Biological Conservation 241 (2020) 108387

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Defining priorities for global snow leopard conservation landscapes

Juan Li[a,b,k,*], Byron V. Weckworth[b], Thomas M. McCarthy[b], Xuchuang Liang[c], Yanlin Liu[d], Rui Xing[e], Diqiang Li[d], Yuguang Zhang[d], Yadong Xue[d], Rodney Jackson[f], Lingyun Xiao[g,k], Chen Cheng[g,k], Sheng Li[h], Feng Xu[i], Ming Ma[i], Xin Yang[j], Kunpeng Diao[k], Yufang Gao[l], Dazhao Song[m], Kristin Nowell[n], Bing He[o], Yuhan Li[k], Kyle McCarthy[p], Mikhail Yurievich Paltsyn[q], Koustubh Sharma[r,s], Charu Mishra[r,s], George B. Schaller[t], Zhi Lu[g,k], Steven R. Beissinger[a,u]

[a] *Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720-3114, USA*
[b] *Panthera, New York, NY 10018, USA*
[c] *Wildlife Conservation Society, Beijing 100101, China*
[d] *Chinese Academy of Forestry, Beijing 100091, China*
[e] *Wildnessxj, Ürümqi, Xinjiang, China*
[f] *Snow Leopard Conservancy, Sonoma, CA 95476, USA*
[g] *Center for Nature and Society, College of Life Sciences, Peking University, Beijing 100871, China*
[h] *College of Life Sciences, Peking University, Beijing 100871, China*
[i] *Key Laboratory of Biogeography and Bioresource in Arid Land, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China*
[j] *Green river, Sichuan, China*
[k] *Shan Shui Conservation Center, Beijing 100871, China*
[l] *School of Forestry and Environmental Studies, Yale University, USA*
[m] *Chinese Felid Conservation Alliance, Beijing 101101, China*
[n] *Cat Action Treasury, Cape Neddick, ME 03902, USA*
[o] *World Wide Fund for Nature, Beijing 100037, China*
[p] *Department of Entomology and Wildlife Ecology, University of Delaware, 250 Townsend Hall, Newark, DE 19716, USA*
[q] *Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, NY, USA*
[r] *Snow Leopard Trust, Seattle, WA 98103, USA*
[s] *Nature Conservation Foundation, Mysore 570002, India*
[t] *Wildlife Conservation Society, New York, NY 10460, USA*
[u] *Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720-3160, USA*

ARTICLE INFO

Keywords:
Panthera uncia
Conservation prioritization
Landscape Conservation Unit
Connectivity
Linkage

ABSTRACT

The snow leopard (*Panthera uncia*) is an apex predator on the Tibetan Plateau and in the surrounding mountain ranges. It is listed as Vulnerable in the IUCN's Red List. The large home range and low population densities of this species mandate range-wide conservation prioritization. Two efforts for range-wide snow leopard conservation planning have been conducted based on expert opinion, but both were constrained by limited knowledge and the difficulty of evaluating complex processes, such as connectivity across large landscapes. Here, we compile > 6000 snow leopard occurrence records from across its range and corresponding environmental covariates to build a model of global snow leopard habitat suitability. Using spatial prioritization tools, we identified seven large continuous habitat patches as global snow leopard Landscape Conservation Units (LCUs). Each LCU faces differing threat levels from poaching, anthropogenic development, and climate change. We identified ten potential inter-LCU linkages, and centrality analysis indicated that Tianshan-Pamir-Hindu Kush-Karakorum, Altai, and the linkage between them play a critical role in maintaining the global snow leopard habitat connectivity.

* Corresponding author at: Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720-3114, USA.
E-mail addresses: lijuan924@gmail.com (J. Li), bweckworth@panthera.org (B.V. Weckworth), tmccarthy@panthera.org (T.M. McCarthy), rockylxc@hotmail.com (X. Liang), plateauhigh@gmail.com (Y. Liu), 394170014@qq.com (R. Xing), lidq@caf.ac.cn (D. Li), yugzhang@sina.com.cn (Y. Zhang), xueyadong334@163.com (Y. Xue), rodney@snowleopardconservancy.org (R. Jackson), ly.xiao@pku.edu.cn (L. Xiao), chengchen@shanshui.org (C. Cheng), shengli@pku.edu.cn (S. Li), xufeng@ms.xjb.ac.cn (F. Xu), maming@ms.xjb.ac.cn (M. Ma), 786084127@qq.com (X. Yang), diaokunpeng@shanshui.org (K. Diao), yufang.gao@yale.edu (Y. Gao), 3beicat@sina.com (D. Song), kristinnowell@gmail.com (K. Nowell), bhe@wwfchina.org (B. He), liyuhan@shanshui.org (Y. Li), mccarthy@udel.edu (K. McCarthy), mypaltsy@syr.edu (M.Y. Paltsyn), koustubhsharma@gmail.com (K. Sharma), charu@snowleopard.org (C. Mishra), gbs.kms@gmail.com (G.B. Schaller), luzhi@pku.edu.cn (Z. Lu), beis@berkeley.edu (S.R. Beissinger).

https://doi.org/10.1016/j.biocon.2019.108387
Received 2 July 2019; Received in revised form 2 December 2019; Accepted 10 December 2019
Available online 20 December 2019
0006-3207/

However, international border fences, railways and major roads can fragment LCUs and potentially obstruct linkages. We propose LCU-specific conservation strategies and transboundary cooperation that should be highlighted in future snow leopard conservation. This effort represents the first range-wide, systematic landscape conservation plan for snow leopards, and provides a rigorous and analytically sound basis for further survey and evaluation.

1. Introduction

To maximize conservation outcomes with limited resources, it is important to identify the regions with the highest conservation priorities. For ease of management or because of political factors, biodiversity conservation planning often sets priorities at regional or national scales based on administrative boundaries, but such efforts can conflict with global conservation priorities (Montesino Pouzols et al., 2014). This is especially true for geographically widespread species, such as large carnivores that require large areas and occur in low densities (Di Minin et al., 2016). Tigers and jaguars are successful cases, where range-wide conservation plans have featured collaboration among all range countries (Dinerstein et al., 2006; Rabinowitz and Zeller, 2010; Sanderson et al., 2002). Following the model of the Global Tiger Initiative's Global Tiger Recovery Program (GTRP), the Kyrgyz Republic initiated the Global Snow Leopard and Ecosystem Protection Program (GSLEP) in 2013, with the participation of governments and NGOs from all 12 snow leopard range countries (Snow Leopard Working Secretariat, 2013). The snow leopard (*Panthera uncia*) is a large cat and apex predator of the mountain ecosystem in the regions centered on the Tibetan Plateau. In contrast to its wide distribution range (1,776,000 to 3,300,000 km^2), the snow leopard has a small population size, which was estimated at 7446 to 7996 and shows a decreasing trend (McCarthy et al., 2017). The main threats come from habitat loss and fragmentation, prey depletion, poaching and retaliatory killing (Snow Leopard Network, 2014; McCarthy et al., 2017). It was estimated that up to 450 snow leopards have been poached annually since 2008 (Nowell et al., 2016). The snow leopard was listed as Endangered in the IUCN's red list from 1972 to 2016. In 2017, it was reassessed as Vulnerable (McCarthy et al., 2017). The downlisting was criticized by some researchers and conservationists who argued that the population size and the mature individuals of snow leopards were overestimated and the threats to snow leopard, such as poaching, were underestimated (Aryal, 2017; Ale and Mishra, 2018). Although downlisting has been debated, there is a consensus that snow leopard conservation efforts must be expanded and improved (Mallon and Jackson, 2017).

Two independent efforts based on expert opinion have been made to identify important landscapes for global snow leopard conservation. The first was a range-wide assessment and conservation planning meeting in Beijing, China in 2008 that was initiated by non-governmental organizations including Panthera, Snow Leopard Trust, Snow Leopard Network and Wildlife Conservation Society. Experts from 11 of the 12 snow leopard range countries conducted a mapping exercise using expert knowledge to demarcate snow leopard range and conservation units (SLCUs) (McCarthy et al., 2016). This meeting produced

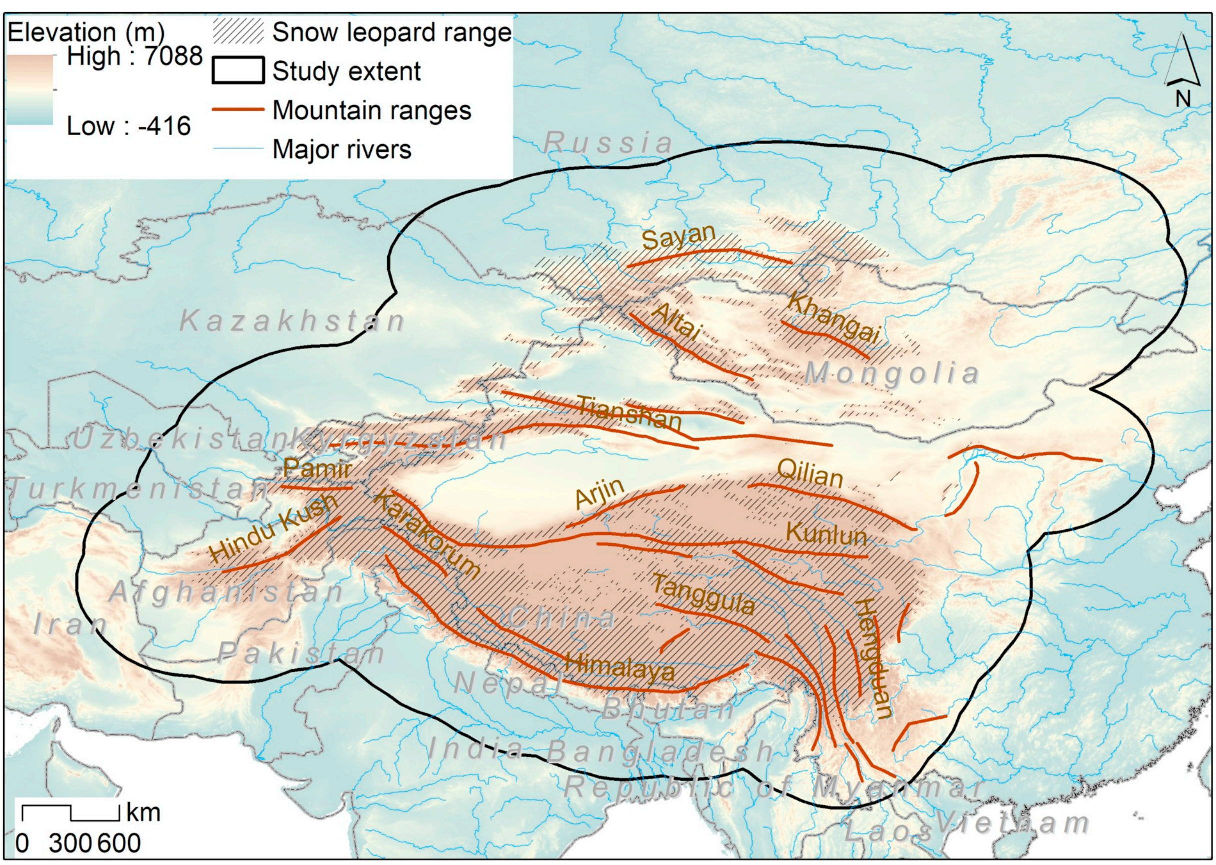

Fig. 1. Topographic features of the snow leopard study area. A 500-km buffer of the snow leopard range and all the snow leopard occurrence points defined the study extent. The main topographic features and snow leopard range are labelled, including the altitude, main mountain ranges (brown lines) and major rivers (blue lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the first range-wide spatially explicit maps of snow leopard conservation units. These maps have provided a sound basis for policymaker and scientists to develop strategies for snow leopard conservation. Five years later, a second assessment conducted under the global snow leopard and ecosystem protection program (GSLEP) used a consultative process involving both government and NGOs within each individual range country to identify snow leopard landscapes (SLLs) (Snow Leopard Working Secretariat, 2013). The involvement of national governments has greatly promoted the law enforcement and environmental-friendly planning of large infrastructure construction in snow leopard range. Both efforts have guided and influenced snow leopard conservation over the past decade and were important for building collaborations among all the snow leopard range countries. However, the conservation priorities that resulted from these efforts differ considerably, partly due to the limited knowledge of snow leopard ecology and the different approaches used for prioritizing conservation actions. Also, neither of the planning efforts adequately addressed landscape connectivity for genetic exchange and long-term survival of snow leopards, or the main threats to snow leopards that should inform conservation strategies. Over the past decade there has been a tremendous increase in the number of publications and sophistication of snow leopard research (Ale et al., 2010, 2014; Alexander et al., 2016; Aryal et al., 2014a, 2014b, 2014c, 2014d, 2016; Janečka et al., 2011; Karmacharya et al., 2011; Li et al., 2014; McCarthy et al., 2008; Zhou et al., 2014). This influx of new information filled key knowledge gaps that are important for rigorously defining snow leopard conservation landscapes.

In this study, we develop a spatial conservation plan for snow leopards by identifying Landscape Conservation Units, linkages and their primary threats using the best, up-to-date data available. First, we compiled > 6000 snow leopard occurrence records across the snow leopard range with fine resolution remote sensing data and environmental covariates to build a model of global snow leopard habitat suitability. We used the model and spatial conservation tools to prioritize global snow leopard habitat and designate global snow leopard Landscape Conservation Units (LCUs). Next, we applied circuit theory to quantify landscape connectivity patterns and identify linkages between the LCUs. Finally, we mapped potential threats to the LCUs and linkages. This effort represents the first range-wide, systematic landscape conservation plan for snow leopard conservation, and provides a rigorous and analytically sound basis for further efforts. The integrated mapping approach that is developed here, which combines habitat, connectivity, and threats, provides a model for conservation planning that could be applied to many species.

2. Methods

2.1. Study area

Our study area covers all putative snow leopard ranges that extend across the 12 known snow leopard range countries: Afghanistan, Bhutan, China, India, Kazakhstan, Kyrgyzstan, Mongolia, Nepal, Pakistan, Russia, Tajikistan and Uzbekistan, as well as Myanmar that has a small area of potential range (Fig. 1) (Snow Leopard Network, 2014). These ranges are distributed on the Tibetan Plateau and in the surrounding mountain ranges, including the Himalaya, Hindu Kush, Pamir, Kunlun, Tian Shan, Pamir, Altai and Hengduan mountain ranges (Fig. 1). These mountains also feed large rivers, such as the Yellow, Yangtze, and Mekong, that provide water to 1 billion people (Fig. 1).

2.2. Habitat suitability

Using maximum entropy, we modeled snow leopard habitat suitability based on occurrence records of snow leopards and related bioclimatic variables (Elith et al., 2010). A total of 6252 snow leopard occurrence records were collected through GPS collars, camera traps, genetically-verified feces, fresh scratches, scent marks, scrapes, and tracks of snow leopards from 1982 to 2017 in all the primary mountain ranges across the snow leopard distribution range. Except for about 5% of these records, most of them have been used in published studies (Ale et al., 2010, 2014; Jackson, 1996; Karmacharya et al., 2011; Li et al., 2016; McCarthy et al., 2008, 2016; Schaller, 2000; Zhou et al., 2014). The distribution pattern of the 6252 snow leopard occurrence records suggests a sampling bias, especially in Northwestern India and Russia (Fig. A1a), probably due to the different survey efforts. To remove aggregations of records, we thinned the occurrence records in geographical space using spThin R package (Aiello-Lammens et al., 2015). Three thinning distances, including 1 km, 10 km and 30 km, were tested, reducing the number of snow leopard occurrence records from 6252 to 2166, 833 and 407, respectively. Thirty km is slightly larger than the greatest distance (27.9 km) snow leopards are known to have travelled between locations on consecutive days (McCarthy et al., 2005). To determine which thinning distance should be used, we chose a region in the northwest India where the occurrence records density is very high (red rectangle in Fig. 1A). This region only corresponds to 0.56% of the total snow leopard range, but the number of snow leopard occurrence records in this region accounts for 7.4% (161/2166) and 6.6% (55/833) of the total snow leopard occurrence records after thinning the records with 1 km and 10 km distance, respectively, and the ratio decreased to 2.7% (11/407) when 30 km is used as the thinning distance, indicating that the 30-km thinning distance is better (Fig. A1b–d). The average test AUC of the habitat suitability model when using 1 km, 10 km and 30 km as the thinning distances are 0.874, 0.894 and 0.901, also suggesting that 30 km is better. Therefore, 30 km was used as the thinning distance.

We selected the following layers as candidate environmental variables, because of their relevance to the ecology of snow leopards: ruggedness, land cover, bioclimatic variables. Ruggedness was calculated from elevation (Shuttle Radar Topography Mission) with the terrain ruggedness index tools in ArcMap using a moving windows size of 3 ∗ 3. Land cover data came from the global 1-km consensus land cover data (with DISCover), which integrates multiple global land-cover products and maximizes accuracy (Tuanmu and Jetz, 2014). Bioclimatic variables for contemporary conditions were downloaded from Worldclim (version 2.0) at 30 second resolution (Hijmans et al., 2005). The study extent was set as a 500-km buffer of the snow leopard current range and all occurrence points (Fig. 1), as a recent range-wide genetic study of snow leopards showed that potential connectivity of dispersing individuals is between 250 and 500 km (Janecka et al., 2017). We analyzed correlation between all the candidate environmental variables. For those highly correlated variables (> 0.8), we kept the one which has direct ecological meaning to snow leopards. Then we removed the variables that contributed < 1% to the maxent model. Finally, ten environmental variables were chosen to build the snow leopard habitat suitability model, including terrain ruggedness index (alt_tri), mixed/other trees (landcover_4), herbaceous vegetation (landcover_6), cultivated and managed vegetation (landcover_7), barren (landcover_11), mean diurnal temperature range (wc2_bio02), max temperature of warmest month (wc2_bio05), mean temperature of coldest quarter (wc2_bio11), precipitation of warmest quarter (wc2_bio18) and precipitation of coldest quarter (wc2_bio19) (Table A1).

To optimize the tradeoff between goodness of fit and overfitting, in the habitat suitability model we tested 32 combinations between 4 feature classes (Linear; Linear and Quadratic; Linear, Quadratic, and Hinge; Linear, Quadratic, Hinge and Product) and 8 regularization multipliers (0.5–4.0 with 0.5 intervals). The model was evaluated using random fivefold cross-validation. AUCDiff (the difference between AUCtrain and AUCtest) was calculated to see the overfitting of the model (Warren and Seifert, 2011). The optimal feature class and regularization multiplier in the model with lowest AICc were selected (Warren and Seifert, 2011). The model evaluation was implemented in

R with ENMeval package (Muscarella et al., 2014).

2.3. Landscape prioritization

We used the planning tool Zonation (v4) to identify priority areas for conservation (Lehtomäki and Moilanen, 2013). Priority ranking was generated by iteratively removing the least valuable remaining grid cells, while accounting for total and remaining distributions of features throughout the entire landscape. We used the core area zonation (CAZ) cell removal method, which retains the locations with highest suitability. We considered connectivity in the Zonation model by setting distribution smoothing at 30 km, the greatest distance snow leopards travelled between consecutive-day locations (McCarthy et al., 2005). Of the priority landscapes (top 10% grid cells delineated by Zonation), we picked continuous areas larger than 10,000 km^2 and defined them as Landscape Conservation Units (LCUs), while areas smaller than 10,000 km^2 were defined as fragments. Snow leopard density varies from 0.15 to 3.1 individuals per 100 km^2 for a study area larger than 500 km^2 (Snow Leopard Network, 2014), a mean home range of male snow leopards based on 95% minimum convex polygon method (Johansson et al., 2016). Using an estimate of 1 individual per 100 km^2, a continuous habitat patch larger than 10,000 km^2 could support 100 individuals, a criteria of prioritized protecting habitat set by GSLEP.

2.4. Landscape connectivity

We applied two commonly used connectivity models to predict landscape connectivity between LCUs: the least-cost path (LCP) model and the circuit model (Cushman et al., 2013). The landscape connectivity was calculated under two scenarios of resistance. In scenario 1, the resistance layer (Fig. A3a) was generated from the habitat suitability map using the following equation (Keeley et al., 2016):

$$Resistance_{natural} = 100–99 * ((1 - \text{Exp}(-c * h))/(1 - \text{Exp}(-c)))$$

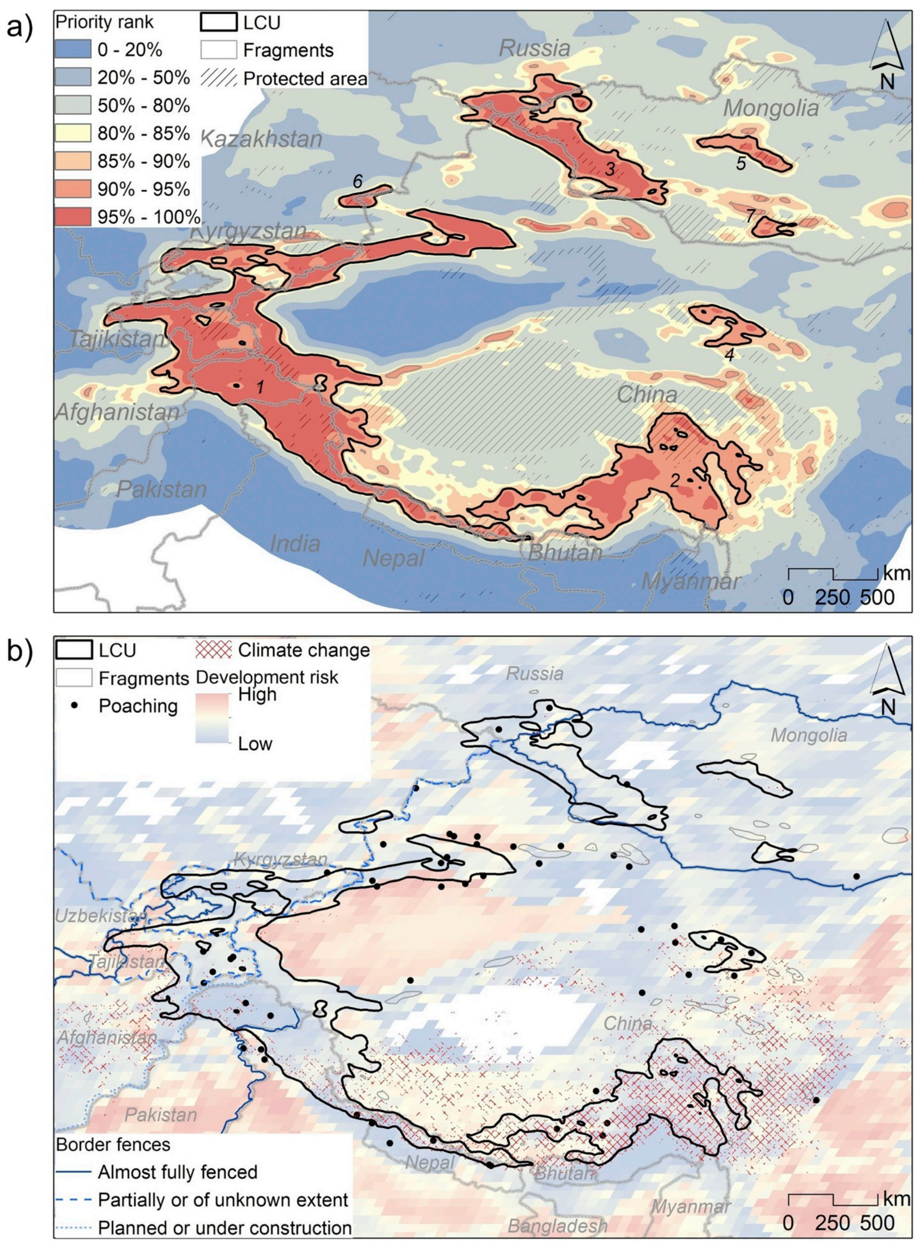

Fig. 2. Proposed global snow leopard Landscape Conservation Units (LCUs) and potential threats. (a) Top 10% prioritized areas are identified as LCUs (≥10,000 km^2) or fragments (< 10,000 km^2) (see Methods). (b) LCUs are facing threats from poaching (Nowell et al., 2016), climate change (Li et al., 2016), future development risk (Heiner et al., 2016), and international border fences (Linnell et al., 2016).

where *h* is the habitat suitability index from the maxent model and *c* is a factor that determines the shape of negative exponential curve. We used 16 as the value of c, the same as that was used to generate a resistance map for the desert bighorn sheep (*Ovis canadensis nelsoni*) (Keeley et al., 2016). Since only natural factors were considered in our maxent model, this resistance layer only reflects the natural resistance.

In scenario 2, we incorporated both the natural resistance and the anthropogenic resistance into the resistance layer. The anthropogenic resistance was calculated by considering both the human footprint index and the influence of border fences (Fig. A3b). The human footprint index, which has a range of 0 to 50, represents the influences of roads, railways, population density, built environments and so on (Venter et al., 2016). Border fences can be classified into three categories: the almost fully fenced border fences, partially or of unknown extent fences, and planned or under construction fences (Linnell et al., 2016). We gave the three categories a resistance value of 100, 50 and 0, respectively. Then we added up the human footprint index and the resistance value of border fences to generate the anthropogenic resistance map:

$$\text{Resistance}_{\text{anthropogenic}} = \text{Human footprint index} + \text{Border fences index}$$

The total resistance map in the second scenario was generated using the following equation:

$$\text{Resistance}_{\text{total}} = \text{resistance}_{\text{natural}} + \text{Resistance}_{\text{anthropogenic}}$$

Linkage mapper (v 2.0) was used to identify the least-cost paths between pairs of adjacent LCUs (McRae and Kavanagh, 2011). The cost-weighted distance (CWD), Euclidean distance (EuD), and least cost path (LCP) were calculated to quantify the linkages between LCUs (Dutta et al., 2016). The higher the ratio of CWD:EucD or CWD:LCP, the more difficulty to move between LCUs. Pinch points within linkages were identified using the pinchpoint mapper module in the linkage mapper. The pinchpoint mapper interfaces with Circuitscape (v4.0.5, McRae et al., 2013) to identify pinch points. Linkages were clipped to a 75 km cost-weighted width cutoff, following a landscape connectivity study done by the Washington Wildlife Habitat Connectivity Working Group (WHCWG, 2010). In that study, 75 km was used as the cost-weighted width cutoff value for the species which accumulate cost quickly when moving through suboptimal habitat, such as where bighorn sheep and Canada lynx (WHCWG, 2010). The centrality mapper module was used to calculate and map current flow centrality across the network, which provides an evaluation of the importance of a habitat patch or linkage in maintaining a connected network (Carroll et al., 2012).

2.5. Threat mapping

Major threats to the snow leopard have been identified as conflict with local people, poaching, and climate change (Snow Leopard Network, 2014), while emerging threats include energy, mineral and other natural resource development associated with transportation infrastructures and habitat modification (Heiner et al., 2016). Conflict with local people over livestock depredation often leads to poaching of snow leopards and illegal trade (Li and Lu, 2014; Nowell et al., 2016). We compiled the best available data of these threats. For poaching, we used the seizures dataset from a newly published report that mapped all available records of snow leopard poaching, smuggling, and illegal trade since 2003 (Nowell et al., 2016). Future energy and mineral development might have direct impacts on snow leopards through land use change, and indirect impacts through habitat fragmentation (Heiner et al., 2016; Oakleaf et al., 2015). We used data from Li et al. (2016) on the impacts of climate change on global snow leopard habitat. Due to insufficient coverage and low resolution of threat datasets, we did not incorporate threats as a data layer in the quantitative prioritization process with Zonation software. Linear infrastructures in this area might divide LCUs or impede dispersal between LCUs (Karlstetter and Mallon, 2014; Ma et al., 2013), so we obtained locations of Eurasia border fences (Linnell et al., 2016) and railroad/roads data from the Natural Earth (http://www.naturalearthdata.com).

3. Results

3.1. Landscape Conservation Units (LCUs)

Our habitat suitability model performed well, with AUCtest of 0.901 (± 0.020) and AUC_{diff} of 0.013 (± 0.019), suggesting that this model has a good discrimination ability (Swets, 1988). Terrain ruggedness index (alt_tri), max temperature of warmest month (wc2_bio05), mixed/other trees (landcover_4), mean diurnal temperature range

Table 1
Global snow leopard Landscape Conservation Units (LCUs) and their characteristics. The three largest and most important LCUs have been bolded.

ID	Name[a]	Area (km^2)	Countries	Protected percentage	Centrality (scenario 1/2)	Threats[b]
1	**TPHK**	*784,226*		*13%*	17.3/15.9	P,D,C
		271,900	*China*	*11%*		*P,D,C*
		121,812	*India*	*19%*		*P,D,C*
		108,696	*Kyrgyzstan*	*5%*		*P,D*
		97,510	*Pakistan*	*6%*		*P,C*
		95,732	*Tajikistan*	*24%*		*P,D*
		44,407	*Afghanistan*	*2%*		*C*
		32,805	*Nepal*	*20%*		*P,C*
		7513	*Uzbekistan*	*57%*		*D*
		3850	*Kazakhstan*	*16%*		*P,D*
2	**Hengduan**	*338,429*	*China*	*17%*	9.2/8.5	P,D,C
3	**Altai**	*175,186*		*18%*	14.3/13.2	P,D
		105,407	*Mongolia*	*25%*		*P,D*
		37,493	*Russia*	*0.5%*		*P*
		24,861	*China*	*20%*		–
		7378	*Kazakhstan*	*11%*		–
4	Qilian	*32,039*	*China*	*7%*	6.1/8.8	P,D
5	Khangai	*25,301*	*China*	*40%*	6.9/6.8	–
6	Jungar Alatau	*12,910*		*42%*	6.0/6.0	D
		8628	*Kazakhstan*	*59%*		*D*
		4282	*China*	*7%*		*D*
7	South Gobi	*10,432*	*Mongolia*	*38%*	8.4/9.2	D
	Total	*1,378,523*		*15%*		

[a] Only subunits larger than 1000 km^2 are listed.
[b] P: Poaching, D: Development, C: Climate change, −: No major threat.

(wc2_bio02) and barren (landcover_11) contributed the most to the model (Table A1). Globally, the highest suitability habitat for snow leopard are in the central regions of the Altai, Khangai, Tian Shan, Pamir, Hindu Kush, Kunlun, Qilian, Hengduan, Tanggula and Himalayan mountain ranges (Fig. A2).

Among the top 10% of the priority habitat, seven continuous habitat patches have an area larger than 10,000 km^2 (Fig. 2, Table 1) and thus were delineated as snow leopard Landscape Conservation Units (LCUs). The Tianshan-Pamir-Hindu Kush-Karakorum (TPHK), Hengduan, and Altai are three largest LCUs, with areas of 784,226 km^2, 338,429 km^2 and 175,186 km^2, respectively (Table 1). The TPHK, Altai and Jungar Alatau LCUs cross national boundaries and were further divided into subunits along country boundaries (Fig. 2a, Table 1). For example, the TPHK LCU is distributed in nine countries including China, Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan, Afghanistan, Pakistan, India and Nepal (Fig. 2a, Table 1).

By overlaying LCUs identified in our study with SLCUs demarcated in 2008 and SLLs identified in 2013, we found that LCUs and SLCUs have similar area and general spatial pattern (Fig. 4). The main differences are in central Tibetan Plateau (Qiangtang region), Arjin mountains and Borohoro mountain ranges, while SLLs only partially overlap with LCUs in the Altai, Tian Shan and Hindu-Kush mountain ranges. (Fig. 4, Table A2). The biggest differences are in China (Fig. 4). Three out of seven LCUs we identified are fully located in China, while 3 are partly in China, with a total area of 670,627 km^2. In contrast, SLLs only have three small landscapes in Qilian, Tianshan and Taxkorgan in China, with a total area of 30,976 km^2 (Fig. 4).

3.2. LCU connectivity

In scenario 1 that only considered natural resistance, eight linkages were identified between the seven LCUs (Table 2, Fig. 3a). The mean length of Euclidean distance (EucD) of the eight linkages is 327 km (range: 17–774 km, Table 2); the mean length of least cost path (LCP) is 531 km (range: 19–1466 km, Table 2). Among them, L1, which connects TPHK (LCU 1) and Hengduan (LCU 2) has the lowest EucD (17 km) and the lowest LCP (19 km) while L3, which connects Qilian (LCU 4) and TPHK (LCU 1), has the highest EucD (774 km) and also the highest LCP (1466 km) (Table 2, Fig. 3a). L3 (EuD: 774 km) may be too long for snow leopards because the dispersal limit of snow leopards was estimated to be between 250 and 500 km (Janecka et al., 2017).

In scenario 2 that considered both natural and anthropogenic resistances, ten linkages are identified between the seven LCUs (Table 2, Fig. 3a). The mean EucD is 372 km (range: 17–774 km, Table 2), and the mean LCP is 549 km (range: 19–1471 km, Table 2). Among them, L1 also has the lowest EucD (17 km) and the lowest LCP (19 km) while L3 has the highest EucD (774 km) and the highest LCP (1471 km), the same as that in scenario 1 (Table 2, Fig. 3a). L9 and L10 have the highest CwD (9481 and 8736 weighted km, respectively) (Table 2, Fig. 3a). The EucD of L3 and L9 (774 and 644 km, respectively) are longer than the estimated dispersal limits of snow leopards (Janecka et al., 2017).

In both scenarios, the TPHK LCU (LCU 1) has the highest centrality in the LCU network. It directly connects to the Hengduan, Altai, Qilian and Jungar Alatau LCUs (LCU 2, 3, 4, 6). The Altai LCU (LCU 3) also has a high centrality (Table 1, Fig. 3a). Correspondingly, the linkage L2 (between LCU 1 and 3) has the highest centrality (Table 2, Fig. A4). Therefore, the TPHK (LCU 1), Altai (LCU 3), and the linkage L2 play an important role in maintaining connectivity of the entire snow leopard Landscape Conservation Unit network. Jungar Alatau (LCU 6) has the lowest centrality (Table 1, Fig. 3a).

Almost every linkage has pinch points where current flow is high, indicating bottlenecks in connectivity between pairwise LCUs (Fig. 3b). In scenario 2, the linkages L2, L4, L5 and L10 have very narrow parts that are critical for snow leopard dispersal (Fig. 3b). L9 and L10 have the highest CWD/LCP ratio, indicating that the cost of moving along them is high (Table 2, Fig. 3b).

3.3. Threat mapping

Snow leopards face various threats throughout their entire range (Figs. 2b, 3b, Table 1). Poaching is a major threat, is widespread across the four largest LCUs, including TPHK, Tianshan (e), Altai, and Qilian LCUs. Anthropogenic development particularly threatens South Gobi, Altai, Qilian and Hengduan LCUs. Climate warming is another major threat. When we overlaid LCUs with predicted snow leopard habitat loss in 2070 (RCP8.5) (Li et al., 2016), we found that Hengduan was the most vulnerable LCU under climate warming, and the western and southern part of TPHK LCU was also threatened (Fig. 2b, Table 1).

In scenario 2 that considered both natural resistance and anthropogenic resistance, LCU connectivity is threatened by linear infrastructures. Three cross-border LCUs, (TPHK, Altai and Jungar Alatau) are fully or partially divided by border fences (Fig. 3b). Railways and major roads in this region cross almost all linkages between these LCUs, and especially they cut right across the narrow pinch points of L2, L4 and L5 (Fig. 3b). In contrast to that in scenario 1, L5 (connecting LCU 2 and LCU 4) and L6 (connecting LCU 3 and LCU 5) chose a completely different path to avoid anthropogenic disturbance in scenario 2 (Fig. 3a).

Table 2
Characteristics of linkages between snow leopard Landscape Conservation Units (LCUs) in two scenarios.

Link ID	From LCU	To LCU	EucD	Scenario 1					Scenario 2				
				LCP	CWD	CWD:EucD	CWD:LCP	Centrality (amps)	LCP	CWD	CWD:EucD	CWD:LCP	Centrality (amps)
L1	1	2	17	19	23	1.37	1.22	8.53	19	128	7.51	6.73	7.45
L2	1	3	384	526	612	1.60	1.16	12.00	520	2149	5.60	4.13	8.55
L3	1	4	774	1466	1510	1.95	1.03	2.16	1471	1899	2.45	1.29	3.71
L4	1	6	131	146	148	1.13	1.01	6.00	160	1154	8.80	7.21	6.00
L5	2	4	425	715	799	1.88	1.12	3.94	667	2044	4.81	3.06	3.50
L6	3	5	245	610	1099	4.49	1.80	3.88	331	1898	7.75	5.73	3.86
L7	3	7	363	413	416	1.15	1.01	6.82	427	716	1.97	1.68	6.08
L8	5	7	284	352	810	2.85	2.30	3.91	324	1625	5.71	5.02	3.81
L9	3	4	644						990	9481	14.72	9.58	1.97
L10	4	7	458						579	8736	19.07	15.08	2.47

EucD: Euclidean distance (km).
LCP: Least cost path length (km).
CWD: Cost weighted distance (weighted km).

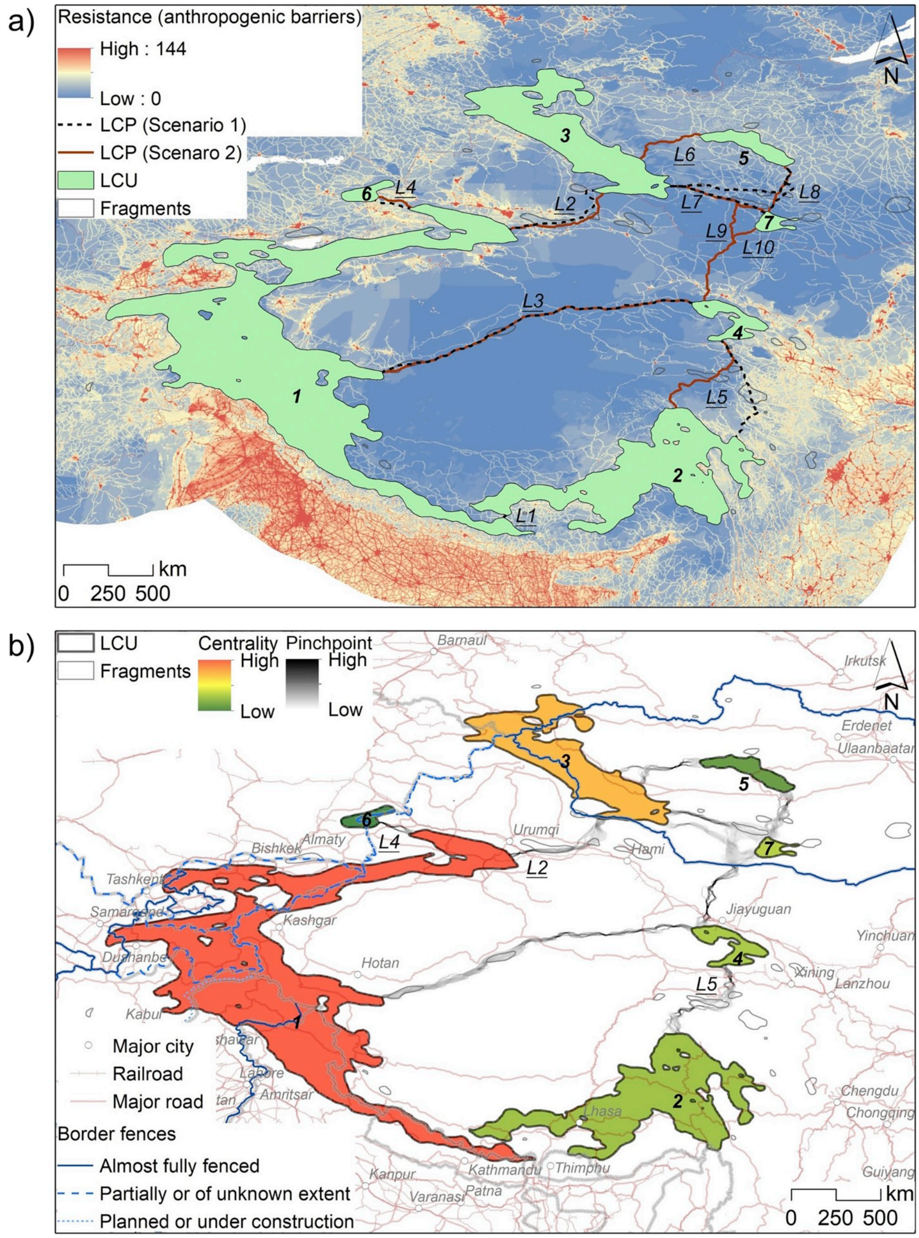

Fig. 3. LCU connectivity pattern and potential barriers of dispersal. (a) The LCPs (least cost path) between LCUs in scenarios 1 and 2. (b) Centrality shows the importance of an LCU to connect the entire LCU network from low (green) to high (red). Current flow of linkages between adjacent LCUs is shown in gradient. Three types of linear infrastructures might be potential barriers to snow leopard dispersal, including border fences, railroads, and major roads. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Comparison of LCUs identified by spatial planning to previous conservation areas

We delineated seven snow leopard Landscape Conservation Units (LCUs) (Fig. 2a) and ten linkages between them (in scenario 2) (Fig. 3). In comparison to expert-opinion based SLCUs and SLLs, our model-driven method identified important habitat patches that previous expert knowledge-based planning efforts failed to distinguish. For example, our results identified the entire Qilian mountains as an LCU. This result appears to be verified by a recent field survey that determined it is a large continuous high-quality snow leopard habitat (Liu Yanlin, unpublished results), whereas previously only a small part of the Qilian mountains was included in the SLCU and SLL (Fig. 4). Also, the central Tibetan Plateau (Qiangtang region) was previously identified as an SLCU (with unknown status) but not as an LCU in our analysis (Fig. 4), because this region only contains fragmented snow leopard habitat with relatively low habitat suitability (Fig. A2). WCS China is currently undertaking a field survey in this region, which should produce a better understanding of the snow leopard's status in this region.

Importantly, our spatial planning approach considered connectivity patterns and linkages among snow leopard LCUs, which were neglected by previous SLL and SLCU efforts (McCarthy et al., 2016; Snow Leopard Working Secretariat, 2013). Our analysis indicated that the largest LCUs in TPHK (LCU 1) and Altai (LCU 2) (Fig. 3) also had high centrality values (Fig. 3). This result is corroborated by a connectivity study, which showed that snow leopard habitat has the highest connectivity in west Tibetan Plateau and Altai-Sayan mountain ranges (Riordan et al., 2016), and matches a recent phylogeography analysis, which found that the snow leopard population in the west Tibetan

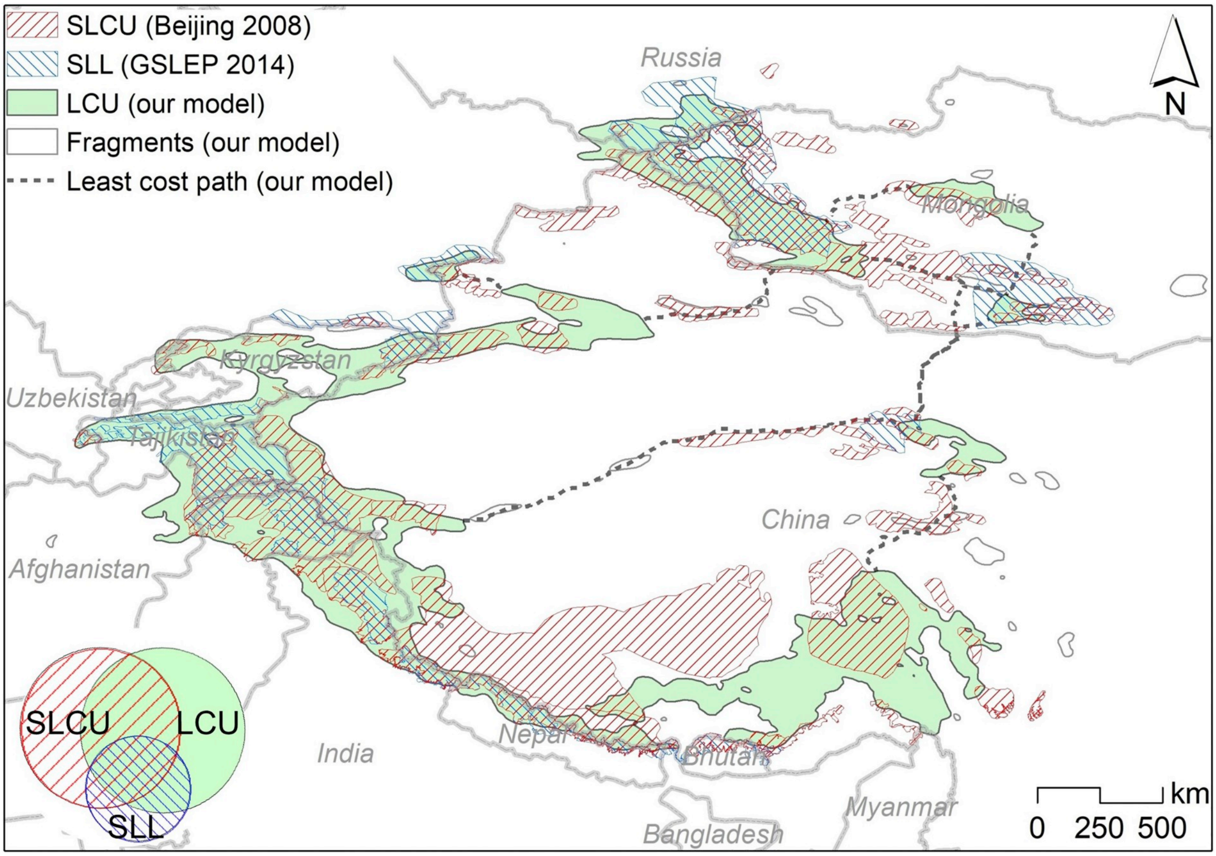

Fig. 4. Difference between LCU and SLCU/SLL. Spatial overlap between the LCUs identified from modeling approaches in this study and the SLCU and SLL identified by experts in two previous global snow leopard conservation planning efforts. Venn diagram showed the overlap percentage among them (detailed numbers are shown in Table A2).

Plateau has the highest genetic diversity (Janecka et al., 2017). The linkages between adjacent LCUs we identified are essential for gene flow and metapopulation dynamics, especially for a low-density species like the snow leopard that persists in naturally fragmented landscapes and has low genetic diversity (Cho et al., 2013; Janecka et al., 2017). Additional efforts are needed to better understand genetic connectivity among fragments and their importance to snow leopard meta-populations.

4.2. LCU-specific conservation strategies based on integrated mapping

Spatial representation of threats is helpful to identify the best conservation actions (Evans et al., 2011; Tulloch et al., 2015). Our study integrated spatial maps of protected areas, connectivity patterns, and the main threats to snow leopards. We found that LCUs varied considerably across size, percentage protected, connectivity, and threats (Fig. 2, Table 1). Thus, below we suggest LCU-specific conservation strategies should be adopted based on site-specific situations.

The second largest LCU, Hengduan (LCU 2, 338,429 km^2), is primarily threatened by climate change (Fig. 2b, Table 1), yet the region is one of the least studied for snow leopards in China (Alexander et al., 2016). Thus, studies of the status and ecology of snow leopard should be prioritized in this LCU. In contrast, the 3rd largest LCU, Altai (LCU 3, 175,186 km^2), extends across four snow leopard range countries, Mongolia, China, Russia and Kazakhstan (Fig. 2, Table 1). It faces relatively high risks of poaching and future anthropogenic development, and only 18% of its area is currently protected (Fig. 2b, Table 1). Hence, multilateral cooperative land-use planning and anti-poaching efforts should be prioritized for the Altai LCU. The pinch point of the L2 linkage connecting LCU 1 and LCU 3 has already been fragmented by three railways and highways to Urumqi (Fig. 3b). The Xinjiang autonomous region is the bridgehead of the One Belt One Road program, which is a development strategy proposed by the Chinese government focusing on building trade deals and infrastructures throughout Eurasia and the Pacific (Debin and Yahua, 2015). New railways, highways, and gas and oil pipelines have already been planned in this region (Tracy et al., 2017), and they might further threaten the linkages L2 and L4. We suggest that wildlife friendly crossing structures should be incorporated in the construction plan. In the future, more fine-scale local information, such as prey availability and abundance, is needed to inform detailed regional conservation planning on the basis of this work.

4.3. Necessity of transboundary cooperation in snow leopard conservation

Ecosystems and species' habitats are separated by political borders all over the world, and transboundary conservation through joint efforts across boundaries can produce conservation successes (Vasilijević et al., 2015). Snow leopards pose extra challenges for transboundary conservation, given that the rugged mountains they inhabit are often used as country borders (Mallon and Kulikov, 2014; Snow Leopard Working Secretariat, 2013; UNDP and GEF, 2016). It has been suggested that up to one third of global snow leopard habitat may be located within 100 km of an international border (Singh and Jackson, 1999; UNDP and GEF, 2016).

Our results highlight the necessity of transboundary cooperation in snow leopard conservation, because three of the seven LCUs cross national boundaries (TPHK, Altai, and Jungar Alatau; Fig. 2a, Table 1). Among them, TPHK (Fig. 2, LCU 1) overlaps some of the world's highest mountain ranges, including the Tian Shan, Pamir, Kunlun, Hindu Kush and Himalaya, and make it the largest continuous snow leopard habitat patch (Fig. 2, LCU 1). However, when considering international boundaries, TPHK occurs in ten Central Asian countries with units of varying sizes (Fig. 2a). On many of these country borders, heavy fencing is already in place as a result of the geopolitical change in the post-9/11 era (Linnell et al., 2016) (Fig. 2b). These fences, and the anthropogenic impacts focused in border regions, could restrict or even preclude important snow leopard dispersal and gene flow within this LCU. The Altai, and Jungar-Alatau LCUs face similar emerging challenges (Figs. 2, 3, Table 1) that, compounded with other threats, could further fragment and imperil populations of a species which demonstratively lack genetic viability (Cho et al., 2013; Janecka et al., 2017). Further genetic erosion due to genetic drift in small and fragmented populations makes the impacts of impending and ongoing climate change even more daunting. The snow leopard, and other species in this region, require the ecological plasticity and adaptive potential to track changes in habitat initiated by global warming, and shift their distributions across international borders (Li et al., 2016).

The increasingly fragmented and fast-changing environment in high Asia leaves little margin for error for conserving snow leopards. The persistence of snow leopards requires improved and effective multilateral cooperation across many actors, such as governments and NGOs. Towards this end, GSLEP has been created to establish channels of cooperation and a platform for progress among all snow leopard range countries (Snow Leopard Working Secretariat, 2013). Internationally coordinated conservation actions targeted to the snow leopard could also help save the sympatric migratory mammals, which are facing similar threats including poaching, habitat loss, barriers to migration, and climate change (UNEP and CMS Secretariat, 2014).

CRediT authorship contribution statement

Juan Li: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Byron V. Weckworth:** Conceptualization, Writing - review & editing, Funding acquisition. **Thomas M. McCarthy:** Conceptualization, Writing - review & editing, Funding acquisition. **Xuchuang Liang:** Investigation, Validation, Writing - review & editing. **Yanlin Liu:** Investigation, Validation, Writing - review & editing. **Rui Xing:** Investigation, Validation, Writing - review & editing. **Diqiang Li:** Investigation, Validation, Writing - review & editing. **Yuguang Zhang:** Investigation, Validation, Writing - review & editing. **Yadong Xue:** Investigation, Validation, Writing - review & editing. **Rodney Jackson:** Investigation, Validation, Writing - review & editing. **Lingyun Xiao:** Investigation, Validation, Writing - review & editing. **Chen Cheng:** Investigation, Validation, Writing - review & editing. **Sheng Li:** Investigation, Validation, Writing - review & editing. **Feng Xu:** Investigation, Validation, Writing - review & editing. **Ming Ma:** Investigation, Validation, Writing - review & editing. **Xin Yang:** Investigation, Validation, Writing - review & editing. **Kunpeng Diao:** Investigation, Validation, Writing - review & editing. **Yufang Gao:** Investigation, Validation, Writing - review & editing. **Dazhao Song:** Investigation, Validation, Writing - review & editing. **Kristin Nowell:** Investigation, Validation, Writing - review & editing. **Bing He:** Investigation, Validation, Writing - review & editing. **Yuhan Li:** Investigation, Validation, Writing - review & editing. **Kyle McCarthy:** Investigation, Validation, Writing - review & editing. **Mikhail Yurievich Paltsyn:** Investigation, Validation, Writing - review & editing. **Koustubh Sharma:** Investigation, Validation, Writing - review & editing. **Charu Mishra:** Investigation, Validation, Writing - review & editing. **George B. Schaller:** Investigation, Validation, Writing - review & editing. **Zhi Lu:** Conceptualization, Writing - review & editing, Funding acquisition. **Steven R. Beissinger:** Conceptualization, Writing - review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

This work was supported by Panthera, UC Berkeley and Shanshui conservation center. We thank Shanshui Conservation Center, WCS, Snow Leopard Trust, Snow Leopard Conservancy, Green River, Wild Xinjiang, Chinese Felid Conservation Alliance, WWF, Chinese Academy of Forestry, Arid Land, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences and many members of the Snow Leopard Network for their sharing of snow leopard occurrence points. Reviews by members of the Beissinger lab greatly improved this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.108387.

References

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B., Anderson, R.P., 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38, 541–545. https://doi.org/10.1111/ecog.01132.

Ale, S.B., Mishra, C., 2018. The snow leopard's questionable comeback. Science 359 (6380), 1110. https://doi.org/10.1126/science.aas9893.

Ale, S.B., Thapa, K., Jackson, R., Smith, J.L.D., 2010. The fate of snow leopards in and around Mt. Everest. Cat News. 53, 19–21.

Ale, S.B., Shrestha, B., Jackson, R., 2014. On the status of Snow Leopard Panthera uncia (Schreber, 1775) in Annapurna, Nepal. J. Threat. Taxa. 6, 5534–5543. https://doi.org/10.11609/JoTT.o3635.5534-43.

Alexander, J.S., Zhang, C., Shi, K., Riordan, P., 2016. A granular view of a snow leopard population using camera traps in Central China. Biol. Conserv.Biological Conservation 197, 27–31. https://doi.org/10.1016/j.biocon.2016.02.023.

Aryal, A., 2017. Poaching: is snow leopard tally underestimated? Nature 550, 457. https://doi.org/10.1038/550457b.

Aryal, A., Brunton, D., Ji, W., Barraclough, R.K., Raubenheimer, D., 2014a. Human–carnivore conflict: ecological and economical sustainability of predation on livestock by snow leopard and other carnivores in the Himalaya. Sustain. Sci. 9, 321–329. https://doi.org/10.1007/s11625-014-0246-8.

Aryal, A., Brunton, D., Ji, W., Karmacharya, D., McCarthy, T., Bencini, R., Raubenheimer, D., 2014b. Multipronged strategy including genetic analysis for assessing conservation options for the snow leopard in the central Himalaya. J. Mammal. 95, 871–881. https://doi.org/10.1644/13-MAMM-A-243.

Aryal, A., Brunton, D., Ji, W., Raubenheimer, D., 2014c. Blue sheep in the Annapurna Conservation Area, Nepal: habitat use, population biomass and their contribution to the carrying capacity of snow leopards. Integr. Zool. 9, 34–45. https://doi.org/10.1111/1749-4877.12004.

Aryal, A., Brunton, D., Raubenheimer, D., 2014d. Impact of climate change on human-wildlife-ecosystem interactions in the Trans-Himalaya region of Nepal. Theor. Appl. Climatol. 115, 517–529. https://doi.org/10.1007/s00704-013-0902-4.

Aryal, A., Shrestha, U.B., Ji, W., Ale, S.B., Shrestha, S., Ingty, T., Maraseni, T., Cockfield, G., Raubenheimer, D., 2016. Predicting the distributions of predator (snow leopard) and prey (blue sheep) under climate change in the Himalaya. Ecol. Evol. 6, 4065–4075. https://doi.org/10.1002/ece3.2196.

Carroll, C., McRAE, B., Brookes, A., 2012. Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of gray wolf populations in western North America. Conserv. Biol. 26 (1), 78–87. https://doi.org/10.1111/j.1523-1739.2011.01753.x.

Cho, Y.S., Hu, L., Hou, H., Lee, H., Xu, J., Kwon, S., Oh, S., Kim, H.-M., Jho, S., Kim, S., Shin, Y.-A., Kim, B.C., Kim, H., Kim, C.-U., Luo, S.-J., Johnson, W.E., Koepfli, K.-P., Schmidt-Küntzel, A., Turner, J.A., Marker, L., Bhak, J., 2013. The tiger genome and comparative analysis with lion and snow leopard genomes. Nat. Commun. 4, 2433. https://doi.org/10.1038/ncomms3433.

Cushman, S.A., McRae, B., Adriaensen, F., Beier, P., Shirley, M., Zeller, K., 2013. Biological corridors and connectivity. In: Macdonald, D.W., Willis, K.J. (Eds.), Key Topics in Conservation Biology 2. Wiley-Blackwell, Hoboken, NJ, pp. 384–404.

Debin, D.U., Yahua, M.A., 2015. One belt and one road: the grand geo-strategy of China's rise. Geogr. Res. 34, 1005–1014.

Di Minin, E., Slotow, R., Hunter, L.T.B., Montesino Pouzols, F., Toivonen, T., Verburg, P.H., Leader-Williams, N., Petracca, L., Moilanen, A., 2016. Global priorities for national carnivore conservation under land use change. Sci. Rep. 6, 23814. https://doi.org/10.1038/srep23814.

Dinerstein, E., Loucks, C., Heydlauff, A., Wikramanayake, E., Bryja, G., Forrest, J., Ginsberg, J.R., Klenzendorf, S., Leimgruber, P., O'Brien, T.G., Sanderson, E., Seidensticker, J., Songer, M., 2006. Setting Priorities for the Conservation and Restoration of Wild Tigers: 2005–2015. A User's Guide. WWF, WCS, Smithsonian, and NFWF-STF, Washington, D.C. – New York.

Dutta, T., Sharma, S., McRae, B.H., Roy, P.S., DeFries, R., 2016. Connecting the dots: mapping habitat connectivity for tigers in central India. Reg. Environ. Chang. 16, 53–67. https://doi.org/10.1007/s10113-015-0877-z.

Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. Methods in Ecol. Evol.Ecology and Evolution 1, 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x.

Evans, M.C., Watson, J.E.M., Fuller, R.A., Venter, O., Bennett, S.C., Marsack, P.R., Possingham, H.P., 2011. The spatial distribution of threats to species in Australia. Bioscience 61, 281–289. https://doi.org/10.1525/bio.2011.61.4.8.

Heiner, M., Oakleaf, J., Davaa, G., Yunden, B., Kiesecker, J., 2016. Emerging threats to snow leopards from energy and mineral development. In: Nyhus, P., Thomas, M., Mallon, D. (Eds.), Snow Leopards. Elsevier, pp. 116–122.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978. https://doi.org/10.1002/joc.1276.

Jackson, R.M., 1996. Home Range, Movements and Habitat Use of Snow Leopard (Uncia uncia) in Nepal. (Doctoral dissertation).

Janečka, J.E., Munkhtsog, B., Jackson, R.M., Naranbaatar, G., Mallon, D., Murphy, W.J., 2011. Comparison of noninvasive genetic and camera-trapping techniques for surveying snow leopards. J. Mammal. 92, 771–783. https://doi.org/10.1644/10-MAMM-A-036.1.

Janecka, J.E., Zhang, Y., Li, D., Munkhtsog, B., Bayaraa, M., Galsandorj, N., Wangchuk, T.R., Karmacharya, D., Li, J., Lu, Z., Uulu, K.Z., Gaur, A., Kumar, S., Kumar, K., Hussain, S., Muhammad, G., Jevit, M., Hacker, C., Burger, P., Wultsch, C., Jackson, R., 2017. Range-wide snow leopard phylogeography supports three subspecies. J. Hered. 108, 597–607. https://doi.org/10.1093/jhered/esx044.

Johansson, Ö., Rauset, G.R., Samelius, G., McCarthy, T., Andrén, H., Tumursukh, L., Mishra, C., 2016. Land sharing is essential for snow leopard conservation. Biol. Conserv. 203, 1–7. https://doi.org/10.1016/j.biocon.2016.08.034.

Karlstetter, M., Mallon, D., 2014. Assessment of Gaps and Needs in Migratory Mammal Conservation in Central Asia. United Nations Environment Programme (UNEP)/ Convention on the Conservation of Migratory Species of Wild Animals (CMS) Secretariat, Bonn, Germany.

Karmacharya, D.B., Thapa, K., Shrestha, R., Dhakal, M., Janecka, J.E., 2011. Noninvasive genetic population survey of snow leopards (Panthera uncia) in Kangchenjunga conservation area, Shey Phoksundo National Park and surrounding buffer zones of Nepal. BMC. Res. Notes. 4, 516. https://doi.org/10.1186/1756-0500-4-516.

Keeley, A.T., Beier, P., Gagnon, J.W., 2016. Estimating landscape resistance from habitat suitability: effects of data source and nonlinearities. Landsc. Ecol.Landscape ecology 31 (9), 2151–2162.

Lehtomäki, J., Moilanen, A., 2013. Methods and workflow for spatial conservation prioritization using zonation. Environ. Model. Softw. Environmental Modelling & Software 47, 128–137. https://doi.org/10.1016/j.envsoft.2013.05.001.

Li, J., Lu, Z., 2014. Snow leopard poaching and trade in China 2000–2013. Biol. Conserv. 176, 207–211. https://doi.org/10.1016/j.biocon.2014.05.025.

Li, J., Wang, D., Yin, H., Zhaxi, D., Jiagong, Z., Schaller, G.B., Mishra, C., McCarthy, T.M., Wang, H., Wu, L., Xiao, L., Basang, L., Zhang, Y., Zhou, Y., Lu, Z., 2014. Role of Tibetan Buddhist monasteries in snow leopard conservation. Conserv. Biol. 28, 87–94. https://doi.org/10.1111/cobi.12135.

Li, J., McCarthy, T.M., Wang, H., Weckworth, B.V., Schaller, G.B., Mishra, C., Lu, Z., Beissinger, S.R., 2016. Climate refugia of snow leopards in High Asia. Biol. Conserv. 203, 188–196. https://doi.org/10.1016/j.biocon.2016.09.026.

Linnell, J.D.C., Trouwborst, A., Boitani, L., Kaczensky, P., Huber, D., Reljic, S., Kusak, J., Majic, A., Skrbinsek, T., Potocnik, H., Hayward, M.W., Milner-Gulland, E.J., Buuveibaatar, B., Olson, K.A., Badamjav, L., Bischof, R., Zuther, S., Breitenmoser, U., 2016. Border security fencing and wildlife: the end of the transboundary paradigm in eurasia? PLoS Biol. 14, e1002483. https://doi.org/10.1371/journal.pbio.1002483.

Ma, M., Xu, F., Cheng, Y., 2013. Snow Leopards in Xinjiang. Science Press, Beijing, pp. 1–588.

Mallon, D., Jackson, R.M., 2017. A downlist is not a demotion: red list status and reality. Oryx 51, 605–609.

Mallon, D., Kulikov, M., 2014. Transboundary Snow Leopard Conservation in Central Asia: Report of the FFI/CMS Workshop. Fauna & Flora International and Convention on Migratory Species, Cambridge, UK & Bonn Germany.

McCarthy, K.P., Fuller, T.K., Ming, M., McCarthy, T.M., Waits, L., Jumabaev, K., 2008. Assessing estimators of snow leopard abundance. J. Wildl. Manag. Journal of Wildlife Management 72, 1826–1833. https://doi.org/10.2193/2008-040.

McCarthy, T., Mallon, D., Sanderson, E.W., Zahler, P., Fisher, K., 2016. What is a snow leopard? Biogeography and status overview. In: Snow Leopards. Elsevier, pp. 23–42. https://doi.org/10.1016/B978-0-12-802213-9.00003-1.

McCarthy, T., Mallon, D., Jackson, R., Zahler, P., McCarthy, K., 2017. Panthera uncia. In: The IUCN Red List of Threatened Species 2017: e.T22732A50664030, https://doi.org/10.2305/IUCN.UK.2017-2.RLTS.T22732A50664030.en.

McCarthy, T.M., Fuller, T.K., Munkhtsog, B., 2005. Movements and activities of snow leopards in Southwestern Mongolia. Biol. Conserv. 124, 527–537. https://doi.org/10.1016/j.biocon.2005.03.003.

McRae, B.H., Kavanagh, D.M., 2011. Linkage Mapper Connectivity Analysis Software. The Nature Conservancy, Seattle WA.

McRae, B.H., Shah, V.B., Mohapatra, T.K., 2013. Circuitscape 4 User Guide. The Nature Conservancy. http://www.circuitscape.org.

Montesino Pouzols, F., Toivonen, T., Di Minin, E., Kukkala, A.S., Kullberg, P., Kuusterä, J., Lehtomäki, J., Tenkanen, H., Verburg, P.H., Moilanen, A., 2014. Global protected area expansion is compromised by projected land-use and parochialism. Nature 516, 383–386. https://doi.org/10.1038/nature14032.

Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P., 2014. ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods Ecol. Evol. 5, 1198–1205. https://doi.org/10.1111/2041-210X.12261.

Nowell, K., Li, J., Paltsyn, M., Sharma, R., 2016. An Ounce of Prevention: Snow Leopard Crime Revisited. TRAFFIC, Cambridge, UK.

Oakleaf, J.R., Kennedy, C.M., Baruch-Mordo, S., West, P.C., Gerber, J.S., Jarvis, L., Kiesecker, J., 2015. A world at risk: aggregating development trends to forecast global habitat conversion. PLoS One 10, e0138334. https://doi.org/10.1371/journal.pone.0138334.

Rabinowitz, A., Zeller, K.A., 2010. A range-wide model of landscape connectivity and conservation for the jaguar, Panthera onca. Biol. Conserv. 143, 939–945. https://doi.org/10.1016/j.biocon.2010.01.002.

Riordan, P., Cushman, S.A., Mallon, D., Shi, K., Hughes, J., 2016. Predicting global population connectivity and targeting conservation action for snow leopard across its range. Ecography 39, 419–426. https://doi.org/10.1111/ecog.01691.

Sanderson, E.W., Redford, K.H., Chetkiewicz, C.-L.B., Medellin, R.A., Rabinowitz, A.R., Robinson, J.G., Taber, A.B., 2002. Planning to save a species: the jaguar as a model. Conserv. Biol. 16, 58–72. https://doi.org/10.1046/j.1523-1739.2002.00352.x.

Schaller, G.B., 2000. Wildlife of the Tibetan Steppe. University of Chicago Press.

Singh, J.J., Jackson, R.M., 1999. Transfrontier conservation areas: creating opportunities for conservation, peace and the snow leopard in Central Asia. Int. J. Wilderness.International Journal of Wilderness 5, 7–12.

Snow Leopard Network, 2014. Snow Leopard Survival Strategy. Seattle, Washington, USA. pp. 145.

Snow Leopard Working Secretariat, 2013. Global Snow Leopard and Ecosystem Protection Program. (Bishkek, Kyrgyz Republic).

Swets, J.A., 1988. Measuring the accuracy of diagnostic systems. Science 240, 1285–1293.

Tracy, E.F., Shvarts, E., Simonov, E., Babenko, M., 2017. China's new Eurasian ambitions: the environmental risks of the Silk Road Economic Belt. Eurasian Geogr. Econ. 58, 56–88. https://doi.org/10.1080/15387216.2017.1295876.

Tuanmu, M., Jetz, W., 2014. A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. Glob. Ecol. Biogeogr. 23, 1031–1045. https://doi.org/10.1111/geb.12182.

Tulloch, V.J., Tulloch, A.I., Visconti, P., Halpern, B.S., Watson, J.E., Evans, M.C., Auerbach, N.A., Barnes, M., Beger, M., Chadès, I., Giakoumi, S., McDonald-Madden, E., Murray, N.J., Ringma, J., Possingham, H.P., 2015. Why do we map threats? Linking threat mapping with actions to make better conservation decisions. Front. Ecol. Environ.Frontiers in Ecology and the Environment 13, 91–99. https://doi.org/10.1890/140022.

UNDP, GEF, 2016. Silent Roar: UNDP and GEF in the Snow Leopard Landscape. UNDP and GEF.

UNEP, CMS Secretariat, 2014. Central Asian Mammals Initiative: Saving the Last Migrations. (Bonn, Germany).

Vasilijević, M., Zunckel, K., McKinney, M., Erg, B., Schoon, M., Rosen Michel, T., 2015. Transboundary Conservation: A Systematic and Integrated Approach. International Union for Conservation of Naturehttps://doi.org/10.2305/IUCN.CH.2015.PAG.23.en.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E.M., 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nat. Commun. 7, 12558. https://doi.org/10.1038/ncomms12558.

Warren, D.L., Seifert, S.N., 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecol. Appl. 21, 335–342. https://doi.org/10.1890/10-1171.1.

WHCWG, 2010. Washington Connected Landscapes Project Statewide Analysis. Washington Departments of Fish and Wildlife, and Transportation, Olympia, WA.

Zhou, Y.Y., Feng, J.C., Duo, H.R., Yang, H.L., Li, J., Li, D.Q., Zhang, Y.G., 2014. Population survey and genetic diversity of snow leopard (Uncia uncia) in Qinghai-Tibet Plateau as revealed by fecal DNA. Acta. Theriol. Sin. 34, 138–148.