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Climate refugia of snow leopards in High Asia

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ABSTRACT

Rapid warming in High Asia is threatening its unique ecosystem and endemic species, especially the endangered snow leopard (*Panthera uncia*). Snow leopards inhabit the alpine zone between snow line and tree line, which contracts and expands greatly during glacier-interglacial cycles. Here we assess impacts of climate change on global snow leopard habitat from the last glacial maximum (LGM; 21 kyr ago) to the late 21st century. Based on occurrence records of snow leopards collected across all snow leopard range countries from 1983 to 2015, we built a snow leopard habitat model using the maximum entropy algorithm (MaxEnt 3.3.3k). Then we projected this model into LGM, mid-Holocene and 2070. Analysis of snow leopard habitat map from LGM to 2070 indicates that three large patches of stable habitat have persisted from the LGM to present in the Altai, Qilian, and Tian Shan-Pamir-Hindu Kush-Karakoram mountain ranges, and are projected to persist through the late 21st century. These climatically suitable areas account for about 35% of the snow leopard's current extent, are large enough to support viable populations, and should function as refugia for snow leopards to survive through both cold and warm periods. Existence of these refugia is largely due to the unique mountain environment in High Asia, which maintains a relatively constant arid or semi-arid climate. However, habitat loss leading to fragmentation in the Himalaya and Hengduan Mountains, as well as increasing human activities, will present conservation challenges for snow leopards and other sympatric species.

1. Introduction

Accelerated global warming over recent decades is altering ecosystems and threatens biodiversity (Thomas et al., 2004; Walther et al., 2002). Known as the "roof of the world", the Tibetan Plateau and surrounding mountain ranges of Central Asia (henceforth referred to as High Asia (Kuhle, 1990), Fig. 1a) have warmed at more than twice the average warming rate of the Northern Hemisphere (Chen et al., 2009; Liu and Chen, 2000). This high rate of warming places the unique ecosystem of High Asia at risk and threatens many endemic mammals, such as the snow leopard (*Panthera uncia*), chiru (*Pantholops hodgsonii*), blue sheep (*Pseudois nayaur*) and wild yak (*Bos mutus*). Among them, the snow leopard is an apex predator that plays an important role in maintaining stability of the alpine ecosystem (Snow Leopard Network, 2014). Due to its small population size and threats posed by habitat loss, a declining prey base, and poaching, the snow leopard was listed as Endangered by the International Union for Conservation of Nature (IUCN) in 1972 (Jackson et al., 2008). The ongoing climate change characterized by rapid warming could further challenge the persistence of remaining snow leopard populations (Forrest et al., 2012).

Large climate shifts have occurred repeatedly in Earth's history, most recently in the glacial-interglacial cycles of the late Quaternary, which played an important role in the extinction of many megafauna species, such as the wooly mammoth (*Mammuthus primigenius*) and giant deer (*Megaloceros giganteus*) (Cooper et al., 2015; Koch and Barnosky, 2006). During cold periods, many warm-adapted species were locally extirpated, due to the advance of major ice sheets, whereas in warm periods the shift of shrubs and forest drove many cold-adapted tundra-steppe species to localized extinction (Guthrie, 2003; Willerslev et al., 2014). Yet some species survived the late Quaternary because of the

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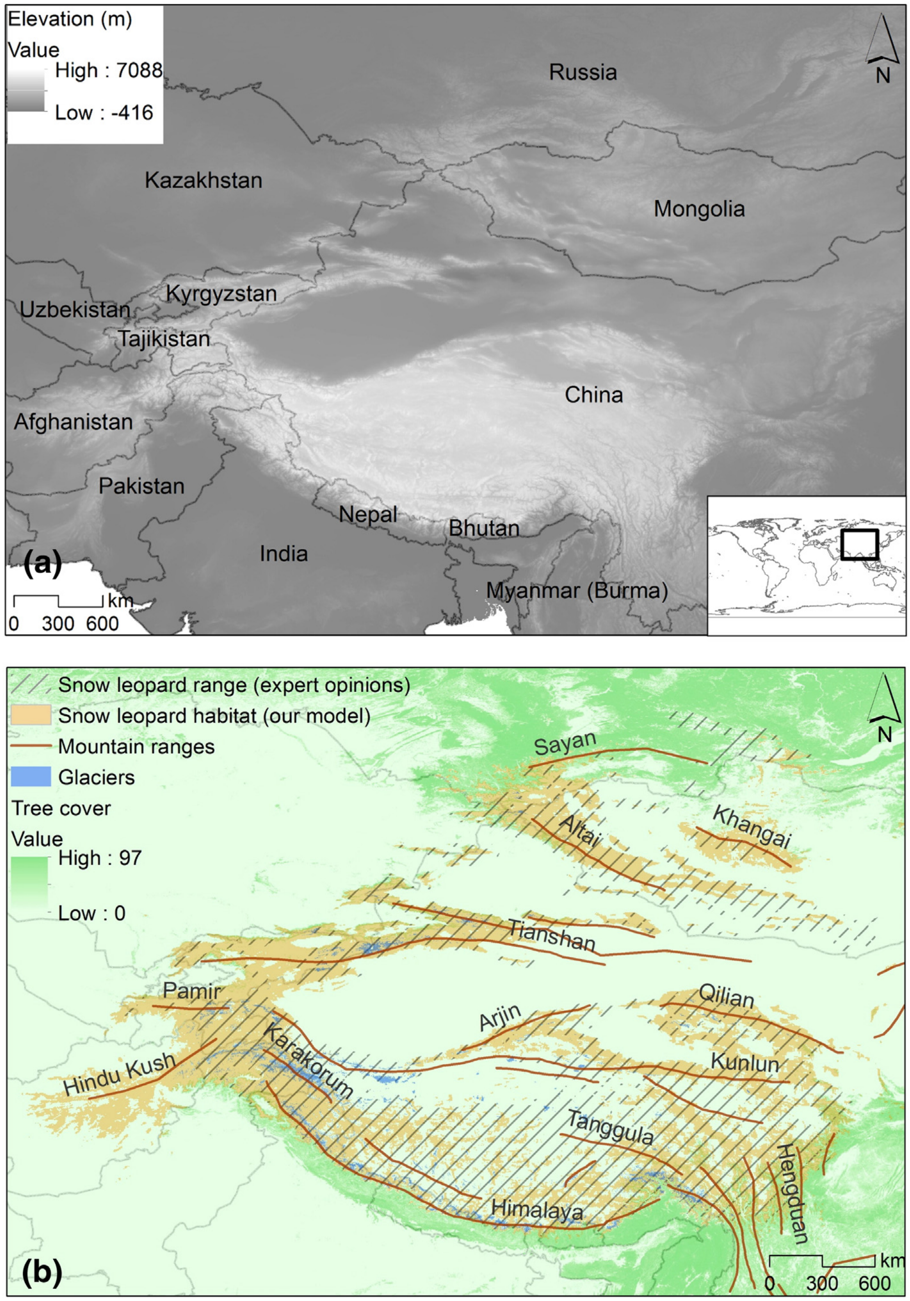

Fig. 1. Distribution of current snow leopard habitat in High Asia. (a), Location of the study region. The study region includes the Tibetan plateau and surrounding mountain ranges (referred to as High Asia). (b), Current snow leopard habitat distribution map. The distribution map predicted by our model (orange) was overlapped with the map derived by expert opinion (McCarthy et al., 2016) (hatched lines). Blue and green colors represent current glaciers (Armstrong et al., 2005) and tree cover (Hansen et al., 2013) ranges, respectively, while brown lines represent the main mountain ranges. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

availability of climate refugia, where they could retreat to, persist in, and expand from under rapid and severe climate changes (Ashcroft, 2010; Keppel et al., 2012). Refugia usually have a relatively stable climate and complex landscape topography, and thus offer the best chance for survival of many taxa when climate changes (Ashcroft, 2010; Morelli et al., 2016). The snow leopard, which originated on the Tibetan Plateau about seven million years ago (Tseng et al., 2014), currently inhabits the alpine zone that lies between the snow line and tree line throughout the mountains of High Asia (Fig. 1) (Snow Leopard Network, 2014). Such alpine zones contracted and expanded greatly during periods of glacier-interglacial cycling (DeChaine and Martin, 2004). Nonetheless, the snow leopard not only survived, but is thought to have had a relatively stable population throughout the late Quaternary (Cho et al., 2013). Analysis of how snow leopards survived the past glacial-interglacial cycles may shed light on understanding the impacts of 21st century climate changes on snow leopards and other species endemic to High Asia.

Here we build a snow leopard distribution model based on contemporary snow leopard occurrences throughout its range and associated bioclimatic variables. Using this model, we assess the impacts of climate change on global snow leopard habitat from the Last Glacial Maximum (LGM) to the late 21st century. We identify climate refugia for snow leopards in High Asia, and analyze the climatic factors and geographical features that promote the existence of refugia. Then we discuss climatic stability of the unique mountain environment in High Asia, which is favorable to snow leopard and other alpine species, and conclude by discussing the challenges to snow leopard conservation.

2. Methods

2.1. Snow leopard occurrence records

We used 2820 snow leopard occurrence records from 1983 to 2008 spanning all 12 snow leopard range countries that were verified by snow leopard experts at the *2008 International Conference on Range-wide Conservation Planning for Snow Leopards* (McCarthy et al., 2016). To diminish potential spatial errors, we retained only 1845 records with a location uncertainty less than 10 km. We also collected camera-trap or genetic-verified snow leopard occurrence records from the published literature, including 17 records in Kyrgyzstan and Xinjiang Autonomous Region in China (McCarthy et al., 2008), 113 records in Qinghai Province in China (Li et al., 2014), and 3 records in Tibet Autonomous Region in China (Zhou et al., 2014). We also have some unpublished data including 15 snow leopard occurrence records based on camera traps in Sichuan Nature reserves, 334 records in Qinghai, Sichuan and Tibet provinces provided by Peking University, Shanshui Conservation Center, and Dr. George Schaller. A final total of 2327 occurrence records were used in this study, and they covered all the main mountain ranges in snow leopard range (Fig. S1).

2.2. Snow leopard habitat distribution model

We employed the maximum entropy algorithm (MaxEnt 3.3.3k), one of the most robust bioclimatic modelling approaches for presence-only data (Elith et al., 2011), to map current snow leopard habitat based on occurrence records. Five bioclimatic variables were chosen to fit the MaxEnt model based on their biological importance to snow leopards and their alpine steppe habitat: altitude and ruggedness (Li et al., 2014), bio10 (mean temperature of warmest quarter), bio11 (mean temperature of coldest quarter), and bio12 (annual precipitation) (Körner, 2012; Ohmura et al., 1992). Ruggedness was calculated from SRTM (Shuttle Radar Topography Mission, 30 m × 30 m) with the VRM (vector ruggedness measure) tools in ArcMap (Sappington et al., 2007) and then rescaled to 2.5 arc-minutes. Gridded bio10, bio11 and bio12 variables (2.5 arc-minutes) for contemporary conditions were downloaded from the WorldClim database to represent the current climate (Hijmans et al., 2005). To control sampling bias, we removed duplicate records in each grid in the MaxEnt software, and then generated a bias layer by calculating kernel density of occurrence points with a 30 km distance for use in the MaxEnt model. We generated a 500 km buffer around all occurrence points and the snow leopard range delineated by expert opinions (McCarthy et al., 2016) to determine the extent of the study region (see the electronic supplementary material, Fig. S1), which is larger than the distribution of known fossil records of snow leopards and their main prey, blue sheep (Brandt, 1871; Dennell et al., 2005; Tscherski, 1892; Tong et al., 2008). We used most default settings for the MaxEnt model (3.3.3k) except we selected the hinge feature (Elith et al., 2010) and generated 30,000 background points across the study region. We reclassified the logistic results of MaxEnt model with the threshold of "equal training sensitivity and specificity" (Liu et al., 2013).

Next, we projected the species distribution model into the LGM (21 kyr ago), mid-Holocene (6 kyr ago), and 2070 (average for 2061–2080) by applying the bioclimatic models to multiple general circulation models (GCMs). To account for uncertainties inherent in climate projections, we used a consensus approach in the LGM, mid-Holocene, and 2070 by showing projected habitat identified as suitable by more than half of the GCMs. All GCMs were downloaded from the WorldClim database, including three GCMs of the LGM, 7 of 9 GCMs of the mid-Holocene from 7 different institutions, and 7 GCMs of 2070 (average for 2061–2080) from the same 7 institutions (see the electronic supplementary material, Table S1). To evaluate model performance, we used five-fold cross-validation and the area under the ROC curve (AUC). All area calculations were done in the projection of Asia North Albers Equal Area Conic. GIS work was done using ArcGIS 10.3.

We calculated the mean values of bio10, bio11 and bio12 in the large refugia (with an area larger than 50,000 km^2), and in habitat lost in the LGM or 2070 (RCP8.5). The error bars in Fig. 3 represent the variation of the mean values when multiple GCMs were chosen to do the calculation.

2.3. Habitat connectivity analysis

To estimate changes in habitat connectivity, we calculated the cost-weighted distances between current patches for comparison with similar measures between patches in 2070 (RCP8.5) with the linkage mapper package in ArcGIS (McRae and Kavanagh, 2011). We used stable snow leopard habitat that existed in all the four time periods as core areas. We used the inverse of the logistic output from our MaxEnt model as a measure of movement cost for snow leopards, and rescaled from 1 (lower cost) to 99 to construct a resistance layer, rather than cost values based on elevation and land cover types (Riordan et al., 2016). For the grid with a value larger than the threshold (equal train sensitivity and specificity given by the MaxEnt model), resistance was set to 1. For the grid with a value smaller than the threshold, resistance was set to (threshold - "value") × 100/threshold. We then used the cost-weighted and Euclidean network analysis method, and pruned the network to the nearest neighbor in Linkage Mapper. We set the bounding circles buffer distance as 12 km, which is a common limit of daily movements for snow leopards (McCarthy et al., 2005). We set the maximum Euclidean corridor distance as 40 km, the longest observed distance travelled in a single day by a snow leopard (McCarthy et al., 2005). All layers were projected to Asia North Equidistance Conic coordinate system for all connectivity analyses.

3. Results

3.1. Current snow leopard habitat

We first built a snow leopard habitat distribution model, and used the five-fold cross-validation procedure and the area under the ROC curve (AUC), as well as true skill statistic (TSS) (Allouche et al., 2006) to evaluate model performance. AUC of the model was 0.900 ± 0.004 (SD) (see the electronic supplementary material, Fig. S2), and TSS was 0.666 ± 0.017 (SD), indicating that this model performed well in the simulation of snow leopard habitat.

The distribution model indicates snow leopard habitat is currently distributed throughout all the main mountain ranges in High Asia, including the Altai, Sayan, Khangai, Tian Shan, Pamir, Hindu Kush, Karakorum, Kunlun, Qilian, Hengduan and Himalaya (Fig. 1b). In addition to these 12 snow leopard range countries, Myanmar is also predicted to support a small area of snow leopard habitat (Table 1), as has been suggested by others (Snow Leopard Network, 2014), although no recent snow leopard occurrence has been reported there.

Model projections of current snow leopard habitat are compatible with the alpine zone that occurs between the current glaciers and forests in High Asia (Fig. 1b). It is also consistent with a snow leopard range map delineated by expert opinion (McCarthy et al., 2016), except that our model projections have a higher spatial resolution (Fig. 1b).

3.2. Simulation of past snow leopard habitat

We used the snow leopard distribution model to project snow leopard habitat in the Last Glacial Maximum (LGM; 21 kyr ago), mid-Holocene (6 kyr ago), and late 21st century (average for 2061–2080). These three periods represent the cold and warm phases of the last glacial period, and a near future scenario of global warming.

In the Last Glacial Maximum, our study region was about 6 °C colder and 13% drier than current conditions according to the general

Table 1
Estimates of snow leopard habitat area (km^2) in all the snow leopard range countries in current stage and in 2070, with accompanying percentage change.

Country	Current	2070			
		RCP2.6	RCP4.5	RCP6.0	RCP8.5
Afghanistan	190,839	165,741 (−13%)	158,107 (−17%)	147,770 (−23%)	133,431 (−30%)
Bhutan	8853	5427 (−39%)	3530 (−60%)	3682 (−58%)	1285 (−85%)
China	1,216,289	1,043,632 (−14%)	896,522 (−26%)	895,888 (−26%)	708,542 (−42%)
India	98,718	97,167 (−2%)	92,402 (−6%)	87,991 (−11%)	81,290 (−18%)
Kazakhstan	49,836	50,730 (2%)	51,128 (3%)	50,979 (2%)	51,951 (4%)
Kyrgyzstan	147,475	147,228 (0%)	146,571 (−1%)	146,024 (−1%)	145,210 (−2%)
Myanmar	1245	551 (−56%)	230 (−81%)	230 (−82%)	14 (−99%)
Mongolia	213,262	229,919 (8%)	244,303 (15%)	247,510 (16%)	275,711 (29%)
Nepal	19,945	14,440 (−28%)	10,496 (−47%)	10,185 (−49%)	3516 (−82%)
Pakistan	94,670	91,344 (−4%)	90,253 (−5%)	89,126 (−6%)	86,325 (−9%)
Russia	72,036	87,477 (21%)	100,107 (39%)	102,465 (42%)	120,434 (67%)
Tajikistan	96,553	96,762 (0%)	96,060 (−1%)	95,279 (−1%)	92,850 (−4%)
Uzbekistan	13,248	12,286 (−7%)	11,659 (−12%)	11,035 (−17%)	10,097 (−24%)
Sum	2,222,970	2,042,703 (−8%)	1,901,369 (−14%)	1,888,162 (−15%)	1,710,655 (−23%)

circulation models (GCMs) (see the electronic supplementary material, Table S1; Fig. S3). Compared with the current distributional range, our model suggests that snow leopard habitat in the LGM was located at lower latitudes and altitudes. Snow leopard habitat loss mainly occurred in the Sayan and Khangai Mountains in the northernmost portion of the snow leopard range, Arjin Shan in the innermost parts, and the mountaintop regions of Tian Shan and the Pamir Mountains (Fig. 2a). This result is supported by moraine evidence that glaciers in the Sayan and Khangai Mountains greatly advanced in the LGM (Rother et al., 2014; Sheinkman, 2011), and the area of glaciers in Tian Shan and Pamir was about three times greater than current size (Shi et al., 2005). Arjin Shan is located at the north edge of the Tibetan Plateau (Fig. 1a), where the annual precipitation was estimated to be only 20–60 mm in the LGM (Hijmans et al., 2005), too dry for the snow leopard and most of its prey. Snow leopard habitat gains in the LGM mainly occurred at the southern end of snow leopard range, including the Himalaya and Hengduan mountain ranges (Fig. 2a).

In the mid-Holocene, temperature was similar to the current climate and precipitation was greater in our study region (see the electronic supplementary material, Fig. S3). Projected snow leopard habitat in the mid-Holocene is similar to the current distribution, except for additional habitat in the western Kunlun Mountains (Fig. 2b). Nowadays, this area is extremely dry, with annual precipitation less than 60 mm, but GCMs suggest precipitation was dozens of millimeters greater 6000 years ago, which was validated by pollen and diatom evidence from the Sumxi-Longmu Co Basin (Elise and Francoise, 1993). Thus, our model indicates this area was suitable habitat for the snow leopard in the mid-Holocene (Fig. 2b).

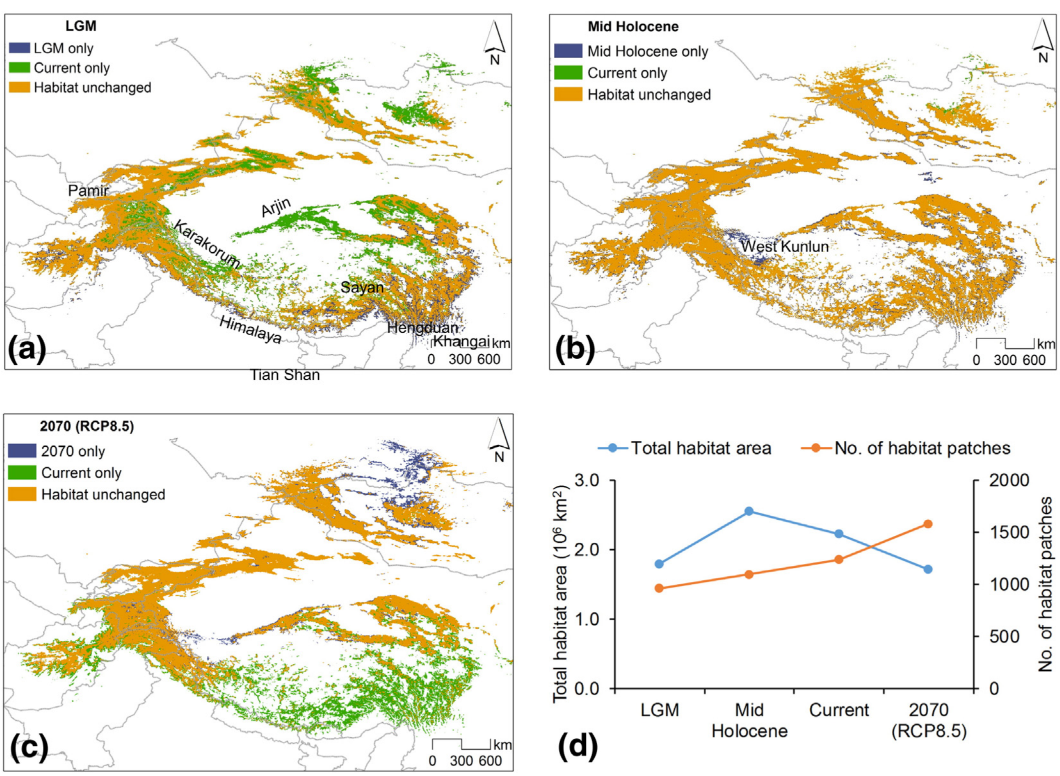

Fig. 2. Snow leopard habitat shifts with climate changes. (a–c), Comparison between current snow leopard habitat and modelled habitat in the LGM (a), mid Holocene (b) and 2070 (RCP 8.5) (c). The unchanged habitat, habitat that only occurs in current stage, and that is projected to only occur in the LGM or mid-Holocene or 2070 (RCP8.5) are colored orange, green, and blue, respectively. (d) Changes of the total habitat area and number of habitat patches over time. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Projected changes to snow leopard habitat in the late 21st century

Projection of climate in the late 21st century depends largely on greenhouse gas emissions. We projected our snow leopard habitat model to 2070 (average for 2061–2080) using the four "Representative Concentration Pathways" (RCPs) scenarios RCP2.6, RCP4.5, RCP6.0 and RCP8.5 adopted by the Intergovernmental Panel on Climate Change (IPCC), which represent low to high greenhouse gas emission rates (Stocker et al., 2013). In the scenario of RCP8.5, the increase of global temperature is greatest, and the winter and summer temperatures in our study region are predicted to increase by 3–7 °C and 3–5 °C in 2070, respectively; annual precipitation will increase by about 10% (see the electronic supplementary material, Fig. S3). Changes of these climate variables from present to 2070 (RCP8.5) vary greatly in current snow leopard range. Bio10 shows larger increase in the Altai, Tianshan, Pamir and Hindu Kush mountain ranges, and smaller increase in the Hengduan, Tanggula, and southeastern Himalaya mountain ranges; in contrast, bio11 is predicted to increase more rapidly in the Himalaya, Tanggula and the northwestern part of Hengduan mountain ranges; the annual precipitation (bio12) would decrease in the Hindu Kush mountain range, but would increase in the Tanggula, Hengduan and eastern Himalaya mountain ranges (see the electronic supplementary material, Fig. S4).

Our model shows that snow leopard habitat would respond by moving northward and upslope (Fig. 2c). Some new suitable habitat would emerge at high latitudes in the eastern Sayan, Khangai Mountains. This conclusion is supported by vegetation modelling that indicated the taiga forest near the border of Mongolia and Russia would be replaced by alpine steppe due to the melting of permafrost (Tchebakova et al., 2010). Snow leopard habitat in the southern portion of the range is predicted to be lost, including that in Himalaya and Hengduan mountains. Scenarios RCP2.6, RCP4.5 and RCP6.0 also predict snow leopard habitat in 2070 to shift northward and upslope, but the area of habitat loss in the southern range and gain in the high latitude area varies greatly (see the electronic supplementary material, Fig. S5). In most countries, snow leopards will suffer habitat loss; notably in Bhutan, Myanmar and Nepal, habitat loss will exceed 80% in 2070 in the scenario of RCP8.5. However, snow leopard habitat in 2070 should increase in Kazakhstan, Mongolia and especially in Russia, where the area of habitat will increase by about 67% in the scenario of RCP8.5 (Table 1).

We quantified trends in snow leopard habitat by calculating change in habitat area and number of habitat patches across all four time periods. Snow leopard habitat in the LGM and 2070 (RCP8.5) accounts for 81% and 77%, respectively, of the current range area (Fig. 2d). This estimate is consistent with genomic evidence that suggested relatively little snow leopard population change in the Quaternary (Cho et al., 2013). However, the number of habitat patches has continued to increase since LGM (Fig. 2d).

3.4. Climate refugia of snow leopards

We identified the overlap of snow leopard habitat in the LGM, mid-Holocene, current stage, and the late 21st century (RCP8.5) (Fig. 3a). These regions are predicted to be suitable snow leopard habitat from LGM to the late 21st century (RCP8.5). They are distributed in the interior of High Asia, including large continuous mountain ranges in the Altai, Tian San, Pamir, Karakorum, Qilian, and many small patches in the Himalaya and Hengduan mountains (Fig. 3a). The total area of these stable snow leopard habitats is 1.1 million km^2, divided into 1317 patches with a median patch size of 38 km^2. Among them, three patches are larger than 50,000 km^2: the Altai, Qilian, and Tian Shan-Pamir-Hindu Kush-Karakoram (TPHK) mountain ranges, with an area of 90,000, 110,000 and 570,000 km^2, respectively (see the electronic supplementary material, Fig. S6; Fig. 3a). The area of the three patches account for about 35% of that of the current snow leopard habitat.

Contemporary snow leopard densities in these three large patches vary from 0.15 to 3.31 individuals per 100 km^2 (Alexander et al., 2015; McCarthy et al., 2008). Using the average density 1.7 snow leopards per 100 km^2 as a rough estimate of snow leopard carrying capacity, the Altai, Qilian, and TPHK could support about 1500, 1800 and 9600 snow leopards, respectively, and would be large enough to function as effective snow leopard refugia (Flather et al., 2011). However, our estimation of carrying capacity should be considered preliminary, as it does not consider water availability, prey abundance or biotic interactions with competitors, which vary throughout the range (Lovari et al., 2013; Lyngdoh et al., 2014).

Other regions of snow leopard habitat were unstable through time. Habitat in the Sayan and Khangai mountain ranges is projected to contract in the LGM, but expand in 2070. In contrast, habitat in the southeastern Tibetan Plateau reached its largest extent in the LGM but should shrink in 2070 (RCP8.5) (Fig. 2a and c; Fig. 3a).

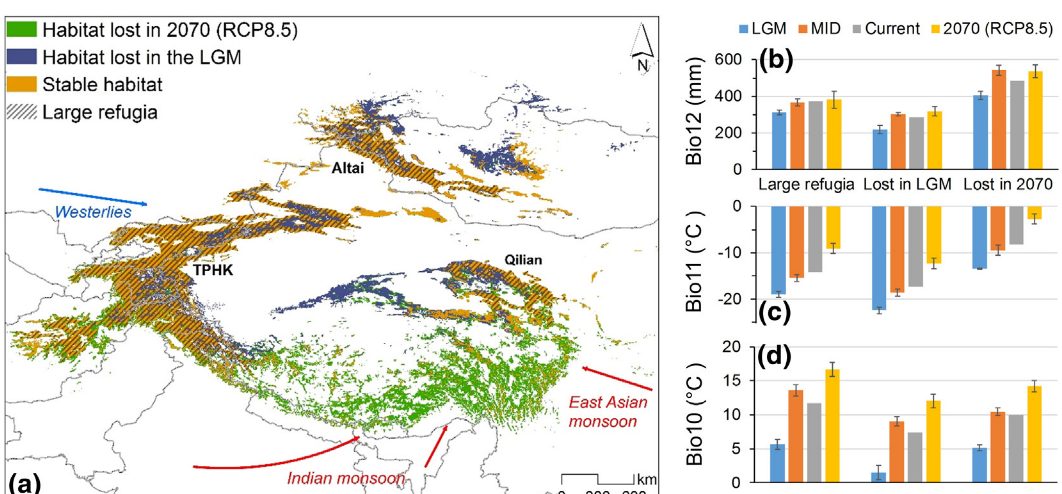

Fig. 3. Climate refugia of snow leopards. (a), Overlap of current snow leopard habitat with habitat in the LGM and in 2070 (RCP8.5). Habitat that persists from the LGM to 2070 (RCP8.5) is colored orange and the three large refugia are indicated by hatched lines. The westerlies and Asian monsoon, which are the dominant atmospheric circulation systems in High Asia, are indicated by blue and red arrows, respectively. (b–d), Changes of climate variables in the three large refugia, and in the habitat that did not occur in the LGM or would be lost in 2070 (RCP8.5). The annual precipitation (bio12) (b), mean temperature of coldest quarter (bio11) (c), and mean temperature of warmest quarter (bio10) (d) in the LGM, mid-Holocene, current stage and 2070 (RCP8.5) are calculated by averaging values from multiple GCMs. Error bar represents the standard deviation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.5. Determinants of snow leopard climate refugia

To understand the climate determinants that underlie the snow leopard refugia, we analyzed mean temperature of the warmest quarter (bio10), mean temperature of the coldest quarter (bio11) and annual precipitation (bio12), in the three large refugia and in habitat lost in the LGM or 2070 (RCP8.5).

In the three large refugia, annual precipitation is projected to increase from 310 mm in the LGM to 380 mm in 2070 (RCP8.5), while temperature in the coldest quarter would rise from −19 °C to −9 °C, and in the warmest quarter fluctuate between 5 °C and 17 °C (Fig. 3b–d). Precipitation and temperature are key factors that shape vegetation types and distribution around the world (Woodward and Williams, 1987). Several climate-vegetation models have been used to simulate global vegetation patterns, such as the BIOME models (Kaplan, 2003). An improved BIOME model, BIOME3China, showed a better ability to simulate the vegetation patterns on the Tibetan Plateau (Ni, 2000). According to this model, the vegetation type in areas with an annual precipitation between 250 mm and 500 mm is steppe. This result broadly agrees with the Köppen climate classification system, in which the three large snow leopard refugia are mainly designated as arid and semi-arid climate (see the electronic supplementary material, Fig. S7) (Peel et al., 2007).

Snow leopard habitat lost in the LGM currently is also mainly arid and semi-arid climate (see the electronic supplementary material, Fig. S7), with an annual precipitation (bio12) of about 280 mm. In the mid-Holocene and in 2070 (RCP8.5), these areas are projected to be slightly wetter, but in the LGM they would have received less precipitation (220 mm) (Fig. 3b). According to the BIOME3China model, regions with an annual precipitation less than 250 mm are desert. Furthermore, in the LGM the mean temperature of the warmest quarter (bio10) was estimated to be less than 2 °C, and the mean temperature of the coldest quarter (bio11) less than −22 °C (Fig. 3c and d). The low annual precipitation and low temperature would limit vegetation growth. Several studies have revealed that glaciers in these areas advanced greatly in the LGM (Rother et al., 2014; Sheinkman, 2011; Shi et al., 2005). As a result, in the LGM these areas would not have been suitable habitat for snow leopards.

Snow leopard habitat lost in 2070 (RCP8.5) is currently found in boreal, hemiboreal and oceanic climates (see the electronic supplementary material, Fig. S7). Annual precipitation in these areas is about 100 mm greater than in the three large refugia, especially in the mid-Holocene and 2070 (RCP8.5) when it is projected to exceed 500 mm (Fig. 3b). The mean temperature of the coldest quarter warmed from −13 °C in the LGM to −8 °C in the current stage, and is projected to exceed −3 °C in 2070 (RCP8.5) (Fig. 3c). Mean temperature of the warmest quarter shows similar changes; it would be 4 °C warmer in 2070 (RCP8.5) than in current stage (Fig. 3d). Temperature is intimately involved in the control of vegetation growth and reproduction, and warming usually leads to advance of the tree line (Grace et al., 2002). As a result of increases of both the annual precipitation and temperature in 2070 (RCP8.5), forest on the Tibetan Plateau will likely displace the current alpine steppe gradually from south and east to north and west with ongoing global warming (Liang et al., 2012), shrinking the alpine zone that is used by snow leopards in this region (Snow Leopard Network, 2014). Tree line has already moved 388 $\pm$ 80 m upward in the Indian Himalaya from 1970 to 2006, and 270 m upward in the southeastern Tibetan Plateau since 1920s (Baker and Moseley, 2007; Singh et al., 2012).

3.6. Habitat connectivity and human activities within the snow leopard range

To evaluate changes in connectivity of snow leopard habitat from present to 2070, we calculated the cost-weighted distance, which represents the least accumulative cost from each habitat patch to its nearest source and has been widely used to quantify habitat connectivity (Adriaensen et al., 2003). The result reveals an obvious increase of cost-weighted distance in the southern portion of the snow leopard range in the late 21st century (Fig. 4a).

We also evaluated human activities within the snow leopard range, because human activities are likely to decrease habitat connectivity. Overlap of our map of current snow leopard habitat with the global Human Footprint Index map (WCS et al., 2005) indicates a low level of human influence in most current snow leopard habitat (Fig. 4b).

4. Discussion

4.1. Climate refugia of snow leopards and alpine animals in High Asia

We identified three large patches of snow leopard refugia (the Altai, Qilian, and TPHK mountain ranges). Our analyses indicate that the refugia are steppes that have persisted since the LGM, and are unlikely to change by 2070. Extensive field work has revealed that steppes on the Tibetan Plateau support snow leopards and their main prey – blue sheep (Snow Leopard Network, 2014), explaining why the stable steppes can serve as snow leopard refugia. The stability of these steppes is closely related to the geography of these regions. The main sources of precipitation here are the winter mid-latitude westerlies and the summer Asian monsoon (Fig. 3a). But the Altai and Khangai mountains in the north block moisture transport of the mid-latitude westerlies (Jeremy et al., 2014), the Himalaya in the south blocks the Indian summer monsoon from the Indian Ocean, and the Hengduan Mountains in the east blocks the East Asian summer monsoon from the Pacific Ocean (Fig. 3a), leaving much of the interior of High Asia as arid or semi-arid zones. The aridity prevents development of forests in this region and also limits downward shifts of glaciers, creating stable conditions conducive to formation of steppes. As evidence of this effect, in the interior of the Tibetan Plateau the equilibrium line altitude (ELA) of glaciers was only 300–500 m lower in the LGM. In contrast, in the Alps in northern Europe, where westerly wind brought heavy precipitation, the ELA was at least 1000 m lower in the LGM. Consequently, no unified ice sheet formed on the Tibetan Plateau in the LGM, while a large ice sheet covered 80% of the Alps (Shi, 2002). Furthermore, analysis of distribution of 290 plant species and the corresponding climatic data on the Tibetan Plateau showed that the biome of the alpine steppe was ecologically stable from LGM to mid-Holocene (Miehe et al., 2011).

The relative stability of High Asia contrasts sharply with the northern Holarctic area, where continental glaciers formed in the LGM and forests spread in the mid Holocene. Such differences may contribute to different destinies of megafaunas in High Asia and that of the northern Holarctic area in the late Quaternary Pleistocene. In other words, our study indicates that climatic stability of the unique mountain environment enables High Asia to shelter snow leopards and other alpine animals during glacial-interglacial cycles. Indeed, mammalian fossil records have revealed that the Altai-Sayan mountains were refugia for several Last Glacial mammals (Ričánková et al., 2015).

4.2. Challenges to snow leopard conservation

Our identification of three large patches of climate refugia may explain how the snow leopard survived glacier-interglacial cycles. However, the rate of warming during recent decades is much greater than that during historical glacier-interglacial cycles. Thus, the window for snow leopards to adapt to climate change will likely be reduced from thousands of years to several decades. This challenge will be greatest for snow leopards inhabiting the Himalaya and Hengduan Mountain ranges, which are the most vulnerable areas to climate warming (see the electronic supplementary material, Fig. S5; Table 1). At the same time, in newly formed habitats that in the eastern Sayan and Khangai Mountains, snow leopards will face direct or indirect competition for resources with other carnivores, such as wolves (*Canis lupus*) and amur tigers (*Panthera tigris*).

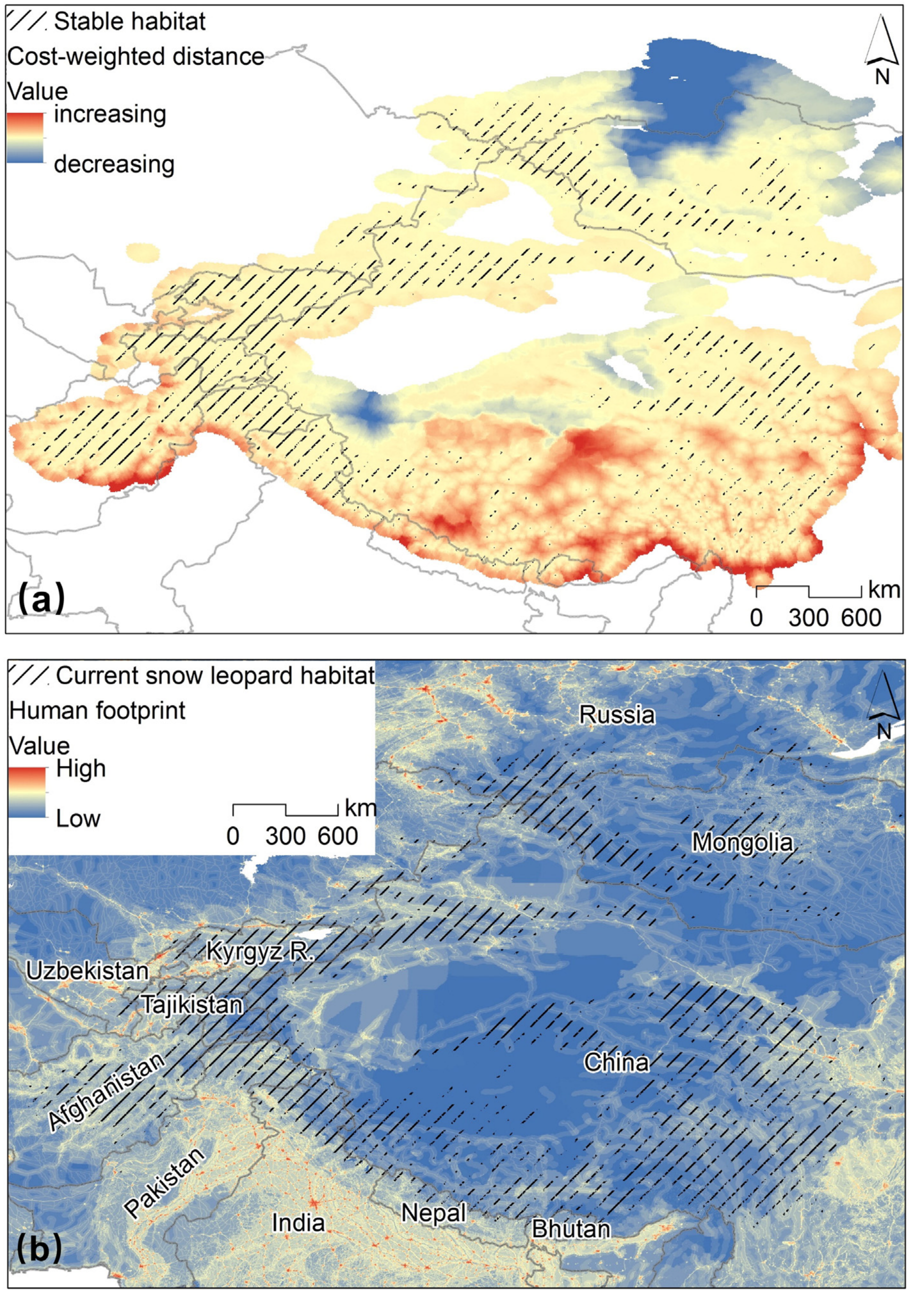

Fig. 4. Challenges to snow leopard conservation. (a), Habitat connectivity change from current stage to 2070 (RCP8.5). Cost weighted distance between stable habitat patches in the southern portion of the range of snow leopard habitat would increase in 2070 (RCP8.5), indicating a decrease of habitat connectivity in these areas. (b), Human footprint map in High Asia. Overlap of current snow leopard habitat with the human footprint map (WCS et al., 2005) reveals an overall low level of human activities in current snow leopard habitat. The harsh environment of the snow leopard range greatly limits human activities, but also results in fragility and low primary productivity of the ecosystem. Increasing human activities in this region challenges snow leopard conservation.

Habitat fragmentation associated with climate warming could present another conservation challenge for snow leopards. Our model shows a loss of 23% of snow leopard habitat area from current conditions to 2070 in the scenario of RCP8.5 (Table 1), and a concomitant increase in the number of habitat patches by about 30% (Fig. 2d). The resulting habitat fragmentation that accompanies habitat loss would decrease connectivity between habitat patches. Habitat connectivity in the southern portion of the snow leopard's range was recently suggested to be high (Riordan et al., 2016), but could be reduced by climate change in the late 21st century. The cost-weight distances of snow leopard habitat in Himalaya and Hengduan Mountains are predicted to increase in 2070 (Fig. 4a), indicating increased habitat fragmentation in these areas driven by climate warming.

Human influence is at a low level in most current snow leopard habitat (Fig. 4b). This occurs because the high altitude, cold, and harsh environment inhabited by snow leopards greatly limits human activities. In addition to the relatively stable climate, little human influence is an important reason why snow leopards can survive in these areas. However, the harsh environment also results in vulnerability of this ecosystem, and growing human activities in High Asia have exacerbated this problem (Cui and Graf, 2009). Human-snow leopard conflicts, represented by depredation on livestock and retaliatory killing (Bagchi and Mishra, 2006; Li et al., 2013; Wilman and Wilman, 2016) and snow leopard poaching and trade (Li and Lu, 2014), are great threats to snow leopard conservation. Herder and farmer interactions with snow leopards may have increased as they followed shifting grasslands and croplands northward and upward in elevation.

To deal with these challenges, establishing nature reserves is likely to be an effective strategy. In 1997, only 6% of snow leopard habitat was included in nature reserves (McCarthy and Chapron, 2003). Currently, reserve coverage has increased to about 19% of the snow leopard's range (Farrington and Li, 2016). There are still large gaps. Establishing nature reserves in snow leopard refugia to limit human activities is very important. At the same time, in the habitat vulnerable to climate warming, long-term efforts are needed to monitor the status of snow leopards and to provide targeted conservation solutions. Because snow leopard habitat occurs in 12 countries and our model shows that large patches of snow leopard habitat are located at the boundaries between countries, it will be especially important to build trans-boundary cooperation to ensure habitat connectivity and to reduce snow leopard poaching and trade.

5. Conclusions

In conclusion, projection of our snow leopard distribution model to the LGM, mid-Holocene and 2070 enabled us to identify climatically stable habitat and habitat that is threatened by climate change. The stable habitat, with a total area of about 1.1 million km^2, accounts for about 50% of the current snow leopard range. Three large patches, the Altai, Qilian, and Tian Shan-Pamir-Hindu Kush-Karakoram (TPHK) mountain ranges, which account for about 35% of the current snow leopard range, should function as effective snow leopard refugia. Existence of the refugia is largely due to the unique mountain environment in High Asia, which maintains a relatively constant arid or semi-arid climate. Aridity in these regions prevents development of forests and glaciers, and thus results in stable alpine steppe for snow leopards to inhabit. The stable alpine steppe may also function as climate refugia for other alpine animals.

Climate refugia sheltered snow leopards during the past glacier-interglacial cycles. However, in the 21st century rapid warming in High Asia will shorten the window for snow leopards to adapt to climate change, increase habitat fragmentation, and increase human activity in the region. Protection and restoration of the fragile alpine steppe ecosystem will be an important conservation action to benefit snow leopards and other sympatric species.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.09.026.

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