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Anthropogenic and environmental correlates of spatial patterns of co-occurrence of small felids in a montane landscape

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ABSTRACT

Understanding how sympatric small felids respond to their environmental surroundings in a human matrix landscape is important to determine their habitat use, distribution and conservation. However, structured survey design and large sample size studies are often rare for cryptic small-and medium-sized felids hindering their reliable and meaningful inferences for conservation management. We employed a multi-species occupancy model on a large-scale camera trap dataset to investigate the effects of environmental and anthropogenic variables on the occupancy, as well as the mechanisms facilitating sympatry among three small felids in Bhutan: the threatened Asiatic golden cat (*Catopuma temminckii*), marbled cat (*Pardofelis marmorata*), and the least concern leopard cat (*Prionailurus bengalensis*). Through their co-occurrence patterns at local and landscape scales, we could identify their potential interactions and the factors influencing them. We found that one species pair (marbled cat: leopard cat) had low co-occurrence at higher elevations. The interactions among the other felid pairs (Asiatic golden cat: marbled cat and Asiatic golden cat: leopard cat) were not directly mediated by human disturbances and were constant across the elevational gradient. We identified important predictors of marginal occupancy for two species: forest cover, river density, and slope for the marbled cat; and housing density, forest cover, and slope for the leopard cat. However, none of the predictor variables significantly influenced Asiatic golden cat occupancy. Our findings suggest that environmental factors, like forest cover and slope, may influence individual felid occupancy and consequently shape their interactions. We recommend that small felid conservation in heterogeneous landscapes need to

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consider the impacts of human land use; limit forest conversion and protect rugged habitats. Through this study, we provide new insights into small felid sympatry in montane landscapes, expanding our understanding of their complex coexistence patterns.

1. Introduction

Compared to other taxa, carnivores get particular attention partly due to their broad ecological roles (Terborgh et al., 1999), including an influence on the structure and composition of ecological communities (Allen et al., 2014), and partly due to their charismatic appeal (Macdonald et al., 2015). Despite advances in carnivore ecology, studies on small felids remain limited (Brodie, 2009; Peterson et al., 2022; Srivathsa et al., 2022) even though they constitute the majority of the Felidae (33 of the 40 species; Sunquist and Sunquist, 2017; Macdonald and Loveridge, 2010). Significant knowledge gaps on small felids concern their population size, habitat use, and behavioral ecology (Can et al., 2020; Chaudhary et al., 2020; Périquet et al., 2015; Taubmann et al., 2016). Small felids can play a crucial role in controlling rodent and other small prey populations, with consequences for agricultural production and food security (Chatterjee et al., 2020; Kamler et al., 2020; Rasphone et al., 2020; Rostro-García et al., 2021). Of the global 33 small felid species, 14 are listed as vulnerable or endangered, by of habitat loss, persecution, and land-use change (Mugerwa et al., 2020).

A species' occurrence and geographic distribution is influenced by its environmental factors and interactions with other species (Pollock et al., 2014). Failure to account for interspecific interactions or co-occurrence patterns may lead to biased inference when modeling habitat associations and the development of ineffective conservation management plans (McLoughlin et al., 2010). However, co-occurrence may be mediated by anthropogenic factors, as some species may benefit from the presence of anthropogenic factors through the human shield effect (protection from dominant predators) and access to food resources (Moll et al., 2018; Gámez and Harris, 2021; Prugh et al., 2023), while others may be negatively impacted by increased human-wildlife conflict or the risk of poaching. The modification of carnivore behaviour in response to human presence may affect the ecological roles each of the interacting species plays and the effect may ripple across the trophic level resulting in the destabilization of ecosystem resilience (Mori et al., 2013).

The landscape of Bhutan, located in the Himalayas, is characterized by rugged and steep topography with significant altitudinal variation. With 69.71 % forest cover and 52 % of the country designated as well-connected protected areas (FMID, 2023), Bhutan is a wild felid hotspot (Tempa et al., 2013). While detailed studies on the spatial distribution (Penjor et al., 2018; 2019), population density (NCD, 2015; Tempa et al., 2019), and interaction (Penjor et al., 2022) of large carnivores have been conducted, there is a lack of knowledge regarding the behavioral ecology and interaction of smaller carnivores. The sympatric felids, namely the Asiatic golden cat (*Catopuma temminckii*) (listed as Near Threatened by the IUCN; McCarthy et al., 2015), marbled cat (*Pardofelis marmorata*) (Near Threatened; Ross et al., 2016), and leopard cat (*Prionailurus bengalensis*) (Least Concern; Ross et al., 2015) with morphological similarities (Grassman et al., 2005), show nuances in behavioral mechanisms like diet partitioning (Kamler et al., 2020) and spatio-temporal segregation (Chatterjee et al., 2020; Rasphone et al., 2020; Vernes et al., 2015). Such sympatry among felid species offers an ideal system to study co-occurrence mechanisms and the influence of anthropogenic and environmental factors. Though small-scale spatiotemporal studies are conducted in protected (Wangmo et al., 2020) and non-protected areas (Vernes et al., 2015; Dhendup and Dorji, 2018; Tenzin et al., 2019; Choki et al., 2023), ecological relationships and co-occurrence in Bhutan are still incompletely described.

Therefore, the objective of this study is to assess the patterns of co-occurrence, and evaluate factors mediating co-occupancy, among the small felid guild in the montane landscape of Bhutan. We hypothesize that human disturbance would affect the co-occurrence of small felids across the altitudinal gradient. The most recent study on large carnivores, involving tigers (*Panthera tigris*), leopards (*Panthera pardus*) and dholes (*Cuon alpinus*) revealed a complex relationship between anthropogenic factors and interspecific interactions (Penjor et al., 2022). The leopard-dhole pair increased their co-occupancy in a landscape composed of higher settlement density, probably avoiding a larger and dominant predator, the tiger (Penjor et al., 2022). Hence, we were intrigued to investigate how small felids occur in the presence of anthropogenic factors in the same landscape. We aim to answer the following questions: 1) What are the effects of environmental and anthropogenic factors on the co-occurrence of small felids at the site and landscape level? 2) Is there influence of human disturbance on the spatial co-occurrence of small felids across the elevational gradient? Based on previous studies in the region (Can et al., 2020; Chatterjee et al., 2020; Cheyne and Macdonald, 2011; Haidir et al., 2013; Hearn et al., 2016; Kawanishi and Sunquist, 2008; Kyaw et al., 2021; Mohamed et al., 2016; Rostro-García et al., 2021; Sunarto et al., 2015), we predict that 1) all three species will respond negatively to anthropogenic variables (housing density and human disturbance). We expect the co-occurrence of species pairs to be negatively affected by housing density at the landscape scale and to vary across altitudinal gradients with higher co-occurrence at lower elevations. 2) We assume that there will be positive co-occurrence among the felids due to their similar choice of prey species (birds and small rodents). The Asiatic golden cat and the marbled cat prefer higher slopes and dense forest cover (Wangmo et al., 2020) and overlap in their temporal activity pattern (mostly diurnal; Rasphone, 2018). Their coexistence may be facilitated by fine-scale habitat segregation, as marbled cats are mainly arboreal (Azlan and Sharma, 2006), while Asiatic golden cats are primarily terrestrial (Kawanishi and Sunquist, 2008). Despite marbled and leopard cat's shared prey preference (Ross et al., 2015; Ross et al., 2016), their different diel activity patterns may enable coexistence as the former is diurnal, and the latter is predominantly nocturnal (Singh and Macdonald, 2017). 3) We expect high forest cover and slope to have a positive influence on marginal occupancies (the probability that a species occurs at some sites) of all three species.

2. Methods

2.1. Study area

Bhutan is a small landlocked country in the eastern Himalayas, sharing borders with China's Tibet region in the north and India in the south. It lies between latitudes 26°45' N and 28° 10' N and longitudes 88°45' E and 92°10' E, spanning across 38,394 km^2 area. The country has rugged terrain, ranging from 97 m above sea level (m.a.s.l) in the south to over 7500 m.a.s.l in the north, with three distinct climatic zones: subtropical, temperate, and alpine zone. It has an annual average temperature of 10.8°C and an average rainfall of 2076.7 mm (NCHM, 2021). Bhutan has the highest proportion of land area under protection in Asia, with a well-designated protected area network (5 National Parks, 4 Wildlife Sanctuaries, 1 Strict Nature Reserve, and 9 biological corridors) and the adjoining landscape comprising 14 Territorial Divisions (non-protected areas). It is recognized as a hotspot of biodiversity, with 11,248 species of plants and animals, including 129 mammal species (NBC, 2017). For a small country, it holds amongst the most diverse wildlife, including charismatic megafauna such as tiger, snow leopard (*Panthera uncia*), clouded leopard (*Neofelis nebulosa*), dhole, and the Asiatic elephant (*Elephas maximus*) supported by a diverse prey community. It is one of the least-populated countries in Asia, with a total population of 727,145 people and a population density of 19 per km^2 (NSB, 2023).

2.2. Camera-trap survey

A nationwide camera-trapping survey was conducted in Bhutan from March 2014 to March 2015. The survey was designed primarily to assess the tiger population and used a grid of 5 × 5 km cells distributed across the country (Fig. 1). The survey was divided into two blocks, north and south, based on logistics and accessibility. Camera traps were established in Protected Areas (PA, n = 10) and Territorial Divisions (TD, n = 11) within the designated grid cells. Grid cells in towns, settlements, large rivers, and alpine habitats were excluded (unless they included over 50 % forest cover). A total of 1129 camera stations were installed, of which 681 were in the north and 448 in the south (Fig. 1). The cameras were placed along animal trails and operated on average for 141 days (March 2014 and June 2014) in the south and 157 days (October 2014 and March 2015) in the north. Each station consisted of a pair of unbaited cameras facing each other, positioned about 45 cm above the ground and 5 m apart. We treated the camera pairs at each trap location as a single station, or single sampling unit, considering it operational as long as at least one camera was functioning. The mean distance

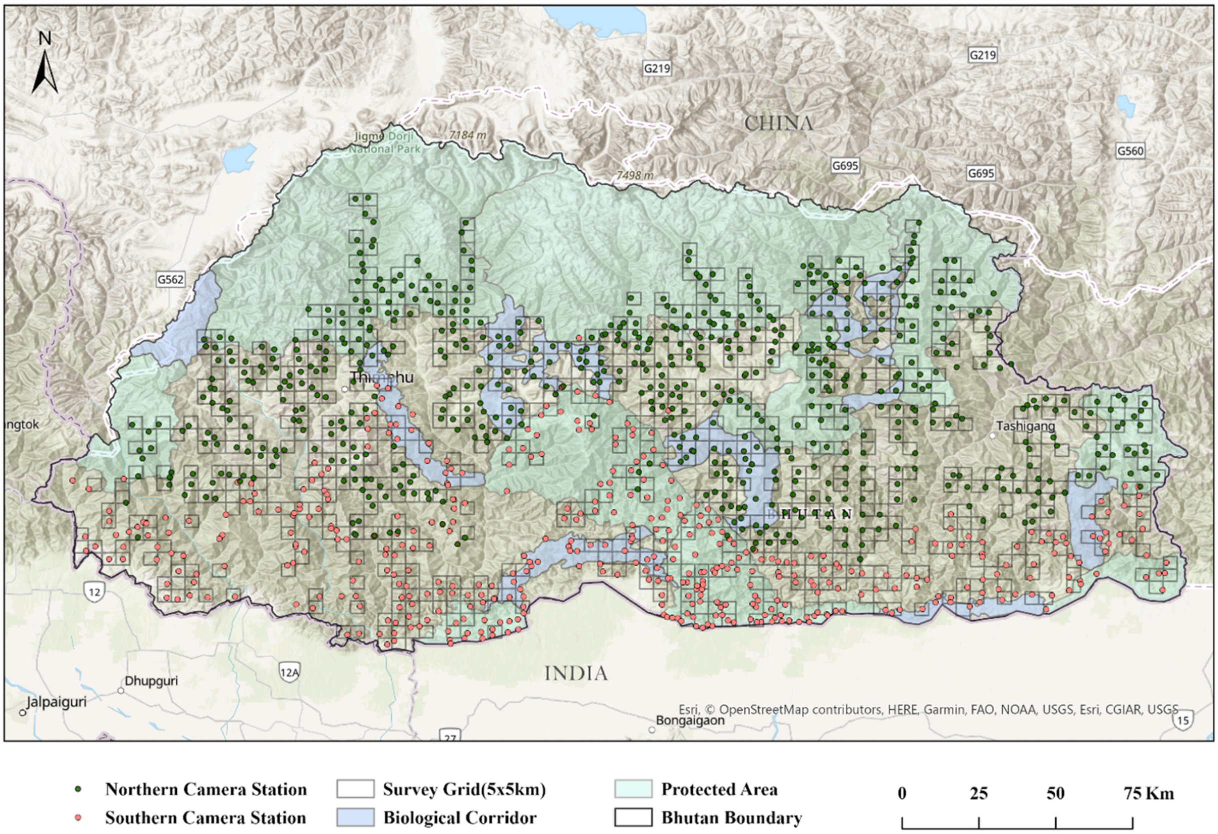

Fig. 1. Distribution of camera traps within 5-km × 5-km survey grids (square boxes) during the national tiger survey (2014–2015). Green circles indicate camera stations in the northern block and pink circles indicate camera stations in the southern block.

between camera stations was 2 km (s.d. = 1.2 km), but varied depending on the terrain and accessibility of the site.

2.3. Anthropogenic and environmental variables

To test our hypothesis, we generated site covariates for each site (camera trap location) using ArcGIS version 10.5 (ESRI, 2016). Failure to account for imperfect detection (or false absence) can underestimate the occupancy of a species when p (detection probability) < 1 (MacKenzie et al., 2002) which is common for any low-density species, like our study species. The imperfection in the observation process may be due to factors such as unequal trap effort and camera trap placement on trails influenced by accessibility and human activity. Detection covariates were trail (coded 1 for cameras on the trail, 0 otherwise), human disturbance measured as daily encounter rates of humans and livestock (cattle, horse, dog) at a camera trap site with independent captures at least 30 minutes apart and trap effort (camera trap functional days) to account for unequal sampling effort. To understand the fine-scale impacts of human activity (Tablado and Jenni, 2017) on felid occupancy, we used the mean daily encounter rate of humans and domestic animals at camera sites to represent human disturbance at the site level.

Based on previous studies (Can et al., 2020; Haidir et al., 2013; Kamler et al., 2020; Mohamed et al., 2013; Naing et al., 2019; Rasphone et al., 2020; Silmi et al., 2021; Sunarto et al., 2015; Wangmo et al., 2020; Grassman et al., 2005), the variables considered for modeling the variation in occupancy probability of each small felid and their co-occurrence were tree cover, slope, prey abundance, river density, disturbance at the camera trap site and housing density. We categorized covariates into two scales: fine-scale (500 m and 1 km) and broad-scale (2 km and 4 km). The scales were chosen to encompass the estimated scale range for each small felid's response to habitat components and anthropogenic variables depending on resource availability and co-occurrence (Penjor et al., 2021). All covariate layers were resampled to 90 m resolution and the value for each variable at each focal scale was then extracted for each camera station. For example, for river density, we rasterized the river shapefile and used a moving window focal mean of radius (500 m, 1 km, 2 km, and 4 km) to determine the percentage of river pixels within each scale radius of a camera station using ArcGIS.

Table 1

Model selection results. $\beta0$ =marginal occupancy intercept; βx = marginal occupancy slopes; $\gamma0$ =two-way interaction intercept; γx = two-way interaction slopes. 0 =no interaction; 1 =constant two-way interaction (intercept only); $\alpha0$ =detection intercept; αx = detection slopes; AICc=Akaike information criterion corrected for small sample size. ΔAICc=delta AIC (difference between AICc of the top and subsequent models).

Marginal Occupancy	Conditional Occupancy*	Detection**	AIC	ΔAIC_c
AGC = $\beta_0 + \beta_1$ Slp4km MC = $\beta_0 + \beta_1$ Treecov4km + β_2 RivDen2km + β_3 Slp500m LC = $\beta_0 + \beta_1$ HDen1km + β_2 Treecov4km + β_3 Slp4km	$\gamma_0 + \gamma_1$ Ele500m + γ_2 HDen4km	$\alpha_0 + \alpha_1$ trail + α_2 Eff + α_3 HDistb	8100.3	0.00
AGC = $\beta_0 + \beta_1$ Slp4km MC = $\beta_0 + \beta_1$ Treecov4km + β_2 RivDen2km + β_3 Slp500m LC = $\beta_0 + \beta_1$ HDen1km + β_2 Treecov4km + β_3 Slp4km	$\gamma_0 + \gamma_1$ HDen4km	$\alpha_0 + \alpha_1$ trail + α_2 Eff + α_3 HDistb	8101.4	1.19
AGC = $\beta_0 + \beta_1$ Slp4km MC = $\beta_0 + \beta_1$ Treecov4km + β_2 RivDen2km + β_3 Slp500m LC = $\beta_0 + \beta_1$ HDen1km + β_2 Treecov4km	0	$\alpha_0 + \alpha_1$ trail + α_2 Eff + α_3 HDistb	8111.0	10.79
AGC = $\beta_0 + \beta_1$ Slp4km MC = $\beta_0 + \beta_1$ Treecov4km + β_2 RivDen2km + β_3 Slp500m LC = $\beta_0 + \beta_1$ HDen1km + β_2 Treecov4km	1	$\alpha_0 + \alpha_1$ trail + α_2 Eff + α_3 HDistb	8112.4	12.14
AGC = $\beta_0 + \beta_1$ Slp4km MC = $\beta_0 + \beta_1$ Treecov4km + β_2 RivDen2km LC = $\beta_0 + \beta_1$ HDen1km + β_2 Treecov4km	$\gamma_0 + \gamma_1$ Ele500m	$\alpha_0 + \alpha_1$ trail + α_2 Eff + α_3 HDistb	8125.6	25.37
AGC = $\beta_0 + \beta_1$ Slp4km MC = $\beta_0 + \beta_1$ Treecov4km + β_2 RivDen2km LC = $\beta_0 + \beta_1$ HDen1km + β_2 Treecov4km	0	$\alpha_0 + \alpha_1$ trail + α_2 Eff + α_3 HDistb	8131.3	31.06
AGC = $\beta_0 + \beta_1$ Slp4km MC = $\beta_0 + \beta_1$ Treecov4km + β_2 RivDen2km LC = $\beta_0 + \beta_1$ HDen1km + β_2 Treecov4km	$\gamma_0 + \gamma_1$ HDen4km	$\alpha_0 + \alpha_1$ trail + α_2 Eff + α_3 HDistb	8137.1	36.86
AGC = $\beta_0 + \beta_1$ Slp4km MC = $\beta_0 + \beta_1$ Treecov4km LC = $\beta_0 + \beta_1$ HDen1km	$\gamma_0 + \gamma_1$ Ele500m	$\alpha_0 + \alpha_1$ trail + α_2 Eff + α_3 HDistb	8143.2	42.90
AGC = $\beta_0 + \beta_1$ Slp4km MC = $\beta_0 + \beta_1$ Treecov4km + β_2 RivDen2km LC = $\beta_0 + \beta_1$ HDen1km + β_2 Treecov4km	$\gamma_0 + \gamma_1$ Ele500m	$\alpha_0 + \alpha_1$ trail + α_2 Eff + α_3 HDistb	8143.4	43.17
AGC = β_0 MC = β_0 LC = β_0	1	α_0	8277.7	177.42
AGC = β_0 MC = β_0 LC = β_0	0	α_0	8283.2	182.91

AGC = Asiatic golden cat; MC = marbled cat; LC = leopard cat; Slp = slope, Treecov = tree cover, RivDen = density of river, HDen = housing density, Ele = elevation, Eff = effort, HDistb = Human disturbance; AIC = Akaike Information Criterion; **Δ** AIC: difference between AIC of top model and subsequent model

[*] same covariate for all interacting pairs

[**] same detection covariate for all species

Similarly, to calculate housing density, we used the point shapefile of all households, rasterized it, and calculated the mean number of houses within each scale radius of camera sites. This variable reflects the density of houses per pixel and when averaged across the 4 km radius characterizes human-related influence at the landscape scale. For tree cover, we used global tree cover data (Hansen et al., 2013) averaged over each focal scale radius. For prey, we calculated the relative abundance of muntjac (*Muntiacus muntjac;* Appendix 1). We used a hierarchical N-mixture model (Royle, 2004) as a function of elevation, extracted from digital elevation raster data (DEM; USGS, 2016), housing density, and tree cover while accounting for imperfect detection using the 'unmarked' package (Fiske and Chandler, 2011) in R (R Core Team, 2022). We then used site-level abundance as prey covariates in occupancy models of the Asiatic golden cat because past studies showed that muntjac was the most consumed prey species of Asiatic golden cat (Kamler et al., 2020). The details on the mean and standard deviation of covariates are in Table S1. Although data on marbled cat diet are limited (Grassman et al., 2005), given its predominantly arboreal nature, it is plausible that marbled cats prey on arboreal species (Hearn et al., 2018), which couldn't adequately be captured by terrestrial camera traps. Likewise, our survey method was unable to capture the leopard cat's prey, which probably mainly comprises rodents not readily sampled using camera traps (Kamler et al., 2020; Rostro-García et al., 2021; Hendry et al., 2023).

To select the optimal scale of each covariate and to examine small felid-habitat relationships, we used a three-step modeling approach (McGarigal et al., 2016). In the first step, we ran univariate single-species single-season occupancy models to investigate the response of each species to a habitat covariate at each scale. The best scale for each variable was selected based on the lowest AICc score (Akaike Information Criterion corrected for small sample size; Burnham and Anderson, 2004). In the second step, we ran Pearson's correlation test to check for multi-collinearity of the selected covariates. No covariate pair showed a high correlation (i.e., $|r| \leq 0.7$; Figure S2). In the final step, we ran multivariate single-species occupancy models on all remaining scale-optimized covariates. We tested all possible combinations of variables and ranked models using ΔAICc (the difference between AICc of subsequent models with the top model) in 'MuMIn' package (Barton, 2020). The variables from the top model of each species were then used in the multispecies occupancy model using the function `occumulti` in the unmarked package. We built a set of 11 biological relevant models to test our hypotheses (Table 1). We compared and ranked the models based on the ΔAICc and selected the model with the lowest score to infer the marginal and conditional occupancy (probability that a species occurs at some sites given that other species are at sites) for each felid species.

2.4. Multi-species occupancy model

To model the co-occurrence among Asiatic golden cat, marbled cat, and leopard cat, we used a multi-species occupancy model for two or more interacting species within single season (Rota et al., 2016). It accommodates two or more co-occurring species without needing an *a priori* assumption of asymmetric interactions (i.e., there is no need to assume that one species dominates the other). Like the single-species model (MacKenzie et al., 2002), it accounts for imperfect detection and allows modeling co-occurrence as a function of covariates. We modeled three co-occurring species by assuming the latent occupancy state of species s at site i as a multivariate Bernoulli random variable, $Z_i \sim \mathrm{MVB}(\quad \Psi_i)$, where Z_i is an S-dimensional vector of 1's and 0's denoting the latent occupancy state (Rota et al., 2016). For example, for three species, $Z = ([000], [001], [011], [100], [110], [010], [101], [111])$, and Ψ_i is the probability of being in one of these states. Each state is first order if it is inhabited by a single species ([001], [100], [010]), second order if it is occupied by two species ([011], [110], [101]), and third order for all three species [111].

We built models for species-specific occupancy (first-order or marginal occupancy) and for pairwise occurrence (second-order or conditional occupancy) to investigate how occupancy varies in response to environmental variables (Twining et al., 2022). In this study, we were interested in examining if the probability of any two of the three sympatric felids co-occurring at the same site was mediated by human disturbance i.e., housing density across an elevational gradient. Using the natural parameters (f) of Rota et al. (2016), the latent states of S species will have $2^s - 1$ possible combinations, so for three species, we have $(f_1), (f_2)(f_3), (f_{12}), (f_{13}), (f_{23}), (f_{123})$ natural parameters. A natural parameter is defined as the log odds that a species occupies a site (Rota et al., 2016). We specify first-order models for each species (f_1, f_2, f_3) i.e., their marginal occupancy as a constant (intercept model) and function of tree cover, slope, river density, and housing density. For second-order models (f_{12}, f_{13}, f_{23}) for each species, first we considered that the species occur independently of one another as a function of habitat covariates only. Second, we considered that species exhibit constant pairwise dependence that does not vary across space, and thirdly that co-occurrence between the species varies as a function of elevation and housing density. We excluded higher-order co-occurrence (i.e., $f_{123} = 0$) as we believe that the probability that three species coexisted was solely a function of species-specific and pairwise occurrence.

To minimize violating the closure assumptions (Rota et al., 2009), we used only the first 120 days of the sampling period for each camera station. This was collapsed into sampling occasions of 15 days each to maximize the temporal independence of captures, and to facilitate model convergence by reducing zero inflation and overdispersion (Dillon and Kelly, 2007). The detection history for each species was binary data with "1" indicating detection and "0" non-detection. We used images captured from both camera traps at the same station to compile the detection data. All continuous site covariates were z-standardized to a mean of 0 and 1 unit standard deviation before the analysis to facilitate model convergence and comparisons among covariates (Stanton et al., 2015).

3. Results

Out of 1129 camera stations, data were retrieved from 849 camera stations across a total effort of 73,259 sampling (trap) days. A total of 490, 363, and 560 independent detections were obtained for the Asiatic golden cat, marbled cat, and leopard cat in 259, 114, and 159 stations, respectively.

The detection probability varied among all three felids. The survey effort was positively associated with detection probabilities of Asiatic golden cat (β=0.17, 0.08 SE, $p = 0.03$) and marbled cat (β=0.17, 0.08 SE, $p = 0.03$). Cameras placed on trails had a strong positive effect on the detection probability of leopard cat (β=1.18, 0.12 SE, $p < 0.001$) and marbled cat (β=0.74, 0.29 SE, $p = 0.01$) whereas human disturbance at the camera site had a negative effect on the marbled cat (β=-0.56, 0.13 SE, $p < 0.001$) but had a positive effect on leopard cat detection (β=0.14, 0.04 SE, $p < 0.001$; Table S4).

At broader scales (2 and 4 km), there is moderate evidence that slope had a positive effect on the marginal occupancy of the Asiatic golden cat (β=0.21, 0.10 SE, $p = 0.04$) and strong evidence of a negative effect on the leopard cat (β=-0.34, 0.11 SE, $p = 0.001$) whereas at the fine scale (500 m and 1 km), there was strong evidence of a positive effect on marbled cats (β=0.59, 0.12 SE, $p < 0.001$). Similarly, there is strong evidence of forest cover having a positive association with the marginal occupancy of the leopard cat (β=0.38, 0.11 SE, $p < 0.001$) and marbled cat (β=0.51, 0.14 SE, $p < 0.001$). Likewise, the density of the rivers was negatively associated with the marginal occupancy probability of the marbled cat (β=-0.34, 0.12 SE, $p = 0.006$). At finer scales (camera site), there is some evidence that housing density had a positive effect on leopard cat marginal occupancy (β= 0.22, 0.11 SE, $p = 0.05$; Fig. 2, Table S2).

Our top multispecies occupancy model provided support for positive co-occurrence for only one species pair (marbled cat: leopard cat), indicated by the exclusion of zero from the 95 % confidence intervals (CI) of the intercept parameter (estimate 0.52; 0.25 SE; 95 % CI 0.04 – 0.99; $p = 0.04$; Table S3). It performed significantly better than models that assumed independent occurrence (no co-occurrence, $\Delta AIC_c > 10$; Table 1). There was strong evidence for negative co-occurrence between marbled cats and leopard cats at higher elevations. At higher elevations, leopard cats were less likely to occupy areas where marbled cats were also present (-0.36; 0.17 SE; 95 % CI $-0.70 - -0.02$, $p = 0.03$, Fig. 3). No support was found that housing density impacted co-occurrence between species pairs as 95 % CI range included zero (Asiatic golden cat: marbled cat 95 % CI $-0.28 - 0.33$, Asiatic golden cat: leopard cat 95 % CI $-0.16 - 0.34$, and marbled cat: leopard cat 95 % CI $-0.48 - 0.17$, Fig. 4).

The probability of occupancy of the Asiatic golden cat was highest (Ψ_{AGC} [95% CI] $= 0.44[0.38 - 0.48]$) followed by leopard cat ($\Psi_{LC} = 0.36[0.32 - 0.42]$) and marbled cat ($\Psi_{MC} = 0.17[0.12 - 0.22]$). Whereas, the detection probability of leopard cat was highest ($p_{LC} = 0.39[0.34 - 0.47]$), followed by Asiatic golden cat ($p_{AGC} = 0.29[0.21 - 0.39]$ and marbled cat ($p_{MC} = 0.06[0.02 - 0.14]$;Fig. 5).

4. Discussion

Our study revealed that co-occurrence of three species of small felid in a montane landscape is not directly mediated by human disturbances, and we observed consistent patterns across the elevational gradient. We found that only one species pair (i.e., marbled cat: leopard cat) negatively occurred at higher elevations. We posit several reasons for this: first, at a higher elevation, the forest cover decreases along with the primary productivity thus reducing prey density for competing similar-sized carnivores (marbled cat and

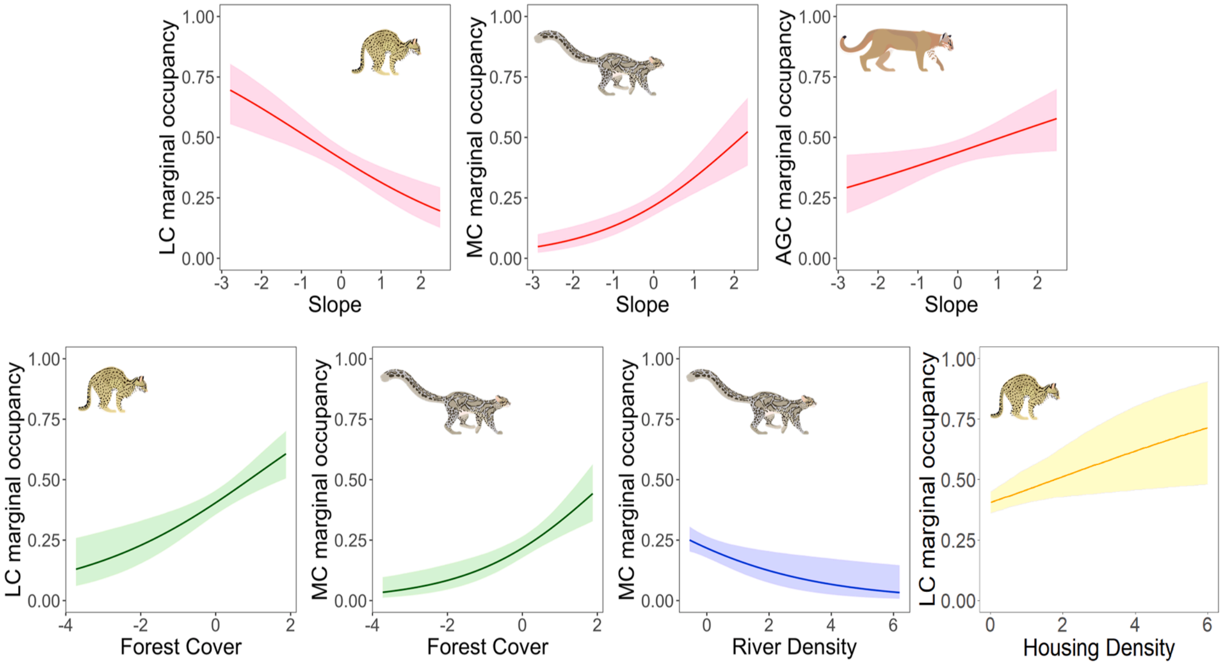

Fig. 2. Marginal occupancy probability of the leopard cat, marbled cat, and Asiatic golden cat as a function of slope, forest cover, river density, and housing density, mean response and associated 95% confidence interval are represented by solid lines and shaded ribbons, respectively. (Animal illustration courtesy: The Faunal Frontier).

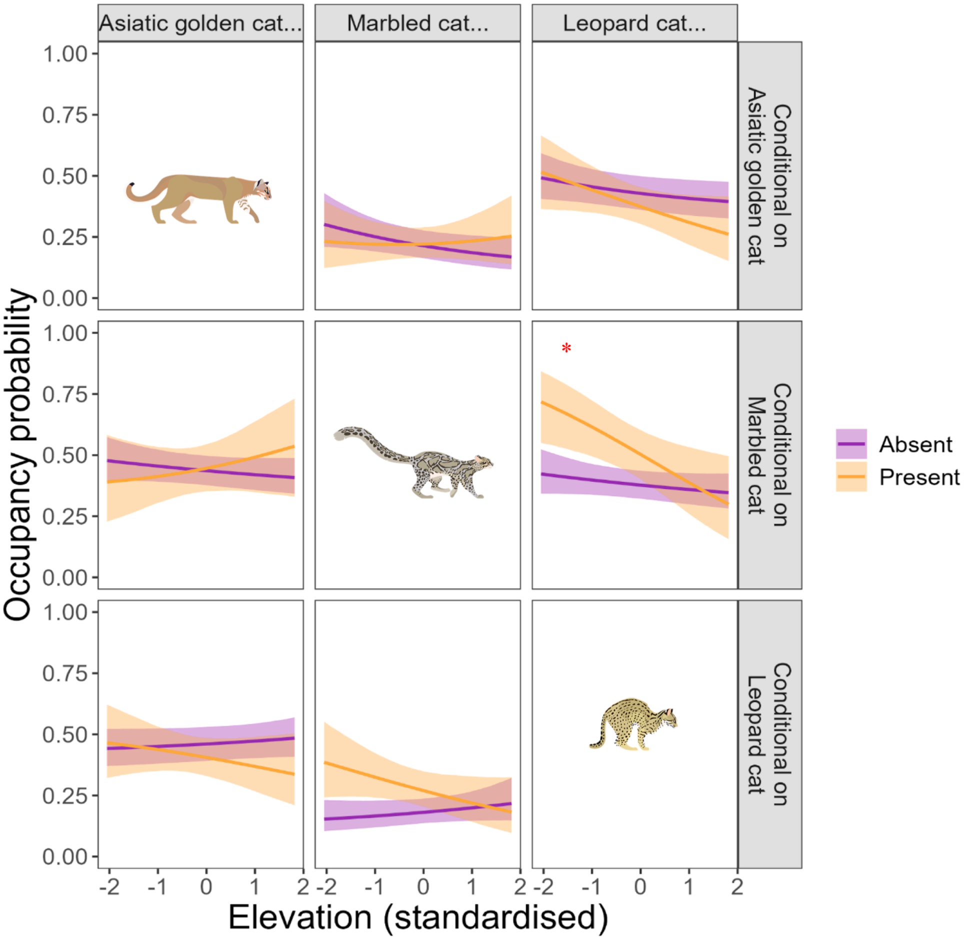

Fig. 3. Occupancy probability of Asiatic golden cat, marbled cat, and leopard cat conditional on the presence and absence of each of the other species along an elevation gradient. The probability of the species in each column is conditional on the presence and absence of the species in each row. The means are represented by solid lines and 95 % confidence intervals by shaded ribbons. The asterisk indicates a significant relationship. (Animal illustration courtesy: The Faunal Frontier).

leopard cat). Hence, the two co-occurring species may have reduced niche dimensions and become intolerant of each other, in contrast to productive habitat at lower elevations that support a higher diversity of prey and hence accommodate a higher diversity of predators. Second, the prey diversity at higher elevations decreases, and this simplification of the prey base may drive negative interactions between the marbled and leopard cats.

We were unable to uncover any concrete evidence of spatial co-occurrence between the Asiatic golden cat: marbled cat pair and the Asiatic golden cat: leopard cat pair. We suspect this could be due to differences in prey choice between slightly larger Asiatic golden cat and marbled cat/leopard cat (but see also study limitations). Asiatic golden cat can hunt prey similar to their body size (e.g., muntjac; Kamler et al., 2020), hence dietary segregation may be possible between Asiatic golden cat and marbled cat or leopard cat, the diet of the latter two mostly constitutes rodents and small birds. However, this is an interesting avenue to explore in the future through dietary and temporal habitat use analyses.

Contrary to our expectations, housing density did not influence the co-occurrence of the three felids (Fig. 4, Figure S1). However, at a fine scale, there was a marginally positive effect of the housing density on leopard cat occupancy. This effect of settlement density on the leopard cat helps to explain why this species is the most common and tolerant of secondary habitats in South and Southeast Asia (Mohamed et al., 2013; Silmi et al., 2021). Leopard cats tend to prefer forest edges and open spaces over dense forests and can tolerate a certain degree of human-modified landscapes (Chua et al., 2016; Rajaratnam et al., 2007). Another reason for the absence of any inimical effect of human settlements (as measured in our data) on leopard cat occupancy could be that rodents occur at higher density in the vicinity of these settlements (Stenseth et al., 2003) offering access to available prey resources. In this sense, space use of leopard cats in the human-modified landscape could be a trade-off between resource availability and the risk of encounters with humans and domestic carnivores (Choki et al., 2023). Alternatively, perhaps because housing density was relatively low in the study area, it may not have had sufficient influence to negatively affect leopard cat occupancy. We caution readers to interpret the effects of human disturbance on felid occupancy with care.

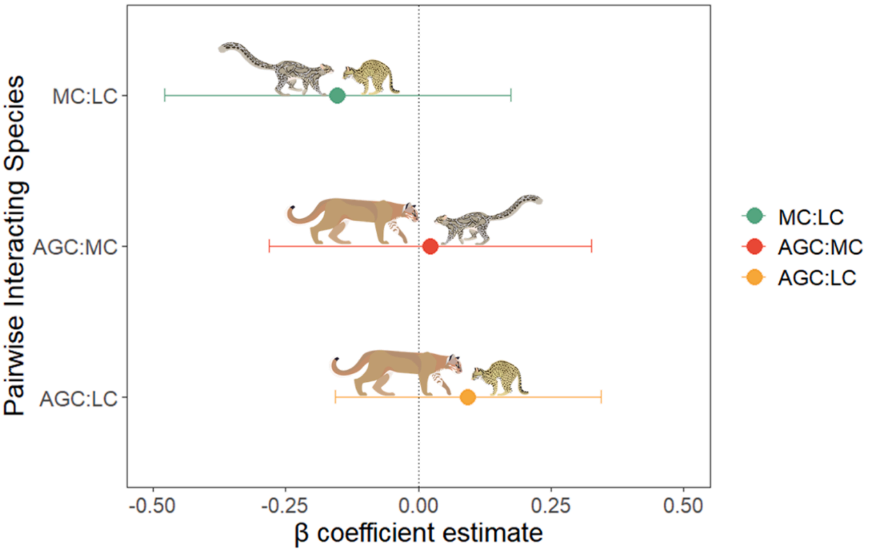

Fig. 4. Human disturbance effects on intraguild co-occurrence (Marbled cat: leopard cat, Asiatic golden cat: marbled cat, Asiatic golden cat: leopard cat) using β coefficient estimates for the housing density covariate represented as mean (dot) and 95 % confidence intervals (whiskers) from the top model (Animal illustration courtesy: The Faunal Frontier).

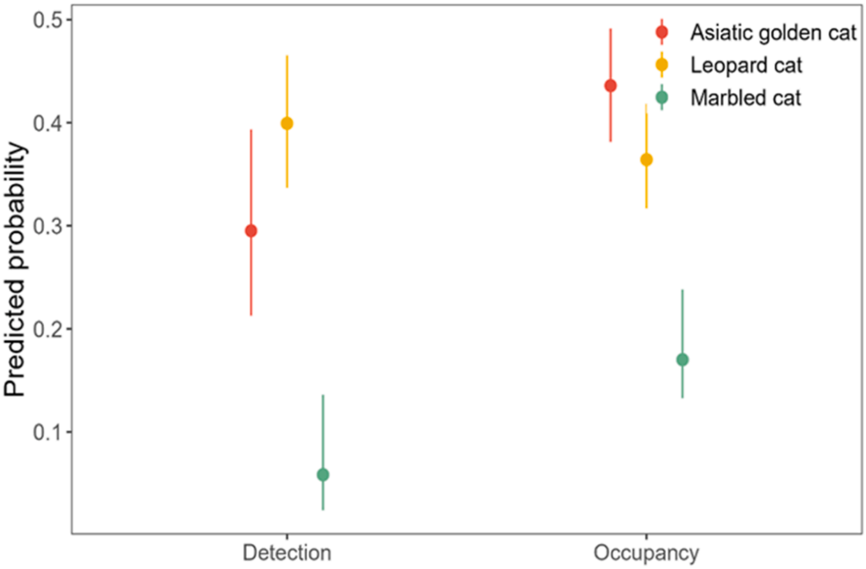

Fig. 5. Predicted marginal occupancy probability and detection probability of Asiatic golden cat, leopard cat, and marbled cat with all the covariates at their means. The means are represented by dots and whiskers represent 95 % confidence intervals.

We identified predictors of marginal occupancy for each species: forest cover, river density and slope were the significant predictors of marbled cat marginal occupancy. For the leopard cat, housing density, forest cover and slope were important predictors, but found no support for any significant predictor of the Asiatic golden cat's marginal occupancy, which might indicate that it is more of a generalist species than the other two felids within the variation of the environmental variables found within our study area.

As hypothesized, high forest cover had a positive influence on the occupancy of marbled cats and leopard cats. This also suggests marbled cat might be an obligate species of forest (Macdonald et al., 2010), primarily associated with moist broadleaved and mixed conifer forests (Thinley et al., 2015) and may also prefer hilly areas (Grassman et al., 2005). On the other hand, leopard cat is a habitat generalist and can be very adaptable to different forest and land-use types (Mohamed et al., 2013; Silmi et al., 2021); thus, this species can adapt to land-use change in ways thought to be problematic for most other small felids. The positive association of marbled cats and leopard cats with the forest cover at the landscape level could be due to the abundance of their primary prey; rodents (Ross et al., 2015) but this could also result in intraguild competition between them (Hearn et al., 2018). We consider that their spatial co-occurrence in forested areas may be supported by temporal segregation, with the marbled cat being mostly diurnal whereas the leopard cat is predominantly nocturnal (Singh and Macdonald, 2017), to maximize encounters with nocturnally active small rodents (Rajaratnam et al., 2007; Kyaw et al., 2021). This highlights the importance and potential conservation values of the intact montane forests of Bhutan for the persistence of these small felids in this landscape (Vernes et al., 2022).

Despite large-scale camera trap surveys spanning a large altitudinal gradient, the detection of all three small felids was relatively low. It revealed the rarity and elusiveness of these small cats, with the Asiatic golden cat being the most common of the three. Although we did not find any evidence of human disturbance (measured by the daily encounter rates of humans and livestock) on the detection probability of the Asiatic golden cat at a camera station level (small-scale), there was strong evidence of its effect on the marbled cat and leopard cat. We show that human disturbance at the camera station level was negatively associated with marbled cat detection, conversely, it had a positive association with leopard cat detection. Indeed, studies elsewhere have shown that leopard cat detection can be most prevalent where people occur most, although this species may alter its activity pattern (become active less during the day) to avoid direct encounters with humans by day (Can et al., 2020). Our results show that, although the species studied are sympatric, they respond differently to the surrounding environment.

Our results suggest that space-use patterns of montane small felid guild are probably influenced by a combination of each species' behavior (i.e., reaction to biotic and abiotic environmental elements) and interactions with competing species as has been observed for larger carnivores in the same landscape (Penjor et al., 2022).

4.1. Limitations

This study adds to the understanding of the patterns of sympatry amongst small felids (including threatened species) in the montane landscape, but due to the nation level methodology implemented, it can do so only at a relatively coarse level. A finer-grained, behavioural ecological appreciation of the species niches, and the dynamics of their co-occurrence will require a more realistic approach, for example radio-tracking of individual movements, attentive to both spatial and temporal aspects, and detailed diet analysis. Also, because our data are from a study design focused on tigers, camera-trap spacing was wider than would have been ideal for small felid studies. Stronger inferences about the underlying processes can be drawn using dynamic models that examine how co-occurrence patterns change over time when data are available from multiple sampling seasons (MacKenzie et al., 2017). Nonetheless, the data we have analyzed add substantially to understanding of the co-occurrence of a montane guild of little-known felids-data that informs both fundamental knowledge of autecology and guild dynamics, and conservation planning.

4.2. Management implications

In conclusion, our results are useful to both national and regional small felid conservation initiatives. The fundamental knowledge gleaned by our study, the first of its kind in Bhutan in particular, and South Asia more generally, will benefit conservation efforts regionally. Small carnivores play an important role in ecosystem structure and function and hence merit targeted conservation. Our findings add to the weight of evidence that limiting the conversion of natural forests, and protecting rugged landscapes, will be crucial for small felid conservation. It is noteworthy that these montane landscapes are often targeted for mining and quarrying (Tobden, 2018). Current conservation efforts, particularly those aimed at reducing threats, indicate that multifaceted and holistic approaches likely will be necessary to make a long-lasting impact on multispecies management.

Ethics Statement

Not applicable: This manuscript does not include human or animal research

CRediT authorship contribution statement

K.C: Conceptualization, Data Curation, Methodology, Formal analysis, Writing – original draft **E.D**: Supervision, Writing – review & editing **C.S.Z**: Supervision, Writing – review & editing **D.W.M**: Funding Acquisition, Supervision, Writing – review & editing **U.P**: Conceptualization, Data Curation, Methodology, Supervision, Writing – review & editing.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03422.

Data Availability

Data will be made available on request.

References

Allen, M.L., Elbroch, L.M., Wilmers, C.C., Wittmer, H.U., 2014. Trophic facilitation or limitation? Comparative effects of pumas and black bears on the scavenger community. PLOS ONE 9 (7), e102257. https://doi.org/10.1371/journal.pone.0102257.

Azlan, J.M., Sharma, D.S.K., 2006. The diversity and activity patterns of wild felids in a secondary forest in Peninsular Malaysia. ORYX 40 (1), 36–41. https://doi.org/10.1017/S0030605306000147.

Barton, K. (2020). *MuMIn: Multi-Model Inference. Model Selection and Model Averaging Based on Information Criterion (AICc and alike)* (R package version 1.43.17.). ⟨https://cran.r-project.org/package=MuMIn⟩.

Brodie, J.F., 2009. Is research effort allocated efficiently for conservation? Felidae as a global case study. Biodivers. Conserv. 18 (11), 2927–2939. https://doi.org/10.1007/s10531-009-9617-3.

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: Understanding AIC and BIC in model selection. Sociol. Methods Res. 33 (2), 261–304. https://doi.org/10.1177/0049124104268644.

Can, Ö.E., Yadav, B.P., Johnson, P.J., et al., 2020. Factors affecting the occurrence and activity of clouded leopards, common leopards and leopard cats in the Himalayas. Biodivers Conserv 29, 839–851. https://doi.org/10.1007/s10531-019-01912-7.

Chatterjee, N., Nigam, P., Habib, B., 2020. Population density and habitat use of two sympatric small cats in a central Indian reserve. PLoS ONE 15 (6). https://doi.org/10.1371/journal.pone.0233569.

Chaudhary, R., Zehra, N., Musavi, A., Khan, J.A., 2020. Spatio-temporal partitioning and coexistence between leopard (Panthera pardus fusca) and Asiatic lion (Panthera leo persica) in Gir protected area, Gujarat, India. PLOS ONE 15 (3), e0229045. https://doi.org/10.1371/journal.pone.0229045.

Cheyne, SM, Macdonald, DW, 2011. Wild felid diversity and activity patterns in Sabangau peat-swamp forest, Indonesian Borneo. Oryx 45 (1), 119–124. https://doi.org/10.1017/S003060531000133X.

Choki, K., Dhendup, P., Tenzin, J., Dorji, D., Tenzin, K., Wangmo, T., Penjor, U., 2023. Conservation potential of non-protected area for sympatric carnivores in Bhutan. Glob. Ecol. Conserv. 42, e02392. https://doi.org/10.1016/j.gecco.2023.e02392.

Chua, M.A.H., Sivasothi, N., Meier, R., 2016. Population density, spatiotemporal use and diet of the leopard cat (Prionailurus bengalensis) in a human-modified succession forest landscape of Singapore. Mammal. Res. 61 (2), 99–108. https://doi.org/10.1007/s13364-015-0259-4.

Dhendup, T., Dorji, R., 2018. Occurrence of six felid species outside protected areas in Bhutan. Catnews 67, 37–39. https://doi.org/10.13140/RG.2.2.26603.59681.

Dillon, A., Kelly, M.J., 2007. Ocelot Leopardus pardalis in Belize: The impact of trap spacing and distance moved on density estimates. Oryx 41 (4), 469–477. https://doi.org/10.1017/S0030605307000518.

ESRI, 2016. ArcGIS Desktop: Release 10.5. Environmental Systems Research Institute, *Redlands, CA*.

Fiske, I.J., Chandler, R.B., 2011. Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43 (10), 1–23. https://doi.org/10.18637/jss.v043.i10.

Forest Monitoring and Information Division. (2023). *National Forest Inventory Report. Department of Forests and Park Services. Ministry of Agriculture and Forests, Thimphu, Bhutan: Vol. I.*

Gámez, S., Harris, N.C., 2021. Living in the concrete jungle: carnivore spatial ecology in urban parks. Ecological Applications 31 (6). https://doi.org/10.1002/eap.2393.

Grassman, L.I., Tewes, M.E., Silvy, N.J., Kreetiyutanont, K., 2005. Ecology of three sympatric felids in a mixed evergreen forest in north-central Thailand. J. Mammal. 86 (1), 29–38. https://doi.org/10.1644/1545-1542(2005)0862.0.CO;2.

Haidir, I.A., Dinata, Y., Linkie, M., Macdonald, D.W., 2013. Asiatic golden cat and Sunda clouded leopard occupancy in the Kerinci Seblat landscape, West-Central Sumatra. CatNews 59 (April 2018), 2013.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-Resolution Global Maps of 21st-Century Forest Cover Change. Science 342 (6160), 850–853. https://doi.org/10.1126/science.1244693.

Hearn, A.J., Cushman, S.A., Ross, J., Goossens, B., Hunter, L.T.B., Macdonald, D.W., 2018. Spatio-temporal ecology of sympatric felids on Borneo. Evidence for resource partitioning? PLoS ONE 13 (7), e0200828. https://doi.org/10.1371/journal.pone.0200828.

Hearn, A.J., Ross, J, Bernard, H, Bakar, S.A., Hunter, L.T.B., Macdonald, D.W., 2016. The First Estimates of Marbled Cat Pardofelis marmorata Population Density from Bornean Primary and Selectively Logged Forest. PLoS ONE 11 (3), e0151046. https://doi.org/10.1371/journal.pone.0151046.

Hendry, A., Amir, Z., Decoeur, H., Mendes, C.P., Moore, J.H., Sovie, A., Luskin, M.S., 2023. Marbled cats in Southeast Asia: Are diurnal and semi-arboreal felids at greater risk from human disturbances? Ecosphere 14 (1), e4338. https://doi.org/10.1002/ecs2.4338.

Kamler, J.F., Inthapanya, X., Rasphone, A., Bousa, A., Vongkhamheng, C., Johnson, A., Macdonald, D.W., 2020. Diet, prey selection, and activity of Asian golden cats and leopard cats in northern Laos. J. Mammal. 101 (5), 1267–1278. https://doi.org/10.1093/jmammal/gyaa113.

Kawanishi, K., Sunquist, M.E., 2008. Food habits and activity patterns of the Asiatic golden cat (Catopuma temminckii) and dhole (Cuon alpinus) in a primary rainforest of peninsular Malaysia. Mammal. Study 33 (4), 173–177. https://doi.org/10.3106/1348-6160-33.4.173.

Kyaw, P.P., Macdonald, D.W., Penjor, U., Htun, S., Naing, H., Burnham, D., Kaszta, Ż., Cushman, S.A., 2021. Investigating carnivore guild structure: Spatial and temporal relationships amongst threatened felids in Myanmar. ISPRS Int. J. Geo-Inf. 10 (12). https://doi.org/10.3390/ijgi10120808.

Macdonald, E.A., Burnham, D., Hinks, A.E., Dickman, A.J., Malhi, Y., Macdonald, D.W., 2015. Conservation inequality and the charismatic cat: felis felicis. Glob. Ecol. Conserv. 3, 851–866. https://doi.org/10.1016/j.gecco.2015.04.006.

Macdonald, D.W., Loveridge, A.J., Nowell, K., 2010. Dramatis Personae: an Introduction to the Wild Felids. Oxford University Press.

Macdonald, D.W., Loveridge, A.J. (Eds.), 2010. The Biology and Conservation of Wild Felids. Oxford University Press, Oxford.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., Langtimm, C.A., 2002. ESTIMATING SITE OCCUPANCY RATES WHEN DETECTION PROBABILITIES ARE LESS THAN ONE. Ecology 83, 2248–2255. https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Hines, J.E., Bailey, L.L., 2017. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Elsevier.

McCarthy, J.L., Wibisono, H.T., McCarthy, K.P., Fuller, T.K., Andayani, N., 2015. Assessing the distribution and habitat use of four felid species in Bukit Barisan Selatan National Park, Sumatra, Indonesia. Glob. Ecol. Conserv. 3, 210–221. https://doi.org/10.1016/j.gecco.2014.11.009.

McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C., Cushman, S.A., 2016. Multi-scale habitat selection modeling: a review and outlook. Landsc. Ecol. 31 (6), 1161–1175. https://doi.org/10.1007/s10980-016-0374-x.

McLoughlin, P.D., Morris, D.W., Fortin, D., vander Wal, E., Contasti, A.L., 2010. Considering ecological dynamics in resource selection functions. J. Anim. Ecol. 79 (1), 4–12. https://doi.org/10.1111/j.1365-2656.2009.01613.x.

Mohamed, A., Ross, J., Hearn, A.J., Cheyne, S.M., Alfred, R., Bernard, H., Boonratana, R., Samejima, H., Heydon, M., Augeri, D.M., Brodie, J.F., Giordano, A., Fredriksson, G., Hall, J., Loken, B., Nakashima, Y., Pilgrim, J.D., Rustam, Semiadi, G., Wilting, A., 2016. Predicted distribution of the leopard cat Prionailurus bengalensis (Mammalia: Carnivora: Felidae) on Borneo. Raffles Bull. Zool. 2016 (May), 180–185.

Mohamed, A., Sollmann, R., Bernard, H., Ambu, L.N., Lagan, P., Mannan, S., Hofer, H., Wilting, A., 2013. Density and habitat use of the leopard cat (Prionailurus bengalensis) in three commercial forest reserves in Sabah, Malaysian Borneo. J. Mammal. 94 (1), 82–89. https://doi.org/10.1644/11-MAMM-A-394.1.

Moll, R.J., Cepek, J.D., Lorch, P.D., Dennis, P.M., Robison, T., Millspaugh, J.J., Montgomery, R.A., 2018. Humans and urban development mediate the sympatry of competing carnivores. Urban Ecosystems 21, 765–778. https://doi.org/10.1007/s11252-018-0758-6.

Mori, A.S., Furukawa, T., Sasaki, T., 2013. Response diversity determines the resilience of ecosystems to environmental change. Biol. Rev 99 (2), 349–364. https://doi.org/10.1111/brv.12004.

Mugerwa, B., Adhya, T., Ratnayaka, A., Thudugala, A., Napolitano, C., Sanderson, J., 2020. Are we doing enough to protect the World's small wild cats? CATnews 71 (Spring) https://www.researchgate.net/publication/342477131.

Naing, H., Ross, J., Burnham, D., Htun, S., MacDonald, D.W., 2019. Population density estimates and conservation concern for clouded leopards Neofelis nebulosa, marbled cats Pardofelis marmorata and tigers Panthera tigris in Htamanthi Wildlife Sanctuary, Sagaing, Myanmar. ORYX 53 (4), 654–662. https://doi.org/10.1017/S0030605317001260.

National Biodiversity Centre. (2017). *Biodiversity Statistics of Bhutan, 2017*.

National Center for Hydrology and Meteorology. (2021). *Bhutan State of the Climate 2020*.

National Statistics Bureau. (2023). Statistical Yearbook of Bhutan (1st ed.). ⟨https://www.nsb.gov.bt/publications/statistical-yearbook/⟩.

Nature Conservation Division*, Counting the Tigers in Bhutan: Report on the National Tiger Survey of Bhutan, 2014-2015.* 2015.

Penjor, U., Astaras, C., Cushman, S.A., Kaszta, Z., MacDonald, D.W., 2022. Contrasting effects of human settlement on the interaction among sympatric apex carnivores. Proc. R. Soc. B: Biol. Sci. 289 (1973). https://doi.org/10.1098/rspb.2021.2681.

Penjor, Kaszta, U., Macdonald, D.W., et al., 2021. Prioritizing areas for conservation outside the existing protected area network in Bhutan: the use of multi-species, multi-scale habitat suitability models. Landsc. Ecol. 36, 1281–1309. https://doi.org/10.1007/s10980-021-01225-7.

Penjor, U., Macdonald, D.W., Wangchuk, S., Tandin, T., Tan, C.K.W., 2018. Identifying important conservation areas for the clouded leopard Neofelis nebulosa in a mountainous landscape: Inference from spatial modeling techniques. Ecol. Evol. 8 (8), 4278–4291. https://doi.org/10.1002/ece3.3970.

Penjor, U., Tan, C.K.W., Wangdi, S., Macdonald, D.W., 2019. Understanding the environmental and anthropogenic correlates of tiger presence in a montane conservation landscape. Biol. Conserv. 238, 108196. https://doi.org/10.1016/j.biocon.2019.108196.

Périquet, S., Fritz, H., Revilla, E., 2015. The lion king and the hyaena queen: large carnivore interactions and coexistence. Biol. Rev. 90 (4), 1197–1214. https://doi.org/10.1111/brv.12152.

Peterson, A.T., Aiello-Lammens, M., Amatulli, G., Anderson, R., Cobos, M., Diniz-Filho, J.A., Escobar, L., Feng, X., Franklin, J., Gadelha, L., Georges, D., Guéguen, M., Gueta, T., Ingenloff, K., Jarvie, S., Jiménez, L., Karger, D., Kass, J., Kearney, M., Zurell, D., 2022. ENM2020: a free online course and set of resources on modeling species' niches and distributions. Biodivers. Inform. 17. https://doi.org/10.17161/bi.v17i.15016.

Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O'Hara, R.B., Parris, K.M., McCarthy, M.A., 2014. Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). Methods Ecol Evol. 5 (5), 397–406. https://doi.org/10.1111/2041-210X.12180.

Prugh, L.R., Cunningham, C.X., Windell, R.M., Kertson, B.N., Ganz, T.R., Walker, S.L., Wirsing, A.J., 2023. Fear of large carnivores amplifies human-caused mortality for mesopredators. Science 380 (6646), 754–758.DOI. https://doi.org/10.1126/science.adf2472.

R Core Team. (2022). *R: A language and environment for statistical computing, Vienna, Austria*. R Foundation for Statistical Computing. ⟨https://www.r-project.org/⟩.

Rajaratnam, R., Sunquist, M., Rajaratnam, L., Ambu, L., 2007. Diet and habitat selection of the leopard cat (Prionailurus bengalensis borneoensis) in an agricultural landscape in Sabah, Malaysian Borneo. J. Trop. Ecol. 23 (2), 209–217. https://doi.org/10.1017/S0266467406003841.

Rasphone, A. (2018). *The intraguild interactions of large carnivores and their impacts on their prey and other smaller carnivores in the Nam Et-Phou Louey National Protected Area, Lao PDR*. University of Oxford.

Rasphone, A., Kamler, J.F., Macdonald, D.W., 2020. Temporal partitioning by felids, dholes and their potential prey in northern Laos. Mammal. Res. 65 (4), 679–689. https://doi.org/10.1007/s13364-020-00524-9.

Ross, J., Brodie, J., Cheyne, S., Hearn, A., Izawa, M., & Loken, B. (2015). *Leopard cat, Prionailurus bengalensis. The IUCN Red List of Threatened Species. Report number: e. T18146A50661611*.

Ross, J., Brodie, J., Cheyne, S., Datta, A., Hearn, A., Loken, B., Lynam, A., McCarthy, J., Phan, C., Rasphone, A., 2016. Pardofelis marmorata. The IUCN Red List of Threatened Species 2016.

Rostro-García, S., Kamler, J.F., Minge, C., Caragiulo, A., Crouthers, R., Groenenberg, M., Gray, T.N.E., In, V., Pin, C., Sovanna, P., Kéry, M., Macdonald, D.W., 2021. Small cats in big trouble? Diet, activity, and habitat use of jungle cats and leopard cats in threatened dry deciduous forests, Cambodia. Ecol. Evol. 11 (9), 4205–4217. https://doi.org/10.1002/ece3.7316.

Rota, C.T., Ferreira, M.A.R., Kays, R.W., Forrester, T.D., Kalies, E.L., McShea, W.J., Parsons, A.W., Millspaugh, J.J., 2016. A multispecies occupancy model for two or more interacting species. Methods Ecol. Evol. 7 (10), 1164–1173. https://doi.org/10.1111/2041-210X.12587.

Rota, C.T., Fletcher, R.J., Dorazio, R.M., Betts, M.G., 2009. Occupancy estimation and the closure assumption. J. Appl. Ecol. 46 (6), 1173–1181. https://doi.org/10.1111/j.1365-2664.2009.01734.x.

Royle, J.A., 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60. https://doi.org/10.1111/j.0006-341X.2004.00142.x.

Silmi, M., Putra, K., Amran, A., Huda, M., Fanani, A.F., Galdikas, B.M., Anggara S, P., Traeholt, C., 2021. Activity and ranging behavior of leopard cats (Prionailurus bengalensis) in an oil palm landscape. Front. Environ. Sci. 9 (March). https://doi.org/10.3389/fenvs.2021.651939.

Singh, P., Macdonald, D.W., 2017. Populations and activity patterns of clouded leopards and marbled cats in Dampa Tiger Reserve, India. J. Mammal. 98 (5), 1453–1462. https://doi.org/10.1093/jmammal/gyx104.

Srivathsa, A., Banerjee, A., Banerjee, S., Chawla, M.M., Das, A., Ganguly, D., Rodrigues, R.G., Adhya, T., Bhatia, S., Kshettry, A., Majgaonkar, I., Punjabi, G.A., Puri, M., Singh, P., Surve, N., 2022. Chasms in charismatic species research: seventy years of carnivore science and its implications for conservation and policy in India. Biol. Conserv. 273. https://doi.org/10.1016/j.biocon.2022.109694.

Stanton, R.A., Thompson III, F.R., Kesler, D.C., 2015. Site occupancy of brown-headed nuthatches varies with habitat restoration and range-limit context. J. Wildl. Manag. 79 (6), 917–926. https://doi.org/10.1002/jwmg.903.

Stenseth, N.C., Leirs, H., Skonhoft, A., Davis, S.A., Pech, R.P., Andreassen, H.P., Wan, X., 2003. Mice, rats, and people: the bio-economics of agricultural rodent pests. Front. Ecol. Environ. 1 (7), 367–375. https://doi.org/10.1890/1540-9295(2003)001[0367:MRAPTB]2.0.CO;2.

Sunarto, S., Kelly, M.J., Parakkasi, K., Hutajulu, M.B., 2015. Cat coexistence in central Sumatra: ecological characteristics, spatial and temporal overlap, and implications for management. J. Zool. 296 (2), 104–115. https://doi.org/10.1111/jzo.12218.

Sunquist, M., Sunquist, F., 2017. Wild Cats of the World. University of chicago press.

Tablado, Z., Jenni, L., 2017. Determinants of uncertainty in wildlife responses to human disturbance. Biological Reviews 92 (1), 216–233. https://doi.org/10.1111/brv.12224.

Taubmann, J., Sharma, K., Uulu, K.Z., Hines, J.E., Mishra, C., 2016. Status assessment of the endangered snow leopard Panthera uncia and other large mammals in the Kyrgyz Alay, using community knowledge corrected for imperfect detection. Oryx 50 (2), 220–230. https://doi.org/10.1017/S0030605315000502.

Tempa, T., Hebblewhite, M., Goldberg, J.F., Norbu, N., Wangchuk, T.R., Xiao, W., Mills, L.S., 2019. The spatial distribution and population density of tigers in mountainous terrain of Bhutan. Biol. Conserv. 238, 108192. https://doi.org/10.1016/j.biocon.2019.07.037.

Tempa, T., Hebblewhite, M., Mills, L.S., Wangchuk, T.R., Norbu, N., Wangchuk, T., Dorji, T., 2013. Royal Manas National Park, Bhutan: a hot spot for wild felids. Oryx 47 (2), 207–210. https://doi.org/10.1017/S0030605312001317.

Tenzin, J., Dhendup, P., Choki, K., Dorji, T., 2019. Six felid species occur outside protected areas in south-central Bhutan. Catnews 70, 25–27. https://doi.org/10.2305/IUCN.UK.2015.

Terborgh, J., Estes, J.A., Paquet, P., Ralls, K., Boyd-Heger, D., Miller, B.J., Noss, R.F., 1999. The role of top carnivores in regulating terrestrial ecosystems. Cont. Conserv.: Sci. Found. Reg. Reserve Netw. 39–64.

Thinley, P., Curtis, P.D., & Lassoie, J. (2015). *Diversity, Occupancy, and Spatio-temporal Occurrences of Mammalian Predators in Bhutan's Jigme Dorji National Park Himalayan Mobilities View project Wildlife Damage Management View project*. https://doi.org/10.13140/RG.2.2.21649.45924.

Tobden, Tobden. (2018). Bhutan and Economic Statistics for Sustainable Development: Focusing on Valuation of Subsoil-Minerals. Asia–Pacific Economic Statistics Week 2018. Bangkok, Thailand. May, 2018.

Twining, J.P., Sutherland, C., Reid, N., Tosh, D.G., 2022. Habitat mediates coevolved but not novel species interactions. Proc. R. Soc. B: Biol. Sci. 289 (1966), 20212338. https://doi.org/10.1098/rspb.2021.2338.

United States Geological Survey. (2016). *Shuttle Radar Topography Mission, Accessed on June 2016.* ⟨https://lta.cr.usgs.gov/SRTM⟩.

Vernes, K., Rajaratnam, R., Dorji, S., 2022. Patterns of species co-occurrence in a diverse Eastern Himalayan montane carnivore community. Mammal. Res. 67 (2), 139–149. https://doi.org/10.1007/s13364-021-00605-3.

Vernes, K., Sangay, T., Rajaratnam, R., Singye, R., 2015. Social interaction and co-occurrence of colourmorphs of the Asiatic golden cat, Bhutan. CATnews 62, 18–20.

Wangmo, S., Lhendup, S., Penjor, S., & Wangchuk, S. (2020). Small felid coexistence in the Royal Manas National Park: Habitat use, spatial and temporal overlap, and implications for management. *Technical Report.Department of Forests and Park Services, Ministry of Agriculture and Forests, Royal Government of Bhutan,* 1–56.