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Border fences reduce potential for transboundary migration of Marco Polo Sheep (*Ovis ammon polii*) in the Pamir Plateau

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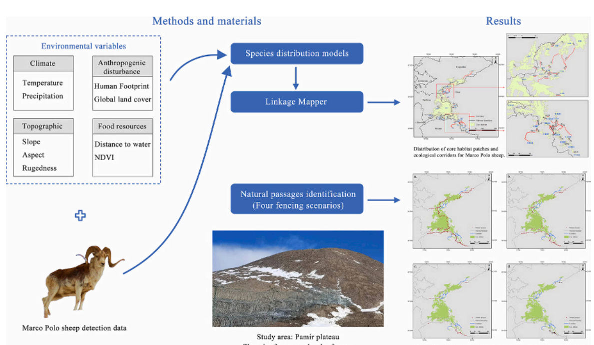
HIGHLIGHTS

- First assessed global habitat and identified ecological corridor of Marco Polo sheep
- Quantifying the effect of border fences on the migration of Marco Polo sheep
- In the most pessimistic scenario, only 25 migratory passages were identified.

GRAPHICAL ABSTRACT



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A B S T R A C T

Border fences have severely impeded the transboundary migration of a number of large mammals worldwide, with central Asia being one of the most impacted. The Marco Polo sheep (*Ovis ammon polii*), an iconic species of Pamir, is threatened in its transboundary movement by increasing border fencing among their five distributed countries, including Tajikistan, Kyrgyzstan, China, Afghanistan, and Pakistan. In this study, by building ensemble species distribution models, we found that eastern Tajikistan had the largest suitable Macro Polo sheep habitat (about 42 % of the total suitable habitat), followed by China (about 32 %). We used least-cost paths to identify 51 ecological corridors including 5 transboundary ecological corridors, which may be important to maintain connectivity in both domestic and transboundary regions. To assess the potential barrier effect of border fences, we assessed four scenarios (30, 40, 50 and 60°) corresponding to the upper limit of the slope for the construction of fences. In areas too steep for fencing, these could be used by wild sheep to cross barriers or borders and may represent migration or movement routes, defined as natural passages. In the most pessimistic Scenario 60, only 25 migratory passages along the border fences were identified, compared to 997 in the most optimistic scenario (Scenario 30), indicating a strong negative effect of intensive border fencing on the transboundary movement of Marco Polo sheep. The establishment of transnational conservation parks, and ensuring permeability is maintained in key areas, could have a positive impact on the connectivity and persistence of Marco Polo sheep populations, and provide important lessons for other large migratory mammals in transboundary regions.

1. Introduction

In recent decades, the loss of biodiversity has increased due to habitat loss and fragmentation caused by the expansion of urban areas and increasing human disturbance (Hooper et al., 2012; Pimm et al., 2014; Ceballos et al., 2015). Migratory species may be particularly vulnerable to range fragmentation, as many need to traverse large areas for breeding or reproduction. In addition, transboundary frontiers (areas near or adjacent to international political boundaries) are becoming increasingly important drivers of range fragmentation, as the implementation of border fences and other barriers may prevent species from successfully accessing parts of their range (Ellison, 2014; Sutherland et al., 2017). The impact of these borders has long been recognized by the Convention on Migratory Species, which has advocated to remove fences across central Asia, yet recent political tensions and major infrastructure initiatives are increasing the development of fences and other barriers across the region (Linnell et al., 2016; UNEP/CMS, 2019).

Existing studies on biodiversity conservation have highlighted the negative impacts of linear infrastructure along borders (e.g., walls, fences) on transboundary species, particularly large mammals (Ellison, 2014; Linnell et al., 2016; Fowler et al., 2018; Liu et al., 2019; UNEP/CMS, 2019; Simkins et al., 2023). In recent years, the rapid development of about 30,000 km of fencing for the whole of Eurasia, with over 21,000 km of fencing in Central Asia, has impeded the transboundary migration of many large mammals (Linnell et al., 2016). The border fences can either create barriers that prevent species from accessing parts of their ranges, or lead to the death of wildlife attempting to cross them (Pokorny et al., 2017; Safner et al., 2021). For example, the US-Mexico border fence and the China-Mongolia border fence disrupt transboundary movement corridors for a variety of species (Flesch et al., 2010; Ito et al., 2013; Chambers et al., 2022). These restrictions both stop gene flow and can make populations inviable by preventing them from accessing critical parts of their range during their seasonal migrations (Linnell et al., 2016; Safner et al., 2019; Li et al., 2020; Sun et al., 2021). One of the solutions to mitigate the negative impacts of border fences on wildlife population and their habitats is to systematically identify potential ecological corridors and develop appropriate conservation strategies. Protecting wildlife habitats and ecological corridors is crucial for the long-term persistence of wildlife populations (Chetkiewicz et al., 2006).

Mapping habitat suitability and identifying potential ecological corridors have been conducted in several cases studied. For example, Almasieh et al. (2019) and Neupane et al. (2022) assessed the amount and quality of habitat available, and the landscape connectivity of Asian elephants (*Elephas maximus*) in the Nepal-India transboundary region, and brown bear (*Ursus arctos*) between the Iran-Iraq border, respectively. A connectivity analysis of brown bears in five European countries by Recio et al. (2020) indicated that maintaining an appropriate transboundary habitat patch network is beneficial for brown bears in expanding and connecting populations in other regions. However, the Pamir plateau is located in the mountains of Central Asia, one of the world's 36 biodiversity hotspots (https://www.conservation.org/priorities/biodiversity-hotspots). Many species distributed across this area are transboundary (UNEP/CMS, 2019), but few studies have been conducted on the transboundary habitats and connectivity of mammals in the region. The Marco Polo sheep (*Ovis ammon polii*), a subspecies of the Argali (*Ovis ammon*), is one of the largest wild sheep and iconic species inhabiting the Pamir plateau (Fedosenko and Blank, 2005). This species seasonally migrates in the border regions of five countries including Tajikistan, Kyrgyzstan, China, Afghanistan, and Pakistan (Schaller et al., 1987; Schaller and Kang, 2008; Chen et al., 2019). The border fences may affect the movement and dispersal of Marco Polo sheep by impeding access to seasonal food resources and restricting or cutting off gene flow between populations (Luikart et al., 2011; CMS, 2014). Unfortunately, we currently lack knowledge of their range of core habitat, locations of habitat connectivity and transnational migration corridors, and information on the severity of the impact of border fences on the migration corridors of Marco Polo sheep across their distributional range (Schaller, 2007; Khan et al., 2016; Salas et al., 2018; Chen et al., 2019; Li et al., 2019). This paucity of information is hampering efforts to develop an effective global Marco Polo sheep conservation strategy.

In our study, we aim to understand the global distribution of Marco Polo sheep, quantify the impact of border fences on their habitat and migration, and provide recommendations for their transboundary conservation. We use detection data from all five Marco Polo sheep range countries to build ensemble species distribution models (eSDMs) and assess habitat suitability across their range. We use spatial analysis to identify appropriate ecological corridors, especially in transboundary regions, where border fences may represent barriers (Liu et al., 2020). In high-elevation border regions, fencing can be particularly difficult because of the steep terrain, which can provide “natural passages” along these fences and other barriers for wildlife to migrate across. We identify the locations of natural passages under four scenarios of fencing, i.e., including fences built on slopes of 30, 40, 50 and 60°, and compared them with transboundary ecological corridors to quantify the potential impact of fencing. We hypothesize that as the intensity of border fence construction increases, there will be a corresponding increase in the difficulty of cross-border migration of Marco Polo sheep, i.e., a decline in the number of natural passages, as well as a gradual loss of available ecological corridors.

2. Methods

2.1. Study area

Our study area (35°10′-42°50′ N, 70°5′-80°1′ E) covers all known range of Marco Polo sheep, which comprises the area along borders between the following countries: Tajikistan, Kyrgyzstan, China, Afghanistan, and Pakistan, including the Pamir, Hindu Kush, Karakoram, Kunlun, and surrounding mountainous landscapes (Schaller and Kang, 2008; Li et al., 2020). The area is characterized by rolling hills and rugged mountains (Luikart et al., 2011), and has a cold and dry alpine climate (Schaller et al., 1987; Salas et al., 2015; Khan et al., 2016). The dominant vegetation communities in the Marco Polo sheep range are dry grassland, including herbaceous, shrub, sparse herbaceous/shrub, and herbaceous with sparse tree/shrub communities (Salas et al., 2018; Wang et al., 2018). The study area is one of the largest wildlife habitats in the mountains of Central Asia, supporting a number of species (Khan et al., 2016; Salas et al., 2018; Chen et al., 2019).

Central Asia is one of the most densely fenced regions in the world, and the 2–3 m high barbed wire fences are present at the majority of international borders in our study area (Linnell et al., 2016). At transboundary frontiers, fences prevent the movement of many animal groups, with barbed wire fences causing injury or death as a result of a collision while running or in an attempt to cross it. However, it is not always possible to construct continuous fences due to the slope of the terrain, which prevents access for people and machinery. Such gaps (natural passages) in the fence can provide an opportunity for wildlife to cross.

2.2. Marco Polo sheep and data collection

2.2.1. Marco Polo sheep

Argali has been classified as Near Threatened (NT) by the International Union for the Conservation of Nature (IUCN) Red List (Reading et al., 2020) and listed in Appendix II of the Convention for the Conservation of Migratory Species of Wild Animals (CMS, 2020). Marco Polo sheep is a transboundary species that is distributed in Tajikistan, Kyrgyzstan, China, Afghanistan, and Pakistan. Tajikistan has the greatest number of individuals of this species, while Pakistan has the smallest (Michel and Muratov, 2010; Haider et al., 2018; Reading et al., 2020). These sheep inhabit rolling hills (Salas et al., 2015) and open areas with gentle slopes (Reading et al., 2020; Odonjavkhlan et al., 2021) and show seasonal movement in the border regions (Schaller et al., 1987; Schaller and Kang, 2008; Chen et al., 2019). During the rutting season (December–January), some males from Tajikistan and Afghanistan may migrate to China to join females (Schaller, 2007; CMS, 2014). Nevertheless, the sheep are severely threatened by human disturbance, e.g., border fences, poaching, and competition with domestic livestock (Reading et al., 2020).

2.2.2. Data collection

Detection data of Marco Polo sheep were collected from field surveys carried out by researchers from different countries, which covered all the known and potential ranges of Marco Polo sheep, using a standardized distance sampling method (Khan et al., 2016; Haider et al., 2018; Wang et al., 2018). However, some areas could only be accessed during limited parts of the year, meaning that detecting different groups of sheep and where they might be crossing structures was not always possible. Using the GPS location of the observers, the distance (measured by a rangefinder, or roughly estimated) and azimuth (measured with an electromagnetic compass) between the observers and target animal/group recorded and sightings were georeferenced (Valdez et al., 2016). Field surveys were conducted by research groups from different countries in December 2009, October and December 2010, every month from 2011 to 2014, and May to November from 2017 to 2021, from 7:00 a.m. to 19:00 p.m. local time. Each transect was conducted by two professionals by vehicle or foot. A total of 1760 sightings were recorded between 2009 and 2021. In Kyrgyzstan, the geographical division between the *O. a. polii* and the *O. a. karelini* is unclear, and the Naryn River is currently considered to be the boundary between the distributions of these two subspecies (Reading et al., 2020). We therefore excluded the detection data from the north of the Naryn River. To avoid overfitting of the model, we used the "spThin" package (version 0.2.0) (Aiello-Lammens et al., 2015) in R (version 4.1.0; (R Core Team, 2022) to spatially thin the detection data, with only one record kept in each 1 km × 1 km grid. This resulted in a total of 797 distribution records that were used in the species distribution model.

2.3. Species distribution modeling

Based on the detection data and environmental variables, ensemble species distribution models were used to assess the habitat suitability for Marco Polo sheep. Climate, topography, human disturbance, and food resources are known to be important factors affecting the distribution of this species (Salas et al., 2015; Khan et al., 2016; Salas et al., 2018). We downloaded bioclimatic variables from WorldClim (version 2.1) with a resolution of 30 s (Fick and Hijmans, 2017). Digital elevation models were downloaded from the Geospatial Data Cloud (www.gscloud.cn) and ruggedness was calculated using ArcGIS 10.6, with the focal statistics tool (square neighborhood of 3 × 3 cell) and the raster calculator tool. Water bodies data was obtained from the Resource and Environmental Science Data Center (www.resdc.cn). The Euclidean distance tool in ArcGIS 10.6 was then used to calculate the distance to the nearest water body. The Human Footprint Index (version 3) was obtained from NASA's Socioeconomic Data and Applications Center (sedac.ciesin.columbia.edu) (Venter et al., 2018). We used land cover and the Normalized Difference Vegetation Index (NDVI) to characterize the availability of forage resources for sheep. Global land cover data were obtained from GlobeLand30 2020 (www.globallandcover.com). We derived the NDVI from the mean of the Modis vegetation indices, with a resolution of 16 days and 250 m (MOD13Q1) between 2009 and 2021 (Didan, 2015). All environmental variable layers were harmonized into a cell size of 1 km × 1 km resolution (Table S1).

Autocorrelation between independent variables would lead to overfitting of the species distribution model. Therefore, we used the package 'usdm' (version 1.1–18) (Naimi et al., 2014) in R to calculate variance inflation factors (VIFs) and exclude those variables with a VIF value >10. We included 15 environmental variables and 797 occurrence points for the eSDMs of Marco Polo sheep (Table S1).

Our eSDMs, constructed using the 'biomod2' package (version 3.5.1) (Thuiller et al., 2021) in R, included eight algorithm: generalized linear models (GLM), generalized boosting models (GBM), generalized additive models (GAM), artificial neural networks (ANN), flexible discriminant analyses (FDA), multivariate adaptive regression splines (MARS), random forests (RF), and MAXENTs. The model performance of presence–absence points is generally better than that of presence-only points (Elith et al., 2006). Therefore, we used the presence–absence points to build the eSDMs of Marco Polo sheep.

We began by randomly creating 10,000 pseudo-absence points (Wisz and Guisan, 2009; Stokland et al., 2011) using the 'biomod2' package in R (Lobo and Tognelli, 2011; Barbet-Massin et al., 2012), which are points with available environmental information within the study area (Phillips et al., 2009). Eighty percent of the presence-absence points (i.e., detection-pseudo absence dataset) were created to train the model, and the remaining 20 % were created for model testing. To reduce the bias both in the modeling and evaluation (Guisan et al., 2017), each of the eight algorithms ran ten times, yielding a total of 80 models (i.e., predictive maps of habitat suitability). The eSDMs were generated by weighting the single models with a TSS (True Skill Statistic) >0.7. Among the 80 models, seven models with TSS values <0.7 were discarded. The average weights of GLM, GBM, GAM, ANN, FDA, RF, MAXENT, and MARS were 0.146, 0.15, 0.075, 0.051, 0.139, 0.152, 0.144, and 0.143, respectively. AUC (area under the relative operating characteristic curve) and TSS are widely used to evaluate the model performance. If AUC was >0.9, or TSS was >0.85, we considered the performance of the model to be excellent (Guisan et al., 2017). To transform the habitat probability distribution into a binary presence-absence distribution, we used the maximized TSS as the threshold for partitioning (Jiménez-Valverde and Lobo, 2007; Liu et al., 2013). Habitats above this threshold were considered suitable, and those below were considered unsuitable. Finally, we used the 'variables_importance' function in the 'BIOMOD2' package in R to calculate the relative importance value of each variable.

2.4. Identification of ecological corridors

The least-cost path is the route of movement between core habitats with the least resistance, shortest Euclidean distance, and minimum cumulative cost between core patches (Adriaensen et al., 2003; Sawyer et al., 2011) which has its own advantages over other methods in analyzing landscape connectivity (Sawyer et al., 2011). Hence, we used least-cost path analysis to map ecological corridors for Marco Polo sheep via Linkage Mapper (version 3.0.0). In our study, we used the following four steps in ecological corridor identification.

First, we defined a patch size >53.3 km^2 with suitable habitat as a core habitat patch, based on the minimum home range size of *Ovis* (Murdoch et al., 2017). Second, we converted the habitat suitability layer into a resistance raster by using a negative exponential function (Keeley et al., 2016; Keeley et al., 2017). Each cell of the resistance raster has a value, and the greater the value, the more difficult it is for the animal to move through (Spear et al., 2010; Beier et al., 2011; Zeller et al., 2012). In this study, the equation for the resistance raster is as follows (Trainor et al., 2013; Keeley et al., 2016; Li et al., 2020):

$$\text{Resistance} = 100 - 99 \bullet \frac{1 - e^{-ch}}{1 - e^{-c}}$$

where c is a constant which determines the shape of the curve and h is the index of habitat suitability. In our study, c is 16 (Keeley et al., 2016).

Third, the Euclidean distances between core habitats were calculated using the Conefor Inputs Tool (http://www.jennessent.com/arcgis/conefor_inputs.htm). Finally, the core habitat patch, resistance raster, and Euclidean distance between core habitats were imported into Linkage Mapper to identify the least-cost paths for Marco Polo sheep.

Cost-weighted distance divided by Euclidean distance (CWD / EucD) and cost-weighted distance divided by least-cost path (CWD / LCP) were used to assess the quality of the corridor (Dutta et al., 2016). The CWD / EucD index is a measure of how difficult it is for a sheep to move between adjacent core patches. The ratio is proportional to the resistance of the corridor, and the quality of the corridor is best when the ratio is 1 (Dutta et al., 2016). CWD / LCP represents the average resistance encountered by animals along the best path chosen when they migrate between adjacent core habitat patches (Dutta et al., 2016).

In addition, we used the Centrality Mapper and Pinchpoint Mapper modules in Linkage Mapper, which are based on circuit theory and called Circuitscape (version 4.0) (McRae et al., 2008; Dickson et al., 2019), to estimate centrality values and identify pinch points in the corridor. The centrality value is an indicator of the rank of the importance of nodes and corridors in the connectivity of habitat patch networks (Carroll et al., 2012). The higher the centrality value is, the more important the node or corridor is. Pinch points, i.e., the location of density of potential flow (current density) is high, are narrow points in the lowest cost corridor, called bottlenecks or choke points (McRae et al., 2008; McRae, 2012; Dutta et al., 2016). The pinch point is the priority area for conservation because its vulnerability and surrounding habitat may affect the connectivity of the corridor (Dutta et al., 2016).

2.5. The identification of natural passage along the border fences

The transboundary borders are difficult for the public to access due to the geopolitical sensitivity of their location and strict military control (Liu et al., 2020). Moreover, information on the countries' border fences, including their exact locations, was not available, so we were unable to obtain the exact distribution of the border fences from all five countries. Due to the steep terrain and average elevations of over 4000 m in the Pamir plateau, it is impossible to build fences in some areas. Therefore, to the best of our knowledge, border fences in Central Asia are not continuous and there might be many natural passages along the fences between countries that provide opportunities for animals such as Marco Polo sheep to cross the border fences. We have assumed four fence construction scenarios based on the steepness (slope) of the terrain to identify potential natural passages for Marco Polo sheep to cross fenced borders. The four scenarios are Scenario 30, Scenario 40, Scenario 50, and Scenario 60, which means the maximum slope for fence construction is 30°, 40°, 50°, 60°, i.e., no fence will be constructed on slopes above 30°, 40°, 50°, 60°, respectively. We assumed these four scenarios based on the actual range of the slope distribution of Marco Polo sheep. We found that Marco Polo sheep are typically found on slopes ranging between 0° and 56.3°, which means that they rarely use slopes >56.3°. We were thus only interested in fenced boundaries located at slopes below 60°. We assumed that any unfenced border could be used as a natural passage for Marco Polo sheep to migrate along. However, natural passages outside the main distribution range of Marco Polo sheep have a very low probability of being used by this species. We created a buffer of 50 km from the core habitat patches and calculated the number of migration corridors for Marco Polo sheep within this area. In addition, the natural passages on either side of the identified ecological corridors are particularly important for Marco Polo sheep. We, therefore, determined the number of natural passages on either side of an ecological corridor within a 5 km radius that were more likely to be used by sheep to cross the border fence.

3. Results

3.1. Habitat suitability

Our ensemble species distribution model showed excellent performance with an AUC value of 0.99 and a TSS value of 0.90. The ranking of the importance of the variables showed that the main factors affecting the distribution of Marco Polo sheep are natural factors. The strongest predictor of presence is the minimum temperature of the coldest month (Table 1). Other main affecting predictors include precipitation seasonality, precipitation of the driest month, precipitation of the warmest quarter, NDVI, and precipitation of the coldest quarter (Table 1).

Table 1
The rank of importance of variables derived from ensemble species distribution models. The numbers in parentheses are the relative importance values of the variables (range between 0 and 1, with 0 indicating no influence of that variable on the model).

Rank	Variable	Rank	Variable
1	Minimum temperature of coldest month (0.51)	9	Isothermality (0.02)
2	Precipitation Seasonality (0.14)	10	Human Footprint (0.01)
3	Precipitation of driest month (0.11)	11	Temperature seasonality (0.01)
4	Precipitation of warmest quarter (0.05)	12	Global land cover (0.01)
5	NDVI (0.05)	13	Distance to water (0.01)
6	Precipitation of coldest quarter (0.05)	14	Slope (0.01)
7	Ruggedness (0.04)	15	Aspect (0.01)
8	Mean temperature of driest quarter (0.03)		

According to the response curve, the highest probability of presence of minimum temperature of the coldest month for Marco Polo sheep was between −19 °C ~ -32 °C (Fig. A.1). The presence probability had an approximatively negative relationship with precipitation seasonality, precipitation of the driest month, precipitation of the warmest quarter, precipitation of the coldest quarter and ruggedness (Fig. A.1).

The total suitable habitat area of Marco Polo sheep was 62,046 km^2, mainly distributed in the center of the Pamir plateau, which includes adjacent areas of western China, eastern Afghanistan, eastern Tajikistan, and eastern Kyrgyzstan (Fig. 1). Among the five countries, Tajikistan has the largest suitable habitat area (26,244 km^2), accounting for 42.3 % of the total suitable area, followed by China, Kyrgyzstan, Afghanistan, and Pakistan (Table 2).

Table 2
The area and proportion of suitable habitat and core habitat of Marco Polo sheep for each country. The unit of area is km^2.

Country	Study area*	Suitable habitat		Core habitat	
		Area	Proportion	Area	Proportion
Tajikistan	80,335	26,244	42.3	25,461	46.0
Kyrgyzstan	190,102	9252	14.9	8027	14.5
China	329,991	19,648	31.7	17,285	31.2
Afghanistan	41,144	3985	6.4	3813	6.9
Pakistan	76,469	2917	4.7	770	1.4

Note: The asterisk (*) means the area refers to the study area within each country rather than the entire area of the country.

3.2. Habitat connectivity corridors

We identified 34 core habitat (hereinafter CH) patches (Fig. 2), with a total area of 55,356 km^2, representing 89.2 % of the total suitable habitat. The area of core habitat for each country was similar to that of its suitable habitat, with Tajikistan having the largest amount of core habitat, followed by China, Kyrgyzstan, Afghanistan, and Pakistan (Table 2). We found the most fragmented core habitat patches in China (Table S2), which had 23 core habitat patches with an average patch size of 751.5 km^2. There were eight transboundary core habitat patches (Table S3), namely patch CH4 (Kyrgyzstan-China, the second largest patch, 9503 km^2), patch CH5 (Kyrgyzstan-China, 951 km^2), patch CH6 (Kyrgyzstan-China, 608 km^2), patch CH7 (Kyrgyzstan-China, 1146 km^2), patch CH19 (Afghanistan-Tajikistan, 174 km^2), patch CH20 (Afghanistan-Tajikistan, 242 km^2), patch CH25 (across all five countries, the largest patch, 38,702 km^2), and patch CH26 (China-Pakistan, 201 km^2). Core habitat patches CH25 and CH7 are the two transboundary patches. The largest patches had the highest centrality values (Fig. 3), indicating that these two patches are important habitats for Marco Polo sheep.

Linkage Mapper identified 51 ecological corridors (thereafter EC) between core habitat patches (Fig. 2, Table S4). The average least cost path of the corridors was 20.24 km (range 1.41–139.02 km, SD 30.02), the average cost-weighted distance was 40.18 km (range 1.42–246.33 km, SD 59.40), and the average Euclidean distance was 12.56 km (range 0–96.7 km, SD 20.42). There were five transboundary ecological corridors (EC11, EC13, EC43, EC44, and EC46), connecting China-Kyrgyzstan (corridors EC11 and EC13) and China-Pakistan (corridors EC43, EC44, and EC46). In addition, China had the largest number of domestic ecological corridors (32), followed by Kyrgyzstan (4), Tajikistan (4), Pakistan (3), and Afghanistan (3) (Table S5).

Ecological corridor EC14 (from patch CH7 to CH25) had the highest

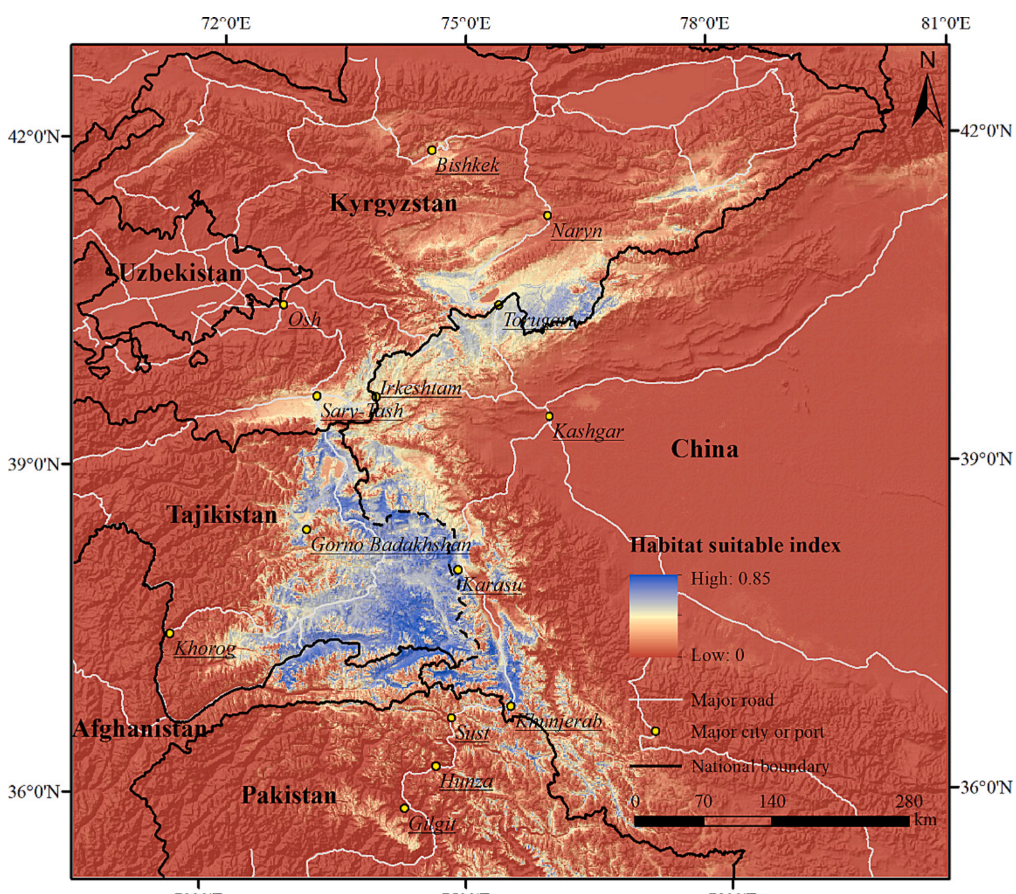

Fig. 1. Habitat suitability map of Marco Polo sheep. The blue-shaded area represents highly suitable habitat, and the red color represents unsuitable habitat. (The standard map number is GS (2016) 2948, the base map is not modified, the following is the same).

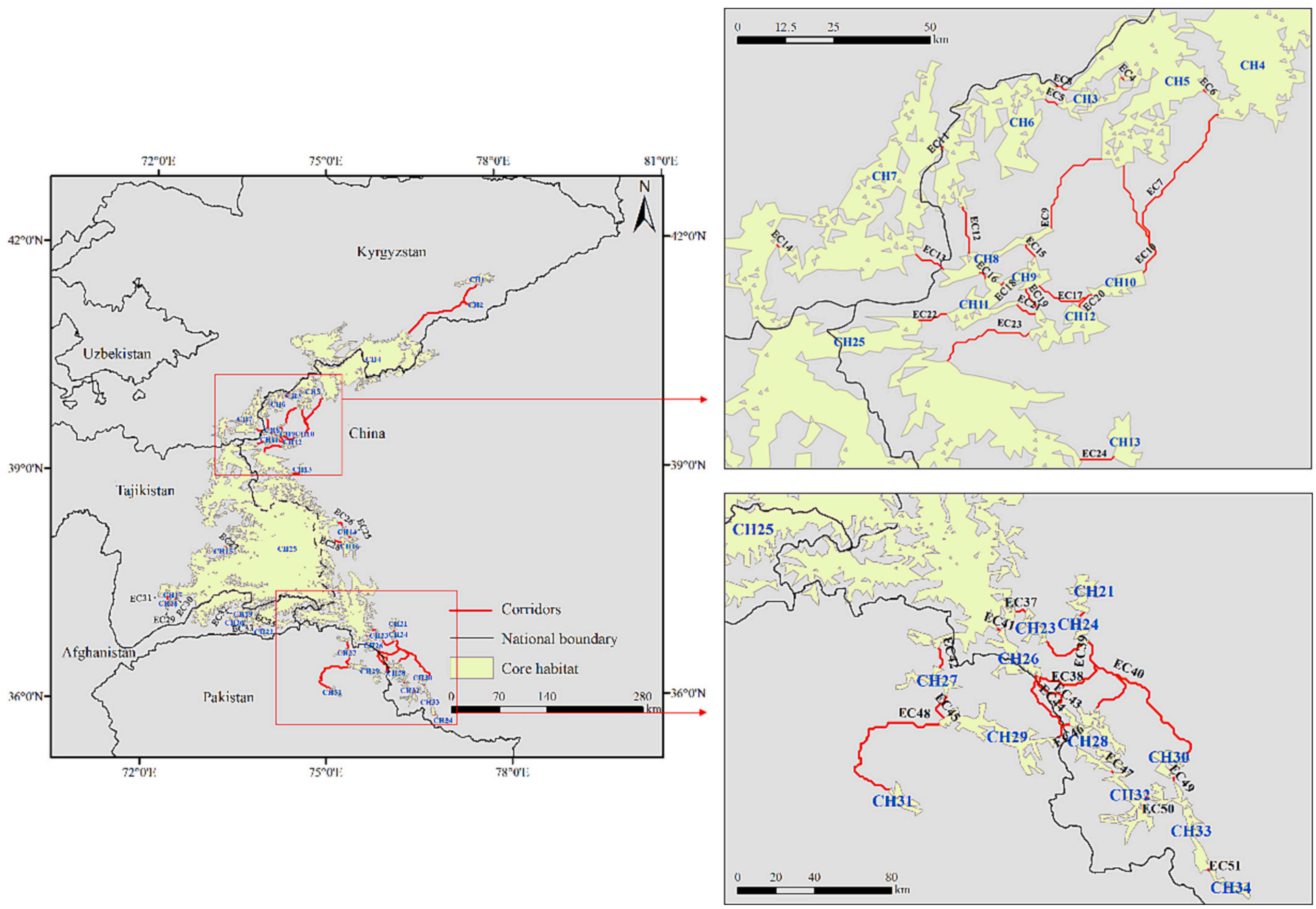

Fig. 2. Distribution of core habitat patches and ecological corridors for Marco Polo sheep, generated by Linkage Mapper. CH1-CH34 are the core habitat patches. EC1 - EC51 are ecological corridors.

centrality, followed by corridor EC41 (from patch CH25 to CH26), EC11 (from patch CH6 to CH7), EC47 (from patch CH28 to CH32), and corridor EC46 (from patch CH28 to CH29) (Table S3). The five corridors with the highest centrality connect seven core habitat patches in five countries (Fig. 3). Meanwhile, the CWD / LCP values for these five corridors were relatively low (the average was 1.18, ranging from 1.00 to 1.38), indicating that the movement resistance for Marco Polo sheep in these five corridors is relatively low (Table S3). It is more difficult for Marco Polo sheep to move through corridors EC19, EC21, EC36, EC38, and EC48, because the CWD / EucD and CWD / LCP for these five corridors were relatively high (Table S3). There was a high density of potential flow in the middle of 10 corridors (EC2, EC9, EC17, EC19, EC23, EC26, EC39, EC43, EC45, and EC48, Fig. 2 and Fig. 3), indicating that these may be the bottlenecks (pinch points) of the ecological corridors that need better protection.

3.3. Natural passage identification

In scenarios with 30, 40, 50, and 60-degree slopes, the number of natural passages was 994, 417, 129, and 25, respectively (Fig. 4), with a density of 2.00, 0.82, 0.26, and 0.05 passages per 10 km. Of these, 135, 29, 2, and 1 natural passage(s) were in core habitat patches, respectively. When a 5 km buffer was added to the corridor, we found that 53, 23, 5, and 1 passage (s) were located within this buffer zone (scenarios 30, 40, 50, and 60, respectively).

4. Discussion

Border fencing, which causes landscape fragmentation and impedes wild animals' access to seasonally important resources, has become a major threat to large mammals all over for the world, especially in Central Asia, North America and Europe (Vasilijevic et al., 2015). As a flagship species of the Pamir plateau, the habitats and ecological corridors of Marco Polo sheep have been studied locally (Khan et al., 2016; Haider et al., 2018; Salas et al., 2018; Chen et al., 2019), but no global studies have been conducted so far on the severity of the issue. There is no doubt that the assessment of habitat, the identification of ecological corridors and natural passages along border fences of Marco Polo sheep on a global scale are crucial for the conservation of the transboundary distribution of species. Our results indicated a strong negative impact of border fences on habitat fragmentation and the potential for transboundary migration of Marco Polo sheep. With the actual state of border fences being unknown, simulating the effects of fences on wildlife migration through different scenarios of fence construction is necessary and provide a new perspective for future work in the field of fencing impacts on wildlife.

4.1. Global patterns of suitable habitat and ecological corridor

Tajikistan has the largest area of suitable contiguous habitat for Marco Polo sheep, so little work is needed to reconnect habitats. A previous study reported that the most suitable habitats for Marco Polo sheep in Tajikistan are located in the eastern part of the country (Salas et al., 2018). Our study confirmed that the core habitat patch CH25 with

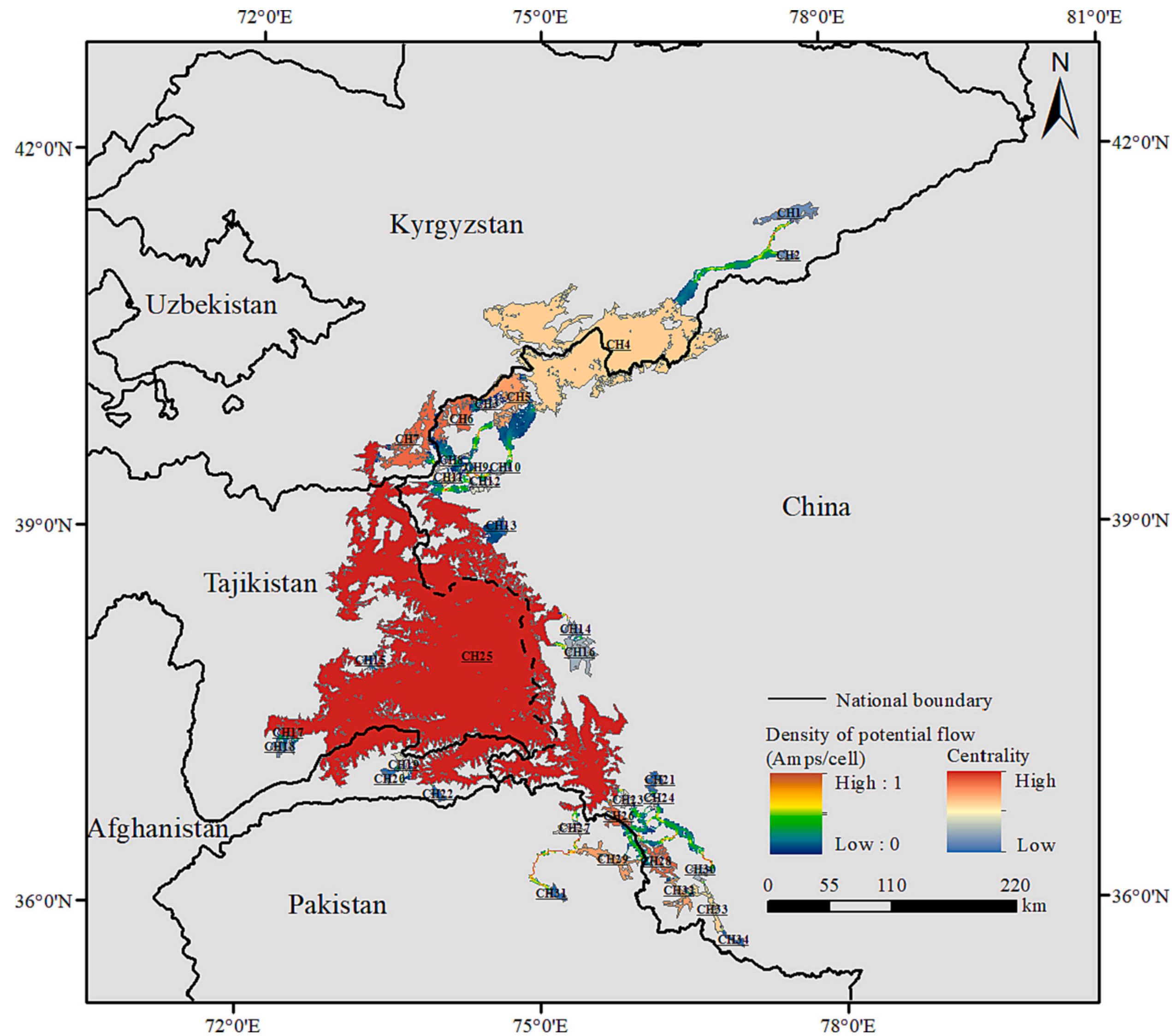

Fig. 3. Map of the study area, showing the centrality of core habitat patches and corridor pinch points (high density of potential flow). CH1-CH34 are core habitat patches. The redder the patch color, the more important the patch is.

the highest centrality relative to other patches, is indeed located in eastern Tajikistan and contains most of the suitable habitat for this species.

China has the second largest suitable habitat for Marco Polo sheep, but habitat fragmentation is severe and many corridors are needed, with up to 32 ecological corridors within China, located at the eastern edge of the global distribution of Marco Polo sheep. New borders resulting from infrastructure associated with the Belt and Road Initiative (BRI) may pose a risk to wildlife (Shi et al., 2023), including the Chinese Marco Polo populations, which requires the formulation of specific conservation measures, such as wildlife-friendly crossing structures (Li et al., 2020). Furthermore, the small core habitat patches CH8–12, located in China, adjacent to the border of Kyrgyzstan and Tajikistan, with a total of 14 potential ecological corridors connecting them, may play an important role as stepping-stones in facilitating these dispersals and migrations of sheep among the three countries. However, our density of potential flow results showed that there are more pinch points in China, which poses a challenge for the conservation and management of these ecological corridors.

Kyrgyzstan has 6.4 % of the suitable habitat for the Marco Polo sheep and the second largest core habitat patch CH4, which straddles China and Kyrgyzstan. The proposed China-Kyrgyzstan-Uzbekistan railway is expected to cross these patches (Li et al., 2021). As a consequence, scientific planning for the railway route prior to its construction, and the construction of wildlife crossing structures at appropriate locations are essential measures to mitigate its impact on wildlife movement in the region (Yang and Xia, 2008; Finka et al., 2019). There are also two transboundary ecological corridors between China and Kyrgyzstan (EC11 and EC13), but unfortunately, these corridors have been rendered dysfunctional by border fencing.

Afghanistan and Pakistan have the smallest areas of suitable habitat and the smallest populations of Marco Polo sheep. These populations will be at risk of regional extinction, especially as data indicates populations may already be declining in these regions (Haider et al., 2018). We identified three transboundary ecological corridors (EC43, EC44 and EC46) between China and Pakistan. If connected, they will facilitate the migration of Marco Polo sheep between China and Pakistan, which may increase the number of these sheep in Pakistan, potentially increasing gene flow and the genetic diversity of sheep between China and Pakistan.

Although our eSDMs showed excellent performance, we recognize that shortcomings in the modeling approach may lead to some biases in the identification of suitable habitat for Marco Polo sheep. The first potential bias is in the collection of species distribution data. If field

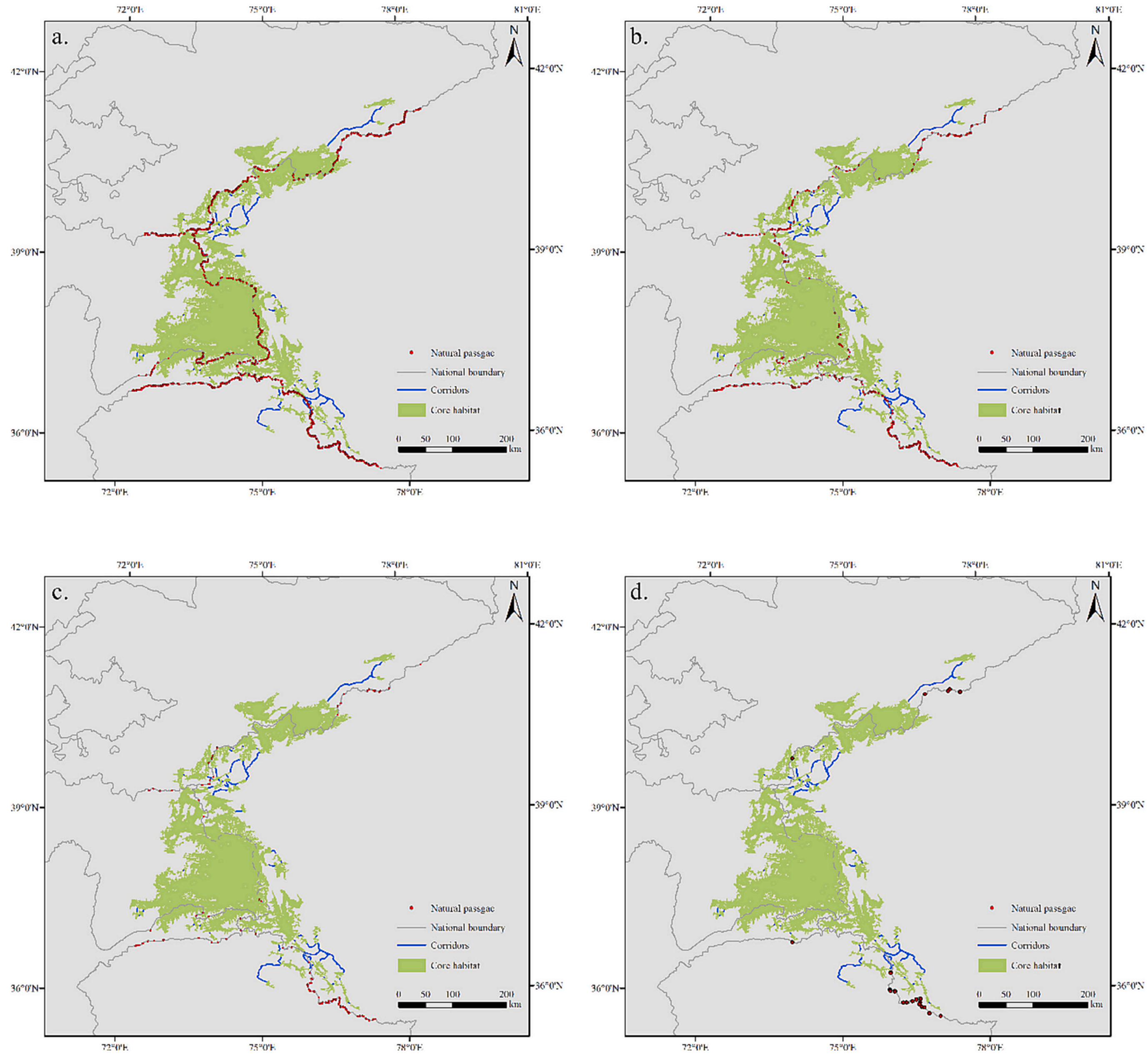

Fig. 4. Map with locations of natural passages (red dots on the border) for Marco Polo sheep across boundaries among the countries, under four different scenarios. (a) if the fence can be built up to a maximum slope of 30°, (b) if the fence can be built up to a maximum slope of 40°, (c) if the fence can be built up to a maximum slope of 50°, and (d) if the fence can be built up to a maximum slope of 60°. Green depicts the core habitat of the Marco Polo sheep range and blue lines indicate movement corridors in otherwise unsuitable habitat.

surveys cannot cover the entire range of the species, it can easily lead to a sampling bias, which in turn affects the results of the model (Jarnevich et al., 2015). Despite our study covering as much of the known and potential distribution of Marco Polo sheep as possible, there are some areas that we have never been able to reach due to the influence of seasons, roads, terrain, and military control, resulting in the inability to obtain data from those areas. The second is the generation of pseudo-absence points in the SDMs. Different strategies for generating pseudo-absence points and the number of generated points can affect the evaluation metrics and results of the model and produce misleading models (Stokland et al., 2011; Jarnevich et al., 2015). In our study, we used a randomized strategy to generate a large number of pseudo-absence points for the purpose of improving model performance and reducing the bias. In addition, the composition of the investigators, the method of transportation for the survey (by car or foot), and transect lengths could also results in potential bias of the models (Lele et al., 2012). For example, the results may be differed when using SDMs that includes empirical non-detection data to assess the distribution of Marco Polo sheep, because transect lengths may affect detection probability of Marco Polo sheep.

4.2. Impact of the border fences on natural passages

As we have hypothesized, our study found that fencing along the borders affects the species' transboundary migration and use of different habitat patches. Patches CH4-CH7, CH19, CH20, CH25, and CH26 are all transboundary core habitat patches and represent 93.08 % of the total core habitat. Habitat fragmentation caused by the border fence is a more serious consequence for population persistence than other factors such as grazing and open roads, as this habitat fragment is no longer connected through ecological corridors. By simulating four scenarios to identify the location of possible migration passages, we found that intensive border fences construction extremely reduces the available migration passages. That is, >97 % of migration passages in the most optimistic scenario 30 (the maximum slope for fence construction is 30°) will disappear compared to the most pessimistic scenario 60 (the maximum slope for fence construction is 60°). The results of our scenarios 30 and 40 (the maximum slope for fence construction is 40°) are consistent with the results of eight Marco Polo sheep migration passages found by Schaller and Kang (2008) on China's borders with Pakistan, Afghanistan and Tajikistan.

Unfortunately, border fences in Central Asia are further being increased or reinforced in response to regional tensions (Linnell et al., 2016), and those fences may pose additional challenges for the dispersal and migration of Marco Polo sheep and sympatric wildlife. The presence of a large number of natural passages would allow Marco Polo sheep to move freely among the five countries, increasing the opportunities for their dispersal and gene flow among populations, and thus contributing to the long-term survival of this species, the sympatric carnivores such as the endangered snow leopard, and the overall contiguity and health of the high altitude ecosystem (Vasilijevic et al., 2015; Thornton et al., 2019; Thornton et al., 2020). These findings provide an important basis for harmonizing the construction of border fences and wildlife migrations in this ecologically sensitive region of the world.

4.3. The necessity and recommendation for transboundary protection of Marco Polo sheep

The capacity and willingness to mitigate the impacts of infrastructure on migratory species vary across Asia. Fences built for border security and to reduce disputes between countries certainly create a barrier to transboundary wildlife migration (Liu et al., 2020). Our study found that >93 % of the core habitat patches are transboundary in distribution. The Xinjiang Uygur Autonomous Region of China is one of the core areas of the Belt and Road Initiative, a cooperative effort by the Chinese government to build trade and infrastructure across Eurasia and the Pacific (Liu, 2015). New railways and highways from the Chinese city of Kashgar to Pakistan, Tajikistan, and Kyrgyzstan have already been built or are being planned in this region (Tracy et al., 2017). These transport networks may further threaten the already declining habitat connectivity of Marco Polo sheep through border fencing. However, conservation successes for the Marco Polo sheep can only be achieved through joint cross-border conservation efforts (Vasilijevic et al., 2015). There are multiple examples of the conservation of isolated or fragmentation habitat network, such as the transboundary conservation of the Amur tiger (*Panthera tigris altaica*) and Amur leopards (*Panthera pardus orientalis*), the transforming the modeling results of habitat and ecological corridors of Giant pandas (*Ailuropoda melanoleuca*) into realistically protected areas and constructed corridors, and Tibetan Antelope (*Pantholops hodgsonii*) using the wildlife underpasses to cross the Qinghai–Tibet railway (Yang and Xia, 2008; Wei et al., 2015; Vitkalova et al., 2018; Kalikhman, 2019; Kang, 2022).

As per our research findings, we suggest the following four proposals for transboundary conservation: First, more organizations such as research institutions and protected areas from the five distributed countries should work together to establish a framework, to the conservation of the sheep. A transnational conservation park that covers at least the range of suitable habitats, ecological corridors, and natural passages should be established. The establishment of the park will not only protect the integrity of the landscapes, but also provide a model for transboundary wildlife conservation in all five countries. For example, the Serengeti National Park-Maasai Mara National Reserve at the Tanzania-Kenya border presents a successful precedent (Veldhuis et al., 2019). The second proposal is to enhance the monitoring of the population dynamics of Marco Polo sheep and to strengthen the satellite collar monitoring of sheep in areas that span across transboundary borders. Monitoring programs using remote sensing techniques can further determine the location of the cross-border migration of Marco Polo sheep and provide a basis for the modification of border fences. Third, implementing monitoring of the genetics of Marco Polo sheep will contribute to the timely detection of the effects of border fences on their genetic diversity. Finally, we should pay continuous attention to the potential effects of climate change and human activities along the BRI on Marco Polo sheep and their habitats, and adapt conservation measures in a timely manner, as our results demonstrated that climate is the key factor influencing their distribution.

5. Conclusions

To our knowledge, this is the first quantitative assessment of the effects of border fences on wild ungulates in their transboundary distribution. This study provides policymakers and scientists with a clearer understanding of the negative impacts of border fences on wildlife and how enhanced connectivity between transboundary habitat patches can help mitigate its effects. Our study is important for guiding the conservation of Marco Polo sheep on the one hand and provides a new perspective to quantify the effects of fences on the migration of wildlife, on the other hand. In addition, the study implies that transboundary cooperation of scientific research and management of wild populations and their habitats are crucial to the ongoing survival of wildlife species across political borders.

CRediT authorship contribution statement

Yingying Zhuo: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis. **Muyang Wang:** Writing – review & editing, Supervision, Methodology, Investigation. **Zhongjun Liu:** Investigation. **Wenxuan Xu:** Writing – review & editing, Investigation. **Abdulnazarov Abdulnazar:** Investigation. **Ali Madad Rajabi:** Investigation. **Askar Davletbakov:** Investigation. **Jibran Haider:** Investigation. **Muhammad Zafar Khan:** Writing – review & editing, Investigation. **Nabiev Loik:** Investigation. **Sorosh Poya Faryabi:** Writing – review & editing, Investigation. **Stefan Michel:** Writing – review & editing, Investigation. **Stephane Ostrowski:** Investigation. **Zalmai Moheb:** Investigation. **Kathreen Ruckstuhl:** Writing – review & editing. **António Alves da Silva:** Writing – review & editing. **Joana Alves:** Writing – review & editing. **Weikang Yang:** Writing – review & editing, Supervision, Project administration.

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.

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

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