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

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Abstract

Conservation planning for large-bodied species in human-dominated landscapes is increasingly compromised by a systematic error in species distribution models (SDMs): the conflation of fundamental environmental suitability—where species could persist—with realized habitat availability—where anthropogenic barriers permit them to do so. This conflation produces overestimates of accessible habitat, misidentifies restoration priorities, and directs mitigation resources away from the human pressures that actually constrain populations. We develop and validate a transferable dual-model framework that resolves this error by pairing an environment-only SDM (Ideal Model, counterfactual for the fundamental niche) with an SDM incorporating anthropogenic variables (Full Model, approximating the realized niche); the pixel-wise difference between outputs constitutes a spatially explicit anthropogenic constraint surface directly actionable for management. Applied to Asian elephants (*Elephas maximus*) across a 2,607 $\mathrm{km}^{\mathbf{2}}$ gradient of protected forest and agricultural frontier in south-central Bhutan, the Full Model substantially outperformed the environment-only model (AUC = $\mathbf{0.896 \pm 0.014}$ vs. $\mathbf{0.848 \pm 0.017}$), confirming that anthropogenic variables capture a dimension of distribution that environmental predictors cannot. Anthropogenic pressure reduced highly suitable habitat by $\mathbf{\sim 57}$ $\mathrm{km}^{\mathbf{2}}$ ($\mathbf{\sim 10\%}$) while degrading a further $\mathbf{\sim 410}$ $\mathrm{km}^{\mathbf{2}}$; human–elephant conflict clustered in high-quality habitat (mean suitability = **0.733** vs. **0.197** landscape-wide), demonstrating that conflict reflects niche overlap in productive landscapes, not displacement into marginal areas. The framework generates a three-category conservation triage map—restoration targets (high Ideal, low Full), mitigation priorities (high both, with conflict), and deprioritized areas (low both)—applicable to any wide-ranging species for which occurrence data and anthropogenic predictor layers are available. As land conversion continues to constrain megafauna populations across Asia, Africa, and beyond, separating environmental suitability from anthropogenic feasibility is a prerequisite for evidence-based conservation investment, not an optional refinement. This framework addresses a general limitation in species distribution modelling under human-dominated conditions and provides a transferable basis for conservation planning across megafauna systems globally.

Keywords: Species distribution modelling; Anthropogenic constraint; Realized niche; Conservation biogeography; Human–wildlife conflict; Land-use planning

1 Introduction

As human land use expands into the last intact habitats of wide-ranging species, conservation planners depend increasingly on species distribution models (SDMs) to determine where wildlife persists, where connectivity is maintained, and where management intervention is most urgent. Yet for large-bodied megafauna—species that require extensive areas of connected habitat and whose ranges overlap most severely with expanding agricultural and infrastructure frontiers—the habitat SDMs predict is progressively disconnected from the habitat animals actually occupy. Most SDM applications estimate the fundamental environmental niche: the set of climatic, topographic, and vegetative conditions under which a species can, in principle, persist (Elith and Leathwick 2009; Guisan et al. 2017). In the Anthropocene, however, megafauna are progressively confined to realized niches constrained by roads, settlements, agriculture, persecution, and behavioral avoidance of human disturbance—none of which are captured by environment-only predictor sets. When SDMs conflate these two niche dimensions, they overestimate habitat availability and generate systematic errors in every downstream decision that depends on them (Guisan et al. 2017).

The management costs of this conflation are concrete and consequential. When a model predicts high habitat suitability in an area from which a species is persistently excluded by infrastructure or agriculture, conservation planners may interpret absence as a survey artefact rather than as evidence of functional inaccessibility—allocating restoration resources to sites that require barrier removal, not habitat management. When human–wildlife conflict is assumed to arise from displacement into marginal environments, but in fact reflects niche overlap in productive landscapes, mitigation strategies target the wrong spatial configurations. When corridor designs rely on environment-only suitability without accounting for anthropogenic barriers, predicted connectivity does not translate into functional movement. Resolving the fundamental–realized conflation is therefore a prerequisite for evidence-based environmental management, not an optional methodological refinement. This gap is especially consequential for the Asian elephant (*Elephas maximus*), whose range has contracted by 30–60% over the past century (de Silva et al. 2023; Ripple et al. 2015), because the productive lowland habitats that define its fundamental niche are precisely the landscapes most attractive for human settlement and agriculture across its 13-country range (Kanagaraj et al. 2019).

Despite widespread recognition that anthropogenic variables shape realized megafauna distributions, most SDM studies for large-bodied species continue to rely on environmental-only predictor sets, implicitly treating modeled suitability as a proxy for realized occupancy (Budhathoki et al. 2023; Sarker and Røskaft 2011; Palei et al. 2024). While a growing number of studies have improved predictive accuracy by including human-footprint variables within a single model (Palei et al. 2024), no study has developed and validated a systematic paired-model approach—training one model on environmental predictors only and a second on combined environmental-plus-anthropogenic predictors, then using the pixel-wise difference between outputs as an anthropogenic constraint surface—that makes the fundamental–realized gap spatially explicit and directly actionable for conservation investment decisions. This absence leaves managers unable to distinguish areas where species are absent because the environment is inherently unsuitable from areas where species are absent because human barriers exclude them from suitable habitat: a distinction that demands different interventions and different investment levels.

South-central Bhutan provides a compelling landscape in which to develop, validate, and demonstrate such a framework. The region encompasses Royal Manas National Park (RMNP), Phibsoo Wildlife Sanctuary (PWS), and the adjoining lowland forests of Sarpang Dzongkhag—a 2,607 km^2 gradient from protected interior forest to rapidly expanding agricultural frontier, supporting approximately 40% of Bhutan's elephant range across a mosaic of protected areas, biological corridors, and intensifying land use (Penjor et al. 2024; Tshering et al. 2024). Human–elephant conflict (HEC) incidents have quadrupled over the past decade in districts such as Sarpang (Dorji et al. 2024), generating acute demand for planning tools that can distinguish ecologically driven from anthropogenically driven habitat unavailability. Critically, the spatial configuration of this landscape—protected areas embedded in an agricultural matrix, with documented conflict, expanding road infrastructure, and verified occurrence and conflict datasets—mirrors the planning context faced by conservation managers across the range of Asian elephants, and more broadly across the ranges of African elephants, tigers, and other wide-ranging megafauna in human-dominated biomes (Ripple et al. 2015). Bhutan is employed as a data-rich test case for a framework designed to be immediately replicable.

This study develops and compares two MaxEnt models: an Ideal Model incorporating only environmental predictors (approximating the fundamental niche) and a Full Model integrating anthropogenic variables (approximating the realized niche). We test the hypothesis that anthropogenic barriers significantly reduce suitable habitat extent relative to environmental potential, with degradation concentrated in productive zones where human activities overlap prime megafauna habitat. Our objectives are to: (1) quantify the divergence between fundamental environmental suitability and realized habitat availability; (2) identify the environmental and anthropogenic predictors most strongly associated with elephant occurrence under each scenario; (3) construct a spatially explicit anthropogenic constraint surface identifying restoration priorities, conflict-mitigation zones, and lower-priority areas; and (4) evaluate relationships between modeled suitability and documented HEC incidents, with implications for conflict management beyond the study landscape. By embedding the fundamental–realized niche distinction within a paired modeling design, this study advances both SDM methodology and environmental management practice: it delivers a transferable decision-support framework for any landscape where large-bodied species persist amid intensifying anthropogenic pressure. This limitation represents a central challenge in conservation biogeography and environmental management, particularly in landscapes where anthropogenic pressures constrain realized species distributions.

2 Methods

2.1 Study Area

The study was conducted in south-central Bhutan, encompassing 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 a critical component of the broader transboundary conservation landscape linking Bhutan's protected areas with Manas Tiger Reserve in Assam, India (Penjor et al.

2024). The spatial configuration of protected areas and connecting corridors sustains landscape-scale permeability for wide-ranging megafauna, with elephants serving as an umbrella species for corridor functionality.

RMNP (1,057 km^2) is situated in Bhutan's southern foothills, bordering Assam and contiguous with Manas Tiger Reserve, creating a transboundary conservation complex. PWS (268.93 km^2) lies southwest of Sarpang and connects to RMNP through BC-03, facilitating species movement across protected areas and international boundaries. Approximately 40% of Bhutan's elephant range occurs in the southern belt, with about 38% located within protected boundaries (Penjor et al. 2024). The region exhibits considerable climatic and topographic variation, with humid subtropical conditions in lowlands (1,500–2,500 mm annual rainfall, summer temperatures 25–35°C) transitioning to temperate conditions at higher elevations. Major river systems including the Punatsangchhu and Manas Chhu traverse the landscape, contributing to formation of alluvial plains and supporting subtropical broadleaf forests, 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 programs, and global biodiversity databases. These records were derived from an initial pool of 82,695 occurrence records and subjected to rigorous spatial filtering and quality control. Primary sources included Department of Forests and Park Services datasets from the National Elephant Survey 2020 and National Tiger Survey 2022, utilizing direct sightings, dung counts, and camera trapping within RMNP, PWS, and Sarpang Forest Division. Supplementary data were obtained from the 2024 field-based habitat study conducted as part of the ACCES project, employing stratified transects and camera traps. To enhance spatial coverage, occurrence records from the Global Biodiversity

Information Facility (GBIF) were included for South Asia, with rigorous data cleaning implemented in R involving spatial thinning to reduce sampling bias, removal of duplicate coordinates, and exclusion of geospatial outliers falling 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-meter 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. These geo-referenced conflict locations were spatially filtered and validated and subsequently used to represent conflict hotspots. HEC points served both as independent validation data and as spatial proxies for anthropogenic pressure in resistance and habitat suitability modeling.

2.3 Environmental and Anthropogenic Variables

Bioclimatic predictors were sourced from WorldClim version 2.1 at 30 arc-second resolutions, representing temperature and precipitation-related variables for baseline conditions (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 captured using Enhanced Vegetation Index (EVI) and Normalized Difference Vegetation Index (NDVI) from MODIS MOD13Q1, accessed via Google Earth Engine, with multi-year mean composites computed for the growing season (April–October).

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-meter resolution using bilinear interpolation for continuous variables and nearest neighbor for categorical layers, with full spatial congruence ensured through `compareGeom()` validation.

2.4 Model Development and Validation

Species distribution modeling was implemented using the `maxnet` package in R, a regularized multinomial logistic regression approach optimized 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 exclusively on environmental predictors (BIO1, BIO12, elevation, slope, aspect, EVI, NDVI), serves as a proxy for the fundamental niche—the range of abiotic conditions under which *E. maximus* could persist in the absence of anthropogenic constraints. The Full Model, integrating additional anthropogenic variables (roads, private lands, settlements, land use, HEC locations), approximates the realized niche—the subset of environmentally suitable space that elephants actually occupy given current human land use. This dual-model structure isolates anthropogenic constraints by comparing spatial predictions and evaluation metrics between scenarios. Conceptually, the Ideal Model serves as a counterfactual—the predicted habitat configuration in the absence of anthropogenic pressure—while the Full Model represents the observed, human-constrained system. The pixel-wise difference between Ideal and Full model outputs constitutes an anthropogenic constraint surface: a spatially explicit map of where, and by how much, human activities have depressed habitat quality below the environmentally determined potential.

Pseudo-absence points were generated at a 10:1 ratio to presence points, applying 1,000-meter spatial thinning to reduce autocorrelation. Sampling was constrained to ecologically accessible areas within a 3-km buffer, excluding protected areas, HEC hotspots, and steep terrain (>30° slope) (Barbet-Massin et al. 2012). Variable selection employed a two-step process: Pearson correlation filtering ($|r| > 0.7$ threshold) followed by Variance Inflation Factor analysis (VIF < 5), retaining only non-collinear predictors based on ecological interpretability (Dormann et al. 2013).

Model training followed a 70:30 stratified train-test split with 5-fold cross-validation to assess robustness. Performance was evaluated using Area Under the Receiver Operating Characteristic Curve (AUC), True Skill Statistic (TSS = sensitivity + specificity -1), sensitivity, specificity, and Cohen's Kappa. Threshold values were selected based on maximum TSS criteria (Liu et al. 2005). Suitability predictions were generated as continuous raster surfaces and reclassified into 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 Human Impact and Conflict Analysis

To quantify anthropogenic habitat degradation, a differential raster was generated by subtracting Full Model output from Ideal Model output. Areas with significant negative values were classified as degraded habitat zones attributable to human activities, while positive values indicated potential restoration areas. The 65 verified human–elephant conflict locations extracted from 2,000 reported incidents were overlaid on the Full Model Habitat Suitability Raster, with pixel values extracted using bilinear interpolation. We explicitly acknowledge that HEC incident locations were also incorporated as predictor variables in the Full Model (Section 2.4), functioning as spatial proxies for zones of concentrated anthropogenic pressure. This introduces a potential structural circularity: HEC locations contribute to model training and simultaneously constitute the spatial pattern being characterized in the conflict analysis. To mitigate 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; the analysis characterizes where conflict occurs relative to habitat quality, not whether the model accurately predicts conflict per se. Multi-scale buffer analysis was conducted at 500 m, 1,000 m, and 2,000 m radii around each HEC point to evaluate local habitat quality surrounding conflict sites. Statistical comparison employed Welch's t-tests to assess differences in habitat suitability between conflict and non-conflict locations, with ANOVA used to test for differences among conflict types (crop damage, property damage, injury/fatality).

3 Results

3.1 Model Performance and Variable Importance

The Full Model achieved superior predictive performance (AUC $= 0.896 \pm 0.014$, TSS $= 0.547 \pm 0.018$) compared to the Ideal Model (AUC $= 0.848 \pm 0.017$, TSS $= 0.532 \pm 0.021$), 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 correctly identify unsuitable areas and avoid false positives in conservation planning. While sensitivity declined slightly in the Full Model (0.667 ± 0.026 vs. 0.700 ± 0.027), overall classification accuracy improved, as evidenced by steeper ROC curves and higher AUC values (Fig. 2). Consistent performance across cross-validation folds, with low standard deviations, reflected high model robustness.

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). These results emphasize that in human-modified landscapes, habitat suitability is governed not only by environmental features but also by spatial patterns of conflict, vegetation productivity, and proximity to infrastructure. In contrast, the Ideal Model was dominated by aspect (4.982), BIO1 (0.940), and elevation (0.457), indicating strong dependence on topographic orientation and climatic gradients in undisturbed habitats. The shift from climate-driven to conflict-driven predictors illustrates adaptive habitat selection under anthropogenic pressure.

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 (>0.90). The Full Model exhibited reductions across all categories: 498.30 km^2 (19.11%) suitable, 276.44 km^2 (10.60%) high, and 60.96 km^2 (2.34%) very high (Table 3; Fig. 3).

This corresponds to a net loss of 56.71 km^2 (∼10.2%) 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, while Moderate and Low classes declined by 47.39 km^2 and 95.71 km^2, respectively. 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). Spatial patterns indicated that degradation was concentrated along the southern border, where linear infrastructure and settlement expansion have converted formerly continuous forest matrices into fragmented mosaics.

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—where paddy cultivation, road networks, and settlement density are highest (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. These areas, primarily located in forest–agriculture transition zones and corridor linkages, represent priority targets for habitat restoration, barrier mitigation, and conflict-sensitive land-use planning. The spatial distribution of restoration opportunities suggests that relatively modest interventions—such as wildlife underpasses, agricultural buffer zones, and corridor reforestation—could recover substantial functional habitat connectivity.

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 to a landscape-wide mean of 0.197—a 3.7-fold difference. Suitability varied among conflict types, peaking for injury/fatality incidents (mean = 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, $p < 0.001$), and ANOVA identified strong differences among conflict types ($F_{(3,1106)} = 129.7$, $p < 0.001$). The spatial distribution of human–elephant conflict incidents relative to predicted habitat suitability is shown in Fig. 6.

Buffer analysis demonstrated 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 disproportionately concentrated in or adjacent to core elephant habitat zones, where environmental conditions most strongly favor elephant occupancy. The pronounced spatial coupling between high-quality habitat and conflict risk underscores a fundamental conservation challenge: communities most exposed to conflict often reside within landscapes simultaneously of greatest ecological importance for *E. maximus.*

The composite spatial pattern of conflict risk derived from habitat suitability, historical conflict records, settlement proximity, and road accessibility is presented in Fig. 7.

4 Discussion

4.1 Fundamental Versus Realized Habitat: The Core Finding

The central result of this study—that environment-only SDMs systematically overestimate realized habitat availability for megafauna by conflating environmental suitability with anthropogenic feasibility—is not a finding specific to Asian elephants or to south-central Bhutan. It is a structural problem with how SDMs are routinely deployed in conservation management, and its consequences play out across every system where large-bodied species persist in human-modified landscapes. The Full Model's superior predictive performance (AUC = 0.896 vs. 0.848) is quantitative confirmation that anthropogenic variables capture a dimension of megafauna distribution that environmental predictors cannot; the $\sim$10% reduction in highly suitable habitat and the $\sim$410 km^2 of degraded suitability identified by the constraint surface represent the type of gap that, replicated across the range of Asian elephants and other megafauna facing equivalent or greater anthropogenic pressure, amounts to systematic misallocation of conservation investment at continental scale. For environmental management practice, the importance of this result lies not in the Bhutan-specific quantities but in what they demonstrate: that paired SDM comparison provides an accessible, repeatable method for measuring this gap wherever occurrence data, anthropogenic predictor layers, and management need co-occur. This study offers three contributions in this context. First, it provides a conceptual advance by explicitly quantifying the fundamental–realized niche divergence for a megafauna species through paired SDM comparison. Second, it introduces a methodological framework—the dual-model paired comparison—that isolates anthropogenic constraints and is directly replicable across taxa and geographies without specialist analytical tools. Third, it provides an empirical finding that human–wildlife conflict concentrates in high-quality, not marginal, habitat, challenging the displacement assumption that underlies many conflict-management programmes worldwide. The management-relevant implications of each contribution are direct: the first enables agencies to audit whether existing habitat inventories overestimate accessible area and, by extension, whether national biodiversity commitments are based on systematically inflated baselines; the second means this audit can be conducted using datasets already assembled for standard biodiversity monitoring, with no additional data collection burden; and the third demands a reorientation of where conflict-management budgets are deployed—away from assumption-based targeting of marginal zones and toward the productive shared landscapes where conflict is structurally inevitable in the absence of proactive intervention.

The shift in predictor importance from climate and topography in the Ideal Model to conflict history, vegetation indices, and infrastructure in the Full Model reflects fundamental changes in habitat selection under anthropogenic stress. In relatively undisturbed scenarios, elephants preferentially select areas based on thermal regime, solar exposure, and elevation-related vegetation variation—consistent with their physiological requirements for cool, resource-rich environments (Wilson et al. 2021). However, in reality, elephants increasingly use habitat patches defined by the absence of human disturbance rather than by optimal environmental conditions, suggesting risk-driven spatial behavior (Vanak et al. 2010). This pattern has been documented across Asian elephant ranges, where human population density and proximity to agriculture emerge as key negative predictors of occurrence (Vasudev et al. 2021). The finding aligns with recent SDM studies demonstrating improved predictive accuracy when incorporating human-footprint data (Palei et al. 2024; Thant et al. 2023).

Beyond the specific empirical outcomes, this study makes an explicit theoretical contribution to species distribution modelling by embedding the fundamental–realized niche distinction—long recognized in niche theory (Elith and Leathwick 2009; Guisan et al. 2017) but rarely operationalized in paired SDM designs—directly into a conservation-applicable workflow. Conventional SDMs that omit anthropogenic predictors implicitly treat observed distributions as approximations of the fundamental niche, a conflation that systematically overstates available habitat in human-modified systems. The dual-model structure addresses this core limitation: by treating the Ideal Model as a counterfactual and the Full Model as the empirically constrained outcome, the framework transforms niche divergence from a theoretical concern into a quantifiable, spatially explicit management variable.

4.2 Spatial Patterns of Habitat Degradation

The concentration of habitat degradation in southern foothill zones reflects a pattern common to agricultural frontiers worldwide: the productive alluvial plains and gentle slopes that constitute optimal megafauna habitat are also the landscapes most attractive for human settlement and cultivation (de la Torre et al. 2021). This spatial overlap creates a classical land-use conflict in which conservation and development objectives compete for the same high-value areas—a dynamic documented for elephants in Peninsular Malaysia, tigers in central India, and large herbivores across sub-Saharan Africa (Ripple et al. 2015). The finding that 285.6 km^2 of degraded habitat retains high environmental suitability represents a spatially explicit restoration-potential estimate directly actionable for land-use planning: it defines the extent and location of areas where policy instruments—ecological restoration designations, agricultural buffer-zone regulations, wildlife corridor easements, and payment-for-ecosystem-services schemes—would yield measurable habitat recovery rather than investment in sites where environmental conditions do not support recovery regardless of management effort.

The spatial pattern of degradation—concentrated along roads and settlements—underscores the barrier effect of linear infrastructure on megafauna movement, a dynamic documented across elephant-range landscapes in South and Southeast Asia and large mammal systems in sub-Saharan Africa (Wilson et al. 2021). Roads fragment habitat not only through direct conversion but also through increased vehicle-collision risk, noise disturbance, and facilitation of human access to formerly remote areas. Where expanding road networks bisect seasonal movement corridors between protected areas, barrier effects compound natural topographic constraints and may restrict gene flow, progressively reducing long-term population viability at a landscape scale. The constraint surface generated by the dual-model comparison directly identifies these infrastructure-driven degradation zones, providing managers with spatial targets for crossing-structure investments, speed-reduction measures, and corridor reforestation—interventions whose general efficacy is well established but whose optimal placement depends precisely on the kind of habitat-feasibility mapping this framework provides.

4.3 Human–Wildlife Conflict in High-Quality Habitat

A pervasive assumption in human–wildlife conflict management is that conflict arises because species are displaced from suitable habitat into marginal, degraded areas where resource scarcity forces animals to use agricultural land. Our results directly contradict this assumption: human–elephant conflict incidents are strongly associated with the highest-quality habitat in the landscape (mean suitability = 0.733, versus 0.197 landscape-wide), demonstrating that conflict is a consequence of niche overlap in productive landscapes, not of animal displacement into marginal environments. This finding has implications that extend far beyond Asian elephants. The same conflict-in-prime-habitat dynamic has been documented in Peninsular Malaysia, where agricultural lands were identified as prime rather than marginal elephant habitat (de la Torre et al. 2021), and in Nepal, where problem elephants utilize the same productive forest–farmland mosaics as non-conflict individuals (Acharya et al. 2016). The consistency of this pattern across independent study systems suggests that it is a predictable structural consequence of niche overlap between megaherbivores and agrarian land use wherever the two co-occur—not a regional anomaly requiring a Bhutan-specific explanation.

This spatial coupling of high suitability and elevated conflict risk generates planning implications that extend beyond any single landscape. It demonstrates that conflict-mitigation policy cannot rely on species voluntarily vacating human-dominated areas or shifting to lower-quality habitat; rather, proactive interventions are required in shared landscapes where conservation and rural livelihood objectives compete for the same productive terrain. Policies premised on the displacement assumption—providing alternative livelihood income in degraded areas to reduce dependence on conflict-prone agriculture, for example—will underperform in systems where conflict occurs because animals and people both occupy high-value habitat, not because animals have been pushed into marginal land. The observed distance–decay pattern in suitability (declining from 0.739 at 500 m to 0.590 at 5 km from conflict sites) provides spatially explicit guidance for targeting mitigation measures: intensive interventions, including electric fencing, early-warning systems, and community-based rapid-response protocols, should prioritize the 1–2 km buffer zone around documented conflict hotspots, where habitat quality and human exposure intersect most strongly, and where investment per conflict-incident-avoided will be lowest.

4.4 Conservation and Management Implications

The dual-model framework provides conservation planners with a spatially explicit tool for differentiating between ecologically suitable areas rendered inaccessible by anthropogenic barriers and intrinsically unsuitable habitat—a distinction that fundamentally shapes the choice and prioritization of management interventions. The approach is applicable wherever large-bodied species persist in human-modified landscapes, from elephant-range countries across Asia and Africa to tiger reserves in the Indian subcontinent and large herbivore landscapes in sub-Saharan Africa (Ripple et al. 2015).

The comparison of Ideal and Full model outputs supports a generalized conservation triage logic structured around three spatial configurations. First, areas of high Ideal-Model suitability but low Full-Model suitability—where environmental conditions are favorable but anthropogenic barriers suppress realized occupancy—constitute priority restoration and reconnection targets: relatively modest interventions (wildlife crossing structures, agricultural buffer zones, corridor reforestation) can recover substantial functional habitat. Second, areas of high suitability in both models that overlap with active conflict zones represent shared resource landscapes requiring simultaneous conservation and conflict-mitigation investment; reactive protection alone is insufficient because the ecological drivers of high occupancy and the human drivers of conflict are spatially inseparable. Third, areas showing low suitability in both models may be deprioritized for megafauna-focused conservation, allowing scarce resources to concentrate on the two higher-value configurations. This three-way triage provides a generalizable, data-driven basis for allocating conservation investment efficiently across heterogeneous landscapes.

In the south-central Bhutan study landscape, as one illustrative application of this globally transferable logic, the triage framework identifies three corresponding spatial priorities: (1) strict protection of core high-suitability areas within RMNP and PWS; (2) restoration and barrier mitigation in degraded corridors, particularly BC-03; and (3) intensive conflict mitigation in the Gelephu–Umling–Dekiling agricultural belt, where high habitat suitability and dense human settlement co-occur. These are not Bhutan-specific prescriptions but reflections of the three universal triage categories—restoration target, mitigation priority, and deprioritized area—applied to one documented landscape. Any region where paired SDM outputs are available can be similarly stratified, making the framework immediately actionable for conservation agencies operating across the Asian elephant's 13-country range and beyond (Nyhus 2016; Shaffer et al. 2019).

4.5 Key Contributions

The principal contributions of this work can be summarized as follows:

- **Conceptual**: First paired SDM comparison designed to explicitly quantify the divergence between fundamental environmental suitability and realized habitat availability for a megafauna species, operationalizing the fundamental–realized niche distinction as a spatially explicit management variable rather than a theoretical abstraction.

- **Methodological**: A dual-model framework that isolates the anthropogenic constraint surface on habitat suitability and is directly replicable across taxa, geographies, and spatial scales using standard SDM tools—requiring no specialized modeling expertise beyond what conservation practitioners already employ.
- **Empirical**: Demonstration that human–wildlife conflict concentrates in high-quality, not marginal, habitat—overturning the displacement assumption embedded in most conflict-management frameworks and establishing niche overlap in productive landscapes as the governing mechanism.
- **Applied**: A three-category conservation triage map (restoration target, mitigation priority, deprioritized area) derived directly from paired model outputs, providing an immediately actionable decision-support tool for conservation investment planning in any human-modified landscape.

4.6 Global Relevance and Transferability

The dual-model framework developed here is applicable to any large-bodied species for which occurrence data, anthropogenic predictor layers, and a management need to distinguish suitable from feasible habitat co-occur—a condition met across the full range of megafauna conservation globally. The fundamental–realized niche divergence documented in south-central Bhutan is likely to be more pronounced, not less, for species facing greater anthropogenic pressure: African savanna elephants navigating expanding agropastoral frontiers across sub-Saharan Africa, tigers in increasingly fragmented forest matrices across South and Southeast Asia, jaguars in agricultural mosaics across Latin America, and large herbivores across rangelands where pastoralism and infrastructure are rapidly intensifying (Ripple et al. 2015). In each of these systems, environment-only SDMs will overestimate available habitat and understate the urgency of anthropogenic barrier removal and conflict mitigation. This methodological limitation is not unique to any region; it is a property of applying environment-only models to species whose realized distributions are governed by human land use as much as by climatic and topographic gradients (Elith and Leathwick 2009; Guisan et al. 2017).

The practical barrier to wider adoption of this framework is low. The paired comparison requires only two standard SDM runs with different predictor sets, a raster difference operation, and a reclassification step—all implementable in standard conservation-software environments. It does not require specialized modeling expertise, new data collection, or institutional resources beyond what regional conservation agencies already deploy for single-model assessments. We argue that paired fundamental–realized SDM comparison should become a standard component of habitat assessments and protected-area planning for species of conservation concern in the Anthropocene, and that the three-category triage output it generates should be treated as a minimum standard for conservation investment prioritization in human-modified landscapes (Nyhus 2016; Guisan et al. 2017).

4.7 Study Limitations and Future Research

Several limitations bound the interpretation of these results and motivate specific directions for future research. First, as presence-only approaches, both MaxEnt implementations are subject to uncertainties associated with sampling bias and the absence of verified absence data (Yackulic et al. 2013). Spatial filtering and cross-validation improve robustness, but absolute suitability values should be treated as relative indices rather than precise probability estimates, particularly at fine spatial scales or in areas with uneven survey coverage. Second, the HEC dataset, while rigorously filtered, is restricted to documented incidents and likely underrepresents the true spatial extent of conflict, particularly for minor crop-damage events that go unreported; this under-representation may compress the estimated suitability–conflict relationship toward its lower bound. This limitation does not affect the framework's primary objective of quantifying anthropogenic constraint, but highlights the need for independent validation in future applications. Third, the analysis is spatially constrained to Bhutan owing to limited data availability from adjacent Assam, which may bias corridor assessments near the transboundary zone and prevent the full characterization of elephant movement across the political boundary.

These limitations suggest three priority directions for extending this work. First, GPS-telemetry data should be incorporated to validate model predictions against observed individual movement trajectories, providing an independent test of the fundamental–realized gap that does not depend on HEC proxy data. Second, ensemble-modeling frameworks would address algorithmic uncertainty by averaging predictions across multiple SDM algorithms, reducing dependence on MaxEnt-specific assumptions. Third, and most important for the framework's global claims, replication of the paired SDM design across multiple elephant-range countries—or across other megafauna systems—would establish empirical benchmarks for the magnitude of anthropogenic habitat degradation across varying land-use intensities, population densities, and institutional contexts, and test whether the conflict-in-prime-habitat pattern documented here is as general as the comparative evidence suggests. Future applications should evaluate model sensitivity to the inclusion of interaction proxies such as conflict data to further disentangle causal and correlative effects.

4.8 Global Lessons for Environmental Management

Five operational lessons for environmental management practice emerge from this analysis, each grounded in the study's findings and applicable beyond the Asian elephant system.

Lesson 1: Environment-only SDMs should not serve as the sole evidence base for habitat conservation planning in human-modified landscapes. They overestimate realized habitat availability by design, and when used uncritically as the primary planning input, they generate an inflated accounting of the area available for population recovery—directly undermining the credibility and achievability of biodiversity commitments.

Lesson 2: The gap between environmental suitability and realized occupancy is itself a primary management variable, not a modeling artefact to be corrected. The anthropogenic constraint surface quantifies where and by how much human activities prevent species from occupying environmentally suitable habitat. This quantity—rather than suitability alone—should anchor restoration investment decisions, because it identifies sites where habitat recovery is ecologically feasible and where the barrier to recovery is removable through management action.

Lesson 3: Human–wildlife conflict management programmes premised on the displacement assumption will be spatially misallocated. Where conflict concentrates in high-suitability habitat—as demonstrated here and corroborated by evidence from Peninsular Malaysia and Nepal—interventions designed for marginal-zone conflict dynamics will fail to address the structural niche overlap that drives incidents. Paired SDM outputs provide the evidential basis for distinguishing these two conflict types and targeting interventions accordingly.

Lesson 4: Ecologically suitable but anthropogenically constrained habitat demands a different policy response than intrinsically unsuitable habitat. The former warrants investment in barrier removal, corridor designation, and land-use transition incentives; the latter requires accepting that conservation objectives must be achieved elsewhere. Conflating the two—as environment-only SDMs require—leads simultaneously to over-investment in unrecoverable sites and under-investment in sites where modest barrier-mitigation expenditure would yield substantial habitat recovery.

Lesson 5: The framework is ready to deploy at scale. The paired SDM design requires no new data collection, no specialized analytical infrastructure, and no institutional capacity beyond what regional conservation agencies already deploy for conventional habitat assessment. The principal barrier to wider adoption is procedural: standard operating procedures for SDM-based environmental assessment must be updated to treat paired fundamental–realized comparison as a minimum requirement wherever model outputs inform protected-area designation, corridor planning, or infrastructure impact assessment.

5 Implications for Environmental Policy and Planning

5.1 Translating Model Outputs into Environmental Management Problems

The fundamental–realized habitat gap documented here represents not merely an ecological finding but a structural failure point in how environmental policies are designed, funded, and evaluated. When conservation agencies, spatial planners, and environmental assessment practitioners base decisions on environment-only SDM outputs—as current standard practice dictates—three categories of policy failure become predictable and, with this framework, preventable.

Misallocation of conservation resources. Investment directed at sites predicted to be suitable but functionally inaccessible due to anthropogenic barriers yields no population recovery outcome. The $\sim$10% reduction in highly suitable habitat and the $\sim$410 km^2 of degraded suitability identified in the Bhutan study landscape illustrate the scale at which this misallocation operates in a single national context; extrapolated across the 13-country range of the Asian elephant, the aggregate misallocation embedded in existing environment-only habitat assessments is substantial. The management-relevant output—the anthropogenic constraint surface—directly identifies which degraded sites are ecologically worth restoring versus which are unsuitable regardless of investment, enabling agencies to reallocate resources from the latter to the former.

Ineffective conflict mitigation. Conflict-management programmes designed around the displacement assumption allocate funding and infrastructure to marginal-zone interventions that do not address the structural source of conflict. Where conflict arises from niche overlap in productive landscapes—as demonstrated by the concentration of incidents at mean suitability 0.733, 3.7 times the landscape-wide mean—this mis-targeting represents a direct efficiency loss. Evidence-based conflict management requires identifying the shared-resource zones where conservation and livelihood pressures intersect, a spatial output the triage map provides.

Planning inefficiencies from SDM limitations. Corridor designs and protected-area expansion proposals built on environment-only suitability overestimate functional connectivity by failing to account for anthropogenic barriers. Infrastructure assessments that use environment-only baselines mischaracterize the ecological status of affected habitat. Both inefficiencies propagate through planning cycles that may span decades, compounding the cost of the initial modeling error.

5.2 Integration with Environmental Decision Systems

The decision-support outputs generated by the dual-model framework connect directly to four environmental planning and policy instruments that currently operate without the analytical precision this framework provides.

Land-use zoning and spatial planning. The three-category triage map constitutes a spatially explicit input for land-use zoning decisions. Restoration-target zones (high Ideal, low Full suitability) warrant designation as ecological restoration areas or wildlife-sensitive land-use categories, with restrictions on further agricultural conversion or infrastructure development. Mitigation-priority zones (high suitability in both models, active conflict) require integrated designations that accommodate both conservation objectives and the rural economies that generate conflict pressure—combining protection obligations with livelihood-support mechanisms in a single spatial planning unit. Lower-priority zones enable planners to defensibly concentrate megafauna-focused investment elsewhere without omitting areas whose environmental conditions do not support recovery. This three-way spatial differentiation is more information-rich than binary protection/non-protection zoning, and provides the specificity that national spatial planning processes require to meet quantitative biodiversity targets.

Protected area expansion and corridor design. National biodiversity strategies that identify priority areas for protected-area expansion or wildlife corridor designation currently rely predominantly on environment-only habitat models. Incorporating the anthropogenic constraint surface into these exercises prevents the designation of corridors in zones where barriers render functional connectivity unachievable without concurrent barrier-removal commitments. The 285.6 km^2 of degraded-but-ecologically-suitable habitat identified in the study landscape directly indicates where corridor designation, paired with binding barrier-mitigation obligations, would deliver measurable connectivity gain—and where, absent such obligations, designation would be an administrative exercise without ecological effect.

Environmental impact assessment. EIA frameworks for infrastructure projects in or adjacent to megafauna habitat assess impact against habitat baselines that, when based on environment-only SDMs, conflate occupied and excluded habitat. The dual-model constraint surface provides a more defensible baseline: it allows EIA practitioners to distinguish whether a proposed development affects habitat that is currently occupied and ecologically functional (high Full Model suitability) from habitat that is already anthropogenically degraded (low Full, high Ideal). This distinction has direct implications for the scale of mitigation required, the stringency of no-net-loss obligations, and the design of biodiversity offset packages under national and international environmental law.

National biodiversity strategies and action plans. Under the Kunming–Montreal Global Biodiversity Framework and national Biodiversity Strategy and Action Plans

(NBSAPs), countries are committed to protecting 30% of land area, restoring 30% of degraded ecosystems, and reducing human–wildlife conflict. The dual-model framework generates quantitative estimates directly relevant to each commitment: the triage map identifies which degraded areas are ecologically viable restoration candidates (because environmental suitability remains high), quantifies their extent, and maps where conflict mitigation must accompany protection to prevent wildlife losses from offsetting protection gains in shared landscapes. These outputs translate directly into the spatial prioritization annexes that NBSAP implementation plans require.

5.3 Five-Step Operational Workflow

The dual-model framework can be operationalized by any conservation agency with access to species occurrence records, standard environmental predictor layers (freely available from WorldClim, MODIS, and SRTM), and anthropogenic infrastructure and land-use datasets—inputs already assembled for most national biodiversity assessments. The implementation pathway proceeds through five steps.

1. **Generate the fundamental niche model (Ideal Model).** Train a standard SDM—MaxEnt or equivalent—using environmental predictors only (climate, topography, vegetation indices) to generate a continuous suitability surface representing conditions under which the target species could persist in the absence of anthropogenic modification.
2. **Generate the realized niche model (Full Model).** Train a second SDM using the same environmental predictors augmented with anthropogenic variables (road networks, settlement density, land use, conflict or mortality incident locations) to generate a suitability surface approximating the observed, human-constrained distribution.

3. **Construct the anthropogenic constraint surface.** Subtract the Full Model output from the Ideal Model output pixel-wise. Negative values (Ideal > Full) identify areas where human activities suppress realized suitability below environmental potential; the magnitude of the difference quantifies the degree of anthropogenic constraint at each location.
4. **Classify triage zones.** Reclassify the paired model outputs and constraint surface into three management-relevant categories: (a) *restoration targets*—high Ideal, low Full suitability—where environmental conditions are favorable but anthropogenic barriers suppress occupancy, and where targeted barrier-removal or land-use transition can recover functional habitat; (b) *mitigation priorities*—high suitability in both models, overlapping with documented conflict or mortality—where conservation and human welfare objectives compete for the same productive landscape, requiring simultaneous habitat protection and conflict-management investment; (c) *lower-priority zones*—low suitability in both models—where neither restoration nor conflict mitigation is the primary megafauna-focused imperative and scarce resources should be concentrated elsewhere.
5. **Allocate management interventions.** Use the triage map as a spatially explicit budget-allocation instrument. Restoration targets receive investment in barrier removal, wildlife crossing structures, corridor reforestation, and land-use transition incentives. Mitigation priorities receive investment in conflict early-warning systems, perimeter fencing, community-based rapid-response protocols, and compensation mechanisms. Lower-priority zones are monitored but not prioritized for active expenditure. The triage output can be overlaid directly with administrative boundaries, road networks, and community land maps to generate agency-level operational plans compatible with annual budgeting and multi-year strategic investment cycles.

This five-step workflow requires no software beyond the standard GIS and SDM platforms already used by regional conservation agencies, and no data inputs beyond those assembled for conventional single-model habitat assessments. It produces outputs that map directly onto the planning categories that environmental management agencies, spatial planners, and EIA practitioners already use—reducing the analytical distance between scientific outputs and management decisions.

5.4 Scalability and Applicability in Developing-Country Contexts

The framework has particular value in the institutional contexts where megafauna conservation is most urgent. In developing-country settings, where conservation agencies operate under severe resource constraints and cannot afford to direct investment toward sites that will not yield population recovery outcomes, the triage map's explicit differentiation of restorable from intrinsically unsuitable habitat is a direct efficiency gain that does not require increased funding—only more precise allocation of existing funding. The framework's dependence on freely available global environmental datasets (WorldClim, MODIS, SRTM, OpenStreetMap) and open-source analytical platforms (R, Python, QGIS) ensures it is accessible without proprietary software licenses or high computational infrastructure. In rapidly changing landscapes, where the boundary between suitable and anthropogenically constrained habitat shifts faster than conventional monitoring can track, the paired SDM design can be updated incrementally as new occurrence and conflict data accumulate, functioning as an adaptive planning tool that keeps pace with landscape change rather than providing a single static assessment.

At continental and range-wide scales, coordinated application of the framework across countries sharing megafauna populations—across the 13-country range of the Asian elephant, across transboundary landscapes of African savanna elephants, or across the contiguous forests of tiger range states—would generate comparable national estimates of anthropogenic habitat loss. Such estimates would enable international conservation bodies and bilateral agreements to prioritize transboundary cooperation investments where the constraint surface indicates that barrier removal would reconnect nationally fragmented populations, and to hold signatory countries accountable to measurable habitat feasibility metrics rather than nominal area-protection commitments.

6 Conclusion

The paired SDM framework developed here demonstrates that a fundamental–realized habitat gap exists wherever megafauna persist in human-modified landscapes, that this gap is quantifiable using standard modeling tools, and that the resulting anthropogenic constraint surface directly supports conservation investment decisions that environment-only models cannot inform. In south-central Bhutan, the comparison of Ideal and Full MaxEnt models showed that anthropogenic pressure has reduced highly suitable Asian elephant habitat by $\sim$10% ($\sim$57 km^2) and degraded suitability across a further $\sim$410 km^2—concentrated precisely in the productive lowland zones where infrastructure and agriculture intersect prime habitat. The Full Model's superior predictive performance (AUC = 0.896 vs. 0.848) confirms quantitatively that environment-only SDMs systematically misrepresent realized occupancy in human-dominated systems.

The finding that human–wildlife conflict incidents cluster in high-quality rather than marginal habitat—with mean suitability at conflict sites 3.7 times the landscape-wide mean—overturns the displacement assumption that underpins many conflict-management programmes and demands a reorientation of where, and how, proactive interventions are deployed. Conservation and human welfare imperatives do not compete at the landscape boundary; they overlap spatially in the same productive terrain, requiring integrated approaches that simultaneously protect core habitat, restore anthropogenically constrained corridors, and mitigate conflict in shared agricultural zones. The three-category triage logic derived from the paired outputs—restoration target, mitigation priority, deprioritized area—provides the spatial structure for making those choices efficiently.

These results are not findings about one country or one species. Across the ranges of African elephants, tigers, large herbivores, and other wide-ranging taxa, environment-only SDMs are generating the same systematic overestimation of accessible habitat and the same misdirection of conservation resources. Separating where species are environmentally able to live from where anthropogenic constraints prevent them from doing so is not a methodological refinement for specialists—it is the foundational step for any evidence-based conservation investment in the Anthropocene, and this framework makes that step accessible to the practitioners and agencies that need it most. This framework provides a defensible and scalable basis for conservation decision-making in human-dominated landscapes globally.

Acknowledgements. The author extends sincere gratitude to the Department of Forests and Park Services, Ministry of Energy and Natural Resources, Royal Government of Bhutan, for providing access to the National Elephant Survey datasets and technical support throughout the study.

Funding. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Competing Interests. The authors declare no competing financial or non-financial interests.

Ethics Approval and Consent to Participate. This research complied with all legal and institutional requirements of the Royal Government of Bhutan. Permissions for the use of Asian elephant occurrence data and human–elephant conflict records were granted by the Department of Forests and Park Services (DoFPS), Ministry of Energy and Natural Resources.

The study was based exclusively on observational records, camera-trap data, and archival administrative datasets; no animals were captured, handled, or experimentally manipulated at any stage. Human–elephant conflict records were anonymized prior to analysis to safeguard the privacy and security of affected households. Institutional animal ethics committee approval was not required because the research involved no direct interaction with wildlife.

Data Availability. Data and code supporting this study will be made available in a public repository upon acceptance, with anonymized access provided during peer review. Bioclimatic and elevation layers were sourced from WorldClim version 2.1.

Author Contributions. Wangdi Wangdi: Conceptualization, Methodology, Formal analysis, Data curation, Visualization, Software, Investigation, Writing – original draft. Tshering Dorji: Data collection, Field investigation, Resources, Validation. Jigme Tenzin: Project administration, Supervision, Writing – review and editing. Tashi Choden: Data collection, Field investigation, Resources, Writing – review and editing.

Declaration of Generative AI Use. During the preparation of this manuscript, the authors used large-language-model tools to assist with language editing and code development. All scientific interpretation, analysis, and final text were produced by the authors. The authors reviewed and edited all AI-assisted outputs and take full responsibility for the accuracy, originality, and integrity of the published work.

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Table 1 Model performance metrics for MaxEnt habitat-suitability models predicting Asian elephant distribution 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 based on permutation importance from MaxEnt models 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 Temp)	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 Precip)	0.001

Table 3 Area (km^2) by habitat-suitability class under Ideal and Full MaxEnt models for Asian elephants in south-central Bhutan. Suitability thresholds represent predicted probability of occurrence. Areas were calculated from 300-m resolution raster outputs clipped to the study extent (n = 256,410 pixels).

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

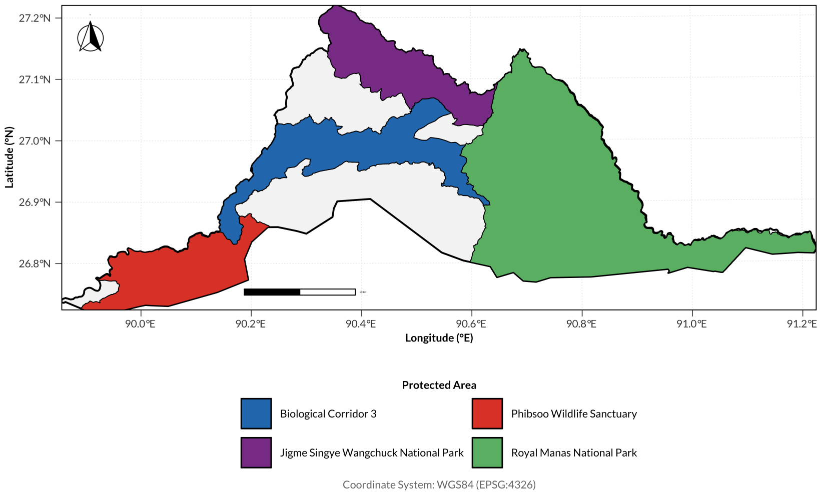

Fig. 1 Study area in south-central Bhutan showing the spatial configuration of Royal Manas National Park, Phibsoo Wildlife Sanctuary, Biological Corridor 03, and surrounding human-modified landscapes. The region spans a gradient from protected lowland forests to agricultural frontiers along the Bhutan–India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

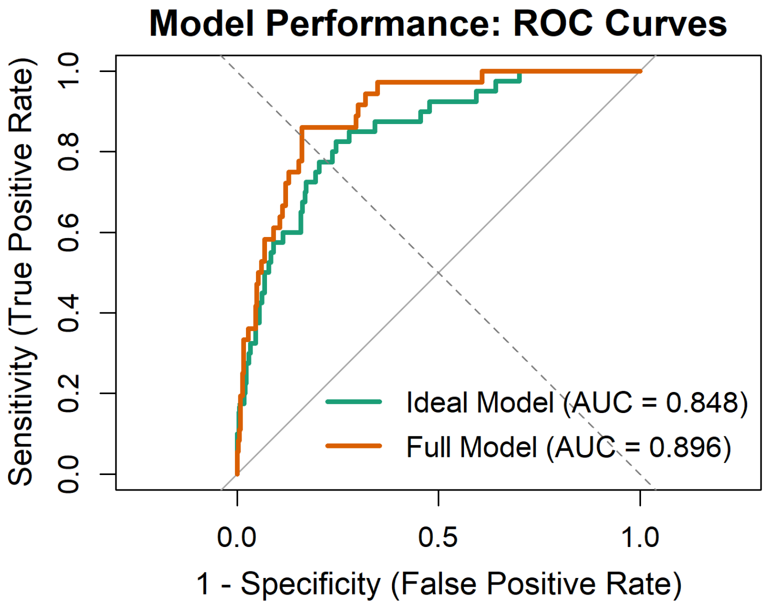

Fig. 2 Receiver operating characteristic (ROC) curves comparing the Ideal Model (environment-only predictors) and Full Model (environment plus anthropogenic predictors). The Full Model's steeper curve and higher AUC (0.896 vs. 0.848) demonstrate that incorporating anthropogenic variables substantially improves prediction of realized elephant distribution.

Table 4 Area (km^2) in each suitability class under Ideal and Full scenarios derived from classified MaxEnt predictions. Areas were derived from classified MaxEnt predictions at 300-m resolution (n = 256,410 pixels).

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

[1]Totals differ slightly from the sum of classes due to rounding.

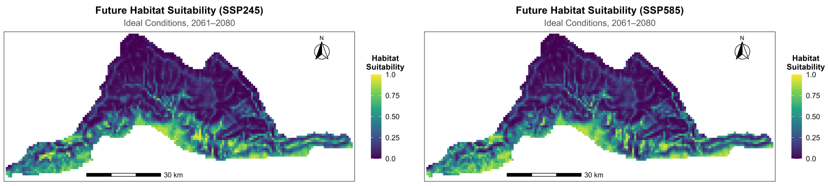

Fig. 3 Anthropogenic constraint on realized habitat: paired suitability maps from the Full Model (observed system, left) and Ideal Model (counterfactual without human pressure, right). Discordance between panels—high suitability in the Ideal Model but reduced suitability in the Full Model—delineates ecologically suitable habitat rendered functionally inaccessible by human activities. Warmer colours indicate higher predicted suitability. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

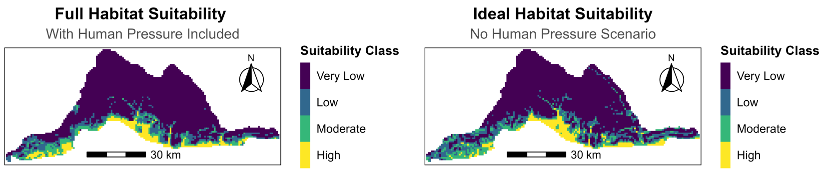

Fig. 4 Classified habitat-suitability maps illustrating the net categorical downgrading of habitat quality from Ideal (right) to Full (left) model predictions. Net expansion of the Very Low suitability class and contraction of Low and Moderate classes quantify the aggregate loss in habitat quality attributable to anthropogenic pressure across the landscape. Suitability classes: Very Low, Low, Moderate, and High. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

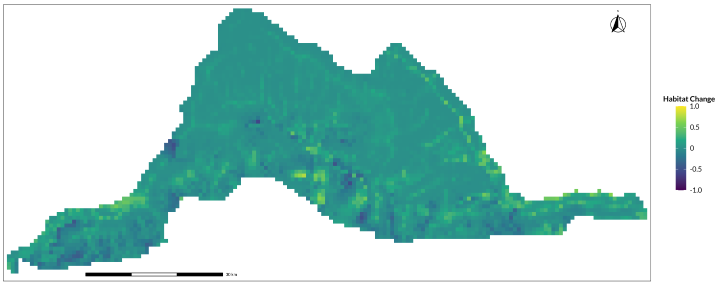

Fig. 5 Spatial patterns of anthropogenic habitat degradation, showing the difference between Ideal and Full model suitability predictions. Warmer colours indicate greater suitability loss attributable to human activities; degradation is concentrated in productive lowland valleys and foothill zones where agricultural expansion and infrastructure development intersect prime elephant habitat. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

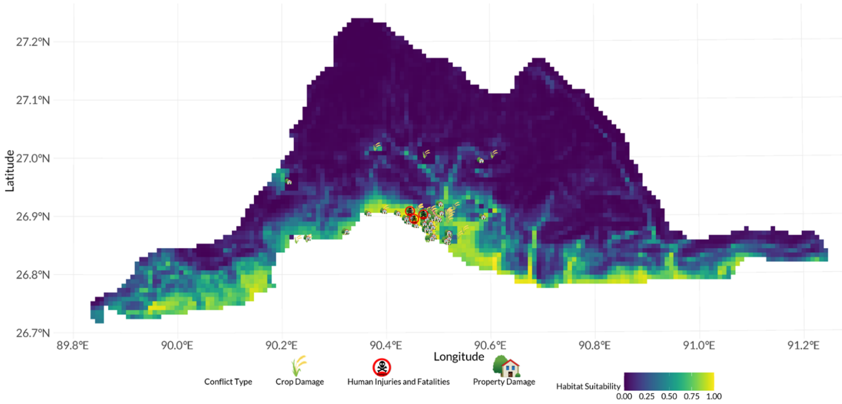

Fig. 6 Human–elephant conflict (HEC) incidents overlaid on Full Model habitat suitability, demonstrating that conflict concentrates in high-quality rather than marginal habitat. Mean suitability at conflict sites (0.733) exceeds the landscape-wide mean (0.197) by 3.7-fold, indicating that communities most exposed to conflict reside within landscapes of greatest ecological importance for *E. maximus*. Points indicate conflict locations categorized by event type. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

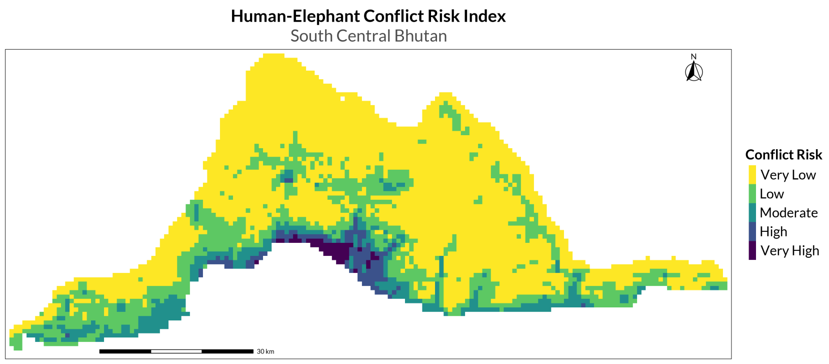

Fig. 7 Composite conflict-risk map integrating habitat suitability (40%), historical conflict density (30%), proximity to settlements (20%), and road accessibility (10%) into five ordinal risk classes. This spatial triage tool identifies where conservation investment should be concentrated to simultaneously protect high-value elephant habitat and reduce conflict exposure for local communities. Map lines delineate study areas and do not necessarily depict accepted national boundaries.