

RESEARCH ARTICLE

Expanding or shrinking? range shifts in wild ungulates under climate change in Pamir-Karakoram mountains, Pakistan

Hussain Ali¹, Jaffar Ud Din², Luciano Bosso³, Shoaib Hameed¹, Muhammad Kabir¹, Muhammad Younas², Muhammad Ali Nawaz^{4*}

1 Department of Zoology, Quaid-I-Azam University, Islamabad, Pakistan, **2** Snow Leopard Trust, Pakistan Program, Islamabad, Pakistan, **3** Wildlife Research Unit, Dipartimento di Agraria, Università degli Studi di Napoli Federico II, Portici, Italy, **4** Environmental Science Program, Department of Biological and Environmental Sciences, Qatar University, Doha, Qatar

* nawazma@gmail.com



Abstract

Climate change is expected to impact a large number of organisms in many ecosystems, including several threatened mammals. A better understanding of climate impacts on species can make conservation efforts more effective. The Himalayan ibex (*Capra ibex sibirica*) and blue sheep (*Pseudois nayaur*) are economically important wild ungulates in northern Pakistan because they are sought-after hunting trophies. However, both species are threatened due to several human-induced factors, and these factors are expected to aggravate under changing climate in the High Himalayas. In this study, we investigated populations of ibex and blue sheep in the Pamir-Karakoram mountains in order to (i) update and validate their geographical distributions through empirical data; (ii) understand range shifts under climate change scenarios; and (iii) predict future habitats to aid long-term conservation planning. Presence records of target species were collected through camera trapping and sightings in the field. We constructed Maximum Entropy (MaxEnt) model on presence record and six key climatic variables to predict the current and future distributions of ibex and blue sheep. Two representative concentration pathways (4.5 and 8.5) and two-time projections (2050 and 2070) were used for future range predictions. Our results indicated that ca. 37% and 9% of the total study area (Gilgit-Baltistan) was suitable under current climatic conditions for Himalayan ibex and blue sheep, respectively. Annual mean precipitation was a key determinant of suitable habitat for both ungulate species. Under changing climate scenarios, both species will lose a significant part of their habitats, particularly in the Himalayan and Hindu Kush ranges. The Pamir-Karakoram ranges will serve as climate refugia for both species. This area shall remain focus of future conservation efforts to protect Pakistan's mountain ungulates.

OPEN ACCESS

Citation: Ali H, Din JU, Bosso L, Hameed S, Kabir M, Younas M, et al. (2021) Expanding or shrinking? range shifts in wild ungulates under climate change in Pamir-Karakoram mountains, Pakistan. PLoS ONE 16(12): e0260031. <https://doi.org/10.1371/journal.pone.0260031>

Editor: Tzen-Yuh Chiang, National Cheng Kung University, TAIWAN

Received: May 31, 2021

Accepted: October 31, 2021

Published: December 31, 2021

Peer Review History: PLOS recognizes the benefits of transparency in the peer review process; therefore, we enable the publication of all of the content of peer review and author responses alongside final, published articles. The editorial history of this article is available here: <https://doi.org/10.1371/journal.pone.0260031>

Copyright: © 2021 Ali et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the manuscript and its [Supporting information](#) files.

Funding: This study received support from the following sources: Snow Leopard Trust (awarded to MAN); and Pakistan Snow Leopard and Ecosystem Protection Program (grant number 9231, awarded to MAN). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

Introduction

Climate change has impacted ecosystems in unprecedented ways globally [1, 2], and appears to be unrelenting. These impacts are further complicated by rapid economic growth [3] and increasing human populations, especially in developing countries [4, 5].

Pakistan is a developing country and ranks as the seventh most vulnerable country to climate change [6]. Extreme temperatures, heavy rainfall, and floods are devastating several ecosystems in the country [7, 8]. Climate change impacts are most frequent in Pakistan's northern mountain ranges, including the Pamir-Karakoram, Himalayas, and Hindu Kush [9] where increasing temperatures, changes in cropping season, receding glaciers or outbursts, and heavy flooding [10–15] are leading to the extinction of several plant and animal species [16, 17]. These mighty mountains are a source of fresh water for half of South Asia [18, 19] and home to many floral and faunal species [20]. Furthermore, the Himalayas and Hindu Kush act as a barrier to monsoon rains [21] which helps the Karakoram range maintain its aridity. Highest and steepest among other ranges, the Karakoram is expected to be the one which is least affected by climate change [22].

Several species of wild ungulate, including the markhor (*Capra facolneri facolneri*), Ladakh urial (*Ovis vignei vignei*), Marco Polo sheep (*Ovis ammon polii*), Kashmir musk deer (*Moschus cupreus*), Himalayan ibex (*Capra ibex sibirica*), and blue sheep (*Pseudois nayaur*) live in these mountains. They play an important role in sustaining mountain ecosystems by influencing vegetation structure, plant composition, and nutrient recycling, in addition to being prey for carnivores [23]. However, climatic variations in recent years have impacted many ungulate species [3], and such impacts could have devastating effects on the ecosystem, including the carnivore community [24]. Climate studies in the Himalayas [25], western Tian Shan and Kyrgyz Alatau mountain ranges in Kazakhstan [26], Ghats in India [27], and Tibetan plateau in China [28] report climate change to be a serious threat to wild ungulates, leading to many species' extinction [3, 25, 27].

The Himalayan ibex is the most common of six wild ungulates in Pakistan. Its range historically extended from Swat to Khunjerab, although it has shrunk to the extreme northern parts of the country [29]. It is found in relatively arid precipitous mountain ranges living well above the tree line at elevations of 3,500–5,000 m [30]. The species does not enter forest zones, preferring steep escape terrain [31]. On the other hand, the blue sheep or *bharal* [32], an intermediate species between the goat and sheep [33] is found in less precipitous areas compared with ibex, at altitudes of 3,500–5,500 m in slopes covered with grasses and sedges, preferably with a southern-east exposition [34, 35].

The persistence of mountain ungulates like the Himalayan ibex and blue sheep in northern Pakistan is important because they are coveted trophies for hunters whose license fees help impoverished communities, who, in turn, help conserve biodiversity in far-flung areas [32]. Conservation planning that targets the long-term survival of these species is not only important from a nature perspective but is also vital for local human populations. Such planning must be informed by both current occurrence and future distribution of these iconic species in response to climate change. Currently, wild ungulate distributions in Gilgit-Baltistan (GB) is only partially known, and knowledge of climate change-induced impacts on species and habitats is insufficient [9]. We considered the ibex and blue sheep as model species to understand range shifts and other associated impacts of climate change on wild ungulates. The selected species represent two different groups—goats and sheep—and distinctive habitats. Inferences drawn from this study will, therefore, build knowledge for the informed management of wild ungulates in northern Pakistan. To achieve this objective, we used species distribution models

(SDMs) which are widely adopted in investigations of species distribution and range shifts [36, 37].

Materials and methods

Study area

Our study was conducted in Gilgit-Baltistan, Pakistan that lies between latitudes 36° N to 37° N and longitudes 74° E to 76° E, with an area ca. 72,200 km², dominated by glaciers and the snow-capped mountains of the Karakoram, Himalaya, Hindu Kush, and Pamir [38, 39]. The area is characterized by a variety of climatic conditions ranging from the monsoon-influenced moist temperate zone in the western Himalayas to the semi-arid cold deserts of the northern Karakoram and Hindu Kush [38]. There are numerous (forest) plant species, including the deodar (*Cedrus deodara*), blue pine (*Pinus wallichiana*), fir (*Abies spectabilis*), spruce (*Picea smithiana*), chilgoza (*Pinus gerardiana*), juniper (*Juniperus spp.*), and birch (*Betula utilis*) [40], and 54 mammalian species [41], including rare ones [30] like the snow leopard (*Panthera uncia*), Astor markhor (*Capra falconeri falconeri*), Ladakh urial (*Ovis vignei vignei*), Marco Polo sheep (*Ovis ammon polii*), grey wolf (*Canis lupus*), Himalayan lynx (*Lynx lynx*), brown bear (*Ursus arctos*), and musk deer (*Moschus spp.*), in addition to the previously mentioned Himalayan ibex and blue sheep.

Collection of presence records

Himalayan ibex and blue sheep presence records (Fig 1) were collected using two methods: camera trapping and double observer surveys.

1. Camera trapping: We installed 225 (Reconyx HC 500 and HC 900; Reconyx, Holmen, USA) cameras during the period 2010–2016 for *C. ibex sibirica* and *P. nayaur*, in different months of the year i.e., Khunjerab National Park (KNP) (November to January, 2010 and September to November, 2011), in Qurumber National Park (QNP) (May to June 2012) in Misgar Valley (May to July, 2013), in Hopper and Hisper Valleys (March to May, 2016) Cameras were left operational for 10 days in the first camera trapping in KNP, but in the latter surveys they were left operational for 40 days to increase the capture rate [42, 43].
2. Double observer Survey: We carried out this survey in 2012–2016 in different parts (KNP, Gojal Valley, Shigar Valley, in Skardu district, and in Gilgit district) of the study area by dividing it into smaller blocks based on watersheds. These watersheds were not larger than daily ungulate/human movement ability. Two observers were sent for survey separated by time (15 minutes) if only one trail was available, or by space, if two trails were available. Each watershed was surveyed by walking along pre-determined routes [44]. The locations where Himalayan ibex and blue sheep were sighted, have been used as presence points to build the MaxEnt model.

We collected 143 and 60 presence points for Himalayan ibex and blue sheep, respectively (S1A and S1B Fig). We then screened these presence points in ArcGIS 10.7 (ESRI, Redland, USA) using nearest neighbor analysis to check spatial autocorrelation [36, 43, 45]. This analysis revealed a high clustering among presence points. Aggregation was, therefore, spatially filtered using SDMTools [46] to ensure independence [36, 43, 47]. This operation led to 36 and 29 presence points for Himalayan ibex and blue sheep, respectively, which we used in MaxEnt models (Fig 1).

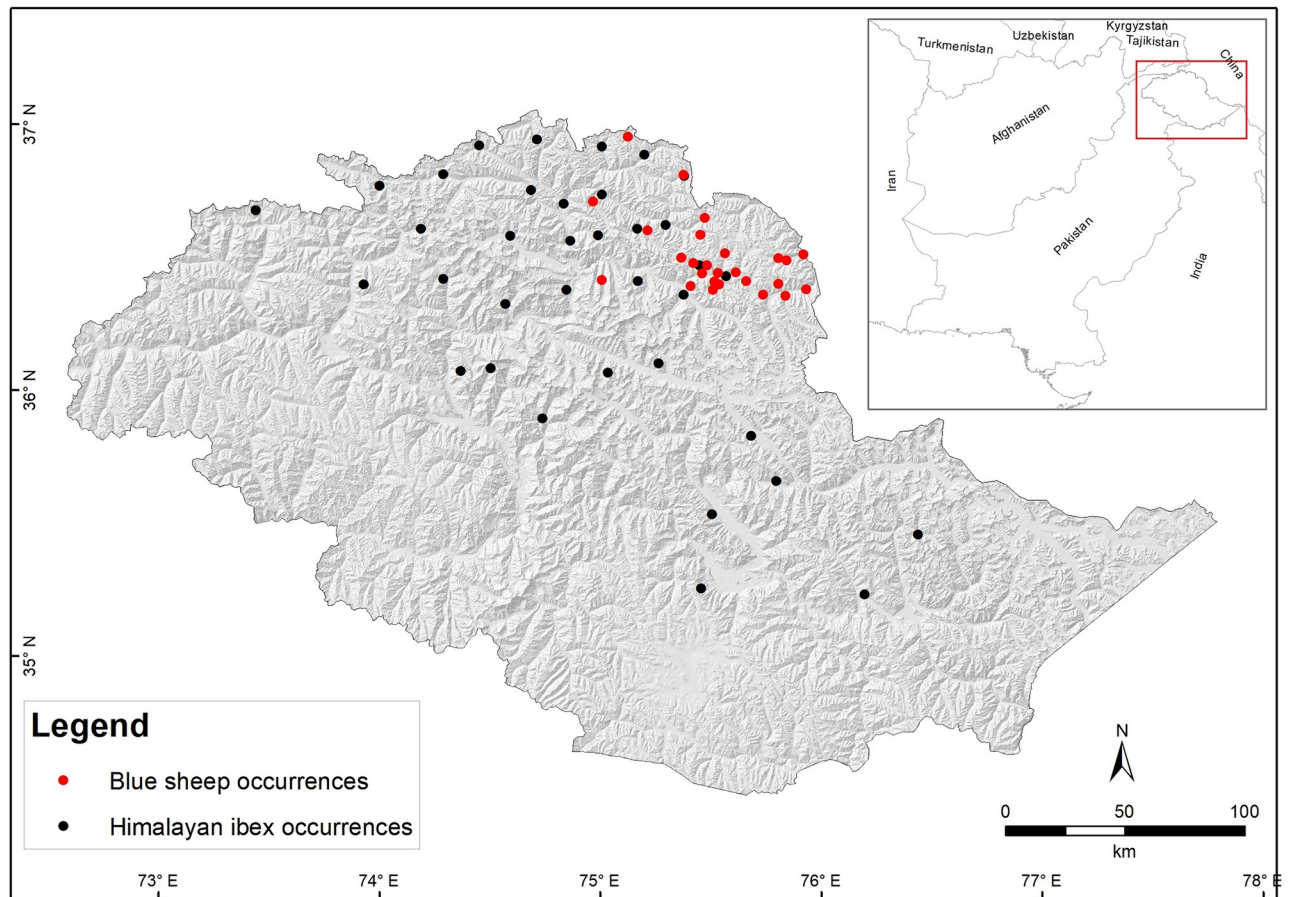


Fig 1. Sampling locations of Himalayan ibex and blue sheep in GB, Pakistan used to build model.

<https://doi.org/10.1371/journal.pone.0260031.g001>

Climatic variables

We downloaded 19 climatic variables from WorldClim 1.4 (<https://www.worldclim.org/current>) [48] to predict currently suitable areas for Himalayan ibex and blue sheep. All the variables were in raster files (grid) with 30-arc second resolution ($0.93 \times 0.93 \text{ km} = 0.86 \text{ km}^2$ at the equator). Further details and information on the realization and interpretation of the WorldClim variables used in this study can be found at <https://pubs.usgs.gov/ds/691/>. We checked all variables for multicollinearity and excluded highly correlated variables i.e., $r \geq 0.70$ (Pearson's correlation coefficient) [43]. This process led to use in the modeling analysis of six environmental variables: annual mean temperature ($^{\circ}\text{C}$), mean diurnal range ($^{\circ}\text{C}$), temperature seasonality [(standard deviation * 100) ($^{\circ}\text{C}$)], mean temperature of wettest quarter ($^{\circ}\text{C}$), mean precipitation (mm), and precipitation seasonality (%).

We used global circulation models (GCMs) MIROC5, BCC-CSM1-1, CCSM4, and HadGEM2ES to predict the future distribution of Himalayan ibex and blue sheep under climate change conditions. Various organizations developed these models under the Coupled Model Intercomparison Project, phase 5 (CMIP5) and are considered highly reliable [36, 49]. The future projections of these GCMs are based on representative concentration pathways (RCPs) which are greenhouse gas (GHG) concentration trajectories on a range of radiative forces suggested in the Intergovernmental Panel on Climate Change's (IPCC) fifth assessment report [50]. We used RCP 4.5 and RCP 8.5 the former is a moderate GHG mitigation scenario [51]

where emissions will peak around 2040 and then decline, while the latter is a scenario where GHG emissions will be the highest of all four RCPs (2.6, 4.5, 6.0 and 8.5) throughout the 21st century [27].

Modeling procedure

We used MaxEnt ver. 3.4.1 [52] to predict the current and future distribution of *C. ibex sibirica* and *P. nayaur* in Pakistan [25]. MaxEnt is a piece of machine learning software used to develop SDMs [53–55]. It is capable of predicting species distribution using presence-only data [56] and predicting the distribution of poorly known species [36, 57]. We built the model using a logistic output format to yield environmental suitability ranging from 0 (unsuitable) to 1 (highly suitable) [58]. We fixed the regularization multiplier to 1, selected 5,000 iterations [27], and ran 20 replicates with cross-validation tests [43].

Different GCM projections can have inherited uncertainties. To avoid this, we used area under the curve (AUC) scores as weighting coefficients that resulted from 20 cross-validations for each of four GCMs and produced a single forecast for each time scale by averaging all individual GCMs for that time slice. [28, 59–61]. We used ten percentile training presence values as the threshold to develop binary presence/absence maps [43].

The model was projected to entire GB. To project the models calibrated for survey area over entire GB, the variables in the projection area must meet a condition of environmental similarity with the environmental data used for calibrating the model. Therefore, we preliminarily ascertained that this condition was verified for both current and future projections by inspecting Multivariate Environmental Similarity Surfaces (MESS), the MESS calculates the similarity of each point in the region of projection to a set of reference points (e.g., background data) and maps the results [56] MESS maps produced by MaxEnt can help users identify extrapolated areas and provide a quantitative measure of projection uncertainty.

Model validation

We tested the predictive performance of the models with different methods: receiver operated characteristics, analyzing the AUC [62], and the true skill statistic (TSS) [63]. AUC assesses models' discrimination ability with values ranging from 0 (equaling random distribution) to 1 (perfect prediction). TSS compares the number of correct forecasts minus those attributable to random guessing, to that of a hypothetical set of perfect forecasts. It considers both omission and commission errors and success as a result of random guessing. Its values range from -1 (a performance no better than random) to +1 (perfect agreement).

Niche overlap

We calculated the niche overlap between *C. ibex sibirica* and *P. nayaur* for predicted habitats using ENMTools [64] in the current time and future climate change scenarios. ENMTools uses MaxEnt map values of habitat suitability for each grid and measures niche overlap using D and I values [64]. It uses Schoener's D value to calculate niche overlap and gives probability distributions with values ranging from 0 (no overlap) to 1 (complete overlap). Similarly, Hellinger's I-statistic in ENMTools measures models' ability to estimate true suitability [64].

Results

Model performance

The AUC values for our models were 0.969 ± 0.025 and 0.821 ± 0.138 for blue sheep and Himalayan ibex, respectively. TSS values were 0.841 ± 0.007 and 0.454 ± 0.281 for blue

sheep and Himalayan ibex, respectively. Both tests suggest strong performances of our models.

Current distribution of Himalayan ibex and blue sheep

Our binary maps showed ca. 26 500 km² (37.71% of total study area) and ca. 6 500 km² (9.26% of total study area) suitable for Himalayan ibex and blue sheep, respectively (Fig 2).

We found that the current habitat predicted for Himalayan ibex included the latitudes from 34° to 37° and the longitudes from 73° to 77°. The most suitable habitats fell in the Karakoram range, followed by the Hindu Kush, and then to a minor extent in the Himalayas (Fig 2A). The habitat suitability of Himalayan ibex was predicted in all ten districts of GB with strongholds in Hunza, Nagar, Shigar, and Ghanche districts. We found that habitats suitable to blue sheep were between the latitudes 35° to 37° and the longitudes 74° to 77° along the Pakistan-China border in the Pamir-Karakorum range that administratively falls in Hunza district, followed by some parts of the Shigar and Ghanche districts along the Pakistan-China border (Fig 2B). We found that annual mean precipitation, mean temperature of the wettest quarter, and temperature seasonality were the most important variables (with 91.6% contribution) in predicting suitable habitats for blue sheep (S1 Table). For ibex, annual mean precipitation, annual mean temperature, and precipitation seasonality were key habitat predictors with an 89% contribution (S2 Table).

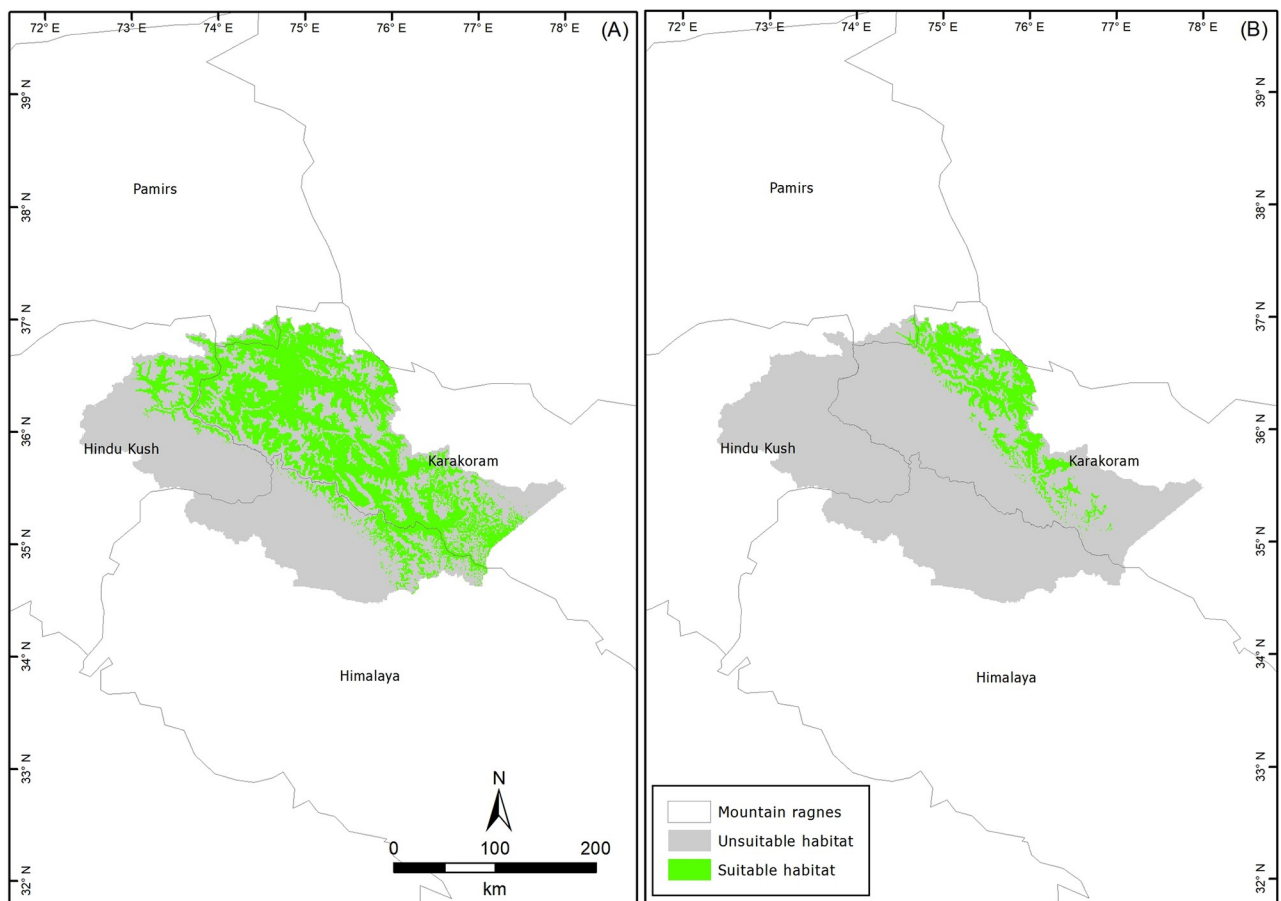


Fig 2. Binary maps of habitat suitability for Himalayan ibex (A) and blue sheep (B) under current climatic conditions.

<https://doi.org/10.1371/journal.pone.0260031.g002>

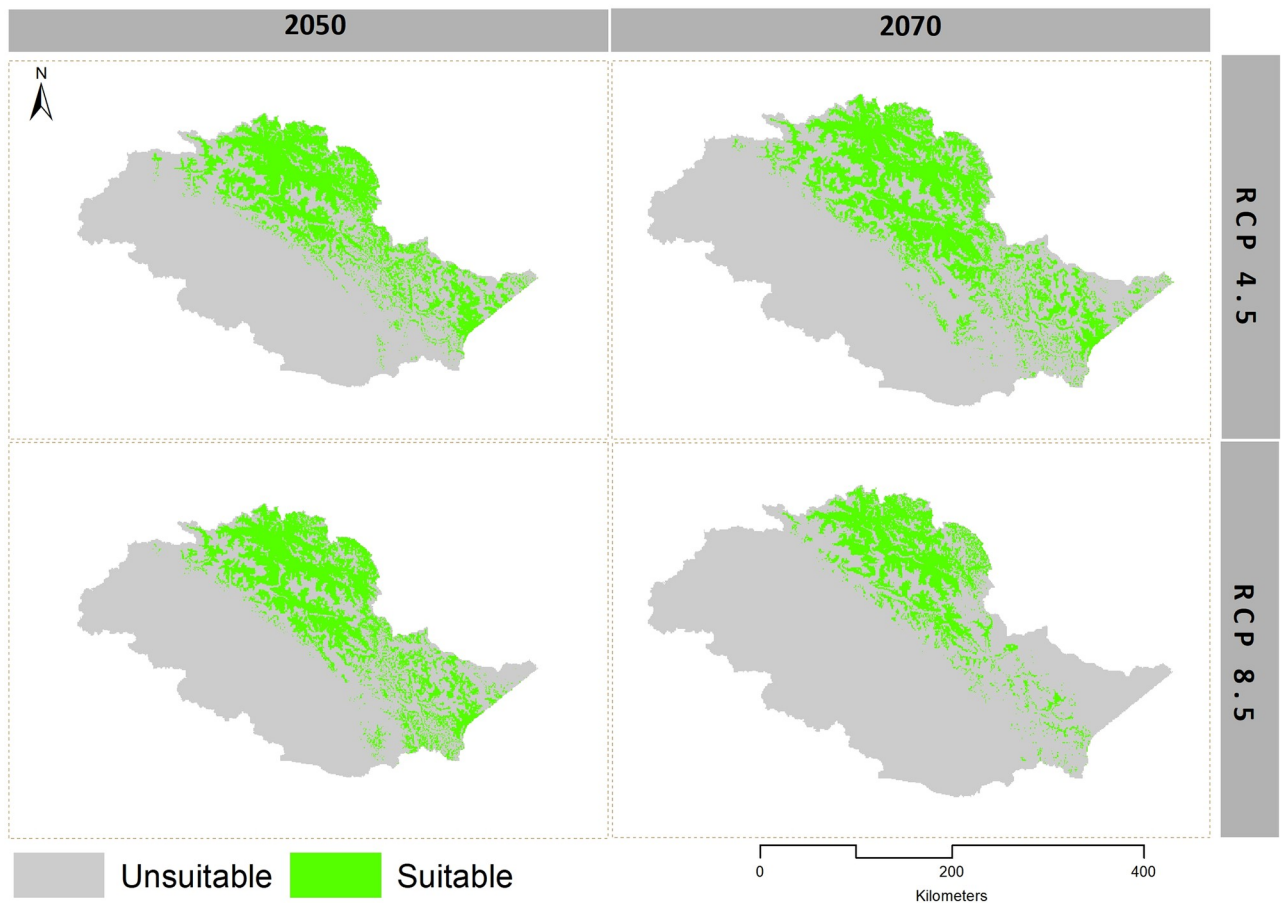


Fig 3. Binary maps of Himalayan ibex under RCP 4.5 and RCP 8.5 scenarios in 2050 and 2070.

<https://doi.org/10.1371/journal.pone.0260031.g003>

Future distribution of Himalayan ibex and blue sheep

Our models showed habitat shrinkage for both Himalayan ibex and blue sheep for RCP 4.5 and RCP 8.5, in 2050 and 2070 scenarios (Figs 3 and 4, Tables 1 and 2).

In the extreme climate change scenario (RCP 8.5 of 2070), blue sheep lost (58%) from the suitable areas that it has currently occupied and gained new suitable areas by extending its current range towards the east. Himalayan ibex gained the least and lost (64.80%) in RCP 8.5 of 2070 (Table 3 and Figs 5 and 6). The model predicted habitat shrinkage to an area of 2,515 km² for blue sheep and 9,248 km² for ibex under the extreme climate change scenario.

The center of suitable Himalayan ibex habitat gradually shifted from the north to the east in RCP 4.5 and RCP 8.5 of 2050, and RCP 4.5 of 2070, while in RCP 8.5 of 2070, it again shifted from the east to the north. The center of the suitable habitat of blue sheep first shifted gradually from the west towards the north in RCP 4.5 and RCP 8.5 of 2050, and RCP 4.5 of 2070. In RCP 8.5 of 2070, it shifted towards the east from the north. The MESS analysis predicted some areas with novel climate conditions across the range for both *P. nayaur* and *C. ibex sibirica* in the future projections. However, these areas were found outside the training range of our model (S1–S8 Figs).

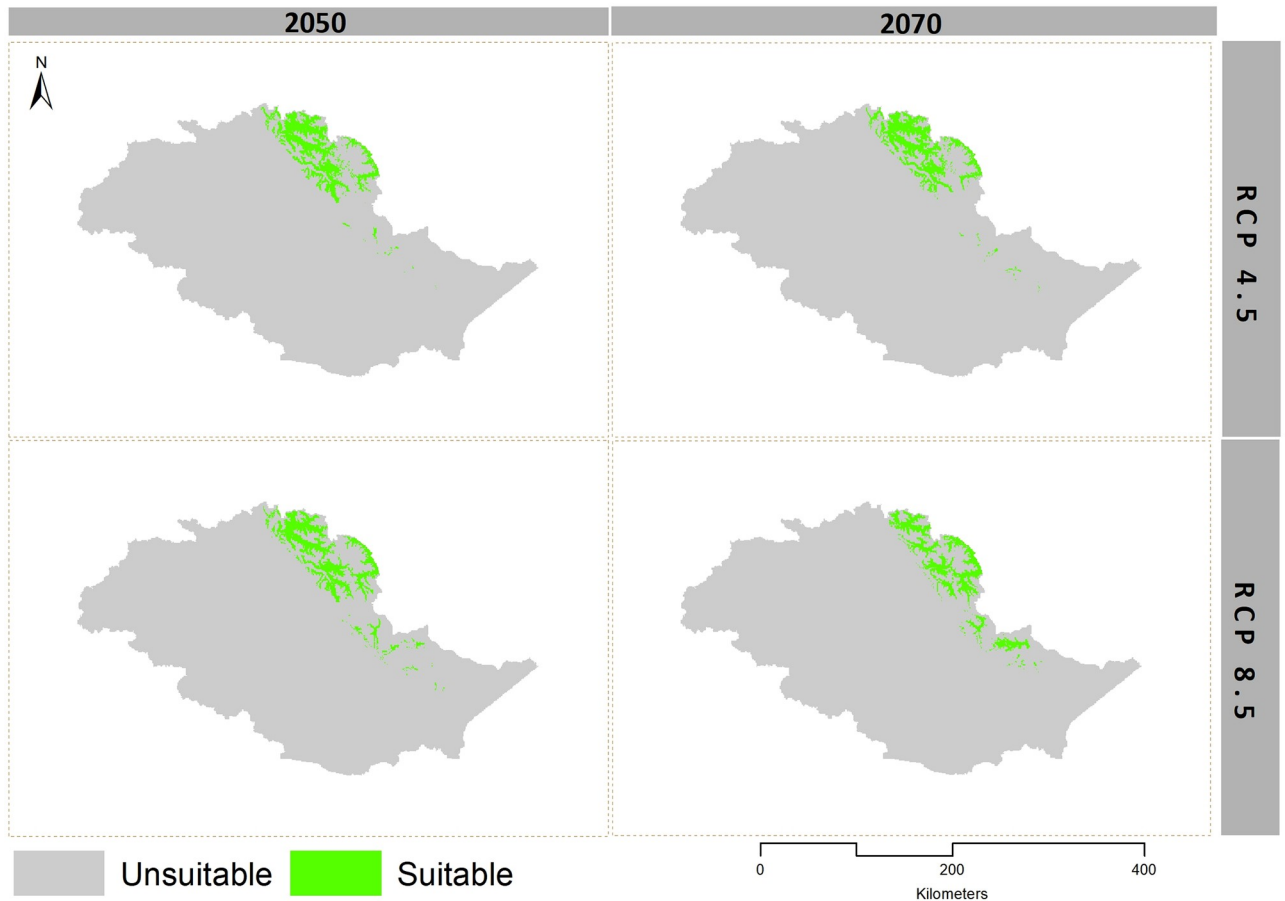


Fig 4. Binary maps of blue sheep under RCP 4.5 and RCP 8.5 scenarios in 2050 and 2070.

<https://doi.org/10.1371/journal.pone.0260031.g004>

Niche overlap

Our analysis of niche overlap between blue sheep and Himalayan ibex indicated a moderate level of niche overlap in the current time. ANOVA test showed that the mean of Schoener's D value for two climate change scenarios (4.5 and 8.5) did not vary significantly ($F(3,12) = 0.15$, $p = 0.68$) on the temporal scale (2050 vs. 2070). Similarly, the probability-based I-statistic values for niche overlap were also not significantly different ($F(3, 12) = 0.37$, $p = .77$) for different RCPs of different years (Table 4 and Fig 7).

Table 1. Area predicted to be suitable in the current and different future climate change scenarios within GB for blue sheep.

	Scenario	No. of pixels predicted to be suitable	Percentage reduction in future scenarios
1	Current	9,035	-
2	2050 RCP 4.5	3,922	56.59
3	2050 RCP 8.5	4,039	55.29
4	2070 RCP 4.5	3,738	58.62
5	2070 RCP 8.5	3,491	61.93

<https://doi.org/10.1371/journal.pone.0260031.t001>

Table 2. Area predicted to be suitable in the current and different future climate change scenarios within GB for *C. ibex sibirica*.

	Scenario	No. of pixels predicted to be suitable	Percentage reduction in future scenarios
1	Current	36,790	-
2	2050 RCP 4.5	23,797	35.31
3	2050 RCP 8.5	23,804	35.29
4	2070 RCP 4.5	24,391	33.70
5	2070 RCP 8.5	12,950	64.80

<https://doi.org/10.1371/journal.pone.0260031.t002>

Table 3. Change resulting from climate change in suitable habitats of blue sheep and Himalayan ibex.

Species	Future	Scenario	Expansion	No occupancy	Stable areas	Habitat loss	Total
Blue sheep	2050	RCP 4.5	3.60	63,779	2,822	3,687	70,291
	2050	RCP 8.5	47.55	63,735	2,906	3,604	70,292
	2070	RCP 4.5	23.05	63,759	2,670	3,839	70,291
	2070	RCP 8.5	125.38	63,657	2,390	4,120	70,292
Himalayan ibex	2050	RCP 4.5	3,024	40,738	14,126	12,460	70,348
	2050	RCP 8.5	2,957	40,805	14,175	12,411	70,348
	2070	RCP 4.5	3,363	40,009	14,102	12,330	69,804
	2070	RCP 8.5	1,035	42,228	8,213	18,255	69,731

<https://doi.org/10.1371/journal.pone.0260031.t003>

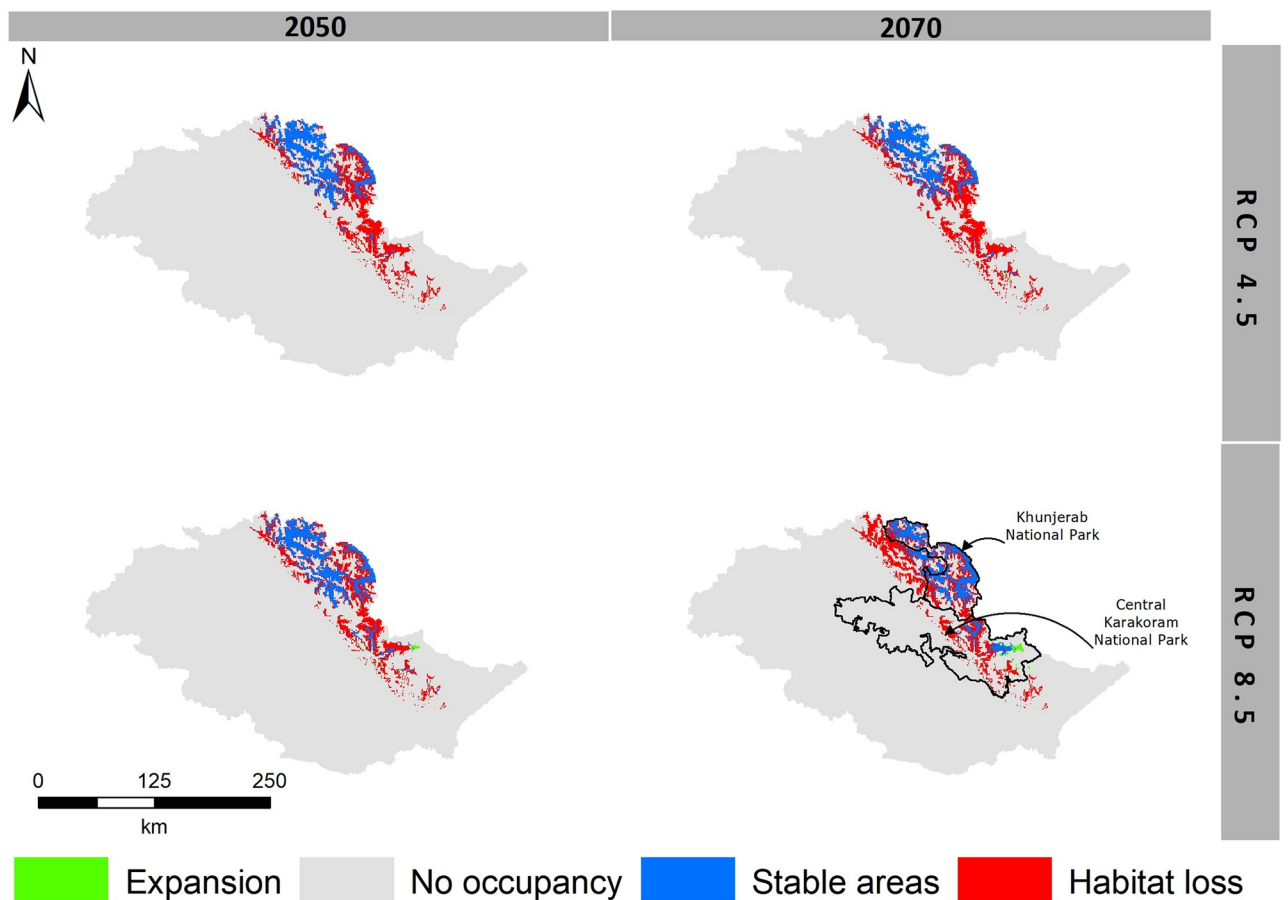


Fig 5. The predicted change in the suitable habitats of blue sheep in 2050 and 2070 under RCP 4.5 and RCP 8.5 scenarios.

<https://doi.org/10.1371/journal.pone.0260031.g005>

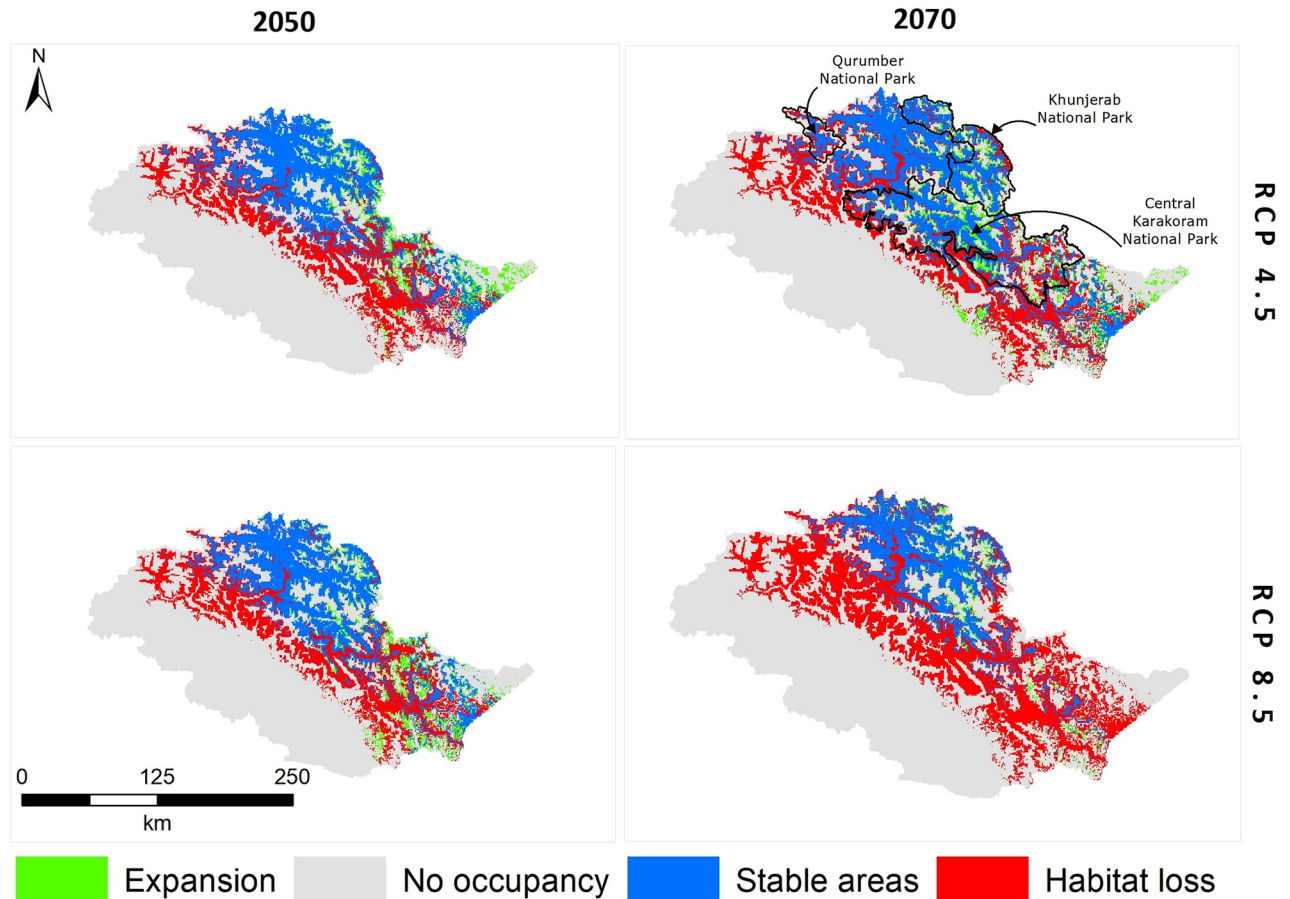


Fig 6. The predicted change in the suitable habitats of blue sheep in 2050 and 2070 under RCP 4.5 and RCP 8.5 scenarios.

<https://doi.org/10.1371/journal.pone.0260031.g006>

Discussion

The use of SDMs for the predictive distribution of biodiversity [65] has increased as the approach is considered efficient in predicting species distribution and climate change impact [66] which aids in species conservation planning [55]. MaxEnt is widely used for its proven ability to construct models using presence-only data [67]. This model worked well on our presence data as indicated by the AUC scores (>0.8), which places it among the best-published models [25, 26, 28, 68]. The higher TSS values further supported the credibility of results [36, 47].

The melting of Himalayan glaciers has increased in the 21st century [69] while the glaciers of the Hindu Kush and Karakoram will melt at a slower rate [70]. In fact, some glaciers in the

Table 4. Estimation of niche overlap between Himalayan ibex and blue sheep under different climate change scenarios.

Schoener's niche overlap metric	Current	2050		2070	
		RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5
<i>D</i>	0.42	0.44	0.46	0.44	0.47
<i>I</i>	0.69	0.72	0.73	0.72	0.74

<https://doi.org/10.1371/journal.pone.0260031.t004>

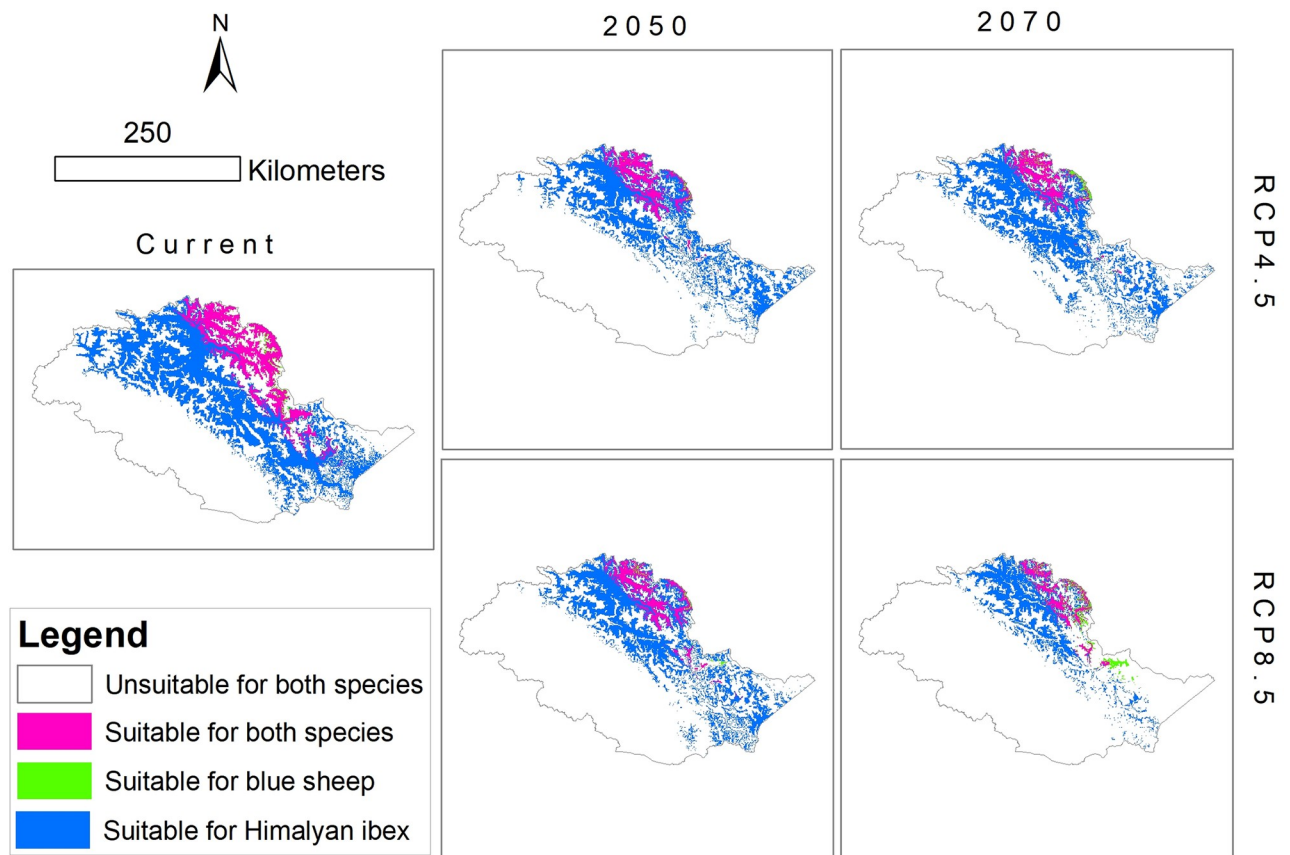


Fig 7. The spatial pattern of niche overlap between blue sheep and Himalayan ibex in current and different climate change scenarios.

<https://doi.org/10.1371/journal.pone.0260031.g007>

higher watersheds of the Karakoram are expanding [71] although at the same time they are thinning. However, regardless of the three described scenarios, the snow on these glaciers regulates ecological processes and patterns [72] and any change in glacier mass, negative or positive, will affect associated biodiversity. Our results for habitat loss and gain were strikingly aligned with the existing knowledge on glaciology. We found that global climate change will have significant effects on the habitats of mountain ungulates in northern Pakistan, though these effects are more pronounced in Hindu Kush, and Himalaya ranges.

Our model for current time predicted 6,510 km² and 26,510 km² of suitable area for blue sheep and Himalayan ibex, respectively. Both model species are present in most of the predicted habitats, or they occupied those areas historically [30, 33]. Ironically, Khan et al., (2014) reported sighting records of ibex in Tangir Valley of Diامر district, which is beyond the suitable habitat predicted in the current study, as well as outside of the former IUCN range [73]. This probably indicates southwards expansion of ibex in recent years. Our model predicted suitable habitat for blue sheep on the Braldu glacier where sheep do not currently exist [74]. Interestingly, older records indicate the presence of blue sheep in this area, e.g., [29] quote a sighting by T. J. Roberts in this area in 1975.

Both blue sheep and Himalayan ibex habitats are usually between the timber and snow lines at elevations of 3,500–5,500 m, and differ as Blue sheep prefers habitats with steep rolling hills and Himalayan ibex prefer precipitous habitats [33]. These habitats are usually

devoid of thick vegetation. Hence, precipitation is a vital factor to sustain life in this zone. We found annual precipitation to be the most contributing variable in predicting suitable habitat for both blue sheep and Himalayan ibex. Annual mean temperature was the second most important variable for Himalayan ibex, and temperature of wettest quarter the second most important for blue sheep. The dry habitats of both ibex and blue sheep have short growing seasons, and any weather fluctuation might leave species starving [75]. *Artemisia* and *Ephedra* shrubs are described as the ibex's main food sources [33]. A year of good winter precipitation and normal mean summer temperature enables shrubs to maximize their growth and green cover [76]. Blue sheep's preferred diet comprises of grasses, forbs, and shrubs *Berberis*, *Polygonum*, and *Ephedra*, respectively [33]. Even in the summers, precipitation at elevations above 4,000 m can bring temperatures below zero and constraint vegetative growth [76]. Hence, temperatures of wettest quarters (June, July, and August) play a decisive role in selecting suitable habitat for blue sheep. Khan et al. (2016) found annual precipitation and minimum temperature to be important variables for developing suitability models for *C. ibex sibirica* and *P. nayaur*, respectively. Aryal et al. (2016) and Luo et al. (2015) reported annual mean temperature as the most influencing variable in predicting suitable habitat for *P. nayaur*.

We observed a sharp decline (56% in RCP 4.5 and 58% in RCP 8.5) in the currently available suitable habitat for blue sheep and (33.70% in RCP 4.5 and 64.80% in RCP 8.5) for Himalayan ibex in extreme climate change scenarios for 2070. This is consistent with [25] who observed a decrease in blue sheep suitable habitat in the future due to climate change in Nepal. Similarly, Luo et al. (2015) reported a 30–50% range reduction for ungulates on the Tibetan plateau under different climate change scenarios.

Climate drives evolutionary processes, forcing animals to migrate to higher elevations or extend their distributional ranges towards the Northern Hemisphere [77] or eastward direction [28]. This process is believed to have occurred in the Miocene Epoch when members of the *Caprinae* in Eurasia and Africa began inhabiting the newly formed mountain ranges of the Himalayas, Karakoram, Hindu Kush, and Pamirs, which emerged from the sea during the Tertiary Period [33]. We expect a similar migration in northern Pakistan because the centers of predicted suitable habitat for Himalayan ibex will shift from north to east in RCP 4.5 and RCP 8.5 of 2050 and 2070 and again from east to the north in RCP 8.5 of 2070. For Himalayan ibex, it will shift from west to north in RCP 4.5 and RCP 8.5 of 2050 and 2070 and from north to east in RCP 8.5 of 2070.

Species co-evolved over millions of years, enabling them to co-exist by selecting different niches [78]. Our model predicted a moderate niche overlap between blue sheep and Himalayan ibex, and this overlap was predicted to increase if the extreme climatic conditions assumed in future scenarios prevail. Increasing temperatures and precipitation have already impacted Himalayan flora [79]. Alpine habitats have short growing seasons [80, 81] and offer relatively few species of grasses, sedges, forbs, shrubs, ferns, lichens, and mosses to Himalayan ibex and blue sheep [82–84]. Hence, these climatic changes in alpine ranges will increase the chances of habitat mismatch for many floral species [28, 80]. Climate change, together with anthropogenic effects transforming land for agriculture or afforestation, road construction, and mining could further shrink habitats suitable for ungulates [28, 68], potentially affecting their perpetuity and the proper functioning of ecosystems [85, 86].

Conservationists emphasize on locating habitats likely to be least affected by climate change and continue serving as suitable habitats (future refugia), and protecting them from anthropogenic activities [21, 87, 88]. Our model predicted such climate refugia for Himalayan ibex to be comprised of three national parks: Khunjerab National Park (KNP), Central Karakoram National Park (CKNP), and Qurumbar National Park (QNP) (Fig 6). For blue sheep, such

refugia exists in the buffer zone of KNP, along with a few patches on the Braldu glacier of CKNP (Fig 5). It is noteworthy, however, that Himalayan ibex will lose most of its current suitable habitat in CKNP in Baltistan division and areas around QNP in the future, but the areas of CKNP in Nagar district will remain stable. All three mountain ranges in our study area provide vital habitats to several mountain ungulates. Unfortunately, most of suitable habitats in Hindu Kush and Himalayas are expected to be altered under future scenarios. On contrary, the Pamir-Karakoram is likely to remain stable and continue accommodating both Himalayan ibex and blue sheep. The relatively lower effect of climate change in this range is likely due to the barrier effect of the Hindu Kush and Himalayas which blunt the monsoon, helping maintain the aridity of the Karakorum's alpine steppes [21, 71].

Conclusions

Our study demonstrate that the current suitable habitat of Himalayan ibex and blue sheep are vulnerable to climate change. Under the rapid climate change Himalayan ibex will lose most of its current suitable habitat in Himalayas and Hindu Kush while blue sheep that currently exists only in Pamir-Karakoram range will be slightly affected. The current network of protected areas (KNP and CKNP) will serve climate refugia for mountain ungulates.

There is urgent need to revisit protected areas management strategies in Pakistan, to enhance their effectiveness for conservation of mountain ungulates. The finding of this study can be used to revisit or align boundaries of existing protected areas with the future predicted habitats. Management and protection efforts shall remain disproportionately higher in parks that encompass climate refugia for mountain ungulates of the region.

Supporting information

S1 Map. Map showing unfiltered and retained occurrences used for the current study A) Himalayan ibex (total 143 points, retained points 36) B) Blue sheep (total 60 points, retained points 29) using SDMtoolbox V1.1(Brown 2014).
(DOCX)

S1 Table. Estimates of relative contributions of the environmental variables used to build MaxEnt model for blue sheep.
(DOCX)

S2 Table. Estimates of relative contributions of the environmental variables used to build MaxEnt model for Himalayan ibex.
(DOCX)

S1 Fig. Maps illustrating multivariate environmental similarity surface (MESS) approach as described in (Elith et al. 2010) and the most dissimilar variables(MOD) for Himalayan ibex under the year 2050 Representative Concentration Pathway (RCP4.5) for different Global Circulation Models. Negative values indicate novel climate in the MESS map across the range. b) Most dissimilar variables (MOD) analysis shows those novel climatic conditions and the associated variables.
(DOCX)

S2 Fig. Maps illustrating multivariate environmental similarity surface (MESS) approach as described in(Elith et al. 2010) and the most dissimilar variables(MOD) for Himalayan ibex under the year 2050 Representative Concentration Pathway (RCP8.5) for different Global Circulation Models. Negative values indicate novel climate in the MESS map across

the range. b) Most dissimilar variables (MOD) analysis shows those novel climatic conditions and the associated variables.

(DOCX)

S3 Fig. Maps illustrating multivariate environmental similarity surface (MESS) approach as described in (Elith et al. 2010) and the most dissimilar variables(MOD) for Himalayan ibex under the year 2070 Representative Concentration Pathway (RCP4.5) for different Global Circulation Models. Negative values indicate novel climate in the MESS map across the range. b) Most dissimilar variables (MOD) analysis shows those novel climatic conditions and the associated variables.

(DOCX)

S4 Fig. Maps illustrating multivariate environmental similarity surface (MESS) approach as described in (Elith et al. 2010) and the most dissimilar variables(MOD) for Himalayan ibex under the year 2050 Representative Concentration Pathway (RCP4.5) for different Global Circulation Models. Negative values indicate novel climate in the MESS map across the range. b) Most dissimilar variables (MOD) analysis shows those novel climatic conditions and the associated variables.

(DOCX)

S5 Fig. Maps illustrating multivariate environmental similarity surface (MESS) approach as described in (Elith et al. 2010) and the most dissimilar variables(MOD) for Blue sheep under the year 2050 Representative Concentration Pathway (RCP4.5) for different Global Circulation Models. Negative values indicate novel climate in the MESS map across the range. b) Most dissimilar variables (MOD) analysis shows those novel climatic conditions and the associated variables.

(DOCX)

S6 Fig. Maps illustrating multivariate environmental similarity surface (MESS) approach as described in (Elith et al. 2010) and the most dissimilar variables(MOD) for Blue sheep under the year 2050 Representative Concentration Pathway (RCP8.5) for different Global Circulation Models. Negative values indicate novel climate in the MESS map across the range. b) Most dissimilar variables (MOD) analysis shows those novel climatic conditions and the associated variables.

(DOCX)

S7 Fig. Maps illustrating multivariate environmental similarity surface (MESS) approach as described in (Elith et al. 2010) and the most dissimilar variables(MOD) for Blue sheep under the year 2070 Representative Concentration Pathway (RCP4.5) for different Global Circulation Models. Negative values indicate novel climate in the MESS map across the range. b) Most dissimilar variables (MOD) analysis shows those novel climatic conditions and the associated variables.

(DOCX)

S8 Fig. Maps illustrating multivariate environmental similarity surface (MESS) approach as described in (Elith et al. 2010) and the most dissimilar variables(MOD) for Blue sheep under the year 2070 Representative Concentration Pathway (RCP8.5) for different Global Circulation Models. Negative values indicate novel climate in the MESS map across the range. b) Most dissimilar variables (MOD) analysis shows those novel climatic conditions and the associated variables.

(DOCX)

Acknowledgments

We acknowledge the support provided by the staff of Parks and Wildlife Department and communities during the field surveys.

Author Contributions

Conceptualization: Hussain Ali, Muhammad Ali Nawaz.

Data curation: Hussain Ali, Jaffar Ud Din, Shoaib Hameed, Muhammad Kabir, Muhammad Younas, Muhammad Ali Nawaz.

Formal analysis: Hussain Ali, Luciano Bosso, Shoaib Hameed, Muhammad Ali Nawaz.

Funding acquisition: Muhammad Ali Nawaz.

Investigation: Jaffar Ud Din, Muhammad Kabir.

Methodology: Hussain Ali.

Project administration: Jaffar Ud Din, Muhammad Ali Nawaz.

Supervision: Muhammad Ali Nawaz.

Visualization: Hussain Ali.

Writing – original draft: Hussain Ali.

Writing – review & editing: Luciano Bosso, Muhammad Ali Nawaz.

References

1. Parmesan C, Yohe G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*. 2003; 421: 37. Available: <https://doi.org/10.1038/nature01286> PMID: 12511946
2. Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, et al. Ecological responses to recent climate change. *Nature*. 2002; 416: 389–395. <https://doi.org/10.1038/416389a> PMID: 11919621
3. Hu J, Jiang Z. Climate change hastens the conservation urgency of an endangered ungulate. *PLoS One*. 2011; 6: e22873. <https://doi.org/10.1371/journal.pone.0022873> PMID: 21826214
4. Ahlburg DA, Kelley AC, Mason KO, Mason eds. KO. The impact of population growth on well-being in developing countries. Springer Science & Business Media; 2013. <http://search.ebscohost.com/login.aspx?direct=true&db=ecn&AN=0392278&site=ehost-live>
5. Schneider UA, Havlik P, Schmid E, Valin H, Mosnier A, Obersteiner M, et al. Impacts of population growth, economic development, and technical change on global food production and consumption. *Agric Syst*. 2011; 104: 204–215. <https://doi.org/10.1016/j.agsy.2010.11.003>
6. Eckstein D, Künzel V, Schäfer L. Global Climate Risk Index 2018. Bonn, Ger Ger. 2017.
7. Rehman A, Rehman A, Jingdong L, Du Y, Khaton R, Wagan SA. Flood Disaster in Pakistan and its Impact on Agriculture Growth (A Review) Flood Disaster in Pakistan and its Impact on Agriculture Growth (A Review). *Env Dev Econ*. 2015; 6: 39–42.
8. Looney R. Economic impacts of the floods in Pakistan. *Contemp South Asia*. 2012; 20: 225–241. <https://doi.org/10.1080/09584935.2012.670203>
9. Ishaq S, Khan MZ, Begum F, Hussain K, Amir R, Hussain A, et al. Climate Change Impact on Mountain Biodiversity: a Special Reference To Gilgit-Baltistan of Pakistan. *J Mt area Res*. 2015; 1: 53–63. 2518-850X
10. Ahmad Z, Hafeez M, Ahmad I. Hydrology of mountainous areas in the upper Indus Basin, Northern Pakistan with the perspective of climate change. *Environ Monit Assess*. 2012; 184: 5255–5274. <https://doi.org/10.1007/s10661-011-2337-7> PMID: 22109645
11. Akhtar M, Ahmad N, Booi MJ. The impact of climate change on the water resources of Hindukush-Karakorum-Himalaya region under different glacier coverage scenarios. *J Hydrol*. 2008; 355: 148–163. <https://doi.org/10.1016/j.jhydrol.2008.03.015>

12. Ashraf A, Naz R, Roohi R. Glacial lake outburst flood hazards in Hindukush, Karakoram and Himalayan ranges of Pakistan: Implications and risk analysis. *Geomatics, Nat Hazards Risk*. 2012; 3: 113–132. <https://doi.org/10.1080/19475705.2011.615344>
13. Joshi S, Jasra WA, Ismail M, Shrestha RM, Yi SL, Wu N. Herders' perceptions of and responses to climate change in Northern Pakistan. *Environ Manage*. 2013; 52: 639–648. <https://doi.org/10.1007/s00267-013-0062-4> PMID: 23674240
14. Tahir AA, Chevallier P, Arnaud Y, Neppel L, Ahmad B. Modeling snowmelt-runoff under climate scenarios in the Hunza River basin, Karakoram Range, Northern Pakistan. *J Hydrol*. 2011; 409: 104–117. <https://doi.org/10.1016/j.jhydrol.2011.08.035>
15. Tahir AA, Chevallier P, Arnaud Y, Ashraf M, Bhatti MT. Snow cover trend and hydrological characteristics of the Astore River basin (Western Himalayas) and its comparison to the Hunza basin (Karakoram region). *Sci Total Environ*. 2015; 505: 748–761. <https://doi.org/10.1016/j.scitotenv.2014.10.065> PMID: 25461078
16. Kulkarni A, Patwardhan S, Kumar KK, Ashok K, Krishnan R. Projected Climate Change in the Hindu Kush–Himalayan Region By Using the High-resolution Regional Climate Model PRECIS. *Mt Res Dev*. 2013; 33: 142–151. <https://doi.org/10.1659/MRD-JOURNAL-D-11-00131.1>
17. Xu J, Grumbine RE, Shrestha A, Eriksson M, Yang X, Wang Y un, et al. The Melting Himalayas: Cascading Effects of Climate Change on Water, Biodiversity, and Livelihoods. *Conserv Biol*. 2009; 23: 520–530. <https://doi.org/10.1111/j.1523-1739.2009.01237.x> PMID: 22748090
18. Kumar P, Kotlarski S, Moseley C, Sieck K, Frey H, Stoffel M, et al. Response of Karakoram-Himalayan glaciers to climate variability and climatic change: A regional climate model assessment. *Geophys Res Lett*. 2015; 42: 1818–1825. <https://doi.org/10.1002/2015GL063392>
19. Bolch T, Kulkarni A, Kääb A, Huggel C, Paul F, Cogley JG, et al. The state and fate of himalayan glaciers. *Science (80-)*. 2012; 336: 310–314. <https://doi.org/10.1126/science.1215828> PMID: 22517852
20. Schild A. ICIMOD's Position on Climate Change and Mountain Systems. *Mt Res Dev*. 2008; 28: 328–331. <https://doi.org/10.1659/mrd.mp009>
21. Li J, McCarthy TM, Wang H, Weckworth B V., Schaller GB, Mishra C, et al. Climate refugia of snow leopards in High Asia. *Biol Conserv*. 2016; 203: 188–196. <https://doi.org/10.1016/j.biocon.2016.09.026>
22. Forsythe N, Fowler HJ, Li X-FF, Blenkinsop S, Pritchard D. Karakoram temperature and glacial melt driven by regional atmospheric circulation variability. *Nat Clim Chang*. 2017; 7: 664–670. <https://doi.org/10.1038/nclimate3361>
23. Bagchi S, Ritchie ME. Herbivore effects on above- and belowground plant production and soil nitrogen availability in the Trans-Himalayan shrub-steppes. *Oecologia*. 2010; 164: 1075–1082. <https://doi.org/10.1007/s00442-010-1690-5> PMID: 20585808
24. Laws AN. Climate change effects on predator–prey interactions. *Curr Opin Insect Sci*. 2017; 23: 28–34. <https://doi.org/10.1016/j.cois.2017.06.010> PMID: 29129279
25. Aryal A, Shrestha UB, Ji W, Ale SB, Shrestha S, Ingty T, et al. Predicting the distributions of predator (snow leopard) and prey (blue sheep) under climate change in the Himalaya. *Ecol Evol*. 2016; 6: 4065–4075. <https://doi.org/10.1002/ece3.2196> PMID: 27516864
26. Holt CDS, Nevin OT, Smith D, Convery I. Environmental niche overlap between snow leopard and four prey species in Kazakhstan. *Ecol Inform*. 2018; 48: 97–103. <https://doi.org/10.1016/j.ecoinf.2018.09.005>
27. Sony RK, Sen S, Kumar S, Sen M, Jayahari KM. Niche models inform the effects of climate change on the endangered Nilgiri Tahr (*Nilgiritragus hylocrius*) populations in the southern Western Ghats, India. *Ecol Eng*. 2018; 120: 355–363. <https://doi.org/https%3A//doi.org/10.1016/j.ecoleng.2018.06.017>
28. Luo Z, Jiang Z, Tang S. Impacts of climate change on distributions and diversity of ungulates on the Tibetan Plateau. *Ecol Appl*. 2015; 25: 24–38. <https://doi.org/10.1890/13-1499.1> PMID: 26255355
29. Hess R, Bollmann K, Rasool G, Chaudhry AA, Virk AT, Ahmad A. Pakistan. In: Shackleton DM, editor. *Wild Sheep and Goats and their Relatives*. Gland, Switzerland: IUCN/SSC Caprinae Specialist Group; 1997. pp. 239–260.
30. Roberts TJ. *The Mammals of Pakistan*. Karachi, Pakistan: Oxford University Press; 1997. <https://books.google.com.pk/books?id=Dph1AAAACAAJ>
31. Fedosenko AK, Blank DA. *Capra sibirica*. *Mamm Species*. 2001; 675: 1–13.
32. Khattak RH, Ali H, Rehman E, Nawaz M. Population Structure of Blue Sheep (*Pseudios nayaur*) in Shimshal Valley Gilgit-Baltistan Pakistan. *Pak J Zool*. 2019.
33. Schaller GB. *Mountain monarchs. Wild sheep and goats of the Himalaya*. University of Chicago Press.; 1977.

34. Wilson P. Ecology and habitat utilisation of blue sheep *Pseudois nayaur* in nepal. *Biol Conserv*. 1981; 21: 55–74. [https://doi.org/10.1016/0006-3207\(81\)90068-9](https://doi.org/10.1016/0006-3207(81)90068-9)
35. Schaller GB. On the behaviour of blue sheep (*Pseudois nayaur*). *J Bombay Nat Hist Soc*. 1973; 69: 523–537.
36. Bosso L, Luchi N, Maresi G, Cristinzio G, Smeraldo S, Russo D. Predicting current and future disease outbreaks of *Diplodia sapinea* shoot blight in Italy: species distribution models as a tool for forest management planning. *For Ecol Manage*. 2017; 400: 655–664. <https://doi.org/10.1016/j.foreco.2017.06.044>
37. Mohammadi S, Ebrahimi E, Shahriari Moghadam M, Bosso L. Modelling current and future potential distributions of two desert jerboas under climate change in Iran. *Ecol Inform*. 2019; 52: 7–13. <https://doi.org/10.1016/j.ecoinf.2019.04.003>
38. Zain OF. A Socio-Political Study of Gilgit Baltistan Province. *Pakistan J Soc Sci*. 2010; 30: 181–190.
39. Dani AH. History of Northern Areas of Pakistan. Lahore, Pakistan: Sang E Meel, Publishers; 2001.
40. Roa AL, Marwat AH. NASSD Background Paper: Forestry. Northern Areas Program, Gilgit; 2003.
41. Virk AT, Sheikh KM, Marwat AH. NASSD Background Paper: Biodiversity. Northern Areas Program, Gilgit; 2003. <http://serenagilgitbaltistan.com/wp-content/uploads/2012/02/11-Water.pdf>
42. Bischof R, Ali H, Kabir M, Hameed S, Nawaz MA. Being the underdog: an elusive small carnivore uses space with prey and time without enemies. *J Zool*. 2014; 293: 40–48. <https://doi.org/10.1111/jzo.12100>
43. Kabir M, Hameed S, Ali H, Bosso L, Din JUJU, Bischof R, et al. Habitat suitability and movement corridors of grey wolf (*Canis lupus*) in Northern Pakistan. *PLoS One*. 2017; 12: 1–17. <https://doi.org/10.1371/journal.pone.0187027> PMID: 29121089
44. Ali H, Younus M, Din JU, Bischof R, Nawaz MA. Do Marco Polo argali *Ovis ammon polii* persist in Pakistan? *Oryx*. 2017/04/12. 2019; 53: 329–333. <https://doi.org/10.1017/S0030605317000229>
45. Abellanas B, Pérez-Moreno PJ. Assessing spatial dynamics of a *Pinus nigra* subsp. *salzmannii* natural stand combining point and polygon patterns analysis. *For Ecol Manage*. 2018; 424: 136–153. <https://doi.org/10.1016/j.foreco.2018.04.050>
46. Boria RA, Olson LE, Goodman SM, Anderson RP. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecol Modell*. 2014; 275: 73–77. <https://doi.org/10.1016/j.ecolmodel.2013.12.012>
47. Smeraldo S, Di Febbraro M, Ćirović D, Bosso L, Trbojević I, Russo D. Species distribution models as a tool to predict range expansion after reintroduction: A case study on Eurasian beavers (*Castor fiber*). *J Nat Conserv*. 2017; 37: 12–20. <https://doi.org/10.1016/j.jnc.2017.02.008>
48. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol*. 2005; 25: 1965–1978. <https://doi.org/10.1002/joc.1276>
49. Khan N, Shahid S, Ahmed K, Ismail T, Nawaz N, Son M. Performance assessment of general circulation model in simulating daily precipitation and temperature using multiple gridded datasets. *Water (Switzerland)*. 2018; 10: 1793. <https://doi.org/10.3390/w10121793>
50. IPCC. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Pachauri RK, Meyer LA, editors. Geneva, Switzerland: IPCC; 2014.
51. Archis JN, Akcali C, Stuart BL, Kikuchi D, Chunco AJ. Is the future already here? The impact of climate change on the distribution of the eastern coral snake (*Micrurus fulvius*). Costello M, editor. *PeerJ*. 2018; 6: e4647. <https://doi.org/10.7717/peerj.4647> PMID: 29736330
52. Phillips SJ, Anderson RP, Dudík M, Schapire RE, Blair ME. Opening the black box: an open-source release of Maxent. *Ecography (Cop)*. 2017; 40: 887–893. <https://doi.org/10.1111/ecog.03049>
53. Balakrishnan B, Nandakumar N, Sebastin S, Kareem KAA. Species distribution models (SDM)—a strategic tool for predicting suitable habitats for conserving the target species: GIS and special distribution modelling (SDM). In: Association IRM, editor. *Environmental Information Systems: Concepts, Methodologies, Tools, and Applications*. Hershey, PA, USA: IGI Global; 2018. pp. 555–568.
54. Byeon D hyeon, Jung S, Lee WH. Review of CLIMEX and MaxEnt for studying species distribution in South Korea. *J Asia-Pacific Biodivers*. 2018; 11: 325–333. <https://doi.org/10.1016/j.japb.2018.06.002>
55. Gomes VHF, Ijff SD, Raes N, Amaral IL, Salomão RP, Coelho LDS, et al. Species Distribution Modelling: Contrasting presence-only models with plot abundance data. *Sci Rep*. 2018; 8: 1003. <https://doi.org/10.1038/s41598-017-18927-1> PMID: 29343741
56. Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. A statistical explanation of MaxEnt for ecologists. *Divers Distrib*. 2011; 17: 43–57. <https://doi.org/10.1111/j.1472-4642.2010.00725.x>
57. Raxworthy CJ, Martinez-Meyer E, Horning N, Nussbaum RA, Schneider GE, Ortega-Huerta MA, et al. Predicting distributions of known and unknown reptile species in Madagascar. *Nature*. 2003; 426: 837–841. <https://doi.org/10.1038/nature02205> PMID: 14685238

58. Phillips SJ, Dudík M. Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography (Cop)*. 2008; 31: 161–175. <https://doi.org/10.1111/j.0906-7590.2008.5203.x>
59. Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W. Evaluation of consensus methods in predictive species distribution modelling. *Divers Distrib*. 2009; 15: 59–69. <https://doi.org/10.1111/j.1472-4642.2008.00491.x>
60. Araújo MB, Whittaker RJ, Ladle RJ, Erhard M. Reducing uncertainty in projections of extinction risk from climate change. *Glob Ecol Biogeogr*. 2005; 14: 529–538. <https://doi.org/10.1111/j.1466-822X.2005.00182.x>
61. Araújo MB, New M. Ensemble forecasting of species distributions. *Trends Ecol Evol*. 2007; 22: 42–47. <https://doi.org/10.1016/j.tree.2006.09.010> PMID: 17011070
62. Fielding AH, Bell JF. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ Conserv*. 2002/05/10. 1997; 24: 38–49. <https://doi.org/10.1017/S0376892997000088>
63. Allouche O, Tsoar A, Kadmon R. Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *J Appl Ecol*. 2006; 43: 1223–1232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>
64. Warren DL, Glor RE, Turelli M. Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution (N Y)*. 2008; 62: 2868–2883. <https://doi.org/10.1111/j.1558-5646.2008.00482.x> PMID: 18752605
65. Araújo MB, Anderson RP, Barbosa AM, Beale CM, Dormann CF, Early R, et al. Standards for distribution models in biodiversity assessments. *Sci Adv*. 2019; 5: eaat4858. <https://doi.org/10.1126/sciadv.aat4858> PMID: 30746437
66. El-Gabbas A, Dormann CF. Wrong, but useful: regional species distribution models may not be improved by range-wide data under biased sampling. *Ecol Evol*. 2018; 8: 2196–2206. <https://doi.org/10.1002/ece3.3834> PMID: 29468036
67. Renner IW, Warton DI. Equivalence of MAXENT and Poisson Point Process Models for Species Distribution Modeling in Ecology. *Biometrics*. 2013; 69: 274–281. <https://doi.org/10.1111/j.1541-0420.2012.01824.x> PMID: 23379623
68. Khan B, Ablimit A, Khan G, Jasra AW, Ali H, Ali R, et al. Abundance, distribution and conservation status of Siberian ibex, Marco Polo and Blue sheep in Karakoram-Pamir mountain area. *J King Saud Univ —Sci*. 2016; 28: 216–225. <https://doi.org/10.1016/j.jksus.2015.02.007>
69. Maurer JM, Schaefer JM, Rupper S, Corley A. Acceleration of ice loss across the Himalayas over the past 40 years. *Sci Adv*. 2019; 5: eaav7266. <https://doi.org/10.1126/sciadv.aav7266> PMID: 31223649
70. Wiltshire AJ. Climate change implications for the glaciers of the Hindu Kush, Karakoram and Himalayan region. *Cryosph*. 2014; 8: 941–958. <https://doi.org/10.5194/tc-8-941-2014>
71. Hewitt K. The Karakoram Anomaly? Glacier Expansion and the 'Elevation Effect,' Karakoram Himalaya. *Mt Res Dev*. 2005; 25: 332–340. [https://doi.org/10.1659/0276-4741\(2005\)025\[0332:TKAGEA\]2.0.CO;2](https://doi.org/10.1659/0276-4741(2005)025[0332:TKAGEA]2.0.CO;2)
72. Niittynen P, Luoto M. The importance of snow in species distribution models of arctic vegetation. *Ecography (Cop)*. 2018; 41: 1024–1037. <https://doi.org/10.1111/ecog.03348>
73. Reading A. *Capra sibirica*, Siberian Ibex. 2015 [cited 22 Apr 2020]. <https://www.iucnredlist.org/species/42398/10695735>
74. Khan MZ, Khan B, Ahmed E, Khan G, Ajmal A, Ali R, et al. Abundance, distribution and conservation of key ungulate species in Hindu Kush, Karakoram and Western Himalayan (HKH) mountain ranges of Pakistan. *Int J Agric Biol*. 2014; 16: 1050–1058.
75. Ciach M, Pęksa Ł. Impact of climate on the population dynamics of an alpine ungulate: a long-term study of the Tatra chamois *Rupicapra rupicapra tatrica*. *Int J Biometeorol*. 2018; 62: 2173–2182. <https://doi.org/10.1007/s00484-018-1619-y> PMID: 30276475
76. Lu X, Huang R, Wang Y, Sigdel SR, Dawadi B, Liang E, et al. Summer Temperature Drives Radial Growth of Alpine Shrub Willows on the Northeastern Tibetan Plateau. *Arctic, Antarct Alp Res*. 2016; 48: 461–468. <https://doi.org/10.1657/AAAR0015-069>
77. Hughes L. Biological consequences of global warming: is the signal already apparent? Hughes, L., 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution*, 15(2), pp.56–61. Available at: <https://www.sciencedirect.com>. *Trends Ecol Evol*. 2000; 15: 56–61. [https://doi.org/10.1016/S0169-5347\(99\)01764-4](https://doi.org/10.1016/S0169-5347(99)01764-4)
78. Finke DL, Snyder WE. Niche Partitioning Increases Resource Exploitation by Diverse Communities. *Science (80-)*. 2008; 321: 1488 LP–1490. <https://doi.org/10.1126/science.1160854> PMID: 18787167
79. Salick J, Ghimire SK, Fang Z, Dema S, Konchar KM. Himalayan Alpine Vegetation, Climate Change and Mitigation. *J Ethnobiol*. 2014; 34: 276–293. <https://doi.org/10.2993/0278-0771-34.3.276>

80. Dolezal J, Dvorsky M, Kopecky M, Liancourt P, Hiiesalu I, MacEk M, et al. Vegetation dynamics at the upper elevational limit of vascular plants in Himalaya. *Sci Rep.* 2016; 6: 24881. <https://doi.org/10.1038/srep24881> PMID: 27143226
81. Uhlig H. Geoeological Controls on High-Altitude Rice Cultivation in the Himalayas and Mountain Regions of Southeast Asia. *Arct Alp Res.* 2006; 10: 519. <https://doi.org/10.2307/1550785>
82. Bagchi S, Mishra C, Bhatnagar Y V. Conflicts between traditional pastoralism and conservation of Himalayan ibex (*Capra sibirica*) in the Trans-Himalayan mountains. *Anim Conserv.* 2004; 7: 121–128. <https://doi.org/10.1017/S1367943003001148>
83. Bhattacharya T, Bashir T, Poudyal K, Sathyakumar S, Saha GK. Distribution, Occupancy and Activity Patterns of Goral (*Nemorhaedus goral*) and Serow (*Capricornis thar*) in Khangchendzonga Biosphere Reserve, Sikkim, India. *Mammal Study.* 2012; 37: 173–181. <https://doi.org/10.3106/041.037.0302>
84. Mishra C, Van Wieren SE, Ketner P, Heitkönig IMA, Prins HHT. Competition between domestic live-stock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya. *J Appl Ecol.* 2004; 41: 344–354. <https://doi.org/10.1111/j.0021-8901.2004.00885.x>
85. Hobbs NT. Modification of Ecosystems by Ungulates. *J Wildl Manage.* 2007. <https://doi.org/10.2307/3802368>
86. Murray BD, Webster CR, Bump JK. Broadening the ecological context of ungulate-ecosystem interactions: The importance of space, seasonality, and nitrogen. *Ecology.* 2013. <https://doi.org/10.1890/12-1582.1> PMID: 23923495
87. Morelli TL, Daly C, Dobrowski SZ, Dulen DM, Ebersole JL, Jackson ST, et al. Managing climate change refugia for climate adaptation. *PLoS One.* 2016; 11: 1–17. <https://doi.org/10.1371/journal.pone.0159909> PMID: 27509088
88. Morelli TL, Maher SP, Lim MCW, Kastely C, Eastman LM, Flint LE, et al. Climate change refugia and habitat connectivity promote species persistence. *Clim Chang Responses.* 2017; 4: 8. <https://doi.org/10.1186/s40665-017-0036-5>