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Multi-species habitat suitability and gap analysis in the Central Western Ghats, India

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Abstract

Protected areas (PAs) are considered core to global biodiversity conservation, but their effectiveness depends on how well they represent habitats required for the species distributions. This study evaluates habitat suitability and conservation gaps for seven large mammal species across protected (Kali Tiger Reserve) and non-protected areas (Karwar and Yellapur Forest Divisions) in Uttara Kannada district, Karnataka, India. We used an ensemble Species Distribution Modelling (SDM) framework with six algorithms: Generalized Linear Model (GLM), Generalized Additive Model (GAM), Maximum Entropy (MaxEnt), Random Forest (RF), Gradient Boosting Machine (GBM), and Multivariate Adaptive Regression Splines (MARS). The models incorporated camera-trap presence-absence data (March -June 2024) and environmental predictors: land-use and land-cover derivatives, elevation, terrain ruggedness, enhanced vegetation index, distance to water bodies, and human disturbance. Model performance was strong for all species (AUC-ROC: 0.68–0.93), with vegetation productivity and proximity to water as key factors influencing distributions. We overlaid binary habitat suitability maps to create a multi-species richness surface and compared Protected and Non-Protected areas categories using Welch's t-test and Cohen's d effect size. While the protected area showed slightly higher mean species richness, significant areas of moderate to high suitability were found in non-protected forest divisions, revealing ongoing gaps in the conservation network. Our results highlight the ecological value of non-protected area forests and support a landscape-level management approach to maintain habitat connectivity across both protected and non-protected areas in this important biodiversity hotspot.

Keywords: Karnataka, Uttara Kannada district, PA & Non-PA Network, Species Distribution Model, Large Mammals

Introduction

Protected areas (PAs) are a key approach to conserving global biodiversity and sustaining ecosystem services (Lecina-Diaz et al. 2019; Neugarten et al. 2020). However, the effectiveness of PA networks depends not only on their spatial extent but also on their capacity to represent species distributions and ecological processes across landscapes (Sundblad et al. 2011; Santini et al. 2016). In many developing countries, existing protected areas do not fully encompass suitable habitats for a broad range of large mammal species that require extensive home ranges and functional connectivity (Minor et al. 2010; Brennan et al. 2022). Large mammals are at risk of habitat loss due to their extensive home ranges and low population densities (Ripple et al. 2014; Ripple et al. 2015). In a fragmented habitat, even small changes can substantially affect their home range and resource availability (Pacifici et al. 2023; IPBES 2024; Keck et al. 2025). One such negative outcome of these fragmented habitats is the disruption of movement patterns, which consequently increases the risk of local extinctions (Crooks and Sanjayan 2006). It is therefore essential to maintain suitable forest habitats and functional corridors across PAs and Non-Protected Areas (non-PAs) to support viable populations of large mammals. These challenges are even more concerning in biodiversity hotspots, where species abundance is under significant threat from land-use change and other anthropogenic pressures.

Globally, 36 regions are defined as biodiversity hotspots, including the Western Ghats in India, which is also a UNESCO World Heritage Site of significant concern (IUCN 2025). The Ghats span across six Indian states (Kerala, Tamil Nadu, Karnataka, Goa, Maharashtra and Gujarat) and harbor a plethora of flora and fauna. The state of Karnataka itself supports a total of 128 mammals, of which 21 are endemic species (Sharma et al. 2025), and has a network of PAs & non-PAs with 5 Tiger Reserves, 30 Wildlife Sanctuaries, 15 Conservation Reserves, and 1 Community Reserve (KSRSAC, 2026). Research indicates that many suitable habitats for wide-ranging species exist outside PA boundaries, highlighting the shortcomings of focusing solely on reserves for conservation (Srivathsa et al. 2014; Ghosh-Harihar et al. 2019). Non-PAs often serve as ecological corridors for large mammals, facilitating movement and dispersal (Karanth et al. 2010; Velho et al. 2016). However, an increase in fragmentation and infrastructure expansion leads to degradation of vital ecological corridors, thereby reducing landscape connectivity, impeding species dispersal and increasing the likelihood of local extirpations. With an incessant increase in the sanctioning and proposal of developmental projects, risks pertaining to fragmentation and alteration of landscape connectivity in the Western Ghats are bound to increase (Gubbi et al. 2014; Puri et al. 2020). These disturbances not only degrade habitat quality but also affect animal behavior and raise mortality risks as the tendency to interact with human-dominated landscapes increases (Naha et al. 2020). Understanding

how habitat quality varies across PAs & non-PAs, and how ecological assessments are affected by loopholes in the context of habitat management is important. Further, based on these loopholes, a strategic plan for expanding the network connectivity between PAs & non-PAs is also necessary to prioritize areas of high conservation importance. As a result, addressing the 'gap' has become a focus of conservation research. Although it is ideal for gap analyses to include all species of conservation concern, it is often impractical to account for the full spectrum of biodiversity, including rare, transient, and poorly detected species, particularly when relying on systematic sampling (Scott et al. 1993). Consequently, conservation planning commonly relies on a subset of representative or indicator species whose ecological requirements capture broader patterns of biodiversity and habitat use. Thus, to some extent, accurately predicting the distributions of such species can substantially improve the effectiveness of gap analyses by enabling the identification of ecologically important areas that are insufficiently protected (Rodrigues et al. 2003).

Species Distribution Models (SDMs) are widely recognized as effective tools for predicting habitat suitability and quantifying the relative influence of environmental and anthropogenic drivers on species distributions (Phillips et al. 2006; Elith et al. 2011). By integrating species occurrence data with spatially explicit environmental covariates, SDMs can facilitate the delineation of ecologically suitable habitats and enable the identification of areas that may be underrepresented within current conservation frameworks or in land-use change. When combined with gap analysis, these methods provide a framework for evaluating the effectiveness of existing PAs networks as well as prioritizing areas for conservation intervention (Rodrigues et al. 2004; Margules and Pressey 2000). Despite these advances, significant gaps remain in understanding habitat suitability patterns for various large mammal species across PAs & non-PAs. In the Western Ghats, most studies have been taxon-specific or restricted to individual PAs, with limited attention to multi-species assessments and landscape-scale connectivity (Srivathsa et al. 2023). Given the accelerating pace of land-use change in biodiversity hotspots like these, there is an urgent need for integrative approaches that concurrently evaluate habitat suitability, connectivity, and conservation gaps across heterogeneous landscapes within the Western Ghats.

In this context, this study aims to assess habitat suitability and conservation gaps for large mammals in the central Western Ghats landscape. Specifically, to (1) assess the habitat suitability of selected large mammals using an ensemble SDM framework, (2) examine the role of both PAs and non-PAs in supporting species richness and distributions, and (3) compare PAs and non-PAs richness to evaluate the conservation effectiveness.

Methods

Study Area

The study was conducted between March and June 2024, within the geographic coordinates 14°55′N to 15°35′N and 74°05′E to 74°45′E, across a proportionate area of the Kali Tiger Reserve (18.37%) and two forest divisions (23.56%) of Karwar and (8.27%) Yellapur, situated in the Uttara Kannada district of Karnataka, India. Within these divisions, sampling was carried out across nine selected forest ranges: Ankola, Anshi Wildlife, Gund, Gopashitta, Idangundi, Mastikatta, Mallapur, Kadra Wildlife, and Ramangulli. Further, within these ranges, there were 49 beats and an area of 804.25 km² (**Fig. 1**). Tropical evergreen and semi-evergreen forests dominate the study area, which gradually transitions into moist and dry deciduous forests towards the eastern boundary of Yellapur Forest Division. The Kali River is the major west-flowing river, along with numerous stream orders that eventually drain into the Arabian Sea. The terrain is highly undulating, with altitude variations from 3 to 700 meters above sea level. Therefore, there is a variety in plant composition (Ramachandra et al. 2018). The climate is, on average, tropical, with mild, warm winters and harsh, humid summers, and a mean annual temperature of 25-28°C. The region receives rainfall during the southwest monsoon, with most places receiving more than 2000 mm a year and the windward slopes of the Sahyadris more than 4000 mm a year (IMD 2023).

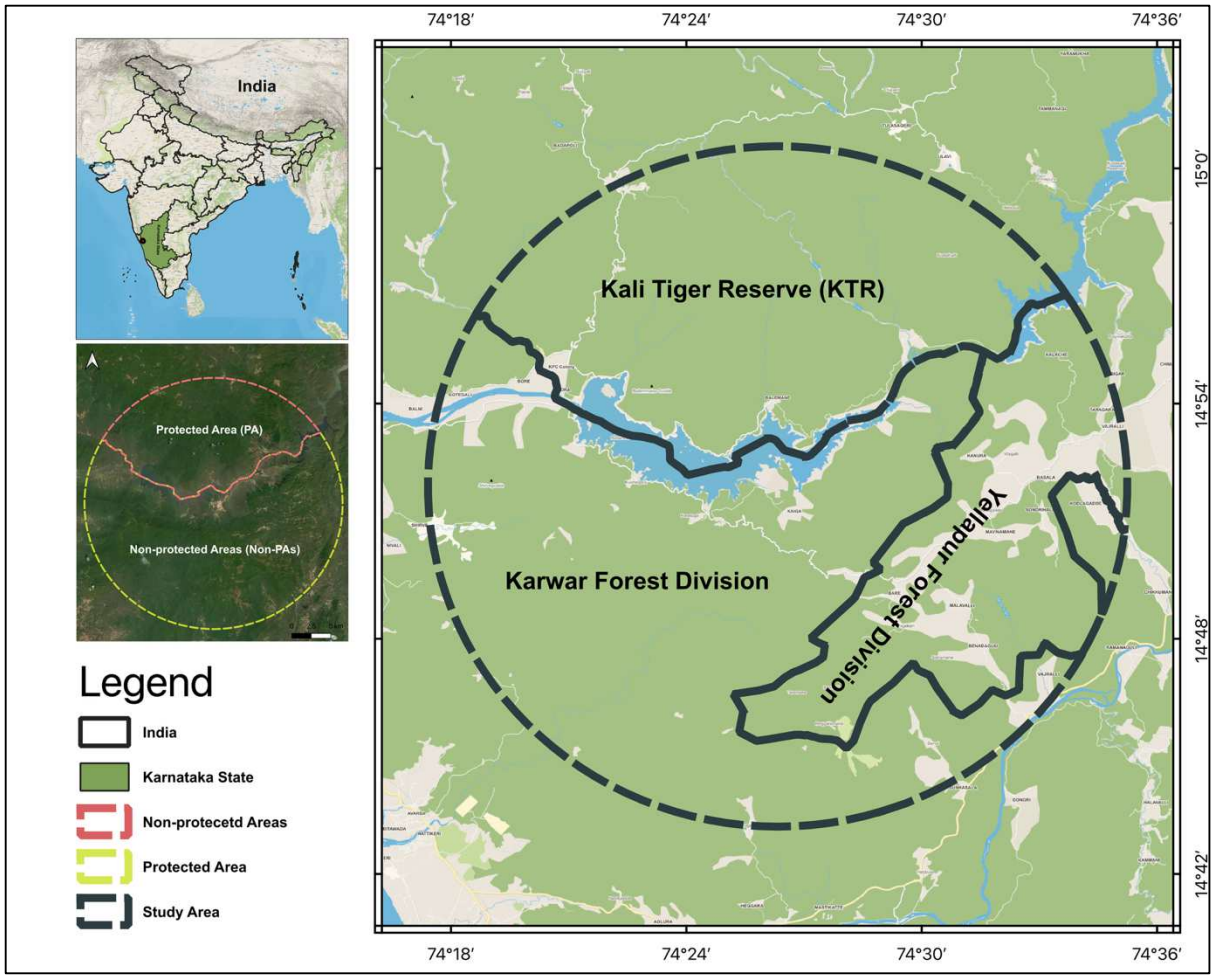


Fig. 1. The Study area, showing the protected area (Kali Tiger Reserve), adjoining non-protected area (Karwar Forest Division and Yellapur Forest Division) in the state of Karnataka, India.

Field Survey

A grid-based stratified random sampling method was applied across the entire study area, dividing it spatially into 4 km² grids (n = 225). Based on the FSI Report (2009), we classified the forest type into four major classes: wet evergreen forest, semi-evergreen forest, tropical moist deciduous forest, and tropical dry deciduous forest, and calculated the area of each class for each grid cell. We excluded large settlements and selected 40% of the area of each forest type for camera trap deployment. We strategically placed 87 camera traps (Browning Trail Cameras Strike Force Pro X1080 model) across 73 unique grids for 1,842 trap nights and recorded 22 mammal species. Camera-trap detections for each species were compiled into detection histories across discrete sampling occasions and subsequently transformed into a binary presence-absence matrix, in which 1 indicated at least one detection at a given site, and 0 indicated no detections. From the recorded assemblage, we selected seven large mammals based on their feeding habits and adequate detection frequencies: Tiger, Common Leopard, Dhole, Gaur, Sambar, Spotted Deer, and Wild Pig. To address potential spatial autocorrelation and sampling bias, our occurrence records were spatially thinned to a 1 km resolution using the *spThin* package in R version 4.3.1 (Aiello-Lammens et al. 2015) (**Table 1**) *(*see Supplementary Information ESM 1 for species occurrence data).

Table 1. Seven selected mammals with their taxonomic information, including species, and common names, along with global conservation status (iucnredlist.org), national conservation status under the Wild Life (Protection) Amendment Act, 2022, total number of occurrence records, and the number of spatially thinned records retained for species distribution modeling.

Species	Scientific Name	Taxonomic families	Global Conservation Status (IUCN)	National Conservation Status (WPA Schedule)	Number of Occurrences	Thinned Location
Common leopard	*Panthera pardus*	Felidae	Vulnerable	Schedule I	37	29
Dhole	*Cuon alpinus*	Canidae	Endangered	Schedule I	7	3
Gaur	*Bos gaurus*	Bovidae	Vulnerable	Schedule I	28	26
Sambar	*Rusa unicolor*	Cervidae	Vulnerable	Schedule I	37	37
Spotted deer	*Axis axis*	Cervidae	Least Concern	Schedule II	15	18
Tiger	*Panthera tigris*	Felidae	Endangered	Schedule I	11	7
Wild pig	*Sus scrofa*	Suidae	Least Concern	Schedule II	48	39

Environmental layers

To minimize redundancy and enhance model robustness, multicollinearity among variables was assessed using pairwise correlation analysis and the Variance Inflation Factor (VIF). Variables exhibiting high correlation coefficients ($|r| > 0.7$) were excluded. Following this selection procedure, nine geospatial predictor layers were chosen from remote-sensing datasets and incorporated as covariates into the SDMs (**Fig. 2**) (see Supplementary Information ESM 2 for environmental predictor variables). Land-use and land-cover (LULC 2024) data obtained from the European Space Agency Climate Change Initiative (ESA CCI, 2024) enabled calculation of the proportional cover of cropland, grassland, shrubland, and forest within a 1 km buffer around each sampling location. Topographic variables, including elevation and Terrain Ruggedness Index (TRI), were generated from a 30-m Digital Elevation Model (DEM) obtained from the Shuttle Radar Topography Mission (SRTM). Distance to water sources was calculated using a merged layer of stream orders, derived through hydrological analysis of the DEM, and surface water bodies extracted from LULC data. Vegetation productivity was quantified using the Enhanced Vegetation Index (EVI), derived from the MODIS MOD13Q1 product (250 m spatial resolution; 16-day composites) for the study period (March to June 2024). Human disturbance was quantified using the Human Settlement Index (HSI) from the Global Human Settlement Layer (GHSL). All predictor variables were standardized to a spatial resolution of 1 km and clipped to the study area extent before analysis. The selected covariates represent key ecological gradients influencing the distribution of large mammals in the Western Ghats. Land use and land cover (LULC) proportions capture habitat heterogeneity and resource availability. Elevation and terrain ruggedness indicate altitudinal and structural variation. Distance to water reflects seasonal resource dependence. The Enhanced Vegetation Index (EVI) measures vegetation productivity and forage availability, while the Human Settlement Index (HSI) indicates anthropogenic disturbance. Together, these variables describe the environmental and human factors shaping species occurrence in the regio

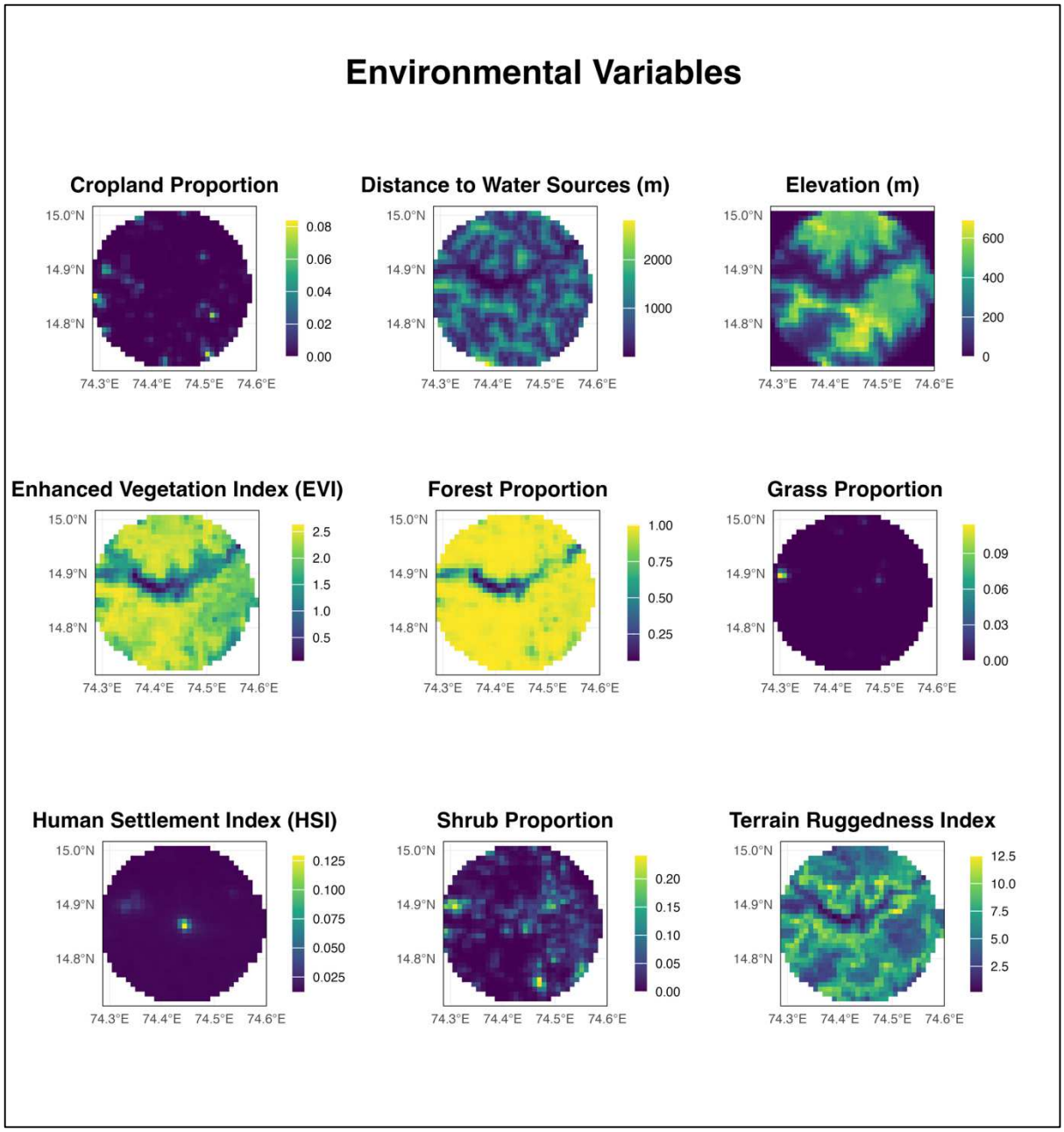


Fig. 2. Environmental predictor variables used in species distribution modelling, showing their spatial variation across the study area.

Species Distribution Modelling

Ensemble SDM was performed for each of the seven species using the "biomod2" package in R version 4.3.1 (Thuiller et al. 2009, 2023), after thinning the occurrence data and formatting the environmental predictors. We choose six modelling algorithms: Generalized Linear Models (GLM), Generalized Additive Models (GAM), Maximum Entropy (MaxEnt), Random Forest (RF), Generalized Boosted Models (GBM), and Multivariate Adaptive Regression Splines (MARS). Model performance was evaluated using K-fold random cross-validation with a 75% training and 25% testing split. The Area Under the Receiver Operating Characteristic Curve (ROC) was the primary evaluation metric. Variable importance for each model was assessed using a permutation-based approach. Once the ensemble output of the individual models was generated, only models with an ROC score ≥ 0.45 were included. The final ensemble predictions gave a 0-1 mean (EMmean).

Gap Analysis

The habitat suitability results for each species were converted to binary maps using the median of species-specific suitability as the threshold. Grid cells at or above the median were marked as predicted presence (1), and those below were marked predicted absence (0). The binary habitat maps for all seven species were overlaid to create a species richness map, showing where predicted presence overlaps across the landscape. To identify conservation gaps, the study area was divided into the following categories: 1. Protected Area (PAs): Kali Tiger Reserve 2. Non-Protected Areas (non-PAs): Karwar and Yellapur Forest Divisions

Species richness was compared between PA and non-PA Categories, and the mean richness, standard deviation (SD), standard error (SE), and 95% confidence intervals (CIs) were calculated. To test for differences in richness between the two landscape types, a Welch's two-sample t-test was performed. Additionally, Cohen's d was calculated to assess the magnitude of the difference.

Results

Species-specific Responses

Dhole

The model performance was ROC (0.85 ± 0.08 SE) (see supplementary Information ESM 4 for ROC scores and model evaluation metrics). Variability contributed to different predictions: EVI (42%), followed by forest proportion (26%), TRI (18%), and elevation (14%). Other variables, such as distance to water (~6%), cropland (~5%), shrub (~4%), grass (~3%), and HSI (~2%), had smaller effects on contributions (see Supplementary Information ESM 5 for variable importance values). The response curves rose sharply at higher EVI values, showing a strong preference for highly productive habitats. Suitability decreased with increasing distance from water bodies, highlighting the species' reliance on water bodies. The model also showed a positive response to terrain ruggedness, suggesting a preference for varied forests. Forest proportions had a unimodal effect, with suitability peaking at intermediate-to-high levels (**Fig. 3a**).

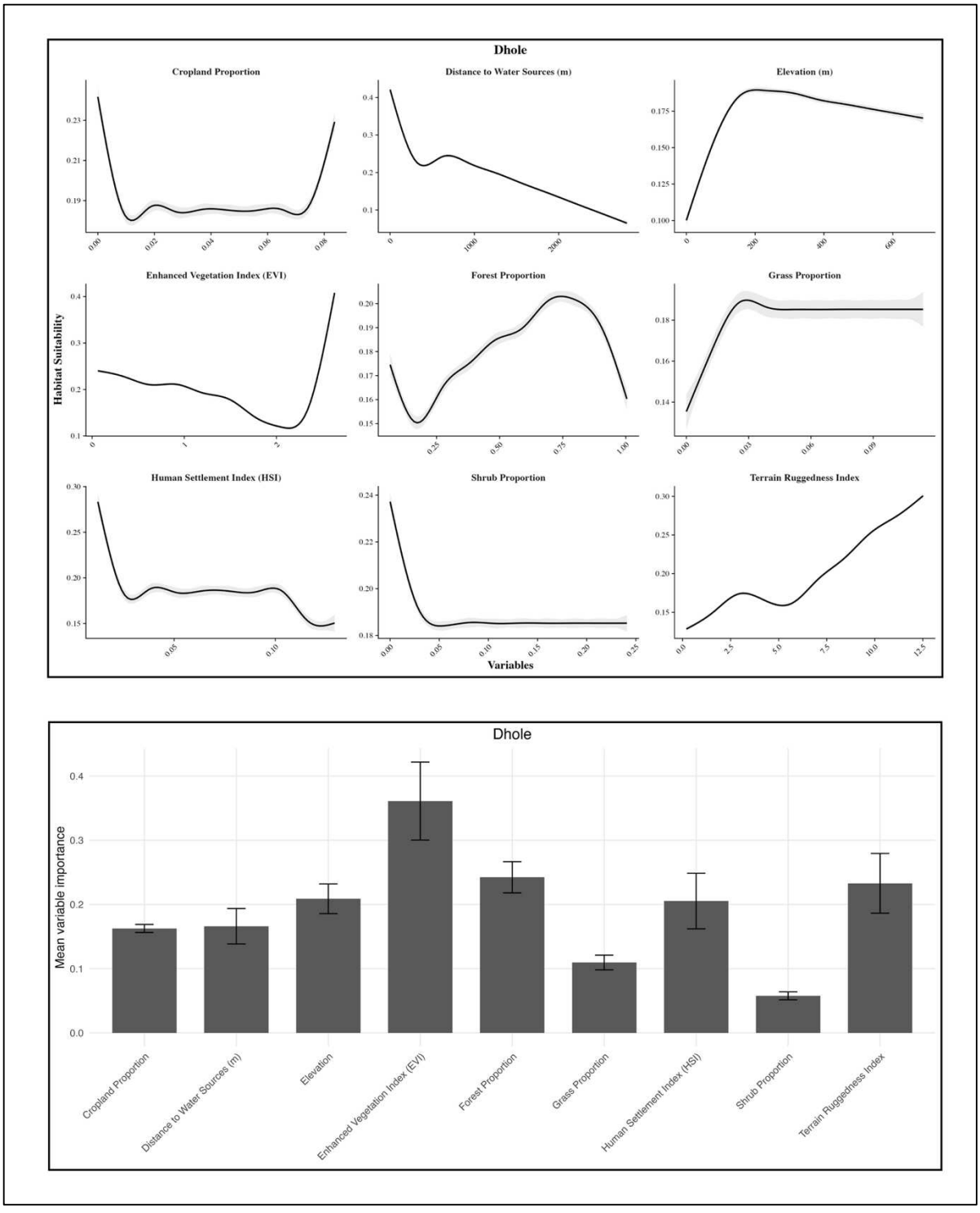


Fig. 3a. Response curves and variable importance for Dhole (*Cuon alpinus*) in the study area.

Common Leopard

The model performance was ROC (0.81 ± 0.03 SE) (see Supplementary Information ESM 4 for ROC scores and model evaluation metrics). Forest proportion (29%), distance to water (24%), and elevation (18%) were the main contributors to the SDM Model. EVI (14%) and TRI (10%) had moderate effects, while shrub (~3%), cropland (~1%), grass (~0.5%), and HSI (~0.5%) had little impact (see Supplementary Information ESM 5 for variable importance values). The response curve states that suitability peaked at intermediate EVI levels. Suitability was highest at moderate distances from water (about 800–1500 m), suggesting the species avoids both dry and highly competitive areas. Suitability decreased with increasing forest cover, indicating a preference for edge habitats and

mixed landscapes. Positive responses to grass and shrub cover supported this, and TRI showed peak suitability at moderate ruggedness (**Fig. 3b**).

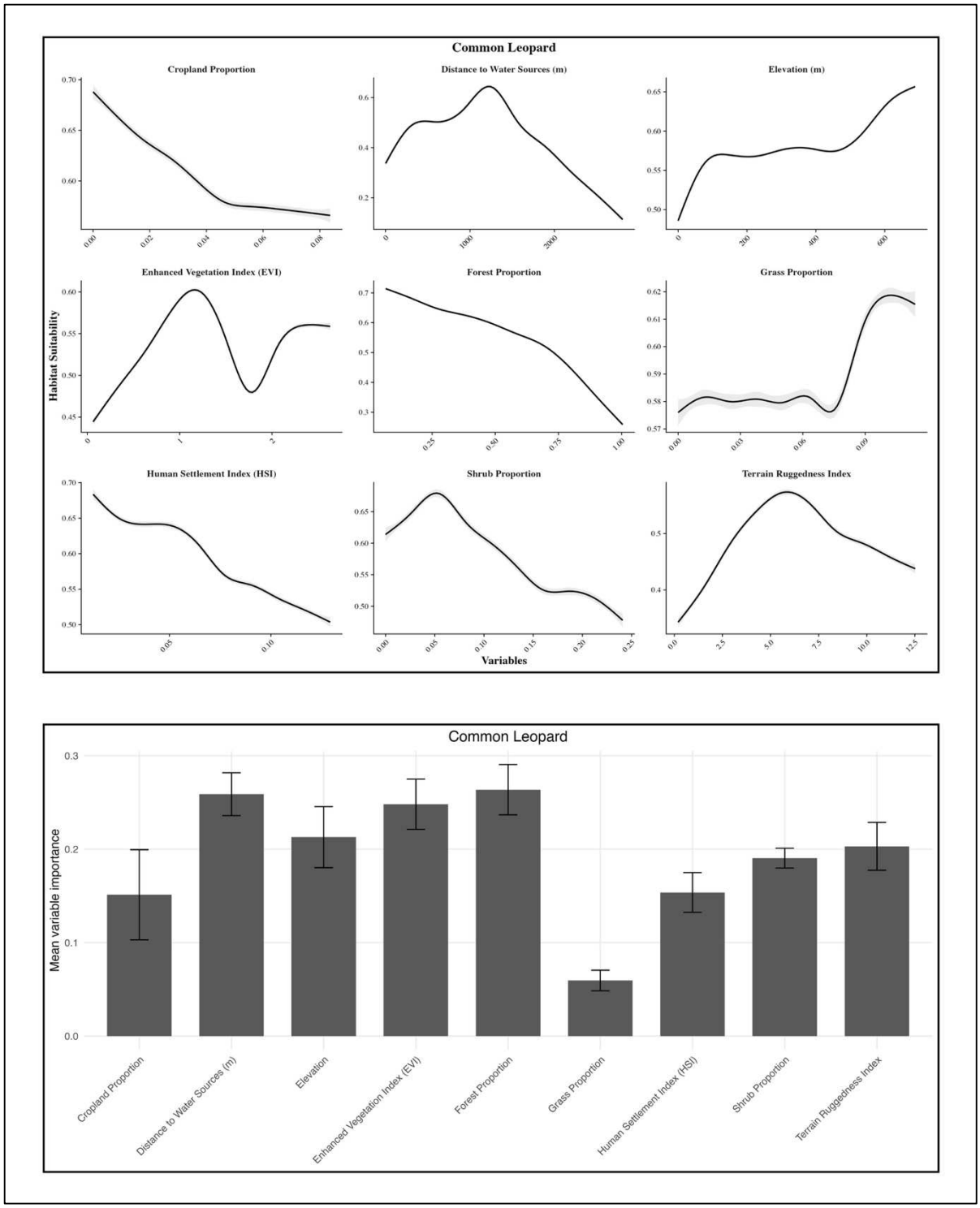


Fig. 3b. Response curves and variable importance for Common Leopard (*Panthera pardus*) in the study area.

Tiger

The model showed excellent performance with tiger ROC (0.93 ± 0.016 SE) (see Supplementary Information ESM 4 for ROC scores and model evaluation metrics). EVI (36%) and HSI (26%) were the most important predictors, together accounting for about 62% of the model's influence. Distance to water (14%), forest proportion (13%), and elevation (9%) also contributed. TRI (~1%), cropland (~0.5%), grass (~0.3%), and shrub (~0.2%) had

little effect (see Supplementary Information ESM 5 for variable importance values). Suitability increases with increasing forest cover, indicating a preference for continuous forest patches. However, suitability declined as EVI increased, suggesting the species avoids very dense vegetation. The model showed a unimodal response to distance from water, with the best suitability at intermediate distances (about 800–1200 m). The species preferred moderate terrain ruggedness, and suitability decreased with increasing elevation (**Fig. 3c**).

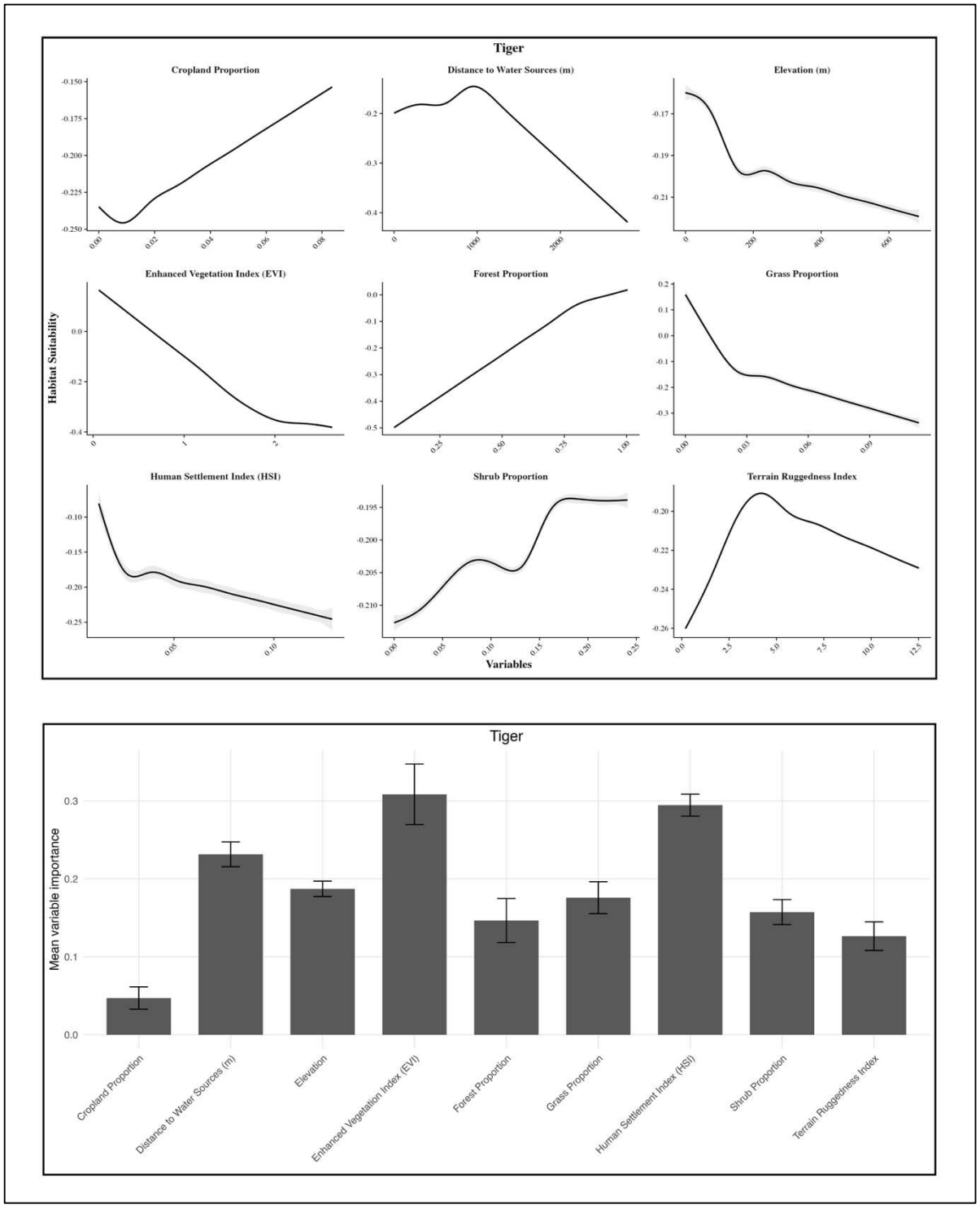


Fig. 3c. Response curves and variable importance for Tiger (*Panthera tigris)* in the study area.

Gaur

The model performed was ROC (0.84 ± 0.03 SE) (see Supplementary Information ESM 4 for ROC scores and model evaluation metrics). EVI was the top predictor (41%), followed by cropland proportion (21%), forest proportion (19%), and grass cover (13%). Other variables, such as elevation (~3%), TRI (~1.5%), shrub (~0.8%), distance to water (~0.5%), and HSI (~0.2%), had minor effects (see Supplementary Information ESM 5 for variable importance values). The response curves exhibited a unimodal relationship with EVI, peaking at intermediate productivity levels. Strong negative responses to cropland, grass, and shrub cover suggested the species avoids open or disturbed habitats. Suitability decreased with increasing forest cover, indicating a preference for mosaic landscapes over dense forests. The species also selected areas with low to moderate terrain ruggedness (**Fig. 3d**).

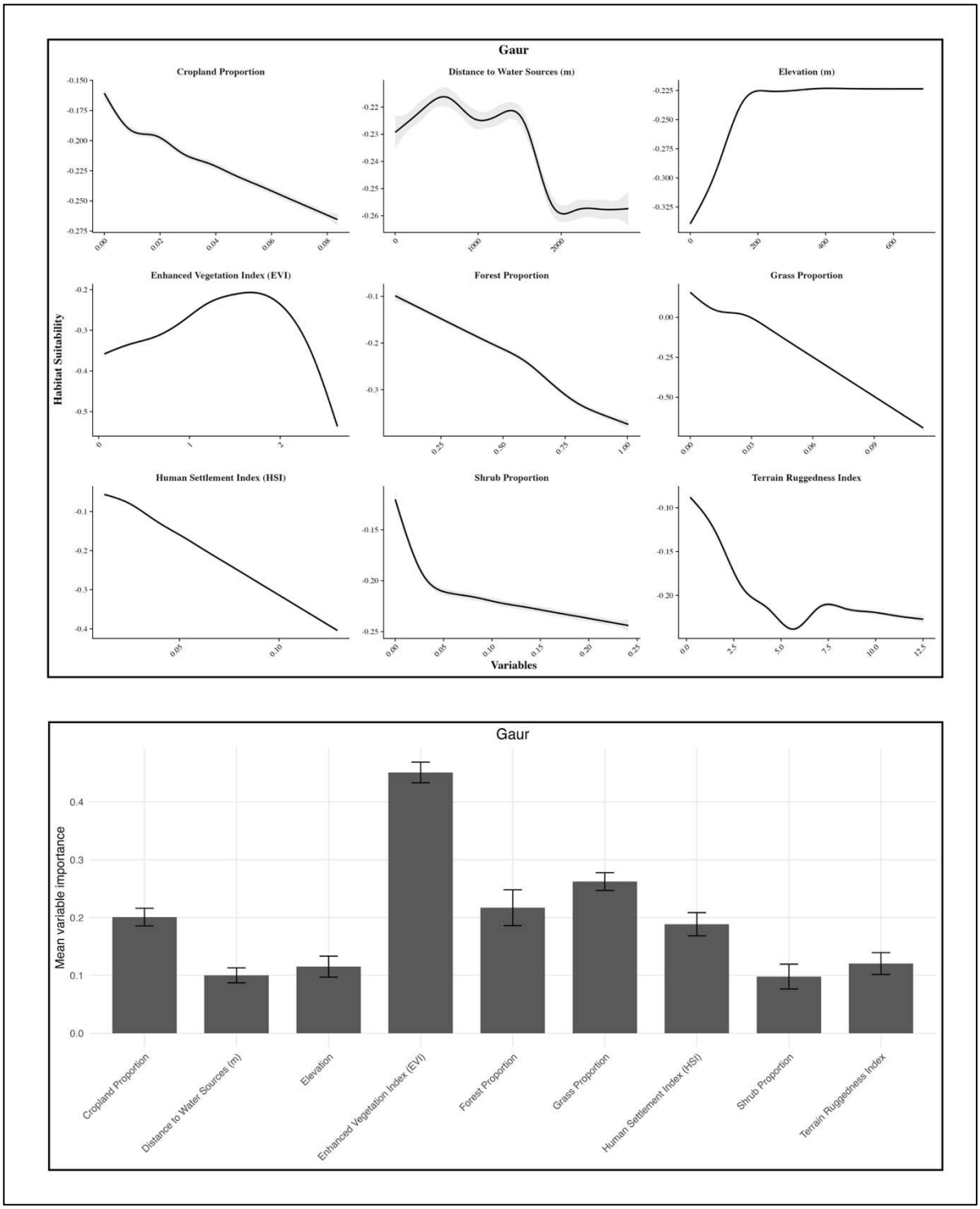


Fig. 3d. Response curves and variable importance for Gaur (*Bos gaurus*) in the study area.

Sambar

The model performed moderately well (0.75 ± 0.03 SE) (see Supplementary Information ESM 4 for ROC scores and model evaluation metrics). EVI (31%), distance to water (27%), and elevation (15%) were the main factors. Forest proportion (14%) and TRI (9%) had moderate effects, while shrub (~2%), grass (~1%), cropland (~0.5%), and HSI (~0.5%) had minor effects (see Supplementary Information ESM 5 for variable importance values). Suitability increased with distance from water up to a moderate range, then levelled off. Suitability declined with increasing EVI, suggesting a preference for moderately productive habitats. Forest cover had a unimodal effect, peaking at intermediate levels (about 0.6–0.8), and grass cover highlighted the importance of forage. The species preferred areas with low to moderate ruggedness and mid-elevations (**Fig. 3e**).

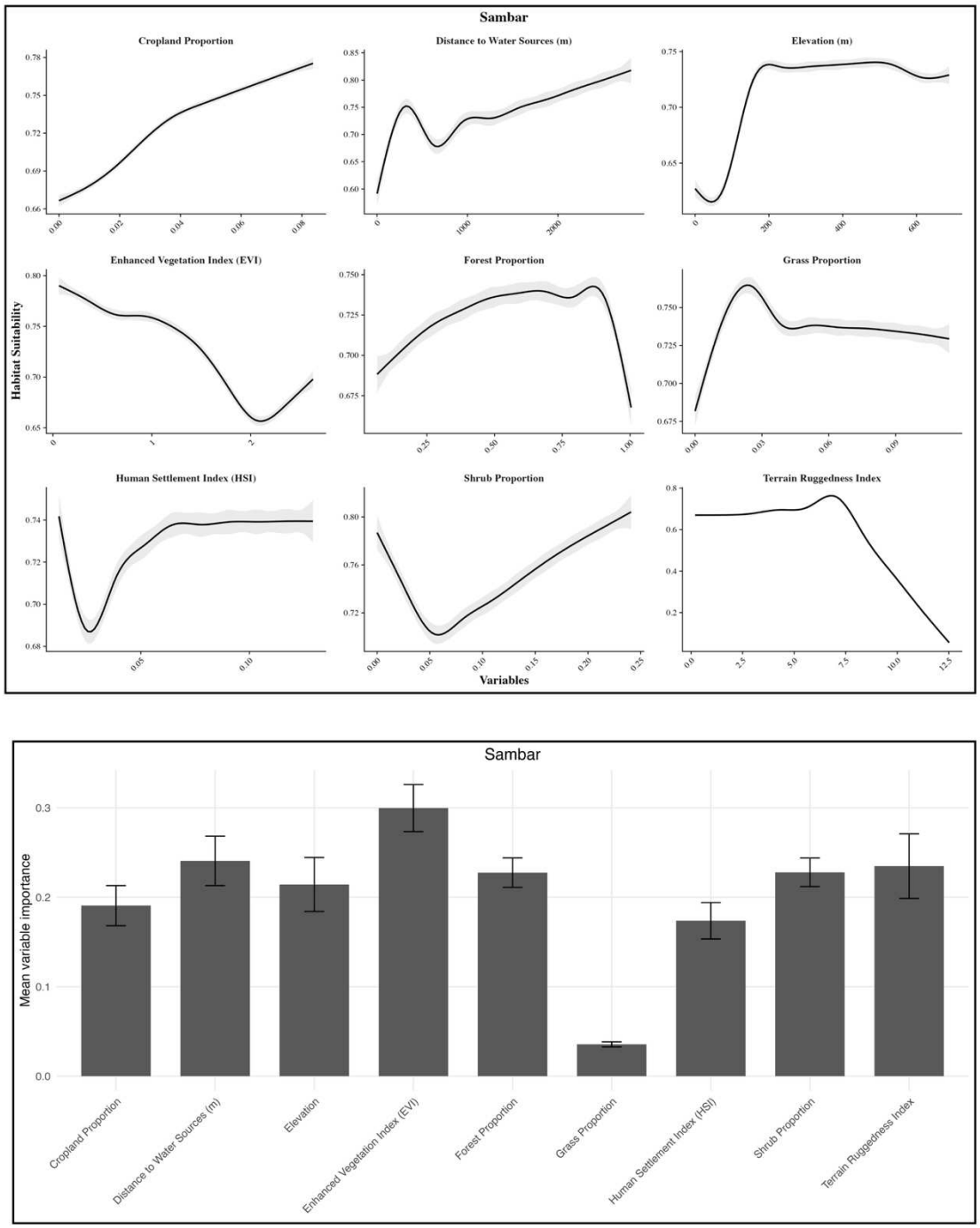


Fig. 3e. Response curves and variable importance for Sambar (*Rusa unicolor*) in the study area.

Spotted Deer

The model performed well (0.88 ± 0.03 SE) (see Supplementary Information ESM 4 for ROC scores and model evaluation metrics). EVI was the most important factor (59%), followed by elevation (16%), TRI (14%), and forest proportion (9%). Other variables, such as distance to water (~1%), grass (~0.5%), shrub (~0.3%), cropland (~0.1%), and HSI (~0.1%), had little effect (see Supplementary Information ESM 5 for variable importance values). The response curves showed a strong negative relationship with EVI, indicating that the species prefers open habitats with low vegetation cover. Suitability increased in areas with moderate forest cover, suggesting the use of forest–grassland edges. Positive responses to grass and shrub cover highlighted the importance of forage. TRI had a negative relationship, showing a preference for flat terrain (**Fig. 3f**).

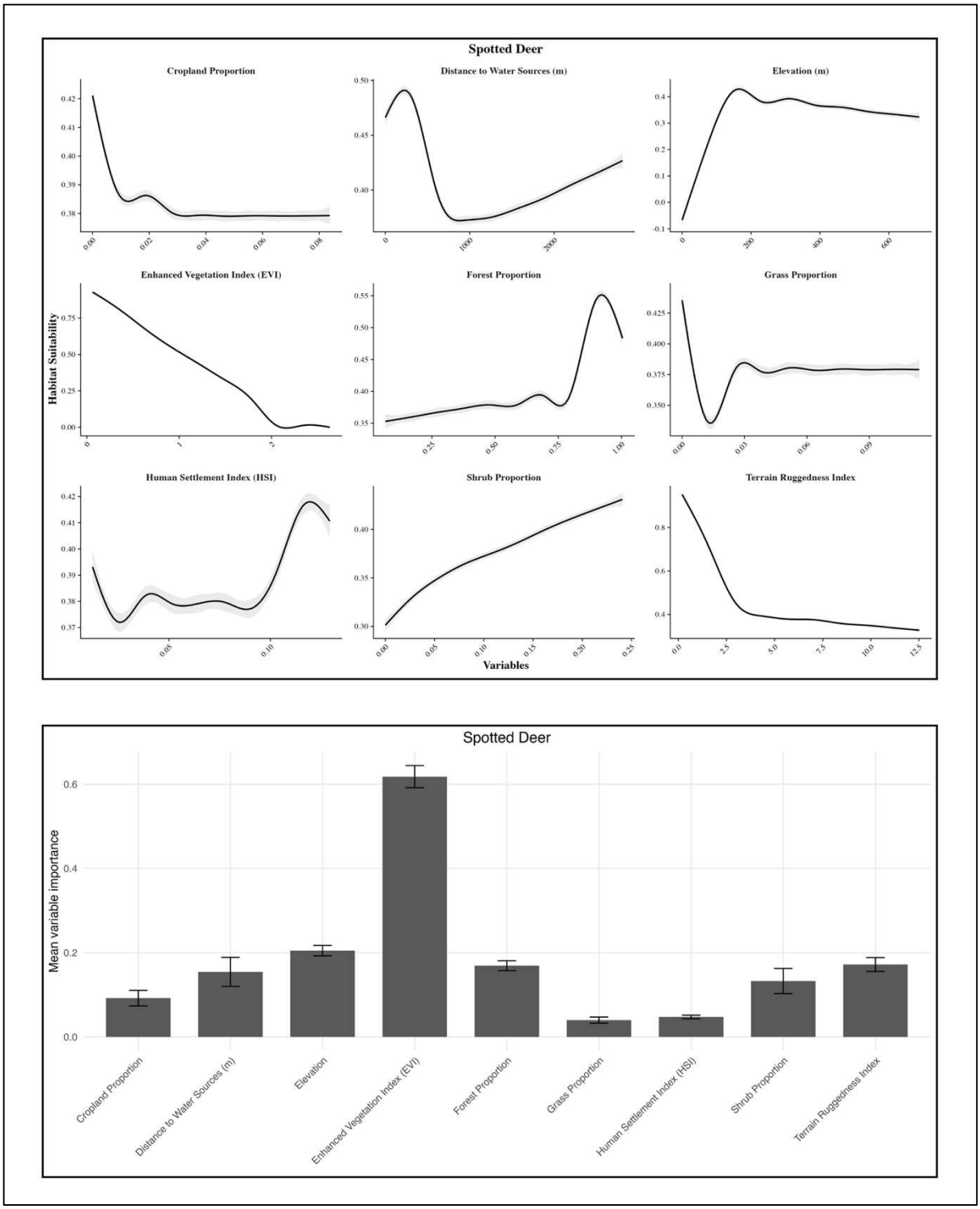


Fig. 3f. Response curves and variable importance for Spotted Deer (*Axis axis*) in the study area.

Wild Pig

The model performed moderately (0.68 ± 0.04 SE) (see Supplementary Information ESM 4 for ROC scores and model evaluation metrics). Shrub proportion was the top predictor (34%), followed by EVI (24%), forest proportion (21%), and elevation (13%). Distance to water (~4%), cropland (~2%), grass (~1%), TRI (~0.8%), and HSI (~0.2%) had smaller effects (see Supplementary Information ESM 5 for variable importance values). The response curves showed broad ecological tolerance, with suitability increasing in mixed forest-shrub landscapes. A negative relationship with EVI suggested a preference for less dense vegetation. Suitability declined with

increasing distance from water, indicating reliance on water. A positive link with cropland suggested adaptability to human-modified areas (**Fig. 3g**).

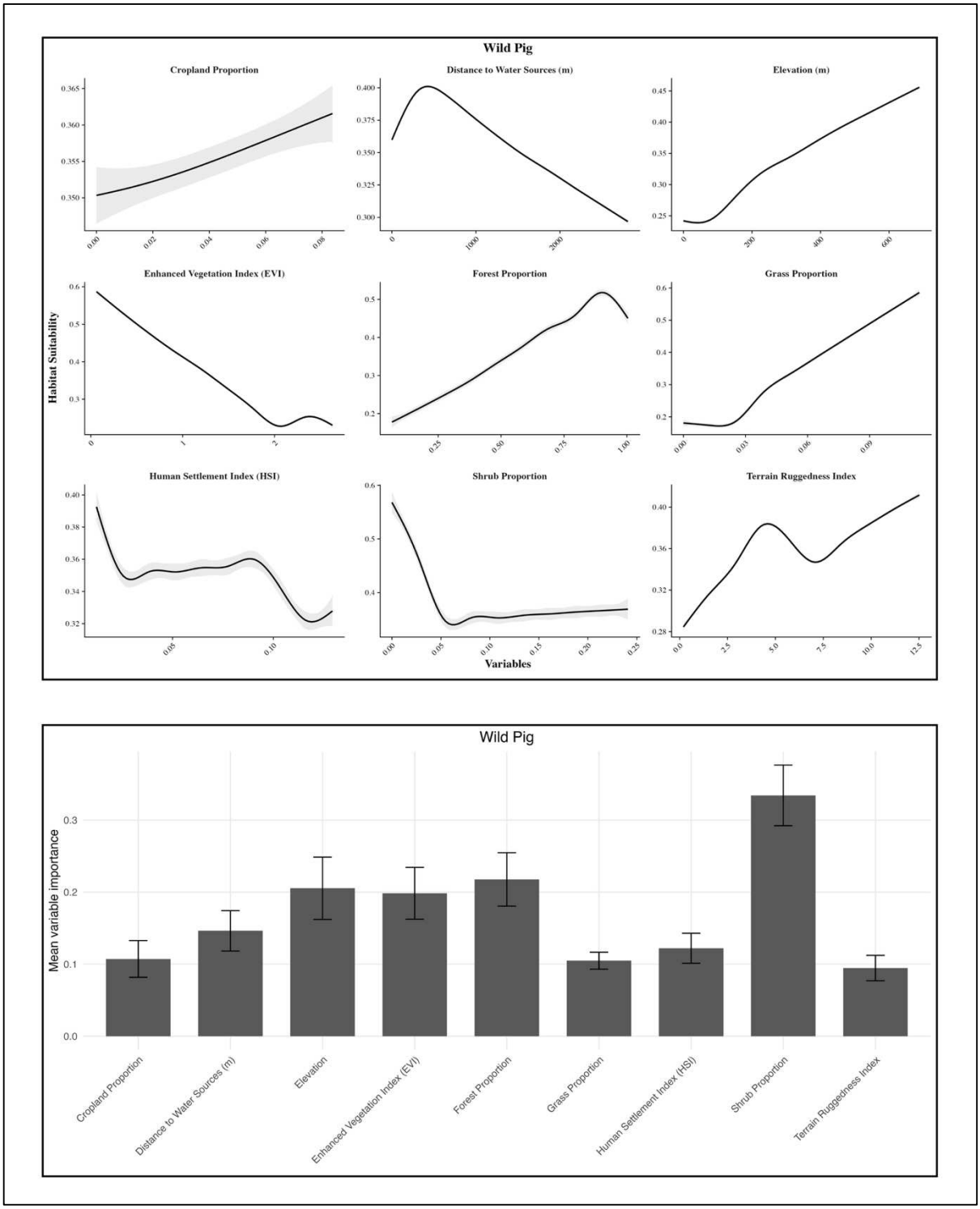


Fig. 3g. Response curves and variable importance for Wild Pig (*Sus scrofa*) in the study area.

Habitat Suitability across Boundaries

Our model yielded different suitability for the selected species based on the proportion of the area. Dhole had the highest suitability in KTR (59.5%) and Karwar (58.5%), followed by Yellapur (18.2%). Gaur had the most suitable area in Yellapur (93.6%), followed by KTR (49.3%) and Karwar (31.9%). Common Leopard had high suitability in Yellapur (66%) and KTR (57.9%), but lower suitability in Karwar (41%). Sambar had moderate

suitability in all three divisions: KTR 55%, Yellapur 60.7%, and Karwar 39.9%. Spotted deer had the most suitable area in Yellapur (67.9%), followed by KTR (45.8%), and then Karwar (43.6%). Tiger had a more suitable area in Yellapur (65.6%) than in Karwar (47.6%) and KTR (41.6%). Wild Pig had high suitability in Yellapur (69.8%) and KTR (66.1%), but lower in Karwar (34.1%) (**Fig. 4**) (see Supplementary Information ESM 3 for species-specific habitat suitability values).

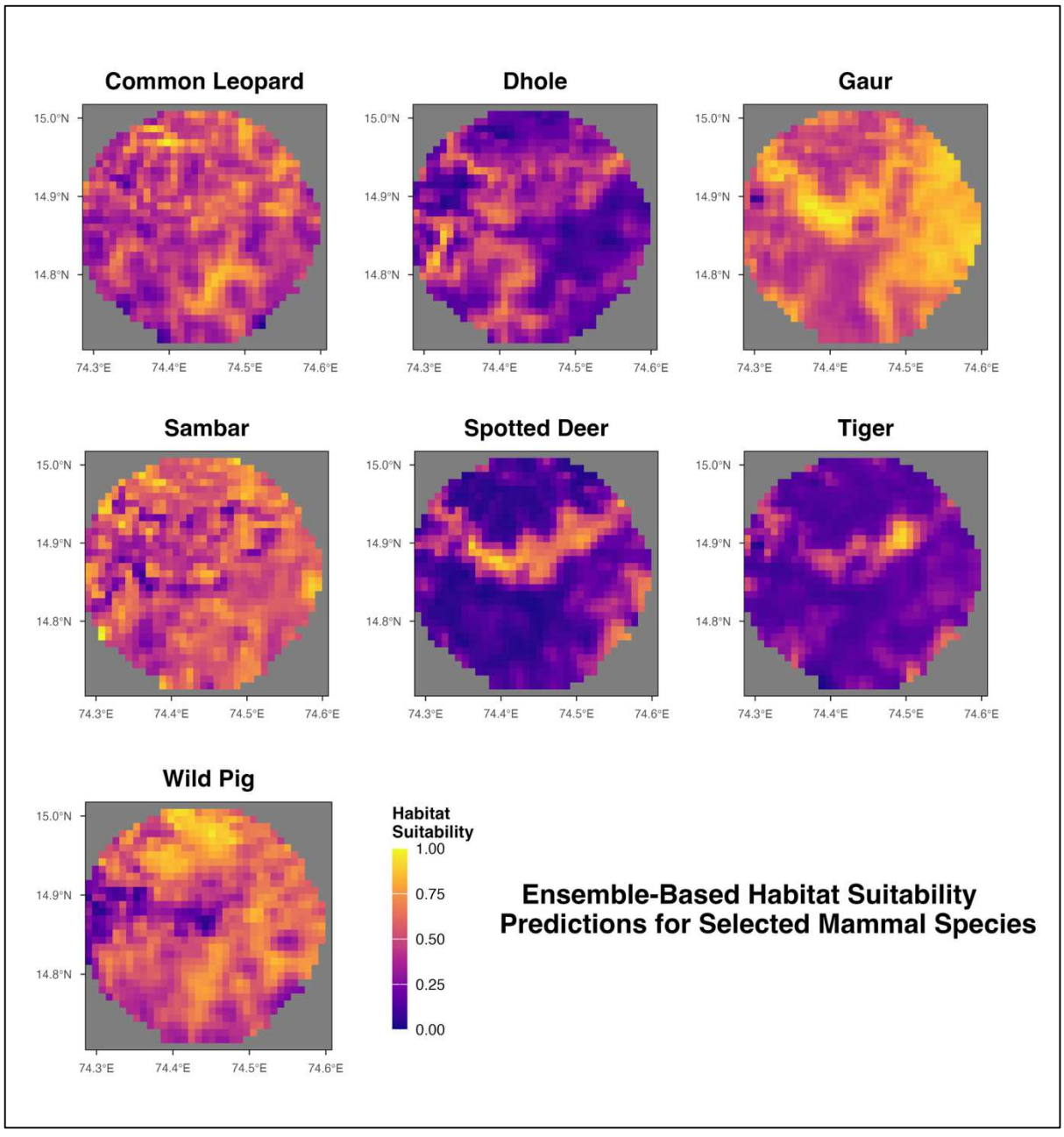


Fig. 4. Ensemble habitat suitability maps for selected mammal species in the study area.

Roles of PAs in Multispecies Conservation

The species richness analysis showed significant variation across PAs & non-PAs (**Fig. 5**). Areas with high richness were mostly found in the continuous forests of PAs, but similar richness was also observed in forests in non-PAs in the Western Ghats. The average predicted species richness was slightly higher in PAs (4.58 ± 1.65 SE, 4.38 - 4.78 95% CI) than in non-PAs (4.09 ± 1.82 SE, 3.94 - 4.24 95% CI). The Welch's t-test showed a significant difference in average species richness ($p < 0.05$) (**Fig. 6**). The effect size (Cohen's $d \approx 0.3$) suggested

a moderate difference between the two groups. Even though PAs had a higher average richness, many pixels with moderate-to-high richness were found in non-PAs.

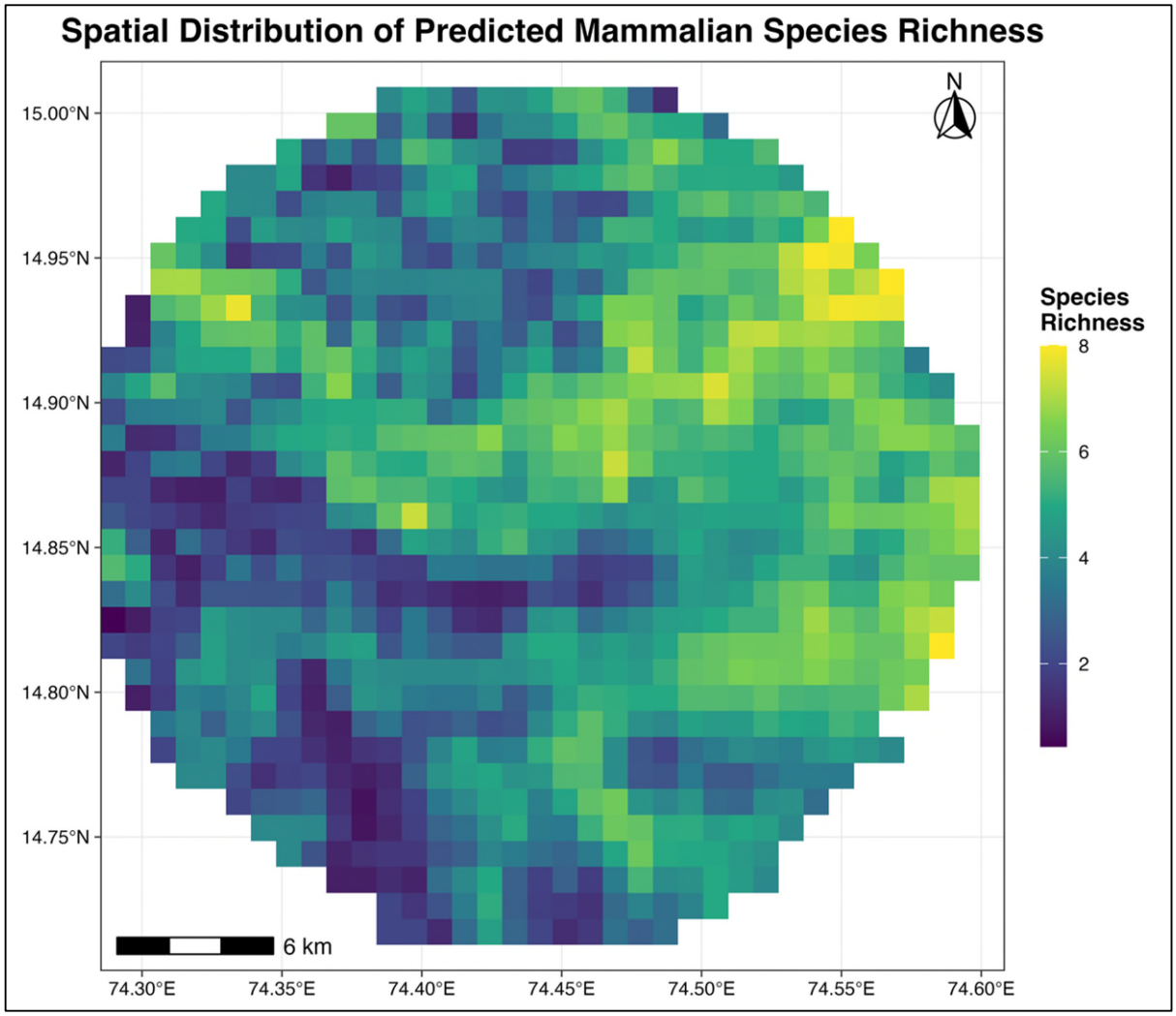


Fig. 5. Predicted species richness across protected and non-protected areas in the study area.

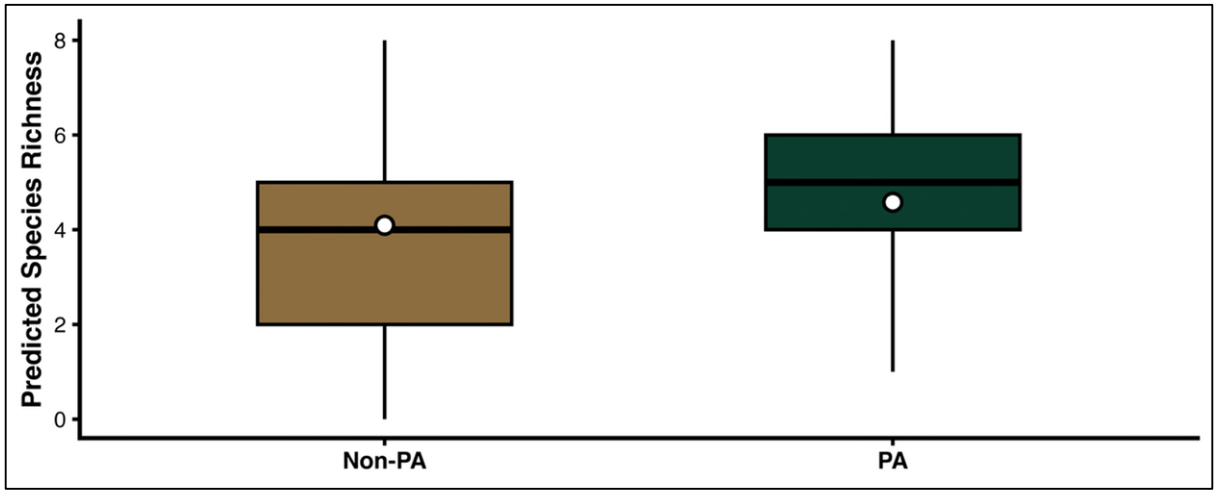


Fig. 6. Comparison of predicted species richness (Welch's t-test) between protected and non-protected areas.

Discussion

Habitat Suitability and Species-Specific Responses in the Central Western Ghats

The results highlight the study area as a significant conservation hotspot for both PAs and non-PAs. The single-season SDM framework showed robust performance (ROC: 0.68–0.93), supporting the utility of multi-algorithm approaches in complex, biodiversity-rich landscapes (Thuiller et al. 2009). Variation in model performance across species suggests that the selected environmental predictors effectively capture species-specific habitat requirements within this heterogeneous landscape (Araújo and New 2007; Marmion et al. 2009; Elith et al. 2011). The EVI was the primary predictor for five of the seven focal species, underscoring the critical role in structuring large mammal assemblages in the Western Ghats (Jathanna et al. 2015; Ramachandra et al. 2018). Spotted deer and wild pig showed strong negative associations with EVI, preferring flat areas with open vegetation cover, consistent with their reliance on ecotones and edge habitats for foraging. The distribution model for gaur indicated pronounced scale and season dependence, with the highest suitability in areas characterized by mixed vegetation structure rather than uniform closed-canopy forest, corroborating findings from Bandipur Tiger Reserve (Barik et al. 2025).

Conversely, the Human Settlement Index (HSI) was negatively correlated with habitat suitability for most species, reflecting landscape changes driven by agricultural expansion and infrastructure development that may disrupt wildlife movement. The HSI had a significant negative effect on tiger habitat suitability and evident that tigers are highly sensitive to anthropogenic disturbance and require large, low-disturbance habitat patches with connectivity to source populations (Karanth et al. 2004; Jhala et al. 2021).

Terrain ruggedness and elevation contributed significantly. Dholes showed a strong preference for rugged terrain, which aligns with evidence that topographic complexity limits human access and provides denning cover (Srivathsa et al. 2014). Notably, metapopulation modeling by Srivathsa et al. (2019) indicated that dhole occupancy dynamics in the Karnataka Western Ghats are more sensitive to colonization in areas adjacent to reserves than to processes within reserves. This finding underscores the conservation importance of the Karwar and Yellapur divisions, which the present study identifies as supporting substantial predicted dhole habitat. These divisions likely serve as movement corridors for dhole packs originating in the adjacent KTR boundary, and their habitat degradation would significantly threaten the viability of the dhole metapopulation at the landscape scale.

Common Leopard exhibited intermediate preferences for terrain ruggedness and EVI, with peak suitability at moderate distances from water and higher suitability at forest-edge interfaces. A statewide ensemble SDM analysis in Karnataka by Kolekar et al. (2024) found that leopard habitat selection is primarily influenced by proximity to forest cover and rocky outcrops and is negatively associated with distance to cropland margins. This supports the present study's interpretation that leopards utilize edge habitats more extensively than tigers and dholes. Such behavioral flexibility is ecologically important, as it enables leopards to maintain a functional presence across the PAs and non-PAs interface in Uttara Kannada, even under moderate human modification. This adaptability may allow leopards to serve as an ecological bridge between wildlife communities in reserves and adjacent unprotected forests. Similarly, Sambar showed unimodal forest preferences, peaking at intermediate closure (0.6-0.8 proportion), with suitability declining sharply in both very open and very dense conditions. As the primary prey species for both tiger and dhole in this landscape, the spatial distribution of Sambar is a key determinant of carnivore habitat suitability. The moderate suitability values observed for Sambar across all three management units highlight the multi-trophic significance of the non-PA forests identified in this study.

Habitat Suitability Across PA and non-PA Boundaries

A principal finding of this study is the prediction of substantial areas of high habitat suitability for all seven focal species outside the KTR. This result is ecologically significant because it indicates that the conservation value of non-PAs forests in the central Western Ghats has been systematically undervalued, consistent with broader assessments of Indian forests (Srivathsa et al. 2014; Ghosh-Harihar et al. 2019). A significant area of suitable tiger habitat (103.43 km²) was identified within the Yellapur Forest Division, which currently lacks formal protection. Given India's recovery obligations under Project Tiger and recent national tiger census data indicating that only

about one-third of the country's approximately 5,83,278 km² of tiger-bearing forests are in relatively healthy condition (NTCA 2023), these findings warrant immediate policy attention.

The predicted extent of suitable dhole habitat was greatest inside KTR, followed by Karwar. Camera-trap records from non-protected forests and secondary habitats adjacent to reserves in the northern and central Western Ghats confirm that unprotected inter-reserve matrices can sustain functional dhole populations when habitat quality is adequate (Srivathsa et al. 2019). In the present landscape, non-PAs meet this threshold, and their loss due to infrastructure development or land-use conversion would have disproportionate consequences for the regional dhole metapopulation. Intensification of infrastructure development or land-use conversion in these divisions could compromise connectivity for Dhole and all wide-ranging species identified in this study. This aligns with broader findings that approvals for developmental projects in ecologically sensitive areas of the Western Ghats are increasing, resulting in cascading effects on landscape permeability (Gubbi et al. 2014; Puri et al. 2020).

Role of PAs and non-PAs in Supporting Multi-Species Conservation

The species richness analysis showed a statistically significant difference in predicted richness between PA and non-PAs (Welch's t-test, $p < 0.05$), with PA exhibiting marginally higher mean richness (4.58 ± 1.65) compared to non-PAs (4.09 ± 1.82). However, the effect size (Cohen's $d \approx 0.3$) was modest, and many pixels in non-PA forests showed moderate-to-high richness values comparable to those in PA forests. This result should not be interpreted as implying functional equivalence between the two forests. Formal protection confers a conservation benefit, consistent with global meta-analyses showing that PAs support higher biodiversity than adjacent unprotected lands (Geldmann et al. 2013). Rather, the modest effect size implies that the functional conservation value of non-PAs forests in the study area is substantially greater than their legal status suggests; with profound policy implications in a region where PA-centric conservation frameworks have historically dominated management planning (Velho et al. 2016).

This interpretation is reinforced by the global analysis of Brennan et al. (2022), which states that a substantial proportion of the world's protected areas are functionally isolated, suggesting that the surrounding unprotected matrix often contributes as much to long-term species persistence as the reserves themselves. In the central Western Ghats, this dynamic appears to be operating: the KTR alone is insufficient to sustain the full complement of large-mammal diversity recorded here. The higher standard deviation in non-PA richness (1.82 vs 1.65 in PA) further indicates spatial heterogeneity in conservation value across unprotected forests and suggests that targeted, spatially explicit management interventions in species rich non-PA patches, rather than blanket management of unprotected areas, would yield disproportionate biodiversity returns (Shigwan et al. 2026). This finding is also consistent with the tree diversity assessment by Shigwan et al. (2026) in the same landscape, which demonstrated that differential protection regimes produce measurable but moderate differences in plant community composition, reinforcing the conclusion that non-PA forests retain substantial ecological integrity and should be treated as active components of the conservation network rather than passive buffers.

Conservation Gaps and Landscape Connectivity

The gap analysis framework identifies a clear and urgent conservation gap in non-PAs, predicted to support high multi-species richness. These areas represent the most immediate priority for conservation action through the implementation of landscape-level wildlife management plans that regulate land use and infrastructure development within ecologically sensitive zones (Rodgers and Panwar 1988; Karanth et al. 2010). Maintaining functional habitat corridors between the KTR and adjacent forest divisions should be recognized as a conservation priority of the highest order. Species such as tigers, dholes, and gaur have substantial suitable habitat in both PA and non-PA units, requiring landscape permeability across management boundaries to sustain viable metapopulations (Crooks and Sanjayan 2006; Karanth et al. 2010). Evidence from camera-trapping operations in unprotected forests across India confirms that tiger densities in some reserve forests outside formal protection are comparable to those within designated tiger reserves (WCT 2021), and that tigers regularly use corridors and non-protected area habitats when landscape permeability is maintained (Jhala et al. 2021). The disruption of these corridors through road or railway expansion, linear infrastructure, or agricultural encroachment in the Karwar-Yellapur matrix would fragment what is currently a functionally connected landscape, with potentially irreversible

consequences for local populations. This concern is heightened by recent trends in the approval of infrastructure projects in ecologically sensitive areas of the Western Ghats and the documented negative relationship between road density and tiger connectivity (Gubbi et al. 2014; Puri et al. 2020).

Limitations and Future Directions

Several limitations of this study warrant consideration. The relatively short camera-trapping period (March to June 2024) and moderate trap density (87 traps across 804.25 km²) may have resulted in incomplete detection of low-density or wide-ranging species, particularly dhole and tiger, for which thinned occurrence records were limited (3 and 7 locations, respectively) (Royle et al. 2009). SDMs constructed from small sample sizes are susceptible to spatial autocorrelation and may overfit to localized habitat conditions (Wisz et al. 2008). While spatial thinning was implemented to reduce sampling bias, future research should incorporate multi-season data and increased detection effort for rare species.

The study period coincides with the pre-monsoon dry season, during which EVI values in the Western Ghats reach their seasonal minimum. This timing introduces a potential systematic bias: evergreen forest patches, which maintain relatively stable productivity year-round, may appear less distinct from seasonal forests in dry-season EVI composites. This effect could compress the observed productivity gradient that underpins several key model predictions. Incorporating multi-season or annual maximum EVI composites in future studies would provide a more ecologically representative characterization of vegetation productivity across forest types (Ramachandran and Mithilasri 2026). Furthermore, the binary thresholding approach used in the gap analysis, which is based on the median suitability value, constitutes a conservative, somewhat arbitrary cutoff. Conducting sensitivity analyses with alternative thresholds (such as maximum specificity plus sensitivity, or P10) would enhance the robustness of gap delineation (Liu et al. 2005).

Future research in this landscape should incorporate fine-scale movement data from GPS-collared Tiger individuals or any dhole pack to empirically validate predicted corridors and assess functional connectivity under both current and projected land-use scenarios. Occupancy modeling frameworks that explicitly account for imperfect detection would yield more statistically rigorous estimates of species distributions and facilitate inference on habitat-use dynamics across the PA–non-PA interface (MacKenzie et al. 2006). Integrating climate projections into SDM frameworks would enable assessment of how changing temperature and precipitation regimes may alter habitat suitability and species richness patterns across this landscape in the coming decades. This is particularly important given the documented vulnerability of Western Ghats biodiversity to climate change, including projected significant declines in suitable habitat for evergreen and deciduous forest types under near-future climate scenarios (Ramachandran and Mithilasri 2026). Additionally, multi-species occupancy models that account for interspecific interactions, such as prey-mediated indirect effects among carnivores or competitive exclusion among co-occurring large ungulates, would provide a more comprehensive mechanistic understanding of community structure across the PA–non-PA gradient

Conclusion

This study provides compelling evidence that conserving large mammals in the central Western Ghats requires action beyond the KTR. The forests of the Karwar and Yellapur divisions provide essential habitat for all seven focal species, with predicted multi-species richness compared to that of the protected area. Although PAs offer a modest but statistically significant advantage in species richness, these findings highlight the necessity of active wildlife management in non-PA forests.

An integrated landscape conservation framework is recommended. This framework should extend formal protection or management mandates to species rich non-PA areas, prioritize corridor maintenance between management units, and explicitly incorporate multi-species habitat suitability into land-use planning and infrastructure approval decisions throughout the central Western Ghats. Implementing such an approach is essential to prevent the gradual loss of landscape connectivity and to ensure the long-term persistence of large mammal communities in this globally significant biodiversity hotspot.

Statement & Declaration

The data are not publicly available due to ethical restrictions. Data are available on reasonable request from the corresponding author.

Author contributions

Conceptualization: Avinash Yadav, Frank S.J.D., Govindan Veeraswami Gopi; Methodology: Avinash Yadav Nonita Rana, Rounak Patra, Frank S.J.D.; Formal analysis and investigation: Avinash Yadav; Writing - original draft preparation: Avinash Yadav; Writing - review and editing: Nonita Rana, Rounak Patra, Frank S.J.D., Govindan Veeraswami Gopi; Funding acquisition: Govindan Veeraswami Gopi; Resources: Govindan Veeraswami Gopi; Supervision: Govindan Veeraswami Gopi.

Research Ethics

We obtained official permission from the Chief Wildlife Warden of Karnataka to conduct the present field study. There were no other ethical issues involved.

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Declaration of competing interest

The authors declare that they have no competing interests.

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