotspot, historically home to an assemblage of six extant felid species: The tiger (*Panthera tigris*), leopard (*P. pardus*), clouded leopard (*Neofelis nebulosa*), Asiatic golden cat (hereafter golden cat; *Catopuma temminckii*), marbled cat (*Pardofelis marmorata*), and leopard cat (*Prionailurus bengalensis*). Although, tigers have not been recorded in field surveys since 2007 (Feng et al., 2008), and the scarcity of leopard records in the area suggests a precarious population status (Cao et al., 2024), Xishuangbanna is one of the most felid-rich regions, receiving highest precedence for felid conservation. However, these felid species are experiencing substantial population decline and range contraction due to human-induced disturbances, such as rapid habitat loss and illegal exploitation of wildlife (Huang et al., 2020). The primary and secondary natural forests in Xishuangbanna continue to be converted into roads, built-up areas, croplands, and commercial plantations (mainly rubber trees *Hevea brasiliensis*) (Xu et al., 2014). The full impact of these anthropogenic disturbances on these species remains unclear, highlighting an urgent need to investigate how these rare and elusive felid species respond to human activities and coexist in disturbed tropical habitats.

In this study, we used non-invasive camera traps in four protected areas, Mengla, Mengyang, Shangyong, and Yiwu, east of the Lancang River in Xishuangbanna from January 2017 to May 2021, to survey the extant felid species. We employed a multi-species occupancy model to evaluate the association between occupancy probability and both natural and anthropogenic disturbance variables, as well as to examine spatial segregation among species, inferred from the residual correlations of the occupancy model (Doser et al., 2022). Furthermore, we compared the species' daily activity patterns to assess their temporal segregation. The aim of this study is to understand 1) how anthropogenic disturbances influence the occupancy of these felid species and potentially shape the co-occurrence patterns in disturbed tropical habitats, 2) how these species facilitate coexistence through spatial and temporal segregations, and 3) to what extent these segregations are correlated with similarities in species traits, specifically in body mass, diet, and scansorial foraging activity.

MATERIALS AND METHODS

Study area

The study was conducted in Xishuangbanna Dai Autonomous Prefecture, Yunnan Province, China (N21°08'–N22°36', E99°56'–E101°50'). The region is situated in southwestern China, sharing borders with Myanmar and Laos, exhibiting rich biodiversity. To safeguard remaining habitats, Xishuangbanna authorities has designated four nature reserves: Xishuangbanna National Nature Reserve (comprising Mangao, Mengla, Menglun, Mengyang, and Shangyong sub-reserves), Naban River Watershed National Nature Reserve, Bulong Prefectural Nature Reserve, and Yiwu Prefectural Nature Reserve. Moreover, conservation efforts have been undertaken to protect and manage primary forests in non-protected areas. These forests constitute the last remaining habitats for felid species in Xishuangbanna. Yet, the Xishuangbanna region continues to experience high levels of human disturbance, resulting in the extensive conversion of tropical forests into agricultural land (crops, rubber, and tea plantations) and urban areas (roads, residential areas, development zones) (Xu et al., 2014). These changes, coupled with persistent illegal hunting and livestock grazing, have significantly impacted wildlife distribution and species coexistence, and continue to be evident even within protected areas. Geographically, Xishuangbanna is bifurcated by the Lancang River into its western and eastern regions, resulting in the relative isolation of habitats. Except for the leopard cats, the other species examined in this study are predominantly

found to the east of the Lancang River, which may be attributed to the large and continuous area of primary forests in this region (Figure 1). Therefore, we focused our field sampling in the eastern region of the Lancang River in Xishuangbanna.

Camera trap survey

We deployed infrared camera traps between January 2017 and June 2021 to conduct field sampling within protected areas in the eastern region of the Lancang River in Xishuangbanna (Figure 1; Table 1). Additionally, we established sampling sites in large core forest areas outside designated protected zones, referred to as Guoyoulin in this study (Figure 1; Table 1). In each sampling block, we set transects mainly along human footpaths or mammal trails, covering both the edge and core areas of the protected area. Camera trap sites were set along the transects, with at least five sites per transect. A total of 65 transects were set up, resulting in 429 study sites (the cameras were neither lost nor damaged). To ensure the independence of sampling sites, the minimum distance between two adjacent sites set was ≥500 m. This separation distance is generally considered adequate for reducing spatial autocorrelation in detection data for a wide variety of mammal species (Lwin et al., 2021; Nichols et al., 2019). The cameras (Yianws L710, China) were set on tree trunks at a height of 0.5–2 m, with placement adjusted to accommodate local terrain and optimize the field of view for detecting felid species. The camera traps operated continuously and recorded the GPS location of each site (Xiao et al., 2014). The camera's battery and the SD card storing the photos were replaced every six months.

Environmental variables

Both natural variables and anthropogenic disturbances are considered key factors influencing the occurrence of felid species. The natural variables included in the analyses related to vegetation, topography, and proximity to water sources. Specifically, the following variables were used: tree density, normalized difference vegetation index (NDVI), elevation, slope, aspect, topographic position index (TPI), and distance to water surfaces (Table 2). These variables are commonly used to predict the potential distribution of felid species (Ashrafzadeh et al., 2020; Santos et al., 2019). In terms of human disturbances, and given the dominant landscape types in Xishuangbanna, we included the following variables: Distance to roads (primarily town-village and county roads), distance to built-up areas (mainly villages), distance to croplands, distance to plantations (mainly rubber *H. brasiliensis* and tea *Camellia sinensis*), relative abundance index (RAI) of human presence, and relative abundance index (RAI) of livestock (domestic cattle) (Table 2). We calculated the distance between each sampling site and the nearest land features (roads, croplands, etc.) using the *near* function in software ArcGIS 10.6. RAI was defined as the number of independent detections per 100 trapping days, whereas an independent detection was defined as consecutive

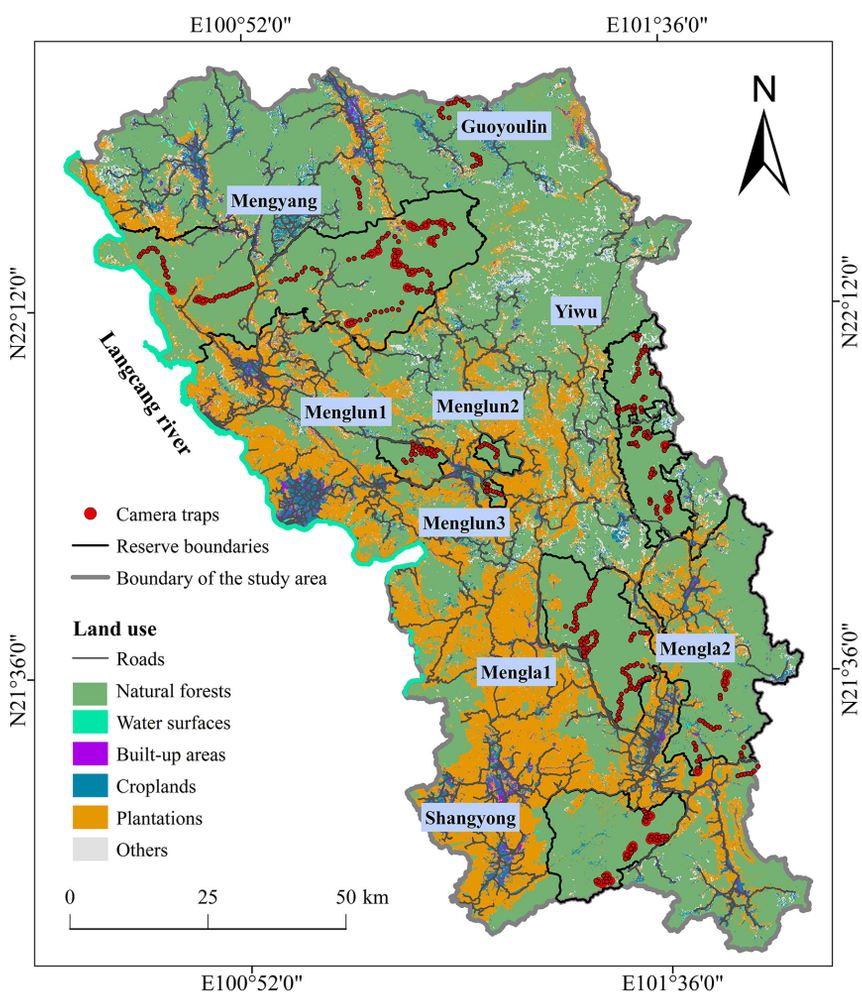

Figure 1 Map depicting the camera deployment sites and the land-use types within the study area

Table 1 The summary information of the camera trap survey for each sampling block

Sampling block	No. transects	No. camera sites	Survey date	Mean no. trapping days
Guoyoulin	2	21	2019.12–2020.12	302.26
Mengla1	12	78	2017.01–2020.07	451.42
Mengla2	7	37	2019.06–2020.06	299.92
Menglun1	2	23	2017.01–2020.10	849.35
Menglun2	1	10	2019.06–2020.12	473.5
Menglun3	2	12	2019.06–2021.04	603.42
Mengyang	12	125	2019.03–2021.05	529.15
Shangyong	6	35	2018.11–2020.01	506.71
Yiwu	21	88	2017.07–2020.06	462.27

Table 2 List of natural and anthropogenic variables used to predict the occupancy of felid species

Variable	Variable type	Range	Source
Tree density	Natural	16 645.56–64 427.45	Derived from the global map of tree density provided by Crowther et al. (2015)
NDVI	Natural	0.24–0.51	Calculated using Landsat 8 digital image (https://earthexplorer.usgs.gov/)
Elevation	Natural	653–1 835	Derived from the ASTER global digital elevation map (https://earthexplorer.usgs.gov/)
Slope	Natural	0.48–49.91°	Calculated using the ASTER global digital elevation map (https://earthexplorer.usgs.gov/)
Aspect	Natural	0–0.99	Calculated using the ASTER global digital elevation map (https://earthexplorer.usgs.gov/) and subsequently transformed to represent a gradient from shady slopes (north-facing, 0) to sunny slopes (south-facing, 1)
TPI	Natural	–7 to 8.56	Calculated using the ASTER global digital elevation map (https://earthexplorer.usgs.gov/)
Distance to water surfaces	Natural	27.09–17 542.41 m	Calculated using the land use map of Xishuangbanna, provided by the Animal Behavior and Changing Environments Research Group, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences
Distance to roads	Anthropogenic disturbance	12.55–8 951.57 m	Calculated using the road network map provided by the Environment Science and Data Center of the Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences (https://www.resdc.cn/)
Distance to built-up areas	Anthropogenic disturbance	507.63–8 646.29 m	Calculated using the land use map of Xishuangbanna, provided by the Animal Behavior and Changing Environments Research Group, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences
Distance to croplands	Anthropogenic disturbance	0–6 727.57 m	Calculated using the land use map of Xishuangbanna, provided by the Animal Behavior and Changing Environments Research Group, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences
Distance to plantations	Anthropogenic disturbance	0–8 162.04 m	Calculated using the land use map of Xishuangbanna, provided by the Animal Behavior and Changing Environments Research Group, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences
RAI of human presence	Anthropogenic disturbance	0–47.09	Calculated based on camera trap records
RAI of livestock presence	Anthropogenic disturbance	0–448.8	Calculated based on camera trap records

photographs of the same species at the same camera station taken more than 30 minutes apart (O'Brien et al., 2003). These above anthropogenic disturbance variables represent the primary types of human disturbances in the Xishuangbanna region and have been used in previous studies to predict the occurrence of other mammal species in this region (He et al., 2024).

Statistical analyses

Species occupancy spatial segregation: We conducted a latent factor multi-species occupancy model (a joint species distribution model with imperfect detection) (Doser et al., 2022) to determine the association between the occupancy probability of the felid species and environmental variables, as well as their spatial segregation. The model was implemented over 53 sampling occasions (with each month treated as a sampling occasion) using the *lfMsPGOcc* function from the package *spOccupancy* 0.7.6 (Doser et al., 2022) in the R Programming Language 4.4.1 (R Core Team, 2024). Monthly presence–absence matrices of felid species served as the dependent variable, with monthly sampling efforts (i.e., how many days a site was sampled in a month) included, while environmental variables served as predictors to calculate occupancy probability. The sampling blocks were included as random effects. The model was run with five chains, each consisting of 300 000 iterations, with a burn-in of 200 000 iterations, thinning set to 100. Two latent factors were used for capturing residual correlations (Vélez et al., 2024). This resulted in a total of 5 000 posterior samples for each parameter, with 1 000 samples obtained from each chain. Parameters were considered to have converged if the R-hat

values were less than 1. Posterior predictive checks were performed using the Freeman-Tukey test with the *ppcOcc* function, where a Bayesian *P*-value within the range of 0.1–0.9 indicated a good model fit. The regression coefficients (mean posterior estimates) were deemed statistically significant if their 90% credible intervals did not include zero (Vélez et al., 2024). To compare the relative contributions of the anthropogenic disturbance and natural variables to the species' occupancy probabilities, we summed the absolute values of the coefficients for each variable type and divided these sums by the total sum of all coefficients (Gross et al., 2017). Spatial segregation among felid species was assessed by calculating the inverse of species-to-species residual correlations, with significant values identified when their 90% credible intervals excluded zero (Vélez et al., 2024).

Temporal segregation: We assessed the temporal segregation among felid species by analyzing the segregation and difference in their daily activity patterns with non-parametric kernel density estimation (NKDE) (Ridout & Linkie, 2009). We treated the occurrence of the same species at the same camera station within a 30-minute interval as an independent event to minimize the overestimation of species occurrences. To eliminate the impact of annual variations in sunrise and sunset times, we converted the clock time of each independent detection into circular solar time using the *solartime* function in package *activity* 1.3.2 (Nouvellet et al., 2012). The coefficients of overlap (Δ) (range 0 to 1) were calculated to determine the temporal overlap using the package *overlap* 0.3.4 (Ridout & Linkie, 2009). We employed Δ1 when the number of detections of at least one species was less than 50, and Δ4 when both species had 50 or more detections (Ridout & Linkie, 2009). The segregation was considered low when 1–Δ<0.25, moderate when 0.25≤ 1–Δ<0.5, and high when 1–Δ≥0.5 (Monterroso et al., 2014). We used Watson's two-sample test of homogeneity to determine the significance of difference in activity patterns using *watson.two.test* function in package *circular* 0.4-95 (Agostinelli & Lund, 2023).

Correlation between trait similarities and segregations: To better understand the drivers of spatial and temporal segregation, Spearman's rank correlation tests were employed to determine the correlation between trait similarities (body mass similarity, dietary similarity, and scansorial foraging similarity) and the strength of segregations. Body mass, diet, and scansorial data were derived from the global mammal traits dataset (Soria et al., 2021). Pairwise body mass similarity was calculated by dividing the smaller species' body mass by that of the larger species. The dietary similarity was calculated using the Pianka index (Pianka, 1973) based on the ten dietary categories provided in the dataset. Scansorial foraging similarity was calculated as the binary categories of scansorial ability between two species (a value of 1 if both species are scansorial and 0 if only one species is scansorial). The pairwise Spearman correlation coefficients (r) were calculated with |r| greater than 0.3, which were considered strong and reported (Gignac & Szodorai, 2016).

RESULTS

Summary of camera trap records

Between January 2017 and May 2021, we recorded a total of 209 921 camera trapping days across 429 sites, with an average of 489.33 days per site. Of these, the leopard cat, marbled cat, golden cat, clouded leopard, and leopard were recorded at 256, 9, 33, 21, and 2 sites, respectively, yielding 1 037, 13, 61, 30, and 4 independent detections. The leopard was excluded from statistical analyses due to the limited number of detections.

Association between occupancy probability of sympatric felid species and environmental variables

The multi-species occupancy model demonstrated a good fit for all felid species (Bayesian *P*=0.12–0.36), with the exception of the leopard cats (Bayesian *P*=0). All parameters showed adequate convergence (mean R-hat±SD=1.01±0.03).

The detection probability of all felid species was positively associated with monthly sampling efforts (standardized coefficients=0.28–0.61, 90% Credible Interval (CI): 0.04–0.2 to 0.38–1.33). The occupancy probability of the leopard cats was higher in areas closer to roads (standardized coefficient= –0.63, 90% CI=–1.15 to –0.15), farther from croplands (standardized coefficient=0.54, 90% CI=0.12–0.95), and in areas with a higher RAI of livestock presence (standardized coefficient=0.98, 90% CI=0.11–2.41) (Figure 2A). For the marbled cats, occupancy probability increased in mountain ridge areas (standardized coefficient=1.53, 90% CI=0.3–3.68)

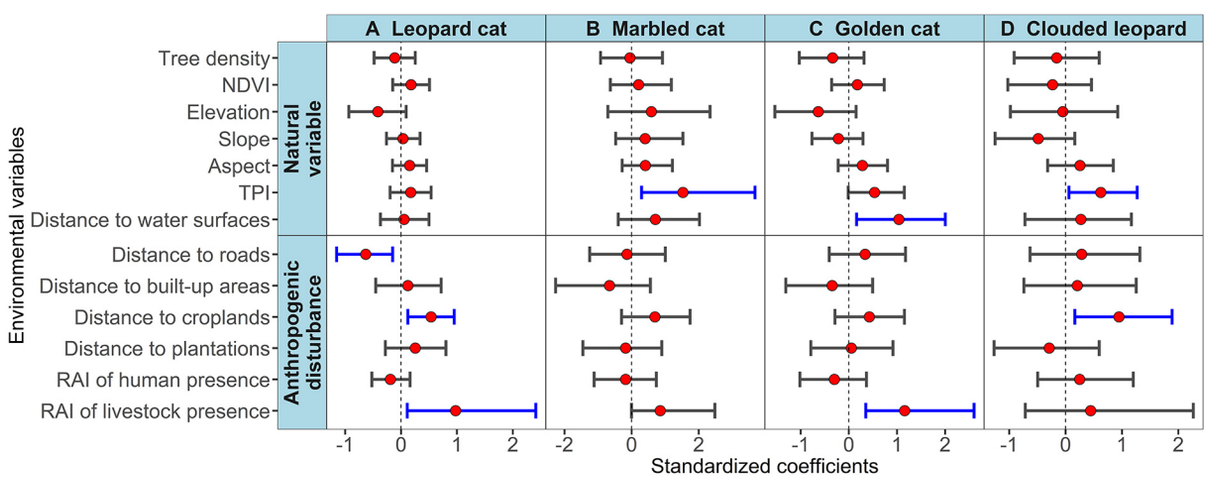

Figure 2 The association between the occupancy probabilities of the felid species and the anthropogenic and natural variables

The dots and the bars represent the standardized coefficients (mean posterior estimates) and the 90% credible confidences, respectively. Blue-colored bars represent statistically significant relationships.

(Figure 2B). The golden cats showed higher occupancy probability in areas farther from water surfaces (standardized coefficient=1.04, 90% CI=0.16–2) and in areas with a higher RAI of livestock presence (standardized coefficient=1.16, 90% CI=0.35–2.6) (Figure 2C). Similarly, the clouded leopards exhibited higher occupancy probability in mountain ridge areas (standardized coefficient=0.62, 90% CI=0.06–1.27) and farther from croplands (standardized coefficient=0.95, 90% CI= 0.16–1.89) (Figure 2D). Among the variables considered in this study, anthropogenic disturbances had a relatively stronger effect on the occupancy probabilities of the leopard cats and clouded leopards compared to natural variables (leopard cats: 70.77% vs. 29.23%; clouded leopards: 53.88% vs. 46.12%). In contrast, the effect of anthropogenic disturbances was relatively weaker for the marbled cats and golden cats (marbled cats: 40.96% vs. 59.04%; golden cats: 44.87% vs. 55.13%).

Spatial segregation of sympatric felid species

The spatial segregation results, derived as the inverse of residual correlations from the multi-species occupancy model, showed that only the golden cat and clouded leopard pair exhibited spatial segregation (residual correlation=–0.57) (Figure 3). However, the residual correlations were not statistically significant, as their 90% credible intervals included zero.

Temporal segregation of sympatric felid species

All felid species had significant or marginal-significant differences in daily activity patterns with each other (Figure 4). However, aside from the leopard cats and the marbled cats, which exhibited high segregation in their daily activity patterns (1–Δ=0.57) (Figure 4A), the other pairwise comparisons among the felid species showed only moderate segregations (0.26≤1–Δ≤0.41) (Figure 4B, D–F), with the exception of the leopard cat and clouded leopard pair, which showed low segregation (1–Δ=0.22) (Figure 4C). The leopard cats displayed a predominantly nocturnal activity pattern, while the marbled cats exhibited a typical diurnal pattern. In comparison, the golden cats and the clouded leopards displayed mainly diurnal activity but also engaged in nocturnal activities. Except for the leopard cats, the other three species had a peak in activity between 8:00 to 10:00 am. The marbled cats and the golden cats showed a more pronounced bimodal activity pattern, with a peak in activity during twilight.

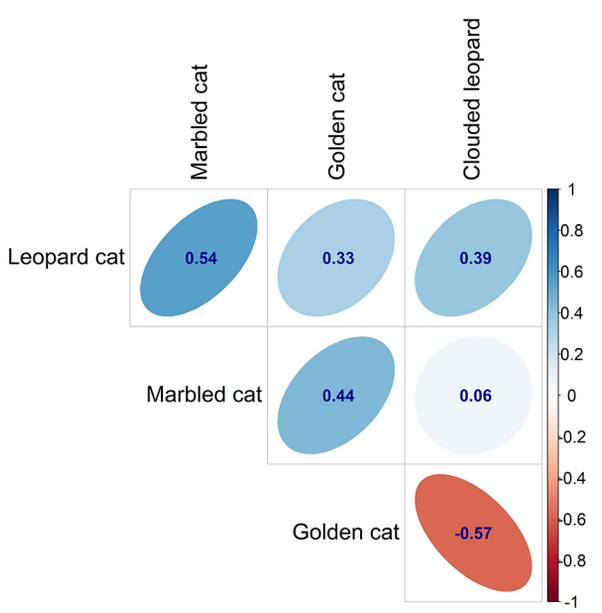

Figure 3 Spatial associations among felid species

The spatial associations were derived from residual correlations of the multi-species occupancy model.

Correlation between segregations of sympatric felid species and trait similarities

In terms of trait similarities and segregations, temporal segregation was positively correlated with both three trait similarities (0.41≤r≤0.5) (Figure 5), while spatial segregation was positively correlated with scansorial foraging similarity (r=0.41). Among the three trait similarities, body size similarity was negatively correlated with both dietary (r=–0.5) and scansorial foraging similarity (r=–0.41), while dietary and scansorial foraging similarities were positively correlated (r=0.85). Among the segregations, spatial segregation was negatively correlated with temporal segregation (r=–0.31).

DISCUSSION

Our findings reveal key information about the coexistence patterns of felid species in disturbed tropical forests, as well as the threats posed by anthropogenic disturbances to them, using the Xishuangbanna region as a case study. With the exception of the marbled cats, all felid species were influenced by anthropogenic disturbances. For the leopard cats and clouded leopards, anthropogenic disturbances had a greater impact than natural variables, with cropland expansion identified as a key factor limiting their occurrences. Furthermore, the leopard cat's responses to croplands and livestock presence mirrored those of the clouded leopards and golden cats, respectively, potentially increasing their co-occurrences. In overlapping habitats, none of the four felid species showed significant spatial segregation (avoidance in sharing site use with one another), which can be primarily attributed to their differing temporal activity patterns. Furthermore, this temporal segregation was positively correlated with species trait similarities, which implies the complementarity and interplay between trait differentiation and behavioral adjustment. Our long-term camera trapping survey across a broad area revealed fewer detections and occupied sites for all felid species except leopard cats, suggesting a concerningly small population status for these species in the Xishuangbanna region of China. Although the relatively limited sample size of our data somewhat reduces the statistical power and the potential for more in-depth data analyses of our analyses, our findings underscore the importance of this work and highlight the urgent need for conservation efforts targeting felid species in the Xishuangbanna region.

Anthropogenic disturbances shape the occupancy and co-occurrence of felid species

The high expansion of human activities has resulted in accelerating land use change. Consequently, the altered anthropogenic landscapes impact carnivores' mechanisms of habitat selection and occurrence patterns (Santos et al., 2019). Felid species typically exhibit strong avoidance of landscape features that are highly disturbed by human activity (Ashrafzadeh et al., 2020), a pattern that was also corroborated in our results. Our findings indicate that leopard cats and clouded leopards prefer habitats farther from croplands, suggesting that agricultural activity, which has intensified due to the region's predominantly agriculture-based

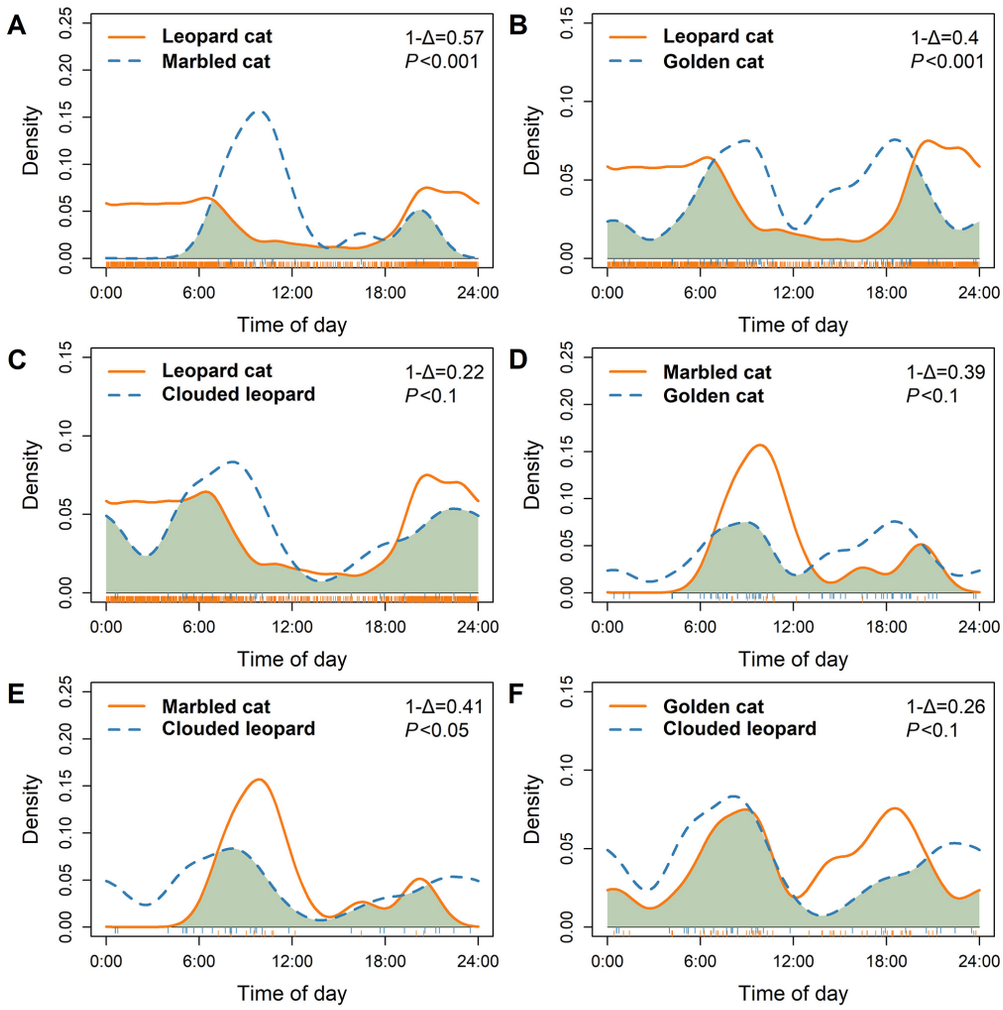

Figure 4 The segregation and difference of felid species in daily activity patterns

The green areas represent pairwise activity overlaps (Δ). The segregation was considered low when 1–Δ<0.25, moderate when 0.25≤1–Δ<0.5, and high when 1–Δ≥0.5.

livelihoods (Xu et al., 2014), restricts the available habitats for these species. Compared to croplands, built-up areas within our sampling regions are relatively scarce, potentially resulting in minimal impact. Roads in these areas are predominantly used for vehicular traffic, with minimal prolonged human presence or activity, unlike trails specifically designed for pedestrian use, which could elicit greater avoidance behavior in mammals (Zhou et al., 2013). Additionally, human activity within plantations tends to be relatively low in intensity. These factors may explain the limited influence of roads and plantations on felid species, with some mammals even utilizing these landscapes as corridors for movement and dispersal (Harich-Wloka et al., 2023; Hill et al., 2021). Interestingly, increased livestock presence within forests was positively associated with a higher occupancy probability of leopard cats and golden cats. This relationship may arise from cascading effects driven by positive interactions between livestock and other small fauna. For example, livestock can attract birds by providing additional food resources in their feces or by exposing arthropods when grazing or disturbing the ground (Gu et al., 2022), potentially increasing prey availability for both leopard cats and golden cats. During our field surveys, we observed phasianids, such as red junglefowl (*Gallus gallus*) and mountain bamboo-partridge (*Bambusicola fytchii*), foraging commensally with domestic cattle. Incidents of livestock predation were scarce within our study area, contrasting with findings reported from other regions in Yunnan province (e.g., Li et al., 2013). Consequently, the stronger impact of anthropogenic disturbances on leopard cats and clouded leopards compared to natural environmental factors underscores their substantial and non-negligible influence on ecological processes within our study area. Additionally, the non-significant effect of anthropogenic disturbances on marbled cats may be attributed to their strong preference for high-elevation habitats (Haidir et al., 2021). However, considering their relatively small population sizes and restricted distribution, this felid species might paradoxically demonstrate heightened susceptibility to anthropogenic pressures through behavioral avoidance mechanisms that limit their utilization of lower elevation areas with intensive human activities (Hearn et al., 2016).

Similar responses to croplands and livestock may enhance the co-occurrences of leopard cats with clouded leopards in areas farther from croplands and with golden cats in areas of higher relative abundance of livestock presence, respectively. This suggests that anthropogenic disturbances impede the differentiation of spatial niches (Sévêque et al., 2020) for sympatric felid species, which aligns with findings from a study on felid species in Colorado, USA (Lewis et al., 2015). This is because most carnivores generally perceive humans as frightening, regardless of whether they are directly threatened

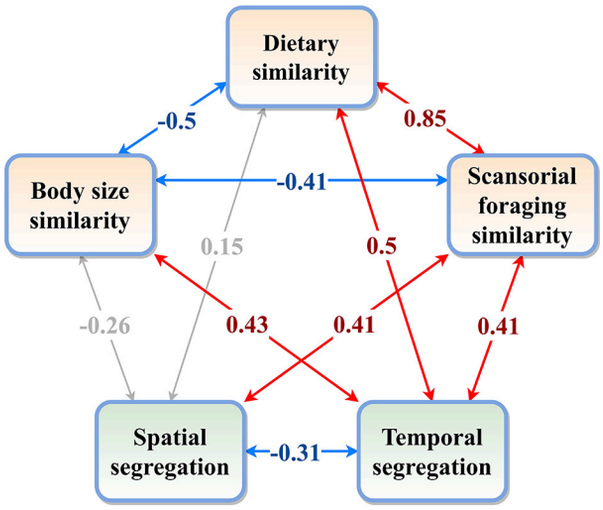

Figure 5 Spearman's rank correlations between trait differences and segregations

|r| values above 0.3 are considered strong associations. Red indicates strong positive correlations, blue indicates strong negative correlations, and grey represents low correlations (|r|<0.3).

by human activities (Sévêque et al., 2020). Therefore, they prefer habitats farther from humans to minimize the risk of anthropogenic mortality (Loveridge et al., 2017). In addition, habitat fragmentation caused by croplands can concentrate competing species into smaller areas, increasing interspecific competition and potentially leading to population declines (Sévêque et al., 2020), though this effect is contingent upon resource availability within the remaining habitat and the intensity of competitive interactions (Karanth et al., 2017).

Temporal segregation, rather than spatial segregation, facilitates the coexistence of felid species in overlapping habitats

Our analysis of spatial segregation demonstrated that sympatric felid species do not exhibit significant segregation or aggregation in their use of sites, thus providing no evidence to support the hypothesis that spatial segregation facilitates coexistence among felid species. In shrunk habitats, spatial avoidance may not appear to be a strategy among felid species for alleviating competition. For example, a study from Sumatra showed that the six sympatric felid species did not avoid each other in site use (Sunarto et al., 2015). Studies from southwestern India and northeastern China have revealed that tigers and leopards demonstrate independent spatial interactions when available habitats are inadequate (Karanth et al., 2017; Li et al., 2019). The lack of spatial avoidance indicates that competitive subordinate species might not be driven to local extinction by heightened competition with dominant species. However, the largest-bodied felid species, the golden cats and the clouded leopards, demonstrate a potential tendency toward spatial segregation (residual correlation=–0.57). This finding further implies that these competing species may employ alternative mechanisms to facilitate coexistence, such as temporal segregation (Schoener, 1974).

Our study revealed that four felid species exhibited significant or marginal-significant differences and had moderate to high segregations in their daily activity patterns with each other. This finding supports the hypothesis that temporal segregation facilitates the coexistence of sympatric felid species (Santos et al., 2019), implying that subordinate species can share high-quality habitat patches with dominant species rather than being excluded through spatial competition (He et al., 2024). The four felid species had distinct differences in their peak activity times of day (Figure 4). Particularly, the leopard cats performed typical nocturnal behavior and observed the highest level of activity during the nocturnal phase than other species but reduced some crepuscular activity observed in a previous study (Li et al., 2022). This may be related to the leopard cats in our study area primarily preying on nocturnal rodents (Grassman et al., 2005). The other three felid species exhibited varying degrees of diurnality, a finding that aligns with the observations of McCarthy et al. (2015). This could be because the activity pattern of the marbled cats partially depends on diurnally active rodents (e.g., squirrels) (Hendry et al., 2023), while the golden cats and the clouded leopards relatively rely on the activity times of ungulates and animal guilds (Kamler et al., 2020; Rasphone et al., 2022). Although evidence is lacking that differences in activity patterns among the four felid species stem solely from competition in our study, variations in their daily active periods effectively reduce the likelihood of encounters, thus enabling their coexistence within the same habitats.

Strength of temporal segregation was correlated with trait similarity among felid species

Drawing on the strong correlations observed within the limited sample size, we investigated the potential relationships between trait similarity and spatio-temporal avoidance. Body size, diet, and scansorial habits represent the three primary traits for understanding the coexistence of these four felid species. This is due to their average body weights ranging from 4.15 to 19.5 kg, relatively distinct dietary niches, and the typical scansorial foraging behaviors exhibited by the marbled cats and clouded leopards (Soria et al., 2021). Temporal segregation, an essential strategy for facilitating shared habitat use, is correlated with trait similarities. Species with greater similarity in body size, diet, and scansorial habits experience intensified competition (Macarthur & Levins, 1967), prompting them to increase temporal segregation to enhance spatial cohabitation. This highlights the complementarity and interplay between trait differentiation and behavioral adjustments. Moreover, the correlations among the three traits and among the three types of segregation reveal complex intrinsic relationships between traits and between segregation mechanisms, respectively. Species with greater similarity in body size are less likely to share similar foraging strategies and diets. However, scansorial foraging strategies are expected to be strongly linked to dietary preferences. Additionally, the negative correlation between temporal and spatial segregations highlights the complementarity of spatio-temporal behavioral displacement (Tian et al., 2022).

Conservation implications

With the rapid advancement of urbanization and agricultural expansion, vast areas of natural forests in Xishuangbanna have been continually converted into croplands. Balancing sustainable economic growth with the conservation of the region's rich biodiversity remains a pressing challenge. Our study reveals that croplands had significant negative effects on the occupancy of endangered felid species and may further shape their patterns of coexistence in shrunk habitats (Figure 2). This highlights that limiting the expansion of croplands could aid in the recovery of felid populations.

However, the lack of significant spatial avoidance patterns implies that sympatric species displaced into overlapping habitats by anthropogenic disturbances do not develop further spatial exclusion. This observed coexistence mechanism may be attributable to temporal niche partitioning, whereby ecologically similar species sequentially utilize identical spatial resources through diel activity pattern differentiation. Furthermore, we recommend that future research include a wider range of species to gain a more comprehensive understanding of the impact of anthropogenic landscapes on biodiversity and ecological processes in Xishuangbanna. Moreover, we observed a positive impact of livestock grazing on the occupancy of leopard cats and clouded leopards, offering valuable data to inform policymakers in reconciling local livestock development with biodiversity conservation efforts. Nonetheless, a comprehensive management approach should also incorporate data on livestock depredation, farmer tolerance of felids, and other potential conflict factors. Given the critical ecological roles that felid species play across ecosystems and their alarming population status, we emphasize that it is essential to increase research efforts focused on these species and implement science-based conservation plans to effectively maintain and restore their populations.

CONCLUSION

Understanding species' responses to anthropogenic disturbances and their coexistence within disturbed habitats is crucial for effective conservation in the Anthropocene. Through spatio-temporal analyses of long-term camera trap data collected in disturbed natural forests in the eastern Lancang River region of Xishuangbanna, we found that anthropogenic disturbances had a greater impact on the occupancy probabilities of leopard cats and clouded leopards compared to natural variables, with their occurrences being negatively impacted by croplands. The leopard cat's response to croplands and livestock, which is similar to the responses of the clouded leopards and golden cats, may contribute to greater co-occurrence with these species. In overlapping habitats, felid species did not exhibit significant spatial segregation, likely because the observed temporal segregation alleviates interspecific competition and facilitates species coexistence. The strength of this temporal segregation was positively correlated with species trait similarities, supporting the predictions of niche theory and underscoring the relationship between species traits and behavioral character displacement. Our study deepens our understanding of how anthropogenic disturbances affect the distribution, coexistence, and community assembly of felid species in disturbed habitats, offering valuable data to support their continued conservation in the Xishuangbanna region.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Our field survey was permitted by Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, the Xishuangbanna National Nature Reserve, and the Yiwu Prefectural Nature Reserve.

DATA AVAILABILITY

The data used in this paper has been submitted to the Science Data Bank (http://www.scidb.cn/) under DOI: https://doi.org/10.57760/sciencedb.zrdc.00030.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

Conceptualization: R.C.Q., Y.L. and R.C.H.; Data curation: Y.L. and R.C.H.; Formal analysis: Y.L. and R.C.H.; Funding acquisition: R.C.Q. and L.W.; Investigation: Y.L. and R.C.H.; Methodology: Y.L., R.C.H. and C.M.; Project administration: R.C.Q.; Resources: R.C.Q. and L.W.; Software: Y.L. and R.C.H.; Supervision: R.C.Q.; Validation: R.C.Q. and L.W.; Visualization: Y.L. and R.C.H.; Writing – original draft: Y.L. and R.C.H.; Writing – review & editing: R.C.Q., L.W. C.M., Y.L. and R.C.H. All authors read and approved the final version of the manuscript.

ACKNOWLEDGEMENTS

We thank the offices of Xishuangbanna National Nature Reserve and Yiwu Prefectural Nature Reserve for supporting and approving this research. We also thank Xiao-Bao Deng, and Guo-Gang Li for field work and Nan Sun, Wei Ao, Jia-Zhou Yang, and Xiao-Ying Mi for the identification of camera-trap photographs.

REFERENCES

Agostinelli C, Lund U. 2023. R package: *Circular Statistics (version 0.4–3)*. https://CRAN.R-project.org/package=circular.

Albuquerque UP, Gonçalves PHS, Ferreira Júnior WS, et al. 2018. Humans as niche constructors: revisiting the concept of chronic anthropogenic disturbances in ecology. *Perspectives in Ecology and Conservation*, **16**(1): 1–11.

Ashrafzadeh MR, Khosravi R, Adibi MA, et al. 2020. A multi-scale, multi-species approach for assessing effectiveness of habitat and connectivity conservation for endangered felids. *Biological Conservation*, **245**: 108523.

Cao H, Quan RC, Bai Y, et al. 2024. Assessment of changes in the composition and distribution of large and medium-sized mammals in Xishuangbanna, Southwest China. *Ecology and Evolution*, **14**(11): e70432.

Dirzo R, Young HS, Galetti M, et al. 2014. Defaunation in the Anthropocene. *Science*, **345**(6195): 401–406.

Doherty TS, Hays GC, Driscoll DA. 2021. Human disturbance causes widespread disruption of animal movement. *Nature Ecology & Evolution*, **5**(4): 513–519.

Doser JW, Finley AO, Kéry M, et al. 2022. spOccupancy: an R package for single-species, multi-species, and integrated spatial occupancy models. *Methods in Ecology and Evolution*, **13**(8): 1670–1678.

Feng LM, Lin L, Zhang LT, et al. 2008. Evidence of wild tigers in Southwest China - a preliminary survey of the Xishuangbanna National Nature Reserve. *Cat News*, **48**: 4–6.

Gignac GE, Szodorai ET. 2016. Effect size guidelines for individual differences researchers. *Personality and Individual Differences*, **102**: 74–78.

Grassman LI, Tewes ME, Silvy NJ, et al. 2005. Spatial organization and diet of the leopard cat (*Prionailurus bengalensis*) in north-central Thailand. *Journal of Zoology*, **266**(1): 45–54.

Gross N, Bagousse-Pinguet YL, Liancourt P, et al. 2017. Functional trait diversity maximizes ecosystem multifunctionality. *Nature Ecology & Evolution*, **1**(5): 0132.

Gu BJ, Weng Y, Diao YX, et al. 2022. Is livestock grazing compatible with green peafowl (*Pavo muticus*) conservation? Potential chance of peafowl-human coexistence. *Biological Conservation*, **275**: 109772.

Haidir IA, Kaszta Ż, Sousa LL, et al. 2021. Felids, forest and farmland: identifying high priority conservation areas in Sumatra. *Landscape Ecology*, **36**(2): 475–495.

Harich-Wloka FK, Treydte AC, Ogutu JO, et al. 2023. Between conflict and coexistence: Wildlife in rubber-dominated landscapes. *Integrative Conservation*, **2**(4): 240–254.

He RC, Wang L, Hughes AC, et al. 2024. Anthropogenic disturbance and competitive avoidance shape the coexistence pattern of macaque species in tropical forests. *Ecosphere*, **15**(9): e70001.

Hearn AJ, Ross J, Bernard H, et al. 2016. The first estimates of marbled cat *Pardofelis marmorata* population density from Bornean primary and

selectively logged forest. *PLoS One*, **11**(3): e0151046.
Hendry A, Amir Z, Decoeur H, et al. 2023. Marbled cats in Southeast Asia: are diurnal and semi-arboreal felids at greater risk from human disturbances?. *Ecosphere*, **14**(1): e4338.
Hill JE, Devault TL, Belant JL. 2021. A review of ecological factors promoting road use by mammals. *Mammal Review*, **51**(2): 214–227.
Huang G, Sreekar R, Velho N, et al. 2020. Combining camera-trap surveys and hunter interviews to determine the status of mammals in protected rainforests and rubber plantations of Menglun, Xishuangbanna, SW China. *Animal Conservation*, **23**(6): 689–699
Kamler JF, Inthapanya X, Rasphone A, et al. 2020. Diet, prey selection, and activity of Asian golden cats and leopard cats in northern Laos. *Journal of Mammalogy*, **101**(5): 1267–1278.
Karanth KU, Srivathsa A, Vasudev D, et al. 2017. Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. *Proceedings of the Royal Society B: Biological Sciences*, **284**(1848): 20161860.
Kronfeld-Schor N, Dayan T. 2003. Partitioning of time as an ecological resource. *Annual Review of Ecology, Evolution, and Systematics*, **34**(1): 153–181.
Lewis JS, Bailey LL, VandeWoude S, et al. 2015. Interspecific interactions between wild felids vary across scales and levels of urbanization. *Ecology and Evolution*, **5**(24): 5946–5961.
Li J, Li DQ, Hacker C, et al. 2022. Spatial co-occurrence and temporal activity patterns of sympatric mesocarnivores guild in Qinling Mountains. *Global Ecology and Conservation*, **36**: e02129.
Li XY, Bleisch WV, Hu WQ, et al. 2023. Human disturbance increases spatiotemporal associations among mountain forest terrestrial mammal species. *eLife*, **12**: RP92457.
Li XY, Buzzard P, Chen YC, et al. 2013. Patterns of livestock predation by carnivores: human-wildlife conflict in Northwest Yunnan, China. *Environmental Management*, **52**(6): 1334–1340.
Li ZL, Wang TM, Smith JLD, et al. 2019. Coexistence of two sympatric flagship carnivores in the human-dominated forest landscapes of Northeast Asia. *Landscape Ecology*, **34**(2): 291–305.
Loveridge AJ, Valeix M, Elliot NB, et al. 2017. The landscape of anthropogenic mortality: How African lions respond to spatial variation in risk. *Journal of Applied Ecology*, **54**(3): 815–825.
Lwin YH, Wang L, Li GG, et al. 2021. Diversity, distribution and conservation of large mammals in northern Myanmar. *Global Ecology and Conservation*, **29**: e01736.
Macarthur R, and Levins R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, **101**(921): 377–385.
MacDougall AS, McCann KS, Gellner G, et al. 2013. Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature*, **494**(7435): 86–89.
McCarthy JL, Wibisono HT, McCarthy KP, et al. 2015. Assessing the distribution and habitat use of four felid species in Bukit Barisan Selatan National Park, Sumatra, Indonesia. *Global Ecology and Conservation*, **3**: 210–221.
Moll RJ, Cepek JD, Lorch PD, et al. 2018. Humans and urban development mediate the sympatry of competing carnivores. *Urban Ecosystems*, **21**(4): 765–778.
Monterroso P, Alves PC, Ferreras P. 2014. Plasticity in circadian activity patterns of mesocarnivores in southwestern Europe: implications for species coexistence. *Behavioral Ecology and Sociobiology*, **68**(9): 1403–1417.
Nichols M, Ross J, Glen AS, et al. 2019. An evaluation of systematic versus strategically-placed camera traps for monitoring feral cats in New Zealand. *Animals*, **9**(9): 687.
Nouvellet P, Rasmussen GSA, Macdonald DW, et al. 2012. Noisy clocks and silent sunrises: measurement methods of daily activity pattern. *Journal of Zoology*, **286**(3): 179–184.
O'Brien TG, Kinnaird MF, Wibisono HT. 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, **6**(2): 131–139.
Pianka ER. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics*, **4**: 53–74.
R Core Team. 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
Rasphone A, Bousa A, Vongkhamheng C, et al. 2022. Diet and prey selection of clouded leopards and tigers in Laos. *Ecology and Evolution*, **12**(7): e9067.
Ridout MS, Linkie M. 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, **14**(3): 322–337.
Ripple WJ, James AE, Robert LB, et al. 2014. Status and Ecological Effects of the World's Largest Carnivores. *Science*, **343**(6167): 1241484
Santos F, Carbone C, Wearn OR, et al. 2019. Prey availability and temporal partitioning modulate felid coexistence in Neotropical forests. *PLoS One*, **14**(3): e0213671.
Saunders DA, Hobbs RJ, Margules CR. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, **5**(1): 18–32.
Schoener TW. 1974. Resource partitioning in ecological communities: Research on how similar species divide resources helps reveal the natural regulation of species diversity. *Science*, **185**(4145): 27–39.
Sévêque A, Gentle LK, López-Bao JV, et al. 2020. Human disturbance has contrasting effects on niche partitioning within carnivore communities. *Biological Reviews*, **95**(6): 1689–1705.
Soria CD, Pacifici M, Di Marco M, et al. 2021. COMBINE: a coalesced mammal database of intrinsic and extrinsic traits. *Ecology*, **102**(6): e03344.
Stone L, Roberts A. 1990. The checkerboard score and species distributions. *Oecologia*, **85**(1): 74–79.
Sunarto S, Kelly MJ, Parakkasi K, et al. 2015. Cat coexistence in central Sumatra: ecological characteristics, spatial and temporal overlap, and implications for management. *Journal of Zoology*, **296**(2): 104–115.
Tian JP, Zou QX, Zhang MM, et al. 2022. Spatial and temporal differentiation are not distinct but are covariant for facilitating coexistence of small and medium-sized carnivores in southwestern China. *Global Ecology and Conservation*, **34**: e02017.
Vélez J, McShea W, Pukazhenthi B, et al. 2024. Implications of the scale of detection for inferring co-occurrence patterns from paired camera traps and acoustic recorders. *Conservation Biology*, **38**(3): e14218.
Wan XR, Jiang GS, Yan C, et al. 2019. Historical records reveal the distinctive associations of human disturbance and extreme climate change with local extinction of mammals. *Proceedings of the National Academy of Sciences of the United States of America*, **116**(38): 19001–19008.
Wearn OR, Rowcliffe JM, Carbone C, et al. 2013. Assessing the status of wild felids in a highly-disturbed commercial forest reserve in Borneo and the implications for camera trap survey design. *PLoS One*, **8**(11): e77598.
Xiao ZS, Li XH, Wang XZ, et al. 2014. Developing camera-trapping protocols for wildlife monitoring in Chinese forests. *Biodiversity Science*, **22**(6): 704–711. (in Chinese)
Xu JC, Grumbine RE, Beckschäfer P. 2014. Landscape transformation through the use of ecological and socioeconomic indicators in Xishuangbanna, Southwest China, Mekong Region. *Ecological Indicators*, **36**: 749–756.
Zanin M, Palomares F, Brito D. 2015. What we (don't) know about the effects of habitat loss and fragmentation on felids. *Oryx*, **49**(1): 96–106
Zhou YB, Buesching CD, Newman C, et al. 2013. Balancing the benefits of ecotourism and development: the effects of visitor trail-use on mammals in a Protected Area in rapidly developing China. *Biological Conservation*, **165**: 18–24.