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Morphological and Spatial Characteristics of Indian Pangolin (*Manis crassicaudata*) Burrows in the Protected Semi-Arid Landscape of Saurashtra, Gujarat, India

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Abstract

The Indian Pangolin (*Manis crassicaudata*) is classified as endangered and is an important ecosystem engineer of the ecosystem where it exists; however, there are very few quantitative baseline studies that evaluate its burrow characteristics and habitat selection. This longitudinal study spanned 2024-2026 and included two different types of natural protected areas located in Saurashtra, Gujarat, India: the basaltic Barda Wildlife Sanctuary and alluvial Mitiyala Wildlife Sanctuary. Using Average Nearest Neighbour analysis, we identified evidence of significant clustering for both feeding burrows ($Z = -13.76$; $P < 0.001$ in Barda; $Z = -9.72$; $p< 0.001$ in Mitiyala) and resting burrows ($Z = -3.99$; $p < 0.001$ in Barda; $Z = -3.39$; $p < 0.001$ in Mitiyala). Using the proximity of commute distances, we calculated an average foraging commute of 331.03 ± 360.59 m in Mitiyala, suggesting that the pangolin spatially separates locations used for feeding versus resting, likely to reduce the risk of predation.

An optimised multi-model ensemble framework (GLM, GAM, RF, MaxEnt) was implemented using 10 environmental covariates to address landscape selection dynamics. The suitability gradient was binarised at an optimised threshold cutoff of 0.431 using Youden's J criterion. Validating the models showed excellent predictive accuracy (TSS > 0.75, $p < 0.01$; AUC > 0.90, $p < 0.01$), identifying land surface temperature and soil texture as the primary determinants of burrow selection. The finding provides fine-scale environmental constraints affecting subterranean ecology and can serve as transferable baseline data for preserving patch-refugia within ecological fragmentation of semi-arid landscapes.

KEY WORDS: Burrow Morphometrics, Ensemble Modelling, Gujarat, *Manis crassicaudata*, Spatial Statistics, Threshold Optimisation

INTRODUCTION

Burrows establish a critical component of animals' life, and this behaviour has evolved as a key adaptive strategy across the animal kingdom. For the majority of fossorial and semi-fossorial taxa, these structures are integral to survival. It is not merely a residence but a critical tool that creates a separate environment or ecosystem in its own, maintains a stable microclimate and humidity, protects against the lethal surface extremes and from hydric fluctuations, which are the major characteristics of the semi-arid landscapes and environment. Beyond this individual survival, the significance of burrows lies in their role in ecosystem functioning. By physically restructuring the soil profile, burrowing animals act as ecosystem engineers, facilitating vertical nutrient cycling, enhancing soil quality with the help of aeration, which also increases the water infiltration capacity of the soil and ultimately promotes habitat heterogeneity. Furthermore, these subterranean structures' excavation creates complex subterranean habitats that support a diverse suite of commensal species from invertebrates to

small vertebrates (Chao 2020; Meng 2023; Sun 2025) by creating space for secondary tenants, which effectively increases local biodiversity, and this underground innovation has allowed diverse lineages to colonise environments ranging from arid deserts to the tundra. While these fossorial lineages are distributed globally across nearly every terrestrial biome, their fossorial evolutionary success is most visible in specialised mammalian assemblages of the Old-World tropics. Across the Indian subcontinent the mammals of fossorial guild represents a diverse and ecologically significant community distributed from high altitude to lowlands few examples are Himalayan Marmot (*Marmota himalayana*), Plateau Pika (*Ochotona curzoniae*), Royle's Pika (*Ochotona roylei*) are the high altitude specialists (Smith & Johnston 2008), Chinese Pangolin (*Manis Pentadactyla*), Hoary Bamboo Rat (*Cannomys badius*), Small-clawed Otter (*Aonyx cinereus*) are the montane and foothills residents (Menon 2014; Challender et al. 2019), Indian Crested Porcupine (*Hystrix indica*), Large Rock Rat (*Cremnomys elvira*) are residing in central plateaus (Prater 1971; Molur & Kennerley 2016), while in lowland and arid zones Indian Pangolin (*Manis crassicaudata*), Indian Desert Gerbil (*Meriones hurrianae*), Honey Badger (*Mellivora capensis*), Indian Fox (*Vulpes bengalensis*), Madras Hedgehog (*Paraechinus nudiyentris*) (Goyal & Ghosh 1993, Molur 2016, Mahmood et al. 2019). In the specific context of Gujarat, the subterranean guild is well represented by Indian Desert Gerbil (*Meriones hurrianae*), Honey Badger (*Mellivora capensis*), Indian Fox (*Vulpes bengalensis*) and Indian Pangolin (*Manis crassicaudata*). Among these, Pangolins (order Pholidota) represent a highly specialised group that depends extensively on burrows for shelter, reproduction and predator avoidance as they possess specialised limb morphology and powerful claws capable of penetrating compacted soils and weathered rock (Mahmood et al. 2019). Despite their ecological importance as underground architects (Swinbourne et al. 2020), they remain poorly understudied due to their elusive and nocturnal behaviour. Broader syntheses further underline the conservation urgency surrounding Pangolins, which are the most threatened and poached mammals globally (Gaubert 2011). Studies across different Pangolin reveals considerable variation in burrow characteristics and habitat associations like Chinese Pangolin (*Manis pentadactyla*), burrow structure and placement are influenced by environmental variables such as slope, vegetation cover, disturbance gradients, and seasonal conditions (Wu et al. 2004; Lin et al. 2010; Zhang et al. 2010; Bao et al. 2013; Sun et al. 2015, Liang et al. 2025), Sunda Pangolin (*Manis javanica*) similarly demonstrates the importance of habitat selection, den use, and landscape context in shaping their burrowing behaviour (Lim & Ng 2007; Challender et al. 2012; Nash et al. 2016). In the African Pangolin species, studies have documented diversity in burrow structure, occupancy, and spatial ecology, linking burrow use with home range dynamics and environmental conditions like thermal regulation (Pagès 1975; Richie 1987; Heath & Coulson 1997; Pietersen et al. 2014; Waterman et al. 2021). Collectively, these studies highlight the ecological significance of burrows while also indicating strong species and habitat-specific variation.

Within this assemblage, we focused on the Indian Pangolin (*Manis crassicaudata* Geoffroy 1803), which is one of the most evolutionarily distinct but globally threatened mammals, currently listed as Endangered on the IUCN Red List and included in Appendix I of CITES (Cota-Larson 2017; Mahmood et al. 2019; Misra & Hanfee 2020) stands out as a uniquely impactful engineer and is widely distributed across South Asia (Prater 1971; Menon 2014; Cota-Larson 2017; Mahmood et al. 2019) and remains comparatively underexplored. Existing literature on the Indian Pangolins is regionally limited to Pakistan (Mahmood et al. 2020; Ahmad et al. 2025), Sri Lanka (Pabasara et al 2015; Karawita et al. 2020; Perera et al. 2022), and the Chota Nagpur Plateau (Prasad & Jha 2021). However, these contributions remain fragmented, and a comprehensive understanding of how burrow characteristics relate to

environmental variables and anthropogenic pressures across different landscapes is still lacking. Most existing literature focuses on the species as a victim of global illegal trade wildlife trade and sighting records leaving its fundamental ecological roles and the logic governing its habitat utilization largely as anecdotal, additional contributions include behavioural observations in captivity (Mohapatra & Panda 2014), morphometric analyses from sequestered individuals (Irshad et al. 2015) and reviews addressing population status and conservation challenges (Misra & Hanfee 2020). Specifically, there is a critical knowledge gap concerning how *M. crassicaudata* adapts its engineering to the unique geological constraints of the Saurashtra landscape. To bridge this particular gap, this study utilises a longitudinal dataset spanning from 2024 to 2026, providing a comprehensive ecological and distributional baseline of burrows of *M. crassicaudata* in Gujarat and the Saurashtra landscape. Beyond anecdotal records, this research seeks to quantify the morphometric characteristics of the functional burrow types across varying substrates while evaluating the spatiotemporal site fidelity (Merkle et al. 2022) through long-term assessment, including camera trapping. Furthermore, we investigate the environmental drivers, specifically soil texture, topography and landscape indices, that govern burrow site selection across the landscape of Saurashtra. By quantifying these habitat requirements, the study will provide baseline data and a scientific foundation that supports the forest departments' efforts in conservation and in maintaining the ecological integrity of the Saurashtra landscape.

MATERIALS AND METHODS

Study area

The research was conducted in two ecologically distinct protected areas within the Saurashtra peninsula of Gujarat, India, i.e. in Barda Wildlife Sanctuary (hereafter Barda) and Mitiyala Wildlife Sanctuary (hereafter Mitiyala). Amidst a rapidly developing landscape, both these sites represent critical undisturbed fragments of the semi-arid biotype and serve as essential refuges for the mammals, including the Indian Pangolin (*Manis crassicaudata*).

Barda is located in Porbandar and Jamnagar districts, spanning across (21°40'N to 21°55'N, 69°40'E to 69°50'E) in 192.31 km^2, and acts as a hilly outlier to the larger Gir forest ecosystem. The terrain is characterised by undulating hills and deep seasonal rivulets, with an elevation range reaching approximately 650m at its highest peaks (Meena & Kumar 2014; Ram 2024). Barda lies under 5A- southern tropical forest, 5A/C3- Southern dry mixed deciduous, and 6B- Northern tropical thorn forest, 6B/DS1- Desert thorn scrub (Champion and Seth 1968; Misra 2005). The vegetation is primarily tropical *Euphorbia* scrub and dry deciduous forest with patches of the same vegetation types and mix as well with 368 recorded floral species, dominated by vegetative species such as *Senegelia senegal, Anogeissus latifolia, Acacia nilotica*, *Syzygium cumini, Ziziphus globarata* and *Euphorbia caducifolia*. Another tree species is *Gardenia resinifera* and *Diospyros melanoxylon*, serving refuges to 376 faunal species showcasing high taxonomic biodiversity, which includes 25 mammals with the Indian Pangolin (Meena & Kumar 2014; Ram 2024). The bioclimatic profile is characterised by three distinct seasons (summer from March to June, with temperatures reaching up to 50°C nowadays; monsoon from June to November, with an average annual precipitation of 650mm; and winter from mid-November to February). The sanctuary's hydrological network is anchored by two perennial arteries, the Kileshwari and Minsar rivers, which serve as the primary drainage

system for the hilly terrain. The soil profile in Barda is largely governed by Deccan trap basalt, resulting in a rocky substrate interspersed with patches of loamy soil (Figure 1).

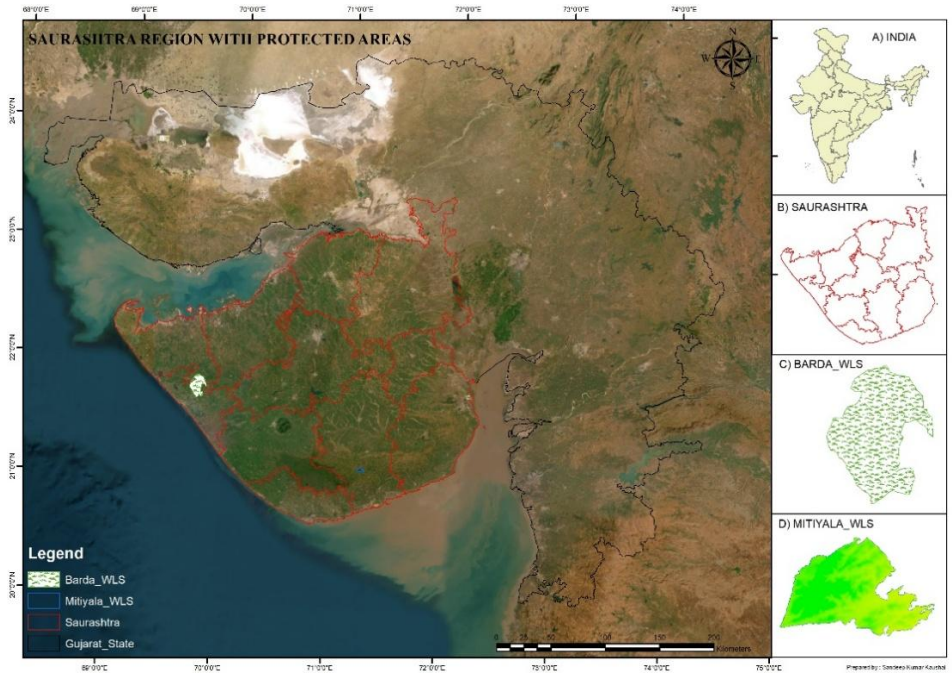


Figure 1 Study area Map insets representing India, Gujarat, Barda, and Mitiyala

While Mitiyala is situated in the Amreli district and is a part of the Gir protected area, serving as a corridor for wildlife movement through the greater Gir landscape, it covers a compact yet ecologically significant area of approximately 18.22 km^2 (Figure 1). Unlike the rugged hills of Barda, Mitiyala is undulating, featuring moderate topography consisting of tall grass patches and open scrubland. This area falls under 6B/DS1- Desert thorn forest and patches of 5B/C2- Northern tropical dry deciduous forest characterised by a mosaic of *Ziziphus* thickets and *Acacia* woodlands with a high proportion of secondary Dry savannah grassland (Champion and Seth 1968), having dominated vegetative species like *Senegalia senegal, Anogeissus latifolia, Boswellia serrata*, *Balanites aegyptica* serving as refuges for higher mammalian biodiversity, including Asiatic lion (*Panthera leo persica*), Indian Leopard (*Panthera pardus fusca*), and Indian Pangolin. Mitiyala also experiences a semi-arid tropical monsoon climate. Similar to the broader Saurashtra landscape, the year is divided into a blistering summer (March to June with temperature reaching up to 50°C), a concentrated monsoon season (June to September precipitation ranging from 615-650mm) and a mild dry winter (October-February temperature gets as low as 8°C) (Kaushal et al., 2026), but overall featured a good compact protected area harbours vast diversity of carnivores and their prey base (Asiatic lion, Indian Leopard, Hyena and Chital, Sambar, Nilgai and Wild boar as prey- predators), Jungle cat and Jackal also founds in the sanctuary.

Methodology

Systematic field surveys were conducted across the Barda and Mitiyala Wildlife Sanctuaries in the Saurashtra region of Gujarat, India, to investigate the morphological and spatial characteristics of Indian Pangolins' burrows. We conducted a survey from 2024 to 2026, spanning three years, allowing longitudinal assessment of burrowing dynamics across multiple climatic cycles. We adopted a hybrid sampling strategy to increase the probability of

encountering this elusive, nocturnal species and their burrows. We divided the study area into a grid, a system adopted for the systematic random sampling methodology, and a 1 km×1km grid overlaid on the study area using QGIS Desktop 3.24.3 *TISLER* version. Within each grid cell, a diagonal line transect was established extending from one vertex to the opposite end. Surveys were conducted along these transects in a consistent direction to maintain sampling rigour. This systematic approach was supplemented by targeted centroid monitoring as well, where intensive searches were conducted within a 100m radius around the centre of each grid, along with camera trapping, and third, random opportunistic surveys or random sightings were also considered. We focused on random opportunities in the microhabitats known to favour Pangolin activity, especially around the burrows of Pangolins, or near the daily movement areas, or wherever indirect evidence has been found. We searched the region with a high density of termitaria or ant colonies. To move beyond static observations, remotely-triggered, motion-sensing infrared camera traps (Cuddeback C1, Cuddeback IR20, Spypoint Solar Dark, and Browning Strike Force ProX) were deployed at active or abandoned burrows. The cameras were positioned at a height of 30 cm above ground to monitor the burrow entrance and kept active for 24 hours a day for a minimum duration of 15 days at the burrows specifically, which provides data on the occupancy and validates the utilisation of burrow sites by *M. crassicaudata*. We also focused on recording the site fidelity of the burrows by Pangolins, defined as the revisit rate by calculating the number of days between consecutive uses of the same burrow by an individual.

For the burrow's identification and characterisation, we identified some features based on which we classified the burrows as belonging to Pangolins, and the diagnostic field signs include tail drag marks, tear drop-shaped tracks and unique claws or scratch marks over the burrows. There were two distinct functional burrow types classified based on the features i.e. (i) Feeding burrows which were characterised by shallow, temporary excavations mostly fresh and loose soil outside burrows and most important it is often located near or at ants and termites colonies, lacking a stabilised tunnel and deep enough maybe found open burrows with claw marks and (ii) living or resting burrows are defined by well-established wider entrance and a permanent deep tunnel extending into earth, fresh and loosen soil can also be found outside entrance if the burrow is fresh or newly excavated, scats or claw marks can also be found once left mostly classified as "abandoned" are the secondary indicators. One of the most important identifying features is the shape shifting of burrows, from circular to having a cut at one lower end, i.e. from O to Q, due to the regular visit of the Pangolins mark a cut because of the tail mainly due to the living burrows are often having curved entrance instead of straight so that's why Pangolins enter circularly daily marking a cut at one end. Living burrows also have loose soil inside, which is used to seal the inner chamber of the burrow (plugging) once a Pangolin enters the burrow to protect from poaching or direct encounters with any other mammals or predators. Upon discovery, each burrow was first classified as a living or feeding burrow. Then each burrow was georeferenced using a high-precision GPS (Garmin eTrex 10 and 30), a mobile application 'GPS Essential' (accuracy verified with Garmin GPS), used in the field. For each burrow, a set of morphometric variables was recorded. Entrance dimension, specifically the horizontal diameter (D_h) and vertical diameter (D_v), was measured to the nearest centimetre. The burrow depth (B) was recorded up to the first major tunnel, or till it was possible without disturbing the animals. If it was suspected that the animals were present inside the burrow, the burrow dimensions were not measured to avoid disturbing the animals. A borescope was also used to record the animals residing inside burrows and their activity (non-invasive method).

The burrow depth was recorded up to the first major tunnel curvature using a flexible tube. Additionally, the entrance orientation (aspect) was determined using a compass to evaluate directional preferences. The slope angle of the terrain at the burrow site was estimated with the help of DEM data and processed with the help of QGIS to assess the species preference for the topographic gradients. The georeferenced burrows data were utilised to assess the spatial distribution and were correlated with multiple landscape-level variables. We used SRTM 1 Arc-Second Global digital elevation model (DEMs) data to derive topographic layers including elevation, slope, aspect, topographic wetness index (TWI), topographic ruggedness index (TRI), topographic position index (TPI), and Hillshade downloaded from (*https://earthexplorer.usgs.gov*). Vegetation (NDVI), canopy moisture (Gao_NDWI), water availability (NDWI), surface temperature (LST) and moisture indices (TWI) were quantified using the Landsat 8-9 OLI/TIRS C2 L2 satellite imagery (*https://earthexplorer.usgs.gov*). The indices were calculated from the bands.

$$\text{NDVI} = \frac{NIR - Red}{NIR + Red}$$

$$\frac{Band\ 5 - Band\ 4}{Band\ 5 + Band\ 4} \quad \text{For Landsat 8-9 satellite imagery}$$

$$\text{NDWI} = \frac{NIR - SWIR}{NIR + SWIR}$$

$$\frac{Band\ 5 - Band\ 4}{Band\ 5 + Band\ 4} \quad \text{For Landsat 8-9 satellite imagery}$$

Furthermore, vector data were utilised to calculate the Euclidean distance from each burrow to the nearest river, road and artificial water point. Edaphic factors were integrated by incorporating soil maps focusing on soil texture and drainage classes. These layers allowed for multidimensional analysis of why certain areas were prioritised for the burrowing over others. For the spatial distribution, niche boundaries and burrowing ecology and preference assessment across the study area and predictively for the Saurashtra region were modelled utilising a spatial grid stack of ten baseline environmental predictors, selected based on the specific a priori hypotheses regarding species-specific habitat selection, micro-climatic shelter requirements and seasonal foraging dynamics. DEM and spectral layer values for each burrow were extracted for the multimodal analysis for their direct biological relevance. To ensure the correct projection, all the environmental layers were processed in Q-GIS and clipped to the geographic boundaries of Mitiyala, Barda and Saurashtra region shapefiles and projected in WGS 84 / UTM Zone 42N coordinate system, and resampled via bilinear interpolation to a standardised pixel resolution of 30 meters.

Data analysis

Morphometric data collected for the burrow characteristics were summarised as Mean ± standard deviation (SD). Prior to statistical testing, the Shapiro-Wilk test was used to evaluate normality. Non-parametric statistical methods were used for the environmental variable comparisons as the structural burrow dimensions exhibited a non-normal distribution ($p < 0.05$). The Two-way ANOVA was used to identify significant differences in burrow dimensions between two study sites and across functional categories. Directional preference of the openings of the burrows was investigated with the help of circular statistics of Rayleigh's Test

for Uniformity of the orientation data to determine if burrow openings displayed a significant directional bias or an isotropic distribution across the landscape. The spatial distribution pattern was analysed using the Average Nearest Neighbour (ANN) index to determine the spatial relationship of burrow distribution patterns, whether they are significantly clustered, dispersed, or randomly distributed. This evaluates the spatial distances between observed mean distance of adjacent burrow connections versus an expected random distribution framework. Nearest Neighbour Ratio (RN) and corresponding *Z*-score were calculated using ArcGIS 10.8 to verify significant geographic clustering and dispersion.

$$\text{ANN} = \frac{\overline{D}_O}{\overline{D}_E}$$

where $\overline{D}_O$ is the observed mean distance between each burrow and its nearest neighbour, while $\overline{D}_E$ is the expected mean distance for the burrows given a random distribution.

Six terrain layers were used as a predictor set derived using DEMs as a primary data source to design the model. Localised landform variations and relative topographic positions are mathematically isolated through the Topographic Position Index (TPI), which evaluates the elevation of a focal cell relative to the mean elevation of its surrounding area within a defined spatial radius according to the formula:

$$TPI = E_{focal} - \frac{1}{n}\sum_{i=1}^{n} E_i$$

Where E_{focal} represents the elevation of the central cell, and E_i represents the elevation of the i^{th} cell within the localised neighbourhood containing n total cells, effectively distinguishing valleys, steep ridges, mid-slope terraces and flat plains. Micro-topographic complexity extracted using the Terrain Ruggedness Index (*TRI*), which quantifies the escape cover availability.

$$\text{TRI} = \sqrt{\frac{1}{8}\sum_{i=1}^{8}(E_{\text{focal}} - E_i)^2}$$

Where E_{focal} is the elevation of the central cell and E_i represents the elevation of its eight adjacent neighbours. Surface moisture accumulation potential and hydrological drainage networks across the terrain were processed as the Topographic Wetness Index *TWI*.

$$\text{TWI} = \ln\left(\frac{\alpha}{\tan(\beta)}\right)$$

where α represents the specific upslope contributing area per unit contour length and β is the localised slope gradient in radians.

Normalised Difference Water Index, following the Gao formulation, was used to predict internal canopy moisture and correlate with the variables affecting the Pangolin.

$$\text{NDWI}_{\text{Gao}} = \frac{\text{NIR} - \text{SWIR}}{\text{NIR} + \text{SWIR}}$$

Table 1 Summary of environmental theme weights, predictor variables, and data sources used in the suitability modelling matrix

Environmental Theme	Baseline Predictor Variable	Theoretical Multiplier Weight (%)	Sources
Topography *(Total Weight: 40%)*	**Elevation**	**15%**	SRTM 1-Arc second Global *https://earthexplorer.usgs.gov*
	Slope Gradient	**10%**	
	TRI (Ruggedness)	**5%**	
	TPI (Position)	**5%**	
	Aspect	**5%**	
Biophysical *(Total Weight: 35%)*	**NDVI (Vegetation)**	**15%**	Landsat 8-9 OLI/TIRS C2 L2 *https://earthexplorer.usgs.gov*
	NDWI (Gao)	**10%**	
	NDWI (McFeeters)	**5%**	
	TWI (Wetness)	**5%**	
Microclimate *(Total Weight: 25%)*	**LST (Surface Temp)**	**25%**	Landsat 8-9 OLI/TIRS C2 L2 *https://earthexplorer.usgs.gov*
TOTAL MATRIX	10 Core Variables	**100%**	

Land Surface Temperature (LST), a critical physiological constraint driving nocturnal den selection, was derived by processing the thermal infrared sensor band 10 through the radiative transfer equation with local atmospheric profiles and surface emissivity to calculate the radiant temperature in Celsius. Euclidean distances to the rivers and forest edges were calculated from vector data. A Pearson correlation matrix and Euclidean distance analysis were executed concurrently to evaluate the relative influence on localised burrow placement, with all significance thresholds fixed at $p < 0.05$. This study utilises weighted overlay analysis for ten spatial predictors classified into three thematic criteria. Topographic factors dictate 40% of the total model weight. Biophysical factors contribute 35%, while Land Surface Temperature (LST) contributes 25% entirely to microclimate. For establishing a consensus suitability framework for predicting optimal micro-habitats, this uses 100 % optimised stacked raster layers (Table 1).

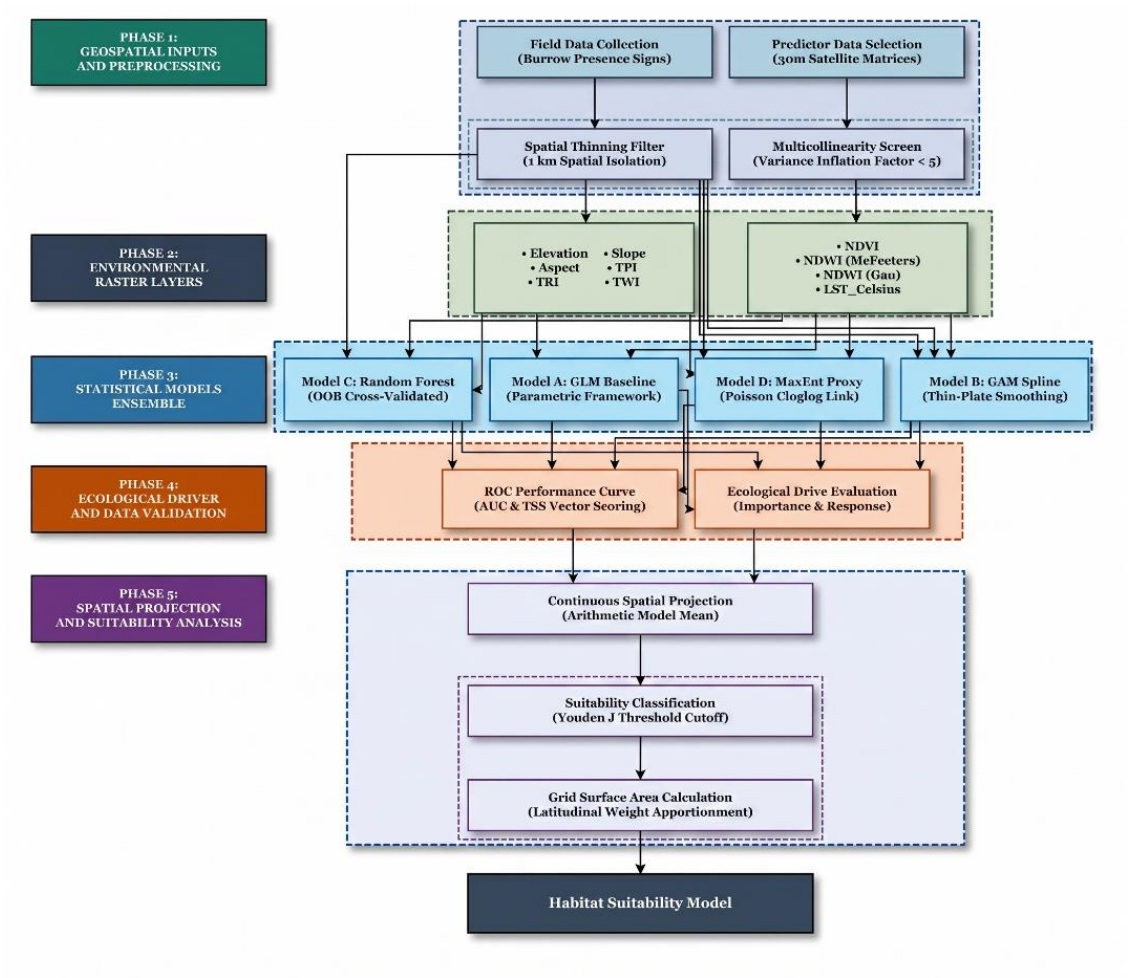


Figure 2 Methodological flowchart outlining the five operational phases of the multi-model ensemble habitat suitability modeling workflow

To overcome the spatial bias and model overfitting, the occurrence data were filtered using a spatial thinning protocol prior to running the analyses. This preprocessing phase constrained presence data to geographically independent locations segregated by a threshold distance of 1 km, eliminating clustered sampling bias and spatial autocorrelation. To reduce statistical redundancy prior to model initialisation, preprocessing was performed to examine the predictor variables processed between geomorphological layers and satellite-derived indices data. Severe multicollinearity magnifies the standard errors of regression coefficients, generates structural instability in the models and distorts the rankings of the variable importance in later ecological interpretations. A complete multicollinearity assessment was conducted across all ten layers to eliminate redundancy. The variance inflation factor (VIF) was computed sequentially for each independent variable utilising an ordinary least squares regression framework against all other covariates in the dataset, following the specified formula:

$$\mathrm{VIF}_i = \frac{1}{1 - R_i^2}$$

Where R_i^2 is the coefficient of determination for the specific regression model in which the primary environmental variable is observed as a dependent function of the other nine parameters. Variables having a variance inflation factor exceeding a specific mathematical

threshold (VIF ≥ 5) were systematically deleted. This filtering assured that no environmental predictor included shared more than 80% of its variance with other predictors and was systematically deleted. This filtering strategy assured that no environmental predictor included shared more than 80% of its variance with other variables in the data matrix, therefore assuring that only independent, non-redundant environmental characteristics were utilised in the subsequent modelling settings. To reduce individual algorithmic bias and summarise the complete complexity of ecological responses within the semi-arid landscape, a multi-model ensemble framework was established, utilising four simultaneous statistical and machine learning configurations derived from 89 independent pre-processed presence records and 10,000 random landscape background points. The baseline parametric trend was determined using a Generalized Linear Model (GLM), which assessed habitat suitability by modelling presence-background data with a binomial error distribution and a logit link function, including both linear and quadratic terms for environmental covariates to represent basic, symmetrical parabolic ecological responses. The rigorous linear assumptions of the baseline model were reduced by incorporating a Generalized Additive Model (GAM), which utilised non-parametric regression smoothing splines enclosed inside an additive structure. This arrangement allowed the form of the link to be characterised experimentally by the data points, with the degrees of smoothing modified using cross-validation to prevent over-fitting. High-order multi-variable interactions and complex thresholds were recorded utilising a non-parametric machine learning Random Forest (RF) bootstrap-aggregation decision tree design. This technique evaluated 1,000 unique regression trees, with a random subset of predictors assessed at each decision threshold and optimised via Out-of-Bag (OOB) cross-validation without requiring explicit distributional assumptions. The modelling matrix was completed by a MaxEnt proxy network utilising a Poisson cloglog link structure. This model minimises the distance between the empirical distribution of presence points and the background landscape constraints through linear, quadratic and hinge feature selections. Model validation evaluation was conducted via a split-sample cross-validation strategy wherein the trimmed occurrence dataset was partitioned into 70% for model training and 30% for independent testing, replicating this validation loop 10 times to obtain stable mean performance. Predictive accuracy was evaluated using two complementary matrices: i) the area under the curve (AUC) of the receiver operating characteristics to measure absolute discrimination capacity across all possible thresholds, and ii) the True Skill Statistic (TSS) to evaluate classification precision independent of prevalence.

$$\mathrm{TSS} = \mathrm{Sensitivity} + \mathrm{Specificity} - 1$$

Values exceeding 0.75 were evaluated as evidence of strong prediction performance. The ecological contribution of each predictor was evaluated using random permutation importance tests that permuted the values of each variable throughout the testing dataset and measured the resulting loss in absolute AUC performance. Partial dependence response curves were also developed to detect nonlinear thresholds and determine the true physiological tolerances of the species along crucial environmental variables.

The different spatial projections from the four models were combined into a single continuous map using the Arithmetic Model Mean. This consensus technique reduced individual model variances and produced an accurate spatial projection of habitat suitability driven only by empirical field data rather than subjective a priori criteria. To transform this continuous probability gradient into independent, binary conservation zones, the analytical technique applied was Youden's J threshold cutoff criterion. The ideal threshold (J) was discovered by maximising the vertical distance on the ROC plot between the curve and the diagonal line.

$$J = \text{Sensitivity} + \text{Specificity} - 1$$

This mathematical method calculated an objective threshold of 0.485, classifying the environment into Suitable habitat core ($\geq J$) and unsuitable habitat core zones ($< J$). In order to determine the geographic surface area of these zones with high precision, a latitudinal weight apportionment technique was included in the final processing phase. Because the research location includes many degrees of latitude throughout the Saurashtra peninsula, traditional cell counting methodologies over-represent surface areas at higher latitudes due to grid cell distortion in projected coordinate systems. The integrated apportionment algorithm updated the surface area computation of each pixel, dependent on its correct geodetic latitude, according to the formula:

$$\text{Area}_{\text{corrected}} = \text{Area}_{\text{nominal}} \times \cos(\text{Latitude})$$

This geodetic development facilitates highly exact calculations of expected habitat availability. All statistical analyses and ensembled model operations were performed in R (version 4.3.1) (R Core Team, 2026), with a significance level set at $p < 0.05$.

RESULTS

A total of 345 burrows were documented and structurally measured across both study locations. In Mitiyala Wildlife Sanctuary, 107 feeding burrows and 25 living burrows were identified. In Barda Wildlife Sanctuary, 176 feeding burrows and 37 living burrows were recorded. Living burrows consistently exhibited larger dimensions than feeding burrows across the sites. In the Barda Wildlife Sanctuary, living burrows were regular and vertically elongated (D_h: 28 ± 1.5 cm, D_v: 34 ± 2.8 cm, $depth$: 162 ± 21 cm) compared to the shallower, near-circular feeding burrows (D_h: 24 ± 1.2 cm, D_v: 26 ± 1.9 cm, $depth$: 129 ± 12 cm). Mitiyala Wildlife Sanctuary was identical to this tendency, as living burrows (D_h: 27 ± 1.7 cm, D_v: 31 ± 2.9 cm, $depth$: 157 ± 18 cm) exceeded the smaller feeding burrows (D_h: 25 ± 1.4 cm, D_v: 27 ± 1.7 cm, $depth$: 126 ± 14 cm). In conclusion, living burrows had substantial vertical elongation ($D_v > D_h$), peaked in Barda, whereas feeding burrows retained a regular, smaller and confined circular contour (Table 2). Two-Way ANOVA was performed to determine the significance of location and burrow type on these morphometrics ($N = 200$). Burrow type strongly correlated with all parameters ($p < 0.001$), indicating that functional utility drives morphological size. For horizontal diameter (D_h), the major impact associated with location was non-significant ($F_{1,196} = 0.04, p = 0.832$). Still, a significant interaction effect ($F_{1,196} = 43.20, p < 0.001$) established that horizontal widening was significantly greater in Barda. The vertical diameter (D_v) exhibited extremely significant results for both the location main effect ($F_{1,196} = 19.28, p < 0.001$) and the interaction factor ($F_{1,196} = 68.14, p < 0.001$), influenced by the distinctive vertical curving characteristics of Barda's living burrows. Conversely, burrow depth was exclusively correlated with functional type ($F_{1,196} = 182.00, p < 0.001$). In contrast, location ($p = 0.135$) and interaction effects ($p = 0.862$) were non-significant, suggesting a substantially conserved structural depth threshold across both sanctuaries.



Figure 3 Feeding Burrows of the Indian Pangolin



Figure 4 Living Burrow of the Indian Pangolin

Table 2 Burrow Morphometrics of Indian Pangolin in Barda and Mitiyala Wildlife Sanctuary

Locations	**Burrows Type**	**Horizontal Diameter (D_h) (in cms.)**	**Vertical Diameter (D_v) (in cms.)**	**Depth (in cms.)**
Barda Wildlife Sanctuary	Feeding	24 ± 1.2	26 ± 1.9	129 ± 12 cm
	Living	28 ± 1.5	34 ± 2.8	162 ± 21 cm
Mitiyala Wildlife Sanctuary	Feeding	25 ± 1.4	27 ± 1.7	126 ± 14 cm
	Living	27 ± 1.7	31 ± 2.9	157 ± 18 cm

The average nearest neighbour (ANN) spatial point pattern analysis indicated that in both distinct landscape conditions, the rugged hills of Barda and the low relief undulating terrain of Mitiyala, the burrow placement by the Indian Pangolin (*Manis crassicaudata*) is influenced by non-random, ecologically driven selection factors. In all evaluated strata, both functional burrow types (living and feeding) exhibited significant structural aggregation, markedly differing from a random geographic distribution ($p < 0.01$). Table 3 provides a comprehensive description of the baseline mapping measurements, spatial ratios, and the associated distributions of statistical significance generated by the ANN processing loop of analysis.

Table 3 Average Nearest Neighbour Pattern of Indian Pangolin Burrow

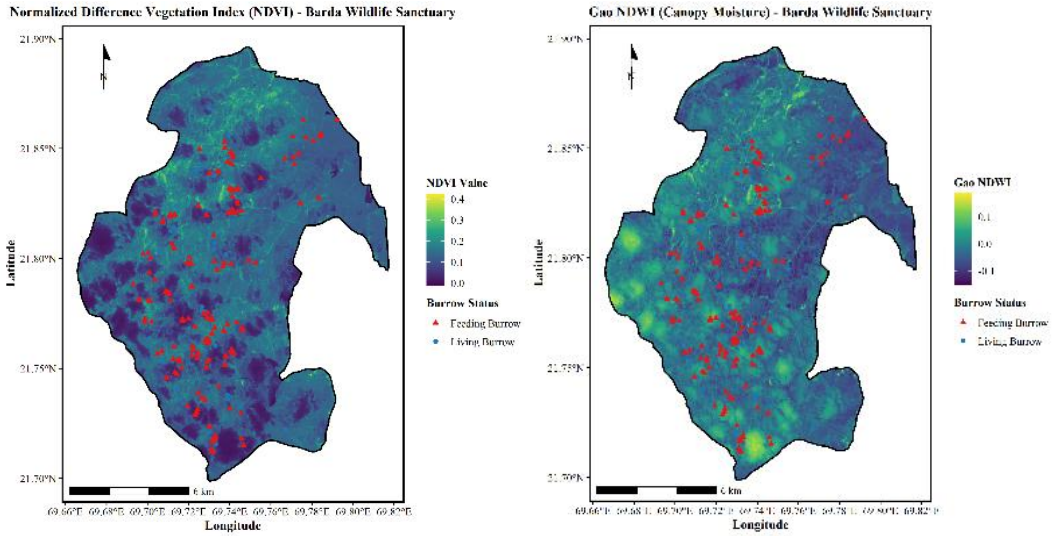
Site	**Burrow Type**	**NN Ratio**	**Z-Score**	**Pattern**
Barda	Living	0.67	-3.99	Clustered
Barda	Feeding	0.46	-13.76	**Highly Clustered**
Mitiyala	Living	0.64	-3.39	Clustered
Mitiyala	Feeding	0.34	-9.72	**Extremely Clustered**

The spatial aggregation metrics for feeding burrows indicated a significant clustering pattern in both wildlife sanctuaries. Within the Barda hilly terrain, feeding burrows indicated a nearest neighbour ratio (NN) of 0.46 with a highly significant Z-score of -13.76 ($p = 0.00$). This high spatial clustering is physically defined by a constrained observed mean distance between clustered burrow sites of just 202 meters. The spatial aggregations became even more prominent inside the alluvial plains of Mitiyala, where feeding burrows attained a NN ratio of 0.34 and a critical Z-score of -9.72 ($p = 0.00$). From an ecological perspective, these extreme mathematical clusters demonstrate that foraging operations are not implemented as random, extensive terrain tracks. Instead, *M. crassicaudata* targets certain microhabitats. The high density of specialised feeding burrows shows that species regularly choose precise colonial insect patches. Foraging behaviour is highly concentrated around certain epigeal termitaria and affluent subterranean art colonies, resulting in unique, dense feeding burrow hotspots where resource availability is maximum.

According to dense clusters of feeding excavations, living burrows demonstrated a more dispersed, yet statistically clustered, spatial pattern across the sanctuaries. In Barda, the instance of living burrows, we discover the burrows were clustered with (*RN*) of 0.67, which mathematically characterises the pattern as clustered. *Z*-score (-3.99) indicates that the species chooses specific locations to thrive, with p=0 indicating highly significant results, with a 531-meter mean distance between two living burrow clusters. A comparable structural distribution was documented in the Mitiyala terrain, providing an *RN* of 0.64 and a *Z*-score of -3.39. Feeding burrows (z= -13.76) are much more clustered than living burrows (z=-3.99). This

significant disparity in spatial density between functional classifications suggests a definite behavioural differential in how the species utilises the landscape. While feeding sites are determined entirely by patchily scattered insect resources, a combination of specialised geomorphological requirements and territorial behaviours regulates living burrows.

Topographic profile extractions across the occurrence datasets revealed the distinct variations in altitudinal selection between the two sanctuaries, contrasted by highly conserved slope preferences. Burrows within Mitiyala were concentrated at higher elevations, exhibiting a median of approximately 265 m within a bounded range of 200 to 390 m. In contrast, Barda occurrences displayed a lower median elevation of 225 m. Still, they occupied a much wider altitudinal gradient, capturing low-lying burrowing activity down to 50m and upper elevation limits reaching 440 m. Conversely, fine-scale terrain micro-topography revealed nearly identical selection patterns for surface gradients across both sides. The median terrain slope at burrow sites was 10° in Barda and 8° in Mitiyala, with both sanctuaries exhibiting an identical upper threshold where specialised burrows persisted on steep slopes up to 32°. This cross-site consistency indicates that while regional geography dictates the absolute elevation, localised micro-habitat selection is structurally constrained by a strong preference for gentle to moderate slopes. In significant contrast to the various terrain baselines, compass-driven vector assessments of the actual burrow openings revealed a highly conserved, non-random orientation rule shared throughout both sanctuaries. In Barda and Mitiyala populations, the morphological opening of both functional burrow classes was exclusively confined to a relatively restricted northern arc extending precisely between 330° and 40°. This tight 'V' shaped directional selection indicates a universal micro-topographic alignment across the Saurashtra region, as *M. crassicaudata* deliberately drives tunnel entrances to face away from the southern and western quadrants.



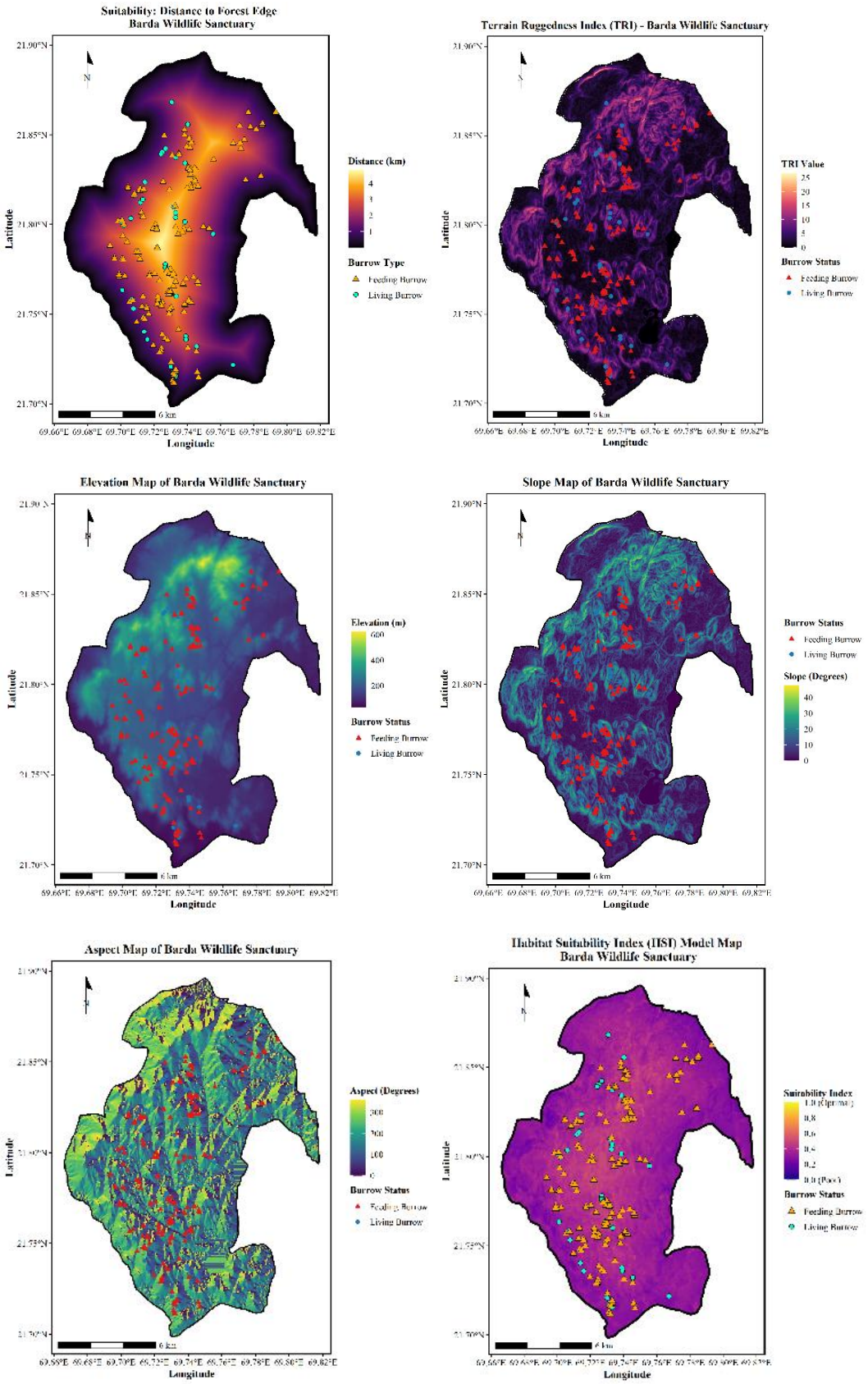


Figure 5 Spatial environmental predictors and the final Habitat Suitability Index (HSI) model map overlaid with burrow distributions in Barda Wildlife Sanctuary

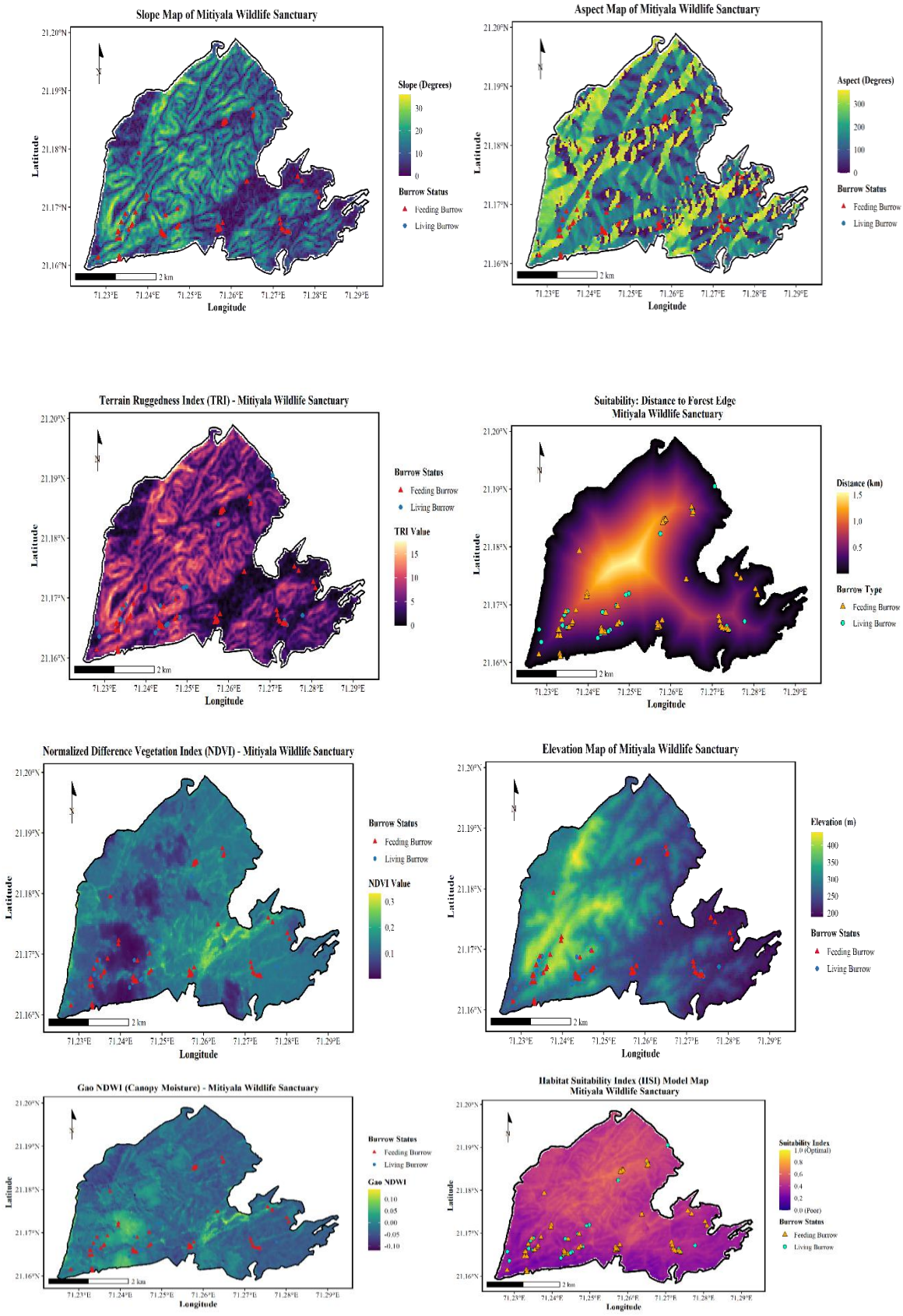


Figure 6 Spatial environmental predictors and the final Habitat Suitability Index (HSI) model map overlaid with burrow distributions in Mitiyala Wildlife Sanctuary

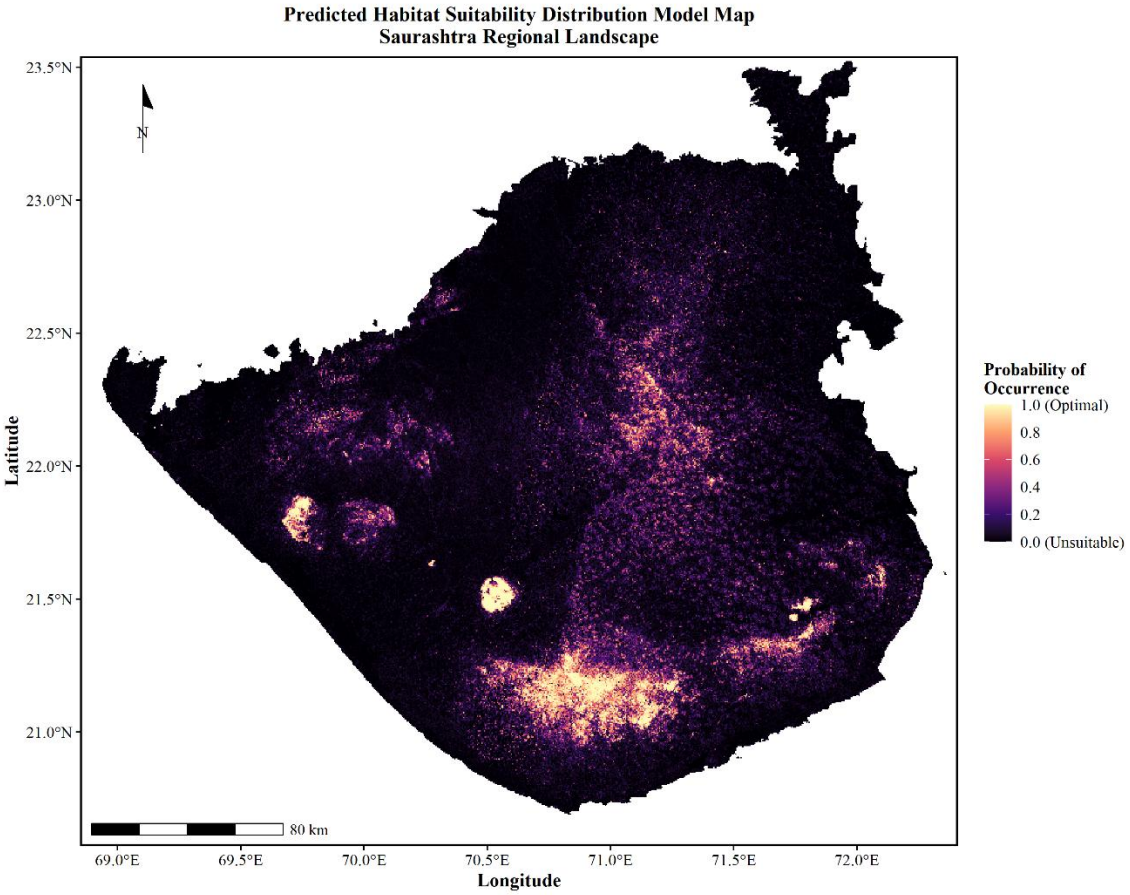


Figure 7 Habitat suitability map of the Indian Pangolin

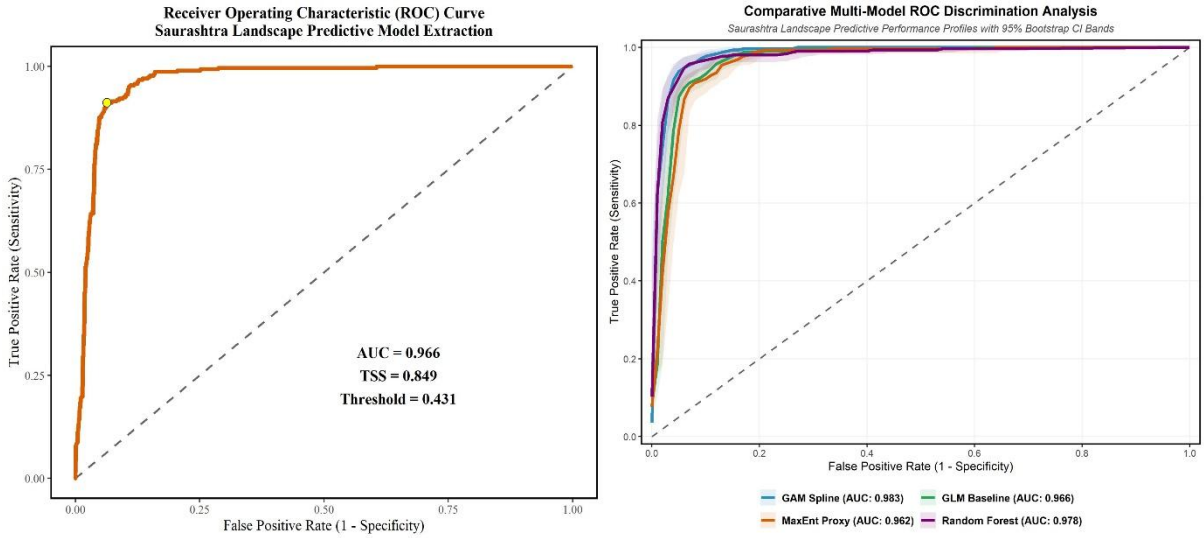


Figure 8 ROC curves for Saurashtra predictive models, showing the ensemble threshold profile (left) and performance comparisons across individual algorithms (right)

The multi-model spatial ensemble framework achieved high predictive accuracy across all four machine-learning and statistical engines (Figure 7). Evaluation of threshold-independent metrices revealed that the semi-parametric Generalized Additive Model exhibited the highest overall discriminatory performance (AUC = 0.983), closely followed by the cross-validated Random Forest Classifier (AUC = 0.978; derived via Out-of-Bag internal voting partitions). The parametric Generalized Linear Model and the presence-background MaxEnt Poisson

proxy demonstrated similarly robust predictive caps with tight confidence intervals (AUC = 0.966 and 0.962, respectively). Overlapping 95% bootstrap confidence interval across all four algorithms remained consistently elevated toward the upper-left quadrant of the receiver operating characteristic space, confirming that the spatial predictor matrix holds exceptionally strong explanatory power for burrow site selection across the Saurashtra regional landscape. Analysis of relative environmental factors contributions based on structural deviance reduction revealed that the topographic paradigm significantly dominated the ensemble matrix. Individually, elevation was found as the single most influential landscape predictor throughout the parametric and semi-parametric computations, preserving feature contributions between 25% and 36%. Notably, transitioning to the non-parametric Random Forest framework exposed high-order micro-topographic interactions; within this machine-learning environment, the absolute influence of local elevation and LST moderately reduced, while fine-scale surface features, specifically slope and the terrain ruggedness index (TRI), abruptly gained ground to account for 19.8% and 19.1% of the model predictive power, respectively. Among the remaining biophysical and hydrological parameters, the topographic wetness index (TWI) exerted a minor structural effect, whereas variables including NDVI, TRI, NDWI, TPI, and aspect provided near-negligible direct contributions to the final deviance model partitions.

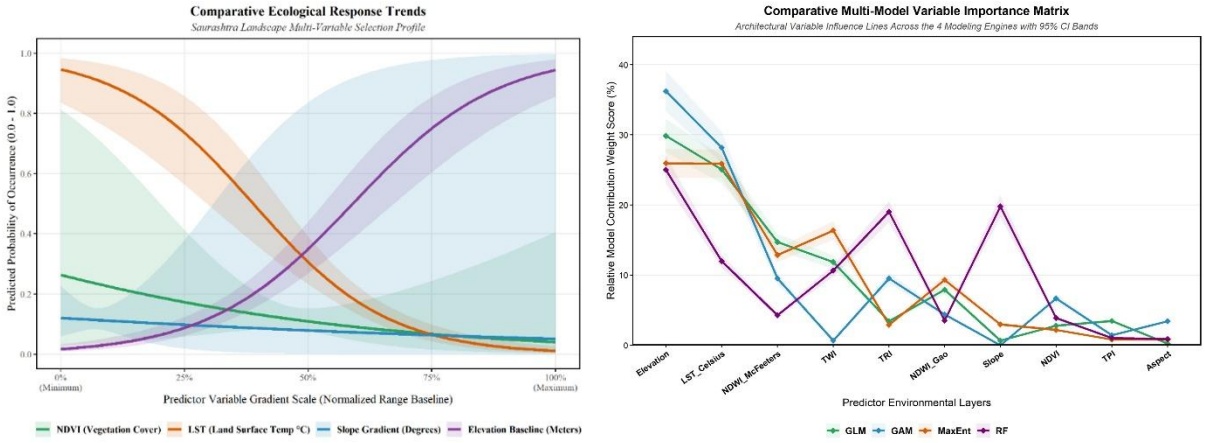


Figure 9 Multi-model habitat suitability response curves (left) and variable importance contribution weights (right) across GLM, GAM, MaxEnt, and Random Forest algorithms

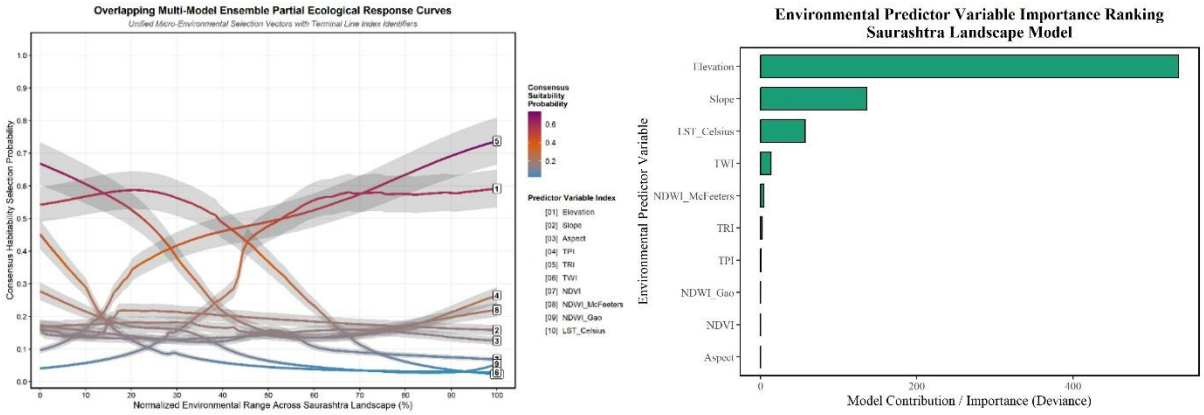


Figure 10 Ensemble partial response curves (left) and variable importance ranking (right) of environmental predictors within the Saurashtra landscape model

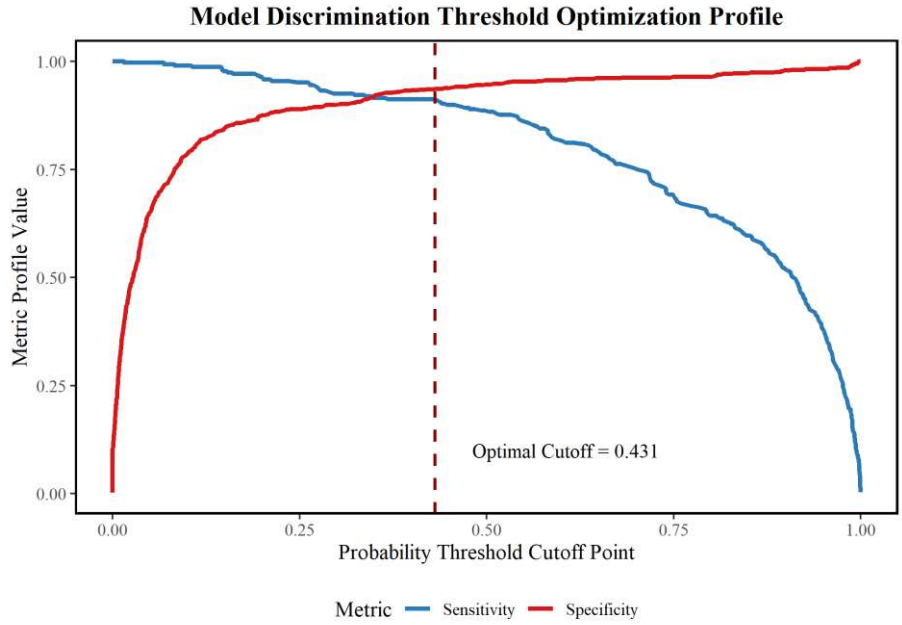


Figure 11 Sensitivity and specificity optimisation curves across probability thresholds, establishing the optimal ensemble model cutoff value at 0.431

Table 4 Total area and percentage distribution of suitable versus unsuitable habitats in the study area

Landscape Suitability Class	**Model Criteria Matrix**	**Spatial Area Coverage (km^2)**	**Relative Proportion of Landscape (%)**
Highly Suitable Habitat	≥ Optimised Threshold Cutoff	3,402.36	5.71%
Unsuitable Landscape	< Optimised Threshold Cutoff	56,135.24	94.29%
Total Area		59,537.60	**100.00%**

The binarization of the continuous consensus probability gradient at the optimal Youden's J threshold of 0.431 delineated a distinctly defined spatial matrix of suitable versus unsuitable conditions across the landscape (Table 4). Of the whole assessed Saurashtra landscape footprint (Area = 59,537.60 km^2), merely 5.71% (Area = 3,402.36 km^2) was classified as a highly suitable habitat. The confined spatial footprints indicate that the target species demonstrates strict, specialised micro-environmental and biophysical constraints throughout the peninsula. A significant majority of the considerable human-influenced agricultural matrices, significantly degraded topographical features, or thermally unstable areas are unsuitable for long-term burrow suitability. The limited and scattered distribution of these 3,402.36 km^2 optimum zones underscores the urgent need for focused, high-intensity conservation zoning with the established protected areas of the Barda and Mitiyala landscape corridors.

DISCUSSION

The significant structural divergence exhibited by the Two-way ANOVA model (n = 200) across burrow dimensions statistically demonstrates that the functional utility drives the architectural engineering of *Manis crassicaudata*. The considerable morphological contrast between functional classes, where

active living burrows typically exhibit larger depth (> 150 cm) and vertically elongated entryways compared to shallow, circular feeding burrows, reflects a specialised energy allocation mechanism. Living burrows operate as crucial, long-term investments targeted towards predator defence, environmental insulation and nurturing of cubs by mother nesting. The large vertical elongation (D_v = 34 ± 2.8 cm in Barda) strengthens the defensive posture of the animal; a higher, narrower structure lets a rolled-up pangolin firmly wedge its scales against the tunnel walls, effectively limiting entry to possible predators. Pangolins basically have two chambers that they use to seal the inner chamber where they rest during the day to avoid interactions and predation (Karawita et al. 2018). Conversely, feeding burrows are temporary, opportunistically built structures designed primarily to extract localised ant and termite biomass. Because these burrows are excavated fast and abandoned after a colonial insect patch is depleted, the energetic investments are optimal, resulting in shallow, unfortified and regular circular profiles across both the sanctuaries. The large interaction effect discovered for horizontal and vertical diameters inside the Barda shows the critical relevance of local substrate geomorphology. Barda's hard, volcanic soil matrices demand a greater energetic excavation cost yet offer remarkable structural stability. This helps the indigenous population to build a deeply carved, elongated tunnel without risking roof collapse. In contrast, the uniform, non-significant interaction found for burrow depth throughout both sanctuaries demonstrates a highly maintained biological threshold. Despite the regional geography or surface soil composition, *M. crassicaudata* enforces a tight substrate depth threshold (averaging 157 to 162 cm for living burrows) to satisfy fundamental physiological safety demands and maintain long-term structural persistence.

The average nearest neighbour (ANN) point pattern analysis reveals conclusive mathematical confirmation that landscape utilisation by *M. crassicaudata* is non-random and highly clustered, which varies significantly from a standard geographic distribution. The significant geographical clustering recorded for feeding excavations, which increased to an extreme RN-ratio of 0.34 and *Z*-score of -9.72 in Mitiyala, demonstrates a severe dependency on patchy resource hotspots. Foraging activities are not implemented as extensive, random trails around the area. Instead, they are determined inside specific micro-habitats that maintain densely populated subterranean ant and epigeal termite colonies. When an abundant dietary patch is identified, the animal performs high-intensity, focused digging activities within a restricted radius, forming dense, clustered feeding burrow hotspots.

However, the significantly reduced spatial clustering observed for living burrows (RN = 0.67 in Barda; RN = 0.64 in Mitiyala) demonstrates an opposing physiological restriction. While foraging footprints fluctuate contingent on seasonal dietary resources, the location of a permanent residential base is heavily limited by territorial exclusion and long-term site protection. The higher RN ratios (0.64:0.67) reported for resting burrows imply that active, permanent burrows are maintained with a higher degree of spatial segregation across the landscape. This pattern reflects the species' need to spread its residential burrows to optimise access to habitat substrates, provide stable micro-climatic conditions inside the deep burrows, and avoid home-range overlap with conspecifics. This spatial separation facilitates the species' solitary behaviour and natural burrow-allocation mechanisms.

Living burrows require a significant mean distance between residential clusters (531 meters in Barda) to avoid overlapping feeding zones and limit intraspecific competition. A significant comparison in spatial density patterns between functional categories (Z = -13.76 vs. Z = -3.99) clearly demonstrates how the Indian Pangolin balances short-term energetic consumption with long-term territorial occupancy over semi-arid terrain landscapes.

The widespread constraint of physical burrow openings to a rather constrained northern arc spanning 330° to 40° across both wildlife sanctuaries is an exceptional behavioural observation. This rigid "V" shaped alignment functions as an obligate micro-topographic buffer against severe bioclimatic stresses, particularly excessive direct solar radiation and catastrophic convective summer winds. In the semi-arid

Saurashtra peninsula, the annual sunlight trajectory is strongly oriented towards the southern sky. Consequently, slopes facing south, south-east and southwest endure significant day-long sun irradiation and high surface heating. By altering burrow entrances to face only toward the northern zone, *M. crassicaudata* exploits maximal natural topographic shadows. This structural alignment ensures that burrow entrances remain entirely shaded from the direct morning solar radiation, thus minimising ambient radiant heat entry during the post-dawn hours when this nocturnal mammal returns from eating.

Furthermore, its northern tilt provides a significant defence against convective thermal heat currents. During the peak dry season, hyper-thermic winds blow predominantly from the west and south-west across the plains. Positioning the burrow apertures inside the 330°- 40° arc keeps the burrow entrance perpendicular or opposed to these hot wind directions. The nearby slope or plateau surrounds and functions as a physical windbreak, preventing hot, arid air masses from rapidly flowing into the subterranean shafts. This effectively safeguards vital internal relative humidity and prevents the species from acute aridity, allowing for a robust physiological hypothesis for the consistent distribution of this confined northern range.

The integration of Digital Elevation Models (DEM) and Landsat spectral indices delineates the rigorous biophysical limitations governing the distribution of *M. crassicaudata*: i) Altitudinal segregation: the altitudinal extractions reveal distinct landscape-level adaptive partitioning. In the complex, hilly landscape of Barda, the species delineates its habitat by occupying a specific mid-elevation zone (180-260 meters), avoiding the flood-prone lowland alluvial basins and the exposed, steep geological slopes. Conversely, the Mitiyala population elevates its home range to a restricted plateau band (240 to 300 meters), which may be due to human movement being more prevalent in low elevation zones. Another reason may be that regional geography influences the absolute altitudinal baseline, whereas micro-habitat selection is governed by localised hazard factors. ii) thermal suppression and canopy cover: the Landsat thermal (LST) and vegetative (NDVI) extractions reveal a strict physiological comfort zone. The complete presence of active living burrows within thermal depressions where dry season land surface temperature values remain around 50°C demonstrates how burrow optimisation is crucial for escaping hyperthermia. This thermal selection indicates the species' presence for moderate canopy densities (NDVI between 0.20 and 0.35) (Sun et al. 2025 a,b). Open hyper-arid desert areas are entirely avoided due to insufficient shade and structural roots, while deep forest interiors are overlooked in favour of fertile scrub-forest boundary zones that sustain huge populations of subterranean prey. iii) moisture optimisation: the correlation of burrow clusters with favourable canopy moisture indices (0-0.1 $NDWI_{Gao}$) suggests that the species depends on particular moisture-retaining micro-refugia that maintain burrow humidity and survive extreme seasonal droughts throughout the Saurashtra region.

The unique predictive accuracy achieved by the multi-model ensemble topology (AUC = 0.96, TSS = 0.84) demonstrates the stability of the environmental predictor matrix. The varied performance hierarchy led by the semi-parametric GAM spline (AUC = 0.98) and the cross-validated Random Forest framework (AUC = 0.97) underlines the complex, non-linear relationships that influence habitat selection by *M. crassicaudata*. The significant shift in variable crucial weight obtained while transitioning into the non-parametric Random Forest setup intricate micro-topographic relationships. While parametric models emphasise macro-scale parameters like absolute elevation, the random forest engine uncovers the crucial importance of fine-scale geomorphological features, with slope gradient (19.8%) and the terrain ruggedness index TRI (19.1%) emerging as major predictive drivers. This statistical shift implies that macro-geographic variables establish the broad distributional limits of the species, whereas localised geomorphological steepness and fragmented terrain characteristics ultimately control the specific coordinates of burrow morphology.

The binarisation of the continuous consensus probability gradient at the optimised Youden's J threshold of 0.431 provides a significant indication for regional conservation management. The mathematical partitioning reveals that out of the large (59,537.60 km^2) Saurashtra regional terrain, a minimal 5.71%

(area = 3,402.36 km^2) is available as highly suitable for the long-term survival of the species. The remaining 94.29% of the landscape is entirely unsuitable due to widespread human-induced agricultural disturbance, high thermal instability, and degraded topographies. The slightly restricted geographical apportionment indicates that broad, unspecific sanctuary restrictions might be challenging. Even within legally protected networks like Barda and Mitiyala, optimal habitat is severely confined to small, isolated interior valley belts and fragile southwestern patches. These isolated habitats serve as critical macro-ecological micro-refugia. Any localised environmental degradation, such as groundwater depletion, depletion of scrub edge layers, or considerable animal overgrazing, can disrupt these fragile interconnections and trigger a rapid localised collapse in suitability.

Regional conservation frameworks must shift focus away from broad boundary enforcement and prioritise the strict zoning and absolute protection of these specific low-temperature, mid-elevation hydrological valleys and forest edge corridors to ensure the long-term persistence of the endangered Indian Pangolin across western India.

CONCLUSION

The multi-model population evaluation carried out in the Saurashtra peninsula established a robust baseline for assessing the systemic vulnerability and highly specialised habitat needs of the endangered Indian Pangolin (*M. crassicaudata*). By demonstrating that structural burrow profiles are strongly controlled by functional utility and geomorphological restrictions, this research turns the focus of pangolin ecology from broad-scale distribution mapping to confined, behaviourally planned micro-refugia. The spatial point patterns and topographic extractions analysed across both populations reveal a species operating under harsh environmental limitations, where foraging habits are rigidly correlated to specialised insect prey patches and residential selections are bound by extreme thermal and altitudinal limits. Crucially, the standardised stability of a narrow northern burrow entrance alignment throughout both the sanctuaries demonstrates a fine-scale behavioural protection mechanism against harsh macro-climatic conditions. When these fine-scale behavioural choices are scaled up to a landscape level using ensemble modelling, they mark an urgent conservation scenario marked by a very limited regional habitat availability that is highly fragmented by human-dominated matrices. This severe erosion of viable zones down to isolated interior regions inside broad sanctuary bounds reveals that historical, wide-area conservation lines struggle to sustain the unique geomorphological and microclimatic niches required by this species to escape localised extinction. To prevent the continuing destruction of these vulnerable ecological environments, forest departments and wildlife managers must quickly switch from passive boundary monitoring to active, micro-refugia protective zoning and should identify the crucial habitats and protect them under provisions of the Indian Wild Life (Protection) Act 1972. Furthermore, landscape management mechanisms must severely penalise extreme livestock overgrazing and tree cutting throughout transitional scrub-forest ecotones to safeguard the leaf-litter biomass and wood-root networks that sustain the pangolin's essential prey base even outside protected forests. Because the vast majority of the remaining optimal habitat areas sit outside protected forests, forest authorities must interact with local agricultural communities to build community-led anti-poaching and citizen science monitoring networks.

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DISCLOSURE STATEMENT

There is no potential conflict of interest.

ETHICAL STANDARD

Fieldwork was carried out with formal research permits granted by the Principal Chief Conservator of Forests (PCCF) and Chief Wildlife Warden, Gujarat Forest Department (Permit No. WLP/RTC/TE-1/C/725-26/2023). We focused on the morphometric characterisation of burrows and used non-invasive motion sensor camera traps. Minimal disturbance was ensured to the surrounding micro-habitat during the measurement of burrow parameters.

AUTHOR CONTRIBUTION

S.K. Kaushal and A.M. Khan planned the study and methodology. S.K. Kaushal conducted a field survey. S.K. Kaushal analyses the data using software. S.K. Kaushal prepared the original draft of the manuscript. S.K. Kaushal and A.M. Khan reviewed and edited the draft. A.M. Khan supervised the study. Both authors have read and agreed to the published version of the manuscript.

DATA AVAILABILITY

The datasets generated and/or analysed during the current study are not publicly available due to strict non-disclosure conditions of the research permit and severe conservation concerns regarding the precise locations of critically endangered species. Data are however available from the corresponding author on reasonable request, strictly subject to prior approval and clearance from the permitting forest department authority.

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SUPPLEMENTARY MATERIAL

The authors declare that no supplementary material is attached to this manuscript.

CONSENT FOR PUBLICATIONS

Both authors consented to the publication of this manuscript in *Scientific Reports.*

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