

Topography shapes the internal organisation of tiger home ranges in the plateau-gorge landscapes of central India

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Abstract

Accurate home-range estimation is central to understanding animal space use, yet most telemetry studies represent terrestrial movement on two-dimensional planimetric surfaces and may therefore overlook the effects of terrain. Although digital elevation model (DEM)-based three-dimensional correction can improve home-range estimates in steep mountainous environments, its ecological relevance in plateau-gorge landscapes remain unclear. We examined how topography influences both home-range estimation and the internal organisation of space use by resident tigers (*Panthera tigris*) in the Vindhyan plateau-gorge landscape of central India. Using long-term GPS telemetry data, we compared two-dimensional and DEM-corrected three-dimensional autocorrelated kernel density estimates for 50% core areas and 95% home ranges across sexes and seasons. We also classified the landscape into six functional landform classes using DEM-derived geomorphometric variables and applied a Bayesian Dirichlet core-shell model to quantify landform enrichment within 50% core areas relative to the surrounding 95 – 50% home-range shell.

Topographic correction produced only negligible increases in estimated home-range area, with 3D-to-2D ratios close to unity, indicating that vertical relief contributed little to the geometric extent of tiger home ranges in this landscape. Terrain nevertheless strongly influenced where intensive space use occurred. Core areas were consistently enriched in rugged refuge and low-drainage landforms, whereas open plateau was systematically under-represented. These patterns were strongest during summer and monsoon and were more pronounced and seasonally consistent in females than in males, suggesting sex-specific differences in the spatial organisation of core use. By contrast, general slope showed little evidence of consistent enrichment across seasons.

Our results show that a limited effect of topographic correction on total home-range area should not be interpreted as evidence that terrain is ecologically unimportant. In this plateau-gorge system, topography shaped the internal distribution of tiger space use more strongly than the outer geometry of the home range. Combining DEM-derived landform classification with Bayesian compositional analysis therefore reveals ecological structure that conventional home-range metrics alone may miss. This framework is broadly transferable to wide-ranging terrestrial mammals in heterogeneous landscapes and can help identify terrain features that contribute disproportionately to habitat quality and conservation value.

Introduction

Understanding how large carnivores use space is one of the central interests in movement ecology, their habitat assessment and conservation planning. Home-range analyses are not just a statistical output around animal locations; it represents the spatial domain within which individuals encounter prey, avoid competitors, access refuge, reproduce and respond to environmental constraints (Burt, 1943; Powell and Mitchell, 2012). For territorial carnivores, home-range structure also reflects the spatial organization of individuals within a landscape, influencing density, overlap, dispersal potential and conflict risk (Dutta and Krishnamurthy, 2025; Nams et al., 2023). Therefore, accurate home-range estimation size and space use patterns is fundamental for interpreting ecological requirements and for translating telemetry data into conservation-relevant spatial information and associated decision making (Jacobson et al., 2023).

Recent advances in movement ecology have substantially improved home-range estimation by accounting for temporal autocorrelation in telemetry data. Autocorrelated kernel density estimation (aKDE) has become particularly useful as it links home-range estimation to continuous-time movement models and avoids several biases associated with conventional kernel methods when GPS relocations are frequent and non-independent (Fleming et al., 2015; Calabrese et al., 2016; Fleming & Calabrese, 2017). However, even when temporal autocorrelation is addressed properly, most of the home-range estimators still represent animal space use as a bivariate utilization distribution (UD) projected on a two-dimensional planimetric surface (2D; Worton, 1989; Sarkar et al., 2016). This implies that the landscape is treated as flat, whereas, in reality animals move through terrain structured by slopes, escarpments, valleys, plateaus and gorges. Thus, a biologically realistic movement model may still be projected onto a geometrically simplified landscape (Farhadinia et al., 2020).

This aspect is particularly important in rugged terrestrial systems. In heterogeneous terrain, the actual surface available to an animal can be substantially larger than the area represented on a two-dimensional planimetric surface (Farhadinia et al., 2020). Digital elevation models (DEM) allow this discrepancy to be quantified by converting planimetric area into topographic surface area (3D). Earlier methodological work demonstrated that DEM-derived surface area provides a more realistic estimate of landscape area than conventional flat-surface calculations, and that explicitly quantify the magnitude of underestimation increases with terrain steepness and complexity (Jenness, 2004). The ratio between DEM-corrected three-dimensional area and conventional two-dimensional area can therefore be expressed as a Topographic Inflation Factor (TIF), providing a direct measure of how much planimetric home-range estimates underestimate the true terrain surface.

Mammals use the rugged terrain in the context of different habitat quality, visibility, thermoregulatory cost, access to mates, and refuge from predators or competitors (Montgomery et al., 2012; Powell and Mitchell, 2012). Previous studies have shown how planimetric and topographically corrected (three-dimensional) home-range estimates differ explicitly, it has been found that herbivores occupying relatively diffident terrain, where topographic correction inflates home-range size by roughly 3–9% (Campbell et al., 2004). In case of meso-predator the topographic correction increased the home-range size by 22% (Monterroso et al., 2013). This bias becoming ecologically meaningful once average slope exceeds roughly 16° or altitudinal range exceeds ~ 1,800 m. In extreme undulating terrain, the bias can be inflated up to 26–38% (Farhadinia et al., 2020).

Large carnivores are especially relevant to address this problem due to their large spatial extent; therefore, their movements often span multiple geomorphic units (McNab, 1963; Krishnamurthy et al., 2016; Dutta and Krishnamurthy, 2024a). In rugged landscapes, ignoring topographic surface area can lead to underestimation of the space used by individuals and potentially overestimation of population density or habitat availability. Farhadinia et al. (2020) provided a clear large-carnivore example by showing that incorporation of vertical relief increased Persian leopard home-range and core-area estimates. However, despite the new advancement in telemetry studies, little attention has been given to landscapes complexity during performing the home-range analysis. Therefore, not only vertical complexity, as expressed as continuous high mountains, but also require to assess the mosaic topographic features, consisting of plateaus, escarpments, ravines, gorges and riverine valleys. Such landscapes may appear moderately rugged at broad spatial scales, yet still impose strong local variation in movement cost, refuge availability, visibility, thermal exposure and access to water (Roshier et al., 2008; Alston et al., 2020). Open plateaus may facilitate travelling, patrolling and prey search, whereas gorges and ravines may provide shaded refugia, water-associated resting areas, ambush terrain or secure movement corridors (LaRue and Nielsen, 2008; Reside et al., 2019).

Beyond estimating the TIF, an equally important question is whether topography structures the internal organisation of home ranges. Sometimes, low TIF indicates no significant change in home range size, however, a tiger's 95% home range may include a broad mixture of terrain types, while its 50% core area may be concentrated in a smaller subset of landforms that provide refuge, water access, resting sites or movement security (Börger et al., 2008; Powell and Mitchell, 2012). Landform composition can therefore complement 2D-3D area correction by identifying how different terrain types are organised within home ranges and core areas. DEM-derived landform classification based on slope, topographic position, ruggedness, local relief and flow accumulation allows landscapes to be divided into ecologically interpretable terrain categories, such as plateau, slope, escarpment/plateau edge, gorge/ravine, valley bottom and riverine low terrain. Such classifications are widely used to describe landform position and terrain heterogeneity, but their interpretation is scale dependent and should be linked to the ecological context of the study system (Weiss, 2001; De Reu et al., 2013; Jasiewicz and Stepinski, 2013). In plateau-gorge landscapes, this approach is particularly useful because ecological terrain structure may be expressed less through large 3D area inflation and more through the selective placement of core areas within rugged refuge terrain or low-drainage terrain that may influence cover, thermal buffering, movement routes, water access and prey encounter opportunities.

The Panna Tiger Reserve (PTR) landscape provides a strong opportunity to examine this knowledge gap. PTR is situated in the Vindhyan landscape of central India, a complex terrain consisting of plateau-gorge system where open plateau surfaces, escarpments, rocky slopes, deep gorges and riverine valleys occur in close spatial proximity. Such terrain creates a structurally complex environment in which animals may shift between open and rugged landforms across seasons, diel periods or behavioural states (Dutta et al., 2026). Previously, conventional two-dimensional home-range estimation could not determine the exact spatial extent of the tigers, nor to address that whether core-use areas are disproportionately used within the complex terrain system (Sarkar et al., 2016; Dutta and Krishnamurthy, 2025). Despite growing recognition that landscape complexity can bias terrestrial home-range estimation, three-dimensional correction has rarely been applied to large felids outside strongly mountainous systems. Moreover, existing studies have largely emphasized on planimetric underestimation, while giving less attention to whether topographic inflation varies between home-range and core-use areas, among individuals, or across seasonal terrain use (Heit et al., 2021). Therefore, it remains unclear how strongly conventional two-dimensional aKDE home-range and core-area estimates underestimate the actual topographic surface used by tigers in plateau-gorge landscapes. Additionally, quantification of different topographic types falling under species home-range was another aspect, that has been received little attention in previous studies.

Addressing this gap would move the analysis beyond a simple 2D-versus-3D comparison and allow topographic inflation to be interpreted as both a methodological correction and an ecological signal of how deeply animal space use is embedded within rugged terrain. This study asks whether topography influences tiger space use primarily by changing the measured size of home ranges or by structuring the internal placement of core areas within those ranges. Specifically, we ask: (1) do sex- and season-specific AKDE home-range and core-area estimates differ after DEM-based 2D-3D correction; (2) does the magnitude of topographic inflation vary between 95% home ranges and 50% core areas across sex and season; (3) are animal core areas compositionally different from the surrounding (95 – 50% home-range shell) in terms of functional landform types; and (4) do males and females show different seasonal patterns of core-area enrichment in plateau, slope, rugged-refuge and low-drainage terrain? We hypothesise that DEM-corrected 3D area will be only moderately larger than 2D planimetric area in the plateau-gorge landscape of Panna, because vertical relief is locally complex but not continuously mountainous. However, we further hypothesise that topography will be ecologically important at the within-home-range scale, with 50% core areas showing stronger enrichment in rugged-refuge terrain, such as escarpments, plateau edges and gorge/ravine systems, relative to the surrounding home-range shell. We also expect this enrichment to vary by sex and season, with males maintaining larger, more plateau-connected home ranges for territorial movement and patrolling, while females show stronger association of core areas with rugged or low-drainage terrain, especially during warmer seasons when shaded refugia, water-associated areas and secure resting sites may become more important. Thus, the central hypothesis is that topography may not substantially inflate tiger home-range area geometrically, but it structures where tigers concentrate their most intensive space use within the home range.

Materials and Methods

Study Area

PTR is situated in the Vindhyan landscape of central India and extends across the Panna, Chhatarpur and Damoh districts of Madhya Pradesh (Fig. 1). Administratively, PTR consists of a 542 km² core area and a 1,032 km² buffer zone. The contiguous Gangau Wildlife Sanctuary, covering 33.47 km², has also been incorporated into the PTR management. The reserve is characterized by a rugged and heterogeneous terrain, with elevations ranging from 164 to 555 m above mean sea level (Fig. 1). Its landscape includes extensive plateaus, deep gorges, rocky escarpments, cliffs and caves. The lowest elevations occur along the Ken River basin. The Ken River is the only perennial water source in the reserve and flows north-south through PTR for approximately 55 km (Dutta and Krishnamurthy, 2024b). The vegetation of PTR is classified as tropical dry deciduous forest, corresponding to Group 5 of Champion and Seth (1968). The dominant forest types include teak (*Tectona grandis*) forests interspersed with tendu (*Diospyros melanoxylon*) and kardhai (*Anogeissus pendula*) forests, along with mixed forests, small bamboo patches, grasslands and riparian vegetation along the Ken River. The region

experiences a tropical dry climate with three distinct seasons. The summer season, from March to June, is hot and dry, with maximum temperatures reaching up to 45°C and relative humidity generally ranging between 15% and 20%. The monsoon season extends from July to October and brings an average annual rainfall of approximately 1,100 mm. Winter lasts from November to February and is cold and dry, with minimum temperatures occasionally dropping to around 5°C. PTR supports a diverse carnivore assemblage. Tiger (*Panthera tigris*) occupies the apex trophic position, while the leopard (*Panthera pardus*) occurs as a sympatric large carnivore. Other carnivores and omnivores recorded from the reserve include golden jackal (*Canis aureus*), striped hyena (*Hyaena hyaena*), dhole (*Cuon alpinus*), Indian wolf (*Canis lupus*), Indian fox (*Vulpes bengalensis*) and sloth bear (*Melursus ursinus*). The buffer zone is a heterogeneous human-dominated mosaic consisting of scattered forest patches, agricultural fields and settlements. It contains 63 villages, with approximately 30,000 people living within the buffer-zone boundary.

[Figure]

Data Collections

Radio telemetry

Telemetry data used in this study were obtained from the long-term project 'Tiger Reintroduction and Recovery Programme in Panna Tiger Reserve, Madhya Pradesh' that continued from 2009 to 2020. During this tenure, we captured and fitted radio collars to 25 tigers (19 females, six males) following the permits from the Madhya Pradesh Forest Department (Permit No. Exp./2009/1205 dated 31 August 2009), in conformity with the provisions under Section 11(1A) of the Wildlife Protection Act, 1972. Each target individual was located and immobilized by a licensed veterinarian using Hellabrunn mixture (125 mg xylazine and 100 mg ketamine/ml; Hafner et al., 1989) through the Tele-Inject projector (Model 4V.31). Individuals were fitted with GPS and VHF collars manufactured by Telonics® Inc, African Wildlife Tracking® Inc and Vetronic Aerospace®. GPS-collared animals were monitored intensively via satellite, and location fixes were acquired at hourly intervals. VHF-collared animals were tracked by a field crew and the researchers together with vehicle-mounted trackers on a 24-hour basis. For this study, we considered long-term telemetry data of 12 tigers (three males and nine females, including founder individuals; Dutta and Krishnamurthy, 2025; Supplementary Table S1). To account for seasonal variation in movement and habitat use, the dataset was stratified into three biologically relevant seasons, and only periods with a minimum of two consecutive months of telemetry data were retained for analysis.

Analytical methods

Missing locations

Location data were originally recorded at hourly intervals, however, missed fixes are an inherent feature of wildlife telemetry studies and may introduce discontinuities in movement trajectories (Frair et al., 2004). Many contemporary movement analyses require temporally regular time series (Dutta and Krishnamurthy, 2024a). Therefore, missing locations were estimated using continuous-time movement models implemented in the *ctmm* package in R (Fleming and Calabrese, 2023; R Core Team, 2025). This approach enabled the reconstruction of continuous movement paths while accounting for spatial and temporal autocorrelation and the stochastic nature of animal movement.

Home-range and core area calculation (UD) in two dimensional planimetric surface

High-frequency GPS data are temporally autocorrelated, conventional kernel density estimators can underestimate uncertainty and produce biased home-range estimates. Therefore, we used autocorrelated kernel density estimation

(aKDE), which estimates the UD while explicitly accounting for the temporal autocorrelation structure of movement data (Fleming et al., 2015; Fleming and Calabrese, 2017). For each collared tiger, home-range estimation was carried out using the continuous-time movement modelling framework by using the *ctmm* package in R (Fleming and Calabrese, 2023; R Core Team, 2025). For each tiger, candidate continuous-time movement models were fitted and compared using model-selection procedures in *ctmm*. The main range-resident models were the Ornstein-Uhlenbeck (OU) and Ornstein-Uhlenbeck Foraging (OUF) models. The OU model represents restricted space use, where an animal's movement remains centred around a home-range area, but without explicitly modelling short-term directional persistence. In contrast, the OUF model incorporates both restricted space use and velocity autocorrelation, making it more suitable for animals that show continuous, directionally persistent movement at short time scales while remaining constrained within a broader home range. Based on the selected movement model, aKDE was used to estimate individual-level UD, from which 95% isopleths were extracted as home-ranges and 50% isopleths as core-use areas. These aKDE-derived polygons provided the spatial basis for subsequent comparison between conventional two-dimensional planimetric area and DEM-corrected three-dimensional topographic surface area. To assess the seasonal change in home-range size, we performed Kruskal Wallis test (KW) in R (Kruskal and Wallis, 1952).

DEM-based two-dimensional to three-dimensional home-range correction

All spatial analyses were conducted in R (R Core Team, 2025) using the *terra* (Hijmans et al., 2026). DEM (USGS/SRTMGL1_003) data was obtained from SRTM via Google Earth Engine. For each collared tiger, to estimate the corresponding three-dimensional topographic surface area, each aKDE polygon was superimposed on a DEM. Following DEM-based surface-area correction approaches, slope was derived for each DEM cell, and the horizontal cell area was corrected by the local slope angle to approximate the true terrain surface area represented by each cell (Jenness, 2004; Monterroso et al., 2013). The three-dimensional area of each aKDE polygon was then calculated by summing all slope-corrected cell areas falling within the polygon boundary using coverage-weighted extraction. To evaluate the effect of topography on home-range estimation was expressed as a Topographic Inflation Factor, calculated as the ratio of DEM-corrected three-dimensional area to conventional two-dimensional area (3D/2D %), where values greater than zero indicate the extent to which conventional planimetric home-range estimates underestimate the actual topographic surface available.

In addition to 2D-3D area correction, a DEM-derived topographic metric matrix was prepared for each 50% and 95% aKDE polygon. Using *terra*, we derived mean slope, Terrain Ruggedness Index (TRI), Topographic Position Index (TPI), absolute TPI, terrain roughness and local relief. Mean slope described average terrain steepness within each isopleth. TRI and roughness quantified local terrain irregularity, while TPI indicated whether areas were positioned on relatively elevated, flat terrain or valley. Absolute TPI was used to measure the strength of topographic contrast irrespective of whether a location occurred on a ridge, plateau edge, valley or gorge. Local relief was calculated as the elevation difference between the maximum and minimum DEM values within a moving neighbourhood, thereby representing short-distance vertical complexity such as ravines, escarpments, gorge walls and plateau edges. Together, these variables allowed us to evaluate whether tiger core-use areas and broader home ranges differed not only in DEM-corrected surface area, but also in their underlying topographic structure.

Landform classification

DEM-based landform classification was performed using *terra* and *whitebox* package in R (Lindsay, 2016; R Core Team, 2025; Wu and Brown, 2025; Hijmans et al., 2026). Following the principle of TPI-based landform classification, where each cell is interpreted according to its elevation relative to the surrounding terrain (Weiss, 2001; De Reu et al., 2013), DEM cells were classified using a rule-based combination of relative topographic position, slope and local vertical complexity. Flow accumulation was derived from a depression-filled DEM using *WhiteboxTools* to distinguish drainage-associated low terrain. Based on these terrain attributes, the landscape was classified into six ecologically meaningful landform classes: plateau, slope, escarpment/plateau edge, gorge/ravine, valley bottom and riverine low terrain (Supplementary Table S2; Figure S1).

Here, we used a hierarchical rule-based classification, Drainage-linked cells were first separated as riverine low terrain using high flow accumulation, negative TPI and low to moderate slope. Remaining low-position cells with low slope were classified as valley bottom, whereas low-position cells with high ruggedness or local relief were classified as gorge/ravine. Steep cells with high local relief and clear topographic break characteristics were classified as escarpment/plateau edge. Low-slope cells with neutral to positive TPI were classified as plateau, and all remaining inclined terrain was assigned to slope. However, this classification was not interpreted as absolute geomorphological units, rather as DEM-derived, exclusive terrain categories to represent ecologically relevant topographic features (Jasiewicz and Stepinski, 2013; De Reu et al., 2013).

Bayesian core-shell topographic model (Dirichlet model)

To investigate whether tiger core areas were topographically structured relative to the terrain available within their own home ranges, we used a core-shell analytical framework. The 50% aKDE isopleth was treated as the core-use area, while the non-overlapping area between the 95% and 50% aKDE isopleths was treated as the available home-range shell. This avoided treating the 95% aKDE as an independent availability unit because the 50% core is nested within it. For each tiger, sex and season, landform composition was calculated separately for the core and shell. The original six DEM-derived landform classes were further grouped into four functional terrain categories: open plateau, general slope, rugged refuge comprising escarpment/plateau edge and gorge/ravine, and low drainage terrain comprising valley bottom and riverine low terrain (Supplementary Figure S2). As these landform proportions are compositional and sum to one, we modelled them using a Bayesian Dirichlet regression, which is appropriate for multivariate proportional data constrained to a simplex (Aitchison, 1986; Douma and Weedon, 2019). The model included zone (core versus shell), sex, season, and the interactions zone*sex and zone*season as fixed effects, with Tiger ID included as a random intercept to account for repeated observations of the same individual across seasons. Bayesian Dirichlet models were fitted in the *brms* package using Hamiltonian Monte Carlo implemented in Stan (Bürkner, 2017; Carpenter et al., 2017). Four Markov chains were run with 10,000 iterations each, including 1,000 warm-up iterations, and convergence was assessed using the potential scale reduction factor ($\hat{R} < 1.01$), effective sample size (ESS). Candidate models were compared using leave-one-out cross-validation (LOO), and the model with the highest expected log predictive density (ELPD) was retained for inference (Vehtari et al., 2017). Posterior predictions were used to estimate the difference in landform composition between core and shell areas for each sex*season combination. For each landform group, we calculated the posterior mean difference, 95% credible interval and the posterior probability that the landform was more represented in the core than in the surrounding shell. Positive core-shell differences were interpreted as core-area enrichment, whereas negative differences indicated under-representation relative to the available home-range shell.

Results

Home-range estimation and DEM corrected topographic inflation

The long-term telemetry dataset of tigers in PTR revealed that males had larger home-range size compared to females. DEM-corrected topographic area differed negligibly from conventional planimetric aKDE estimates. Across seasons, male 95% aKDE home ranges increased from 229.91-243.75 km² in 2D to 231.15-245.08 km² after DEM correction, corresponding to an average topographic inflation of only ~ 0.4% (Table 1; Suppeltmentary Table S3-5). Male 50% core areas similarly increased by ~ 0.5%. Female 95% aKDE home ranges showed almost similar topographic inflation, increasing by ~ 0.6–0.7% across seasons, while 50% core areas increased by ~ 0.6–0.7% (Supplementary Table S6-8). As there were no major changes in topographic inflation, therefore, we performed the KW test for 2D based home range. The KW test indicated that there was a non-significant difference seasonally for both 95% ($\chi^2 = 1.6$, p 0.44) and 50% ($\chi^2 = 2.79$, p 0.24) home-range isopleths.

Table 1

Sex- and season-specific comparison of planimetric (2D) and DEM-corrected topographic (3D) aKDE home-range estimates of tigers in Panna Tiger Reserve.

Sex	Season	Planimetric (2D) aKDE (95%) (mean km ² ± SE)	Planimetric (2D) aKDE (50%: core area) (mean km ² ± SE)	Topographic (3D) aKDE (95%) (mean km ² ± SE)	Topographic (3D) aKDE (50%: core area) (mean km ² ± SE)	Avg. aKDE 95% 3D/2D (%)	Avg. aKDE 50% 3D/2D (%)	Mean local relief 95% (m)	Mean local relief 50% (m)
Male	Summer [Table S3]	229.91 ± 46.64	60.86 ± 12.51	231.15 ± 46.91	61.23 ± 12.57	0.4	0.5	9.87	11.02
	Monsoon [Table S4]	243.75 ± 40.52	64.69 ± 9.69	245.08 ± 40.84	65.08 ± 9.77	0.4	0.5	9.66	10.55
	Winter [Table S5]	236.17 ± 30.19	63.61 ± 8.27	237.41 ± 30.4	64 ± 8.33	0.4	0.5	9.40	10.34
Female	Summer [Table S6]	48.33 ± 4.10	10.94 ± 1.16	48.68 ± 4.14	11.02 ± 1.17	0.6	0.7	12.17	12.99
	Monsoon [Table S7]	55.52 ± 4.92	14.02 ± 1.43	55.91 ± 4.95	14.11 ± 1.44	0.7	0.7	12.43	13.07
	Winter [Table S8]	54.89 ± 4.96	13.32 ± 1.42	55.27 ± 4.99	13.4 ± 1.43	0.7	0.6	12.33	11.54

[Table 1]

Landform based space use

In contrast, landform composition revealed stronger ecological differentiation between 95% home ranges and 50% core-use areas. Male tiger home ranges were consistently plateau-dominated, with plateau comprising 57.83–59.25% of 95% aKDE areas across seasons. However, plateau representation declined within male 50% core areas to 54.19–55.94%, while escarpment/plateau-edge and gorge/ravine classes increased (Supplementary Table S9-11). For example, in summer, escarpment/plateau-edge increased from 6.61% in 95% home ranges to 8.27% in 50% cores, and gorge/ravine increased from 7.54% to 9.68% (Table 2). A similar pattern occurred in monsoon and winter, suggesting that male core areas were slightly but consistently shifted away from broad plateau surfaces and toward more dissected terrain. Female home ranges contained less plateau and more complex terrain than male home ranges. Plateau accounted for only 47.69–48.11% of female 95% aKDE areas, compared with ~ 58–59% in males. Female 50% core areas showed a further reduction in plateau during summer and monsoon, declining to 41.73% and 44.54%, respectively (Table 2; Supplementary Table S12-14). The clear patterns occurred in summer, when female core areas showed higher representation of gorge/ravine terrain, valley bottoms and riverine low terrain compared with their 95% home ranges. This suggests that although DEM-based area correction was weak, tiger core areas were structured by landform type, particularly in females and during the summer season.

Table 2

DEM-derived landform composition of tiger 95% home ranges and 50% core-use areas across sex and season.

Sex	Season	aKDE isopleths	Different landforms (Mean %)					
			Plateau	Slope	Escarpment/ plateau edge	Gorge/ ravine	Valley bottom	Riverine low terrain
Male	Summer	95	57.83	16.13	6.61	7.54	9.60	2.26
	[Table S9]	50	54.19	15.7	8.27	9.68	9.71	2.42
	Monsoon	95	59.25	16.12	5.77	6.84	9.72	2.28
	[Table S10]	50	55.94	16.12	7.22	8.32	9.97	2.39
	Winter	95	58.5	16.16	6.25	7.29	9.52	2.25
	[Table S11]	50	55.93	15.78	7.27	8.76	9.86	2.37
Female	Summer	95	47.69	17.36	9.08	11.41	11.67	2.75
	[Table S12]	50	41.73	16.64	9.8	13.9	14.4	3.46
	Monsoon	95	48.11	16.96	9.66	11.59	11	2.65
	[Table S13]	50	44.54	16.38	10.23	14.18	11.71	2.92
	Winter	95	47.78	17.59	9.13	11.52	11.2	2.75
	[Table S14]	50	46.36	18.26	8.10	10.6	13.56	3.09

[Table 2]

Bayesian Dirichlet model

The LOO cross-validation indicated that the parsimonious Bayesian Dirichlet model provided the best predictive performance ($\Delta\text{ELPD} = 0$), whereas the more complex model did not improve predictive accuracy ($\Delta\text{ELPD} = -5.3 \pm 6.4 \text{ SE}$); therefore, the simpler model (zone* sex + zone*season) was retained for subsequent inference (Supplementary Table S15). The selected model exhibited excellent convergence, with all parameters such as $\hat{R} = 1.00$ and high effective sample sizes (Bulk ESS = 15,598 to 56,622; Tail ESS = 21,640 to 31,262), indicating stable posterior estimation. Random intercepts revealed moderate among-individual variation in landform composition, particularly for rugged refuge ($\text{SD} = 1.13$, 95% CI = 0.71 to 1.84), while the estimated Dirichlet precision parameter was relatively high ($\phi = 34.97$, 95% CI = 31.88 to 38.20), suggesting well-defined compositional responses across individuals.

The Bayesian Dirichlet model revealed clear differences in landform composition between tiger core-use areas and the surrounding home-range shell, although the magnitude and consistency of enrichment varied between sexes and seasons (Table 3). Across different landforms, rugged refuge emerged as the landform most consistently enriched within core areas, whereas general slopes generally exhibited weak or no evidence of preferential representation relative to the surrounding home-range shell. Among males, core areas were strongly enriched in rugged refuge during summer (posterior mean log-ratio = 0.388, 95% CI = 0.153 to 0.623), corresponding to an approximate 47.4% greater representation than in the surrounding shell (Table 3). This enrichment became even stronger during the monsoon (63.1% increase; posterior mean = 0.489, 95% CI = 0.247 to 0.736), whereas no clear evidence of enrichment was detected during winter. Low-drainage terrain showed only moderate enrichment during summer and monsoon, while general slopes remained largely indistinguishable from the surrounding home-range shell across all seasons (Table 3). Females exhibited stronger and more seasonally

consistent landform enrichment than males, with positive core-shell differences persisting across multiple landform categories. During summer, core areas were enriched in both rugged refuge (44.2%) and low-drainage terrain (54.6%), whereas general slopes showed only moderate support for enrichment. During the monsoon, all three non-reference landforms displayed positive enrichment within female core areas, with the strongest effects observed for rugged refuge (59.5%) and low-drainage terrain (52.0%). In winter, enrichment remained evident only for low-drainage terrain (35.5%), while neither rugged refuge nor general slopes differed substantially from the surrounding shell (Table 3).

Table 3

Posterior estimates of core-shell differences in landform composition derived from the Bayesian Dirichlet model for male and female tigers across seasons.

Sex	Season	Landform	Posterior mean (log-ratio)*	SE	95% CI	Relative change in core (%)	Evidence for core enrichment
Male	Summer	General slope	0.038	0.115	-0.186 to 0.266	+ 3.9	No evidence
		Rugged refuge	0.388	0.120	0.153 to 0.623	+ 47.4	Strong evidence
		Low drainage	0.161	0.124	-0.082 to 0.405	+ 17.5	Moderate evidence
	Monsoon	General slope	0.147	0.119	-0.086 to 0.382	+ 15.8	Moderate evidence
		Rugged refuge	0.489	0.125	0.247 to 0.736	+ 63.1	Strong evidence
		Low drainage	0.145	0.130	-0.110 to 0.399	+ 15.6	Moderate evidence
	Winter	General slope	-0.001	0.117	-0.231 to 0.229	-0.1	No evidence
		Rugged refuge	0.025	0.125	-0.220 to 0.268	+ 2.5	No evidence
		Low drainage	0.029	0.127	-0.221 to 0.279	+ 2.9	No evidence
Female	Summer	General slope	0.168	0.092	-0.012 to 0.349	+ 18.3	Moderate evidence
		Rugged refuge	0.366	0.090	0.190 to 0.541	+ 44.2	Strong evidence
		Low drainage	0.436	0.097	0.247 to 0.627	+ 54.6	Strong evidence
	Monsoon	General slope	0.278	0.096	0.091 to 0.467	+ 32.0	Strong evidence
		Rugged refuge	0.467	0.095	0.281 to 0.653	+ 59.5	Strong evidence
		Low drainage	0.419	0.103	0.216 to 0.622	+ 52.0	Strong evidence
	Winter	General slope	0.129	0.099	-0.063 to 0.325	+ 13.8	Moderate evidence
		Rugged refuge	0.003	0.101	-0.194 to 0.202	+ 0.3	No evidence
		Low drainage	0.304	0.106	0.098 to 0.514	+ 35.5	Strong evidence

* Open plateau was specified as the reference landform in the Bayesian Dirichlet model. Posterior coefficients therefore represent log-ratio differences between each landform and the reference category.

[Table 3]

Bayesian model diagnostics indicated excellent model performance (Fig. 2). Posterior distributions were unimodal and well defined, and MCMC trace plots showed complete mixing and substantial overlap among the four independent chains, indicating stable posterior sampling with no evidence of convergence failure. These diagnostics were consistent with the numerical convergence statistics ($R = 1.00$ and high effective sample sizes), indicating that the posterior estimates used to evaluate sex- and season-specific differences in landform composition were robust. Equivalent convergence diagnostics for the complementary Bayesian log-enrichment model are presented in Supplementary Figure S3.

Posterior summaries further supported these findings (Supplementary Table S16). Rugged refuge consistently exhibited posterior enrichment probabilities specifically during summer and monsoon, whereas low-drainage terrain also showed high posterior support, particularly in females. In contrast, open plateau consistently produced negative posterior log-enrichment values and enrichment ratios below one, indicating systematic under-representation within tiger core areas relative to the surrounding home-range shell. General slopes mostly showed enrichment ratios close to one with comparatively low posterior support, suggesting little evidence of preferential concentration. Together, these results demonstrate that although topographic inflation of aKDE home-range area was minimal, tiger core-use areas were organised non-randomly within the landscape, being disproportionately concentrated in rugged refuge and low-drainage landforms, with stronger and more seasonally consistent patterns in females than in males.

[Figure 2]

Discussion

Topographic correction

This study is the first ever attempt to understand the impact of topography on large carnivore within a plateau-gorge landscape complex. The small difference between planimetric and DEM-corrected aKDE estimates indicates that vertical relief had limited influence on the geometric size of tiger home ranges in PTR. This contrasts with studies from steeper or more mountainous landscapes, where incorporating terrain surface area can substantially increase home-range estimates (Farhadinia et al., 2020). Previous studies have shown that average slope was being a key driver of the geometric correction, average-slope threshold beyond 16° , where planimetric underestimation becomes substantial (Monterroso et al 2013). Therefore, PTR's plateau-gorge terrain is ecologically heterogeneous, but not sufficiently steep across entire aKDE polygons to produce large 3D area inflation. Similarly, residential tigers did not exhibit any significant change in home-range size across the season, reflecting their area dominance and territoriality throughout the study period, similar patterns have also been observed in different large carnivores (Mancinelli et al., 2018; Thompson et al., 2021).

Although weaker 2D-3D correction should not be interpreted as evidence that topography has no significant role in habitat selection. Rather, the landform composition analysis indicates that topography may influence tiger home-ranges. Male and female tigers both used broad plateau-dominated landscapes at the 95% aKDE scale, but their 50% core areas showed greater representation of escarpment, gorge/ravine and drainage-associated terrain, indicating that topography may not expand home-range area geometrically, but it may still determine where animals concentrate intensive use within the home range (Dickson et al., 2013; Blake and Gese, 2016). Male tigers occupied much larger and more plateau-dominated home-ranges, which is consistent with the socio-spatial organisation of solitary felids, where male ranges are typically shaped by territorial patrolling and overlap with multiple female ranges (Sandell, 1989; Sunquist, 1981; Goodrich et al., 2010). However, male 50% core areas still showed a consistent increase in escarpment and gorge/ravine terrain, indicating that intensive use was concentrated in more structurally complex zones. Female home ranges were smaller but contained proportionally more rugged and low-lying terrain, particularly in summer, when 50% cores showed reduced plateau representation and higher contribution of gorge/ravine, valley-bottom and riverine low-terrain classes. In the dry deciduous landscape of PTR, such terrain may provide shaded resting sites, drainage-linked movement routes, water-associated resources, cover and potential prey-interception areas (Gupta and Krishnamurthy, 2023).

Bayesian core-shell

The Bayesian core-shell analysis extends the interpretation beyond descriptive differences in landform composition by demonstrating that tiger core areas are not simply smaller subsets of the broader home range, but are disproportionately concentrated within particular geomorphic settings. Although the overall three-dimensional correction to home-range area was minimal, the Bayesian model consistently identified rugged refuge and low-drainage terrain as the landforms most strongly enriched within core-use areas relative to the immediately available home-range shell. This distinction is ecologically important because it separates the effect of landscape geometry from the internal spatial organisation of home ranges. In other words, while topography contributed little to geometric inflation of home-range area, it strongly influenced where tigers concentrated their most intensive use. Such scale-dependent responses are consistent with hierarchical habitat selection theory (Johnson, 1980; Mayor et al., 2009).

The consistent enrichment of rugged refuge within tiger core areas suggests that structurally complex terrain provides ecological conditions that are disproportionately important for intensive space use. Escarpments, rocky ravines and dissected terrain may offer greater visual concealment, secure resting locations, thermally buffered microhabitats and natural travel corridors than the surrounding plateau surface (Dickson et al., 2013; Blake and Gese, 2016). Similar associations between rugged terrain and space use have been reported for several large carnivores, including leopards, cougars and wolves, where complex topography enhances refuge availability, reduces disturbance and influences movement efficiency (Farhadinia et al., 2020). Male cores retained a stronger residual attachment to open plateau, better suited to the long-distance travel and territorial patrol that structure a wide-ranging (LaRue and Nielsen, 2008; Montgomery et al., 2012), and showed refuge enrichment concentrated mainly in the summer, when rugged terrain's value for concealment and ambush hunting would matter most (Dickson et al., 2013; Blake and Gese, 2016). Female cores, by contrast, showed a broader and more seasonally persistent shift toward refuge and drainage-associated terrain, consistent with the resource and security demands typical of female felid space use: predictable access to water and prey, thermally buffered rest sites, and reduced exposure during a period when reproductive investment and cub-rearing constrain movement (Sunkist, 1981; Sandell, 1989; Goodrich et al., 2010). Central Indian dry deciduous forest offers an obvious mechanism for this asymmetry: valley bottoms, drainage lines and riverine depressions retain moisture and denser vegetation for longer than the surrounding plateau (Roshier et al., 2008; Alston et al., 2020), likely concentrating both prey activity and sheltered movement routes in exactly the terrain classes enriched within female cores (Gupta and Krishnamurthy, 2023). Although the present analyses do not directly evaluate behavioural mechanisms, it indicates that geomorphological heterogeneity contributes more strongly to the spatial organisation of female core areas than to male territorial space use. The consistent under-representation of open plateau within tiger core areas reinforces the view that extensive plateau surfaces primarily function as movement or territorial space rather than locations of prolonged activity.

The closest comparison available comes from Farhadinia et al. (2020), who also reported sex-specific consequences of vertical relief in Persian leopards, but through a different mechanism: relief there helped separate the ranges of neighbouring individuals in space, reducing overlap across a landscape steep enough to support that kind of geometric segregation. PTR's tigers appear to reach a broadly similar functional outcome, sex-differentiated space use, without any comparable geometric separation, because the terrain is not steep enough to pull whole ranges apart. Instead, the differentiation is achieved by reorganising activity within an already-shared range rather than by separating the ranges themselves. At the scale of an entire home range, slope determines how much extra surface area topography adds. At the scale of a core area nested within an already-fixed range, whether an individual specifically seeks out sloped ground depends on what that ground offers functionally, and in PTR that functional pull was detectable only when conditions plausibly made it worth something, heavy monsoon rain and saturated low ground favouring firmer, better-drained footing near refuge and drainage features.

Limited literature is available to address DEM-based 3D correction paired with a Bayesian compositional model of internal terrain use. Earlier studies were concentrated on whether and by how much topography inflates home-range area without

asking whether the same terrain restructures activity inside the range. Studies addressing the compositional question, in the tradition established by Aebischer et al. (1993), generally start from a two-dimensional home range and rarely carry a 3D-corrected baseline, or a fully propagated measure of uncertainty, into the comparison. The present analysis sits between these two traditions rather than directly within either.

Together, these findings demonstrate that evaluating only the magnitude of topographic correction can underestimate the ecological role of terrain. Although three-dimensional correction altered tiger home-range area only marginally, the Bayesian core-shell analysis revealed a clear internal reorganisation of space use, indicating that landscape structure influences where intensive use occurs rather than simply how much area is occupied (Burt, 1943; Powell & Mitchell, 2012). This distinction aligns with the growing recognition that home ranges contain hierarchical patterns of use, where core areas represent locations of disproportionate behavioural importance rather than random subsets of the broader UD (Fleming et al., 2015).

Caveats and Limitations

The Bayesian core-shell framework identified consistent differences in landform composition between tiger core areas and the surrounding home-range shell, the analysis was based exclusively on terrain characteristics derived from a DEM. Therefore, the observed enrichment patterns should be interpreted as spatial associations rather than direct evidence of habitat selection or behavioural preference. Other ecological factors, including prey distribution, vegetation structure, water availability, human disturbance and interspecific interactions, were not explicitly incorporated and may also contribute to the observed patterns. Furthermore, the study represents a single plateau-gorge landscape within the Vindhyan Range, and caution is therefore required when extrapolating these findings to tiger populations occupying contrasting ecological settings. Future studies integrating high-resolution environmental covariates with movement-based habitat selection models would help identify the ecological mechanisms underlying terrain-associated space use.

Conservation Implications

The findings show that even in cases where topographic correction does not have much impact on the estimation of the home-range size, the landscape structure still plays a significant role in terms of the arrangement of space by the tigers within their territory. The core use areas were significantly associated with rugged refuge and low-drainage terrain characteristics, indicating the greater contribution of these geomorphological characteristics in performing certain ecological roles. These include safe movement, resting possibilities, and availability of perennial drainage systems. Therefore, conservation plans need to go beyond the estimation of the home-range size to incorporate the fine-scale geomorphological variation for identification of habitat refugia, habitat restoration, and landscape connectivity (Zeller et al., 2012; Tucker et al., 2018). In case of plateau-gorge landscapes, such as those of the Vindhyan Range, conservation prioritization should incorporate escarpments, ravines, and drainage corridors, not the habitat types alone, may improve habitat quality within the tiger territories even in landscapes that have limited presence of these structures.

Conclusion

More broadly, the Bayesian compositional framework demonstrates the value of examining where animals concentrate their activity rather than only how much area they occupy. Conventional comparisons of two- and three-dimensional home-range estimates quantify geometric bias arising from terrain, but provide little insight into how landscape structure influences the allocation of space within individual territories. By explicitly comparing the 50% core with the surrounding 95 – 50% home-range shell, the present analysis controlled for individual differences in home-range location and availability, allowing inference to focus on the internal distribution of landforms within each territory. This core-shell framework therefore complements traditional home-range analyses by linking topographic heterogeneity with fine-scale spatial organisation, offering a practical approach for identifying terrain features that disproportionately contribute to intensive use by wide-ranging carnivores.

Declarations

All animal was captured and collared under permit by the Madhya Pradesh Forest Department (Permit No. Exp./2009/1205, dated August 31, 2009), under Section 11(1A) of the Indian Wildlife (Protection) Act, 1972.

Open Research Statement: Due to security considerations associated with collared tigers, we refrain from publicly disclosing any location-specific information, including GPS tracking data, home range estimates, and revisitation sites.

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Author Contributions

SD: Conceptualization (lead), Methodology (lead), Data collection and processing (lead), Analysis (lead), Visualization (lead), Writing - original draft preparation (lead), Writing - review and editing (equal).

RK: Conceptualization (supporting), Project administration (lead), Supervision (lead), Funding procurement (lead), Writing - review and editing (equal).

Conflict of Interest

The authors have no conflict of interest.

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Figures

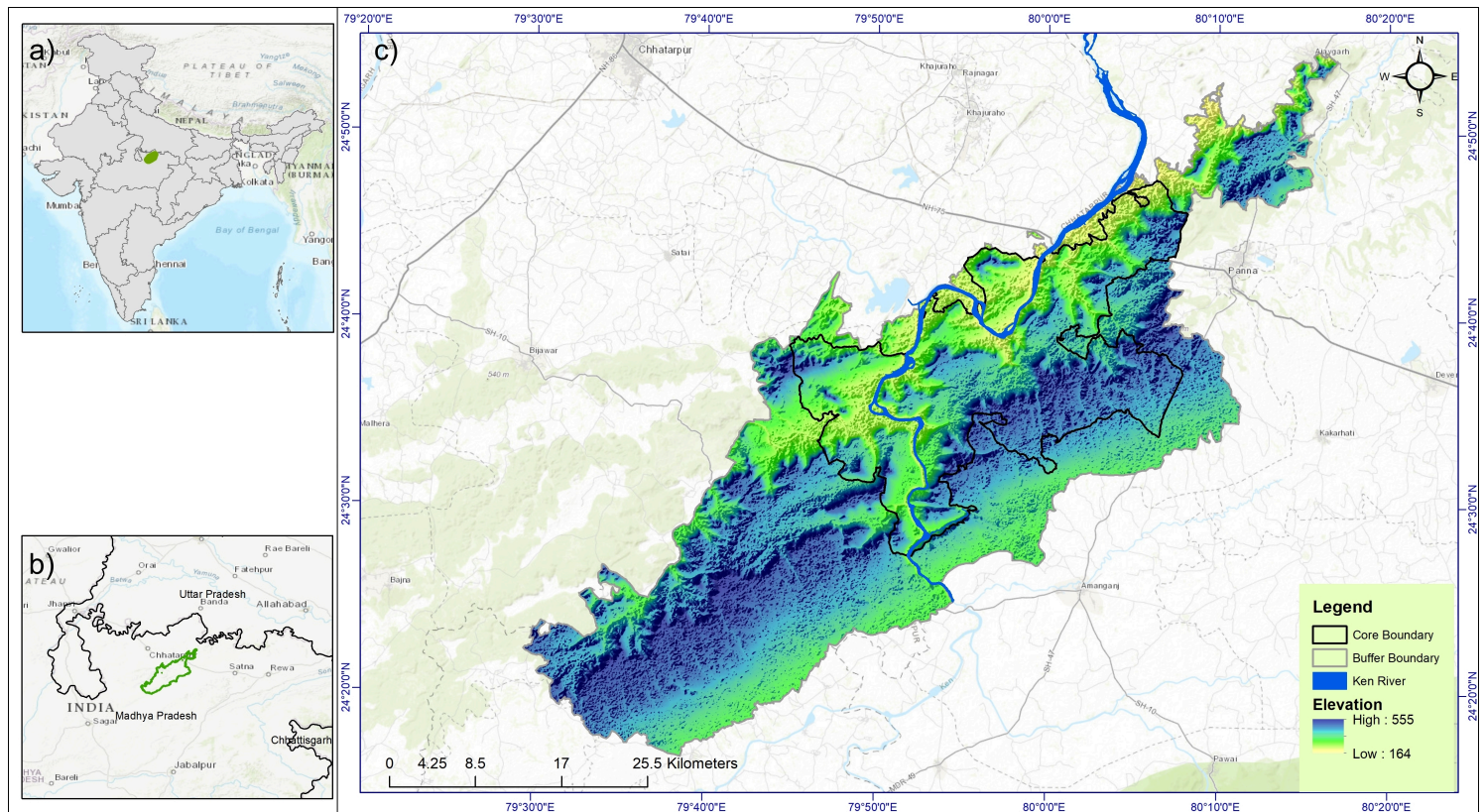


Figure 1

Map showing the position of the study area. Map (a) India, (b) the states of Madhya Pradesh, Uttar Pradesh and Rajasthan and (c) Panna Tiger Reserve.

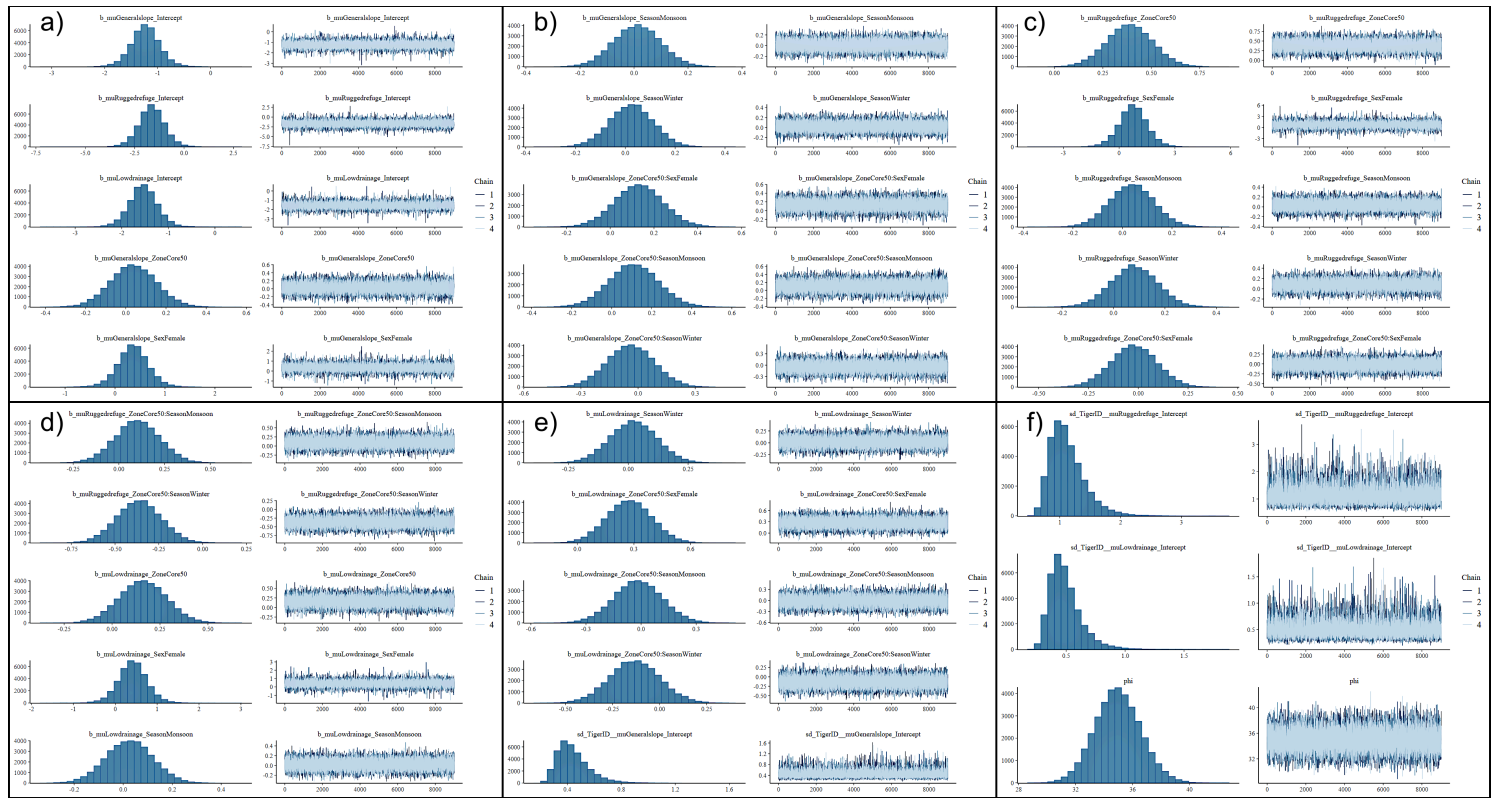


Figure 2

Posterior distributions and MCMC convergence diagnostics of the Bayesian Dirichlet model describing tiger core-shell differences in landform composition across sex and season. Panels illustrate the principal model components: **(a)** intercept and baseline effects for the reference landform, **(b)** fixed effects of season and core-shell interactions for general slope, **(c)** fixed effects associated with rugged refuge, **(d)** interaction effects involving rugged refuge and low-drainage landforms, **(e)** remaining interaction terms together with individual (Tiger ID) random-effect variance, and **(f)** random-effect variance components and the Dirichlet precision parameter (ϕ). The unimodal posterior distributions, good overlap among the four MCMC chains, and absence of systematic trends indicate satisfactory model convergence and stable posterior estimation.

Supplementary Files

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