



Tiger and leopard habitat use in Bhutan revealed by Bayesian multi-scale spatial occupancy models

Singye Wangmo^{a,b,*}, Marc Kéry^c, David W. Macdonald^a, Abishek Harihar^d,
Caroline C. Sartor^a, Samuel A. Cushman^a, Patrick Burns^e, Andrew J. Loveridge^{a,d},
Amy Dickman^a

^a Wildlife Conservation Research Unit (WildCRU), Department of Biology, University of Oxford, South Parks Road, Oxford, OX1 3EL, United Kingdom of Great Britain and Northern Ireland

^b Department of Forests and Park Services, Ministry of Energy and Natural Resources, Bhutan

^c Swiss Ornithological Institute, Seerose 1, CH-6204, Sempach, Switzerland

^d Panthera, 104 West 40th, New York, NY, 10018, United States

^e Northern Arizona University, School of Informatics, Computing & Cyber Systems, 1295 Knoles Dr, Flagstaff, AZ, 86011, United States

ARTICLE INFO

Keywords:

Bhutan
Occupancy model
Panthera tigris tigris
Panthera pardus fusca
Spatial autocorrelation
Habitat use
Protected area

ABSTRACT

The increasing ecological costs and constraints facing large carnivores, driven by habitat loss, poaching and human–wildlife conflict, represent a major challenge for global conservation. Although tigers have received significant conservation attention, knowledge gaps remain regarding their fundamental biology, including how they differ from sympatric carnivores such as leopards in habitat use and ecological requirements. We studied these two species across Bhutan's mosaic of protected and non-protected areas, using camera trap data from the second National Tiger Survey (2021–2022). We applied a scale-optimised spatial hierarchical occupancy model to examine habitat use by tigers and leopards, compare their ecological niches, and assess their co-occurrence patterns.

Tigers were estimated to occupy 7359 km² (~19% of Bhutan), whereas leopards occupied 15,842 km² (~41%), reflecting their broader distribution and Bhutan's disproportionate contribution to the global ranges of both species. For tigers, maintaining the ecological integrity of existing protected areas is more critical than expanding their coverage. Conservation strategies should prioritise core habitats and connectivity beyond protected areas and across multi-use landscapes, while addressing developmental pressures. In contrast, higher leopard occupancy in non-protected, human-modified landscapes, highlights their adaptability but also signals greater risks of human–carnivore conflict. We recommend community-driven coexistence frameworks tailored to species-specific ecological and socio-economic contexts. Building on its strong conservation ethos, Bhutan is well-positioned to lead multidisciplinary strategies that secure the long-term persistence of both species while contributing to biodiversity gains regionally and globally.

1. Introduction

The interlinked processes of habitat degradation and climate change have marked the onset of the Anthropocene, an epoch defined by human-driven ecosystem modification and accelerated species extinction rates (Ceballos et al., 2005; Ripple et al., 2014; Keck et al., 2025). Consequences are especially severe for large carnivores, whose extensive spatial requirements and frequent conflict with humans complicate

conservation efforts (Wikramanayake et al., 2004; Goodrich et al., 2022). Despite their ecological, cultural, and economic importance (Macdonald et al., 2017), large carnivores continue to experience substantial range contractions and population declines due to habitat loss, prey depletion, and poaching (Karanth et al., 2004a; Ripple et al., 2019). These pressures are further intensified by national and transboundary development agendas prioritising infrastructure expansion and transformative land-use changes (Ash et al., 2022; Kaszta et al., 2024).

* Corresponding author at: Wildlife Conservation Research Unit (WildCRU), Department of Biology, University of Oxford, South Parks Road, Oxford, OX1 3EL, United Kingdom of Great Britain and Northern Ireland.

E-mail address: Singye.wangmo@wolfson.ox.ac.uk (S. Wangmo).

<https://doi.org/10.1016/j.biocon.2026.112050>

Received 21 September 2025; Received in revised form 21 July 2026; Accepted 5 August 2026

0006-3207/© 2026 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Among Asia's most emblematic large carnivores are tigers (*Panthera tigris*) and leopards (*Panthera pardus*), apex predators that have experienced dramatic range contractions compared to the extent of their historical ranges, approximately 93% for tigers and around 50% for leopards (Hunter, 2015; Jacobson et al., 2016; Sanderson et al., 2023). These species are central to ecosystem function, playing a key role in prey regulation and trophic balance, and they serve as both flagship and umbrella species for broader biodiversity conservation (Macdonald et al., 2017; Shivakumar et al., 2023). Yet conservation investment remains disproportionately focused on tigers, with leopards receiving comparatively little attention (Jacobson et al., 2016; Kafley et al., 2019).

Despite their overlapping ranges, tigers and leopards differ markedly in their ecological flexibility and tolerance to human disturbances (Kafley et al., 2019; Penjor et al., 2022b). Conservation strategies often rely on the umbrella species concept, suggesting that the protection of wide-ranging apex predators indirectly benefits co-occurring species (Caro, 2003). However, in heterogeneous, human-modified landscapes, interspecific differences in carnivore responses to disturbance may limit their effectiveness as reliable biodiversity surrogates (Dalerum et al., 2008). Targeted management interventions and shifts in carnivore guild dynamics can influence broader ecosystem functions (Ritchie and Johnson, 2009; Levi and Wilmers, 2012). Intraguild competition, particularly among carnivores with overlapping diets (Schoener, 1974), drives spatial and temporal partitioning, shaping species diversity and distribution patterns. These interactions are further influenced by landscape-level factors, including anthropogenic disturbances and management regimes (Blaum et al., 2009; Schuette et al., 2013).

Understanding these dynamics is particularly relevant in regions where protected and human-modified areas occur in close proximity. One such setting is Bhutan. The country lies within the world's largest Tiger Conservation Landscape, the Northern Triangle, which spans 298,847 km² across India, Myanmar, China, and Bhutan. Here, both species persist across a mosaic of protected areas and adjoining landscapes that differ in habitat conditions, human disturbance, and management regimes (Wangchuk et al., 2004; Tempa et al., 2013; Tempa et al., 2019). Bhutan maintains more than 70% forest cover, and its protected area network system spans 19,750 km², 52% of the national land area, across ten protected areas and nine biological corridors (NCD, 2020; FMID, 2023). This system is managed through a zonation framework that strictly protects core zones, while allowing regulated resource use in buffer, transition, and multiple-use zones (DOFPS, 2011).

Over half of Bhutan's human population, primarily in rural communities, resides within or near these protected areas, where they have legal access to resources, reflecting a conservation model that integrates biodiversity protection and community livelihoods. In contrast, non-protected areas, which comprise over 14,000 km² and approximately 49% of the country's forest cover, are managed by Divisional Forest Offices (DFO) under a broader mandate emphasising sustainable forest management and rural development (NCD, 2020; Tshewang et al., 2021). The ongoing rapid land-use changes in the country, driven by urban development, agriculture, road construction, and associated human–wildlife conflict (Tshewang et al., 2021; Wangchuk et al., 2023), combined with its legacy of rich biodiversity, offer an important opportunity to examine how large carnivores such as tigers and leopards respond to different management approaches across a conservation–development landscape. Understanding these responses requires assessing habitat use in relation to environmental and anthropogenic factors and interspecific interactions that shape carnivore community structure and dynamics (Sunarto et al., 2015; Gompper et al., 2016; Miller et al., 2018).

Occupancy models are commonly used to infer species distribution while accounting for imperfect detection, a widespread challenge in ecological surveys that can result in overlooking the presence of a species (MacKenzie et al., 2002; Tyre et al., 2003; Kéry and Royle, 2016, 2021). As datasets expand in spatial extent and increase in resolution (i.

e., decrease in site area), accounting for residual spatial autocorrelation may become crucial for avoiding biased estimates and enhancing predictive accuracy (Johnson et al., 2013; Guélat and Kéry, 2018). Standard occupancy models use spatially indexed covariates but do not explicitly model spatial dependence; in this study, we refer to these as non-spatial occupancy models to distinguish them from spatial models that incorporate autocorrelation through correlated random effects (Doser et al., 2022a). Spatial dependence often arise from habitat features that are themselves spatially structured but not included in a model, or from biotic processes such as dispersal patterns, territorial behaviour, and interactions with sympatric species, including source–sink dynamics and spatial avoidance between dominant and subordinate species (Guélat and Kéry, 2018).

Penjor et al. (2019) established a baseline for tiger distribution and habitat use in Bhutan using a non-spatial occupancy model and data from the first National Tiger Survey 2014–2015. Here, we analysed camera trap data from Bhutan's largest biodiversity survey, the second National Tiger Survey from 2021 to 2022, using spatial occupancy models that account for residual spatial autocorrelation (Doser et al., 2022b) and using scale-optimised environmental covariates (McGarigal et al., 2016). Specifically, we addressed the following three main questions: 1. What are the spatial patterns of occupancy and what is the current geographic range size for tigers and leopards in Bhutan? 2. Which key environmental and anthropogenic variables, including protection status (PAs vs NonPAs), and at what spatial scales, most strongly influence tiger and leopard habitat use? 3. Do tigers and leopards exhibit spatial co-occurrence or avoidance? Although interspecific interactions were not the primary focus of our study, we analysed spatial overlap post-hoc, based on the estimated presence/absence of both species to examine patterns of coexistence and segregation.

We tested the following hypotheses: (a) tiger occupancy is higher in protected areas than in non-protected areas, reflecting the positive response of this species to formal protection, avoidance of human disturbance (e.g., proximity to roads and agriculture), tendency to avoid steep terrain, and preference for structurally complex forests i.e., with high canopy cover and foliage height diversity (Goodrich et al., 2010; Karanth et al., 2011; Penjor et al., 2019; Sanderson et al., 2023; Jhala et al., 2025) (b) leopard occupancy is higher in non-protected forests than in protected areas, owing to leopards' broader ecological tolerance and adaptability to human-modified landscapes (e.g., GMI, road density and agriculture), and increases with foliage height diversity (i.e., structurally complex, multi-layered forests) (Hayward et al., 2006; Athreya et al., 2016; Gubbi et al., 2020; Penjor et al., 2022a), and (c) spatial overlap between tigers and leopards is limited, such that leopard occupancy declines where tiger occupancy is high, consistent with patterns reported elsewhere that may reflect competitive interactions (Harihar et al., 2011; Chatterjee et al., 2023).

The comparisons we make here between spatial processes, habitat use and co-occurrence of tiger and leopard, and of their species-specific responses to environmental and anthropogenic variables, offer critical information and a more nuanced understanding of these at-risk species. Our findings provide important insights to support their conservation planning efforts in Bhutan and beyond, especially as regional development accelerates and pressure on large carnivore habitats intensifies.

2. Methods

2.1. Study area

Bhutan is a small, mountainous country situated on the southern slopes of the Eastern Himalayas, bordered by China to the north and India to the east, west, and south. It covers an area of 38,394 km², with a total human population of only 784,043 corresponding to a density of 19 km⁻² (NSB, 2025). Elevation ranges from less than 100 m in the southern foothills to over 7500 m in the north, with an average elevation of 3280 m, spanning three distinct climate zones: subtropical foothills,

temperate mid-elevations, and high alpine regions. Forests cover around 26,800 km² (70%) of the total area, composed of approximately 68% broadleaf and 32% coniferous species (FMID, 2023).

Bhutan lies within the Northern Triangle Tiger Conservation Landscape (TCL), the world's largest at 294,847 km² and representing more than 32% of the global TCL extent (Sanderson et al., 2023).

2.2. Camera trap survey and design

Under the aegis of the Department of Forests and Park Services (DoFPS), the second National Tiger Survey was conducted from October 2021 to July 2022 in 10 Protected Areas (PAs) and 14 Territorial Forest Divisions (Fig. 1). A total of 1043 grid cells, each measuring 5 × 5 km² (25 km²), were uniformly laid out across the country based on the combined distributional range of tigers and leopards at elevations from 90 to 4500 m a.s.l. (DoFPS, 2023; Tempa et al., 2019). Much of the high-elevation terrain in the north of the country was excluded from the sampling frame because both species are known to be largely absent from these areas (Fig. 1). The camera trap survey, conducted using standard block trapping methods (Karanth & Nichols, 2002), took place in two major survey blocks: North and South, owing to logistic and weather constraints.

The Northern Block had 527 camera stations from 11th October 2021 to 31st January 2022, spanning 13 field offices: seven Protected Areas and six Divisional Forest Offices. The Southern Block consisted of 672 camera stations from 21st February 2022, to 30th July 2022, spread across 15 field offices: four Protected Areas and 14 Divisional Forest Offices (See Appendix A for details). A small number of additional camera stations were installed outside the predefined grids to improve coverage in areas with logistical or accessibility constraints, and in locations identified through local knowledge of reported large carnivore

presence.

A 5 × 5 = 25 km² grid was initially selected following the density sampling protocol, which recommends placing at least 2–3 camera stations within the average home range of a female tiger (Karanth & Nichols, 2002). This design was supported by GPS and VHF telemetry data from Bhutan, which estimated female tiger home ranges at 28–34 km² in the south (DoFPS, 2023; DoFPS, unpublished data) and up to 150 km² for a single female in central Bhutan (DoFPS, 2023). However, we conducted our analyses at a finer spatial grain of 2 × 2 km² to represent spatial variation in carnivore habitat use with a greater spatial resolution, while ecological scale dependence was addressed through multi-scale covariates. This yielded 9704 grid cells of 4 km² each. Since tiger and leopard home ranges in Bhutan far exceed 4 km² in size, we interpreted the occupancy parameter in our analysis as the probability of site use during the survey period, rather than as the probability of permanent presence (Steenweg et al., 2017), and we take the liberty to use both as synonyms. Home ranges exceeding a grid cell are in fact one of the factors that may lead to residual spatial autocorrelation in an occupancy model and our spatial occupancy model addressed this (MacKenzie et al., 2017; Gould et al., 2019); see below.

Given the low density and detectability of large felids, cameras were strategically placed along likely travel routes such as forest trail intersections, ridgelines, rivers, saltlicks, and waterholes (Karanth & Nichols, 2002). Each station consisted of two cameras mounted 45–60 cm above the ground and 2–3 m from the trail to capture full-body images. We used the Camera Trap File Manager (CTFM, Panthera) tool and CAMTRAPR (Niedballa et al., 2016), to manage camera trap data by assigning metadata including date, time, species, and sex, and to generate species-specific detection histories for occupancy modeling.

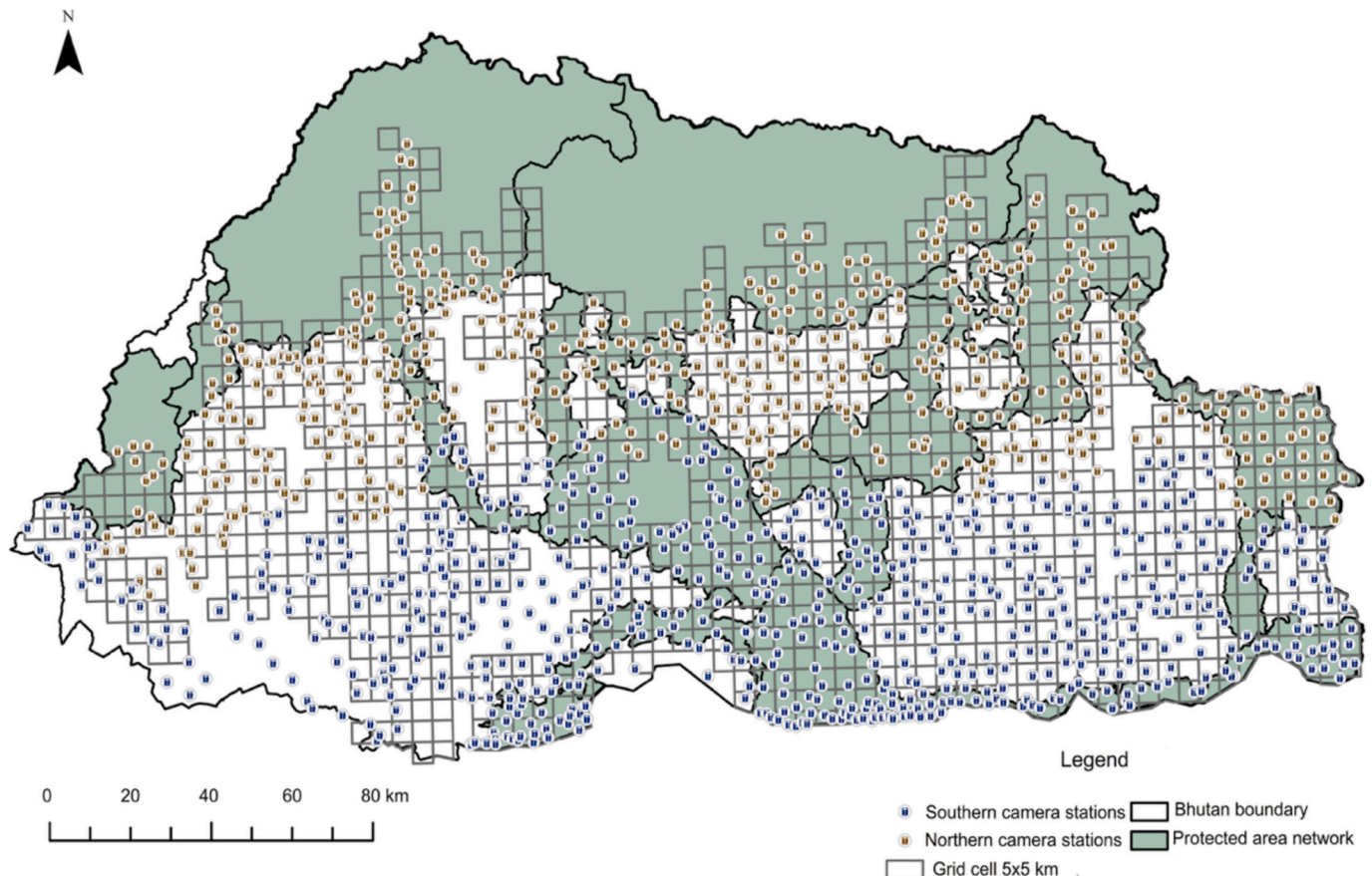


Fig. 1. Map of the study area in Bhutan showing camera-trap locations arranged in a 5 × 5 km grid during the Second National Tiger Survey (2021–2022).

2.3. Covariates

Drawing on ecological knowledge and prior studies, we selected a suite of 19 covariates that potentially influenced tiger and leopard habitat use (Perez et al., 2006; Athreya et al., 2016; Tempa, 2017; Penjor et al., 2019; Penjor et al., 2022b; Perez et al., 2022; Wen et al., 2022; Milda et al., 2023; Poudel et al., 2023) and grouped them into four categories: vegetation, topographic, anthropogenic, and climatic factors.

Vegetation covariates included five structural metrics derived from NASA's GEDI LiDAR dataset (Dubayah et al., 2020) providing fine-scale information about three-dimensional forest structure. These metrics included the total plant area index (TPAI), plant area volume density of the understory from 0 to 5 m (PAVD), Foliage Height Diversity (FHD), canopy cover, and forest canopy height (FCH). Since GEDI makes sparse observations of forest structure, we developed a Random Forest model based on GEDI footprint observations and several ancillary data layers, including Sentinel-2 optical satellite imagery and ALOS-2 PALSAR-2 L-band radar data. We made spatially-continuous prediction maps of each of the five structural metrics at 100 m spatial resolution (see Appendix G for details). We also included Gross Primary Production (GPP; MOD17A2H, 1 km, 8-day composite) as a continuous proxy for vegetation productivity and greenness (Running and Zhao, 2015).

Topographic covariates included elevation (SRTM 30 m), roughness, topographic position index (TPI), and compound topographic index (CTI), all derived from digital elevation models (MERIT-DEM at 90 m and SRTM at 30 m spatial resolution (NASA JPL, 2013)). We also included a river layer from the Land Use Land Cover (LULC) dataset provided by the Department of Forest and Park Services, Royal Government of Bhutan (RGoB).

Anthropogenic covariates included four variables representing human land use and infrastructure. The Global Human Modification (GHM) index (1 km resolution) quantifies cumulative human pressure from settlements, agriculture, transportation, energy and mining, and electrical infrastructure (Kennedy et al., 2019). We further included road, agriculture and protected areas and biological corridor polygon layers, all derived from the LULC dataset of the DoFPS, RGoB.

Climatic covariates included four variables derived from the CHELSA-W5E5 v1.1 dataset at a spatial resolution of approximately 1 km: mean annual temperature, mean annual precipitation, temperature seasonality, and precipitation seasonality (Karger et al., 2023). These variables capture long-term climate averages and seasonal variability across Bhutan.

2.4. Obtaining covariates at multiple spatial scales

We first resampled all the predictor rasters to a resolution of 90 m. Using Google Earth Engine (GEE) (Gorelick et al., 2017), we then computed weighted focal statistics at seven spatial extents (250 m, 500 m, 1 km, 2 km, 4 km, 8 km, and 16 km) using a moving-window approach with Gaussian distance-decay kernels (radius = scale; σ = scale/2), following McGarigal et al. (2016). We then extracted the covariate values at camera trap locations in GEE using a custom zonal-statistics function. For continuous variables, we calculated the Gaussian-weighted focal mean at each scale, whereas for binary categorical variables (e.g., river, protected area; coded as 1 = presence, 0 = absence), we calculated the focal mean as the weighted proportion of the surrounding landscape classified as present.

2.5. Occupancy modeling

We used the R package *spOccupancy* (Doser et al., 2022b) to fit spatial and non-spatial occupancy models (MacKenzie et al., 2002; Tyre et al., 2003) for both species separately. We first selected the optimal spatial scale for each environmental covariate that potentially affected tiger or leopard distribution, followed by covariate selection to obtain our final

models for inference.

Detection histories were compiled for each camera station using 30-day intervals as sampling occasions, with a '1' denoting a detection, and '0' denoting a non-detection. The first 529 camera stations were deployed sequentially in the northern block during days 1–150 of the study, followed by deployment of the remaining 673 stations in the southern block during days 151–268. Thus, in the first period, only the northern stations contributed data, whereas the southern stations were inactive, and vice versa in the second period. Therefore, occasions with inactive cameras were coded as NA.

2.5.1. Optimisation of spatial scale of covariates

To identify the spatial extent around camera trap sites at which covariates best predicted the distribution of tigers and leopards, we implemented a multi-scale optimisation approach (McGarigal et al., 2016; Macdonald et al., 2019). For each species, we evaluated 19 covariates (all normalised prior to analysis) at seven spatial scales from 250 m to 16 km; see above. To avoid excessive computational costs, we used for this a non-spatial occupancy models (see below). For each species separately, we used the Widely Applicable Information Criterion (WAIC) to compare the predictive performance of the model across these seven scales (Watanabe and Opper, 2010) and selected the optimal scale for each covariate and species. To avoid excessive multicollinearity among scale-optimised covariates, we next calculated pairwise Pearson correlation coefficients and excluded one variable from each pair with $|r| > 0.7$ using the `vifcor()` function in the `usdm` R package (Naimi, 2023). Finally, we iteratively removed variables with a stepwise variance inflation factor of > 5 . This resulted in 11 covariates for leopards and 9 for tigers (see Appendix H(a) and H(b) for details).

2.5.2. Covariate selection

To identify a useful model for inference of tiger and leopard distribution in Bhutan, we first fitted a non-spatial occupancy model with linear and quadratic terms of all 11 and 9 predictors for leopards and tigers, respectively, using the function `PGOcc` (Doser et al., 2022b) and then dropped all quadratic terms that were statistically unsupported, i.e., had 0 inside of their 95% credible interval. We then retained that covariate structure and fitted a spatial occupancy model to the tiger and the leopard data using the function `spPGOcc` (Doser et al., 2022). For comparison we also fitted the corresponding two models without spatial autocorrelation using `PGOcc`.

2.5.3. Fitting the non-spatial and the spatial occupancy models

For tiger, we modelled occupancy probability using gross primary productivity (GPP), protected areas and biological corridors, mean annual precipitation, precipitation seasonality, river density, road density, terrain roughness, proportion of agricultural cover, and topographic position index (TPI). For leopard, we used foliage height diversity (FHD), elevation, global human modification (GHM), GPP, mean annual precipitation, precipitation seasonality, river density, road density, terrain roughness, proportion of agricultural cover, and TPI.

Detection probability for both species was specified as a function of Julian date (linear and quadratic, both standardised) and the logarithm of the trap effort (i.e., of the number of trap nights per occasion).

To accommodate residual spatial autocorrelation, i.e., spatial structure in occupancy probability at the scale of our 4 km² grid cells that was not accounted for by the covariates in the model, we fitted a spatial occupancy model using Nearest Neighbour Gaussian Processes (NNGPs) as implemented in the `spOccupancy` package (Doser et al., 2022). Here, the linear predictor of occupancy probability at grid cell j comprises a spatially structured random effect $W = (W_1, \dots, W_j)^T$, modelled as a draw from a multivariate normal distribution $W \sim \text{MVN}(0, \Sigma)$, where Σ is the variance-covariance matrix containing the pairwise spatial covariances between sites i and j and is defined as $\Sigma_{ij} = \sigma^2 \exp(-\phi d_{ij})$, i.e., the exponential covariance model. Here, d_{ij} denotes the

Euclidean distance between each pair of sites i and j , σ^2 represents the spatial variance, and ϕ is the spatial decay parameter that controls how quickly residual spatial autocorrelation declines with increasing distance. We assigned a weakly informative prior to the spatial variance term $\sigma^2 \sim \text{Inverse Gamma}(\alpha = 1, \beta = 2)$, and independent uniform priors for the spatial decay parameter $\phi \sim \text{Uniform}(0.001, 0.5)$. As a sensitivity analysis, we fitted the spatial occupancy models with four different NNGP configurations, with 5, 15, 20, and 30 neighbours, which we compared using WAIC. For both the tiger and leopard, the formulation with 5 NNGP proved to have the lowest (or best) value of WAIC and hence, we present the results for these. We ran all models for sufficiently long that all chains had reached convergence based on a visual assessment of trace plots and values of the Rhat convergence statistics of ≤ 1.1 (Brooks and Gelman, 1998). We report posterior means as point estimates and symmetric 2.5 and 97.5% percentiles for a 95% credible interval (CRI). To convey the uncertainty in estimated species distribution maps, we also show the posterior standard deviation.

Model fit was evaluated via posterior predictive checks (PPC) using the Freeman–Tukey discrepancy statistic (Freeman and Tukey, 1950) implemented in the `ppcOcc()` function of `spOccupancy`.

For comparison, to evaluate the error in tiger and leopard range size estimates from ignoring imperfect detection, we fitted a variant of our best-fit spatial model (5-NNGP) in `spOccupancy` without the detection component. We collapsed detections across all sampling occasions into a single presence–absence indicator (1 if detected at least once, 0 otherwise) and duplicated this column to create a pseudo-detection history of two identical occasions. This forced the model to assume perfect detection ($p = 1$) while maintaining the same structure as the full 5-NNGP spatial occupancy model, thereby allowing us to fit an equivalent spatial logistic regression without explicitly modeling imperfect detection.

2.5.4. Prediction of species presence and absence and estimation of range size and overlap metrics

We used predictions from the fitted spatial models to estimate tiger and leopard range size in Bhutan, their overlap with protected and non-protected areas, and spatial overlap between the two species. For comparison, we also generated the same estimates using the non-spatial models. These quantities were estimated by summing the predicted values of presence and absence of a pixel over suitable areas, for example, across all grid cells in Bhutan to estimate national range size. Repeating these calculations across posterior draws from the Bayesian analysis allowed uncertainty in the estimates to be propagated.

To compare occupancy between protected areas (PAs) and non-protected areas (NonPAs), we calculated the fractional overlap of each grid cell with the two management zones using `terra::extract` in R. For each pixel, we multiplied the estimated occupancy probability (ψ) by the proportion of the pixel within each zone, thereby apportioning occupancy proportionally between PAs and NonPAs. Posterior samples of presence–absence states (z) were drawn from the spatial occupancy model, and mean occupancy was summarised separately for PAs and NonPAs. We then evaluated the posterior distribution of occupancy differences (NonPA – PA). The same comparison was conducted separately for the 24 management strata comprising 10 PAs and 14 DFOs.

To evaluate spatial overlap between tiger and leopard distributions in Bhutan, we used posterior samples of the estimated occupancy states (z) from the two independently fitted spatial models and classified each of the 9704 sites across 2500 MCMC draws into four states: neither species present, leopard only, tiger only, or both species present. These classifications were used to calculate site-level co-occurrence frequencies, conditional occupancy probabilities, and associated contrasts, with full propagation of uncertainty. The corresponding equations are provided in Appendix I.

3. Results

We recorded 405 independent tiger events and 796 independent leopard events over a total sampling effort of 96,857 effective trap nights (median 3927 per station; range 2068–8725). Tigers were detected at 187 stations (15% of the total), whereas leopards were detected at 265 camera stations (22% of the total) (see Appendix A for details).

3.1. Scale of covariates influencing habitat use

The scale of habitat use differed between tigers and leopards for seven of the eight shared covariates (Tables 1 and 2). Leopards responded to topographic covariates at broader scales, with Topographic position index (TPI) and terrain roughness optimised at 8 km and rivers at 16 km, whereas tiger occupancy was best explained by these covariates at finer scales, with TPI and terrain roughness optimised at 4 km and rivers at 250 m. Elevation was important only for leopards at 2 km.

Among anthropogenic variables, both species responded to roads at 250 m, whereas agricultural land best described patterns in tiger habitat use at a spatial scale of 16 km and 8 km for leopards. The Global Modification Index (GMI) and PA network system were selected at 16 km for leopards and tigers, respectively. Responses to climate also

Table 1

Posterior means with 95% CRIs in parentheses for non-spatial and for spatial occupancy models for tigers L and Q denote the linear and quadratic terms of a covariate. Estimates with 95% CRIs that do not overlap 0 (and thus are “significant”) are highlighted in boldface.

Parameter and parametric form	Scale (kms)	Non-spatial model	Spatial model (5 NNGP)
Occupancy probability			
Intercept		−0.82 (−1.24;−0.38)	−2.02 (−4.09−0.14)
Gross Primary Productivity (L)	1	0.04 (−0.23−0.30)	0.42 (−0.69−1.57)
Gross Primary Productivity (Q)	1	−0.41 (−0.68−0.13)	−0.69 (−1.59−0.07)
Protected Areas and Biological			
Corridors (L)	16	0.68 (0.43−0.94)	1.11 (0.03−2.43)
Protected Areas and Biological	16	−0.29 (−0.54;−0.03)	−0.63 (−1.62−0.16)
Corridors (Q)		0.1359 (−0.06−0.33)	−0.10 (−0.53−0.29)
Precipitation (L)	1	0.51 (0.26−0.77)	0.98 (−0.42−2.39)
Precipitation Seasonality (L)	8	−0.35 (−0.57;−0.13)	−1.09 (−2.30;−0.05)
Precipitation Seasonality (Q)	8	−0.33 (−0.57;−0.09)	−0.48 (−1.07−0.002)
River (L)	0.25	−0.08 (−0.33 − 0.16)	−0.16 (−0.67−0.34)
Road (L)	0.25	−0.83 (−1.09;−0.60)	−1.26 (−2.20;−0.59)
Roughness (L)	4	−0.59 (−0.87;−0.30)	−0.98 (−1.98;−0.17)
Agriculture (L)	16	−0.56 (−0.83;−0.30)	−0.91 (−1.68;−0.30)
Topographic Position Index (L)	4	−	19.54 (6.23–52.28)
Spatial variance (σ^2)	–	–	0.052 (0.02–0.09)
Spatial range (ϕ)	–	–	
Detection probability			
Intercept		−2.36 (−3.04;−1.71)	−2.42 (−3.08;−1.78)
Month (L)		−0.003 (−0.21−0.19)	−0.024 (−0.23−0.19)
Month (Q)		−0.14 (−0.37−0.08)	−0.14 (−0.36−0.09)
Log effort (L)		0.66 (0.66–0.87)	0.67 (0.48–0.88)

Table 2

Posterior means with 95% CRIs in parentheses for non-spatial and for spatial occupancy models for leopards. L and Q denote the linear and quadratic terms of a covariate. Estimates with 95% CRIs that do not overlap 0 (and thus are “significant”) are highlighted in boldface.

Parameter and parametric form	Scale (kms)	Non-spatial model	Spatial model (5 NNGP)
Occupancy probability			
Intercept		−0.90 (−1.43;−0.360)	−1.68 (−4.27;−1.30)
Foliage Height Diversity (L)	16	0.54 (0.13–0.99)	1.16 (−0.46–3.09)
Elevation (L)	2	−1.55 (−2.15;−0.98)	−2.82 (−5.27;−0.71)
Global Human Modification (L)	16	−0.08 (−0.38–0.20)	−0.11 (−1.86–1.90)
Gross Primary Productivity (L)	0.5	−0.19 (−0.76–0.35)	0.79 (−1.30–3.37)
Gross Primary Productivity (Q)	0.5	0.36 (0.01–0.70)	0.62 (−0.85–2.07)
Precipitation (L)	16	−0.06 (−0.29–0.16)	−0.43 (−1.53–0.41)
Precipitation Seasonality (L)	2	−1.05 (−1.36;−0.76)	−1.12 (−3.33–1.28)
Precipitation Seasonality (Q)	2	−0.50 (−0.73;−0.27)	−1.0846 (−2.69–0.16)
River (L)	16	−0.090 (−0.51–0.37)	0.39 (−1.60–2.62)
River (Q)	16	0.39 (0.07–0.75)	0.50 (−0.61–1.93)
Road (L)	0.25	−0.89 (−1.87–0.08)	−1.68 (−4.09–0.68)
Road (Q)	0.25	0.21 (0.04–0.49)	0.53 (0.03–1.22)
Roughness (L)	8	0.23 (−0.075–0.57)	0.47 (−1.20–2.16)
Agriculture (L)	8	0.15 (−0.05–0.36)	0.78 (0.002–1.99)
Topographic Position Index (L)	8	−0.02 (−0.27–0.25)	−0.57 (−2.17–0.50)
Spatial variance (σ^2)	–	–	120.12 (14.44–489.03)
Spatial range (ϕ)	–	–	0.083 (0.03–0.16)
Detection probability			
Intercept		−3.78 (−4.47;−3.11)	−3.74 (−4.43;−3.08)
Month (L)		−0.08 (−0.25–0.09)	−0.05 (−0.21 – 0.11)
Month (Q)		−0.11 (−0.30–0.08)	−0.12 (−0.32–0.08)
Log effort (L)		0.98 (0.78–1.19)	0.98 (0.78–1.18)

differed among the species. Tigers showed scale-specific responses to precipitation at 1 km and precipitation seasonality 8 km, while leopards responded at 16 km and 2 km, respectively. For vegetation metrics, tigers responded to Gross Primary Productivity (GPP) at 1 km and leopards to Foliage Height Diversity (FHD) at 16 km.

3.2. Comparisons between inferences by spatial versus non-spatial models

The best spatial model greatly outperformed the corresponding non-spatial model in terms of WAIC for both species (tiger: spatial = 1513.24, non-spatial = 1705.17; leopard: spatial = 2315.29, non-spatial = 2564.22). Posterior predictive Bayesian p-values for the 5–NNGP spatial models were 0.19 for both tigers and leopards, suggesting adequate model fit.

For tigers, the spatial variance was estimated at a much lower value than for leopards (Tables 1 and 2), indicating stronger spatial structure in leopard occurrence that was not explained by the covariates in each model. The estimate of the spatial decay parameter (ϕ) was higher for leopard (0.0826) than for tiger (0.0522). In the exponential correlation

model, $\left(\frac{3}{\phi}\right)$ gives the distance between two sites over which residual spatial correlation drops to 0.05, and thus ‘almost zero’. This distance was estimated at 57.5 km and 36.3 km, for tiger and leopard, respectively (Tables 1 and 2).

3.3. Habitat use inferred from spatial models

Posterior occupancy estimates from the spatial model showed clear differences between the two large carnivores. Tigers had a lower overall occupancy, with a countrywide mean of 0.19 (0.16–0.22), indicating a much more restricted distribution in Bhutan. In contrast, leopards had a higher mean occupancy of 0.41 (0.36–0.46), suggesting broader spatial distribution.

For leopards, the detection probability for a single trap night was estimated at 0.03 (0.01–0.04) and increased to 0.40 (0.35–0.45) when cumulated over 30 trap days. For tigers, the detection probability for a single trap day was higher at 0.08 (0.04–0.14) and increased to 0.46 (0.39–0.53) over 30 trap days (Figs. 2–5).

3.4. Estimated covariate relationships from spatial occupancy models

Of the nine covariates in the spatial tiger model, five had “significant” effects where the 95% CRI did not contain 0 (see Table 1). Occupancy increased with protected area and biological corridor coverage, indicating greater habitat use within the protected area and biological corridor network, with a slight plateau at high coverage. “Significant” negative effects were observed for precipitation seasonality (quadratic), terrain roughness (linear), topographic position index (TPI; linear), and agricultural land (linear), suggesting that tigers prefer gentle terrain and low-lying ridges while avoiding steep slopes and agricultural areas. Occupancy peaked at intermediate precipitation seasonality, with greater uncertainty at the extremes (Fig. 6).

For leopard, three of the 11 covariates were “significant”. Elevation (linear) had a strong negative effect, indicating a preference for lower elevation. Unlike tigers, leopard occupancy was positively associated with agricultural land (linear) and with intermediate road densities (quadratic; Fig. 7).

The two species responded differently to vegetation covariates. Leopards showed a weak association with foliage height diversity (FHD) at the 16 km scale (linear) and a weak U-shaped response to GPP at the 500 m scale, whereas tigers exhibited a unimodal response to GPP at the 1000 m scale (linear; Figs. 6 and 7).

Detection probability increased with survey effort for both species, with a stronger rate of increase per camera trap night for leopards ($\beta = 0.98$) than for tigers ($\beta = 0.67$; Appendix B). Seasonal variation, modelled with linear and quadratic terms of Julian date, was weak and “non-significant”.

3.5. Range sizes computed from spatial occupancy models

For tigers, the spatial model estimated a range size (posterior mean) of 7359 km² (CRI: 6153–8724), whereas the non-spatial model yielded a slightly higher estimate (7641 km²; CRI: 6566–8843). For leopards, the range size estimate was 15,842 km² (14,186–17,778), i.e., approximately 2.1 times larger than that for tigers, whereas the non-spatial model estimated the range size at 16,640 km² (14,975–18,361; Fig. 8). For comparison, spatial models that failed to account for imperfect detection produced considerably smaller range size estimates: 5605 km² (4682–6746) for tigers and 10,897 km² (9900–11,984) for leopards (Fig. 8). Thus, in our case a species distribution model that ignored imperfect detection would have led to an underestimation of the range size of 24% and 31% for the two study species, highlighting the importance of accounting for imperfect detection to avoid biased inference about range size.

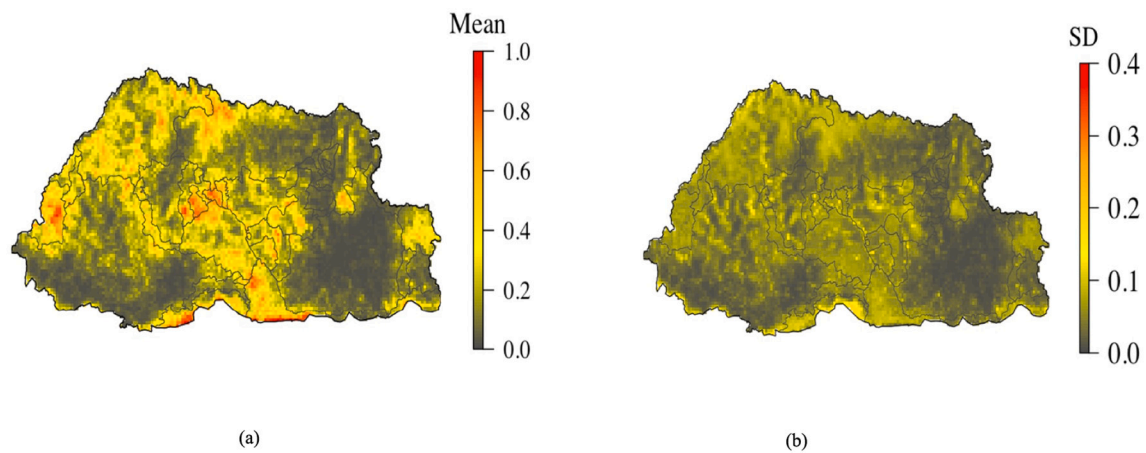


Fig. 2. Predicted occupancy probability for tigers from the non-spatial occupancy model: (a) posterior mean and (b) posterior standard deviation as a measure of uncertainty of the map in (a).

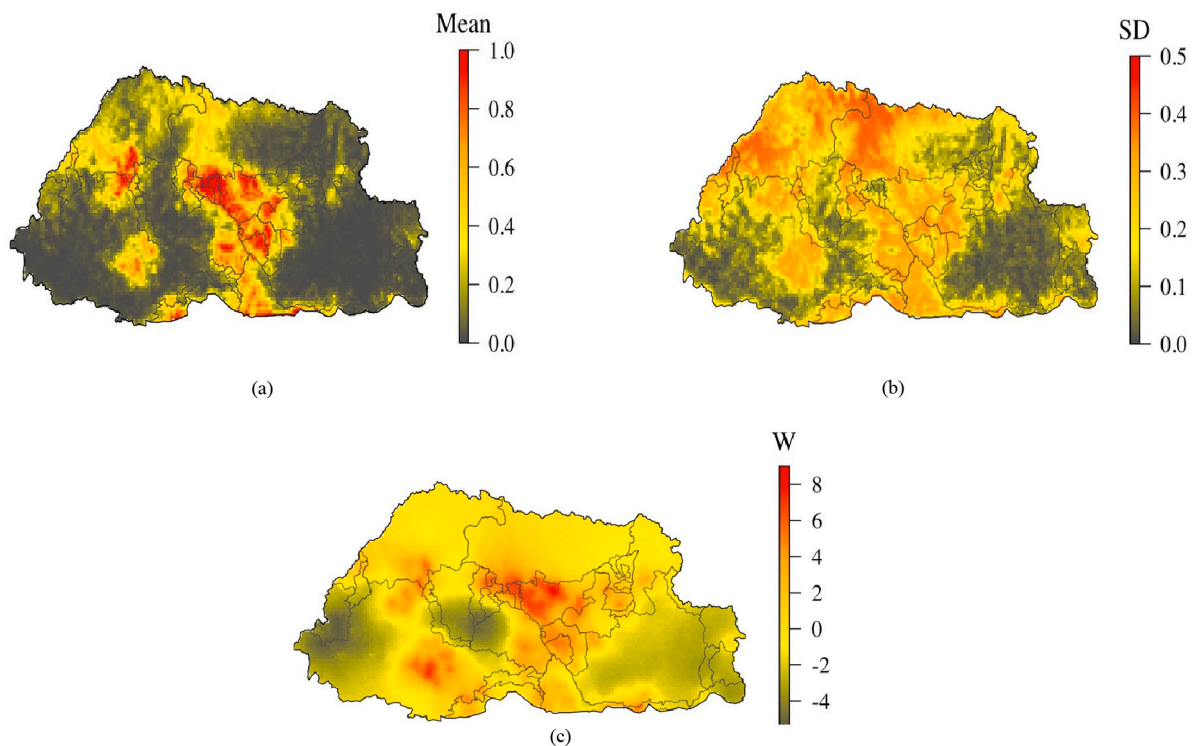


Fig. 3. Predicted occupancy probability for tigers from the spatial occupancy model: (a) posterior mean, (b) posterior standard deviation, and (c) posterior mean of the spatial random effect (w).

3.6. Comparison of occupancy (ψ) inside and outside protected areas

Tigers and leopards showed contrasting associations with PAs and NonPAs, respectively. Tiger occupancy was higher within PAs (0.24, 0.18–0.30) than outside of them (0.16, 0.13–0.19), whereas leopard occupancy was higher outside PAs (0.47, 0.41–0.53) than within (0.33, 0.27–0.40). The mean difference between NonPAs and PAs was 0.14 (0.05–0.22) for leopards and -0.08 (-0.15 to -0.02) for tigers. Thus, leopard occupancy was “significantly” higher in NonPAs and tiger occupancy “significantly” higher in PAs (Fig. 9).

3.7. Realised occupancy (ψ) at the Protected Area (PA) and Non-PA/ Divisional Forest Office (DFO) level

Tiger occupancy varied widely across different management zones,

from 0.63 (0.48–0.78) in Bumthang Forest Division (NonPA) to 0.013 (0.00–0.06) in Samtse Forest Division (NonPA). Among PAs, the highest estimates were in Royal Manas National Park (0.48, 0.31–0.64), Phibsoo Wildlife Sanctuary (0.47, 0.25–0.70), and Jigme Singye Wangchuck National Park (0.32, 0.21–0.44), whereas most NonPAs had values < 0.30 .

Leopard occupancy also varied considerably, ranging from 0.89 (0.77–0.98) in Pemagatshel Forest Division (NonPA) to 0.085 (0.01–0.24) in Jigme Khesar Strict Nature Reserve (PA). Several Non-PAs, including Pemagatshel, Mongar (0.82, 0.72–0.90), and SamdrupJongkhar Forest Divisions (0.79, 0.64–0.92), had higher values of occupancy than many PAs, with the highest PA estimates for leopard recorded in Jomotsangkha Wildlife Sanctuary (0.75, 0.49–0.99), Royal Manas National Park (0.74, 0.61–0.87), and Phibsoo Wildlife Sanctuary (0.66, 0.41–0.87) (Fig. 12 and Appendix C and D for details).

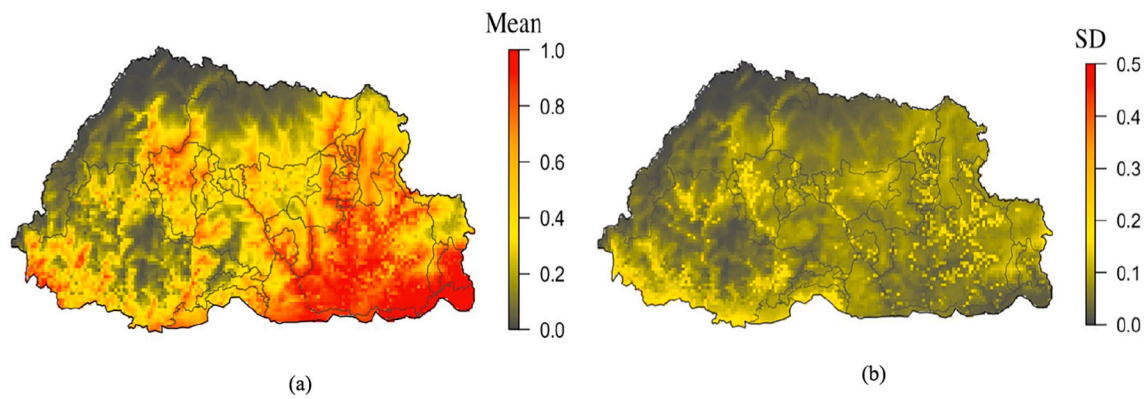


Fig. 4. Predicted occupancy probability for leopards from the non-spatial occupancy model: (a) posterior mean and (b) posterior standard deviation.

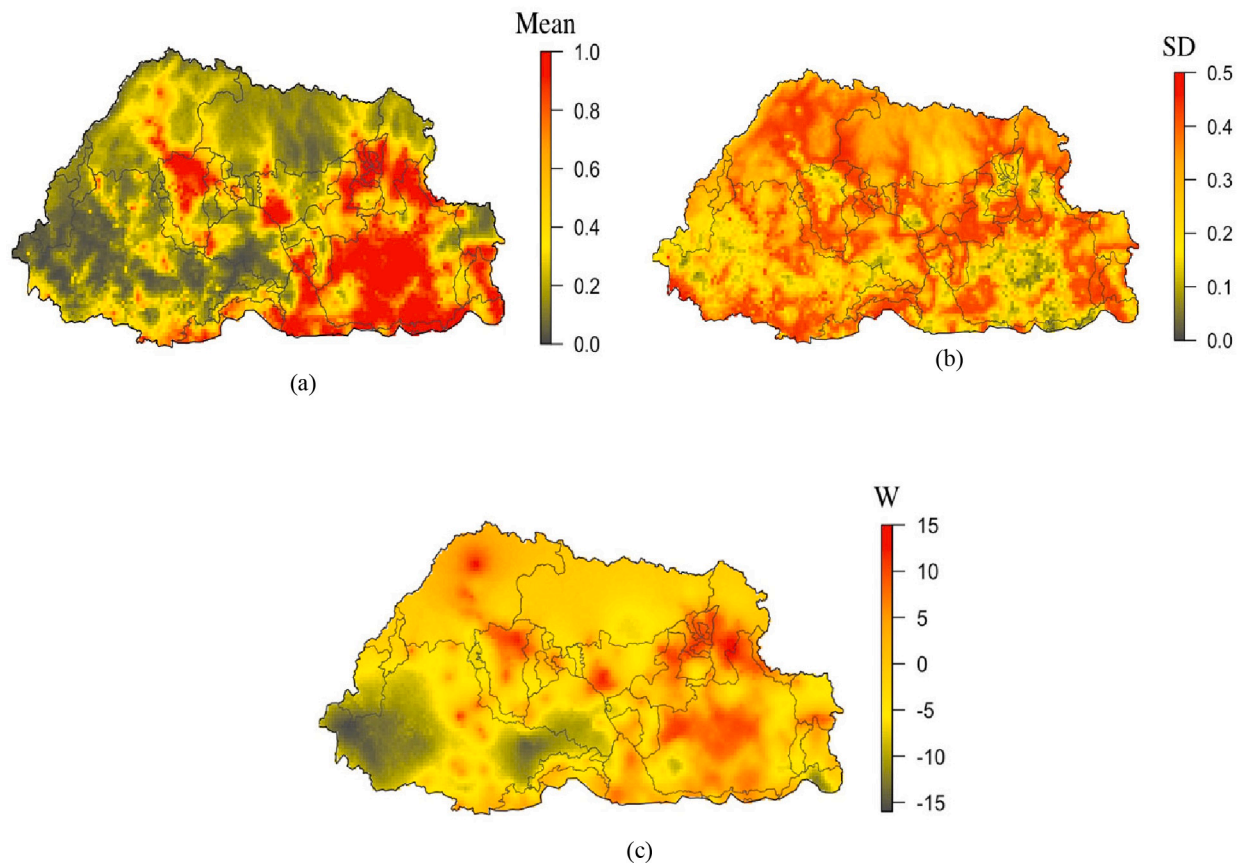


Fig. 5. Predicted occupancy probability for leopards from the spatial occupancy model: (a) posterior mean, (b) posterior standard deviation, and (c) posterior mean of the spatial random effect (w).

3.8. Occupancy overlap between tiger and leopard

The two spatial occupancy models for tiger and leopard predicted leopard-only occupancy (i.e., presence of leopards and absence of tigers) at 46% of Bhutan, more than four times more than the tiger-only occupancy (i.e., presence of tigers and absence of leopards) of 8.5%. Areas predicted to be jointly occupied by both species accounted for 15% of Bhutan, indicating a generally low spatial overlap between tiger and leopard during our study period (Fig. 10). The largest area of Bhutan was for sites where both species were absent, which was estimated to be 18,452 (16,629–20,061) km². Leopard-only sites covered 13,005 (11,585–14,628) km², whereas tiger-only sites were much smaller at 4522 (3601–5611) km². The smallest area, 2837 (2228–3577) km², was

predicted for sites where both species co-occurred, indicating a limited spatial overlap (Fig. 13; Appendix E).

3.9. Conditional occupancy probabilities for the two species

The probability of tiger presence given leopard presence was estimated at 0.179 (0.145, 0.215), compared to 0.197 (0.160, 0.244) when leopards were absent. Conversely, the probability of leopard presence given tiger presence was estimated at 0.386 (0.318, 0.460) and at 0.414 (0.369, 0.463) given tigers were absent. Differences between conditional probabilities showed little evidence of avoidance as both CRIs overlapped zero. Tiger presence was slightly lower when leopards were present than absent ($\Delta T = -0.018$, 95% CRI: -0.059 – 0.021 ; $\Pr(\Delta T <$

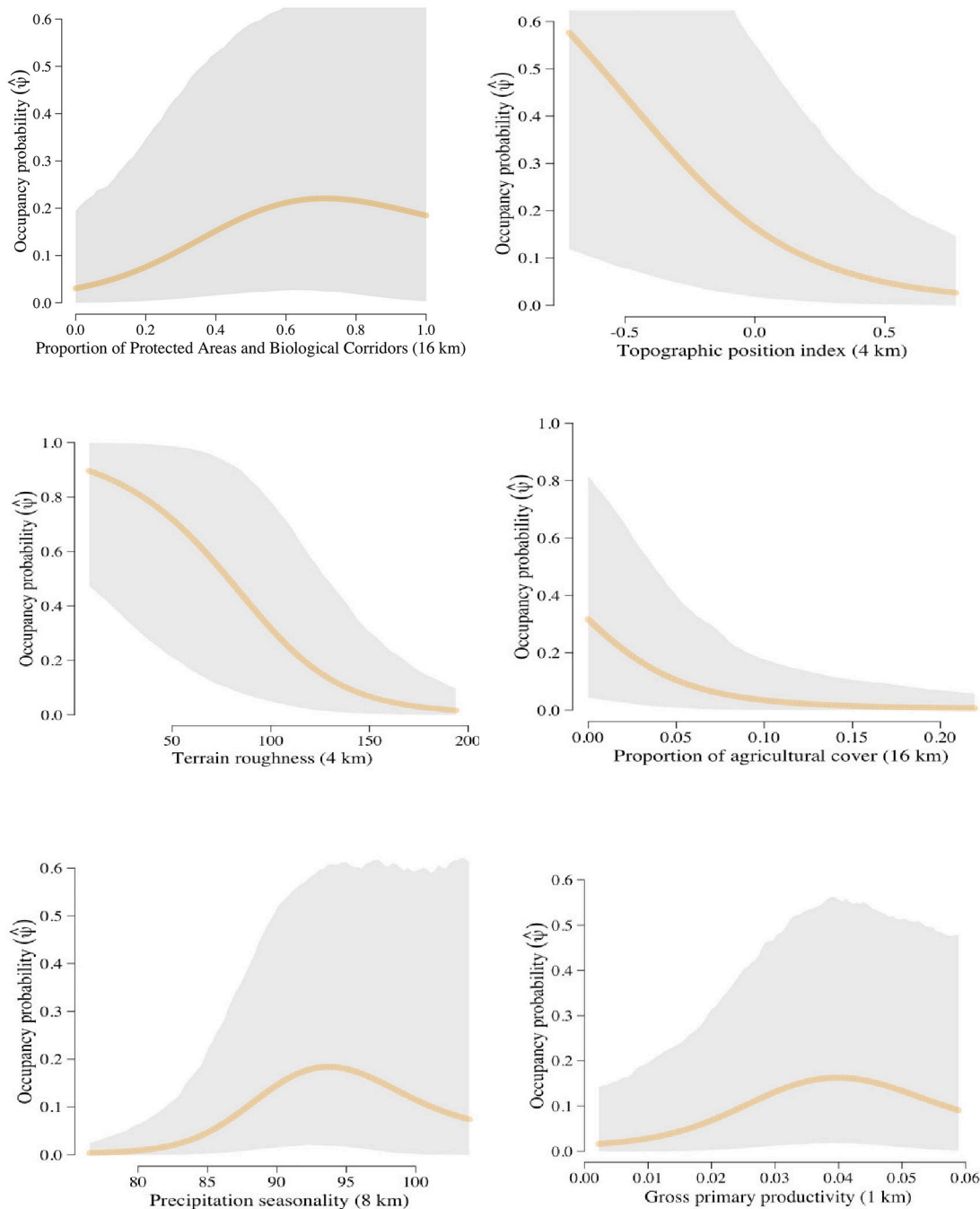


Fig. 6. Predictions of occupancy probability as a function of the covariates in the spatial model for the tiger. The plots illustrate the marginal effects of individual covariates on occupancy probability, holding all other variables constant at their means. Tiger illustration: Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu).

0) = 0.82), and leopard presence was similarly lower when tigers were present ($\Delta L = -0.028$, 95% CRI: -0.089 – 0.035 ; $\Pr(\Delta L < 0) = 0.82$). These patterns indicate no credible displacement, though the posterior distributions suggest a weak tendency toward reduced co-occurrence (Fig. 14; Appendix F).

4. Discussion

We have applied spatial occupancy models with scale-optimised environmental predictors and provided a comparative assessment of habitat use and range size for tigers and leopards in Bhutan. Using

camera trap data from Bhutan's largest biodiversity survey, the second National Tiger Survey (2021–2022), we demonstrated that spatial occupancy models provide better predictive performance than corresponding non-spatial models. Posterior predictions of presence and absence in each grid cell of Bhutan obtained from our model provided a methodology for simultaneously estimating range size, quantifying the overlap in the distribution of the two large carnivores with management zones, and assessing species co-occurrence, offering a valuable approach directly applicable to conservation planning and management.

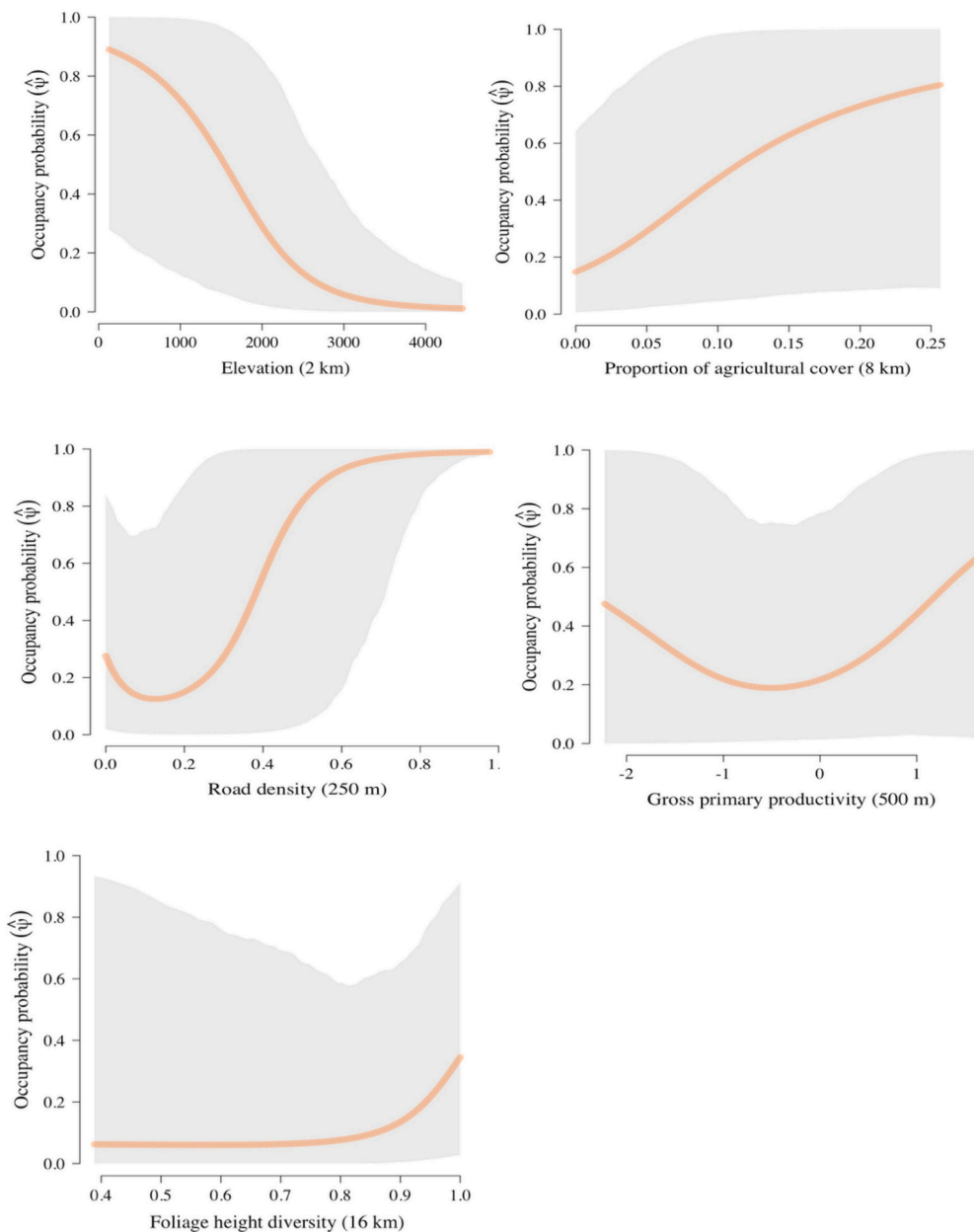


Fig. 7. Predictions of occupancy as a function of the covariates in the spatial model for the leopard. The plots illustrate the effect of individual covariates on occupancy probability, holding other variables constant at their means. Leopard illustration: Pixabay.

4.1. Mean geographical range size and habitat use

Using a spatial occupancy model, we estimated tiger occupancy in Bhutan at 7359 km² (95% CRI: 6153–8724), i.e., about one-fifth of the country. This highlights Bhutan's disproportionate importance for global tiger conservation despite its small geographic size. The mean probability of tiger occupancy (interpreted as habitat use; $\hat{\psi}$) was 0.19. For comparison, [Penjor et al. \(2019\)](#), using a non-spatial occupancy framework with 25 km² grid cells, reported a higher mean posterior probability of habitat use (0.335; SD = 0.291, 95% CRI = 0.157–0.561). However, the two values are not comparable because their grid cells were much larger than the 4 km² cells used in our study. All else being equal, larger grid cells will always lead to higher values of occupancy

([Kéry and Royle, 2016](#): chapter 1). One additional factor that will tend to increase the size of the earlier range estimate by [Penjor et al. \(2019\)](#) was their use of a non-spatial model. Such models have a tendency to lead to larger range size estimates than spatial models, as we also noted in one of the comparisons in our study. Reanalysing the 2nd National Tiger Survey data at a 25 km² resolution, or the 1st National Tiger Survey data at a 4 km² resolution within a spatial framework, would produce estimates that are comparable.

Leopards exhibited more than twice the geographical range size (~15,842 km² vs. ~7359 km²) than tigers, indicating a much wider distribution. The spatial model was again better in terms of prediction success than was the non-spatial model. Compared to spatial models with detection, an occupancy models that omitted spatial

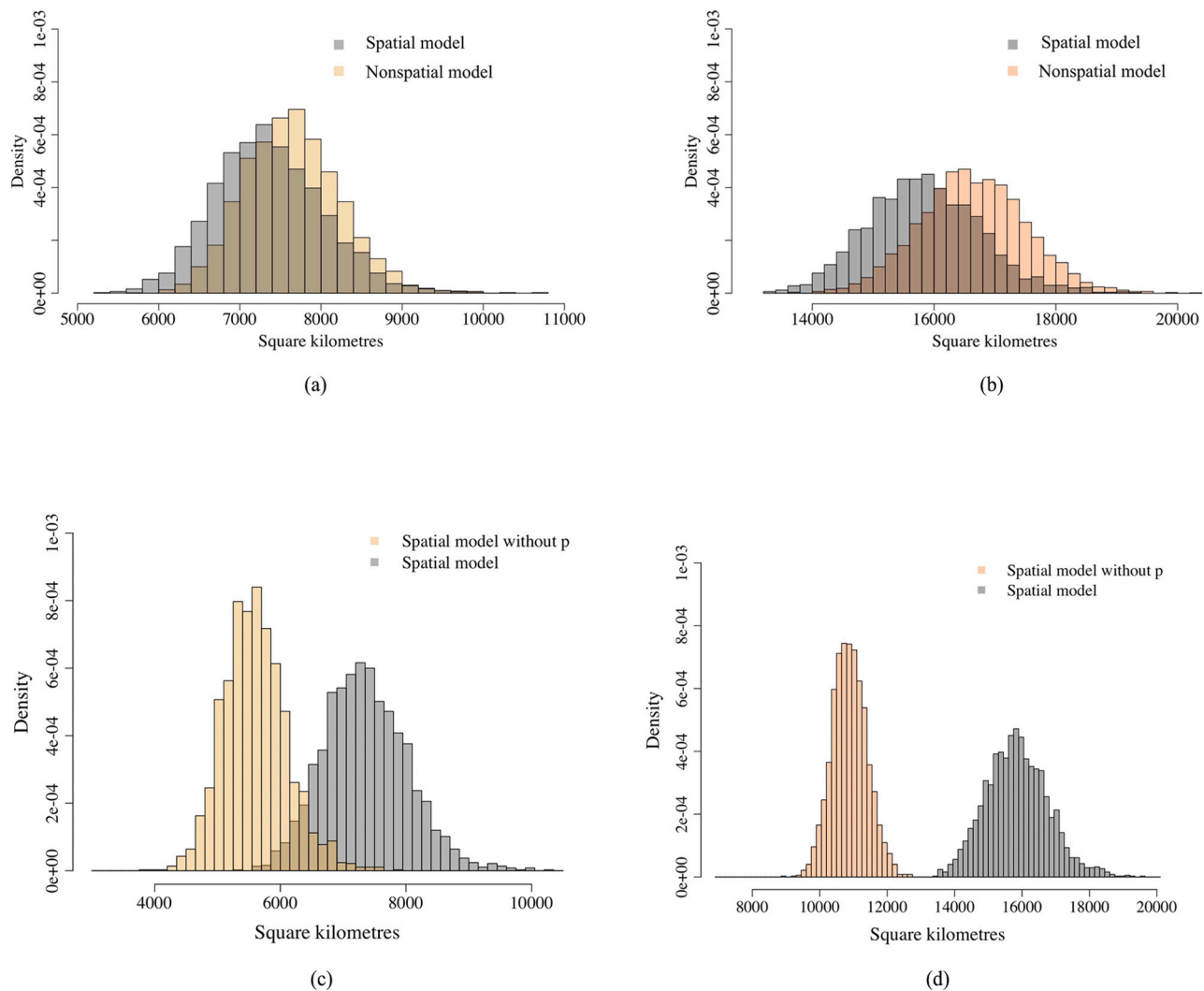


Fig. 8. Posterior distributions of the estimated range size (km^2) in Bhutan for tigers (a), and leopards (b), obtained from spatial and non-spatial occupancy models. Panels (c) and (d) compare the estimated range sizes (km^2) from the spatial model that ignores imperfect detection (without p) and the full spatial occupancy model that accommodates p for tigers and leopards, respectively.

autocorrelation overestimated range size by $\sim 4\%$ for tigers and $\sim 5\%$ for leopards. In addition, incorporating imperfect detection into the range size assessment was vital, since spatial models that omitted detection underestimated ranges by $\sim 24\%$ and $\sim 31\%$, respectively.

This pattern is consistent with findings by Guélat and Kéry (2018), who demonstrated that ignoring spatial autocorrelation can bias species distribution estimates, even with extensive datasets. Notably, spatial models produced more localised patterns of high and low occupancy than non-spatial models, together with wider uncertainty intervals after accounting for residual spatial autocorrelation. This indicates that non-spatial models may smooth over geographically concentrated occupancy patterns and understate uncertainty in spatial predictions.

4.2. Species-specific scale-dependent responses

Our results demonstrated distinct scale-dependent habitat associations, reinforcing the importance of multi-scale analyses in carnivore ecology (McGarigal et al., 2016). Tiger habitat use was primarily driven by protected areas and biological corridor coverage and agricultural extent at broader scales. In contrast, terrain roughness, topographic position index, and seasonal precipitation influenced occupancy at finer scales, consistent with evidence that broad-scale anthropogenic pressures and fine-scale topographic heterogeneity jointly shape large

carnivore distributions (Sunarto et al., 2012; Krishnamurthy et al., 2016; Macdonald et al., 2019; Atzeni et al., 2024). Road and river proximity were retained at a finer scale but was non-significant, indicating limited sensitivity to edge habitats.

Leopards responded to anthropogenic variables across finer spatial scales, including road proximity at 250 m and agricultural extent at 8 km, indicating greater adaptability to human-modified landscapes. In contrast, tiger occupancy was primarily influenced by broader-scale variables such as protected area and biological corridor coverage and agricultural extent at 16 km, indicating a dependence on coarse-scale habitat structure. Such divergence between the two species highlights the need for species-specific conservation strategies that explicitly account for scale-dependent habitat associations (McGarigal et al., 2016).

Furthermore, distinct patterns in spatial variance (σ^2) and spatial decay (ϕ) parameters support divergent scale-dependent habitat use between these carnivores. Both parameter values were substantially higher for leopards than for tigers, indicating stronger fine-scale spatial clustering in leopards and a broader-scale spatial dependence in tigers. For leopards, this residual spatial autocorrelation likely reflects their ecological flexibility and use of fine-scale habitat features, particularly in human-modified landscapes. Consistent with our findings and previous studies, leopards responded positively to agricultural land and to road proximity (Athreya et al., 2016; Poursalem et al., 2021; Loveridge

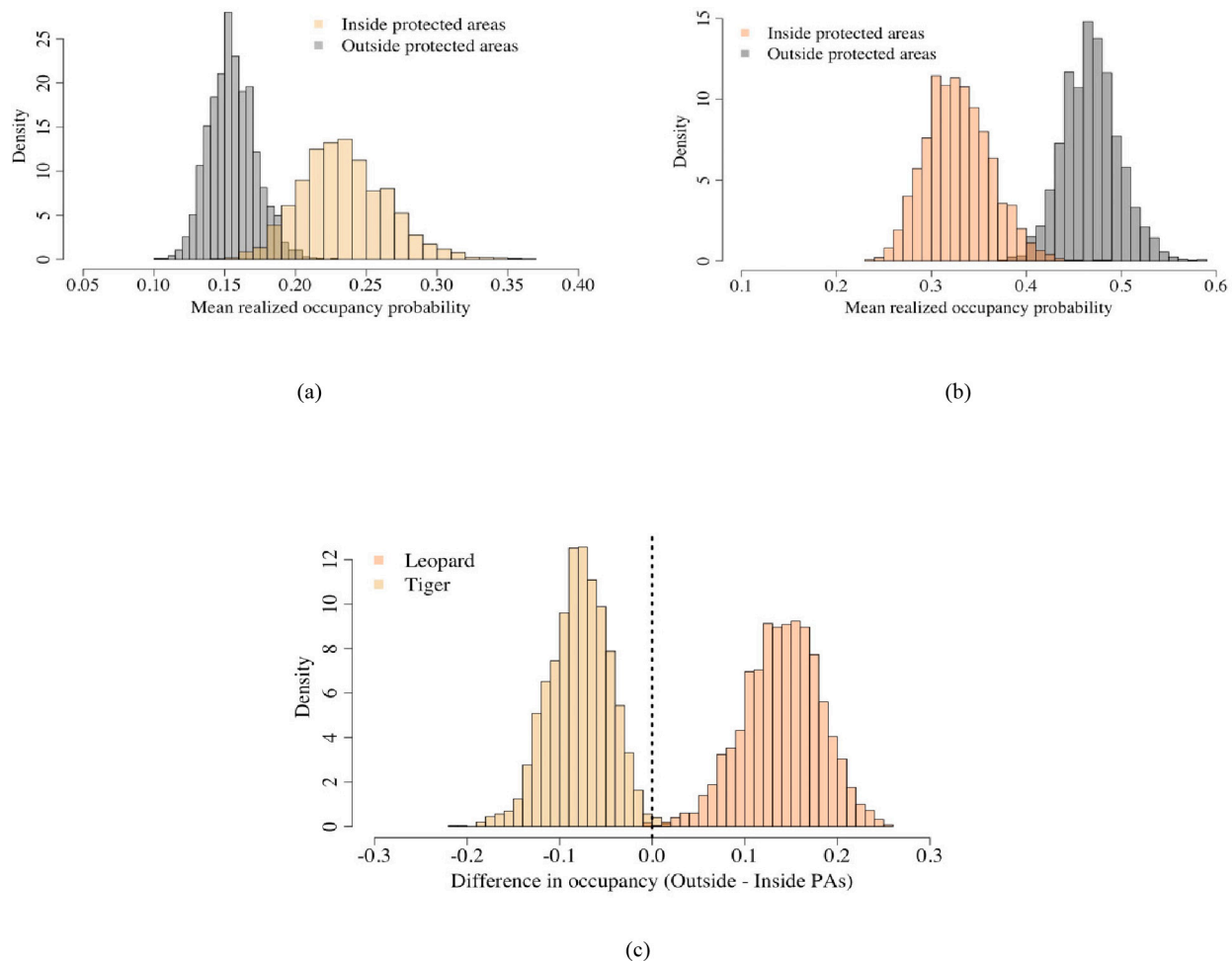


Fig. 9. Posterior distributions of the realised occupancy probabilities for tigers (a) and leopards (b) inside and outside protected areas (PAs). Panel (c) shows the posterior distributions of the differences in realised occupancy probabilities between areas outside and inside PAs for both species.

et al., 2022; Poudel et al., 2023). These anthropogenic features are often spatially clustered at fine scales, driving localised occupancy patterns that are not fully captured by broader environmental covariates. This highlights the importance of spatially explicit models in accounting for residual spatial structures that non-spatial models may overlook (Dormann et al., 2007; Guélat and Kéry, 2018). Tigers exhibited broader-scale spatial dependence, which aligns with their reliance on extensive protected habitats (at the 16 km scale) and larger home-range requirements (Sunquist and Sunquist, 2002; Hunter, 2015; Karanth and Nichols, 2017).

4.3. Large carnivore occupancy and co-occurrence across management zones

Our findings revealed differences in habitat use between tigers and leopards across Bhutan's management zones. Tiger habitat use was significantly higher in Protected Areas (PAs), whereas leopard habitat use was notably higher in non-protected areas (NonPAs). Although some NonPAs, such as Bumthang, Zhemgang, Thimphu, and Dagana Forest Divisions, supported relatively higher tiger occupancy, the highest values of occupancy probability occurred within the central and south-central PAs. These results reinforce the importance of formally protected landscapes as demographic strongholds for tigers. Given their wide-ranging behaviour and vulnerability to human pressures, tigers will continue to depend on the ecological integrity and management effectiveness of Bhutan's PA network for their survival. This aligns with strong evidence highlighting the irreplaceable role of PAs in maintaining

the source populations of tigers and their prey (Balme et al., 2010; Wikramanayake et al., 2011; Jhala et al., 2025).

The positive contribution of the protected area and biological corridor network was further supported by a strong linear relationship between tiger occupancy and protected area and biological corridor coverage within a 16-km landscape window (Fig. 6). However, this effect was constrained by significant negative associations with terrain roughness and the Topographic Position Index (TPI), suggesting that some high-coverage protected area and biological corridor landscapes, which are often steep and rugged, may offer lower suitability (Fig. 6). Tiger occupancy was also high in several DFOs outside the protected area network, highlighting the complementary importance of NonPA habitats (Fig. 12).

Contrary to our hypothesis, forest structure variables such as foliage height diversity, shrub density, canopy height, and cover were not significant predictors of tiger occupancy, likely due to overlap with protected area and biological corridor coverage, which reflects intact, low-disturbance habitat (Tshewang et al., 2021). Gross primary productivity (GPP), a proxy for vegetation productivity, was retained but was not significant, possibly reflecting moderate productivity in intact forests limited by elevation and climate (Malhi et al., 2017). Its weak unimodal relationship with tiger's habitat use is consistent with broader evidence that carnivore communities peak at intermediate productivity levels (Sultaire et al., 2025).

One notable finding was that tiger occupancy was low in the southwest, northeast, and southeast of Bhutan, whereas leopard occupancy was relatively high in these regions largely outside protected

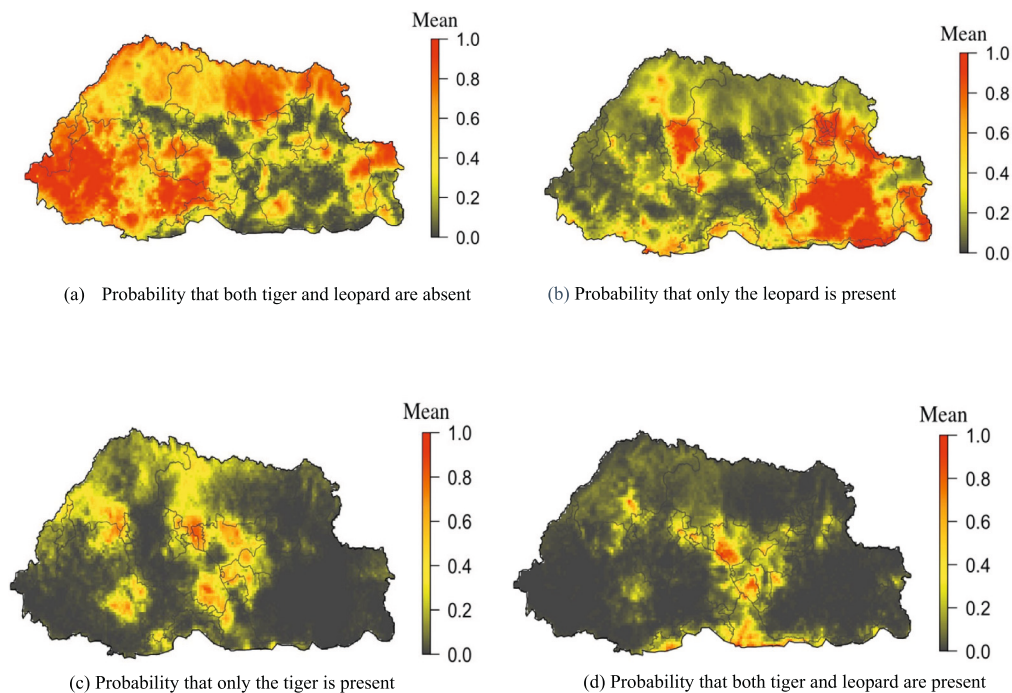


Fig. 10. Co-occurrence probabilities of tigers and leopards in Bhutan, obtained from spatial occupancy models. Maps show: (a) probability that both species are absent, (b) probability that only leopards are present, and tigers are absent, (c) probability that only tigers are present, and leopards are absent, and (d) probability that both species are present.

areas. Leopards also exhibited significantly higher occupancy in non-protected areas compared to tigers, consistent with our hypothesised limited spatial overlap between the two species, with leopards using edge habitats and human-modified landscapes more extensively than tigers (Fig. 9). This is further supported by the positive influence of road density and agricultural land on leopard occupancy, highlighting their ecological flexibility and tolerance to human presence (Fig. 7). Similar patterns have been reported across Asia, where leopards persist in buffer zones, agroforestry systems, and forest edges (Ngoprasert et al., 2007; Athreya et al., 2020; Moradi et al., 2024). Together, these findings challenge the assumption that protected areas alone are sufficient to conserve wide-ranging carnivores, highlighting the importance of habitats outside the formal protected area network where effective human–carnivore conflict prevention measures support coexistence under species- and landscape-specific conditions (Woodroffe & Ginsberg, 1998; Jones et al., 2024).

From a conservation perspective, the leopard's adaptability to disturbance and tolerance of human presence is a double-edged sword. These traits support their persistence outside protected areas but also heighten conflict risks in Bhutan, where leopards more frequently occupy human-dominated landscapes than tigers. Such risks include increased livestock depredation, road mortality, and retaliatory persecution (Athreya et al., 2020; Baral et al., 2024; Harihar et al., 2011). With 90% of Bhutan's rural population reliant on agro-pastoral livelihoods, livestock depredation represents both a conservation and economic challenge (Wang and Macdonald, 2006). Reports collected from 2010 to 2023 (DoFPS, unpublished data) confirm rising human–large carnivore conflict, particularly in central and eastern Bhutan. Our findings emphasise the need for integrated approaches that address both sympatric carnivore management and conflict mitigation, tailored to the ecological and socio-economic contexts of each species. Conservation strategies must also account for species interactions and community-level dynamics, ensuring that efforts do not focus solely on a single apex predator (Caro, 2010; Ripple et al., 2014; Thanet et al., 2025).

At the landscape scale, our findings point to habitat partitioning between the two species, with tigers strongly associated with protected

areas and leopards more common in non-protected areas (Fig. 10 and 13). The limited spatial overlap (~15% of Bhutan) points to broad-scale segregation in habitat use. Interestingly, however, this pattern did not translate into strong evidence of direct avoidance at finer spatial scales. At the site scale, co-occurrence analyses based on conditional probabilities, suggested that, where the two species do overlap, the presence of one does not measurably suppress occupancy of the other. In other words, tigers and leopards occupy largely distinct areas across Bhutan, but where their ranges intersect, they are able to coexist without measurable suppression of one by the other. This pattern may reflect intraguild competition, whereby tigers dominate core habitats and resources while leopards are displaced to marginal areas (Odden et al., 2010; Harihar et al., 2011; Pokheral and Wegge, 2019). Alternatively, bottom-up influences of prey availability may be the primary driver, with both species maximising resource acquisition in prey-rich environments, as reported by recent studies in Bhutan and India's Manas Tiger Reserve (Lahkar et al., 2021; Penjor et al., 2022a).

Although interspecific interactions were not our primary focus and were not represented by any parameters in the separate models fitted to the two species, we leveraged posterior samples of the presence/absence indicators, (z), from independently fitted spatial occupancy models to explore tiger–leopard co-occurrence. This highlights the strength of the Bayesian framework, which enables both descriptive and empirical inferences about spatial overlap even without a joint species distribution model. Our findings provide preliminary insights into co-occurrence that could be further explored with hierarchical multispecies occupancy models or joint species distribution (Dorazio and Royle, 2005; Rota et al., 2016; Kéry and Royle, 2021), particularly within a spatial framework (Doser et al., 2022b).

One typical limitation of our study is that we did not include direct prey availability as a covariate. Prey data were available only as unevenly distributed point-level camera-trap observations and could not be incorporated into our multi-scale raster-based covariate framework without generating a spatially explicit prey surface, which would have introduced additional assumptions and uncertainty. Some covariates may partly reflect prey-related habitat conditions, but they are not

substitutes for direct prey data (Karanth et al., 2004b; Harihar and Pandav, 2012).

5. Conservation implications

Our study revealed scale-dependent differences in how two sympatric large carnivores, tigers and leopards, respond to environmental and anthropogenic drivers, reflecting differences in ecological requirements and adaptability. In a landscape such as Bhutan's, which retains extensive natural habitat and a strong network of protected areas and biological corridors, an important question remains: should conservation prioritise land-sparing, by protecting intact habitats from conversion, or land-sharing, by fostering coexistence in multifunctional landscapes?

Our findings suggest that both approaches are needed, but in species-specific ways. For tigers, long-term persistence will depend on maintaining the ecological integrity of Bhutan's protected area and biological corridor network while also securing core habitats and connectivity in non-protected landscapes, particularly under current and planned development. Ecologically based planning tools are nowadays available to evaluate compromises between species conservation and development (Jantz et al., 2025). We therefore recommend strong protection of core tiger habitats, complemented by targeted coexistence strategies in human-modified areas where governance, socio-economic incentives, and cultural tolerance can support persistence (Dickman et al., 2013; Treves and Bruskotter, 2014; Jhala et al., 2025). We also recommend systematic inclusion of leopard monitoring and habitat-use assessments within Bhutan's current tiger monitoring mandate.

For leopards, whose adaptability supports their occurrence in human-modified landscapes as reflected in their high occupancy in non-protected areas, coexistence frameworks must be central. However, this adaptability also signals an increased risk of human–carnivore conflict in the future. Given the distinct ecological niches and responses of tigers and leopards, coexistence and mitigation frameworks must be explicitly tailored to each species.

Our findings provide clear policy guidance: invest in improving the quality and connectivity of core habitats while simultaneously developing innovative coexistence mechanisms outside PAs and multi-use landscapes that integrate the ecological requirements of large carnivores with the priorities of local communities through participatory, culturally appropriate, and locally driven solutions. Bhutan's conservation legacy has established its status as a stronghold for global tiger recovery. Maintaining these gains will require addressing complex trade-offs between biodiversity conservation and economic development through a holistic, transdisciplinary approach that integrates science, policy, and practical interventions, including innovative conservation finance mechanisms (Macdonald, 2019).

CRedit authorship contribution statement

Singye Wangmo: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marc Kéry:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **David W. Macdonald:** Writing – review & editing, Supervision. **Abishek Harihar:** Writing – review & editing. **Caroline C. Sartor:** Writing – review & editing, Supervision. **Samuel A. Cushman:** Writing – review & editing. **Patrick Burns:** Writing – review & editing. **Andrew J. Loveridge:** Writing – review & editing, Supervision. **Amy Dickman:** Writing – review & editing, Supervision.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author (s) used *Grammarly* in

order to check grammar, spelling, and language editing. The author (s) reviewed and edited the content as needed and take(s) full responsibility for the content of the published article.

Funding

No direct funding was received for this research. The camera trap data used in this study were collected by the Department of Forests and Park Services, Royal Government of Bhutan, as a part of the second NTS.

Declaration of competing interest

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

Acknowledgements

We thank the current and former Directors of the Department of Forests and Park Service (DoFPS), Mr. Karma Tenzin and Mr. Lobzang Dorji, for their support and for granting permission to use the camera trap data from the second cycle of the National Tiger Survey (NTS). We are deeply grateful to the foresters of the DoFPS from 24 field offices for their commitment and dedication to data collection during the COVID-19 pandemic. We acknowledge Bhutan for Life, UNEP's Vanishing Treasures Programme, WWF Bhutan, the Bhutan Trust Fund for Environmental Conservation, and the Bhutan Foundation for providing generous financial support to the DoFPS in implementing the NTS.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2026.112050>.

Data availability

The authors do not have permission to share data.

References

- Ash, E., Cushman, S.A., Redford, T., Macdonald, D.W., Kaszta, Z., 2022. Tigers on the edge: mortality and landscape change dominate individual-based spatially-explicit simulations of a small tiger population. *Landsc. Ecol.* 37, 3079–3102.
- Athreya, V., Isvaran, K., Odden, M., Linnell, J.D., Kshetry, A., Krishnaswamy, J., Karanth, U.K., 2020. The impact of leopards (*Panthera pardus*) on livestock losses and human injuries in a human-use landscape in Maharashtra, India. *PeerJ* 8, e8405.
- Athreya, V., Odden, M., Linnell, J.D.C., Krishnaswamy, J., Karanth, K.U., 2016. A cat among the dogs: leopard *Panthera pardus* diet in a human-dominated landscape in western Maharashtra, India. *Oryx* 50, 156–162.
- Atzeni, L., Ilany, A., Geffen, E., Cushman, S.A., Kaszta, Z., Macdonald, D.W., 2024. Reviving the Arabian leopard: harnessing historical data to map habitat and pave the way for reintroduction. *Biol. Conserv.* 291, 110440.
- Balme, G.A., Slotow, R., Hunter, L.T.B., 2010. Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze Complex, South Africa. *Anim. Conserv.* 13, 315–323.
- Baral, K., Bhandari, S., Adhikari, B., Kunwar, R.M., Sharma, H.P., Aryal, A., Ji, W., 2024. Prey selection by leopards (*Panthera pardus fusca*) in the mid-hill region of Nepal. *Ecol. Evol.* 14 (2), e10924.
- Blaum, N., Tietjen, B., Rossmanith, E., 2009. Impact of livestock husbandry on small and medium-sized carnivores in Kalahari savannah rangelands. *J. Wildl. Manag.* 73, 60–67.
- Brooks, S.P., Gelman, A., 1998. General methods for monitoring convergence of iterative simulations. *J. Comput. Graph. Stat.* 7, 434–455.
- Caro, T., 2003. Umbrella species: critique and lessons from East Africa. In: *Animal Conservation Forum*. Cambridge University Press, pp. 171–181.
- Caro, T., 2010. *Conservation by Proxy: indicator, Umbrella, Keystone, Flagship, and Other Surrogate Species*. Island Press.
- Ceballos, G., Ehrlich, P.R., Soberón, J., Salazar, I., Fay, J.P., 2005. Global mammal conservation: what must we manage? *Science* 309, 603–607.
- Chatterjee, A.B., Sankar, K., Jhala, Y.V., Qureshi, Q., 2023. Spatio-temporal patterns of co-occurrence of tigers and leopards within a protected area in central India. *Web Ecol.* 23, 17–34.

- Dalerum, F., Somers, M.J., Kunkel, K.E., Cameron, E.Z., 2008. The potential for large carnivores to act as biodiversity surrogates in southern Africa. *Biodivers. Conserv.* 17, 2939–2949.
- Dickman, A., Marchini, S., Manfredo, M., 2013. The human dimension in addressing conflict with large carnivores. In: *Key Topics in Conservation Biology* 2, pp. 110–126.
- DOFPS, 2011. Forestry development in Bhutan: Policies, Programmes and institutions. In: *Forest Resources Management Division, Department of Forests and Parks Services. Ministry of Agriculture and Forests, Thimphu, Bhutan.*
- DoFPS, 2023. Status of Tigers in Bhutan: The National Tiger Survey Report 2021–2022. Bhutan Tiger Center, Department of Forests and Park Services, Ministry of Energy and Natural Resources, Royal Government of Bhutan, Thimphu, Bhutan.
- Dorazio, R.M., Royle, J.A., 2005. Estimating size and composition of biological communities by modeling the occurrence of species. *J. Am. Stat. Assoc.* 100, 389–398.
- Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 609–628.
- Doser, J.W., Finley, A.O., Kéry, M., Zipkin, E.F., 2022. spOccupancy: an R package for single-species, multi-species, and integrated spatial occupancy models. *Methods Ecol. Evol.* 13, 1670–1678.
- Dubayah, R., Blair, J.B., Goetz, S., Fatoyinbo, L., Hansen, M., Healey, S., Hofton, M., Hurtt, G., Kellner, J., Luthcke, S., 2020. The global ecosystem dynamics investigation: high-resolution laser ranging of the Earth's forests and topography. *Sci. Remote. Sens.* 1, 100002.
- Forest Monitoring, Information, Division, 2023. National forest inventory. In: *State of Forest Carbon Report, vol. Volume II. Department of Forests and Park Services, Thimphu, Bhutan (ISBN 978-99980-791-1-3).*
- Freeman, M.F., Tukey, J.W., 1950. Transformations related to the angular and the square root. *Ann. Math. Stat.* 607–611.
- Gompper, M.E., Lesmeister, D.B., Ray, J.C., Malcolm, J.R., Kays, R., 2016. Differential habitat use or intraguild interactions: what structures a carnivore community? *PLoS One* 11, e0146055.
- Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Kerley, L.L., Quigley, H.B., Hornocker, M. G., 2010. Spatial structure of Amur (Siberian) tigers (*Panthera tigris altaica*) on Sikhote-Alin Biosphere Zapovednik, Russia. *J. Mammal.* 91, 737–748.
- Goodrich, J., Wibisono, H., Miquelle, D., Lynam, A., Sanderson, E., Chapman, S., Gray, T., Chanchani, P., Harihar, A., 2022. *Panthera tigris*. The IUCN Red List of Threatened Species 2022: E. T15955A214862019.
- Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google Earth Engine: planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.* 202, 18–27.
- Gould, M.J., Gould, W.R., Cain III, J.W., Roemer, G.W., 2019. Validating the performance of occupancy models for estimating habitat use and predicting the distribution of highly-mobile species: a case study using the American black bear. *Biol. Conserv.* 234, 28–36.
- Gubbi, S., Sharma, K., Kumara, V., 2020. Every hill has its leopard: patterns of space use by leopards (*Panthera pardus*) in a mixed use landscape in India. *PeerJ (San Francisco, CA)* 8, e10072-e10072.
- Guélat, J., Kéry, M., 2018. Effects of spatial autocorrelation and imperfect detection on species distribution models. *Methods Ecol. Evol.* 9, 1614–1625.
- Harihar, A., Pandav, B., 2012. Influence of connectivity, wild prey and disturbance on occupancy of tigers in the human-dominated western Terai Arc Landscape. *PLoS One* 7, e40105.
- Harihar, A., Pandav, B., Goyal, S.P., 2011. Responses of leopard *Panthera pardus* to the recovery of a tiger *Panthera tigris* population. *J. Appl. Ecol.* 48, 806–814.
- Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., Kerley, G.I.H., 2006. Prey preferences of the leopard (*Panthera pardus*). *J. Zool.* 270, 298–313.
- Hunter, L., 2015. *Wild Cats of the World*. Bloomsbury Publishing.
- Jacobson, A.P., Gerngross, P., Lemeris, J.J.R., Schoonover, R.F., Anco, C., Breitenmoser-Würsten, C., Durant, S.M., Farhadina, M.S., Henschel, P., Kamler, J.F., Laguardia, A., Rostro-García, S., Stein, A.B., Dollar, L., 2016. Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. *PeerJ (San Francisco, CA)* 4, e1974.
- Jantz, P., Macdonald, D.W., Gonzalez, I., Hearn, A.J., Kaszta, Z., Landguth, E.L., Burnham, D., Goetz, S.J., Zeller, K.A., Loveridge, A.J., 2025. Connecting landscapes: a decision support system to facilitate conservation led development. *Environ. Model. Softw.* 192, 106576.
- Jhala, Y.V., Mungi, N.A., Gopal, R., Qureshi, Q., 2025. Tiger recovery amid people and poverty. *Science* 387, 505–510. %@ 0036-8075.
- Johnson, D.S., Conn, P.B., Hooten, M.B., Ray, J.C., Pond, B.A., 2013. Spatial occupancy models for large data sets. *Ecology* 94, 801–808.
- Jones, E.M., Koch, A.J., Pay, J.M., Mann, D.F., Jones, M.E., Hamede, R.K., 2024. Movements and habitat selection of a marsupial carnivore in a modified landscape. *Conservation Science and Practice* 6 (3), e13098.
- Kafley, H., Lamichhane, B.R., Maharjan, R., Khadka, M., Bhattarai, N., Gompper, M.E., 2019. Tiger and leopard co-occurrence: intraguild interactions in response to human and livestock disturbance. *Basic Appl. Ecol.* 40, 78–89.
- Karanth, K.U., Nichols, 2002. *Monitoring Tigers and their Prey: A Manual for Researchers, Managers, and Conservationists in Tropical Asia*. Centre for Wildlife Studies.
- Karanth, K.U., Nichols, J.D., 2017. *Methods for Monitoring Tiger and Prey Populations*. Springer, Singapore.
- Karanth, K.U., Chundawat, R.S., Nichols, J.D., Kumar, N.S., 2004a. Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture–recapture sampling. *Anim. Conserv.* 7, 285–290.
- Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A., Hines, J.E., 2004b. Tigers and their prey: predicting carnivore densities from prey abundance. *Proc. Natl. Acad. Sci. U. S. A.* 101, 4854–4858.
- Karanth, K.U., Gopalaswamy, A.M., Kumar, N.S., Vaidyanathan, S., Nichols, J.D., MacKenzie, D.I., 2011. Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. *J. Appl. Ecol.* 48, 1048–1056.
- Karger, D.N., Lange, S., Hari, C., Reyer, C.P., Conrad, O., Zimmermann, N.E., Frieler, K., 2023. CHELSA-W5E5: daily 1 km meteorological forcing data for climate impact studies. *Earth Syst. Sci. Data* 15, 2445–2464.
- Kaszta, Z., Cushman, S.A., Hearn, A., Sloan, S., Laurance, W.F., Haidir, I.A., Macdonald, D.W., 2024. Projected development in Borneo and Sumatra will greatly reduce connectivity for an apex carnivore. *Sci. Total Environ.* 918, 170256.
- Keck, F., Peller, T., Alther, R., Barouillet, C., Blackman, R., Capo, E., Chonova, T., Couton, M., Fehlinger, L., Kirschner, D., 2025. The global human impact on biodiversity. *Nature* 1–6.
- Kennedy, C.M., Oakleaf, J.R., Theobald, D.M., Baruch-Mordo, S., Kiesecker, J., 2019. Managing the middle: a shift in conservation priorities based on the global human modification gradient. *Glob. Chang. Biol.* 25, 811–826.
- Kéry, M., Royle, J.A., 2016. *Applied Hierarchical Modeling in Ecology: Analysis of Distribution. Abundance and Species Richness in R and BUGS* 1.
- Kéry, M., Royle, J.A., 2021. *Applied Hierarchical Modeling in Ecology: Analysis of Distribution. Abundance and Species Richness in R and BUGS: Volume 2: Dynamic and Advanced Models*. Academic Press.
- Krishnamurthy, R., Cushman, S.A., Sarkar, M.S., Malviya, M., Naveen, M., Johnson, J.A., Sen, S., 2016. Multi-scale prediction of landscape resistance for tiger dispersal in central India. *Landscape Ecol.* 31, 1355–1368.
- Lahkar, D., Ahmed, M.F., Begum, R.H., Das, S.K., Harihar, A., 2021. Inferring patterns of sympatry among large carnivores in Manas National Park—a prey-rich habitat influenced by anthropogenic disturbances. *Anim. Conserv.* 24 (4), 589–601.
- Levi, T., Wilmsers, C.C., 2012. Wolves–coyotes–foxes: a cascade among carnivores. *Ecology* 93, 921–929.
- Loveridge, A.J., Sousa, L.L., Seymour-Smith, J.L., Mandisodza-Chikerema, R., Macdonald, D.W., 2022. Environmental and anthropogenic drivers of African leopard *Panthera pardus* population density. *Biol. Conserv.* 272, 109641.
- Macdonald, D.W., 2019. Mammal conservation: old problems, new perspectives, transdisciplinarity, and the coming of age of conservation geopolitics. *Annu. Rev. Environ. Resour.* 44, 61–88.
- Macdonald, D.W., Bothwell, H.M., Kaszta, Z., Ash, E., Bolongon, G., Burnham, D., Can, Ö. E., Campos-Arceiz, A., Channa, P., Clements, G.R., Hearn, A.J., Hedges, L., Htun, S., Kamler, J.F., Kawanishi, K., Macdonald, E.A., Mohamad, S.W., Moore, J., Naing, H., Onuma, M., Penjor, U., Rasphone, A., Mark Rayan, D., Ross, J., Singh, P., Tan, C.K. W., Wadey, J., Yadav, B.P., Cushman, S.A., 2019. Multi-scale habitat modelling identifies spatial conservation priorities for mainland clouded leopards (*Neofelis nebulosa*). In: *Multi-scale Habitat Modelling Identifies Spatial Conservation Priorities for Mainland Clouded Leopards (Neofelis nebulosa)*. John Wiley & Sons Ltd.
- Macdonald, E., Hinks, A., Weiss, D., Dickman, A., Burnham, D., Sandom, C., Malhi, Y., Macdonald, D., 2017. Identifying ambassador species for conservation marketing. *Glob. Ecol. Conserv.* 12, 204–214.
- 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.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L., Hines, J.E., 2017. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Elsevier.
- Malhi, Y., Girardin, C.A., Goldsmith, G.R., Doughty, C.E., Salinas, N., Metcalfe, D.B., Huaraca Huasco, W., Silva-Espejo, J.E., del Aguila-Pasquell, J., Farfán Amézquita, F., 2017. The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective. *New Phytol.* 214, 1019–1032.
- McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C., Cushman, S.A., 2016. Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecol.* 31, 1161–1175. %@ 0921-2973.
- Milda, D., Ashish, K., Ramesh, T., Kalle, R., Thanikodi, M., 2023. Evaluation of anthropogenic pressure on the occupancy patterns of large mammals in the Western and Eastern Ghats. *Landscape Ecol.* 38, 409–422.
- Miller, J.R.B., Pitman, R.T., Mann, G.K.H., Fuller, A.K., Balme, G.A., 2018. Lions and leopards coexist without spatial, temporal or demographic effects of interspecific competition. *J. Anim. Ecol.* 87, 1709–1726.
- Moradi, A., Ahmadi, A., Toranjzar, H., Shams-Esfandabad, B., 2024. Survey of attitudes of human local communities of conservation areas of Kohgiluyeh and Boyer-Ahmad Province toward Persian leopard (*Panthera pardus saxicolor*). *Rangel. Ecol. Manage.* 93, 24–32.
- Naimi, B., 2023. usdm: Uncertainty Analysis for Species Distribution Models (Version 2.1-7)[Computer Software].
- NASA JPL, 2013. *NASA Shuttle Radar Topography Mission Global 1 Arc Second [Dataset]*. NASA Land Processes Distributed Active Archive Center. <https://doi.org/10.5067/MEASURES/SRTM/SRTMGL1.003> (Date Accessed: 2026-08-07).
- National Statistics Bureau, 2025. Socio-economic Indicators (SEI) Bhutan: First Quarterly Issue, January–March 2025. Royal Government of Bhutan, Thimphu.
- Nature Conservation Division, 2020. Protected Area Zonation Guidelines of Bhutan. Department of Forest and Park Services, Ministry of Energy and Natural Resources, Royal Government of Bhutan, Thimphu, Bhutan.

- Ngoprasert, D., Lynam, A.J., Gale, G.A., 2007. Human disturbance affects habitat use and behaviour of Asiatic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. *Oryx* 41 (3), 343–351.
- Niedballa, J., Sollmann, R., Courtiol, A., Wilting, A., 2016. camtrapR: an R package for efficient camera trap data management. *Methods Ecol. Evol.* 7, 1457–1462.
- 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.
- Odden, M., Wegge, P., Fredriksen, T., 2010. Do tigers displace leopards? If so, why? *Ecol. Res.* 25 (4), 875–881.
- Penjor, U., Astaras, C., Cushman, S.A., Kaszta, Z., MacDonald, D.W., 2022a. Contrasting effects of human settlement on the interaction among sympatric apex carnivores. *Proc. R. Soc. B Biol. Sci.* 289.
- Penjor, U., Astaras, C., Cushman, S.A., Kaszta, Z., MacDonald, D.W., 2022b. Contrasting effects of human settlement on the interaction among sympatric apex carnivores. *Proc. Biol. Sci.* 289, 20212681.
- Perez, F., Piao, Z., Liu, X., 2022. Habitat suitability for a community of Amur tigers (*Panthera tigris altaica*) and their prey in Changbaishan. *Environ. Sci. Pollut. Res.* 29, 12249–12260.
- Perez, I., Geffen, E., Mokady, O., 2006. Critically endangered Arabian leopards *Panthera pardus nimr* in Israel: estimating population parameters using molecular scatology. *Oryx* 40, 295–301.
- Pokheral, C.P., Wegge, P., 2019. Coexisting large carnivores: spatial relationships of tigers and leopards and their prey in a prey-rich area in lowland Nepal. *Ecoscience* 26 (1), 1–9.
- Poudel, S., Twining, J.P., Stedman, R.C., Ghimire, S.K., Fuller, A.K., 2023. Ecological and anthropogenic drivers of leopard (*Panthera pardus fusca*) attack occurrence on humans in Nepal. *People Nat.* 5, 1977–1988.
- Poursalem, S., Amininasab, S.M., Zamani, N., Almasieh, K., Mardani, M., 2021. Modeling the distribution and habitat suitability of Persian leopard *Panthera pardus saxicolor* in southwestern Iran. *Biol. Bull.* 48, 319–330.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., 2014. Status and ecological effects of the world's largest carnivores. *Science* 343, 1241484.
- Ripple, W.J., Wolf, C., Newsome, T.M., Betts, M.G., Ceballos, G., Courchamp, F., Hayward, M.W., Van Valkenburgh, B., Wallach, A.D., Worm, B., 2019. Are we eating the world's megafauna to extinction? *Conserv. Lett.* 12, e12627.
- Ritchie, E.G., Johnson, C.N., 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecol. Lett.* 12, 982–998.
- Rota, C.T., Winkle, C.K., Kays, R.W., Forrester, T.D., McShea, W.J., Parsons, A.W., Millsaugh, J.J., 2016. A two-species occupancy model accommodating simultaneous spatial and interspecific dependence. *Ecology* 97, 48–53.
- Running, S.W., Zhao, M., 2015. Daily GPP and Annual NPP (MOD17A2/A3) Products NASA Earth Observing System MODIS Land Algorithm. MOD17 User's Guide 2015, pp. 1–28.
- Sanderson, E.W., Miquelle, D.G., Fisher, K., Harihar, A., Clark, C., Moy, J., Potapov, P., Robinson, N., Royte, L., Sampson, D., 2023. Range-wide trends in tiger conservation landscapes, 2001–2020. *Front. Conserv. Sci.* 4, 1191280 %@ 1192673-1191611X.
- Schoener, T.W., 1974. Resource partitioning in ecological communities: research on how similar species divide resources helps reveal the natural regulation of species diversity. *Science* 185, 27–39.
- Schuetz, P., Wagner, A.P., Wagner, M.E., Creel, S., 2013. Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biol. Conserv.* 158, 301–312.
- Shivakumar, S., Khettry, A., Surve, N., Rahman, H., Ghimire, Y., Tharchen, L., Zaw, T., Waseem, M., Jhala, Y., 2023. *Panthera pardus ssp. fusca*. The IUCN Red List of Threatened Species 2023. : e. T215195524A215195533.
- Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J.T., Burton, C., Townsend, S.E., Carbone, C., Rowcliffe, J.M., Whittington, J., 2017. Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. *Front. Ecol. Environ.* 15, 26–34.
- Sultaire, S.M., Millsaugh, J.J., Jackson, P.J., Montgomery, R.A., 2025. Identifying factors mediating the carnivore richness–productivity relationship across a precipitation-driven ecotone. *J. Biogeogr.* 52, 161–171.
- Sunarto, S., Kelly, M.J., Parakkasi, K., Klenzendorf, S., Septayuda, E., Kurniawan, H., 2012. Tigers need cover: multi-scale occupancy study of the big cat in Sumatran forest and plantation landscapes. *PLoS One* 7, e30859.
- 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, 104–115.
- Sunquist, M., Sunquist, F., 2002. *Wild Cats of the World*. University of Chicago Press.
- Tempa, T., 2017. The Ecology of Montane Bengal Tigers (*Panthera tigris tigris*) in the Himalayan Kingdom of Bhutan. ProQuest Dissertations Publishing.
- Tempa, T., Hebblewhite, M., Mills, L.S., Wangchuk, T.R., Norbu, N., Wangchuk, T., Nidup, T., Dendup, P., Wangchuk, D., Wangdi, Y., 2013. Royal Manas National Park, Bhutan: a hot spot for wild felids. *Oryx* 47, 207–210.
- 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.
- Thanet, D.R., Regmi, P.R., Lamichhane, B.R., Naha, D., Kupferman, C., Beasley, J.C., et al. Subedi, N., 2025. Coexistence of sympatric large carnivores: Spatio-temporal interactions between tigers and leopards in Parsa National Park, Nepal. *Ecol. Evol.* 15 (6), e7154.
- Treves, A., Bruskotter, J., 2014. Tolerance for predatory wildlife. *Science* 344, 476–477.
- Tshewang, U., Tobias, M.C., Morrison, J.G., Tshewang, U., Tobias, M.C., Morrison, J.G., 2021. State of environment in Bhutan. In: *Bhutan: Conservation and Environmental Protection in the Himalayas*, pp. 1–24.
- Tyre, A.J., Tenhumberg, B., Field, S.A., Niejalke, D., Parris, K., Possingham, H.P., 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecol. Appl.* 13, 1790–1801.
- Wang, S.W., Macdonald, D.W., 2006. Livestock predation by carnivores in Jigme Singye Wangchuck National Park, Bhutan. *Biol. Conserv.* 129, 558–565.
- Wangchuk, S., Bond, J., Thwaites, R., Finlayson, M., 2023. Exploring human–wildlife conflict and implications for food self-sufficiency in Bhutan. *Sustainability* 15, 4175.
- Wangchuk, T., Thinley, P., Tshering, K., Tshering, C., Yonten, D., Wangdi, K., 2004. *A Field Guide to the Mammals of the Bhutan (No Title)*.
- Watanabe, S., Opper, M., 2010. Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *J. Mach. Learn. Res.* 11.
- Wen, D., Qi, J., Long, Z., Gu, J., Tian, Y., Roberts, N.J., Yang, E., Kong, W., Zhao, Y., Sun, Q., Jiang, G., 2022. Conservation potentials and limitations of large carnivores in protected areas: a case study in Northeast China. *Conserv. Sci. Pract.* 4 n/a.
- Wikramanayake, E., McKnight, M., Dinerstein, E., Joshi, A., Gurung, B., Smith, D., 2004. Designing a conservation landscape for tigers in human-dominated environments. *Conserv. Biol.* 18, 839–844.
- Wikramanayake, E., Dinerstein, E., Seidensticker, J., Lumpkin, S., Pandav, B., Shrestha, M., Mishra, H., Ballou, J., Johnsingh, A., Chestin, I., 2011. A landscape-based conservation strategy to double the wild tiger population. *Conserv. Lett.* 4, 219–227.
- Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280 (5372), 2126–2128.