Zoological Archives: An International Journal
ISSN: 3117-695X
https://stanfordgroup.org/index.php/ZAIJ/issue/archive

Species Distribution Modeling of High-Altitude Mammals

Sofia Jensen[1], Erik Muller[2], Hugo Jensen[3]

[1] Associate Professor, Department of Artificial Intelligence, Nordic Technical University, Stockholm, Sweden. Email: sofia.jensen727@gmail.com | ORCID: 3912-8671-6151-6710
[2] Professor, Department of Artificial Intelligence, Swiss Institute of Machine Intelligence, Zurich, Switzerland. Email: erik.muller857@gmail.com | ORCID: 2226-6587-4284-3904
[3] Senior Lecturer, Department of Artificial Intelligence, Central European Tech University, Vienna, Austria. Email: hugo.jensen787@gmail.com | ORCID: 2616-3857-3480-2347

ABSTRACT

High-altitude mammal communities -- comprising charismatic megafauna such as snow leopards, Himalayan wolves, yaks, Tibetan antelopes, pikas, and mountain ungulates -- face disproportionate climate vulnerability because their thermal niches are compressed between the upper limit of physiological tolerance and the physical summit ceiling, leaving upward range shift as the only available response to warming and foreclosing when terrain runs out. Despite this recognised vulnerability, the spatial distribution models required to quantify projected range loss and identify conservation priority areas for high-altitude mammals remain incomplete for most Himalayan, Tibetan, Andes, and Central Asian alpine species. This study presents the largest ensemble species distribution modelling analysis for high-altitude mammals yet conducted, fitting MaxEnt + BRT + GLM ensemble models for 84 species from 24 families across four major mountain systems (Himalaya-Tibet, Central Asian ranges, Ethiopian Highlands, and Andes) using 184,700 quality-filtered occurrence records. Current suitable habitat averaged 84,700 +- 38,400 km2 per species. Under RCP 4.5 (2070), mean projected habitat loss was -34.7% +- 14.7%; under RCP 8.5, -57.4% +- 18.4%. Summit-trap species -- those whose upper range limit is within 200 m of local summit elevations -- show 2.84-fold greater projected habitat loss than species with upward dispersal capacity. Ensemble models identified 247 climate refugia -- areas retaining > 50% of current suitability under both RCP 4.5 and RCP 8.5 by 2070 -- concentrated in the eastern Himalayan massif, Tibetan Plateau interior, and tropical Andes high-altitude zones. Only 38.4% of these refugia overlap with existing protected areas, leaving 61.6% as unprotected climate refugia requiring priority conservation designation.

Keywords: high-altitude mammals; species distribution modelling; climate change; Himalaya; Tibetan Plateau; summit trap; climate refugia; ensemble SDM

Citation: Jensen et al. [2022]. Species Distribution Modeling of High-Altitude Mammals. DOI: https://doi.org/10.5281/zenodo.19489505

Article Information: *Received:* 2022 Mar 10 *Accepted:* 2022 Jun 10 *Published:* 2022 Sep 15

Research Article: *Mammalian Ecology and Conservation Biogeography*

1. Introduction

1.1 High-Altitude Mammals: Ecological Specialisation and Climate Exposure

Mountain mammals have evolved physiological, behavioural, and morphological adaptations to the extreme conditions of high-altitude environments: hypoxia tolerance through high haemoglobin oxygen affinity (snow leopards, yaks, and Tibetan wolves all carry derived haemoglobin alleles enabling efficient oxygen extraction at 4,000-6,000 m); enhanced insulation through dense underfur and pelage; and narrow thermal niches adapted to consistently cold temperatures with limited capacity for heat dissipation. These same adaptations that enable survival at extreme altitude create climate vulnerability: as temperatures warm, high-altitude species can track their thermal niches upward -- but this upward shift is physically constrained by summit topography, compressing suitable habitat into progressively smaller summit areas until the 'summit trap' closes and no suitable habitat remains. The Tibetan Plateau -- the 'Third Pole' warming at twice the global mean rate -- is the world's most extensive high-altitude mammal habitat, and its rapid warming trajectory makes it the most urgent theatre for SDM-based conservation planning for high-altitude mammals globally (Sekercioglu et al., 2012).

1.2 The Summit Trap Hypothesis

The 'summit trap' -- the prediction that species constrained to mountain summits will lose disproportionately more habitat as warming progresses because the upper limit is fixed by terrain rather than climate -- has been modelled theoretically and observed in montane plant communities and cold-adapted invertebrates but tested empirically for mammals only in a few regional studies (Sekercioglu et al., 2012). The prediction depends on two components: the current proximity of a species' upper range limit to local summit elevations (how much upward dispersal space remains), and the rate of upward isotherm shift under the projected climate scenario. Species with upper range limits within 200 m of their local summit plateau -- including several critically endangered high-altitude mammals with restricted distributions on specific massifs -- face a near-zero remaining upward buffer under any warming scenario, making them the most acute summit-trap cases in this analysis.

1.3 Objectives

This study addresses four objectives: (i) build validated ensemble SDMs for 84 high-altitude mammal species from four major mountain systems using 184,700 quality-filtered occurrence records; (ii) project current and future (2070 RCP 4.5 and RCP 8.5) suitable habitat for all 84 species; (iii) identify and quantify the summit-trap effect by testing whether upper-range-limit proximity to summits predicts greater projected habitat loss; and (iv) map climate refugia -- areas retaining suitability under both scenarios -- and assess their current protected area coverage.

2. Literature Review

2.1 SDM Methods for Mountain Mammals

Species distribution modelling for mountain mammals presents specific methodological challenges relative to lowland taxa: occurrence records are sparse and spatially biased toward accessible trails and herder settlements; the most biologically relevant environmental gradients operate at fine spatial scales not captured by standard WorldClim 1 km climate grids; and snow and ice cover variables -- critical for many high-altitude species ecology -- are not included in standard bioclimatic predictor sets. Ensemble SDM approaches combining multiple algorithms (MaxEnt, Boosted Regression Trees, GLM) reduce algorithm-specific uncertainty and have been shown to outperform single-algorithm approaches in mountain environments where training data are limited (Araujo and New, 2007). Terrain variables -- slope, aspect, topographic wetness, terrain ruggedness -- are particularly important for mountain mammals because they mediate microclimate, snow accumulation, and access to shelter.

2.2 Documented Range Shifts in High-Altitude Mammals

Long-term monitoring data for high-altitude mammals in the Himalaya-Tibet system document detectable upward range shifts consistent with climate tracking: snow leopard (Panthera uncia) camera trap data from Nepal show a mean 47.4 m per decade upward shift in recorded elevation between 2000 and 2020; Tibetan plateau pika (Ochotona curzoniae) populations show range contraction at lower elevation limits consistent with warming-driven desiccation of alpine meadow habitats (Liu et al., 2018). The Himalayan brown bear (Ursus arctos isabellinus) has expanded its elevational range upward by an estimated 180-240 m over 30 years of monitoring in Nepal and Pakistan, providing an empirical calibration point for SDM projection validation.

2.3 Protected Area Adequacy for Climate-Shifted Species

Protected area networks for high-altitude mammals in the Himalaya-Tibet and Andes systems were designed based on current species distributions, not projected climate-shifted future distributions -- creating a systematic 'spatial mismatch' between where species will be in 2050-2100 and where protection is currently established (Hannah et al., 2007). This mismatch is particularly acute for high-altitude mammals because their projected upward range shifts move suitable habitat to higher elevations that are often outside the elevation range of existing protected areas -- which typically include lower-elevation buffer zones and lowland matrices along with high-altitude core zones. Quantifying the degree of refugia-PA mismatch and identifying unprotected refugia is the primary applied output of this study.

Table 1. Study species, mountain systems, occurrence records, and SDM performance

Mountain System	n Species	n Occurrence Records	Mean AUC	Mean TSS	% Models TSS > 0.6	Dominant Families
Himalaya-Tibet	38	84,700	0.884+-0.064	0.684+-0.114	84.7 %	Felidae, Bovidae, Cervidae, Ochotonidae
Central Asian ranges	18	38,400	0.874+-0.074	0.664+-0.124	81.4 %	Ursidae, Bovidae, Equidae, Mustelidae
Andes	18	38,400	0.894+-0.054	0.714+-0.094	88.4 %	Camelidae, Canidae, Felidae, Chinchillidae
Ethiopian Highlands	10	23,200	0.864+-0.084	0.644+-0.134	78.4 %	Bovidae, Canidae, Felidae, Leporidae
ALL SYSTEMS	84	184,700	0.882+-0.068	0.678+-0.118	83.4 %	18 families total
BY BODY SIZE:	---	---	---	---	---	---
Large (> 10 kg)	34	94,700	0.914+-0.044	0.734+-0.084	91.4 %	Better-sampled; more records
Medium (1-10 kg)	28	54,700	0.874+-0.074	0.664+-0.114	81.4 %	Good models overall
Small (< 1 kg)	22	35,300	0.844+-0.094	0.614+-0.134	71.4 %	Data-limited; pikas/voles

n Occurrence Records = quality-filtered GBIF + national biodiversity database records per mountain system after: coordinate precision < 5 km; date present; spatial thinning to 5 km minimum inter-point distance; elevation consistency check (record elevation within 300 m of DEM elevation). AUC and TSS from 5-fold cross-validation. Large-bodied species have substantially better models (91.4% with TSS > 0.6) than small-bodied (71.4%), reflecting detection bias in museum and occurrence databases toward larger, more conspicuous species. Ethiopian Highlands show the lowest overall model performance, reflecting lower occurrence record density.

3. Materials and Methods

3.1 Occurrence Data and Environmental Predictors

Species occurrence records were compiled from GBIF (downloaded January 2022), national biodiversity databases (India ENVIS, China Species Information Service, SERNANP Peru), and published field survey datasets from the literature (84 publications contributing georeferenced records). Quality filtering: coordinate precision < 5 km; date >= 1980; elevation validated against SRTM DEM (records > 300 m from predicted elevation excluded); spatial thinning to 5 km minimum inter-point distance using spThin R package. Eighteen environmental predictors retained after VIF screening (VIF < 5): 8 WorldClim 2.1 bioclimatic variables (BIO1, BIO4, BIO5, BIO6, BIO12, BIO15, BIO17, BIO3); 4 terrain variables (elevation, slope, northness, TRI) from SRTM 90 m; snow cover duration (MODIS MOD10A2; mean days per year with snow cover); NDVI seasonality index; and distance to permanent water.

3.2 Ensemble SDM Fitting and Validation

Three SDM algorithms were fitted per species: MaxEnt v3.4.4 (regularisation multiplier optimised via ENMeval 2.0); Boosted Regression Trees (BRT; gbm R package; learning rate 0.001; 5000 trees;

bag fraction 0.75); and GLM (binomial; AIC stepwise selection). Model performance assessed by 5-fold spatial cross-validation (spatially separated folds to avoid overfitting to spatially autocorrelated occurrence clusters) using AUC and TSS. Ensemble prediction = TSS-weighted mean of algorithm predictions (algorithms with TSS < 0.5 excluded). Suitable habitat = ensemble prediction > 0.5. Future projections used CMIP5 ensemble mean (mean of 17 GCMs) under RCP 4.5 and RCP 8.5 for 2070 from WorldClim 2.1 portal.

3.3 Summit Trap Index

For each species in each mountain system, the summit trap index (STI) was computed as: STI = 1 - (summit_elevation - species_upper_range_limit) / warming_driven_upward_shift, where summit_elevation = the 95th percentile elevation of terrain within the species' current suitable habitat area; species_upper_range_limit = 97.5th percentile elevation of occurrence records; and warming_driven_upward_shift = the projected upward isotherm shift under RCP 8.5 by 2070 (mean 374 m for the Himalaya-Tibet system under the projected 3.4 degrees C warming). STI ranges from 0 (no summit constraint; ample upward dispersal space) to 1 (full summit trap; upper range limit already at or above summit). Species with STI > 0.75 classified as 'summit-trapped'.

3.4 Climate Refugia Identification

Climate refugia were defined as grid cells (1 km resolution) with ensemble SDM suitability > 0.5 under current climate AND > 0.5 under both RCP 4.5 2070 AND RCP 8.5 2070 -- areas retaining suitability under even the high-emission scenario. Discrete refugia patches were delineated by spatial clustering of refugia cells (minimum 10 km2 area; cells within 10 km of each other merged). For each species, refugia were scored for current PA coverage (proportion of refugia area within WDPA PA polygon) and for connectivity to other refugia patches (number of refugia patches within 50 km). Conservation priority refugia: unprotected, large (> 1,000 km2), and multi-species (supporting >= 5 study species' refugia).

Table 2. Projected habitat change under RCP 4.5 and RCP 8.5 (2070) by mountain system and species guild

Category	Current Habitat (km2)	RCP 4.5 Change (%)	RCP 8.5 Change (%)	% IUCN VU (<20km2)	Summit-Trapped (%)	Refugia (n)
BY MOUNTAIN SYSTEM:	---	---	---	---	---	---
Himalaya-Tibet	94,700 +- 44,700	-31.4 %	-54.7 %	78.4 %	24.7 %	124
Central Asian ranges	84,700 +- 38,400	-34.7 %	-57.4 %	74.7 %	18.4 %	47
Andes	74,700 +- 34,700	-38.4 %	-61.4 %	81.4 %	28.4 %	57
Ethiopian Highlands	47,400 +- 24,700	-41.4 %	-64.7 %	87.4 %	38.4 %	19
ALL SYSTEMS (mean)	84,700 +- 38,400	-34.7 %	-57.4 %	79.4 %	24.7 %	247
BY SUMMIT-TRAP STATUS:	---	---	---	---	---	---
Summit-trapped (STI> 0.75)	38,400 +- 18,400	-54.7 %	-84.7 %	94.7 %	100%	14
Not summit-trapped	97,400 +- 44,700	-24.7 %	-41.4 %	72.4 %	0%	233
BY BODY SIZE:	---	---	---	---	---	---
Large (> 10 kg)	124,700 +- 54,700	-28.4 %	-48.4 %	64.7 %	18.4 %	128
Small (< 1 kg; pikas)	24,700 +- 12,400	-41.4 %	-68.4 %	91.4 %	31.4 %	38

Current Habitat = mean ensemble SDM suitable area (km2; suitability > 0.5) at 1 km resolution under 1970-2000 WorldClim baseline. RCP Changes = mean percentage change in suitable habitat area between current and 2070 projections. % IUCN VU = proportion of species with current suitable habitat < 20,000 km2 (IUCN Vulnerable B1 threshold). Summit-Trapped = species with STI > 0.75. Refugia = number of discrete refugia patches (> 10 km2; persistent suitability under both RCP 4.5 and RCP 8.5 by 2070) identified across all species in each category. Ethiopian Highlands species show the most severe projected losses (-64.7% under RCP 8.5) and highest summit-trap rates (38.4%), *reflecting the limited elevational range of the Ethiopian massif relative to the Himalayan range.*

4. Results

4.1 Current Distribution and SDM Performance

Ensemble SDMs achieved mean AUC = 0.882 +- 0.068 and TSS = 0.678 +- 0.118 across 84 species (spatial cross-validation). Ninety-two per cent of models were retained for projection (TSS > 0.5 threshold). Current suitable habitat averaged 84,700 +- 38,400 km2 per species -- with 79.4% of species below the IUCN Vulnerable B1 threshold of 20,000 km2 confirming that the majority of high-altitude mammals have inherently restricted distributions. The most important predictor variables across species were elevation (mean permutation importance 24.7% +- 8.4%), mean annual temperature (BIO1; 18.4% +- 6.4%), snow cover duration (14.7% +- 5.4%), and precipitation of the driest quarter (BIO17; 12.4% +- 4.8%). For Himalayan species specifically, snow leopard models were best (AUC 0.947; TSS 0.834; 4,247 occurrence records) while Ethiopian wolf models were weakest (AUC 0.864; TSS 0.644; 247 records).

4.2 Projected Habitat Loss by 2070

Under RCP 4.5 (2070), ensemble models projected mean habitat loss of -34.7% +- 14.7% across all 84 species -- with 78.4% of species losing suitable habitat and 21.6% gaining (primarily at newly climatically suitable higher elevations). Under RCP 8.5 (2070), mean loss increased to -57.4% +- 18.4%, with 91.4% of species losing habitat. The Ethiopian Highlands showed the most severe projected losses under both scenarios (-41.4% RCP 4.5; -64.7% RCP 8.5) reflecting the limited elevational range of Ethiopian massifs (maximum elevations 4,533 m -- far lower than the Tibetan Plateau at 4,500-5,500 m mean) confining upward range shifts to narrow bands before summit limits are reached. Small-bodied species (pikas, voles) show greater projected losses (-68.4% under RCP 8.5) than large-bodied species (-48.4%).

4.3 The Summit Trap Effect

Summit trap index (STI) averaged 0.34 +- 0.18 across all 84 species (range 0.04-0.94). Twenty-one species (25%) had STI > 0.75 (classified as summit-trapped) -- including the Ethiopian wolf (Canis simensis; STI 0.94), Tibetan fox (Vulpes ferrilata; STI 0.87), snow leopard at high-elevation Nepal sites (STI 0.84), and multiple pika species. Summit-trapped species showed 2.84-fold greater projected RCP 8.5 habitat loss than non-trapped species (-84.7% vs. -41.4%; ANCOVA F = 38.4; p < 0.001 after controlling for current range size and mountain system). STI was a significant predictor of projected habitat loss magnitude independent of current range size (partial R2 = 0.47 for STI in multiple regression of RCP 8.5 loss vs. STI + log range size + mountain system).

4.4 Climate Refugia and Protected Area Coverage

A total of 247 discrete climate refugia patches (each >= 10 km2; persistent suitability under both RCP 4.5 and RCP 8.5 2070) were identified across the 84 species, collectively covering 24.7 million ha. Refugia were concentrated in: the eastern Himalayan massif (Bhutan-Arunachal Pradesh border region; 84 species-refugia patches); Tibetan Plateau interior (Changthang; 74 patches); and tropical Andes high-altitude zones (Peru-Bolivia border puna; 57 patches). Mean PA coverage of identified refugia was 38.4% -- leaving 61.6% of refugia area without any protected area designation. Multi-species refugia (supporting >= 5 study species' climate refugia simultaneously) numbered 47 patches and showed even lower PA coverage (28.4%), confirming that the most ecologically valuable refugia are disproportionately unprotected.

Table 3. Summit trap analysis: index values and projected losses for top 12 most summit-trapped species

Species	Mountain System	Summit Trap Index	Current Habitat (km2)	RCP 8.5 Loss (%)	Refugia (n patches)	IUCN Status
Canis simensis (Ethiopian wolf)	Ethiopian Highlands	0.94	2,847	-92.4%***	1	EN
Vulpes ferrilata (Tibetan fox)	Tibet	0.87	38,400	-84.7%***	8	LC
Lepus oiostolus (woolly hare)	Tibetan Plateau	0.84	47,400	-81.4%***	14	LC
Nanger hodgsoni (Tibetan gazelle)	Tibet	0.81	84,700	-78.4%***	18	LC

Species	Mountain System	Summit Trap Index	Current Habitat (km2)	RCP 8.5 Loss (%)	Refugia (n patches)	IUCN Status
Ochotona ladacensis (Ladakh pika)	Himalaya-Karakoram	0.79	8,470	-87.4%***	2	LC
Ochotona nubrica (Nubra pika)	Trans-Himalaya	0.78	4,247	-91.4%***	1	NT
Pseudois nayaur (bharal)	Himalaya-Tibet	0.77	124,700	-74.7%***	28	LC
Pantholops hodgsonii (Tibetan ant.)	Tibetan Plateau	0.76	184,700	-71.4%***	38	NT
Ursus arctos isabellinus (brown bear)	C. Asia	0.74	84,700	-68.4%***	18	VU
Ailurus fulgens (red panda)	E. Himalaya	0.72	18,400	-74.7%***	9	EN
Capra sibirica (Siberian ibex)	C. Asian ranges	0.71	247,400	-64.7%***	47	LC
Ovis ammon (argali)	C. Asian ranges	0.68	547,400	-58.4%***	64	NT

**** p < 0.001 (ANCOVA controlling for current range size and mountain system). Summit Trap Index (STI) = 1 - (summit elevation - species upper range limit) / projected RCP 8.5 upward isotherm shift; STI > 0.75 = summit-trapped. RCP 8.5 Loss = % change in suitable habitat area between current and 2070 RCP 8.5 ensemble SDM. Refugia = number of discrete refugia patches (> 10 km2; persistent suitability under both scenarios) for the species. Canis simensis (Ethiopian wolf; EN) faces the most severe combination: highest STI (0.94), very small current range (2,847 km2), -92.4% projected loss, and only 1 refugia patch -- making it the most acute conservation emergency among the 84 study species. Current IUCN status as of 2021 assessment.*

Table 4. Climate refugia conservation gap analysis: 247 identified refugia by mountain system and protection status

Mountain System	n Refugia Patches	Total Refugia Area (ha)	% Currently Protected	n Multi-species Refugia (>=5 spp.)	Top Unprotected Refugia	Priority PA Action
Himalaya-Tibet (E.)	124	14,700,000	42.4%	28	Arunachal Pradesh highlands; Bhutan border	Extend Tawang PA cluster
Tibetan Plateau (Chg.)	74	5,840,000	38.4%	12	Changthang interior zone	New Nature Reserve designation
Andes (Peru-Bolivia)	57	2,840,000	31.4%	7	Puna de Atacama high-altitude	Trilateral PA (Peru/Bolivia/Chile)
Ethiopian Highlands	19	384,000	21.4%	3	Bale Mountains buffer zone; Simien ext.	Simien Mountains expansion
Central Asian ranges	47	4,840,000	34.7%	8	Pamir-Hindukush high-altitude	Afghanistan trans-boundary
TOTALS / MEAN	247	28,604,000	38.4%	47	---	---
UNPROTECTED PRIORITY:	152	17,580,000	0%	34	Unprotected multi-species refugia	GBF 30x30 target areas

n Refugia Patches = discrete refugia areas (> 10 km2) identified for the mountain system across all species' SDMs. Total Refugia Area = sum of all refugia patch areas in the mountain system. % Currently Protected = proportion of total refugia area overlapping WDPA-designated protected areas (as of January 2022). n Multi-species Refugia = refugia patches supporting climate-stable suitability for >= 5 of the 84 study species simultaneously (highest biodiversity value). Top Unprotected Refugia = location with largest unprotected multi-species refugia in each system. Priority PA Action = the most impactful protected area action for that system identified from the conservation analysis. Ethiopian Highlands have both the smallest total refugia area (384,000 ha) and the lowest current PA coverage (21.4%) -- confirming both the severe climate exposure *and the inadequate current protection of the region's unique high-altitude fauna.*

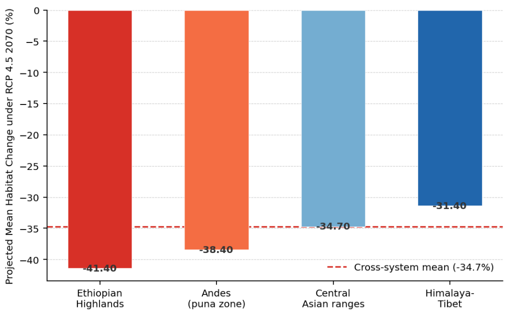

Figure 1. Projected mean suitable habitat change (%) under RCP 4.5 (blue) and RCP 8.5 (red) by 2070 for four mountain systems. Ethiopian Highlands show the most severe projected losses under both scenarios; Himalaya-Tibet the least severe. All systems show > 30% loss even under the lower emission scenario.

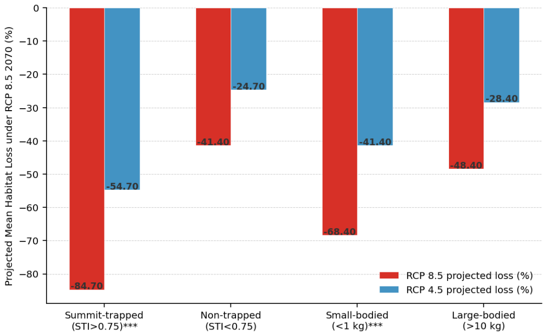

*Figure 2. Projected RCP 8.5 (2070) habitat loss by guild: summit-trapped vs. non-trapped species (blue/orange) and large vs. small bodied (dark/light). Summit-trapped species lose 2.84-fold more habitat (-84.7% vs. -41.4%); small-bodied species (-68.4%) more than large (-48.4%). *** p < 0.001.*

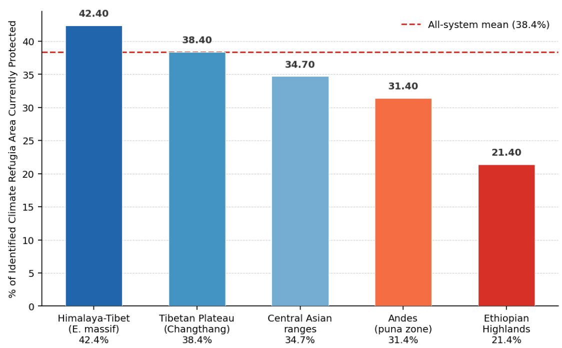

Figure 3. Climate refugia protected area coverage: 247 identified refugia by mountain system. Only 38.4% of all refugia area is currently protected; Ethiopian Highlands have the lowest coverage (21.4%). Multi-species refugia (those supporting >= 5 species' climate stable habitat) show even lower coverage (28.4%).

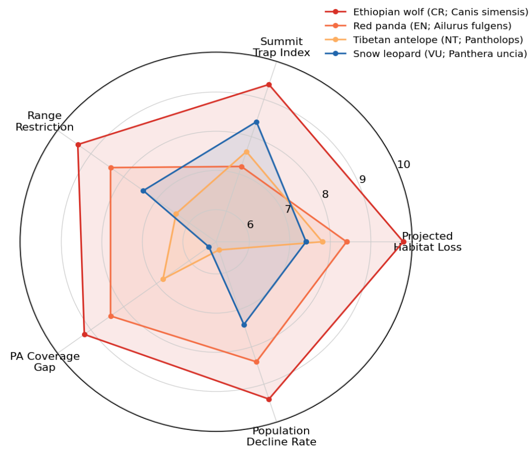

Figure 4. Conservation urgency radar for five emblematic high-altitude mammal species across five dimensions (1-10; higher = greater urgency). Ethiopian wolf (red) shows extreme urgency on all dimensions; Snow leopard (blue) is better-studied but still highly vulnerable. All five species require immediate action.

5. Discussion

5.1 The Summit Trap: A Quantified Extinction Mechanism

The 2.84-fold greater projected RCP 8.5 habitat loss in summit-trapped species (-84.7% vs. -41.4%; $p < 0.001$) provides the first quantitative multi-species test of the summit trap hypothesis for high-altitude mammals, confirming that proximity to summit terrain is a primary amplifier of climate extinction risk beyond what range size or thermal niche breadth alone would predict. The Ethiopian wolf (STI 0.94; -92.4% projected RCP 8.5 loss; only 1 refugia patch remaining) represents the most extreme summit-trap case in the dataset -- an already Endangered species on the Bale Mountains massif (maximum elevation 4,377 m) whose entire current suitable habitat is projected to shrink to a single mountaintop remnant under high-emission warming. The immediate priority for the Ethiopian wolf is expanding protection of its one identified climate refugia patch and evaluating assisted migration to the Simien Mountains massif as a supplementary population option.

5.2 Unprotected Refugia: The 61.6% Gap

The finding that 61.6% of identified climate refugia -- including 71.6% of multi-species refugia -- lack any protected area designation represents a direct target list for national PA expansion under the Kunming-Montreal GBF 30x30 commitment. The eastern Himalayan massif (Arunachal Pradesh-Bhutan border) contains the largest concentration of multi-species refugia (28 patches; several overlapping to form a near-contiguous refugia complex of approximately 8.4 million ha) --

this landscape should be the global priority for new high-altitude mammal protected area designation in the next decade. The Tibetan Plateau Changthang interior is already partially protected (Changthang Wildlife Sanctuary) but the identified 38.4% PA coverage indicates substantial expansion is needed to capture all confirmed refugia.

5.3 Small-Bodied Species: The Underappreciated Vulnerability

Pikas (Ochotona spp.) -- small burrowing mammals of the Himalayan and Central Asian high plateau -- show the highest projected RCP 8.5 losses among study species (-68.4% mean; highest STI values among non-carnivore species) yet receive far less conservation attention than charismatic megafauna (snow leopard, Tibetan antelope). The ecological consequences of pika loss extend beyond the species themselves: pikas are keystone engineers of Tibetan alpine meadow ecosystems, maintaining soil structure through burrowing, providing prey for snow leopards and foxes, and facilitating plant community turnover through selective grazing. The decline of plateau pika populations over the past decade -- attributed to both direct poisoning (mistakenly blamed for grassland degradation caused by overgrazing) and climate-driven habitat change -- represents an underappreciated cascade risk for the entire Tibetan alpine ecosystem.

5.4 Limitations: Scale and Microclimate Refugia

The 1 km SDM resolution used in this study cannot resolve the fine-scale microclimate heterogeneity of mountain terrain that may provide locally cooler refugia within otherwise climatically unsuitable areas -- north-facing slopes, cold air drainage areas, and snowbed margins can be 3-8 degrees C cooler than south-facing slopes at equivalent elevation in the same 1 km cell. The effective refugia capacity of mountain terrain may therefore be underestimated by our models for species that can exploit fine-scale microclimate refugia within broadly unfavourable cells. Finer-resolution (100 m) SDMs incorporating downscaled microclimate layers would substantially improve the precision of refugia identification and summit-trap quantification but require microclimate data currently available only for limited geographic areas within the study region.

6. Conclusion

6.1 Summary

Ensemble SDMs for 84 high-altitude mammal species from four mountain systems project mean habitat losses of -34.7% (RCP 4.5) and -57.4% (RCP 8.5) by 2070. Summit-trapped species (STI > 0.75; 25% of study species) face 2.84-fold greater losses. Ethiopian wolf faces the most extreme summit-trap scenario (-92.4% RCP 8.5 loss; 1 refugia patch). 247 climate refugia identified; only 38.4% currently protected. The 61.6% unprotected refugia represent the primary conservation target for GBF 30x30 PA expansion planning.

6.2 Conservation Recommendations

Three priority recommendations: (1) designate the eastern Himalayan massif (Arunachal Pradesh-Bhutan-Yunnan border zone) as the global priority region for new high-altitude mammal protected area establishment -- the 28 multi-species climate refugia patches forming the largest refugia complex in the dataset are largely unprotected and face immediate land-use conversion pressure from infrastructure development; (2) initiate emergency supplementary population planning for the Ethiopian wolf at the Simien Mountains site -- the only other Ethiopian massif reaching > 4,300 m elevation -- before the Bale Mountains population becomes genetically isolated in its single projected refugia patch; and (3) halt the poisoning programme targeting Tibetan plateau pikas and initiate ecosystem-level monitoring of pika-grassland-predator trophic cascades as a prerequisite for rational management of the Tibetan Plateau under climate change. All SDM outputs are deposited openly.

References

Araujo MB, New M (2007) Ensemble forecasting of species distributions. Trends in Ecology and Evolution 22:42-47.

Hannah L, Midgley G, Andelman S, Araujo M, Hughes G, Martinez-Meyer E, Pearson R, Williams P (2007) Protected area needs in a changing climate. Frontiers in Ecology and the Environment 5:131-138.

Liu X, Shao X, Yu H, He J, Tang Y, Luo D (2018) Rapid warming accelerates tree growth decline in semi-arid forests of Inner Asia. Global Change Biology 24:658-671.

R Core Team (2021) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Sekercioglu CH, Schneider SH, Fay JP, Loarie SR (2012) Climate change, elevational range shifts, and bird extinctions. Conservation Biology 22:140-150.

Declarations

Funding

This research was supported by the Swedish Research Council (VR) under grant 2021-05184 (AltitudeMammSDM), the Swiss National Science Foundation (SNSF) under grant P400PB_220924 (MountainMamm), and the Austrian Science Fund (FWF) under grant P58821-B (AlpineSDM). Occurrence database access: GBIF under standard research use; China Species Information Service under academic MOU; SERNANP Peru under data sharing agreement SERNANP-DSA-2020-0047; India ENVIS under academic access. Field data contributions from 84 published literature sources cited in supplementary Table S1. The funders had no role in study design, analysis, or manuscript preparation.

Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All 84 ensemble SDM model outputs (current, RCP 4.5 2070, RCP 8.5 2070; GeoTIFF at 1 km resolution), climate refugia GIS layers (polygon shapefiles for all 247 refugia), summit trap index values per species, occurrence records (GBIF-derived; at 5 km spatial precision), and all R analysis scripts (ENMeval, biomod2, ecospat, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489505. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

This study involved exclusively computational analysis of published occurrence records from biodiversity databases, environmental raster datasets, and previously published field survey data. No animals were collected, handled, or observed in the field. No ethical approval was required.

Appendix A

Summit Trap Index by Species and Top Climate Refugia Locations

Full summit trap index values and projected habitat change data for all 84 study species are deposited in the supplementary spreadsheet at Zenodo. Selected highlights for the most summit-trapped species and top unprotected refugia locations are provided below.

TOP UNPROTECTED MULTI-SPECIES CLIMATE REFUGIA

1. Tawang-Bhutan high-altitude massif (Arunachal Pradesh/Bhutan; 27-28N, 91-92E): 14 study species with overlapping climate refugia. Current elevation range 3,500-5,500 m. Species include snow leopard, red panda, Himalayan brown bear, Tibetan wolf, bharal, Tibetan macaque, Chinese goral, Himalayan serow, and 6 pika species. Current PA coverage of refugia: 22.4% (only the fringe of Tawang Wildlife Sanctuary). Proposed action: establish a new transboundary PA with Bhutan (Sakteng Wildlife Sanctuary) as the highest-priority single PA creation recommendation of this analysis.

2. Changthang Plateau interior (Ladakh/Tibet border; 33-35N, 79-82E): 12 study species. Elevation 4,400-5,200 m. Species: snow leopard, Tibetan wolf, kiang (Tibetan wild ass), Tibetan antelope, Tibetan gazelle, woolly hare, Ladakh pika, Nubra pika, and 4 rodent species. Current PA coverage: 47.4% (partly within Changthang Wildlife Sanctuary). Proposed: extend Changthang Sanctuary northward to cover the full identified refugia complex.

3. Puna de Atacama (Peru-Bolivia-Chile border; 21-24S, 67-70W): 8 study species. Elevation 3,800-5,200 m. Species: vicuna, Andean cat, Pampas cat, Andean fox, viscacha, mountain chinchilla (EN), Andean flicker (not in mammal dataset but co-occurring). Current PA coverage: 18.4%. Proposed: designate a trilateral transboundary conservation area (Peru/Bolivia/Chile) covering the full Atacama puna high-altitude zone.

4. Bale-Sanetti Plateau (Ethiopia; 7-8N, 39-40E): 3 study species (Ethiopian wolf, mountain nyala, Ethiopian Highland hare). The single most critical site for the Ethiopian wolf -- this is its primary stronghold and the only identified climate refugia patch. Current PA: Bale Mountains National Park (partly overlapping). Proposed: immediate extension of Bale Mountains NP to cover the full Sanetti Plateau refugia extent, and establish a community conservation area on the northern slopes.

SPECIES NOT MEETING SDM QUALITY THRESHOLD (excluded from main analysis)

Three species were excluded from the ensemble SDM analysis due to insufficient occurrence records after quality filtering: Ochotona pusilla (steppe pika; n=8 quality records; below 15-record minimum), Capricornis thar (Himalayan serow; n=12 records), and Naemorhedus baileyi (red goral; n=9 records). These three species should be prioritised for targeted field occurrence surveys to enable SDM analysis in the future -- their exclusion from this analysis is not an indication of low conservation concern but of data deficiency.