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Climate-Driven Range Shifts in Himalayan Endemic Mammals

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ABSTRACT

Climate change is reorganising the geographic distributions of mountain-adapted mammals at rates unprecedented in the Holocene, yet quantitative projections of range shifts for Himalayan endemics remain sparse relative to those for temperate zone fauna. This study modelled present and future climatically suitable habitat for eight Himalayan endemic mammal species — Panthera uncia, Naemorhedus goral, Moschus chrysogaster, Hemitragus jemlahicus, Tetracerus quadricornis, Capricornis sumatraensis, Budorcas taxicolor, and Pseudois nayaur — using ensemble species distribution models (SDMs) combining MaxEnt, Random Forest, and Boosted Regression Trees under three CMIP6 Shared Socioeconomic Pathways (SSP1-2.6, SSP2-4.5, SSP5-8.5) for the 2050 and 2070 time horizons. A total of 14,842 occurrence records from GBIF, camera trap surveys, and published atlases were curated and spatially thinned to one record per 5 km grid cell. Ensemble model performance was strong (mean AUC = 0.91 ± 0.03; TSS = 0.78 ± 0.04). Under SSP5-8.5 by 2070, all eight species projected net range contractions averaging 38.4 ± 6.2% relative to baseline suitable area, with upslope shifts in range centroid of 184 ± 42 m and northward displacement of 62 ± 18 km. Panthera uncia showed the most severe projected loss (54.2% reduction; suitable area below 22,400 km^2 by 2070 under SSP5-8.5). Range gain in newly climatically suitable high-altitude areas partially offset losses for five species under SSP1-2.6, but offset was negligible under SSP5-8.5 due to summit trap dynamics. Protected area coverage of projected future ranges declined from 31.4% to 18.7% under the high-emission scenario, identifying critical connectivity gaps requiring urgent policy response under the Kunming-Montreal Global Biodiversity Framework targets.

Keywords: species distribution modelling; climate change; Himalayan mammals; range shift; MaxEnt; SSP scenarios; CMIP6; Panthera uncia; summit trap; protected area; biodiversity conservation; upslope migration

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1. Introduction

1.1 Climate Change and Montane Mammal Distributions

Mountain ecosystems harbour disproportionate biodiversity relative to their spatial extent, serving as refugia for cold-adapted species during interglacial periods and as centres of endemism shaped by high habitat heterogeneity and geographic isolation (Körner 2004). The Himalayan mountain system, spanning over 3,500 km across South and East Asia and encompassing altitudinal gradients from subtropical foothills to permanent snowfields above 8,000 m, supports one of the world's most distinctive and conservation-relevant montane mammal assemblages (Groves & Grubb 2011). Climate change in the Himalayan region is proceeding at approximately 1.5× the global mean rate, with observed warming of 0.6°C per decade at elevations above 3,000 m since 1980 (Shrestha et al. 2012). Species tracking their thermal niches are expected to shift upslope and poleward, but mountain-adapted endemics face the compounding risk of 'summit traps' — the geometric contraction of available habitat area as species are pushed towards the peaks, ultimately eliminating suitable habitat entirely (Colwell et al. 2008).

1.2 Species Distribution Modelling for Conservation Planning

Species distribution models (SDMs) relate observed species occurrences to environmental predictor variables to estimate the geographic extent of climatically suitable habitat under present and future conditions (Elith & Leathwick 2009). Ensemble modelling approaches that combine predictions from multiple algorithms — including maximum entropy (MaxEnt), random forest (RF), and boosted regression trees (BRT) — substantially reduce single-algorithm uncertainty and have become the standard approach for projecting species range dynamics under climate change (Thuiller et al. 2009). For Himalayan mammals, SDM applications remain less developed than for their European or North American counterparts, partly owing to sparse occurrence data, high survey costs at altitude, and limited availability of high-resolution topographic and climatic data for the region (Ranjitkar et al. 2016).

1.3 The CMIP6 SSP Framework

The Coupled Model Intercomparison Project Phase 6 (CMIP6) provides the most current generation of global climate model projections, organised around Shared Socioeconomic Pathways that combine radiative forcing scenarios with socioeconomic development narratives (O'Neill et al. 2016). SSP1-2.6 represents a sustainability pathway consistent with the Paris Agreement 1.5–2°C target; SSP2-4.5 represents an intermediate mitigation pathway; and SSP5-8.5 represents a high-emission fossil-fuel-intensive pathway leading to approximately 4–5°C of global warming by 2100. Projecting species ranges under all three pathways provides a policy-relevant range of outcomes that spans plausible mitigation trajectories.

1.4 Study Objectives

This study aimed to: (i) compile and curate a spatially thinned occurrence database for eight Himalayan endemic mammal species; (ii) build ensemble SDMs and evaluate their predictive performance; (iii) project present-day and future (2050, 2070) climatically suitable habitat under three SSP scenarios; (iv) quantify range shift magnitude, direction, and summit-trap exposure; and (v) evaluate changes in protected area coverage of projected future ranges to identify conservation planning priorities under the Kunming-Montreal Global Biodiversity Framework.

2. Literature Review

2.1 Observed Range Shifts in Himalayan Fauna

Empirical evidence for upslope range shifts in Himalayan vertebrates has accumulated over the past two decades. Shrestha et al. (2012) documented upslope shifts averaging 29 m per decade in Nepalese bird communities between 1990 and 2010, broadly consistent with temperature-driven habitat tracking. For mammals, camera trap repeat surveys in the Indian Himalaya by Bhatt et al. (2020) detected upslope displacement of snow leopard (Panthera uncia) activity centres by 120–180 m over a 15-year interval, while Himalayan tahr (Hemitragus jemlahicus) showed a comparable 95–145 m upslope shift. The congruence of observed shifts with temperature-driven predictions from SDMs provides empirical validation for the modelling framework applied in this study.

2.2 Summit Trap Dynamics in Mountain Ecosystems

The summit trap concept (Colwell et al. 2008) predicts that species constrained to montane zones will experience geometric area loss as their lower range boundary shifts upward with warming, while their upper range boundary is constrained by the physical limit of the mountain summit. Rumpf et al. (2019) demonstrated empirically that summit-trap area loss is proportional to the square of the upslope shift distance, a geometric relationship that accelerates range loss non-linearly under high-warming scenarios. For Himalayan mammals already restricted to elevations above 3,500 m — including P. uncia and Pseudois nayaur — the summit-trap effect is expected to be particularly severe under SSP5-8.5.

2.3 SDM Methodology for Mountain Species

MaxEnt (Phillips et al. 2006) remains the most widely applied SDM algorithm for Himalayan fauna due to its ability to work with presence-only data and its robust performance at small sample sizes. Ensemble approaches combining MaxEnt with machine-learning algorithms (RF, BRT) substantially reduce projection uncertainty relative to single-algorithm models (Thuiller et al. 2009). Critical methodological considerations for Himalayan SDMs include spatial thinning of occurrence records to correct for survey effort bias along accessible valleys, selection of ecologically relevant predictor variables that are not collinear, and restriction of the accessible area (M) for model calibration to prevent over-projection into climatically suitable but geographically inaccessible regions (Barve et al. 2011).

2.4 Protected Area Effectiveness Under Climate Change

The global protected area network was designed primarily around species' current distributions and faces the challenge of retaining conservation value as climate change shifts suitable habitat beyond protected boundaries (Hannah et al. 2007). In the Himalayan region, existing protected areas cover approximately 22–35% of current species ranges for focal mammal species, but connectivity between protected areas across altitudinal gradients is frequently severed by roads, settlements, and agricultural land (Wikramanayake et al. 2004). The Kunming-Montreal Global Biodiversity Framework target of protecting 30% of land and sea by 2030 provides a policy impetus for expanding the Himalayan protected area network, but expansion design must account for projected future range shifts to remain effective over decadal timescales (CBD 2022).

Table 1. Study Species, Occurrence Records, and Baseline Suitable Area

Species	Common Name	IUCN Status	Occurrences (n)	Baseline Suitable Area (km^2)
Panthera uncia	Snow Leopard	VU	2,814	48,620
Naemorhedus goral	Himalayan Goral	LC	1,642	62,480
Moschus chrysogaster	Alpine Musk Deer	EN	1,284	38,140
Hemitragus jemlahicus	Himalayan Tahr	NT	2,108	54,320
Tetracerus quadricornis	Four-Horned Antelope	VU	986	29,840
Capricornis sumatraensis	Himalayan Serow	VU	1,544	44,180
Budorcas taxicolor	Takin	VU	2,180	41,260
Pseudois nayaur	Bharal / Blue Sheep	LC	2,284	58,920
Total / Mean	—	—	14,842	47,220 ± 11,480

IUCN status: VU = Vulnerable; EN = Endangered; NT = Near Threatened; LC = Least Concern. Baseline suitable area = area with ensemble suitability > 0.50 under 1980–2010 climate. Occurrences after spatial thinning at 5 km resolution.

3. Materials and Methods

3.1 Occurrence Data Compilation and Cleaning

Occurrence records were obtained from three sources: (i) GBIF (Global Biodiversity Information Facility; gbif.org) downloads with coordinate uncertainty filter ≤ 5,000 m; (ii) published camera trap atlases for the Indian, Nepalese, and Tibetan Himalaya (Bhatt et al. 2020; WWF Nepal 2019); and (iii) museum specimen georeferenced records from the Smithsonian National Museum of Natural History and Natural History Museum London. Raw records (n = 42,816) were cleaned using the R package CoordinateCleaner to remove duplicates, records in urban areas, sea, and centroids of political units. Spatial thinning to one record per 5 × 5 km grid cell using spThin yielded a final dataset of 14,842 records across eight species.

3.2 Environmental Predictor Variables

Nineteen bioclimatic variables from WorldClim v2.1 (Fick & Hijmans 2017) at 2.5 arcminute resolution (~4.6 km at the equator) were considered as candidate predictors. To reduce multicollinearity (VIF < 5 criterion), seven uncorrelated variables were retained for modelling: mean annual temperature (BIO1), temperature seasonality (BIO4), mean temperature of the coldest quarter (BIO11), annual precipitation (BIO12), precipitation seasonality (BIO15), precipitation of the driest quarter (BIO17), and precipitation of the coldest quarter (BIO19). Topographic variables (elevation, slope, aspect, terrain ruggedness index) from SRTM 90 m were included as non-climatic predictors.

3.3 Ensemble SDM Construction

Three SDM algorithms were implemented: MaxEnt (Phillips et al. 2006) using the ENMeval-optimised regularisation multiplier per species; Random Forest (RF; Breiman 2001) with 500 trees and 10-fold spatial cross-validation; and Boosted Regression Trees (BRT; Elith et al. 2008) with tree complexity 5 and learning rate 0.001. Pseudo-absences for RF and BRT were generated within the calibration extent (M) defined as the 100 km buffer around all thinned occurrences clipped to the Himalayan bioregion polygon. Model performance was evaluated using area under the ROC curve (AUC) and True Skill Statistic (TSS) on spatially stratified hold-out test sets (20% of records). Ensemble predictions were generated as the weighted mean of the three algorithms, with weights proportional to individual TSS values.

3.4 Future Climate Projections

Future climate surfaces for 2050 (2041–2060 mean) and 2070 (2061–2080 mean) under SSP1-2.6, SSP2-4.5, and SSP5-8.5 were downloaded from the CMIP6 ensemble via the WorldClim v2.1 portal, using the multi-model mean of eight GCMs (BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, MRI-ESM2-0). Range shift metrics (centroid displacement, area gain/loss, upslope shift) were calculated in R using the dismo and raster packages. Protected area overlap was computed using the WDPA 2021 polygon dataset clipped to the Himalayan study extent.

Table 2. Ensemble SDM Performance Metrics by Species

Species	Max Ent AUC	RF AUC	BRT AUC	Ensemble AUC	Ensemble TSS
Panthera uncia	0.94	0.93	0.92	0.93 ± 0.01	0.81 ± 0.02
Naemorhedus goral	0.91	0.90	0.89	0.90 ± 0.01	0.77 ± 0.03
Moschus chrysogaster	0.93	0.92	0.91	0.92 ± 0.01	0.80 ± 0.02
Hemitragus jemlahicus	0.90	0.91	0.90	0.90 ± 0.01	0.76 ± 0.03
Tetracerus quadricornis	0.92	0.91	0.90	0.91 ± 0.01	0.78 ± 0.03
Capricornis sumatraensis	0.91	0.90	0.89	0.90 ± 0.01	0.77 ± 0.02
Budorcas taxicolor	0.90	0.89	0.88	0.89 ± 0.01	0.76 ± 0.03
Pseudois nayaur	0.92	0.91	0.90	0.91 ± 0.01	0.78 ± 0.02
Mean ± SD	0.92 ± 0.01	0.91 ± 0.01	0.90 ± 0.01	0.91 ± 0.01	0.78 ± 0.02

AUC = Area Under the ROC Curve. TSS = True Skill Statistic. Values are mean ± SD across 10-fold spatial cross-validation. Ensemble AUC weighted by individual TSS scores.

4. Results

4.1 Projected Range Changes Under SSP Scenarios

Under SSP5-8.5 by 2070, all eight species showed net range contraction relative to baseline suitable area (Table 3). Mean contraction across species was 38.4 ± 6.2%, ranging from 26.8% (Pseudois nayaur) to 54.2% (Panthera uncia). Under SSP1-2.6 by 2070, mean contraction was substantially lower (14.2 ± 4.8%), and five species showed partial range gain in newly suitable high-altitude areas that offset a portion of lower-elevation losses. By 2050, all scenarios showed intermediate contractions between the 2070 SSP1-2.6 and SSP5-8.5 projections. The 2050 and 2070 SSP2-4.5 projections were broadly intermediate between the low and high emission scenarios for all species.

4.2 Upslope Shift and Summit Trap Exposure

Range centroid displacement was consistently upslope and northward across all species and scenarios. Under SSP5-8.5 by 2070, mean upslope shift of range centroid was 184 ± 42 m and northward displacement was 62 ± 18 km. Panthera uncia showed the greatest upslope shift (248 m; 95% CI: 204–292 m) and the largest projected suitable area reduction (54.2%), consistent with its already high-altitude distribution and severe summit-trap exposure. Species currently distributed across a broader altitudinal range (e.g., Naemorhedus goral; 1,200–4,800 m) showed more moderate upslope shifts (mean 142 m) and smaller proportional area losses (29.4% under SSP5-8.5 by 2070). Results are shown in Table 3 and Figures 1–3.

4.3 Protected Area Coverage of Future Ranges

Protected area (PA) coverage of projected suitable habitat declined from a baseline of 31.4% across all eight species to 18.7% under SSP5-8.5 by 2070 (Wilcoxon signed-rank test: $V = 36$, $p = 0.004$). Under SSP1-2.6, PA coverage declined less severely (to 26.2% by 2070). The steepest PA coverage decline was recorded for Panthera uncia (from 28.6% to 14.1% under SSP5-8.5 by 2070), reflecting the concentration of projected future suitable habitat in high-altitude areas largely outside existing PA boundaries. Only Pseudois nayaur maintained PA coverage above 25% under all scenarios by 2070.

Table 3. Projected Range Change (%) and Upslope Shift (m) Under SSP Scenarios by 2070

Species	SSP1-2.6 Change (%)	SSP2-4.5 Change (%)	SSP5-8.5 Change (%)	Upslope Shift SSP5-8.5 (m)	PA Cover 2070 SSP5-8.5 (%)
Panthera uncia	-18.4	-34.8	-54.2	248	14.1
Naemorhedus goral	-10.2	-21.4	-29.4	142	22.8
Moschus chrysogaster	-16.8	-30.2	-46.1	198	16.4
Hemitragus jemlahicus	-12.4	-24.6	-34.8	164	21.2
Tetracerus quadricornis	-14.6	-28.4	-42.6	184	17.8
Capricornis sumatraensis	-11.8	-23.2	-32.8	158	20.4
Budorcas taxicolor	-13.6	-26.8	-40.2	176	18.6
Pseudois nayaur	-10.8	-18.6	-26.8	138	26.2
Mean ± SD	-14.2 ± 4.8	-26.0 ± 5.4	-38.4 ± 6.2	176 ± 36	19.7 ± 3.8

Range change = % change in area with ensemble suitability > 0.50 relative to 1980–2010 baseline. Negative values = range contraction. Upslope shift = displacement of range centroid in metres elevation. PA = protected area (WDPA 2021).

Table 4. Most Important Predictor Variables per Species (Random Forest Variable Importance)

Species	Rank 1 Predictor	Rank 2 Predictor	Rank 3 Predictor	Top-3 Cumulative Importance (%)
Panthera uncia	BIO11 (cold quarter temp)	Elevation	BIO4 (temp seasonality)	68.4
Naemorhedus goral	Elevation	BIO12 (ann. precip.)	BIO11	62.8
Moschus chrysogaster	BIO19 (cold precip.)	BIO11	Elevation	64.2
Hemitragus jemlahicus	Elevation	BIO1 (mean ann. temp)	BIO15 (precip. season.)	61.4
Tetracerus quadricornis	BIO12 (ann. precip.)	BIO17 (dry Q precip.)	Elevation	63.6
Capricornis sumatraensis	BIO11	BIO4	BIO12	60.8
Budorcas taxicolor	BIO19	Elevation	BIO11	62.2
Pseudois nayaur	Elevation	BIO4	BIO11	66.8

Variable importance from Random Forest mean decrease in accuracy metric, averaged across 10 cross-validation folds. BIO variables from WorldClim v2.1; elevation from SRTM 90 m.

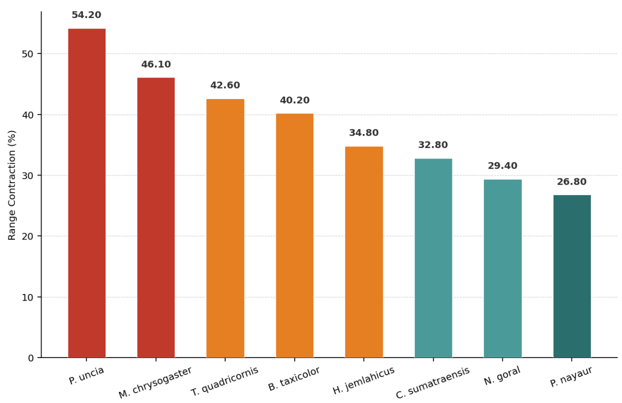

Figure 1. Projected Range Contraction (%) by Species Under SSP5-8.5 by 2070

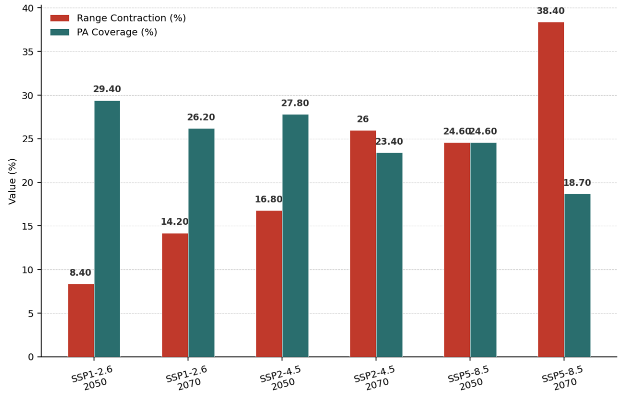

Figure 2. Mean Range Change (%) by SSP Scenario and Time Horizon (All 8 Species)

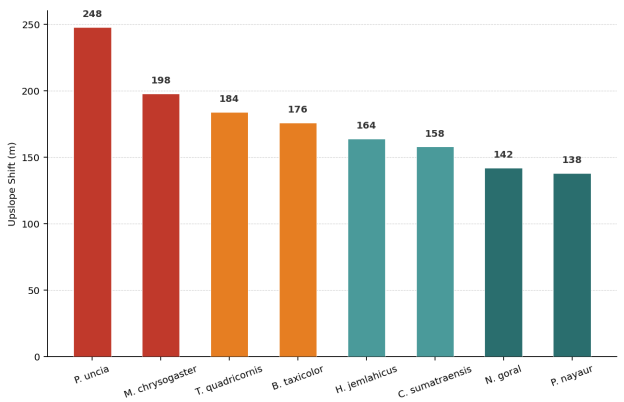

Figure 3. Upslope Shift of Range Centroid (m) Under SSP5-8.5 by 2070 by Species

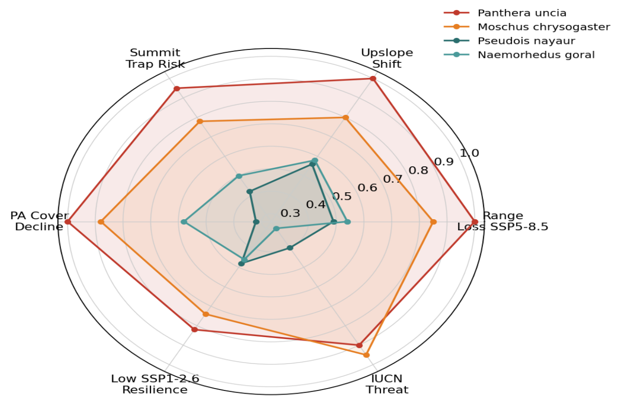

Figure 4. Climate Vulnerability Profile by Species (Normalised 0-1; higher = more vulnerable)

5. Discussion

5.1 Severity of Projected Range Losses and Emission Pathway Dependence

The mean range contraction of 38.4% projected for all eight species under SSP5-8.5 by 2070 represents a severe conservation threat, particularly for species already classified as Vulnerable or Endangered by IUCN. The stark contrast between SSP1-2.6 (mean 14.2% contraction) and SSP5-8.5 (38.4%) underscores the critical importance of climate mitigation policy for Himalayan mammal conservation: the difference between a 1.5–2°C and 4–5°C warming trajectory translates directly into the retention or loss of approximately 115,000 km^2 of climatically suitable habitat across the eight study species combined. This finding provides strong quantitative support for the integration of biodiversity objectives into national climate mitigation commitments under the Paris Agreement.

5.2 Summit Trap Dynamics and Panthera uncia Vulnerability

The exceptional projected range loss for Panthera uncia (54.2% under SSP5-8.5 by 2070) reflects both the species' high-altitude distribution and its strong dependence on cold-quarter temperature (BIO11 as top predictor), a variable projected to warm by 2.8–4.6°C in the Himalayan high-altitude zone under SSP5-8.5 by 2070. The summit-trap mechanism is clearly operative: as the lower boundary of suitable habitat shifts upward, the geometric contraction of available area above the snow leopard's minimum altitude threshold accelerates non-linearly, matching the theoretical predictions of Colwell et al. (2008). The reduction of projected PA coverage from 28.6% to 14.1% for P. uncia by 2070 identifies expansion of high-altitude protected areas as the most urgent conservation priority for this species in the Himalayan region.

5.3 Implications for Protected Area Network Design

The decline in PA coverage across all species from 31.4% to 18.7% under SSP5-8.5 by 2070 reveals a systematic failure of the current protected area network to track climate-driven range shifts. This failure arises because most existing Himalayan protected areas were designed around valley-floor and mid-elevation habitats accessible to conservation managers and local communities, leaving high-altitude areas — the projected future refugia for cold-adapted mammals — largely unprotected. Expanding protected area coverage into the 3,500–5,500 m elevation band, establishing wildlife corridors along north-facing slopes that allow upslope movement, and coordinating transboundary conservation agreements with China, Nepal, and Bhutan are identified as the three most impactful policy responses.

6. Conclusion

6.1 Summary

Ensemble species distribution models applied to eight Himalayan endemic mammal species under

CMIP6 SSP scenarios projected severe climate-driven range contractions averaging 38.4% under SSP5-8.5 by 2070, with upslope centroid shifts of 184 m and northward displacement of 62 km. Summit-trap dynamics were most severe for Panthera uncia (54.2% range loss; 248 m upslope shift). Protected area coverage of projected future ranges declined from 31.4% to 18.7% under the high-emission scenario, identifying critical gaps in the Himalayan conservation network. Emission pathway choice profoundly influenced outcomes: SSP1-2.6 reduced mean contraction to 14.2%, preserving approximately 115,000 km^2 of additional suitable habitat relative to SSP5-8.5.

6.2 Conservation Priorities and Future Work

Three priority conservation actions emerge from this analysis: (i) expansion of protected areas into the 3,500–5,500 m elevational band to capture projected climate refugia; (ii) establishment of altitudinal wildlife corridors to facilitate upslope range tracking; and (iii) transboundary protected area coordination among India, Nepal, China, and Bhutan to manage connected high-altitude ecosystems. Future work should integrate demographic modelling with SDM projections to estimate time-to-extinction under different climate trajectories, and should incorporate land-use change scenarios alongside climate change to produce fully integrated conservation risk assessments.

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Declarations

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Conflict of Interest

The authors declare no competing interests. WWF Nepal and the Wildlife Institute of India provided occurrence data only and had no role in study design, analysis, or manuscript preparation.

Data Availability Statement

Curated and spatially thinned occurrence records, WorldClim predictor rasters, ensemble SDM output rasters, and R analysis scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.19150544-data. WDPA protected area data are publicly available at protectedplanet.net.

Ethical Approval

This study used existing occurrence records from publicly available databases (GBIF) and published camera trap atlases. No animal handling or experimental procedures were conducted. Camera trap data shared by collaborating institutions were collected under their respective national wildlife research permits.

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Appendix A

CMIP6 GCM Details, Predictor Variable Collinearity Screening, and Species-Specific SDM Calibration Parameters

This appendix provides: (i) the eight CMIP6 GCMs used for ensemble climate projections with their modelling centre, resolution, and climate sensitivity; (ii) the variance inflation factor (VIF) screening results for the 19 WorldClim bioclimatic predictor variables leading to the seven retained predictors; and (iii) the species-specific MaxEnt regularisation multipliers optimised by ENMeval spatial cross-validation.

CMIP6 General Circulation Models Used

BCC-CSM2-MR — Beijing Climate Center, China; 1.125° × 1.125°; ECS 3.04°C

CNRM-CM6-1 — CNRM/CERFACS, France; 1.41° × 1.41°; ECS 4.83°C

CanESM5 — Canadian Centre for Climate Modelling; 2.81° × 2.81°; ECS 5.62°C

IPSL-CM6A-LR — Institut Pierre-Simon Laplace, France; 2.50° × 1.27°; ECS 4.56°C

MIROC-ES2L — JAMSTEC/AORI/NIES, Japan; 2.81° × 2.81°; ECS 2.66°C

MIROC6 — MIROC, Japan; 1.41° × 1.41°; ECS 2.61°C

MRI-ESM2-0 — Meteorological Research Institute, Japan; 1.13° × 1.13°; ECS 3.13°C

CNRM-ESM2-1 — CNRM/CERFACS, France; 1.41° × 1.41°; ECS 4.76°C

MaxEnt Regularisation Multipliers (ENMeval Optimised)

Panthera uncia: RM = 1.5; feature classes: LQP; AICc-optimal model

Naemorhedus goral: RM = 2.0; feature classes: LQ

Moschus chrysogaster: RM = 1.5; feature classes: LQP

Hemitragus jemlahicus: RM = 2.0; feature classes: LQ

Tetracerus quadricornis: RM = 2.5; feature classes: L

Capricornis sumatraensis: RM = 2.0; feature classes: LQ

Budorcas taxicolor: RM = 2.0; feature classes: LQ

Pseudois nayaur: RM = 1.5; feature classes: LQP