

Trophic Cascades and Habitat Suitability in Udanti Sitanadi Tiger Reserve: Impacts of Prey Depletion and Climate Change on Predator-Prey Dynamics

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This study investigates the trophic cascades and habitat suitability in Udanti Sitanadi Tiger Reserve (USTR), highlighting the roles of apex predators, subordinate predators, and prey species in maintaining ecosystem balance. Using the Trophic Species Distribution Model (Trophic SDM), we explored prey-predator interactions and habitat suitability, revealing that tigers respond to prey depletion by increasingly relying on cattle, while leopards adapt by preying on smaller species. Additionally, climate change projections for 2021–2040 and 2081–2100 under CMIP6 scenarios SSP245 and SSP585 indicate significant regional habitat shifts, necessitating adaptive management strategies. Kulhadighat is projected to face habitat contraction, while Sitanadi may experience habitat expansion. This study emphasizes the need for effective conservation efforts such as habitat restoration, prey augmentation and predator recovery are the most important steps needed to maintain the purpose of a Tiger reserve and conservation potential of Chhattisgarh-Odisha Tiger Conservation Unit (TCU). To achieve these dynamics, focusing on community participation, anti-poaching measures, and scientific recommendations are the most crucial components to focus on. This comprehensive analysis underscores the critical role of targeted conservation activities in prey-depleted landscapes to ensure the long-term survival of tigers and the overall health of forest ecosystems, enhancing biodiversity and mitigating human-wildlife conflicts in USTR.

Key words: Climate impact, Prey-predator interaction, Species distribution modeling, Trophic interaction, TrophicSDM

BACKGROUND

A trophic cascade is described as a process by which a perturbation propagates either up or down a food web with alternating negative and positive effects at different successive levels (Terborgh et al. 2006). Large carnivores are categorized by their large body size and for being apex predators, placed high in the trophic ladder (Edwards 2014). As top predators, they can inhibit the explosion of herbivore and subordinate predator populations in ecosystems, an effect that cascades throughout ecological communities and promotes biodiversity (Wallach et al. 2015). The effect of disappearance of such apex predators proceeds downwards successively across the lower trophic levels, resulting in population increases of mid-sized predators *i.e.*, mesopredator release (Crooks and Soulé 1999; Prugh et al. 2009) or a higher abundance of subordinate predators, which may affect herbivores and local vegetation in various ways.

Various ecosystems globally are facing heavy extirpation of apex predator populations due to habitat loss and persecution from humans. This has impacts down the line on the lower trophic levels and leads to “mesopredator release” (Estes et al. 2011; Ripple et al. 2014). The mesopredator-release hypothesis predicts that, if present, apex or top predators dominate their subordinate trophic levels, and, if removed, the successive counterparts will be ‘released’ from dominance and may increase in their numbers (Prugh et al. 2009).

Studies in North America, Europe, and Australia indicate that wolves *Canis lupus*, lynx *Lynx pardinus*, and dingoes *Canis lupus dingo* are the top predators that control subordinate predators like coyotes *Canis latrans* and foxes *Vulpes vulpes*, and further investigate their impact on lower successive levels (Elmhagen and Rushton 2007; Berger et al. 2008; Letnic et al. 2012; Sarmiento et al. 2021). In Asia, tiger *Panthera tigris* is the most iconic predator species, although it suffered serious population decline from anthropogenic pressures such as: prey depletion by human hunting, elimination of tigers for conflict mitigation, hunting for trading of their body parts, and habitat loss or degradation. In spite of conservation efforts over 50 years, wild tigers now occupy < 7% of their historic range. Reproducing tiger populations survive in < 1% of the ~1.6 million km² potential habitat (Karanth et al. 2020).

In India, the tiger is identified as a large predator that occupies the apex position in the food web/ trophic structure of most of the terrestrial ecosystems. They play a crucial role by exerting

regulatory pressure on subordinate predators and herbivore populations, thereby regulating and maintaining the balance of forest ecosystems. Removal or local extinction of such predators may alter the stability of the ecosystem and bring considerable adverse changes. Securing tigers thus safeguards micro-niches in the forest ecosystem, which conserves life forms at the smallest levels, ensuring water and climate security as well (Jhala et al. 2020). Moreover, as a highly threatened and flagship species, the tiger absorbs a continuous flow of funding, which in turn serves a wide range of conservation benefits in India. As a top predator, tiger is successfully surviving in the country as compared to other tiger-ranging countries in Asia. In the last few decades, studies and monitoring programs aimed at large carnivore ecology in India has revealed that the tiger population is largely stable and increasing in the country. The project Tiger, started in 1972 with nine tiger reserves (~18,278 km²), has now extended to 53 tiger reserves (~75,796 km²) and successfully engaged about 2.23% of the geographical area of India that supports conservation of representative ecosystems and biodiversity therein (Qureshi et al. 2023). This rising population of tigers is sharing their space and resources with other co-predators. Among these, leopards *Panthera pardus* are most frequently found to co-occur with tigers in various landscapes across India. Due to various ecological and administrative factors, the abundance of tigers is not evenly distributed in India; rather, many of the tiger reserves have insignificant number of tigers or no tigers at all, allowing the subordinate predators to utilize all the trophic levels in a habitat.

This study was conducted in the Udanti Sitanadi Tiger Reserve (USTR), in central India. This forest is famous for its tiger population, a relict population of Asiatic wild buffalo *Bubalus arnee* and its rich avian and reptile diversity. From the time of its establishment in 2009, it is facing political unrest that has restricted all the ecological monitoring activities and paid a toll in terms of wildlife management (Stripes 2011; Putul 2021; Noronha 2022). Previous studies revealed that despite the designation of a tiger reserve, USTR had only one or two tigers from 2016–2022 (Jhala et al. 2020; Qureshi et al. 2023; Basak et al. 2023) in the entire tiger reserve encompassing an area of 1842.54 km².

Few studies have previously investigated the status of tigers, its co-predators and their prey species in USTR along with the possible threats to the tiger reserve (Basak et al. 2020; Basak et al. 2023). In these studies, the authors explored the role of wildlife conservation in this landscape which was unnoticed for a long period of time since it was considered as an area of serious political insurgencies. They highlighted that generally, removal of top predators results in releases/increase of subordinate predators into the habitat, but in case of USTR despite the low population size of tigers, the leopard population did not increase as expected. Rather, it was found to be plummeting along with their sparse prey population in the presence of high human activity across the landscape (Basak et al. 2023). Forest dwelling communities living inside and outside the reserve are using

USTR as their hunting ground and continue their traditional practice in the areas of the reserve (Basak et al. 2020). Their age-old uncontrolled hunting traditions pose serious threats to the wild ungulate populations, consequently affecting the food resources of carnivore populations in the study area. Moreover, USTR was under prolonged political violence and social unrest that acted as potential hindrance for curbing illegal activities in USTR within the existing legal frameworks. In this critical situation of wildlife conservation in USTR, interventions through species recovery plans are needed urgently. Recovery projects need selection of suitable sites that match the biotic and abiotic needs of the focal species under current and future climatic conditions. Therefore, in this study, we have aimed at unfolding the prey-predator interactions and habitat suitability for tiger and leopard by using the trophic SDM (webSDM, <https://github.com/giopogg/webSDM>) model (Trainer et al. 2014; Poggiato et al. 2022; Cosentino et al. 2023) in USTR. The Trophic SDM is a statistical distribution model that models the distribution of species by involving known trophic interactions among the species network present in an area. It provides a useful insight into the concept of trophic cascades in ecological science, which is practical in conservation and management demands. Careful use of the outcomes of the TrophicSDM analysis can be highly useful for wildlife managers and decision makers to predict and prioritize areas for species recovery in a prey-depleted landscape like USTR with the assistance of local communities.

The objective of our study is three-fold, (1) Understanding the Trophic Cascade of USTR: This objective aims to investigate the cascading effects within the Udanti Sitanadi Tiger Reserve (USTR). By examining the interactions between different trophic levels, we will gain insights into how the presence or absence of apex predator, such as tigers, influences the population of subordinate predator leopard and prey species, ultimately affecting the entire ecosystem, (2) Establishing a Trophic Species Distribution Model (SDM): The goal here is to develop a Trophic SDM that incorporates known trophic interactions among species in USTR. This model will help us understand the intricate connections between tigers, leopards, and their prey. By integrating biotic and abiotic factors, the model aims to provide a detailed analysis of species distributions and habitat suitability, offering valuable insights for conservation efforts and (3) Formulating Comprehensive Recommendations for Apex Predator Habitat Recovery: Based on the findings from the trophic SDM and field observations, this objective focuses on developing actionable recommendations for the recovery and management of apex predator habitats in USTR. These recommendations will be grounded in mathematical modeling and empirical data, aiming to enhance habitat suitability, mitigate human-wildlife conflicts, and support the long-term survival of tigers and other co-predators within the reserve.

Study Area

USTR is spread over 1842.54 km² of Gariyaband and Dhamtari districts of Chhattisgarh, central India (Fig. 1). It constitutes of Udanti and Sitanadi Wildlife Sanctuaries as cores and Taurenga, Indagaon, and Kulhadighat Ranges as buffers. The topography of the area includes hill ranges with intercepted strips of plains and lies in the basin of the Mahandi River. The forest types are chiefly dry tropical peninsular sal forest and southern tropical dry deciduous mixed forest (Champion and Seth 1968). Sal *Shorea robusta* is dominant, mixed with *Terminalia* sp., *Anogeissus* sp., *Pterocarpus* sp., and bamboo species. Sitandi includes dry teak forest, dry peninsular sal forest, and north dry mixed deciduous forest, as per Champion and Seth, 1968. Natural teak forests are mostly found in patches on the alluvial soil along the streams and rivers, while teak plantations have been established in other areas (Kanoje, 2008). *Schleichera oleosa*, *Terminalia arjuna*, *Terminalia tomentosa*, *Mangifera indica*, *Syzigium cumini*, *Eugenia heyneana*, *Ficus racemosa*, *Ficus lacor*, *Ficus bengalensis*, and *Stereospermum chelonoides*, all of which are characteristic of riverine or riparian areas.

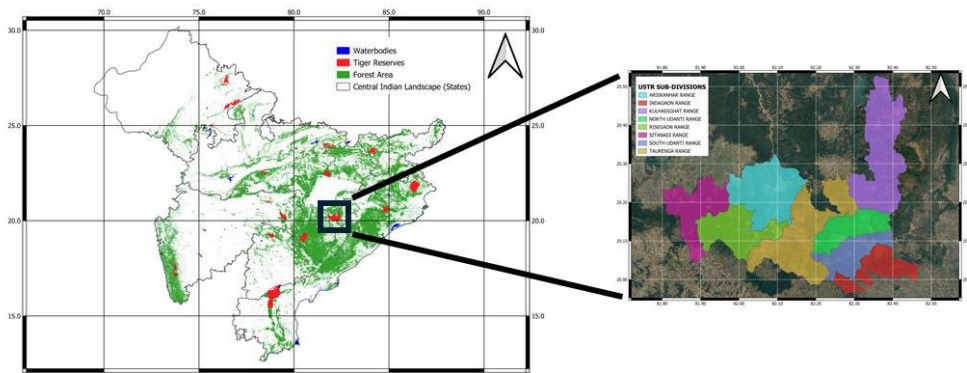


Fig. 1. Map of Central Indian landscape complex (CILC) showing location of present study area Udanti-Sitanadi Tiger Reserve (USTR). (Map Data: Google Satellite Basecamp).

The tiger *Panthera tigris* is the apex predator in USTR, and other co-predators are the leopard *Panthera pardus*, dhole *Cuon alpinus*, Indian grey wolf *Canis lupus*, striped hyena *Hyaena hyaena*, and sloth bear *Melursus ursinus*. Various wild ungulate species are available as prey bases in the tiger reserve, ranging from small-sized Indian mouse deer *Moschiola indica*, four-horned antelope *Tetraceros quadricornis*, and barking deer *Muntiacus vaginalis*, to mid-sized spotted deer *Axis axis* and wild pig *Sus scrofa*, to large-sized gaur *Bos gaurus*, sambar *Rusa unicolor*, and nilgai *Boselaphus tragocamelus*. Smaller carnivores include the jungle cat *Felis chaus*, rusty-spotted cat *Prionailurus rubiginosus*, and golden jackal *Canis aureus*. Apart from these, this landscape has a small population of Asiatic wild buffalo *Buablus arnee* and forest areas with recently invaded

transient herds of elephants *Elephas maximus*. Moreover, it houses 246 species of terrestrial and wetland birds (Bharos et al. 2018). Hence, this landscape supports high diversity and is worthy of conservation efforts. The area's hilly topography is intercepted by plain strips which together play an important role in connectivity of the Chhattisgarh-Odisha Tiger Conservation Unit (TCU). In the east, the tiger reserve is contiguous with the proposed Sonabeda Tiger Reserve in Odisha, forming the Udanti-Sitanadi-Sonabeda Landscape which spreads over 3000 km². In the west, the tiger reserve is connected to Indravati Tiger Reserve in the Bastar region, and in the north, it is connected to Dhamtari and Gariyaband Forest Divisions and further to Barnawapara Wildlife Sanctuary in Mahasamund District. Thus, this TCU has the potential to be of significant importance in the future of wildlife conservation (Qureshi et al. 2023; Basak et al. 2023).

MATERIALS AND METHODS

Collection of Species-Occurrence Data

The National Tiger Conservation Authority (NTCA) and the Wildlife Institute of India (WII) developed a protocol for nationwide estimation and monitoring of tiger and prey populations, as well as their habitats, outlined in A Protocol on Phase-IV Monitoring (Technical Document No. 1/2011). Under this framework, it is essential to monitor changes in tiger populations through intensive surveillance of source populations within tiger reserves and protected areas across tiger landscape complexes (Phase-IV). This approach includes maintaining a centralized photo database of tigers at the NTCA, derived from camera traps deployed throughout the reserves. Occurrence data were collected by repeatedly conducting camera trapping surveys in USTR from 2016 to 2017 and in 2018. We conducted camera trap-based surveys under Phase IV tiger monitoring framework, in 2016–17 to obtain captures of large predators in USTR mainly focused on tiger bearing areas and areas where the chances were higher of having photo-captures of co-predators. The standard protocol involves a camera trap density of one camera pair within a 4–5 km² grid. However, the placement of cameras is flexible and depends on the intensity of animal movements within the grid. While the center of the grid is generally considered optimal, cameras can be positioned anywhere within the grid where focal animal activity is observed to be high.

The ranges were divided into 4 km² grids and those grids were used for deploying cameras. Overall, 136 camera trap stations were installed in this session, in three different blocks across North Udanti, South Udanti, and Kulhadighat ranges. The next camera trapping session was carried out during All India Tiger Monitoring (AITM) program in 2018 when 2 km² grid size was used for

camera trapping. During this session, we covered Arsiakanhar, Risgaon, Sitanadi and Kulhadighat ranges by installing 182 cameras. We deployed the cameras as per the results obtained from carnivore sign surveys before camera trapping. The total sampling duration was 90 days (about 3 months) each for 2016–17 and 2018 camera trapping sessions, while cameras were operational for 30 days in each block. Two camera traps were deployed in each location around forest trails based on indirect evidence of wild carnivore utilization, where possibility of photo-capturing them was higher. We deployed each camera at least 4–5 m from the center of each trail to capture full frame pictures of predators. All cameras were placed at knee height (1.5 feet) from the ground level to obtain identifiable animal-flank photographs. Photo-captures of various herbivore and carnivore species obtained from these two camera trapping sessions were arranged to organize the data based on their presence and absence in the study area. We assigned 1 and 0 values for species presence and absence respectively for each camera point within the sampling time frames.

Collection of Animal-Trap Data

Hunting by using animal traps is now an alarming issue in places where biodiversity and hunting communities co-occur. Wild animals are often scared, suffocated and killed brutally while entrapped in such animal traps. The list of species that suffer traumatic killing in traps may start from a small rodent to an animal as large as an elephants. Controlling or reducing such criminal activities need very tedious and hard efforts from the concerned conservation authorities. Chhattisgarh is no exception in this case. USTR homes hunting communities who use these forests as their traditional hunting ground. With the advancement of the surrounding world gradually these communities have also adapted urban materials to manufacture traps to catch animals instead using traditional bows, arrows and natural materials. This landscape is a mosaic of forests and human dominated areas. Villages in this landscape have mostly tribal populations belonging to Kamars, Baigas, Gonds, Bhunjias and miscellaneous tribes who continued their traditional hunting for bush meat consumptions, illegal livelihoods, recreation and sports as well. Under such conditions, Anti-Snare Walks were conceptualized and conducted in 2021 to create awareness, reduce the effect of snare traps and wildlife poaching in the area and to initiate a practice of curbing down wildlife related crimes by involving the communities and the concerned Government authority. In addition to these, as a part of this program, frontline forest staffs were also trained to detect and destroy various animal traps that are used by the local communities to kill various mammalian species that ranges from small rodents to large herbivores like sambar. Overall, 97 beats were walked to uninstall snares and other traps. On average overall search effort was 6.21 km/walk, for USTR.

GIS-Data Pre-processing

As per the methodology, camera traps could be positioned anywhere within the designated grids based on animal movement intensity. So it was determined that the minimum distance between camera traps was 200 meters. Therefore, in our GIS analysis, we utilized a 100-meter grid, which is half of the estimated minimum distance, to ensure finer spatial resolution and more detailed extraction of zonal statistics. To improve model performance, we applied a quantile transform to the input variables with a target normal distribution. In this manuscript, we did not conduct formal collinearity checks because we were unsure of how they would affect the Trophic SDM, especially given our use of quantile-transformed variables. Nonetheless, we acknowledge that collinearity among predictor variables can potentially influence model performance, and we plan to explore appropriate variable-filtering approaches in future studies. These variables encompass a wide range of environmental and geographical attributes, including distances, aspect categories, land cover, and bioclimatic variables (Table S1). Further details are in the supplementary material section 1.

Trophic Model

The Trophic Species Distribution Model (TrophicSDM) (Poggiato et al. 2022) utilized in this study provides a sophisticated framework for understanding predator-prey interactions within the Udanti-Sitanadi Tiger Reserve (USTR). By integrating trophic relationships alongside abiotic factors, such as climate, terrain, land cover, and distance from anthropogenic layers, this model offers a detailed analysis of species distributions and habitat suitability. TrophicSDM sheds light on the ecological consequences of varying apex predator populations, such as tigers, and their influence on subordinate predators, such as leopards, and their prey species. This approach is especially pertinent in ecosystems like USTR, where apex predator numbers are critically low, allowing for the examination of ecological changes. In USTR, TrophicSDM was used to identify interactions between tigers, leopards, and their prey, which in turn was used to propose effective conservation practices.

The hypothesized trophic connectivity diagram (Fig. 2) shows the interactions between prey and their predator species in USTR, specifically with tigers and leopards as the primary predators. Tigers are connected to a range of prey species, including sambar, nilgai, Indian gaur, wild pig, spotted deer, and cattle; this supports that the tigers are majorly inclined towards the large to middle sized prey species (Karanth and Sunquist 1995; Hayward et al. 2012; Basak et al. 2018 2020). Tiger's preference for larger prey provides insights into their requirement of substantial biomass,

which aligns with their status as apex predators requiring significant energy intake. Tigers' inclusion of livestock in their diet can be attributed to the availability of higher biomass cattle, especially when wild prey is scarce. On the other hand, leopards are known for their adaptability to changing environment, often by widening their food choices as per the availability of prey species that includes varied prey sizes as well (Eisenberg and Lockhart 1972; Santiapillai et al. 1982; Johnsingh 1983; Rabinowitz 1989; Seidensticker et al. 1990; Bailey 1993; Karanth and Sunquist 1995; Daniel 1996; Edgaonkar and Chellam 1998; Sankar and Johnsingh 2002; Qureshi and Edgaonkar 2006; Edgaonkar 2008; Mondal et al. 2011; Sidhu et al. 2017). This flexibility in turn allows them to survive in diverse environments, including areas close to human settlements where livestock might be more accessible. In this landscape too, leopards are known to showcase their adaptability and opportunistic feeding behaviour (Basak et al. 2020). TrophicSDM analysis supports this too as we see that leopard's prey includes both smaller animals, like Indian hare, northern plains langur, four horned antelope, mid-sized prey, such as wild pig to large sized preys like spotted deer and cattle.

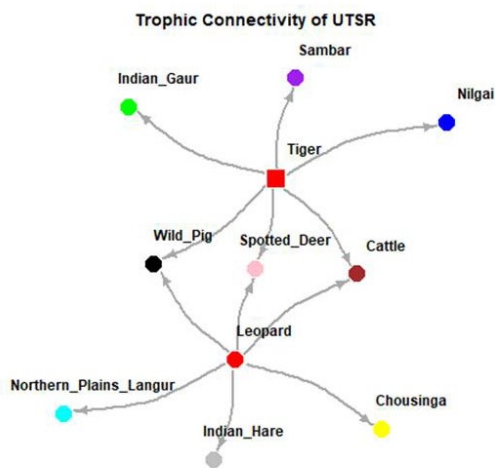


Fig. 2. The Trophic connectivity expected in Udanti-Sitanadi Tiger Reserve (USTR), Chhattisgarh, Central India.

Figure 2 highlights the differences in biomass and size preferences between tigers and leopards. Tigers prefer larger prey that meets their high energy demands, while leopards exhibit a broader dietary range, adapting to prey availability and habitat conditions. The model has derived trophic relations between the predator and prey species of USTR and enhanced our understanding of how the bottom-up effect can impact the predators in such landscape where availability of both large and middle-sized prey species is shaping the large predator interactions and population dynamics. Trophic connections were derived at different confidence levels: 90% (a), 80% (b), and 70% (c). It is predicted that at 90% confidence, the connections will be conservative and show only significant relations. Whereas 80% and 70% confidence level will make the limit flexible and

hence, can exhibit wider ranges of interactions that will be suitable for tigers in USTR, if prey sample increases.

Model Setup for Trophic Interactions

To set up our trophic model, we utilized a Bayesian framework implemented in the `stan_glm` function. Our model was designed with a binomial output using a logit-link function to accurately capture the probabilistic nature of abiotic and biotic interactions. We ran two independent Markov Chain Monte Carlo (MCMC) chains, each with a total of 2000 samples. To ensure the convergence and stability of our estimates, we specified a burn-in period of 1000 samples for each chain, discarding these initial samples to mitigate the influence of the starting values.

Justification for using Trophic Model

The justification for using the trophic model over the non-trophic model for tigers and leopards is compelling based on the provided statistics. For tigers, the trophic model exhibits a higher AUC (0.84 vs. 0.79) and TSS (0.66 vs. 0.51) based on the mean from a 5-fold cross-validation experiment, indicating superior predictive performance. Although the non-trophic model shows slightly higher AUC (0.69 vs. 0.66) and TSS (0.33 vs. 0.27) for leopards, the overall fit statistics favor the trophic model, which has a lower AIC (4442.54 vs. 4449.92) and a higher log-likelihood (-1817.27 vs. -1828.96), indicating a better fit to the data. The lower AUC for leopards could be due to their behavior as habitat generalists, thriving in diverse environments and making their presence more challenging to predict. In summary, the trophic model demonstrates better predictive power and fitness, particularly for tigers. By capturing crucial ecological interactions, it offers a more accurate and comprehensive representation of their natural habitats and behaviors, making it a valuable tool for conservation efforts.

Trophic interaction

In this experiment, we aimed to compare the observed habitat (Fig. 3a) with a hypothetical habitat of tigers (Fig. 4) by manipulating prey availability. Specifically, we excluded cattle from the tiger's diet and made sambar and spotted deer available throughout the study area. The observed habitat represents the actual conditions and resources a species utilizes in the presence of biotic interactions, such as competition and predation, while the hypothetical habitat encompasses the potential range of conditions and resources a species could theoretically use without such

interactions. Tigers have increasingly relied upon cattle due to the low wild ungulate population and the high biomass of available livestock. By ensuring the widespread availability of their preferred natural prey, such as sambar and spotted deer, and removing the availability of livestock, we observed changes in the tigers' habitat use and distribution (Fig. 4). This adjustment was made to understand the tiger's natural dietary preferences and habitat requirements better, free from the constraints of current prey availability.

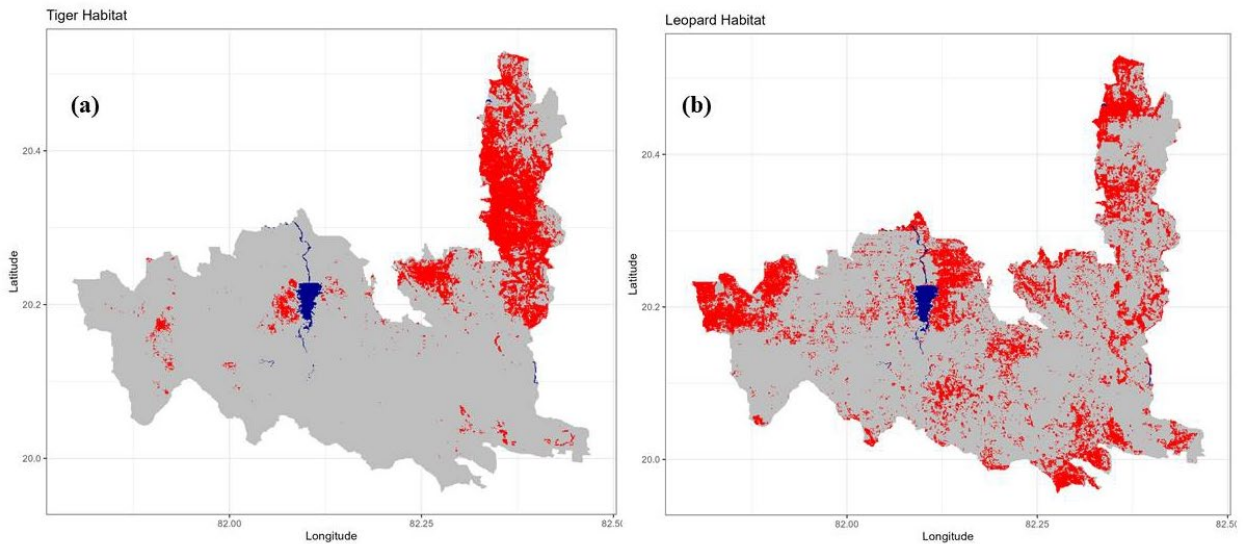


Fig. 3. Habitat of (a) tiger, and (b) leopard in USTR, estimated using the optimal threshold from Youden method.

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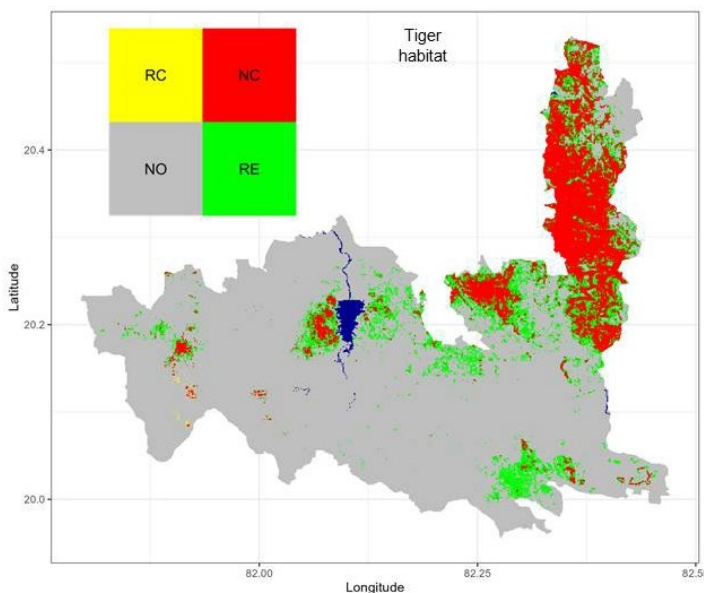


Fig 4. Hypothetical tiger habitat assuming absence of cattle and maximum abundance sambar and spotted deer. (RC* Range contraction , RE*Range expansion , NC*No Change , NO*No habitat).

Habitat Experiments

We estimated the optimal threshold for each of the 200 MCMC inference samples using the Youden method, which identifies the threshold that maximizes the sum of sensitivity and specificity, thereby balancing true positive and true negative rates. Then, using a 90% confidence level of prediction, we set the 10th percentile of the sample optimum thresholds as a fixed threshold for experiments. Subsequently, we classified any region with a habitat suitability value higher than this threshold as Habitat, and values lower than this threshold as Not Suitable. For the subsequent habitat change experiment, we compared the realized habitat with the post-experiment simulated habitat. Grids that are not habitat in both scenarios are classified as NO (no habitat). Habitats that remain unchanged are classified as NC (no change). Areas where habitat expands are classified as RE (range expansion), and areas where habitat contracts are classified as RC (range contraction).

Climate Change Experiment Setup

For our climate change impact assessment on habitat suitability in the Udanti Sitanadi Tiger Reserve, we utilized habitat projections for the periods 2021–2040 and 2081–2100 under scenarios from the Coupled Model Inter-comparison Project Phase 6 (CMIP6), specifically SSP245 (low-emission scenario) and SSP585 (high-emission scenario). We employed four climate models: CMCC-ESM2, GISS-E2, HadGEM3-GC3, and UKESM1. The methodology involved swapping the bioclimatic variables from the abiotic layers with their equivalent bias-corrected bioclimatic variables for each model-scenario-time slice combination.

RESULTS

This section presents an in-depth analysis of habitat suitability for tigers and leopards in USTR, exploring the key predictors and ecological factors influencing their distribution. Subsequent subsections delve into trophic interactions between predators and prey, examine the impacts of habitat manipulation experiments on tiger distribution, and evaluate projected habitat shifts under climate change scenarios for both mid-century (2021–2040) and late-century (2081–2100) timeframes across various climate models and emission pathways.

Predictor Significance Analysis of Habitat Suitability in USTR

The habitat suitability analysis for various species in the Udanti Sitanadi Tiger Reserve provides insights into the critical abiotic and biotic factors influencing their distribution (Table 1). This discussion aims to elucidate these factors to develop effective conservation and management strategies within the reserve.

Table 1. Contribution of Environmental variables and selected prey species in suitable habitats of tiger and leopard in USTR. Min_Snare_Distance (Minimum distance to snare within a 0.1 km grid), ASPECT_cat_1 (North facing slopes), ASPECT_cat_2 (East facing slope), ASPECT_cat_4 (West facing slope), wc2.1_30s_bio_5 (Max Temperature of Warmest Month), wc2.1_30s_bio_8 (Mean Temperature of Wettest Quarter), wc2.1_30s_bio_11 (Mean Temperature of Coldest Quarter), wc2.1_30s_bio_12 (Annual precipitation), wc2.1_30s_bio_13 (Precipitation for wettest month), ESRI_LULC_cat_11 (Forests), ESRI_LULC_cat_2 (rangelands/croplands), Slope_cat_3 (steep slopes, 15–30 degree), Slope_cat_4 (very steep slopes, >30 degree), Cattle, Wild Pig, Northern Plains Langur and Indian Hare

Tiger			
Variable	mean	5%	95%
Intercept	-9.452	-14.666	-4.595
Min_Snare_Distance	-1.480	-2.483	-0.614
ASPECT_cat_2	0.365	0.027	0.758
SLOPE_cat_4	0.799	0.267	1.355
wc2.1_30s_bio_12	-5.491	-10.461	-0.563
wc2.1_30s_bio_13	5.464	0.498	11.499
Cattle	2.601	1.097	4.219
Leopard			
Variable	mean	5%	95%
Intercept	-2.868	-4.858	-0.849
ASPECT_cat_1	0.151	0.057	0.250
ASPECT_cat_4	-0.124	-0.222	-0.034
ESRI_LULC_cat_11	6.134	2.650	9.404
ESRI_LULC_cat_2	6.226	2.694	9.564
SLOPE_cat_3	0.163	0.018	0.320
wc2.1_30s_bio_11	6.362	1.248	11.791
wc2.1_30s_bio_12	1.284	0.165	2.372
wc2.1_30s_bio_5	2.278	0.204	4.633
wc2.1_30s_bio_8	-3.890	-7.738	-0.243
Wild_Pig	0.538	0.010	1.087
Northern_Plains_Langur	1.046	0.550	1.575
Indian_Hare	0.796	0.269	1.351

Tiger Habitat Suitability

In our trophic species distribution model (SDM) for tiger habitat, several variables emerged as significant predictors, each contributing differently to the model. The intercept, with a mean value of -9.45, represents the baseline log-odds of tiger presence when all predictor variables are set to zero. This negative value suggests that, in the absence of other factors, the likelihood of tiger presence is inherently low, highlighting the importance of the additional variables in predicting suitable tiger habitats. We have observed tigers mostly in Kuladighat and Phase IV Block 2, with

detections at 22 sites, and a total count of 45 observations. In our analysis, 255.88 km² is found to be suitable for tiger habitat (Fig. 3a).

One of the most significant variables is the minimum distance to the nearest snare (Min_Snare_Distance), which has a mean coefficient of -1.48. This indicates that tigers are more likely to be found near snares, suggesting higher habitat suitability in these areas, likely due to higher prey abundance. However, this proximity increases the risk of animals being caught in traps, underscoring the urgent need for anti-poaching measures. Addressing this issue is crucial for protecting both prey and predator species within the reserve.

Aspect category 2 (ASPECT_cat_2), representing East-facing slopes, has a positive mean coefficient of 0.36. This suggests that tigers are more likely to be found in habitats with these slope characteristics. Additionally, steep slopes categorized under SLOPE_cat_4 (very steep slopes, > 30 degrees) also positively influence tiger presence, with a mean coefficient of 0.80. These findings indicate that tigers may prefer certain topographical features, possibly due to the cover and hunting advantages they provide.

Among the bioclimatic variables, wc2.1_30s_bio_12 (Annual Precipitation) and wc2.1_30s_bio_13 (Precipitation of Wettest Month) show contrasting effects. Annual precipitation has a negative mean coefficient of -5.49, suggesting that higher annual precipitation levels are associated with lower tiger presence. In contrast, precipitation during the wettest month has a positive mean coefficient of 5.46, indicating that areas with high precipitation in the wettest month may be more favourable for tigers. This contrast highlights the complex relationship between precipitation patterns and tiger habitat suitability.

Lastly, the presence of cattle is a significant positive predictor, with a mean coefficient of 2.60. This suggests that even though tigers prefer to hunt wild ungulates with large biomass, when there is critically low abundance of such large-sized ungulates in USTR, they exploit available cattle population to meet their energy needs in the reserve. This practice of preying on cattle indicates a potential for human-tiger conflict in this area.

Leopard Habitat Suitability

In our trophic species distribution model (SDM) for leopard habitat, several variables emerged as significant predictors, each contributing differently to the model. The intercept, with a mean value of -2.87, represents the baseline log-odds of leopard presence when all predictor variables are set to zero. This negative value suggests that, in the absence of other factors, the likelihood of leopard presence is inherently low, underscoring the importance of the additional variables in predicting suitable leopard habitats. Unlike tiger we have observed Leopard presence in

almost all the subdivisions, with detections at 159 sites, and a total count of 388 observations. In our analysis, 430.17 km² is found to be suitable for Leopard habitat (Fig. 3).

Aspect categories play a notable role in determining leopard habitat preferences.

ASPECT_cat_1 (North-facing slopes) has a positive mean coefficient of 0.15, indicating that leopards are more likely to be found on these slopes. Conversely, ASPECT_cat_4 (West-facing slopes) has a negative mean coefficient of -0.12, suggesting that these slopes are less suitable for leopards. This highlights the importance of specific topographical features in influencing leopard distribution.

Land Use and Land Cover (LULC) categories also significantly impact leopard habitat suitability. ESRI_LULC_cat_11 (forests) has a substantial positive mean coefficient of 6.13, indicating that forested areas are highly favourable for leopards. Similarly, ESRI_LULC_cat_2 (rangelands/croplands) also shows a strong positive influence with a mean coefficient of 6.23. These findings suggest that leopards prefer a mix of forested and open landscapes, which provide both cover and hunting opportunities.

Slope category 3 (SLOPE_cat_3), representing steep slopes (16–30 degrees), has a positive mean coefficient of 0.16. This indicates a slight preference for steeper slopes, which may offer advantages in terms of cover and vantage points for hunting.

Among the bioclimatic variables, wc2.1_30s_bio_11 (Mean Temperature of Coldest Quarter) and wc2.1_30s_bio_12 (Annual Precipitation) both show positive influences on leopard presence, with mean coefficients of 6.36 and 1.28, respectively. This suggests that leopards are more likely to be found in areas with moderate to high precipitation and cooler temperatures during the coldest quarter. Conversely, wc2.1_30s_bio_8 (Mean Temperature of Wettest Quarter) has a negative mean coefficient of -3.89, indicating that higher temperatures during the wettest quarter are less favorable for leopards. Additionally, wc2.1_30s_bio_5 (Max Temperature of Warmest Month) has a positive mean coefficient of 2.28.

Prey availability is another crucial factor influencing leopard habitat suitability. The presence of wild pigs (Wild_Pig) has a positive mean coefficient of 0.54, indicating that areas with higher wild pig populations are more likely to support leopards. Similarly, the presence of northern plains gray langurs (Northern_Plains_Langur) and Indian hares (Indian_Hare) positively influences leopard presence, with mean coefficients of 1.05 and 0.80, respectively. These prey species provide essential food resources for leopards, enhancing habitat suitability.

Trophic interaction

The figure 5 illustrates significant trophic connections between predators and prey at USTR across three confidence levels: (a) 90%, (b) 80%, and (c) 70%. At 90% confidence (Fig. 5a), the connections are conservative, showing only the most significant interactions, such as tigers connected to cattle, and leopards to northern plains langur and wild pig. As the confidence level decreases to 80% (Fig. 5b) and then to 70% (Fig. 5c), the tiger exhibits increasing prey width, adding connections to sambar and spotted deer. This suggests that due to a lower tiger population and the higher biomass availability of cattle, tigers have shifted their diet towards cattle. However, tigers have a natural dietary preference for sambar and spotted deer, which are not available in abundance within their habitat area due to low populations. In contrast, the leopard's interactions remain largely unchanged across the different confidence levels, indicating a consistent prey base. This expansion of prey connections for tigers at lower significance levels highlights the complexity and broader scope of their trophic interactions compared to leopards.

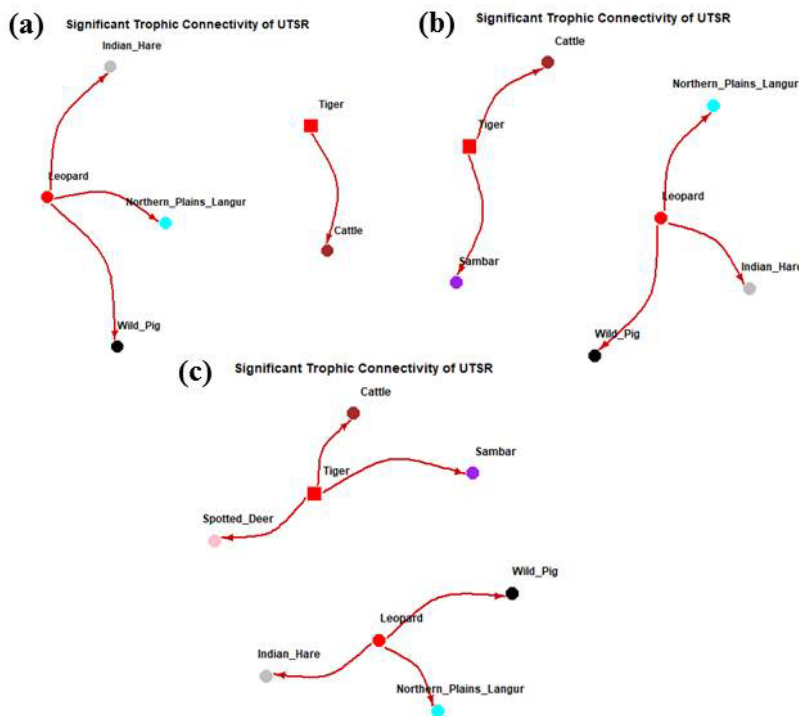


Fig. 4. The significant trophic connection between predators and prey at USTR, at 90% confidence level (a), at 80% confidence level (b), and at 70% confidence level (c).

In this experiment, we observed the following positive habitat metrics: 1512.37 km² of No Occurrence (NO), a minimal 1.08 km² of Habitat Contraction (RC), a substantial 194.45 km² of Habitat Expansion (RE), and a stable 254.8 km² of No Change (NC). These results provide a solid reference point for understanding the beneficial impact of prey manipulation on tiger habitat dynamics, highlighting the potential for improved habitat conditions when tigers' natural prey preferences are supported.

Climate Change Scenario Analysis

The habitat projections for 2021-2040 under scenarios CMIP6 SSP245 and SSP585, using models CMCC-ESM2, GISS-E2, HadGEM3-GC3, and UKSM1 reveal significant changes across the Kuladighat and Sitanadi regions (Fig. 6). The analysis indicates considerable habitat changes in both scenarios (Table 2), with more pronounced impacts under the high-emission SSP585 scenario.

For period of 2021-2040, in the SSP245 scenario (Fig. 6a), the CMCC-ESM2 model shows habitat expansion in Sitanadi (RE: 1519 km²) with no contraction. However, under the SSP585 scenario (Fig. 6b), this model projects small habitat expansions in Sitanadi (RE: 273 km²) and range contraction in Kuladighat (RC: 238 km²). In the SSP245 scenario (Fig. 6c), the GISS-E2 model highlights new habitat expansions in Sitanadi (RE: 1339 km²) with negligible range contraction (RC: 7 km²). Under the SSP585 scenario (Fig. 6d), the GISS-E2 model shows the range expansion in Sitanadi (RE: 173 km²) and range contraction Kuladighat (RC: 206 km²). In the SSP245 scenario (Fig. 6e), the HadGEM3-GC3 model predicts habitat extinction in Kuladighat (RC: 230 km²) and shifting of habitat to Sitanadi (140 km²). Under the SSP585 scenario (Fig. 6f), this model shows significant habitat contractions in Kuladighat (RC: 157 km²) and habitat expansion in Sitanadi (RE: 529 km²). In the both the scenario (Fig. 6g and 6h), the UKSM1 model shows almost similar patterns of change as HadGEM3 with habitat extinction in SSP245 scenario (RC: 247 km², RE: 6 km²) and under SSP585 habitat shifting from Kuladighat to Sitanadi (RE: 253 km², RC: 222 km²).

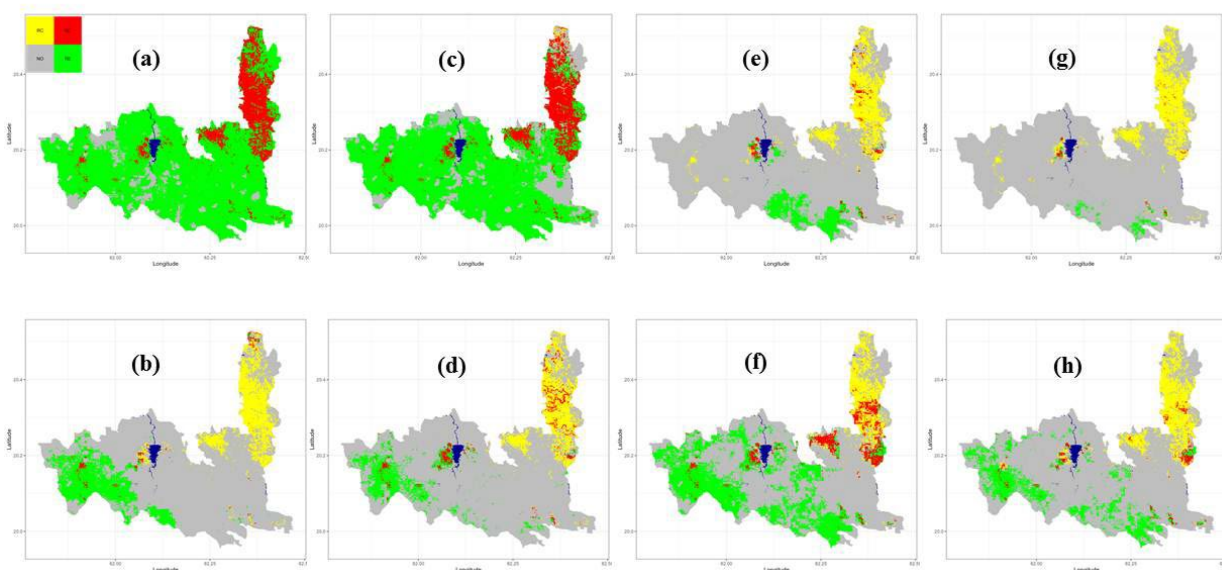


Fig. 6. The projected tiger habitat change for the future scenario 2021-2040, for scenario CMIP6 SSP245 (row 1) and SSP585 (row 2) for models CMCC-ESM2 (column 1), GISS-E2 (column 2), HadGEM3-GC3 (column 3), and UKSM1 (column 4): (a) CMIP6 SSP245 for model CMCC-

ESM2, (b) CMIP6 SSP585 for model CMCC-ESM2, (c) CMIP6 SSP245 for model GISS-E2, (d) CMIP6 SSP585 for model GISS-E2, (e) CMIP6 SSP245 for model HadGEM3-GC3, (f) CMIP6 SSP585 for model HadGEM3-GC3, (g) CMIP6 SSP245 for model UKSM1, (h) CMIP6 SSP585 for model UKSM1.

Table 2. Table presents tiger habitat changes across different climate change scenarios for the periods 2021-2040 and 2081-2100, using models GISS-E2, HadGEM3-GC3, and UKESM1 under SSP245 and SSP585 scenarios. The categories include No Occurrence (NO), Habitat Contraction (RC), Habitat Expansion (RE), and No Change (NC)

Experiment	NO	RC	RE	NC
CMCC-ESM2_ssp245_2021-2040	187.52	0	1519.3	255.88
CMCC-ESM2_ssp245_2081-2100	1706.82	254.25	0	1.63
CMCC-ESM2_ssp585_2021-2040	1433.64	238.96	273.18	16.92
CMCC-ESM2_ssp585_2081-2100	183.74	21.54	1523.08	234.34
GISS-E2-1-G_ssp245_2021-2040	367.78	7.17	1339.04	248.71
GISS-E2-1-G_ssp245_2081-2100	400.74	1.69	1306.08	254.19
GISS-E2-1-G_ssp585_2021-2040	1532.88	206.8	173.94	49.08
GISS-E2-1-G_ssp585_2081-2100	1706.63	254.32	0.19	1.56
HadGEM3-GC31-LL_ssp245_2021-2040	1565.47	230.43	141.35	25.45
HadGEM3-GC31-LL_ssp245_2081-2100	1706.82	255.88	0	0
HadGEM3-GC31-LL_ssp585_2021-2040	1177.78	157.62	529.04	98.26
HadGEM3-GC31-LL_ssp585_2081-2100	703.52	177.93	1003.3	77.95
UKESM1-0-LL_ssp245_2021-2040	1677.19	247.69	29.63	8.19
UKESM1-0-LL_ssp245_2081-2100	1706.53	255.78	0.29	0.1
UKESM1-0-LL_ssp585_2021-2040	1453.21	222.45	253.61	33.43
UKESM1-0-LL_ssp585_2081-2100	571.05	195.45	1135.77	60.43

For the period 2081-2100, the CMCC-ESM2 model under SSP245 (Fig. 7a) continues to predict complete habitat extinction (RC: 254 km²). Under the SSP585 scenario (Fig. 7b), this model projects vast expansion of habitat in Sitanadi (RE: 1523 km²) and negligible habitat contraction in Kuladighat (RC: 20 km²). The GISS-E2 model under SSP245 (Fig. 7c) shows habitat expansion significantly in Sitanadi (RE: 1306 km²) and no discernable habitat contraction (RC: 1 km²). However, under the SSP585 scenario (Fig. 7d), the GISS-E2 model is showing habitat extinction (RC: 254 km²). The HadGEM3-GC3 model under SSP245 (Fig. 7e) is showing habitat extinction (RC: 255 km²). Under the SSP585 scenario (Fig. 7f), this model shows the shifting of habitat from Kuladighat to Sitanadi (RC: 177 km², RE: 1003 km²). The UKSM1 model again follows the HadnGEM3 model. In SSP245 (Fig. 7g) it is showing habitat extinction (RC: 255 km²) and in SS585 (Fig. 7h) it showing habitat shifting from Kuladighat to Sitanadi (RC: 195 km², RE: 1135 km²).

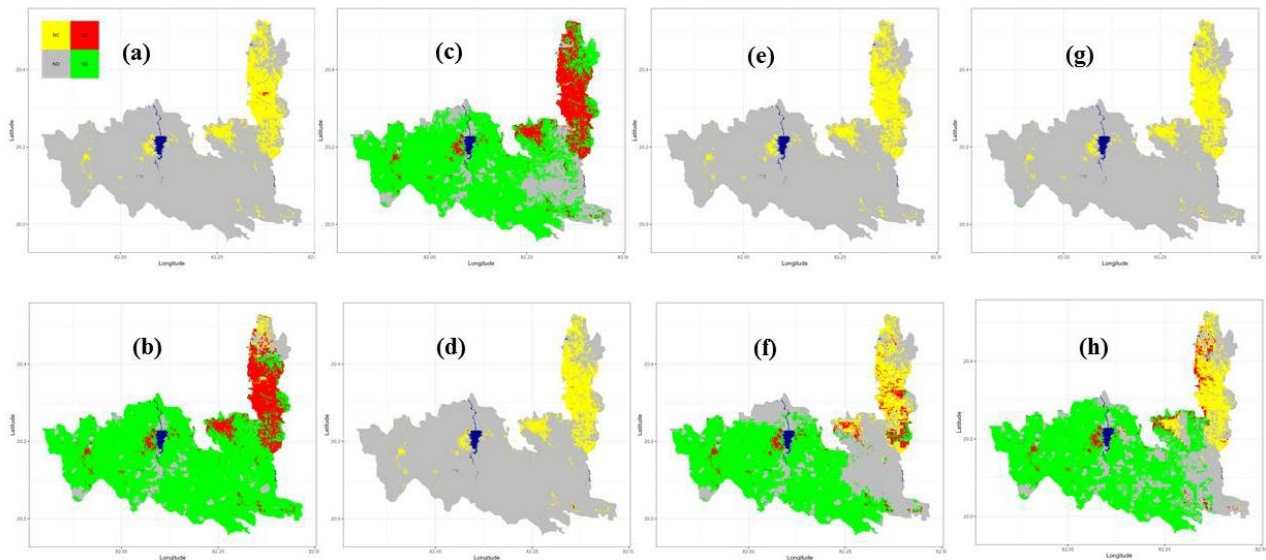


Fig. 7. The projected tiger habitat change for the future scenario 2081-2100, for scenario CMIP6 SSP245 (row 1) and SSP585 (row 2) for models CMCC-ESM2 (column 1), GISS-E2 (column 2), HadGEM3-GC3 (column 3), and UKSM1 (column 4): (a) CMIP6 SSP245 for model CMCC-ESM2, (b) CMIP6 SSP585 for model CMCC-ESM2, (c) CMIP6 SSP245 for model GISS-E2, (d) CMIP6 SSP585 for model GISS-E2, (e) CMIP6 SSP245 for model HadGEM3-GC3, (f) CMIP6 SSP585 for model HadGEM3-GC3, (g) CMIP6 SSP245 for model UKSM1, (h) CMIP6 SSP585 for model UKSM1.

DISCUSSION

Trophic interactions play a significant role in maintaining healthy predator and prey population dynamics in diverse ecosystems that simultaneously sustain the ecological balance of the ecosystem. Apex predators majorly occupy high trophic levels; their presence may regulate other predators and prey species at lower levels through trophic cascades (Ripple et al. 2014). Therefore, in the absence of predators, ecosystem functionality may face various risks (Ripple et al. 2014). In the case of African lions, their density is strongly correlated to prey density (Van Orsdol et al. 1985) and thus they faced a decline in response to prey depletion (Vinks et al. 2021) in various areas of African continent. The survival rates and population densities of subordinate competitors in those ecosystems, such as the African wild dog and cheetah show lower correlation to prey density but are negatively correlated with the density of dominant competitors (Creel and Creel 1996; Kelly et al. 1998; Mills and Biggs 1993; Mills and Gorman 1997; Swanson et al. 2014). On the contrary, a long-term study in the Greater Kafue Ecosystem (GKF), Zambia found a general decline in all large predator populations at the same time. In Zambia, African wild dog population was found to be

comparatively low when the lion population in the area declined severely, in response to declining prey population. It was expected that African wild dogs would take advantage of the reduced competition from the apex predator, the African lions, leading to an increase of their population size at that time. However, the opposite scenario had unfolded, which the African wild dog population continuing to exhibit with comparatively low population density (Goodheart et al. 2021).

In the Indian context, large predators like tigers exert competitive pressure on other subordinate or co-predators, which in turn may positively influence the prey populations. Therefore, in tiger-ranging areas, studies have observed that decline in the population of top predators like tigers leads to an increase in the subordinate predators like leopards. Similarly, reintroducing tigers to its past range can significantly lower the leopard population due to increased spatial and dietary competition from tigers (Harihar et al. 2011; Mondal et al. 2013). Previous studies conducted in USTR had indicated that the area has nearly lost its tiger population, with only one or two individuals still remaining (Qureshi et al. 2022; Basak et al. 2023). In response to the absence of apex predators, the leopard population was expected to flourish, but leopards were found to survive with a comparatively low population density of 1.56 ± 0.36 SE/100 km² (citation again). Subsequently, the prey species, especially the ungulate species of every size, exhibited the same trend; the derived ungulate density was only 8.46 ± 2.1 SE individuals/km² (Basak et al. 2023). Globally, prey depletion is known to result in decline of large carnivores and this is found to be a very prominent issue in USTR as well. This bottom-up effect was seen in the trophic experiment using Trophic SDM to check the trophic interaction between the available prey and predators. In this study, the predicted trophic connections at 90% confidence highlighted that tigers only have interactions with cattle and leopards have significant interactions with northern plains gray langur, Indian Hare, and wild pig, but by lowering the confidence level to 80% and 70% with much more flexible options, the model indicated connections between tigers and sambar and spotted deer, whereas leopards remained more or less unchanged and maintained the relationship with northern plains gray langur, wild pig, and Indian hare. Overall, this study revealed that in a situation where the prey population has significantly plummeted, leopards have expanded their diet to include medium- and small-sized prey like Indian hare, northern plains gray langur, and wild pig. Tigers, on the other hand, have shifted towards free-ranging domestic cattle available in the forest villages or hamlets to fulfill their energy requirements in the absence of large herbivores with larger biomass that are ideally their preferred prey. Therefore, increasing the population size for various preys can change the scenario of predator-prey interactions; recruiting various prey species, especially large and medium-sized ungulates like the gaur, sambar, wild pig, and spotted deer for tigers, is highly crucial for the long-term survival of the species with other co-predators.

Apart from trophic interactions among prey and predator species in USTR, this study investigated prey-mediated habitat utilization and predator distribution in this landscape. The spatial utilization of a large predator reflects the interactions between various biotic and abiotic factors, bioclimatic parameters, human influences, the presence of competitors, and access to water (Bailey 1993; Marker and Dickman 2005; Vanak et al. 2013; Snider et al. 2021). Central India and the Eastern Ghats tiger landscape complex comparably have the highest tiger population and remarkable spatial occupancy in India, due to good habitat conditions and corridor connectivity among the tiger reserves and other forested areas. This tiger landscape complex spread across the states of Rajasthan, Maharashtra, Madhya Pradesh, Chhattisgarh, Jharkhand, and Odisha. Additionally, it includes the areas from Eastern Ghats in Telangana, Andhra Pradesh, and Odisha, and certain parts of the Northern Western Ghats (Sahyadri) in Maharashtra to maintain the characteristic integrity of the landscape complex (Qureshi et al. 2022). Despite being part of a region that supports the highest density of tigers, there are areas like Udanti Sitanadi Tiger Reserve that lack proper habitat conditions for tigers to thrive, the observed population size is significantly lower than the expected viable population size for this region. The reserve spans over an area of 1843 km² but only 13% of it is suitable for tigers. Severely depleted prey populations in the area have pushed tigers to be reliant on cattle as their primary food source, as evident from our study. The suitability experiment predicted that only 23% of the total area is suitable for even the highly adaptable big cat, the leopards. Leopards occupy a prominent position in the trophic pyramid alongside tigers, exhibiting adaptability in habitat and dietary preferences, and playing a vital role as top predators in a wide array of landscapes across India (Qureshi et al. 2024). Therefore, we considered analysis of leopards' habitat in USTR as well. Our study revealed that leopards were also surviving in a low density in the area. To adapt to the conditions there, leopards have shifted to small sized prey species like langur, Indian hare, medium sized prey like wild pig and also opportunistically kill cattle they come across in the reserve. High spatial occurrence of animal traps in the reserve indicates poaching activities prevalent within the reserve. This contributes to the large degree of depletion of animal in the area which eventually plays a role in prey and predator population across time scales. Thus, protection measures and effective interventions are needed to be implemented to curb the challenges of human dependence in USTR.

Ideal tiger habitat consists of areas suitable for hunting and raising cubs, sufficient availability of prey biomass, preferentially medium- and large-sized ungulates, and freedom from persecution by humans, the tiger's main competitor (Gittleman and Harvey 1982; Karanth and Sunquist 1992; Smith 1993; Miquelle et al. 1999a; Darimont et al. 2023). If we keep aside the anthropogenic parameters, climate change predominantly shapes tigers' habitat in the wild (Cooper et al. 2016). Climate change is globally altering natural ecosystems, habitats and thus niches and

their biodiversity (Bellard et al. 2012). In future, climate change together with human activities will cause severe habitat degradation, biodiversity loss, habitat loss and eventually extinction of species and can potentially push the apex predators such as tiger towards extinction too.

Our study suggests that slope orientation influences predator habitat selection differently, potentially due to factors such as prey distribution, microclimate, or hunting efficiency. East-facing slopes often receive more sunlight in the morning, creating warmer microclimates that may attract prey species and, consequently, tigers. Conversely, north-facing slopes are typically cooler and might provide better cover for leopards, which are known for their stealth and adaptability in diverse environments. These preferences could also be tied to species-specific behaviors and physiological needs, which warrant further investigation.

In our study area, the detailed analysis of effect of climate change in certain time periods highlights the differential impacts on Kuladighat and Sitanadi areas. The projected habitat changes for 2021–2040 (Fig. 6) and 2081–2100 (Fig. 7) under CMIP6 scenarios SSP245 and SSP585 using CMCC-ESM2, GISS-E2, HadGEM3-GC3, and UKSM1 models reveal significant regional differences in habitat dynamics in USTR. Kuladighat region, which is the last remaining tiger habitat in USTR, faces substantial habitat changes, while Sitanadi region, where tigers have not been recorded in the last decade, is projected to experience expansions and new occurrences. The hilly Kulhadighat, with its less dense human population, appears more vulnerable to habitat changes, and can even experience habitat extinction as models predicted, while the plains and lower hills of Sitanadi, with higher human population density, are likely to see increased habitat suitability.

This dichotomy of habitat gains and loss in tiger reserve areas necessitates a dual approach in conservation strategies. For Kulhadighat, efforts should focus on preserving the remaining habitats and restoration of degraded habitats through targeted conservation programs and mitigation of climate impacts. In contrast, Sitanadi will require strategies to manage the influx of new habitats and potential species migrations. Proactive measures such as creating wildlife corridors and buffer zones can help mitigate human-wildlife conflicts and promote biodiversity resilience. Human activities can make the parameters such as maintaining habitat connectivity and species influx vulnerable in future and thus need to be safeguarded with strong protection measures in the landscape. This underlines the necessity to account for both climate change model-scenario uncertainty and inter-model variability. These variations in projections among models must be considered whenever these future projections are used to inform conservation planning.

Globally, tigers experienced 150 years of decline; after which the habitat for the tigers seems to have stabilized at around 16% of its indigenous extent (1.817 million km²). There were 63 Tiger Conservation Landscapes in the world as of 1st January 2020; spread over 911,920 km² shared

across 10 of the 30 present-day countries which once harboured tiger populations. Over the last 20 years, the total area of Tiger Conservation Landscapes (TCLs) has declined from 1.025 million km² in 2001, a range-wide loss of 11%, with the greatest losses in Southeast Asia and southern China. Meanwhile there was significant increase in Tiger Conservation landscapes in India, Nepal, Bhutan, Northern China and South-eastern Russia. Overall, 226 restoration landscapes in these areas can result in 50% rise in tiger population (Sanderson et al., 2023). We found that USTR represents a landscape where careful integration of conservation strategies, positive community participation and continuous input of strong scientific recommendations can secure a thriving future for tigers, co-predators and their prey species. This in turn could restore the functionality of the Chhattisgarh-Odisha Tiger Conservation Unit (TCU) and establish it as a reservoir of biodiversity. These findings highlight the urgent need for adaptive management and conservation strategies tailored to the specific challenges and opportunities presented by the USTR landscape. USTR falls approximately under 35% of the tiger reserves in the country, which urgently needs efficient and effective planning for habitat restoration, ungulate augmentation, and subsequent tiger reintroduction. This will be highly crucial to ensuring sustainable coexistence between human and natural systems in the face of ongoing climate change.

Our results highlight the importance of implementing adaptive regional management and conservation tools to adequately address local threats while utilizing new opportunities. The future of biodiversity and a sustainable coexistence of human systems with natural systems in the backdrop of continued climate change will largely depend on successful planning and implementation. By accounting for these uncertainties, conservation strategies can be made more robust and resilient, ensuring they remain effective under a range of possible future climate scenarios.

CONCLUSION

The study assesses trophic cascades and habitat suitability in the Udanti Sitanadi Tiger Reserve (USTR) with a focus on interactions among apex predators, subordinate predators, and prey species using comprehensive analytical tools. The results highlight the importance of tigers and leopards in ecosystem regulation, as well as the negative consequences of depleting prey populations and human activity.

The study uses the Trophic Species Distribution Model (SDM) to provide an understanding of the spatial and trophic dynamics of USTR. The findings highlight the need for focused

conservation strategies, including habitat restoration and prey supplementation, to help sustain apex predator populations as well as ecological diversity.

Our climate change projections reveal the need for rapid adaptive management to ameliorate habitat shifts and also maintain the ecosystem resilience of USTR. The successful implementation of these approaches will require collaborative efforts with local communities, government agencies, and conservation organizations.

Together, this study leads to better insights into ecological interactions and a strong framework for designing conservation action plans with priorities that are implemented in prey-depleted landscapes such as USTR. Conservation of these iconic species effectively secures their prey base and the overall health of forests. It not only contributes to tiger conservation but also provides ecosystem services such as clean drinking water and air quality improvement. This overall study suggests maintaining a healthy environment in the tiger reserve. To achieve that, the USTR authority must integrate community-based protection strategies into their conservation planning. Regular engagement with local communities is essential, with targeted awareness programs designed for children, students, youth, and adults. These initiatives foster rapport between management and villagers, which is critical for reducing activities such as trapping and poaching. Building strong and efficient networks with communities residing within the reserve can further strengthen these efforts. Additionally, implementing regular anti-snare walks and snare removal programs will significantly curb poaching activities. Such proactive measures ensure a safer habitat for wildlife.

Strengthening legal actions against poaching is equally vital to reinforce the rule of law and demonstrate the effectiveness of legal institutions in combating wildlife crimes. To address human-wildlife conflicts, specialized teams should be deployed to report incidents, follow up on cases, and assist villagers in filing for compensation. Providing timely support in securing compensation from the concerned authorities can build trust and reduce conflict between the communities and the reserve authority. These supportive measures can positively impact local communities, encouraging cooperation and enabling authorities to better manage conflicts in the future.

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REFERENCES

- Bailey TN. 1993. The African leopard: ecology and behavior of a solitary felid. Columbia University Press.
- Basak K, Mandal D, Babu S, Kaul R, Ashraf NVK et al. 2018. Prey animals of tiger (*Panthera tigris tigris*) in Dudhwa landscape, Terai Region, North India. *Proc Zool Soc* **71**:92–98. doi:10.1007/s12595-016-0196-5.
- Basak K, Ahmed M, Suraj M, Reddy BV, Yadav OP et al. 2020. Diet ecology of tigers and leopards in Chhattisgarh, central India. *J Threatened Taxa* **12**:15289–15300. doi:10.11609/jott.5526.12.3.15289-15300.
- Basak K, Suraj M, Ahmed M, Kumar U, Bhattacharjee S. 2023. The first attempt of assessing the population status of large predators and their prey in an unexplored central Indian Protected Area. *Wildlife Lett* **1**:47–58. doi:10.1002/wll2.12015.
- Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. 2012. Impacts of climate change on the future of biodiversity. *Ecol Lett* **15**:365–377. doi:10.1111/j.1461-0248.2011.01736.x.
- Berger KM, Gese EM, Berger J. 2008 Indirect effects and traditional trophic cascades: A test involving wolves, coyotes, and pronghorn. *Ecol* **89**:818–828. doi:10.1002/ece3.9855
- Bharos AMK, Bux F, Basak K, Ahmed M, Bharos A. 2018. Avian diversity and range extensions records from Udanti-Sitanadi tiger reserve, Chhattisgarh, India. *Int J Fauna Biol Stud* **5**:214–227.
- Champion HG, Seth SK. 1968. The Forest Types of India. The Government of India press, New Delhi, pp. 1–404.
- Cooper DM, Dugmore AJ, Gittings BM, Scharf AK, Wilting A et al. 2016. Predicted Pleistocene–Holocene range shifts of the tiger (*Panthera tigris*). *Divers Distrib* **22**:1199–1211. doi:10.1111/ddi.12484.
- Cosentino F, Seamark E, Cakenberghe VV, Maiorano L. 2023. Not only climate: The importance of biotic interactions in shaping species distributions at macro scales. *Ecol and Evol* **13**:e9855. doi:10.1002/ece3.9855.
- Creel S, Creel NM. 1996. Limitation of African wild dogs by competition with larger carnivores. *Conserv Biol* **10**:526–538. doi:10.1046/j.1523-1739.1996.10020526.x.
- Crooks KR, Soulé ME. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nat* **400**:563–566. doi:10.1038/23028
- Daniel JC. 1996. The Leopard in India. Natraj Publishers, Dehra Dun, pp. 1–228.
- Darimont CT, Cooke R, Bourbonnais ML, Bryan HM, Carlson SM et al. 2023. Humanity’s diverse predatory niche and its ecological consequences. *Commun Biol* **6**:609. doi:10.1038/s42003-023-05112-5.

- Edgaonkar A, Chellam R. 1998. A preliminary study on the ecology of the Leopard, *Panthera pardus fusca* in Sanjay Gandhi National Park, Maharashtra. Wildlife Institute of India, Dehradun, Park, Maharashtra. RR-98/002, pp. 1–33.
- Edgaonkar A. 2008. Ecology of the leopard (*Panthera pardus*) in Bori Wildlife Sanctuary and Satpuda National Park, India. Dissertation, University of Florida, Gainesville, Florida, USA.
- Edwards M. 2014. A review of management problems arising from reintroductions of large carnivores. J Young Investigators **27**:11–16.
- Eisenberg JF, Lockhart M. 1972. An ecological reconnaissance of Wilpattu National Park, Ceylon. Smithsonian Contrib Zool **101**:1–118. doi:10.5479/si.00810282.101.
- Elmhagen B, Rushton SP. 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? Ecol Lett **10**:197–206. doi:10.1111/j.1461-0248.2006.01010.x.
- Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JB, Marquis RJ. 2011. Trophic downgrading of planet Earth. Sci **333**:301–306. doi:10.1126/science.1205106.
- Gittleman JL, Harvey PH. 1982. Carnivore home-range size, metabolic needs and ecology. Behav Ecol Sociobiol **10**:57–63. doi:10.1007/BF00300060.
- Goodheart B, Creel S, Becker MS, Vinks M, Schuette P et al. 2021. Low apex carnivore density does not release a subordinate competitor when driven by prey depletion. Biol Conserv **261**:109273. doi:10.1016/j.biocon.2021.109273.
- Harihar A, Pandav B, Goyal SP. 2011. Responses of leopard *Panthera pardus* to the recovery of a tiger *Panthera tigris* population. J Appl Ecol **48**:806–814. doi:10.1111/j.1365-2664.2011.02007.x.
- Hayward MW, Jedrzejewski W, Jedrzejewska B. 2012. Prey preferences of the Tiger *Panthera tigris*. J Zool **286**:221–231. doi:10.1111/j.1469-7998.2011.00871.x.
- Jhala YV, Qureshi Q, Yadav SP. 2020. Status of leopards in India, 2018. National Tiger Conservation Authority, Government of India, New Delhi, and Wildlife Institute of India, Dehradun. Technical Report TR/2020/16.
- Johnsingh AJT. 1983. Large mammalian prey-predators in Bandipur. J Bombay Nat Hist Soc **80**:1–57.
- Kanoje RS. 2008. Nesting sites of Indian giant squirrels in Sitanadi wildlife sanctuary, India. Curr Sci **94**:882–884.
- Karanth KU, Sunquist ME. 1992. Population structure, density and biomass of large herbivores in the tropical forests of Nagarhole, India. J Trop Ecol **8**:21–35. doi:10.1017/S0266467400006040.

- Karanth KU, Sunquist ME. 1995. Prey selection by tiger, leopard and dhole in tropical forests. *J Anim Ecol* **64**:439–450. doi:10.2307/5647
- Karanth KU, Kumar NS, Karanth KK. 2020. Tigers against the odds: Applying macro-ecology to species recovery in India. *Biol Conserv* **252**:108846. doi:10.1016/j.biocon.2020.108846.
- Kelly MJ, Laurenson MK, Fitzgibbon CD, Collins DA, Durant SM et al. 1998. Demography of the Serengeti cheetah (*Acinonyx jubatus*) population: The first 25 years. *J Zool* **244**:473–488. doi:10.1017/S0952836998004014.
- Letnic M, Ritchie EG, Dickman CR. 2012. Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biol Rev* **87**:390–413. doi: 10.1111/j.1469-185X.2011.00203.x.
- Marker LL, Dickman AJ. 2005. Factors affecting leopard (*Panthera pardus*) spatial ecology, with particular to Namibian farmlands. *S Afr J Wildl Res* **35**:105–115.
- Mills MGL, Biggs HC. 1993. Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. *Symp Zool Soc Lond* **65**:253–268.
- Mills MG, Gorman ML. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conserv Biol* **11**:1397–1406. doi:10.1046/j.1523-1739.1997.96264.x.
- Miquelle DG, Smirnov EN, Merrill TW, Myslenkov AE, Quigley HB et al. 1999a. Hierarchical spatial analysis of Amur tiger relationships to habitat and prey. *In: Riding the Tiger: tiger conservation in human-dominated landscapes*. Cambridge University Press, Cambridge, UK, pp. 71–99.
- Mondal K, Gupta S, Qureshi Q, Sankar K. 2011. Prey selection and food habits of leopard (*Panthera pardus fusca*) in Sariska Tiger Reserve, Rajasthan, India. *Mammalia* **75**:201–205. doi:10.1515/mamm.2011.018.
- Mondal K, Sankar K, Qureshi Q. 2013. Factors influencing the distribution of leopard in a semi-arid landscape of Western India. *Acta Theriol* **58**:179–187. doi:10.1007/s13364-012-0104-3.
- National Tiger Conservation Authority (NTCA). 2011. A protocol on Phase-IV Monitoring (Technical Document No. 1/2011) New Delhi, India: NTCA.
- Norohna R. 2022. Losing its stripes. Available at: <https://www.indiatoday.in/india-today-insight/story/losing-its-stripes-1604995-2019-10-01>.
- Putul AP. 2021. Maoist insurgency in all three of Chhattisgarh's tiger reserves has made conservation difficult. Available at: <https://scroll.in/article/1003162/maoist-insurgency-in-all-three-of-chhattisgarhs-tiger-reserves-has-made-conservation-difficult>.
- Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ et al. 2009. The rise of the mesopredator. *Biosci* **59**:779–791.
- Poggiato G, Andréoletti J, Shirley L, Thuiller W. 2022. Integrating food webs in species distribution models improves ecological niche estimation and predictions. *Authorea*. November 15, 2022.

doi:10.22541/au.166853394.45823739/v1.

- Qureshi Q, Edgaonkar A. 2006. Ecology of Leopard in Satpura-Bori conservation area, Madhya Pradesh. Final Report. Wildlife Institute of India, Dehradun, pp. 1–119.
- Qureshi Q, Jhala YV, Yadav SP, Mallick A. eds. 2022. Status of tigers, co-predators and prey in India, 2022. National Tiger Conservation Authority, Government of India, New Delhi, and Wildlife Institute of India, Dehradun.
- Qureshi Q, Jhala YV, Yadav SP, Mallick A. eds. 2023. Status of tigers, co-predators and prey in India, 2022. National Tiger Conservation Authority, Government of India, New Delhi, and Wildlife Institute of India, Dehradun. .
- Qureshi Q, Jhala YV, Yadav SP, Tiwari VR, Garawad R, Mallick A. eds. 2024. Status of Leopards in India, 2022. National Tiger Conservation Authority, Government of India, New Delhi, and Wildlife Institute of India, Dehradun.
- Rabinowitz A. 1989. The density and behaviour of large cats in a dry tropical forest mosaic in Huai Kha Khaeng Wildlife Sanctuary, Thailand. Nat Hist Bull Siam Soc **37**:235–251.
- Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG et al. 2014. Status and ecological effects of the world’s largest carnivores. Sci **343**:1241484. doi:10.1126/science.1241484.
- Sanderson EW, Miquelle DG, Fisher K, Harihar A, Clark C et al. 2023. Rangewide trends in tiger conservation landscapes, 2001–2020. Front Conserv Sci **4**:1191280. doi:10.3389/fcosc.2023.1191280.
- Sankar K, Johnsingh AJT. 2002. Food habits of tiger (*Panthera tigris*) and leopard (*Panthera pardus*) in Sariska Tiger Reserve, Rajasthan, India, as shown by scat analysis. Mammalia **66**:285–289. doi:10.1515/mamm.2002.66.2.285.
- Santiapillai C, Chambers MR, Ishwaran N. 1982. The Leopard *Panthera pardus fusca* (Meyer 1794) in the Ruhuna National Park, Sri Lanka and observations relevant to its conservation. Biol Conserv **23**:5–14. doi:10.1016/0006-3207(82)90003-2.
- Sarmiento P, Bandeira V, Gomes P, Carrapato C, Eira C, Fonseca C. 2021. Adapt or perish: How the Iberian lynx reintroduction affects fox abundance and behaviour. Hystrix **32**:48–54.
- Seidensticker J, Sunquist ME, McDougal C. 1990. Leopards living at the edge of the Royal Chitwan National Park, Nepal. In: Daniel JC, Serrao JS, eds. Conservation in developing countries: Problems and prospects. Proc Centenary Seminar of the Bombay Natural History Society and Oxford University Press, Bombay, pp. 415–423.
- Sidhu S, Raghunathan G, Mudappa D, Raman TRS. 2017. Human-Leopard interactions in a plantation landscape in Anaimalai hills, India. Conserv Soc **15**:474–482. doi:10.4103/cs.cs_16_111.

- Smith JLD. 1993. The role of dispersal in structuring the Chitwan tiger population. *Behav* **124**:165–195. doi:10.1163/156853993X00500.
- Snider MH, Athreya VR, Balme GA, Bidner LR, Farhadinia MS et al. 2021. Home range variation in leopards living across the human density gradient. *J Mammal* **102**:1138–1148. doi:10.1093/jmammal/gyab050.
- Stripes. 2011. Bi-monthly outreach journal of National Tiger Conservation Authority Government of India. Vol. 3, Issue 1.
- Swanson A, Caro T, Davies-mostert H, Mills MGL, Macdonald W et al. 2014. Cheetahs and wild dogs show contrasting patterns of suppression by lions. *J Anim Ecol* **83**:1418–1427. doi:10.1111/1365-2656.12231.
- Terborgh J, Feeley K, Silman M, Nuñez P, Balukjan B. 2006. Vegetation dynamics on predator-free land-bridge islands. *J Ecol* **94**:253–263.
- Trainor AM, Schmitz OJ, Ivan JS, Shenk TM. 2014. Enhancing species distribution modeling by characterizing predator-prey interactions. *Ecol Appl* **24**:204–216. doi:10.1890/13-0336.1
- Van Orsdol K, Hanby JP, Bygott JD. 1985. Ecological correlates of lion social organization (*Panthera leo*). *J Zool* **206**:97–112. doi:10.1111/j.1469-7998.1985.tb05639.x.
- Vanak AT, Fortin D, Thaker M, Ogden M, Owen C, Greatwood S, Slotow R. 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecol* **94**:2619–2631.
- Vinks MA, Creel S, Schuette P, Becker MS, Rosenblatt E et al. 2021. Response of lion demography and dynamics to the loss of preferred larger prey. *Ecol Appl* **31**:e0298. doi:10.1002/eap.2298.
- Wallach AD, Izhaki I, Toms JD, Ripple WJ, Shanas U. 2015. What is an apex predator? *Oikos* **124**:1453–1461. doi:10.1111/oik.01977.