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Research article

Tiger habitat use dynamics in Bardia-Banke Complex, Nepal using camera trap-based multi-season occupancy framework

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Abstract

Understanding fine-scale habitat use dynamics within species home range is crucial for long term conservation planning. We used multi-season occupancy models incorporating field and landscape level covariates to tiger camera trap data collected during the systematic periodic survey from 2013 to 2022. Habitat use probabilities varied across primary sessions, peaking at 0.56 in 2013 and dropping to 0.49 in 2022, indicating negative and positive rate of change in tiger habitat use probabilities (average lambda $\lambda_{2013\text{-}2018} = 0.60$, - 40% decline; average lambda $\lambda_{2018\text{-}2022} = 2.28$, +128% increase) between survey period 2013–2018 and 2218–2022 respectively. Local colonization probabilities fluctuated between 0.39 (SE = 0.09) during 2013–2018 and 0.48 (SE = 0.04) during 2018–2022, while local extinction remained stable at 0.50 (SE = 0.005), suggesting high site turnover. The effects of covariates on tiger habitat use dynamics varied over time. Tiger habitat use probabilities increased with proximity to waterholes and distance from settlements and decreased with elevation. However, the influence of habitat productivity and prey availability on tiger habitat use was contrary to our expectations. Colonization probability increased with prey availability and proximity to waterholes. Habitat productivity positively influenced local extinction, contrary to a priori expectations. Our findings highlight the critical role of waterhole distribution in shaping tiger habitat use in water-limited landscape. Enhancing water and prey availability can support colonization, promoting long-term persistence of tigers. Tiger habitat use dynamics highlight the importance of targeted, site-specific conservation strategies aimed at enhancing habitat suitability and promoting landscape connectivity. We emphasize the importance of long-term, multi-year camera trap monitoring to track persistence of tigers across the Complex. The study's combination of estimated tiger habitat use and grid-based approaches offers a valuable framework for implementing targeted conservation interventions.

Keywords: Camera trap; Detection probability; Habitat use probability; Multi season occupancy models; Tiger

1 | Introduction

Understanding ecosystem dynamics that influence species persistence is crucial for effective conservation and wildlife management (Farris et al. 2016; Rota et al. 2016). Long-term species persistence is shaped by demographic factors such as birth, death, immigration, and emigration, as well as environmental covariates including habitat alterations, climate change, disease, prey availability, and human disturbances (Garcia et al. 2014; Farris et al. 2016; Rota et al. 2016). Ecological variables such as prey availability (Everatt et al. 2019; Abade et al. 2020), water sources (Mondal et al. 2013; Oriol-Cotterill et al. 2015), forest cover (Cristescu et al. 2019; Cimatti et al. 2021), and proximity to human settlements (Mondal et al. 2013; Abade et al. 2020), roads (Carter et al. 2020), and trails (Thapa et al. 2021) strongly influence the occurrence of large carnivores.

Large carnivores, such as tigers (*Panthera tigris*), face severe threats, with populations declining to fewer than 5,660 individuals (Sanderson et al. 2023) and their geographic range contracting to less than 10% of its historic extent (Goodrich et al. 2022). These declines are primarily driven by poaching (Oswell 2010), land use changes, and human population growth (Wolf & Ripple 2017; Van der Weyde et al. 2018). Tiger recovery now largely depends on the protection and effective management of approximately 42 "source sites" within the broader Tiger Conservation Landscape (TCL), which forms the foundation for global tiger conservation strategies (Goodrich et al. 2022; Gray et al. 2023; Jhala et al. 2025). Ensuring the long-term persistence of tigers in these source sites is crucial for facilitating natural dispersal into new areas, particularly across South and East Asia (Qi et al. 2021). The multi-year surveys are essential for capturing dynamic processes and identifying key factors influencing species persistence and local population dynamics (MacKenzie et al. 2006; Magurran et al. 2010; Rosenblatt et al. 2014).

Tiger population studies are often limited to a single-year camera trap survey designed to estimate key population metrics such as occupancy (Thapa et al. 2016; Shah et al. 2025), abundance, or density (Thapa et al. 2017; Shah et al. 2024) in Nepal. However, a single-year snapshot survey fail to capture the complex processes of local colonization and extinction that influence species persistence (Kuussaari et al. 2009; Wearn et al. 2012; Essl et al. 2015). To address this gap, we conducted three periodic camera trap surveys between 2013 and 2022, allowing us to examine tiger habitat use dynamics and assess their response to habitat and anthropogenic factors using robust dynamic occupancy models, while accounting for imperfect detection (MacKenzie et al. 2006).

In this study, we aimed to investigate the temporal and spatial dynamics of tiger habitat use and its underlying drivers within Bardia-Banke Complex, Nepal using detection and non-detection data from periodic camera trap surveys conducted in 2013, 2018, and 2022. We applied single-species multi-season occupancy models (MacKenzie et al. 2006) incorporating landscape and field level covariates related to habitat, prey availability, water sources, and environmental characteristics to investigate factor affecting tiger habitat use over the period of time including local dynamic process such as colonization (also defined as new site use) and local extinction (also defined as site abandonment) probabilities over the sampling period between 2013-2022. We hypothesized that tiger habitat use over the years, increases with survey specific habitat productivity, spatial distribution of waterholes, and prey availability, and decreases with proximity to human settlements, while local colonization (and extinction) by tigers over the period positively (negatively) influenced by seasonal habitat productivity, spatial distribution of waterholes and prey availability (see more in method sections).

2 | Materials and methods

2.1 | Study area

Bardia-Banke Complex (Area: 2,876 km^2; N 27^0 58′13″ to 28^0 35.5′; E 80^{0}10′ to 82^0 12′19″) encompasses Bardia National Park (BNP), one of the 42 global tiger source sites (Walston et al. 2010), Banke National Park (BaNP) and surrounding forest areas (Figure 1). The East-West National Highway cuts across both parks, spanning 30 km in BNP and 72 km in BaNP, while the North-South Ratna Highway, power transmission lines, and an irrigation canal further intersect the landscape. It lies within the transboundary Terai Arc Landscape recognized as a global priority Tiger Conservation Landscape (Thapa et al. 2016).

The Complex has played a crucial role in tiger recovery, with the population increasing from 18 individuals in 2010 to 150 in 2022 (DNPWC & DFSC 2022). Prey density was estimated at 68.26 individuals per km^2 (CV = 15.06%, range: 50.8 - 91.6) in Bardia National Park and 29.01 individuals per km^2 (CV = 26.13%, range: 17.5 - 48.2) in Banke National Park in 2022 (Shah et al. 2024).

Key ungulate prey species for tigers, leopards *Panthera pardus*, and dholes *Cuon alpinus* in the Complex includes sambar *Rusa unicolor*, chital *Axis axis*, wild boar *Sus scrofa,* and northern red muntjac *Muntiacus vaginalis*. In addition, the Complex is home to several threatened mammals such as Asian elephants *Elephas maximus*, greater one-horned rhinoceros *Rhinoceros unicornis*, gharials *Gavialis gangeticus*, sloth bears *Melursus ursinus* and river dolphins *Platanista gangetica*, along with over 500 bird species, many of which are endangered (Wegge & Storaas 2009; Shah et al. 2024).

The Complex potential tiger habitat spans ~2,876 km^2 encompassing diverse subtropical deciduous vegetation, from early successional floodplain communities to mature Sal *Shorea robusta* forests, alluvial floodplain grasslands, rivers and both natural, and man-made waterholes (Barber-Meyer et al. 2013). Dense human populations surround the Complex, averaging about ~243 people/km^2 (CBS Nepal 2022).

The Complex also contains crucial forest corridors that connect it to India's Katarniaghat Wildlife Sanctuary through the Khata Corridor and Suhelwa Wildlife Sanctuary through the Kamdi Corridor. Perennial rivers (Karnali, Babai, West Rapti) and over 50 ephemeral streams originating from the Churia Hills channel rainwater during the monsoon season but remain dry for the rest of the year (Shah et al. 2024).

2.2 | Methods

We used National Tiger Surveys data of 2013, 2018 and 2022. We followed a grid-based approach to design the camera trap survey for detection and non-detection of tigers and prey species. We sampled 2,876 km^2 of potential tiger habitat and divided the study area into four survey blocks with each block being divided further into 2 × 2 km^2 grid cells and we deployed camera stations within each cell (Figure 1). One pair of digital cameras were set in each grid mounted on wooden poles or trees, approximately 45-60 cm off the ground and ~3 m away on either side of existing human and/or game trails. No bait or lure was used (Shah et al. 2025). Cameras were set to run 24 hours a day for an average of 15-20 days in each block (Supportive Information S2). We set camera stations at 1 to 4 km apart between two adjoining grids of 2 × 2 km^2 at locations that would have the highest probability of photo-capturing of tigers (Thapa & Kelly 2017). Cameras were programmed to record a burst of three photos in 30-second intervals. We surveyed the entire study area during winter season from November to early February in 2013, 2018, and 2022.

2.3 | Data analysis

We used the multi-season occupancy model (MacKenzie et al. 2003) to analyze the trends in tiger habitat use dynamics. We employed multi-season, single-species (dynamic) occupancy modeling, which explicitly account for spatial autocorrelation in detection within each grid cell (Hines et al. 2014), where 'season' refers to consecutive yearly surveys. This approach explicitly models yearly changes in the probability of occupancy (ψ) as well as probabilities of local colonization (γ) and extinction (ε). Local colonization is defined as the probability of an unoccupied site during time t becoming occupied at t+1. Conversely, local extinction is defined as the probability of a previously occupied site during time t becoming unoccupied at t+1 (MacKenzie et al. 2006). This modeling approach employs a Pollock's robust design, meaning parameters (detection, occupancy, colonization, and extinction) are geographically 'closed' to movement (e.g., immigration and/or emigration) during surveys, but 'open' between survey years (MacKenzie et al. 2006).

For animals with larger home ranges than our 2 × 2 km^2 grid cells, such as tigers, occupancy models yield reliable estimates of probability of detection and habitat use (rather than true occupancy) at finer spatial scales (Mackenzie et al. 2018). Within the home range, occupancy can be seen as a metric of intensity of habitat use, which has been successfully used in earlier studies for tigers (Sunarto et al. 2012; Shah et al. 2025), dholes (Srivathsa et al. 2014), and elephants (Thapa et al. 2019). In this context, each cell can be used to gather information about patterns in space-use within the home-range or habitat use (Kshettry et al. 2017). During each survey, tiger detections were coded "1" and non-detection as "0" for each grid cell to develop the detection history. We have a maximum of 16 sampling occasions within each grid cell in each of the three primary sessions. In the detection histories matrix, in situations where there was no survey a missing value entry (-) was incorporated into the matrix.

We also used the combination of one field level and four landscape level covariates (Table 1) to assess its influence on tiger habitat use dynamics across the grid cells in the Bardia-Banke Complex. These covariates include prey photo-capture frequency as an index of prey availability (PREY) influencing the tiger habitat use (Barber-Meyer et al. 2012; Harihar & Pandav 2012). We used the prey index as detection rate (number of photo events per 100 trap nights) of prey species at each camera station as measure of prey availability (Carter et al. 2012). Landscape covariates such as elevation (ELE) was found to influence the distribution of tigers along its potential habitat (Thapa et al. 2022). We computed elevation from digital elevation model with 90 m resolution data (downloaded from https://srtm.csi.cgiar.org/). Remotely sensed vegetation indices such as index of vegetation characteristics that indicates the amount of primary productivity: Normalized Difference Vegetation Index

(NDVI) was extracted for winter (Thapa & Kelly 2016). Distance to the nearest waterholes (DWAT) from the grid cells were extracted from field survey and park records. We also used the distance to the nearest settlement (DSET) extracted as a surrogate measure of disturbance at the landscape level (Thapa et al. 2019). All variables were extracted from GIS public domain, and values were averaged at the grid cell level. We hypothesized tiger intensity of habitat use over time (aka probability of habitat use) to be positively influenced by prey availability, NDVI, distance away from settlement, and negatively influenced by elevation, distance to waterholes (Table 1).

We fitted a set of 39 candidate models to evaluate hypotheses regarding the effects of covariates on probability of habitat use (17 potential models), colonization (8 potential models), extinctions (7 potential models) and detection processes (7 potential models) in Program PRESENCE Ver 2.13.47 (Hines 2006). Prior to modeling, all covariates were screened for collinearity. Highly correlated variables ($|rs| \geq 0.70$) were either removed or not used in combination within the same model (Supportive Information S1).

All covariates used in modelling were normalized using the z transformation and/or scaled using a constant value (Thapa & Kelly 2016). We used a step wise approach to model the parameter of interest at the grid cell level (Karanth et al. 2011; Mackenzie et al. 2018). In the first step, we modelled detection probability either as constant/season or varying by covariates using a global model (model containing all the five covariates: DWAT+NDVI+PREY+ DSET+ELE). In the second stage, we fixed the top model for detection and built models using different combinations of covariates influencing probability of colonization. We followed similar approach, we fixed top model for colonization and built models using different combinations of covariates influencing probability of extinction. At last, we fixed top model for detection, colonization, extinction, and built models using different combinations of covariates influencing probability of tiger habitat use.

For model selection, we ranked all models using Akaike's Information Criterion (AIC) and chose the best model based on lowest AIC scores. We considered all models with $\Delta AIC < 2$ as competing models (Burnham & Anderson 2002). We used model averaging techniques to determine the grid cell-specific probabilities of habitat use (ϕ), colonization (γ), extinction (ε), and detection (p) considering all the competing models. The value of untransformed coefficients (i.e., betas, β) reflects the magnitude and direction (sign) of the influence of covariates on the probabilities of tiger habitat use (ϕ), colonization (γ), extinction (ε), and detection

Table 1. Field level and landscape level predictor variables (including their justification) evaluated as covariates affecting tiger habitat use dynamics in the Complex. The "+" and "-" indicate positive versus negative a priori predictions regarding the hypothesized direction of the effect of the covariate on probabilities of habitat use, colonization, extinction, and detection of tigers.

Covariates	General justification for the selection of the covariates	Description	Hypothesized a priori relationship			
			Ψ	γ	ε	p
Prey index (PREY)	Tiger habitat use is largely influenced by prey availability, with wild ungulate density serving as a key determinant of tiger presence (Karanth et al. 2004; Karanth et al. 2011). This prey index was used as a measure of relative prey availability, rather than estimates of prey occupancy, because it provides more detailed information regarding the local activity levels of prey species (Shah et al. 2024).	We sorted all the camera trap pictures of wild prey and considered photos as independent events if they were 30 minutes or more apart, unless we could tell there were distinctly different individuals, as is commonly done in camera trap studies (Di Betti et al. 2009). Computed from detection rate (number of photo events per 100 trap nights) of prey species at each camera station as an index to prey availability (Carter et al. 2012). Capture events of all prey species were summed for each location to obtain prey index.	+	+	-	+
Elevation (ELE)	Tigers are primarily found in the Terai region at elevations below 700 meters (Thapa et al. 2022). Low-elevation areas are favorable for tigers and their prey base, as highlighted by Karanth et al. (2009), Kafley et al. (2016), and Thapa et al. (2021).	Computed using the Shuttle Radar Topography Mission (SRTM) digital elevation model-90m (Riley et al. 1999)	-	-	+	-
Normalized Difference Vegetation Index (NDVI)	NDVI has been used as a measure of vegetation primary productivity (Nathalie Pettorelli et al. 2009; Thapa & Kelly 2016). Tiger habitat use tends to increase with increase in vegetation productivity (NDVI).	Derived from Landsat 6 Thematic Mapper imagery (28.5 m X 28.5 m resolution) of the study area during the 'winter season' in three primary surveys (November- February, 2013-2018-2022). Download from: (downloaded from https://land.copernicus.eu/en/products/vegetation).	+	+	-	+
Distance to waterholes (DWAT)	Water availability becomes a limiting factor in the Bardia-Banke Complex during the dry months (Thapa et al. 2023). Proximity to waterholes enhances habitat suitability for both tiger populations and their prey base (Kafley et al. 2016; Thapa et al. 2016).	Generated a surface by calculating the Euclidean distance from waterhole spatial data extracted from Bardia and Banke National Park Management Plan.	-	-	+	-
Distance to settlements (DSET)	Tigers prefer undisturbed forests that offer optimal conditions for survival. Greater distance from human settlements further supports the persistence of both tiger populations and their prey base (Sunarto et al. 2012; Kafley et al. 2016).	Generated a surface by calculating the Euclidean distance from settlement data extracted from Nepal Survey Department 1996 digital topographic data and world settlement data.	+	+	-	+

Table 2. Summary of model selection statistics for the 7 candidate models depicting detection probability of tigers in the Bardia-Banke Complex, Nepal. K represents the number of parameters in the model. AIC is Akaike information criterion; ΔAIC represents the difference in AIC value relative to the top model (Burnham & Anderson 2002); AIC_{wt} is AIC weight for each model; ψ is probability of site occupancy/ habitat use; p is the probability of detection; γ is the probability of colonization; ε is the probability of extinction. GM is the Global Model.

Detection model	**AIC**	**AIC**	**AIC_{wt}**	**Model likelihood**	**K**
ψ (GM), γ (seasonal GM), ε (seasonal GM),p(seasonal)	8032.18	0	1	1	21
ψ (.),γ (.),eps(.),p(.)	8248.78	216.6	0	0	4
ψ (GM), γ (seasonal GM), ε (seasonal GM), p(seasonal DWAT+NDVI+PREY)	10930.97	2898.79	0	0	27
ψ (GM), γ (seasonal GM), ε (seasonal GM), p(seasonal DWAT+NDVI)	10931.49	2899.31	0	0	24
ψ (GM), γ (seasonal GM), ε (seasonal GM), p(seasonal DWAT)	10960.48	2928.3	0	0	21
ψ (GM), γ (seasonal GM), ε (seasonal GM), p(seasonal PREY)	11628.23	3596.05	0	0	21
ψ (GM), γ (seasonal GM), ε (seasonal GM), p(seasonal NDVI)	11657.2	3625.02	0	0	21

DWAT: distance to the nearest waterholes; DSET: distance to the nearest settlement; ELE: Elevation; NDVI: normalized difference vegetation index; PREY: prey index.

(p). We considered the influence of covariates as important and supported if their β estimates and the 95% confidence limits did not include zero (Dupont 2002). We used estimates from model averaged estimates to map the site level tiger habitat use, colonization, and extinctions probabilities over three primary survey periods in the Bardia-Banke Complex. We also reported the rate of changes in tiger habitat use (Lambda, λ) between primary sessions from the top habitat use model.

3 | Results

3.1 | Summary of trap efforts and tiger detections

The survey team spent 28,687 camera trap days, with effort varying across three primary survey seasons in 2013 (5,340 trap days), 2018 (9,982 trap days), and 2022 (13,365 trap days), and recorded 281unique tiger photo detections at 588 grids of the total 1,652 grids surveyed in the Bardia-Banke Complex (Supportive Information S2). For prey detection, the survey team recorded prey photo detections at 1,373 grids of the total 1,652 grids surveyed in the Complex.

3.2 | Modelling detection and dynamic occupancy probability

The global models for occupancy (habitat use), colonization, and extinction, incorporating landscape and field level covariates, revealed a strong influence of survey season on detection probabilities across grid cells (AIC weight = 1) (Table 2). Therefore, we used seasonal variation in detectability in subsequent analyses for modelling probability of tiger habitat use, colonization, and extinction.

After modeling detection probability, we applied the same global model for tiger habitat use and seasonal global model for local colonization and extinction using seasonal covariates. Among eight candidate models, the additive model incorporating PREY, DWAT, and seasonal NDVI emerged as the top model (AIC weight = 1.0, Table 3), influencing the tiger probability of local colonization along grid cells. Based on β values, the effect of PREY seems to have significant positive effect suggest higher colonization with increase in prey index (CI's do not overlap zero), while DWAT has a possible negative but not significant effect (CI's overlapped zero) was found

Table 3. Summary of model selection statistics for the top 8 models depicting probability of local colonization of tigers in the Bardia-Banke Complex, Nepal.

Local Colonization models	**AIC**	**ΔAIC**	**AIC_{wt}**	**Model likelihood**	**K**
ψ (GM), γ (seasonal DWAT+NDVI+PREY), ε (seasonal GM),p(seasonal)	8032.18	0	1	1	21
ψ (GM), γ (.), ε (seasonal GM),p(seasonal)	8053.14	20.96	0	0	16
ψ (GM), γ (seasonal NDVI+DWAT), ε (seasonal GM),p(seasonal)	8061.61	29.43	0	0	19
ψ (GM), γ (seasonal PREY+DWAT), ε (seasonal GM),p(seasonal)	8071.5	39.32	0	0	19
ψ (GM), γ (seasonal DWAT), ε (seasonal GM),p(seasonal)	8104.72	72.54	0	0	17
ψ (GM), γ (seasonal NDVI+PREY), ε (seasonal GM),p(seasonal)	8116.87	84.69	0	0	19
ψ (GM), γ (seasonal NDVI), ε (seasonal GM),p(seasonal)	8133.84	101.66	0	0	17
ψ (GM), γ (seasonal PREY), ε (seasonal GM),p(seasonal)	8168.62	136.44	0	0	17

DWAT: distance to the nearest waterholes; DSET: distance to the nearest settlement; ELE: Elevation; NDVI: normalized difference vegetation index; PREY: prey index. K represents the number of parameters in the model. AIC is Akaike information criterion; ΔAIC represents the difference in AIC value relative to the top model (Burnham & Anderson 2002); AIC_{wt} is AIC weight for each model; ψ is probability of site occupancy/ habitat use; p is the probability of detection; γ is the probability of colonization; ε is the probability of extinction. GM is Global Model.

Table 4. Summary of model selection statistics for the top 7 models depicting probability of local extinction of tigers in the Bardia-Banke Complex, Nepal.

Local extinction models	**AIC**	**ΔAIC**	**AIC_{wt}**	**Model likelihood**	**K**
ψ (GM), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),p(seasonal)	8029.98	0	0.5244	1	19
ψ (GM), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI),p(seasonal)	8031.65	1.67	0.2275	0.4339	17
ψ (GM), γ (seasonal DWAT+NDVI+PREY), ε (seasonal DWAT+NDVI),p(seasonal)	8032.18	2.2	0.1746	0.3329	21
ψ (GM), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+PREY),p(seasonal)	8034.16	4.18	0.0649	0.1237	19
ψ (GM), γ (seasonal DWAT+NDVI+PREY), ε (seasonal PREY+DWAT),p(seasonal)	8038.56	8.58	0.0072	0.0137	19
ψ (GM), γ (seasonal DWAT+NDVI+PREY), ε (seasonal DWAT),p(seasonal)	8041.84	11.86	0.0014	0.0027	17
ψ (GM), γ (seasonal DWAT+NDVI+PREY), ε (seasonal PREY),p(seasonal)	8048.98	19	0	0.0001	17

DWAT: distance to the nearest waterholes; DSET: distance to the nearest settlement; ELE: Elevation; NDVI: normalized difference vegetation index; PREY: prey index. K represents the number of parameters in the model. AIC is Akaike information criterion; ΔAIC represents the difference in AIC value relative to the top model (Burnham & Anderson 2002); AIC_{wt} is AIC weight for each model; ψ is probability of site occupancy/ habitat use; p is the probability of detection; γ is the probability of colonization; ε is the probability of extinction. GM is Global Model.

Table 5. Summary of model selection statistics for the top 18 models depicting probability of habitat use by tigers in the Bardia-Banke Complex, Nepal.

Occupancy models	**AIC**	**ΔAIC**	**AIC_{wt}**	**Model likelihood**	**K**
ψ (DWAT+DSET+NDVI+ELE+PREY), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8029.98	0	0.5059	1	19
ψ (DWAT+NDVI), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8030.73	0.75	0.3477	0.6873	16
ψ (DWAT+NDVI+PREY), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8032.46	2.48	0.1464	0.2894	17
ψ (NDVI), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8059.32	29.34	0	0	15
ψ (NDVI+PREY), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8060.67	30.69	0	0	16
ψ (NDVI+DSET+PREY+ELE), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8062.32	32.34	0	0	18
ψ (DWAT), γ (seasonal DWAT+NDVI+PREY),eps(seasonal NDVI+DWAT),*p*(seasonal)	8069.55	39.57	0	0	15
ψ (DWAT+ELE), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8070.48	40.5	0	0	16
ψ (DWAT+PREY), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8071.22	41.24	0	0	16
ψ (DWAT+DSET), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8071.33	41.35	0	0	16
ψ (DWAT+DSET+ELE), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8072.48	42.5	0	0	17
ψ (DWAT+PREY+DSET+ELE), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8074.27	44.29	0	0	18
ψ (DSET+ELE), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8133.08	103.1	0	0	16
ψ (DSET+PREY+ELE), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8133.98	104	0	0	17
ψ (ELE), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8141.6	111.62	0	0	15
ψ (DSET), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8150.33	120.35	0	0	15
ψ (PREY), γ (seasonal DWAT+NDVI+PREY), ε (seasonal NDVI+DWAT),*p*(seasonal)	8173.13	143.15	0	0	15
ψ (PREY), γ (seasonal PREY + DWAT), ε (seasonal NDVI + DWAT),*p*(seasonal)	8269.59	69.76	0	0	12

DWAT: distance to the nearest waterholes; DSET: distance to the nearest settlement; ELE: Elevation; NDVI: normalized difference vegetation index; PREY: prey index. K represents the number of parameters in the model. AIC is Akaike information criterion; ΔAIC represents the difference in AIC value relative to the top model (Burnham & Anderson 2002); AIC_{wt} is AIC weight for each model; ψ is probability of site occupancy/ habitat use; *p* is the probability of detection; γ is the probability of colonization; ε is the probability of extinction.

on colonization suggesting more colonization near water sources, and while the seasonal NDVI seems to have negative on colonization, opposite to apriori with inconclusive effect (Table 6).

We therefore fixed the top colonization model with additive effects of PREY, DWAT, and NDVI and developed a set of models exploring different covariate combinations influencing local extinction probability and occupancy (tiger habitat use).

Among the seven candidate models, the additive model incorporating seasonal NDVI and DWAT ranked highest (AIC weight = 0.52, Table 4), influencing the probability of local tiger extinctions

Table 6. Summary of the β coefficient estimates derived using the logit link function from the top-ranked model, as well as from univariate models either within 2 ΔAIC units of the top model or with model weights exceeding 95%. These estimates are based on field- and landscape-level covariates hypothesized to affect tiger habitat use probability (Ψ_{GRID}), colonization (*γ*), extinction (*ε*), and detection (*p*) at 2 × 2 km^2 grid level.

Scale	**Model**	**β_{DWAT} (SE)**	**β_{DSET} (SE)**	**β_{ELE} (SE)**	**β_{NDVI} (SE)**	**β_{PREY} (SE)**
Ψ_{GRID}	Best model	***-0.87 (0.16)***	***0.55 (0.19)***	**-0.31(0.21)**	***-2.09 (0.38)***	**-0.07 (0.11)**
	Univariate	*-1.29 (0.17)*	*-0.75 (0.16)*	*-1.16(0.21)*	*-2.45 (0.57)*	-0.04 (0.08)
$\gamma_{2013-2018}$/ $\gamma_{2018-2022}$	Best model	**-1.63 (1.01)/** ***-1.60 (0.24)***			***-5.34(0.39)/*** **-0.08 (0.14)**	**0.20 (0.50)/** ***1.74 (0.43)***
	Univariate	-0.69 (0.16)/ *-1.18 (0.17)*			-2.57(3.09)/ -0.06 (0.10)	-0.05(0.11)/ *0.66 (0.21)*
$\varepsilon_{2013-2018}$/ $\varepsilon_{2018-2022}$	Best model	***-0.49 (0.19)*/** **0.01 (0.20)**			***-0.36(0.11)/*** ***0.52 (0.22)***	
	Univariate	*-0.71 (0.21)*/ 0.18 (0.18)			*-0.43(0.10)*/ *0.55 (0.21)*	*0.33 (0.12)*/ *-0.54 (0.25)*

Ψ indicates the probability of site occupancy or habitat use at the grid scale (Ψ_{GRID}); β refers to the coefficient reflecting the magnitude and direction of a covariate's influence in the model; β_0 denotes the intercept. DWAT represents the distance to waterholes, DSET is the distance to human settlements, ELE indicates elevation, NDVI stands for the normalized difference vegetation index, and PREY refers to the prey availability index. SE denotes the unconditional standard errors; NC indicates models that did not converge. Models shown in **bold** represent the best-supported models, **underlined** models align with a priori hypotheses, and ***italicized*** models highlight covariates with significant influence on tiger habitat use (i.e., 95% confidence intervals exclude zero).

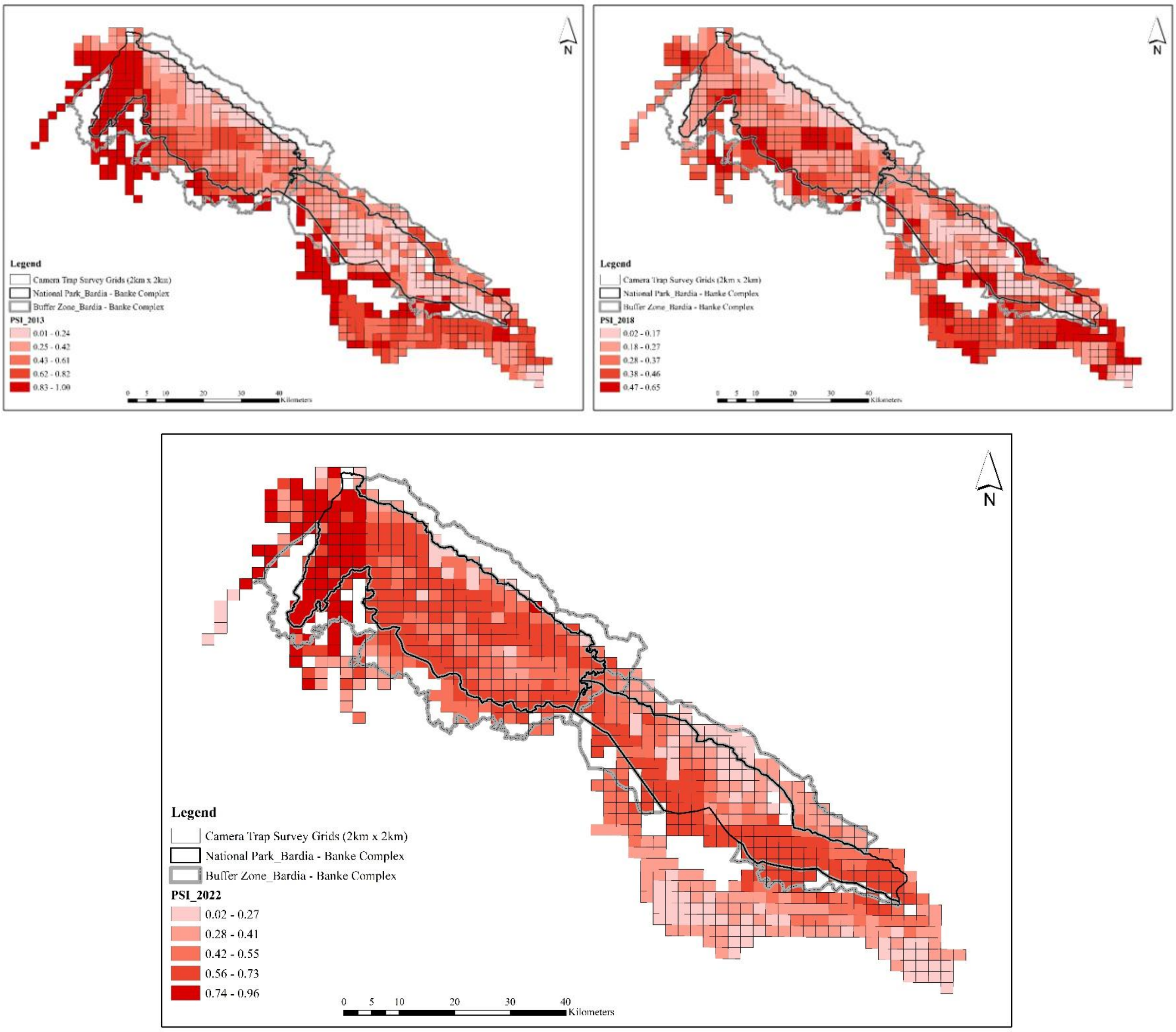

Figure 2. Maps of estimated mean site level habitat use probabilities (Ψ_{GRID}) for tigers in the Bardia – Banke Complex during the first primary session in 2013 (top-left), the second primary session in 2018 (top-right), and the third primary session in 2022 (bottom).

along grid cells. Based on β values, the seasonal NDVI seems to have a positive effect on local extinction from 2018-2022 and a negative effects from 2013-2018, contrary to a priori expectations. However, the results remain inconclusive, as the confidence intervals overlap zero. In contrast, DWAT shows a possible negative effect on local extinction from 2013–2018 and a positive effect from 2018–2022. However, neither effect is statistically significant, as the confidence intervals overlap zero. These patterns may suggest abandonment of grid cells further from water sources between the two survey periods (Table 6).

We fixed the top local extinction model with additive effects of NDVI and DWAT, and subsequently built models using different combinations of covariates to assess their influence on the probability of tiger habitat use.

3.3 | Modelling occupancy for tiger habitat use and influencing covariates

The large number of competing models using landscape and field level covariates highlights uncertainties in modeling probability of tiger habitat use in the study areas. However, certain variables consistently appeared in all top models (Table 5). Among the 18 candidate models, the top model (AIC weight = 0.51) included a global model which included the additive effects of distance to water (DWAT), distance to settlement (DSET), habitat productivity (NDVI), wild prey index (PREY), and elevation (ELE). DWAT had a significant negative effect on probability of tiger habitat use, consistent with the priori hypothesis, as indicated by confidence intervals not overlapping zero. DSET was associated with lower probability of tiger habitat use near villages, aligning with expectations. Contrary to the priori hypothesis, NDVI significantly reduced the probability of tiger habitat use, with confidence intervals excluding zero. Unexpectedly, PREY had a negative effect on probability of tiger habitat use, but its confidence intervals overlapped at zero, suggesting an inconclusive effect. Similarly, ELE showed a negative but non-significant influence, with confidence intervals overlapping zero (Table 5).

3.4 | Estimates of tiger habitat use dynamics in the Badia-Banke Complex

At the grid level (2 X 2 km^2), survey season influenced the probability of tiger detections, ($\hat{p}$ (SE ($\hat{p}$)). Detection probability was significantly higher in 2018 at 0.31 (0.01) compared to 0.09 (0.01) in 2013 and 0.12 (0.01) in 2022 when using the global model for occupancy (tiger habitat use). The multi-season occupancy models estimated the probability of colonization (gamma, $\hat{\gamma}$ (SE ($\hat{\gamma}$)) and

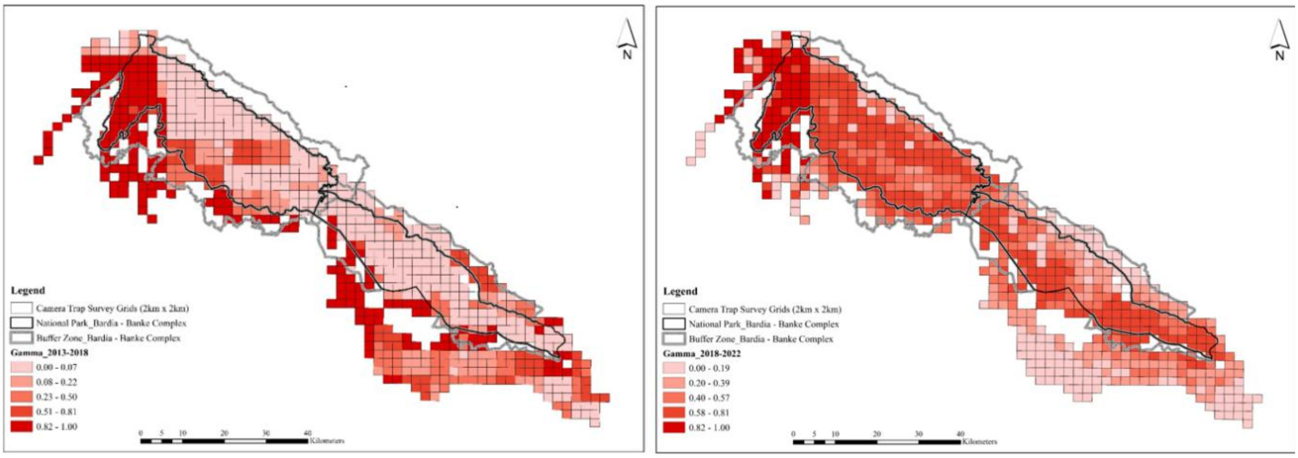

Figure 3. Maps of colonization probabilities for tiger in the Bardia–Banke Complex for the periods ($\gamma_{2013\text{-}2018}$) (left) and in ($\gamma_{2018\text{-}2022}$) (right).

showed positive increase between subsequent surveys, with a model-averaged estimate of 0.39 (SE 0.09, CV=23%) between 2013–2018 and 0.48 (SE 0.04, CV=8%) between 2018–2022. The multi-season occupancy models estimated the probability of extinction (epsilon,$\hat{\varepsilon}$ (SE ($\hat{\varepsilon}$)) and showed positive increase with similar estimates between subsequent surveys, with a model-averaged estimate of 0.50 (SE 0.01) between 2013–2018 and 0.50 (SE 0.01) between 2018–2022. Model-averaged estimates of habitat use ($\hat{\Psi}$ (SE ($\hat{\Psi}$)) (initial Ψ), based on a combination of landscape and field level covariates, were 0.56 (SE 0.011) in 2013, 0.32 (SE 0.004) in 2018, and 0.49 (SE 0.002) in 2022.

4 | Discussion

This study is the first to use multiyear, systematic camera trap survey data to analyze tiger habitat use over time and the environmental factors shaping site-use dynamics in Nepal. Using a robust multi-season occupancy framework (MacKenzie et al. 2006), we examined habitat use across a gradient from floodplain to seasonally dry deciduous forests in the Bardia-Banke Complex. Our periodic monitoring (every four to five years) protocol and relative ease in collecting detection and non-detection data through camera trap surveys provide a powerful approach in estimating and predicting intensity of tiger habitat use (Jhala et al. 2025) across the source sites (Figure 2). Habitat use probabilities varied across primary sessions, peaking at 0.56 in 2013, dipping to a low of 0.32 in 2018, and rising again to 0.49 in 2022, indicating substantial habitat use by tigers. One possible reason for the observed variation in tiger habitat use is the increase in sampling effort due to the expansion of the area surveyed. This artefact, driven by greater sampling in peripheral zones of protected areas, typically less used by tigers, may have influenced the results. In contrast, in 2013 survey focused primarily in core protected areas, which are more intensively used by tigers.

A potential explanation for drop in tiger habitat use probability in 2018 could be habitat disturbances such as prolonged forest fire or flood-induced stagnant water in the habitat between 2013 and 2018 (DNPWC 2018).

Tiger habitat uses over time indicate a positive trend, with the highest gains observed between 2018 and 2022. The driving forces behind these changes are primarily linked to the distance to water sources and the presence of waterholes. The spatial distribution of these water sources plays a key role in influencing tiger habitat use. Despite the parks having few perennial water sources aside from the major rivers, the construction of waterholes through habitat management programs may significantly contribute to creating suitable habitats for the species.

This is biologically plausible, given that the Banke-Bardia Complex is primarily located in the Churia and Bhabhar regions, where water sources are critical factors influencing tiger presence. The declaration of Banke National Park as a protected area in 2010 was likely a key driver of habitat development and protection for tigers. Two perennial rivers, the Karnali and the Babai, pass through the Bardia National Park creating floodplain habitats that are highly productive for prey species. Instead, Banke National Park is dominated by the Sal-forest in Churia hills, with porous alluvial substrates running from east to west in the northern part of the park.

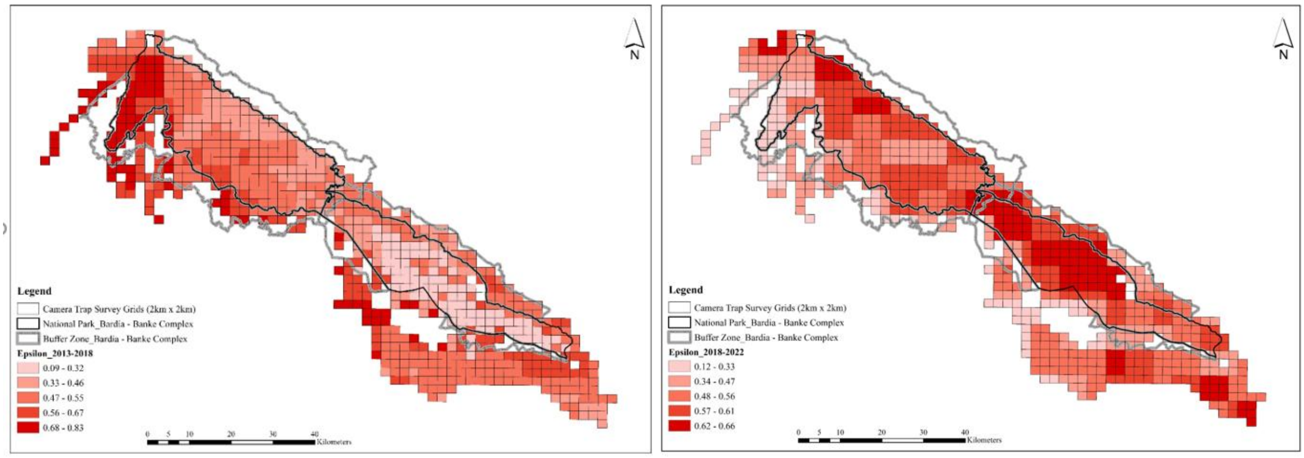

Figure 4. Maps of extinction probabilities for tigers in the Bardia – Banke Complex for the period ($\varepsilon_{2013\text{-}2018}$) (left) and in ($\varepsilon_{2018\text{-}2022}$) (right).

The streams originating from the Churia Hills permeate the porous sediment and flow beneath the land surface, reemerging south of the park, thereby restricting water availability in over 80% of the park during dry months. Most of the artificial waterholes created to provide water for wildlife do not retain water during dry months, when water is a key limiting factor for wildlife in Banke National Park. Metrics indicate spatial variation in tiger habitat use within core areas and temporal variation over time. Habitat factors, such as the presence of waterholes and distance from settlements, are major contributors to the observed patterns of tiger habitat use in the Complex. The extensive spatial coverage of Churia and Bhabhar regions, areas are typically characterized by lower productivity, influences tiger habitat use within protected areas (PAs) and surrounding landscapes. Disturbances such as proximity to human settlements and forest fires may have significant negative impacts, whereas active habitat management is likely to play a key role in enhancing tiger habitat use across the range.

Our results demonstrate that tigers are unevenly distributed across the Bardia-Banke Complex, with sink-like habitats occurring outside the core tiger areas of the Complex, which is embedded within globally prioritized tiger conservation landscape, Terai Arc Landscape. We observed a higher concentration of tiger habitat use in Bardia National Park, suggesting it may serve as a source population for both existing and potential corridors, namely Kamdi and Khata (Figure 2; see habitat use map of 2022). Our results reveals site specific and temporal variations in tiger habitat use, consistent with findings from other studies (example Kafley et al. 2016; Thapa & Kelly 2017) and studies on other species (example elephants - Thapa et al. 2020; Ram et al. 2024). Identifying site-and species-specific hotspot-areas with a higher probability of habitat use (Figure 2) can help managers develop targeted conservation strategies to enhance tiger habitat use.

Our top model indicates that landscape-level covariates primarily drive tiger habitat use in the Bardia-Banke Complex, supporting three of the five priori hypotheses. However, considerable model selection uncertainty remains, with the top model ($w = 0.50$) incorporating the additive effects of distance to waterhole (DWAT), distance to settlement (DSET), prey index (PREY), habitat productivity (NDVI), and elevation (ELE). Tiger habitat use fluctuates in a high-low-medium pattern over time reflecting the interplay of ecological, environmental variables and disturbance factors. Our findings align with previous studies on tiger and leopard occupancy at the landscape scale (Barber-Meyer et al. 2013; Thapa et al. 2021) as well as fine-scale studies in source sites such as Chitwan National Park (Kafley et al. 2016; Thapa & Kelly 2017).

As expected, tiger habitat use increased near waterholes (DWAT) and decreased in areas with higher levels of disturbance (DSET; Barber-Meyer et al. 2013; Harihar & Pandav 2012) and elevation (ELE; Thapa et al. 2022). However, in the prominent Churia habitat of the Complex, tiger habitat use unexpectedly declined with increasing NDVI and prey index, although the effect size was small. This pattern contradicted our predictions but was consistent with previous findings for tigers by Thapa & Kelly (2017) and for leopards by Lamichhane et al. (2021) in the Churia range.

In agroecosystems, tigers exhibited a high probability of using agricultural areas during the winter (0.64; SE = 0.08), coinciding with increased vegetation cover. During this season, tigers preferred densely vegetated areas and avoided regions with dense human settlements (Warrier et al. 2020). Vegetation cover also had a strong positive effect on mammalian community occupancy, particularly among large-bodied or diurnal species (Feng et al. 2021). As habitat generalists, tigers have been recorded at high densities in open forest habitats. The observed negative relationship with NDVI in forest ecosystems may reflect their ecological flexibility.

Our findings indicate that colonization probabilities increased (gamma, $\hat{\gamma} = 0.39$ to 0.48) between survey periods, suggesting potential new site use or an expansion of tiger presence (Figure 3). This trend may be linked to substantial conservation investments within the Terai Arc Landscape (TAL) (Thapa et al. 2020). Key management interventions aimed at achieving tiger conservation goals included the construction and maintenance of waterholes, restoration of wetlands and springs, development of solar-powered deep bore ponds to ensure year-round water availability, and targeted grassland management through cutting and controlled burning. Additionally, the creation of fire line networks to mitigate wildfire risks, increased patrolling, and the establishment of new guard posts have contributed to improved habitat conditions. These interventions, particularly between 2013 and 2022, have enhanced the distribution and reliability of water sources, thereby supporting greater habitat suitability for tiger colonization (DNPWC 2019). Moreover, the integrated development of waterholes, grasslands, and fireline networks as cohesive management units is likely to further promote tiger persistence and long-term habitat use in key source sites.

However, extinction probabilities also increased between surveys, underscoring ongoing habitat dynamics. The consistent extinction estimate across the periods 2013–2018 and 2018–2022 ($\hat{\varepsilon} = 0.50$) suggests persistent site turnover, emphasizing the need for targeted conservation interventions (Figure 4). We propose two plausible drivers for this continued turnover in the Bardia-Banke Complex. First, tourism-related disturbances, particularly from jungle safaris and guided walks that follow tiger presence, may be disrupting habitat use, given the tiger's status as a flagship attraction. Second, the limited application of consistent and adaptive habitat management may be allowing successional changes that render previously used sites unsuitable for long-term tiger occupancy.

Understanding habitat use dynamics is crucial for adaptive management strategies aimed at stabilizing populations and improving long-term habitat suitability for tigers. We developed dynamic models (colonization and extinction) using a combination of field and landscape level variables influencing these processes. The model weight was concentrated on the most influential covariates: one for survey specific detectability, three seasonal covariates for colonization, two for local extinction, and five for habitat use. Supporting our priori hypothesis, detection probability varied across survey periods. This variation may be attributed to the type of detector (camera trap model) used during the three sampling periods (Shah et al. 2025) in the winter season. A combination of covariates was found to both positively and negatively influence colonization and extinction probabilities specific to survey sessions in the Complex, with each model supporting two to three of the three a priori hypotheses. Although none of the covariates had a consistently conclusive effect on tiger habitat use dynamics, factors such as distance to waterholes, prey index (i.e., prey availability) and habitat productivity (measured by NDVI during the winter season) were found to influence both new site use and site abandonment by tigers in the Bardia-Banke Complex. Tiger colonization between the successive surveys, supporting two of the three a priori hypotheses, may be attributed to the spatial distribution of waterholes and prey availability in the source sites (Shah et al. 2024; Shah et al. 2025). Habitat productivity, as a measure by NDVI, showed contradicting results; its effect on both local colonization and extinction was therefore inconclusive and inconsistent across survey sessions — contrary to our a priori prediction.

The spatial location of waterholes had an effect; however, low water availability within them, along with the omission of external factors related to habitat management (such as forest fire) or other disturbance drivers may need to be assessed in future surveys. Our estimates show an increase in the proportion of habitat used by tigers, starting from an initial 1,611 km^2 with fluctuation in habitat use between the periods 2013–2018 and 2018–2022. These trends indicate a negative rate of change between 2013-2018 (average lambda $\lambda_{2013\text{-}2018} = 0.60$, representing 40% decline) and a positive rate of change between 2018-2022 (average lambda $\lambda_{2018\text{-}2022} = 2.28$, representing a 128% increase) in tiger habitat use probabilities. This suggests that Banke National Park, one of the newest protected areas in the country, has recently played an effective role in supporting tiger recovery within the Bardia-Banke Complex (DNPWC & DFSC 2022).

5 | Conclusions

A positive trajectory in tiger habitat use, characterized by distinct spatial and temporal variation, appears to be primarily driven by the distribution of water sources. Tigers are progressively expanding into new potential habitats, with increasing local colonization probabilities accompanied by consistent site turnover, as indicated by local extinction probabilities. These dynamics highlight the importance of targeted, site-specific conservation strategies aimed at enhancing habitat suitability and promoting landscape connectivity.

Understanding habitat use patterns within a species' home range is crucial for devising effective conservation strategies at a source site. In water-limited habitats, especially during the dry season, the spatial distribution of waterholes significantly influences tiger habitat use, along with prey availability, and extent of forest and grass cover. An integrated habitat management approach such as maintaining waterholes and ensuring prey availability can enhance tiger habitat use and promote colonization, thereby supporting their long-term persistence (occupied grid cells over the years) in the Bardia-Banke Complex. The study's combination of estimated tiger habitat use and grid-based approaches offers a valuable framework for implementing targeted conservation interventions. Bardia and Banke National Park have played a crucial role in the recovery of the tiger population (Shah et al. 2024). The systematic survey methods employed in the study can be replicated to monitor long-term persistence of tigers across the Complex.

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Ethics approval

We obtained research approval from the Department of National Parks and Wildlife Conservation, Nepal (Ref. No: 2443/075/76 Eco. 207; April 22, 2019). No experiments involving live animals were conducted. Field surveys, data collection and the use of data were carried out with prior approval from the department. We duly acknowledged supporting organizations for this research.

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Data availability

Data will be made available upon reasonable request to the corresponding author (s).

Authors' contributions

S.K.S.: Conceptualization (Lead), Data Curation (Lead), Formal Analysis (Lead), Methodology (Lead), Writing – Original draft (Lead), Writing – review and editing (Lead); J.B.K.: Conceptualization (Equal), Methodology (Equal), Supervision (Lead), Writing – review and editing (Equal); B.B.: Conceptualization (Equal), Investigation (Equal), Methodology (Equal), Supervision (Equal), Writing – review and editing (Equal); N.S.: Conceptualization (Equal), Investigation (Equal), Formal Analysis (Equal), Supervision (Equal), Validation (Equal), Methodology (Equal), Writing – review and editing (Equal); R.B.K.: Data Curation (Equal), Investigation (Equal), Formal Analysis (Equal), Methodology (Equal), Writing – Original draft (Equal), Writing – review and editing (Equal); K.T.: Data Curation (Equal), Investigation (Equal), Formal Analysis (Equal), Writing – Original draft (Equal), Writing – review and editing (Equal).

Conflicts of interest

The authors declare no conflict of interest.

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Supportive Information (S1–S2):

S1. Spearman correlation coefficients between the predictor variables. Those with very high correlations (|rs| ≥ 0.70) were not used together in the same model. Number of grid cells surveyed = 1652.

Covariates	**DSET**	**SLOPE**	**ELE_2013**	**DWAT 2022**	**DWAT 2018**	**DWAT 2013**	**NDVI_2022**	**NDVI_2018**	**NDVI_2013**	**PREY_2022**	**PREY_2018**	**PREY_2013**
DSET	1.00											
SLOPE	0.16	1.00										
ELE_2013	0.06	0.67	1.00									
DWAT_2022	0.04	-0.11	0.04	1.00								
DWAT_2018	0.10	-0.01	0.12	0.72	1.00							
DWAT_2013	0.30	0.05	-0.05	-0.04	0.06	1.00						
NDVI_2022	0.35	0.40	0.40	-0.06	0.02	0.12	1.00					
NDVI_2018	0.36	0.45	0.44	-0.07	0.04	0.15	0.97	1.00				
NDVI_2013	0.33	0.48	0.48	-0.06	0.03	0.11	0.98	0.97	1.00			
PREY_2022	0.00	-0.17	-0.26	-0.18	-0.15	0.06	-0.10	-0.10	-0.12	1.00		
PREY_2018	-0.16	-0.19	-0.19	-0.05	-0.09	-0.16	-0.42	-0.40	-0.45	0.15	1.00	
PREY_2013	0.16	-0.02	-0.16	-0.35	-0.17	0.44	0.05	0.07	0.04	0.08	0.01	1.00

DSET: distance to nearest settlement; DWAT: distance to nearest water sources; ELE: Elevation; NDVI: normalized difference vegetation index; SLOPE: slope; PREY: prey index.

S2. Summary of survey effort and detection of tigers in the Bardia-Banke Complex, western TAL, Nepal.

Descriptions	**2013**	**2018**	**2022**
Number of 2 X 2 km^2 grid cells surveyed	356	577	719
Survey trapping efforts	5,340	9,982	13,365
Grid cells with tigers detections	113	187	288
Naïve Occupancy *	0.32	0.32	0.40

*number of sites where the species was detected divided by total number of sites surveyed.