

A prediction for the possibility of the transboundary import of Peste des petits ruminants in western China by validation of transboundary transmission paths

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Abstract

Peste des petits ruminants (PPR) is a highly infectious transboundary disease of small ruminants caused by peste-des-petits-ruminants virus. It is one of the most destructive diseases in sheep industry in Africa, Asia and the Middle East. In Pamir Plateau, India, Pakistan, Afghanistan, Tajikistan, Kazakhstan and other countries bordering Tibet and Xinjiang of China are all PPR epidemic areas. Within this region, there are many big population size wild small ruminants, moving freely across the border. The time-honored transboundary nomadic lifestyle results in transboundary migration of livestock too. China has experienced two national epidemics, which can be sourced back to Tibet and Xinjiang. In order to reach the China National Plan for the Eradication of Peste des Petits Ruminants and construct a national wide free zone without immunization in 2020, effective control of transboundary spreading and imported cases is an unavoidable choice. For the countries in the pan Pamir Plateau, the spatial risk distribution of PPR were predicted by a variety of eco-geographical, anthropoid and meteorological variants first time; by the resistance surface analysis, maximum available transboundary paths for PPR spreading by small ruminants were calculated. Finally, 5 paths were obtained, respectively from Kazakhstan, Tajikistan, Pakistan and Kashmir to enter Xinjiang and Tibet of China through different channels. This study not only confirmed the fact of transboundary communication of small ruminants for the first time, but also provided specific objectives for PPR prevention. This research can also provide new methods for the prevention and control of other transboundary infectious diseases.

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Summary

Peste des petits ruminants (PPR) is a highly infectious transboundary disease of small ruminants caused by peste-des-petits-ruminants virus. It is one of the most destructive diseases in sheep industry in Africa, Asia and the Middle East. In Pamir Plateau, India, Pakistan, Afghanistan, Tajikistan, Kazakhstan and other countries bordering Tibet and Xinjiang of China are all PPR epidemic areas. Within this region, there are many big population size wild small ruminants, moving freely across the border. The time-honored transboundary nomadic lifestyle results in transboundary migration of livestock too. China has experienced two national epidemics, which can be sourced back to Tibet and Xinjiang. In order to reach the China National Plan for the Eradication of Peste des Petits Ruminants and construct a national wide free zone without immunization in 2020, effective control of transboundary spreading and imported cases is an unavoidable choice. For the countries in the pan Pamir Plateau, the spatial risk distribution of PPR were predicted by a variety of eco-geographical, anthropoid and meteorological variants first time; by the resistance surface analysis, maximum available transboundary paths for PPR spreading by small ruminants were calculated. Finally, 5 paths were obtained, respectively from Kazakhstan, Tajikistan, Pakistan and Kashmir to enter Xinjiang and Tibet of China through different channels. This study not only confirmed the fact of transboundary communication of small ruminants for the first time, but also provided specific objectives for PPR prevention. This research can also provide new methods for the prevention and control of other transboundary infectious diseases.

Keyword : Peste des petits ruminants, MaxEnt, Least Cost Path

INTRODUCTION

Peste des petits ruminants (PPR) is an acute, serious, contact infectious disease caused by peste des petits ruminants virus (PPRV) belonging to the genus of morbilliviruses(Li et al., 2018). PPR is characterized by sudden depression, high fever, anorexia, nasal and ocular discharge, mouth erosive lesions, pneumonia and severe diarrhea(Alemu et al., 2019, Alfred et al., 2018). PPRV is mainly transmitted through direct or indirect contact, and the incubation period is typically 2-7 days(Kumar et al., 2014). The morbidity rate can reach 100% with a high case fatality with the acute form of disease(Parida et al., 2016). Both the domestic and wild ruminants are susceptible to PPRV, while the goats and sheep are the most susceptible hosts. The pig was recorded to be infected(Nawathe and Taylor, 1979){Shabbir, 2020 #5;Nawathe, 1979 #16}. At present, the prevention and control measures for PPRV are mainly based on herd immunity by live attenuated vaccine in endemic area(Enchery et al., 2019). In PPR free area, slaughtering of infected animals, environmental sanitation sustainability, prohibition of animal transportation and quarantine are measures adopted generally(Couacy-Hymann et al., 1995). Although many measures have been taken in prevention, PPR is still widely distributed worldwide(Banyard et al., 2010). Above 63% of the domestic small ruminants in the world remains under the threat of PPR, and the risk to wildlife is unknown(Baazizi et al., 2017). The livestock industry has been greatly ruined or decreased by PPR in the affected countries and regions, and even jeopardized the food security system, causing economic recession(Baron et al., 2017). PPR has attracted the attention of international organizations and relevant national authorities, which is listed as a transboundary animal disease need to be controlled and eradicated by FAO and OIE(OIE and FAO, 2015a).

PPR was first discovered in the early 1940s in Cote d'Ivoire and then expanded cross over nearly the whole world(OIE and FAO, 2015b). Now around 70 countries have either reported infection to the OIE or are suspected of being infected(Shaila et al., 1996). Of these, more than 60% are in Africa and the others are in Asia and the Middle East. There are another 50 countries are considered to be at risk for PPR(Liu et al., 2018). In China PPR first outbreak in the Ngari region of Tibet in 2007 with a 5751 death of sheep and goats accounting for 16% motility rate(Wang et al., 2009). This epidemic was effectively controlled by ways combing slaughter, mass immunity and restriction of animal transportation. However, PPR re-emerged in Xinjiang, China in December 2013 and rapidly spread to much of China in the first half of 2014 through

the large live-sheep trading network(Bao et al., 2014). 23 provinces, autonomous regions and municipalities (P/A/M) of PR China (PR China is administratively divided into 34 P/A/M) have been involved into this pandemic and caused a heavy loss of sheep and goat industry of China(Bao et al., 2017).

There are four known lineages of PPRV (I-IV). The lineage I and II are distributed in the West Africa; the lineage III are popular in East Africa, the Arabian Peninsula and southern India; the lineage IV is popular in the Arabian Peninsula, the Middle East, South Asia and Africa(Kwiatek and Olivier, 2011). Phylogenetic analysis revealed that the Chinese 2013–2014 strains and Tibet strains isolated previously in 2007, both belonged to lineage IV but in different sub-branches. Nevertheless, compared with the Tibet strains, the Chinese 2013–2014 strains shared high degree of genetic homology with those from Pakistan and Tajikistan(Xia et al., 2016). As early as 1991, an outbreak of PPR was reported in Pakistan bordering Xinjiang(Anees et al., 2013). Similarly, outbreaks of PPR were reported in Tajikistan bordering Xinjiang in March 2004, and phylogenetic analysis indicated that the isolates belonged to lineage IV as well(Kwiatek et al., 2007). So we consequently speculated that the Chinese PPR epidemic was spread more possibly from bordering countries into China.

The part of the western border of China (N29°54' - 44°32') borders 7 countries, 6 of which are PPR endemic countries (India, Pakistan, Afghanistan, Tajikistan, Kazakhstan and Russia). Though the epidemiological situation in Kyrgyzstan, another neighbor, is not clear, serum positive reports of PPR are existed. In the border areas of China-northern India, China-Pakistan, China-Afghanistan, China-Tajikistan, China-Kyrgyzstan and China-Kazakhstan, crisscrossed huge high mountains and low valleys is the dominant landform. Since ancient times to now, the nomadic nations constitute the main part of local population. Therefore, transboundary grazing is the local typical style of production and life and domestic ruminant exchanges and migration frequently(Padhi and Ma, 2014). Due to the existence of large area of no man's land and harsh environment, border control between countries is always difficult to be fully realized, and transboundary grazing is still widespread until 1990s here. Moreover, in this region many wildlife protected areas host a large number of wild ruminants (*Ovis ammon*, *Capra ibex*, *Gazella subgutturosa*, *Procapra picticaudata*, *Pantholops hodgsonii*, *Pseudois nayaur*), which provide a big sum of carriers of PPRV for transboundary spreading(Li et al., 2017). Wild ruminants, goats and sheep all are capable to cross the barbed wire mesh on the boundary in the need of foraging, migration and other activities. Also due to the imperfect establishment of the barbed wire mesh in some areas the transboundary spread of PPR has become natural(Liu et al., 2020). Combined with the above possibilities, all susceptible animals in this area contact frequently by common utilization of water sources, food and habitat, so the virus is particularly easy to spread from one side to another(Rahman et al., 2019).

In 2013, after the PPR epidemic which caused huge economic losses to China's sheep industry, in December 2015, the Ministry of Agriculture of China officially issued the National Plan for the Eradication of Peste des Petits Ruminants (2016-2020). It planned that by 2020, except constructing a 30 km width immune isolation belt in the border counties and plantations along the border line, the whole nation is going to achieve the goal of a national wide "free zone without immunization". Considering the impossibility of immunization of wild ruminants, the construction of the free zone should be based on cutting off all possible routes of transmission and eliminating imported cases firstly.

In ecology, resistance coefficient is used to express the willingness of a species to pass through a specific landscape unit or the suitability index of the landscape unit for a species(Zeller et al., 2012). In the process of passing through a specific environment, if the energy and time consumption of individuals is small and the mortality rate is low, it means that the environmental resistance is low(Hashmi et al., 2017). the possibility of animals passing through the area is high. Then the landscape unit is regarded as a corridor (migration paths)(F. et al., 2003). We assume that there are natural migration paths for wild and domestic ruminants in the N 29°54'-44°32' section of the western border of China, and transboundary spreading of PPRV exist. Therefore, this study mainly focuses on the risk analysis of PPR and the verification of transboundary paths in the above-mentioned multinational border areas, and try to block the local transboundary communication of PPR, so as to provide valuable suggestions for the prevention and control for border areas worldwide.

MATERIALS AND METHODS

Research area

The study area is located between N 29°54'-44°32', E 64°0'-85°17', namely the Pamir Plateau and its huge mountain range that extended to the surrounding area (Pan Pamir Plateau)(Fig.1). Located in the southeast of Central Asia and the western most end of China, Pamir Plateau straddles the south of Tajikistan and the north of Afghanistan. It is a huge junction of Kunlun Mountains, Karakoram mountains, Hindu Kush mountains and Tianshan Mountains, covering an area of about 1×10^5 square kilometers. The Pamir Plateau is composed of several groups of mountains and wide valleys and basins between mountains, with an average altitude of more than 5000 meters. It is a strong continental alpine climate with severe cold, especially in the eastern Pamirs, with a long winter (October to April of the next year). The difference between the East and the west of Pamir Plateau is significant. The west Pamir Plateau is a typical high mountain plateau with very large absolute and relative height and the complex terrain. The abundant rainfall helps to develop large dense net of rivers and prospective vegetation. The absolute and relative height of the East Pamir Plateau are small compare with its west part. The significant features of east are wide valleys and widespread 1085 glaciers covering an area of 8041 square kilometers. It is the breeding ground for many small wild ruminants. Since the hostile nature of habitat on the high, huge mountains in Tashkurgan in Pamirs Plateau, it drives the migration of large populations of ruminants, such as yak, camel and ovis ammon regularly and shed a great risk to countries on the both sides of the boarder.

Date processing

67 environmental factors from 1979 to 2013 were extracted from CHELSA database (V.1.2) with a resolution of 30 arc-seconds. The monthly precipitation (n=12), monthly mean/minimum/maximum temperature (n=36), derived bio climatic variants (n=19), slope, vegetation cover layer (ESA CCI), population density (Asia Continental Population Data sets (2000-2020) were used. Slope and Euclidean distances to rivers are extracted from DEM (<http://www.gscloud.cn/>)(Table1). 396 geographical locations of PPR case from OIE report and published articles were used for model production. The rarefying of spatial autocorrelation refers to Joka(Joka et al., 2019). The multi-collinearity among variants is identified and limited by Principal component analysis (PCA) by SPSS 22.0(Moriguchi et al., 2016). The VIF value <10 was set as the threshold of multi-collinearity(Duque-Lazo et al., 2016, Leanne et al., 2018).

Prediction for the Spatial distribution of PPR

Due to the large height difference in study area, the areas were analyzed separately as $\geq 1500\text{m}$ group and $< 1500\text{m}$ group(Himeidan et al., 2009). The disease distribution points were screen by spatial rarefying for the model. The environmental variables and non environmental variables are diagnosed to exclude multiple collinearity. Then MaxEnt model analysis is carried out to eliminate the factors with low contribution rate. The final factor obtained is used for the prediction of the final MaxEnt model(Gils et al., 2014). The prediction map obtained by overlaying of results of the two groups by spatial analysis fuzzy overlay in ArcGIS. The setting and self-test of MaxEnt refer to Joka (Joka et al., 2019).

Prediction of the maximum available transboundary paths

Corresponding to least cost path (LCP) and according to the research purpose, all transboundary channels available to ruminants are named as maximum available paths (MAP)(Balbi et al., 2019). Cluster analysis by ArcGIS 10.2 were performed for the outbreak points of PPR both in China and abroad(Zulu et al., 2014). The LCP model of ArcGIS 10.2 was supplied for the results of cluster by pair-wised calculation (China versus abroad) to obtain transboundary paths(Ray, 2004). By excluding those that with a starting point far away from the border and those finally incorporated into other most convenient channels, the maximum available transboundary paths were reached. For this research, the resistance coefficient is defined by land

cover and altitude. Further, the land cover (land cover data was extracted from ESA CCI Land Cover project database, containing 9 categories 21 subcategories) and altitude are categories as available and unavailable according to expert experience and the ethology of small ruminants; the available land cover and altitude were reclassified into 1 and 9 scales to construct the resistance layer(Sawyer et al., 2011). 1 for low resistance and 9 for high resistance.

RESULTS

Result of data processing

In areas above 1500 meters, 99 geographical locations of PPR cases left by 30 km rarefying. The minimum temperature of June was selected as the environmental variant. No multi-collinearity was detected by a VIF values within 0 to 2(<10). The variant of vector distance from the river (river distance) was excluded due to its high standard deviation. Finally, the minimum temperature of June, vegetation, population density and slope were adopted for the final model(fig.2).

In areas below 1500 meters, 81 geographical locations of PPR cases left by 40 km rarefying. The mean temperature of September was selected as the environmental variant. No multi-collinearity was detected by a VIF values within 0 to 2 (<10). The variant of vector distance from the river (river distance) was excluded due to its high standard deviation. Finally, the mean temperature of September, vegetation, population density and slope were adopted for the final model(fig.3 Table.2).

Result of prediction for the Spatial distribution of PPR

The AUC and SD values of the both models of above and below 1500 m are 0.825, 0.027and 0.890, 0.005 respectively, indicating a better prediction. The Pamirs Plateau and its extended mountains are in high-risk areas, and the Tibet and Xinjiang in western china are surrounded by these risks. From the perspective of administrative divisions, the countries bordering China are all high-risk areas of PPR, while the high-risk areas on the China side are relatively weak(fig.4).

Result of prediction of the maximum available transboundary paths

Were obtained Five groups of PPR distribution points outside China and three groups in China were obtained by ArGis cluster analysis. We got five transboundary paths: 1.Kazakhstan-Confluence of Ili River and Horgos River- Xinjiang (Huocheng county); 2.Tajikistan-WestPamirPlateau-Xinjiang(Kashgarcity);3.Pakistan-WestPamirPlateau-Xinjiang(Kashgarcity);4.Kashmir-Pakistan-WestPamirPlateau-Xinjiang (Kashgarcity); 5.Kashmir-Bangon lake-Tibet (Ritu county)(fig.5).

DISCUSSION

Xinjiang and Tibet, as well as neighboring countries are all contaminated regions of PPR and resulted in large scale of deaths(Wu et al., 2016). Though this area is an important geographical region for PPR spreading from the west to the east, there is not an integrated study on the spatial distribution of PPR here. For the first time, the spatial distribution risk of PPR in this region was accurately assessed by multiple eco-geographical, anthropoid and meteorological variables. The results show that western border of Xinjiang and the northwest border of Tibet are high risk areas for PPR, which are consistent with the historical distribution of PPR. High-risk areas of PPR was also verified in Pakistan, Afghanistan, Kazakhstan, Kyrgyzstan and other bordering countries, while the distribution area is larger than that in China, showing the possibility of risk export. Previously, it was thought that there had been PPR communication between China and its western neighboring countries, but no evidence was found. Though the genetic relationship of PPRV isolated in countries within this region can be determined by phylogenetic analysis, the origin country of PPRV from the aspect of epidemiology can not be answered yet(Sahu et al., 2017). Then the source of

PPR in China is still a mystery. In this paper, the validation of the available transboundary paths for PPR spreading are proved first time by spatial and habitat analysis techniques. Combining with the migration of wildlife and transboundary grazing, the integrated transboundary situation of PPR in this region was effectively revealed(Stewart and Belote, 1976). Currently, different elevation areas are dealt with separately to overcome the incapability of the model in dealing with DEM with great difference(Himeidan et al., 2009). We also categorized the target areas into two and taken 1500 m as the threshold. After analysis, the accuracy of these two models is optimal and the prediction is reliable. The predicted high-risk area completely covered all known historical epidemic areas. To adopt 1500 meters as the threshold to distinguish the high altitude areas from the low altitude areas is based on the internationally standard for altitude division.

In our research, the densities of wild and domestic small ruminants animals are not used because of their uneven distribution and the difficulty in population size assessment, which is influenced greatly by the migration habits of wild small ruminants animals and nomadic lifestyle. Such behaviors of migration and nomadism are sensitive to temperature, precipitation, altitude, slope and human population distribution(Carlson et al., 2019). They are natural responses to the natural seasonal factors, or in other words, regulated by the above factors. Therefore, the risk analysis based on the above variants can effectively reflect the actual distribution of PPR.

The LCP analysis is the most commonly used method to assess the connectivity between habitats(Cushman et al., 2013). It designs a landscape resistance surface based on the assumed "cost" of landscape components versus species movement, and determines the minimized cumulative cost path between sites(Ntassiou et al., 2015). The minimum cost model can integrate the geographic information and behavior information. In our maximum available path's analysis, based on special purposes, we did not assign a value to DEM and LC after reclassification according to the expert experience as usual. For transboundary spreading of PPR, except the unavailable paths, all paths can be utilized by small ruminants and responsible for PPR spreading. Therefore, all available paths should be kept without further classification. In terms of the number of transboundary path, we focus on the calculation on risk areas close to the border on both sides. A band of paths that did not cross the boundary itself and finally partially overlapping with the transboundary paths were removed. Correspondingly, the transboundary paths were kept priority.

In 2018 in Xinjiang the 3 parallel border separation fences were built(Liu et al., 2020), which severely restricted the transboundary migration of wildlife and grazing of livestock, and to some extent, it is beneficial to the control the spreading of PPR(Cui et al., 2017). However, from the experience of the construction and lesson of damaging of the border fences in northeast border of China, it is impossible to build a large-scale border separation fences without any escape intervals for wildlife, even in the hilly and plain areas such as the northeastern China; secondly, in some special environments, such as rivers which can not be completely enclosed and remain for wildlife migration; Finally, the capability to damage fences of wild animals can not be ignored, such as the usual seen damage of boar to the border fences. Therefore, we can neither ignore nor be too optimistic about the obstructive role of the border fence for the migration of wild animals. To barrier the transboundary communication of human and animals does reduce the transboundary spreading of PPR(Didelot et al., 2015). While in the long run, the changes of the behaviors of human and animal will certainly lead to the changes of the landscape and then to the spatial distribution of wildlife diseases at the landscape scale(M. and Munir, 2014). Therefore, in the future, we will pay attention to the spatiotemporal dynamics of PPR in this region, in order to provide experience for the study of PPR distribution and decision making in other similar regions in the world.

Density of population is the most important factor affecting the distribution of PPR, in pastoral areas, herdsmen mainly raise small ruminants as their economic source, and the number of small ruminants is closely related to PPR epidemic. In the border areas of western China, the nomadic nations are dominant. In the area above 1500 m, with the human population density increasing gradually, the risk of PPR increases slowly, and followed by a platform period. This is because most of the high-altitude areas are pastoral areas and with the increase of small ruminants raised by people, the risk of disease also increased. In the area below 1500 m, with the human population density increasing, the risk of disease increases first, and then

decreases rapidly. This is because the low altitude areas are mostly occupied by cities and towns. In small towns (less urbanization), the risk of disease is higher in accordance with the density of livestock where small ruminants are still kept as economic sources (Keesing et al., 2010). While in urban areas, the lower risk of disease is the reason of the unsuitability of livestock raise.

Some studies have pointed out that temperature rise plays a key role in diseases outbreak and spreading (Aguilar et al., 2018). In this study, the minimum temperature of June is the main variable in the category above 1500 m. In June with the gradually increase of the average minimum temperature (within 0-13), the PPR risk increases gradually; The mean temperature of September is the main factor in the category below 1500m. In September with the gradually increase of the average temperature (within 0-31), the probability of PPR increases gradually. It has been found that with the increase of temperature, the risk of animal disease increases (Nicholls, 2015). Richard Kock pointed out that temperature rise plays a key role in disease (Kock et al., 2018).

China share a long border with many neighboring countries and facing a great risk of PPR cross-border import by the cross-border activities of small ruminants. Five cross-border import paths are predicted in this study, among which path h is from Kazakhstan through the junction of Khorgos River and Ili River into Xinjiang, China. The homology of PPRV strains isolated from Kazakhstan and China is 99.8%, which reflects the cross-border communication between the two countries (Kock et al., 2015). Huocheng County, Ili Kazak Autonomous Prefecture, Xinjiang, China is located in the open area in the northwest of Ili River Valley. It borders Kazakhstan, and the Khorgos river is in the west. Planting and animal husbandry are the main local production mode, and there are bilateral cross-border grazing. It has been reported that Saiga antelopes which widely distributed in Kazakhstan migrates to the north and south twice a year, and they migrate to Xinjiang, China through Kazakhstan to give birth, which also provides the possibility for PPR cross-border transmission (Cui et al., 2017, Bekenov et al., 2010). The cross-border paths a.b.c enters China from the west of Pamir Plateau. Western Pamir has abundant rainfall, abundant vegetation and wide distribution of wild small ruminants. As there are many mountain passes, it can lead to India in the south and to Afghanistan in the west, and may also be a natural channel for PPR transmission. On the Pamir Plateau, China's Tashkurgan Wildlife Nature Reserve, which borders Pakistan, is where rare wildlife such as *Procapra przewalskii*, *Ovis ammon polii*, *Pseudois Nayar* and *Capra sibirica* roam. Wild animals are easy to cross into China. Therefore, Pamir Plateau is also an important cross-border passage for wildlife, which is a high-risk area for PPR cross-border import. The cross-border paths d is from Kashmir along the Bank of Bangongcuo lake into Ritu County, Tibet, China. Bangongcuo Lake runs through Kashmir and Tibet, China. It is a natural ranch, among which *Equus Kiang*, *Pantholops hodgsonii* and *Ovis ammon* are widely distributed. These wild animals can adapt to the harsh environment and survive in the area of 4600-6000 altitude. They can live in the area of ultra-high altitude. The natural channel carries out cross-border activities. There are abundant grasslands in Ritu County in China. Most of them are semi-agricultural and semi pastoral nomads. Wild animals and domestic animals share the same water source, food and frequent contact in the activity area. It is suspected that PPR has been introduced into Ritu County in Tibet since 2005. It has also been reported that wild animals in this area have died of small ruminant epidemic (Bao et al., 2011b).

PPR has been transmitted to China twice. The western border of China is long and borders many countries, and there are many transboundary channels. In order to control the introduction of diseases from abroad, it is necessary to strengthen the monitoring on the available transboundary paths. Especially during the suitable seasons for PPR spreading, to forbid grazing and set barriers within the path range should be done. Compulsory immunization should be carried out in densely populated border towns and pastoral areas to reach a highly effective immune response in case of contacting with infected wild animals (Bao et al., 2011a). Due to the reason of broad distribution of PPR, multiple hosts and strong migration of hosts, large-scale vaccination is impossible for prevention, so prevention and control has been difficult. This research not only provides more accurate prevention and control strategies for the prevention of the introduction of PPR into China, but also provides better suggestions for the prevention and control of PPR in neighboring countries, and provides an important rationale for the complete elimination of PPR in China in 2020 (Albina et al.,

2013).

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COMPETING INTERESTS

The authors declare that they have no conflict of interest.

Author Contributions

Wang XiaoLong conceived and supervised the study. Gao Shan carried out the spatial modeling, the Least Costs Path analysis, interpretation of results, map design and draft writing. Lv JiaNing also contributed to the data filtering and the map design. Wang XiaoLong, Wang HaoNing and Huang LiYa contributed to the discussion and manuscript writing. Xu GuoYong provides DEM data and help in cartography. All authors significantly contributed to the final manuscript and gave final approval for publication.

Ethical Statement

The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to. No ethical approval was required.

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Table 1 Details of the variables

Variables classification	Variable details	Source
Climate ^a	Bioclimatic	http://chelsa-climate.org
	Monthly P	
	Monthly mean T	

Terrain^b	Monthly min T	
	Monthly max T	
	DEM	http://www.gscloud.cn/
	Slope angle	
Human impact	Distance to river	
	Population	http://www.worldpop.org.uk/data/summary/?doi=10.5258/SOTON/WP0
Land cover	Land cover	http://maps.elie.ucl.ac.be/CCI/viewer/download.php

Table 2 Estimates of relative contributions of the environmental variants to the final models

Above 1500m		
variant	Contribution%	Permutation importance
Population Density	32.2	30.3
Min T June	28.4	45.9
Slop	22.7	10.2
Land Cover	16.6	13.6
Below 1500m		
variant	Contribution%	Permutation importance
Population Density	46.8	21.9
Mean T Sep	38.8	69.7
Land Cover	10.7	5
Slop	3.7	3.3

Figure 1 Research area

Figure 2 Response curves for PPR above 1500. The curves show the mean response (red) and the mean standard deviation (blue)

Figure 3 Response curves for PPR below 1500. The curves show the mean response (red) and the mean standard deviation (blue)

Figure 4 Probability of occurrence of PPR with the high-risk sectors of the international borders

Figure 5 PPR transboundary input paths

(In this study, the boundary line is a schematic boundary line, not as any basis for demarcation.)





