Separating Fundamental from Realized Habitat: A Dual-Model Framework for Quantifying Anthropogenic Constraints on Species Distributions in Human-Dominated Landscapes

Short running title: Fundamental and realized habitat

Abstract

Aim Species distribution models (SDMs) used in conservation often estimate environmental suitability without distinguishing it from the human constraints that limit realized occupancy. We developed a paired-model framework to separate these two dimensions for Asian elephants and to test whether human–elephant conflict (HEC) is associated with marginal habitat or with high-quality shared landscapes.

Location South-central Bhutan, including Royal Manas National Park, Phibsoo Wildlife Sanctuary, Biological Corridor 03, and adjacent agricultural landscapes.

Methods We compiled 1,049 elephant occurrence records and 65 verified HEC locations, harmonized environmental and anthropogenic predictors to 841.916-m resolution, and fitted two MaxEnt models. The Ideal Model used environmental predictors only as a proxy for fundamental suitability, whereas the Full Model added roads, settlements, land use, private lands, and HEC interaction hotspots to approximate realized habitat. Pixel-wise differences between models were used to map anthropogenic constraints. HEC locations were then analysed descriptively in relation to predicted suitability.

Results The Full Model outperformed the Ideal Model (AUC = 0.896 ± 0.014 vs. 0.848 ± 0.017) and reduced suitable habitat (> 0.50) from 555.01 to 498.30 km^2. Anthropogenic pressure lowered highly suitable habitat by approximately 57 km^2 and degraded approximately 410 km^2 overall, especially in lowland forest–agriculture mosaics. HEC locations occurred in high-suitability areas (mean suitability = 0.733) rather than in marginal habitat.

Main conclusions Environment-only SDMs can overestimate accessible habitat in human-dominated landscapes. Paired comparison of fundamental and realized habitat surfaces provides a practical way to identify restorable but constrained habitat, shared landscapes requiring conflict mitigation, and lower-priority areas. For Asian elephant conservation in Bhutan, and potentially for other wide-ranging megafauna, separating environmental potential from anthropogenic feasibility improves the basis for land-use planning and conservation investment.

Keywords: anthropogenic constraint surface, Asian elephant, conservation biogeography, human–elephant conflict, land-use planning, realized niche, species distribution modelling

1 Introduction

As human land use expands into the remaining habitat of wide-ranging species, conservation planning depends increasingly on species distribution models (SDMs) to identify where wildlife persists, where connectivity remains functional, and where intervention is most urgent. Yet many SDMs used in applied conservation estimate only the fundamental environmental niche: the climatic, topographic, and vegetative conditions under which a species could persist in principle (Elith and Leathwick, 2009; Guisan et al., 2017). In human-dominated landscapes, realized occupancy is filtered by roads, settlements, agriculture, persecution, and behavioural avoidance of disturbance. When environment-only SDMs are interpreted as if they represent accessible habitat, they can overestimate habitat availability and mislead downstream decisions about protection, restoration, corridor design, and conflict mitigation.

The management consequences of this conflation are practical rather than merely conceptual. Areas predicted as suitable may be functionally unavailable because infrastructure or settlement patterns exclude wildlife. Conflict may be treated as evidence of displacement into marginal habitat when it instead reflects overlap between productive habitat and human land use. Corridor plans based only on environmental suitability may therefore fail to capture the barriers that determine whether movement is actually possible. Although many recent SDM studies improve prediction by adding anthropogenic variables (Palei et al., 2024; Thant et al., 2023), fewer studies make the gap between environmental potential and human-constrained reality explicit through a paired modelling design that compares the two surfaces directly.

South-central Bhutan provides an informative test case for such a framework. The landscape includes Royal Manas National Park (RMNP), Phibsoo Wildlife Sanctuary (PWS), Biological Corridor 03 (BC-03), and adjacent agricultural frontiers, covering 2,607 km^2 and approximately 40% of Bhutan's elephant range (Penjor et al., 2024; Tshering et al., 2024). It combines protected forest, corridor habitat, rapid land-use change, and recurring human–elephant conflict (HEC), thereby reflecting a planning context common across elephant-range landscapes. We developed two MaxEnt models: an Ideal Model using environmental predictors only, and a Full Model integrating environmental and anthropogenic predictors. Our objectives were to: (1) quantify the divergence between fundamental environmental suitability and realized habitat availability; (2) identify the predictors most strongly associated with elephant occurrence under each scenario; (3) map anthropogenic constraint surfaces relevant to restoration and mitigation; and (4) examine whether documented HEC incidents are associated with marginal habitat or with high-quality shared landscapes.

2 Methods

2.1 Study area

The study was conducted in south-central Bhutan across a 2,607.07 km^2 landscape spanning Sarpang Dzongkhag, Royal Manas National Park (RMNP), Phibsoo Wildlife Sanctuary (PWS), and Biological Corridor 03 (BC-03) (Fig. 1). This region forms part of a broader transboundary conservation landscape linking Bhutanese protected areas with Manas Tiger Reserve in Assam, India (Penjor et al., 2024). The protected-area and corridor configuration sustains landscape-scale permeability for wide-ranging megafauna, with elephants serving as an umbrella species for corridor functionality.

RMNP (1,057 km^2) borders Assam and is contiguous with Manas Tiger Reserve, whereas PWS (268.93 km^2) lies southwest of Sarpang and connects to RMNP through BC-03. The southern belt holds roughly 40% of Bhutan's elephant range, with about 38% falling inside protected areas (Penjor et al., 2024). The region spans humid subtropical lowlands to higher-elevation temperate conditions and includes major river systems, alluvial plains, subtropical broadleaf forest, chirpine zones, and dense riverine vegetation.

2.2 Species occurrence data

Species presence records (n = 1,049) of Asian elephants (*Elephas maximus*) were compiled from multiple sources, including national surveys, local monitoring programmes, and the Global Biodiversity Information Facility. These records were derived from an initial pool of 82,695 occurrences and subjected to spatial filtering and quality control. Core sources included the National Elephant Survey 2020 and National Tiger Survey 2022, which used direct sightings, dung counts, and camera trapping within RMNP, PWS, and Sarpang Forest Division. Supplementary data were obtained from a 2024 field-based habitat study associated with the ACCES project. Additional GBIF records from South Asia were cleaned in R through grid-scale spatial thinning, duplicate removal, and exclusion of geospatial outliers outside terrestrial habitat boundaries (Hijmans et al., 2017).

Only high-precision records (coordinate uncertainty < 1 km) with valid date and location metadata were retained. All occurrence points were projected to Bhutan's national coordinate reference system (EPSG:5266) and standardized to 841.916-m resolution. For spatial conflict analysis, 65 verified human–elephant conflict (HEC) locations were extracted from approximately 2,000 reported incidents recorded in the Forest Information Reporting & Monitoring System between 2018 and 2024. Verification retained only records with sufficient locality and date metadata for confident georeferencing to the analysis grid; duplicate, ambiguous, and spatially imprecise reports were excluded. These geo-referenced conflict locations were subsequently used to represent conflict hotspots and, in the Full Model, zones of concentrated human–elephant interaction rather than as an independent validation dataset.

2.3 Environmental and anthropogenic variables

Bioclimatic predictors were sourced from WorldClim version 2.1 at 30 arc-second resolution, representing baseline temperature and precipitation conditions for 1970–2000 (Fick and Hijmans, 2017). Terrain variables including elevation, slope, and aspect were derived from the WorldClim elevation layer using the `terra::terrain` function in R. Vegetation dynamics were represented using Enhanced Vegetation Index (EVI) and Normalized Difference Vegetation Index (NDVI) from MODIS MOD13Q1, accessed via Google Earth Engine and summarized as multi-year growing-season means.

Anthropogenic variables included road networks, private lands, and building footprints obtained from official cadastral and infrastructure datasets. Protected-area boundaries, water sources, and third-order stream networks were included to represent ecological boundaries and hydrological influences. HEC incident points from the Forest Information Reporting

& Monitoring System provided spatial indicators of human–elephant interaction zones. All raster layers were harmonized to EPSG:5266 at 841.916-m resolution using bilinear interpolation for continuous variables and nearest-neighbour resampling for categorical layers, with full spatial congruence checked through `compareGeom()` validation.

Human–elephant conflict (HEC) incident locations ($n = 65$) were incorporated as spatial predictors to represent zones of concentrated human–elephant interaction. These locations are not interpreted as independent causal drivers of habitat suitability, but as emergent socio-ecological features reflecting areas where high-quality elephant habitat spatially overlaps with human land use. As such, HEC points capture fine-scale interaction intensity that may not be fully represented by conventional anthropogenic variables such as roads, settlements, or land-use categories. Their inclusion in the Full Model is therefore intended to improve representation of the realized, human-constrained distribution of elephants, rather than to model conflict occurrence itself.

2.4 Model development and validation

Species distribution modelling was implemented using the `maxnet` package in R, a regularized multinomial logistic-regression approach for presence-background data (Phillips et al., 2017). Two models were developed to separate fundamental environmental suitability from realized habitat availability. The Ideal Model, trained only on environmental predictors (BIO1, BIO12, elevation, slope, aspect, EVI, NDVI), served as a proxy for the fundamental niche. The Full Model added anthropogenic predictors (roads, private lands, settlements, land use, and HEC locations) to approximate the realized niche under current human land use. Pixel-wise subtraction of the Full surface from the Ideal surface yielded an anthropogenic constraint layer indicating where human activities depress suitability below environmental potential.

Pseudo-absence points were generated at a 10:1 ratio to presence points, with 1,000-m spatial thinning to reduce autocorrelation. Sampling was constrained to ecologically accessible areas within a 3-km buffer, excluding protected areas, HEC hotspots, and slopes steeper than 30 degrees (Barbet-Massin et al., 2012). Variable selection followed Pearson correlation filtering ($|r| > 0.7$) and Variance Inflation Factor screening (VIF < 5), retaining predictors on the basis of collinearity and ecological interpretability (Dormann et al., 2013).

Models were trained with a 70:30 stratified train-test split and evaluated through five-fold cross-validation. Performance metrics included Area Under the Receiver Operating Characteristic Curve (AUC), True Skill Statistic (TSS), sensitivity, specificity, and Cohen's Kappa. Thresholds were selected by maximizing TSS (Liu et al., 2005). Continuous suitability predictions were reclassified into four ordinal categories: Low (0.00–0.25), Moderate (0.25–0.50), High (0.50–0.75), and Very High (0.75–1.00).

2.5 Anthropogenic constraint and conflict analysis

To quantify anthropogenic habitat degradation, a differential raster was generated by subtracting Full Model output from Ideal Model output. Areas with negative values were interpreted as degraded habitat zones attributable to human activities, whereas positive values indicated areas with restoration potential. The 65 verified HEC locations were overlaid on the Full Model suitability raster, and pixel values were extracted using bilinear interpolation. We explicitly acknowledge that HEC incident locations were also incorporated as predictor variables in the Full Model, functioning as spatial proxies for zones of concentrated anthropogenic pressure. This introduces a potential structural circularity: HEC locations contribute to model training and also constitute the spatial pattern characterized in the conflict analysis.

To avoid interpretive over-reach, all HEC–suitability comparisons are presented as descriptive characterizations of the ecological context of conflict zones rather than as independent model validation. Multi-scale buffer analysis was conducted at 500 m, 1,000 m, 2,000 m, and 5,000 m radii around each HEC point to evaluate local habitat quality around conflict sites. Welch's t-

tests were used to compare suitability between conflict and non-conflict locations. Differences among conflict types and buffer distances were summarized descriptively because extracted raster values around HEC points were not treated as independent validation samples.

3 Results

3.1 Model performance and variable importance

The Full Model achieved superior predictive performance (AUC = 0.896 ± 0.014, TSS = 0.547 ± 0.018) compared to the Ideal Model (AUC = 0.848 ± 0.017, TSS = 0.532 ± 0.021), demonstrating the importance of anthropogenic variables in capturing realized elephant distribution (Table 1). The Full Model exhibited enhanced specificity (0.880 ± 0.012 vs. 0.832 ± 0.015), indicating improved ability to identify unsuitable areas and reduce false positives in conservation planning. Sensitivity declined slightly in the Full Model (0.667 ± 0.026 vs. 0.700 ± 0.027), but overall classification accuracy improved, as shown by steeper ROC curves and higher AUC values (Fig. 2).

Permutation-based importance scores revealed distinct predictor hierarchies between models (Table 2). In the Full Model, HEC incident locations (importance = 3.021) emerged as the dominant predictor, followed by NDVI (2.081), EVI (1.255), and aspect (0.974). Because HEC points were included as a proxy for concentrated human–elephant interaction, their prominence is interpreted as evidence that realized elephant distribution tracks fine-scale socio-ecological overlap not fully captured by broader anthropogenic layers, rather than as proof that conflict occurrence is an independent causal driver of suitability. In contrast, the Ideal Model was dominated by aspect (4.982), BIO1 (0.940), and elevation (0.457), indicating stronger dependence on topographic orientation and climatic gradients when anthropogenic filtering is omitted.

3.2 Current habitat suitability patterns

Habitat-suitability predictions revealed marked differences between the Ideal and Full models. Under Ideal conditions, total suitable habitat (> 0.50 threshold) covered 555.01 km^2 (21.29% of the landscape), with 284.95 km^2 (10.93%) classified as high suitability (> 0.70) and 64.50 km^2 (2.47%) as very high suitability (> 0.90). The Full Model reduced these totals to 498.30 km^2 (19.11%), 276.44 km^2 (10.60%), and 60.96 km^2 (2.34%), respectively (Table 3; Fig. 3).

This corresponds to a net loss of 56.71 km^2 of suitable habitat attributable to anthropogenic pressure, with degradation most pronounced in southern foothill zones where roads, settlements, and agriculture intersect prime elephant habitat. Categorical reclassification revealed systematic habitat degradation (Table 4). The area classified as Very Low suitability increased by 142.62 km^2 under human influence, whereas Moderate and Low classes declined by 47.39 km^2 and 95.71 km^2, respectively. The slight increase in the High class (+0.48 km^2) is best interpreted as threshold reallocation at class boundaries rather than as a biologically meaningful gain in habitat quality. Statistical comparison confirmed a significant reduction in habitat quality, with mean suitability class decreasing by 0.069 units (Welch's $t = 8.96$, df = 4,335, $p < 0.001$, 95% CI [0.054, 0.085]) (Fig. 4).

3.3 Anthropogenic impact quantification

Differential analysis indicated that approximately 409.7 km^2 of the landscape experienced habitat-suitability degradation attributable to anthropogenic factors, with mean landscape suitability declining from 0.235 under Ideal conditions to 0.202 in the Full Model. Degradation was most severe in productive lowland valleys and foothill zones where agricultural expansion and infrastructure development have created barriers to elephant movement. Areas showing the strongest degradation signals (> 0.30 reduction in suitability) were concentrated in Sarpang Dzongkhag, particularly around Gelephu, Umling, and Dekiling Gewogs (Fig. 5).

Restoration-potential mapping identified 285.6 km^2 where the Ideal Model predicted moderate-to-high suitability but the Full Model indicated degraded conditions. Most of these areas occur in forest–agriculture transition zones and corridor linkages. They represent priority targets for habitat restoration, barrier mitigation, and conflict-sensitive land-use planning.

3.4 Human–elephant conflict relationships

Spatial analysis revealed a strong association between HEC incidents and high-quality elephant habitat. The 65 geo-referenced conflict locations exhibited mean habitat suitability of 0.733 (median = 0.821), compared with a landscape-wide mean of 0.197, a 3.7-fold difference. Suitability varied among conflict types, with the highest mean values for injury or fatality incidents (0.969), followed by property damage (0.759) and crop damage (0.691). Welch's t-test confirmed that habitat suitability at conflict locations was significantly higher than in non-conflict areas ($t = 18.69$, df = 131.2, $p < 0.001$). Because HEC points also served as predictors in the Full Model, contrasts among conflict types are interpreted descriptively rather than as independent inferential tests (Fig. 6).

Buffer analysis showed a clear distance-decay in habitat suitability around conflict sites: mean suitability was 0.739 within 500 m, declining to 0.710 at 1 km, 0.689 at 2 km, and 0.590 at 5 km. This gradient indicates that HEC events are concentrated in or adjacent to core elephant habitat, where favourable environmental conditions and human exposure overlap most strongly. The composite spatial pattern of conflict risk derived from habitat suitability, historical conflict records, settlement proximity, and road accessibility is shown in Fig. 7.

4 Discussion

4.1 Separating fundamental and realized habitat

The paired-model comparison shows that environment-only SDMs can materially overestimate accessible habitat when human land use filters occupancy. The Full Model's improvement over the Ideal Model, together with the reduction in suitable and highly suitable habitat, indicates that anthropogenic predictors capture an additional dimension of elephant distribution that climate, topography, and vegetation alone do not recover. The main contribution is therefore not the Bhutan-specific magnitude of habitat loss, but the demonstration that the gap between environmental potential and realized habitat can be quantified with a routine paired SDM workflow. This makes anthropogenic constraint a measurable management variable rather than an implicit source of model error.

The shift in predictor importance from climate and topography in the Ideal Model to vegetation, infrastructure, and human–elephant interaction proxies in the Full Model further reinforces this interpretation. In relatively unconstrained settings, elephants are expected to track productive environments and topographic refugia. In modified landscapes, however, realized use is conditioned by whether those same environments remain accessible in the presence of roads, settlements, and land conversion. Because HEC locations were used here as proxies for overlap zones, their importance is best interpreted as evidence of fine-scale socio-ecological interaction not fully represented by broader anthropogenic layers, not as evidence that conflict occurrence is itself a stand-alone driver of habitat suitability.

4.2 Conflict in shared high-quality habitat

HEC incidents were concentrated in high-suitability habitat rather than in marginal areas. This pattern challenges the common assumption that conflict is primarily a consequence of elephants being displaced into poor habitat. Instead, the results are more consistent with niche overlap in productive forest–agriculture mosaics, where the same lowland environments are valuable to elephants and to people. The buffer analysis supports this interpretation by showing that suitability remains high close to conflict locations and declines with distance from them.

This pattern matters for interpretation as well as management. Because HEC points were incorporated into the Full Model, the conflict analysis should not be treated as an independent validation test. Even so, the descriptive result is informative: conflict is concentrated where ecological value and human exposure coincide. Similar patterns have been reported from other elephant landscapes, suggesting that conflict mitigation should focus on shared high-value habitat rather than assuming that incidents occur mainly at the ecological margins (Acharya et al., 2016; de la Torre et al., 2021). For conservation planning, the key inference is that conflict zones may also be priority habitat rather than areas of low ecological importance.

4.3 Conservation implications

This study meets the journal's conservation-biogeography criterion most clearly through the management value of the paired surfaces. Comparing Ideal and Full predictions generates three operational classes for conservation action. First, areas with high Ideal suitability but low Full suitability represent restoration targets: the environment remains suitable, but anthropogenic barriers currently suppress occupancy. These locations are candidates for corridor restoration, barrier removal, reforestation, or wildlife-crossing investments. Second, areas with high suitability in both models that overlap with conflict records represent mitigation priorities: they are ecologically important and socially contested at the same time, so conservation action must be paired with conflict prevention, early-warning systems, fencing, and rapid-response measures. Third, areas with low suitability in both models can be treated as lower-priority zones for elephant-focused investment.

In south-central Bhutan, this logic highlights three immediate planning applications: stronger protection of core habitat within RMNP and PWS, restoration and reconnection along degraded corridor segments such as BC-03 and adjacent forest–agriculture transitions, and concentrated mitigation in the Gelephu–Umling–Dekiling belt where high suitability and dense human activity overlap. More broadly, the approach can support land-use zoning, corridor design, and infrastructure review wherever managers need to distinguish intrinsically unsuitable habitat from habitat that remains ecologically suitable but functionally inaccessible. Transferability to other wide-ranging megafauna is plausible because many species face equivalent human filtering of realized distributions, but the effect sizes reported here should not be generalized without replication across additional taxa and landscapes.

4.4 Limitations and future research

Several limitations bound interpretation of these results. First, both models are presence-only MaxEnt implementations and therefore remain sensitive to sampling bias and the absence of verified absence data (Yackulic et al., 2013). Second, because HEC locations were included as predictors and then examined descriptively in relation to suitability, the HEC–suitability pattern should be interpreted as a characterization of socio-ecological overlap rather than as an independent test of model performance; a sensitivity analysis excluding HEC from the Full Model would be an important next step. Third, the HEC dataset is restricted to documented incidents and probably underrepresents the full spatial extent of conflict, particularly where minor crop damage goes unreported. Fourth, the analysis remains spatially bounded by Bhutanese data availability and therefore cannot fully characterize transboundary movements into adjacent Assam.

Future work should therefore combine telemetry-based movement data, ensemble modelling, and predictor-specific sensitivity analyses to test how robust the paired-surface framework remains when HEC is excluded or replaced by other anthropogenic indicators. Replication across multiple elephant landscapes, and eventually across other megafauna systems, will be necessary to determine how general the magnitude and spatial form of the fundamental–realized habitat gap actually are.

4.5 Concluding remarks

Separating where elephants could persist environmentally from where they can persist under current human pressure changes the interpretation of habitat maps in conservation practice. In south-central Bhutan, the paired SDM framework showed that anthropogenic pressure reduces access to otherwise suitable habitat and that conflict clusters in productive shared landscapes rather than in marginal refuges. The practical value of the framework lies in converting that distinction into spatially explicit restoration and mitigation priorities. For conservation biogeography, this provides a more defensible basis for allocating effort in landscapes where habitat quality and human pressure are inseparable.

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Data Accessibility Statement

An anonymized submission package containing processed elephant occurrence data, coarsened HEC coordinates, predictor-layer metadata, model outputs, and R scripts required to reproduce the analyses will be deposited in an anonymous public repository before submission. The repository DOI or anonymous review link should be inserted here prior to journal upload. Because Asian elephants are sensitive to persecution and poaching, any publicly released coordinate data should be provided at a coarser spatial resolution consistent with the journal's policy for threatened species, while retaining sufficient analytical detail for reproducibility.

Table 1: Model performance metrics for Asian elephant MaxEnt habitat-suitability models in south-central Bhutan. Values are means ± SD across five-fold cross-validation.

Model	AUC (±SD)	TSS (±SD)	Sensitivity (±SD)	Specificity (±SD)	Kappa
Ideal	0.848 ± 0.017	0.532 ± 0.021	0.700 ± 0.027	0.832 ± 0.015	0.371
Full	0.896 ± 0.014	0.547 ± 0.018	0.667 ± 0.026	0.880 ± 0.012	0.376

Table 2: Top-ranked predictors for Asian elephant MaxEnt models in south-central Bhutan under Ideal and Full scenarios. Importance scores represent relative contributions within each model and are not directly comparable between scenarios.

Model	Rank	Variable	Importance score
Full	1	HEC incident locations	3.022
Full	2	NDVI	2.081
Full	3	EVI	1.255
Full	4	Aspect	0.974
Full	5	Distance to roads	0.493
Full	6	Distance to streams	0.258
Full	7	Slope	0.057
Full	8	Water source density	0.016
Ideal	1	Aspect	4.982
Ideal	2	BIO1 (annual temperature)	0.940
Ideal	3	Elevation	0.457
Ideal	4	Stream density	0.212
Ideal	5	Distance to streams	0.202
Ideal	6	Slope	0.022
Ideal	7	Water source density	0.002
Ideal	8	BIO12 (annual precipitation)	0.001

Table 3: Area (km^2) by habitat-suitability class for Asian elephant models in south-central Bhutan under Ideal and Full scenarios. Suitability thresholds represent predicted probability of occurrence. Areas were calculated from classified model outputs clipped to the study extent.

Suitability class	Threshold	Full Model		Ideal Model	
		Area (km^2)	%	Area (km^2)	%
Total area	—	2,607.07	100	2,607.07	100
Suitable	>0.50	498.30	19.11	555.01	21.29
High	>0.70	276.44	10.60	284.95	10.93
Very High	>0.90	60.96	2.34	64.50	2.47

Table 4: Area (km^2) in each suitability class for Asian elephant habitat in south-central Bhutan under Ideal and Full scenarios. Areas were calculated from classified model outputs clipped to the study extent.

Suitability class	Ideal (km^2)	Full (km^2)	Change (km^2)
Very Low	1,706.26	1,848.88	+142.62
Low	431.21	335.50	−95.71
Moderate	281.28	233.89	−47.39
High	188.32	188.80	+0.48
Total[1]	2,607.07	2,607.07	0.00

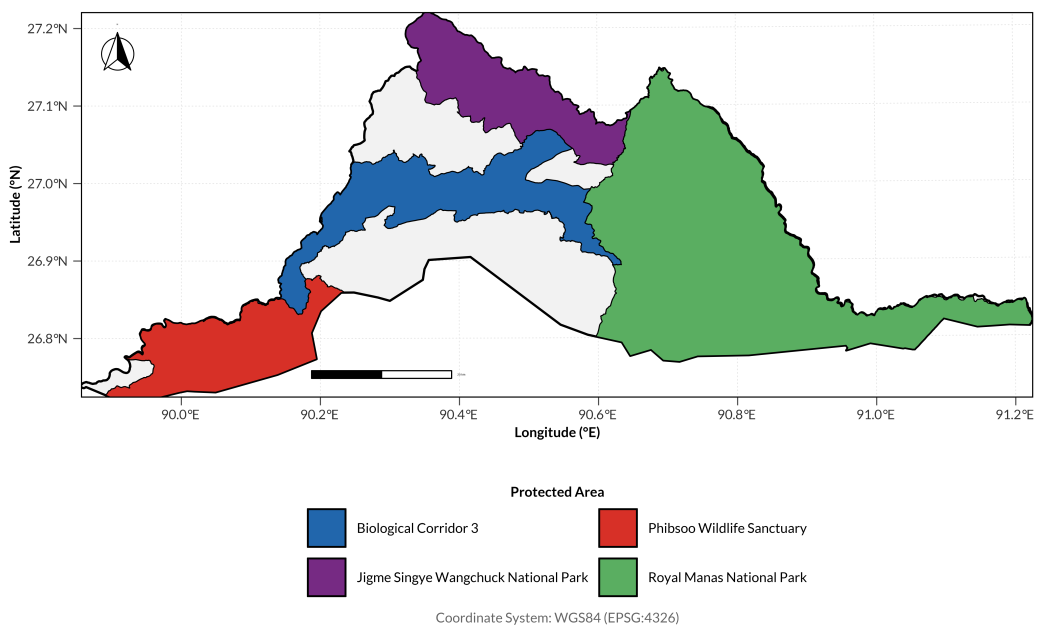

Figure 1: Study area for Asian elephant habitat modelling in south-central Bhutan, showing Royal Manas National Park, Phibsoo Wildlife Sanctuary, Biological Corridor 03, and surrounding human-modified landscapes. The region spans a gradient from protected lowland forests to agricultural frontiers along the Bhutan–India transboundary zone. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

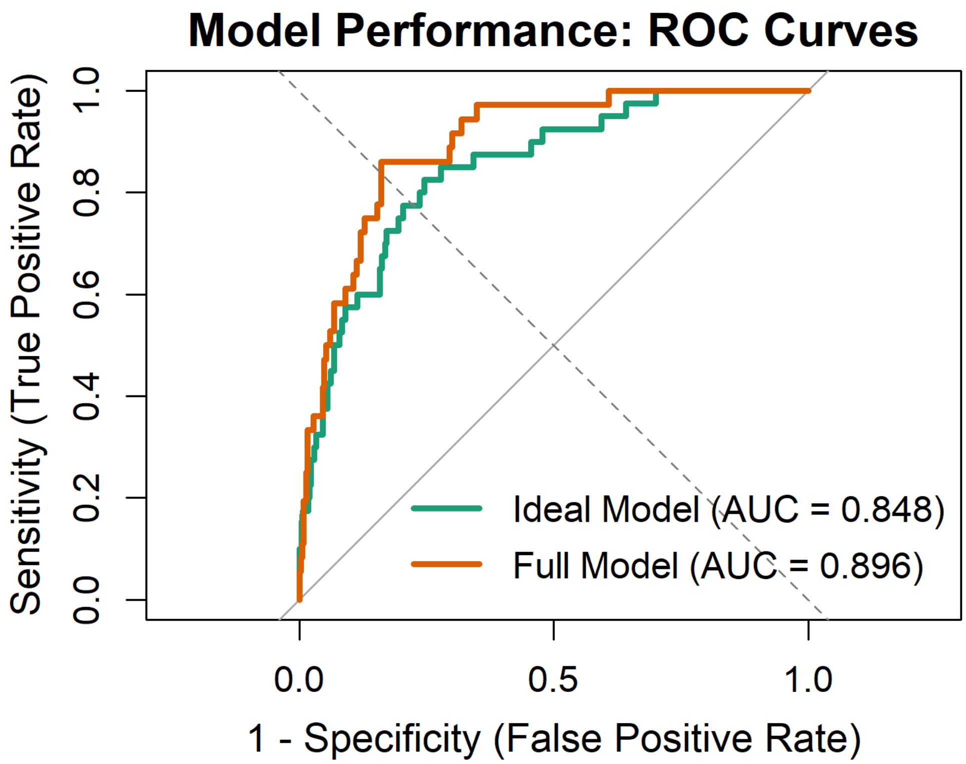

Figure 2: Receiver operating characteristic curves for Asian elephant habitat-suitability models in south-central Bhutan. The Full Model, which includes environmental and anthropogenic predictors, shows a steeper curve and higher AUC than the environment-only Ideal Model.

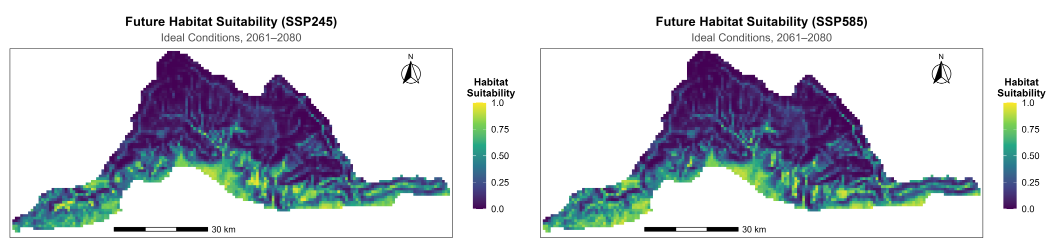

Figure 3: Paired habitat-suitability maps for Asian elephants in south-central Bhutan from the Full Model (left) and Ideal Model (right). Differences between panels identify environmentally suitable habitat rendered less available by anthropogenic pressure. Warmer colours indicate higher predicted suitability. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

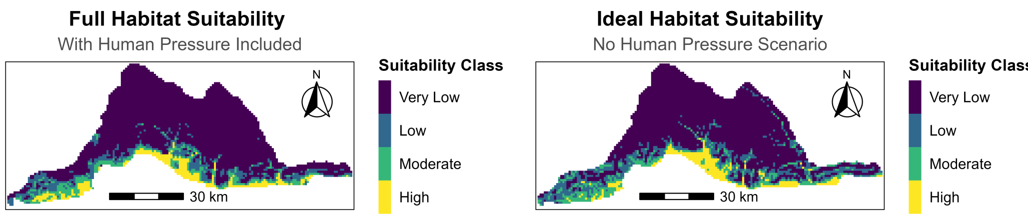

Figure 4: Classified Asian elephant habitat-suitability maps for south-central Bhutan illustrating the net downgrading of habitat quality from Ideal (right) to Full (left) model predictions. Expansion of the Very Low class and contraction of the Low and Moderate classes summarize the cumulative effect of anthropogenic pressure. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

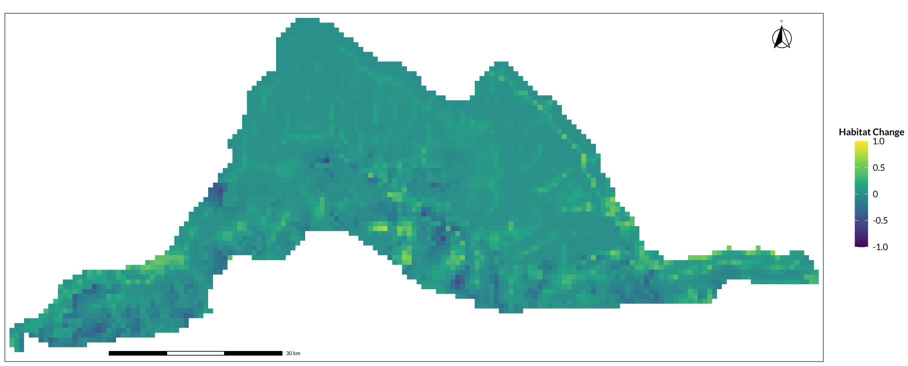

Figure 5: Spatial pattern of anthropogenic habitat degradation for Asian elephants in south-central Bhutan, calculated as the difference between Ideal and Full model suitability predictions. Warmer colours indicate greater suitability loss attributable to human activities. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

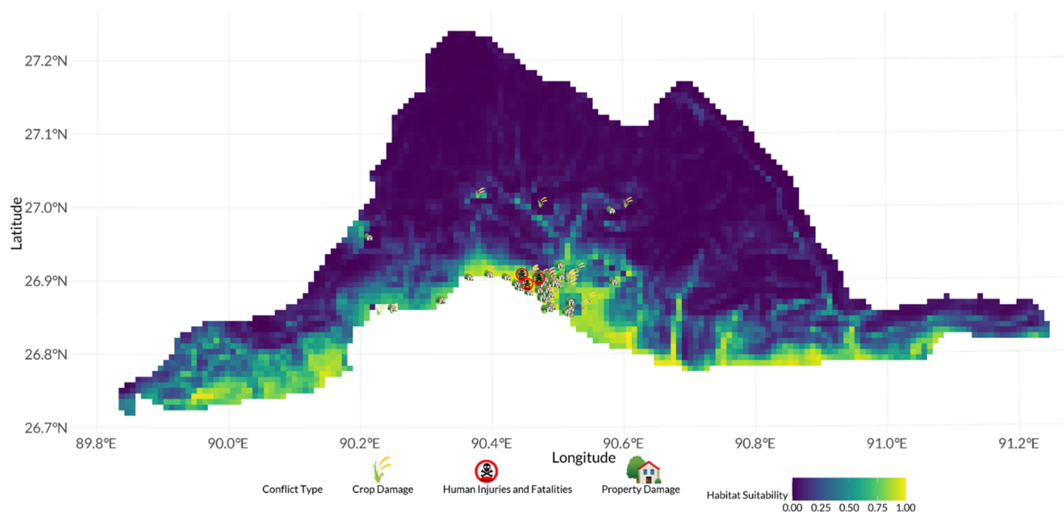

Figure 6: Human–elephant conflict incidents overlaid on Full Model habitat suitability for Asian elephants in south-central Bhutan. Conflict is concentrated in high-suitability habitat, indicating overlap between ecologically important elephant habitat and human land use. Points indicate conflict locations categorized by event type. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

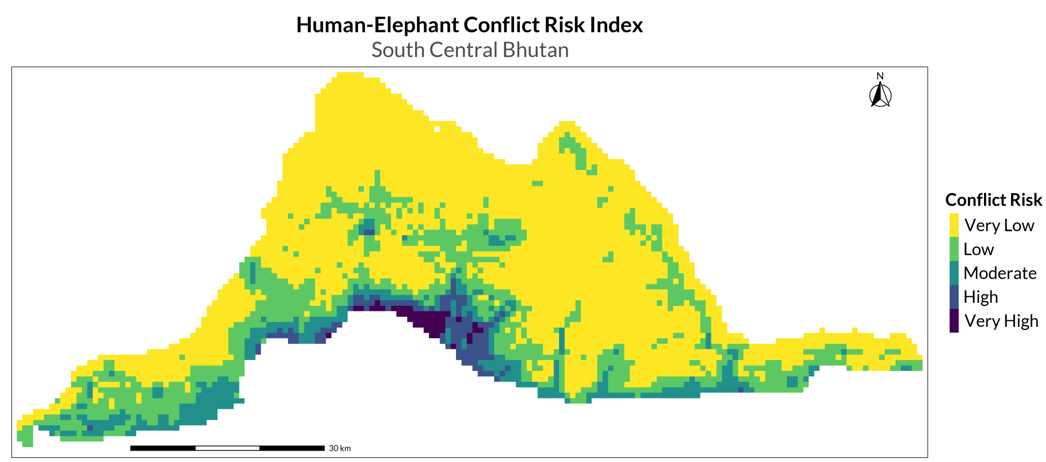

Figure 7: Composite conflict-risk map for Asian elephants in south-central Bhutan integrating habitat suitability, historical conflict density, proximity to settlements, and road accessibility into five ordinal risk classes. The map identifies areas where conservation investment and conflict mitigation are most likely to coincide. Map lines delineate study areas and do not necessarily depict accepted national boundaries.