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Urbanization and Habitat Characteristics Associated with the Occurrence of Peste des Petits Ruminants in Africa

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Abstract: As a highly contagious viral disease, peste des petits ruminants (PPR) can cause severe socio-economic impacts in developing countries due to its threat to sheep and goat production. Previous studies have identified several risk factors for PPR at the individual or herd level. However, only a few studies explored the impacts of landscape factors on PPR risk, particularly at a regional scale. Moreover, risk factor analyses in Africa usually focused on sub-Saharan Africa while neglecting northern Africa. Based on regional occurrence data during 2006–2018, we here explored and compared the risk factors, with a focus on factors related to ruminant habitats, for the occurrence of PPR in sub-Saharan and northern Africa. Our results demonstrated different risk factors in the two regions. Specifically, habitat fragmentation was negatively correlated with PPR occurrence in sub-Saharan Africa, while positively correlated with PPR occurrence in northern Africa. Moreover, urbanization showed a positive association with PPR occurrence in sub-Saharan Africa. Our study is among the first, to our knowledge, to compare the risk factors for PPR in sub-Saharan and northern Africa and contributes to a better understanding of the effects of habitat characteristics on PPR occurrence at a regional scale.

Keywords: landscape factor; PPRV; urbanization; habitat fragmentation; livestock; risk factor

1. Introduction

Land use change (such as urbanization, habitat fragmentation, deforestation, agricultural intensification, livestock grazing, etc.) can dramatically alter host–pathogen interactions and disease risks by its impacts on host/vector movements and distributions, pathogen survival and activity, and microenvironments [1,2]. Although many studies have been conducted on the relationship between land use change and infectious diseases in the last two decades, our understanding of this relationship is still incomplete [2], partly due to its complexity caused by many involved processes. For example, A previous study found that forest fragmentation in the eastern United States had inconsistent effects on Lyme disease risk in different study periods [3]. Therefore, more studies are needed to deepen our understanding of the relationship between land use change and infectious diseases, particularly in those regions that are still undergoing rapidly growing population and increasing demands on land for urban development or agricultural industry.

Peste des petits ruminants (PPR) is a highly contagious viral disease of small ruminants caused by the peste des petits ruminants virus (PPRV) of the genus *Morbillivirus*, family *Paramyxoviridae* [4,5]. It is mainly transmitted through direct contact between infected and susceptible hosts [6]. PPR prevails in a wide range of areas in Africa, Asia, and the Middle East [7], of which Africa and Asia have the highest disease outbreak rates [8]. In recent years, it has also been reported that PPR is occurring in European ruminant populations [9].

PPRV can spread rapidly in wild and domestic ruminant populations [10,11], posing a huge threat to animal husbandry, particularly sheep and goat production in developing countries [8,12,13]. In 2015, the World Organization for Animal Health (OIE) and the Food and Agriculture Organization of the United Nations (FAO) prioritized PPR for control and launched a joint plan to eradicate the disease by 2030 [14].

Previous studies have identified many risk factors that may contribute to the outbreak and spread of PPR at the herd level [15–19]. For example, an investigation among sheep and goat flocks in northern Jordan found that PPR infection prevalence was higher in larger herds with higher numbers of sheep and goats [18]. Herzog et al. found that herds with cattle kept separate from goats and sheep had a higher infection rate than those with three species kept together [19]. This may be caused by the fact that cattle, as an incompetent host with a low ability to secrete and spread PPRV, can reduce the contact rate between competent hosts such as goats and sheep [19–21]. Besides risk factors at the herd level, studies also identified several risk factors at the individual level. For example, PPR prevalence was significantly higher in goats aged 4–6 months than in those aged less than 4 months [22]. Mahamat et al. found that seroprevalence in female goats and sheep was higher than in males [23].

In addition to host factors, landscape factors can also influence PPR risk by influencing host movements and distributions. For example, Rahman et al. found a positive correlation between road length and PPR cumulative incidence in Bangladesh, which may be related to animal movement [24]. PPR incidence in sheep and goats was the highest in plains and hilly areas of Punjab and Sindh in Pakistan, as nomadic grazing in these areas could promote contact between animals [25]. A serological survey in Ethiopia in 1999 showed similar results, indicating that the seroprevalence of PPR was higher in lowlands than in highlands [26]. In contrast, Ruget and Fournié conducted a predictive study in this region and showed that highlands had a greater risk of PPR outbreaks and transmission than lowlands. The contradictory results of these two studies might be attributed to the fact that the serological survey was not conducted in many highlands, missing some high-risk highland areas to which PPRV could be spread through the movement of animals such as sheep [6,27]. Furthermore, factors related to land cover could also be associated with PPR outbreaks. For example, by predicting the outbreak risk of PPR in western China and the Trans-Himalayan region, Gao and Zeng et al. found that PPR was more likely to occur in grasslands, deciduous broad-leaved forests, shrub lands, and urban areas, which may be related to ruminants' habitat preference and the impact of humans on ruminant activity [28,29].

As the first region to report PPR, Africa still has one of the highest PPR outbreak rates in the world [8], playing an important role in PPR removal programs. In some countries in sub-Saharan Africa, the economic losses caused by PPR can account for up to 70% of the total household income, particularly for families in pastoral areas with livestock as their main economic source [30]. However, only a few studies have been conducted to investigate the factors associated with PPR risk in Africa, particularly at a regional scale. For example, Ruget et al. proposed that some landscape factors such as water bodies, road density, and arid or semi-arid areas might be associated with PPR spread and outbreaks in East Africa and the Union of Comoros [27], but these proposed associations were not tested with statistical methods. Moreover, there have been rare studies focusing on PPR risk in northern Africa. It has been suggested that the frequent animal trade and transboundary movements from northern Africa to Europe and other parts of Africa promote the spread of PPR among these regions [31]. In fact, the recurrence of PPR in the Maghreb region of Africa has been considered one of the major challenges to achieving the global PPR eradication target by 2030 [31].

Therefore, in this study, we explore the spatial patterns of PPR occurrence during 2006–2018 in Africa and investigate the risk factors with a focus on both host and landscape characteristics. Considering the differences in climate and landscape conditions between northern Africa and sub-Saharan Africa, we perform analyses for the two regions in order to better compare the risk factors between these two regions. This study can provide new insights into understanding the risk factors of PPR occurrence in Africa and contribute to a better prediction of the future in the context of global land use change.

2. Materials and Methods

2.1. Disease Data

Data on PPR presence/absence in Africa from 2006 to 2018 were collected from the World Animal Health Information System coordinated by OIE, which provides data on PPR outbreaks in domestic animals with a one-year resolution. Some countries reported PPR only at the country level, while others reported it at a smaller administrative level. In this study, we only used the data reported at the administrative level. Moreover, only the countries that reported at least one PPR case during the study period were included in the analyses, in order to avoid potential false absences. We divided African countries into northern and sub-Saharan African regions according to the Statistics Division of the United Nations (UNSD, https://unstats.un.org/unsd/methodology/m49, accessed on 1 December 2021). The final dataset for the analyses includes 4449 cases of PPR presence/absence for 26 countries in sub-Saharan Africa, while 1051 cases of PPR presence/absence for 6 countries in northern Africa (Figure 1).

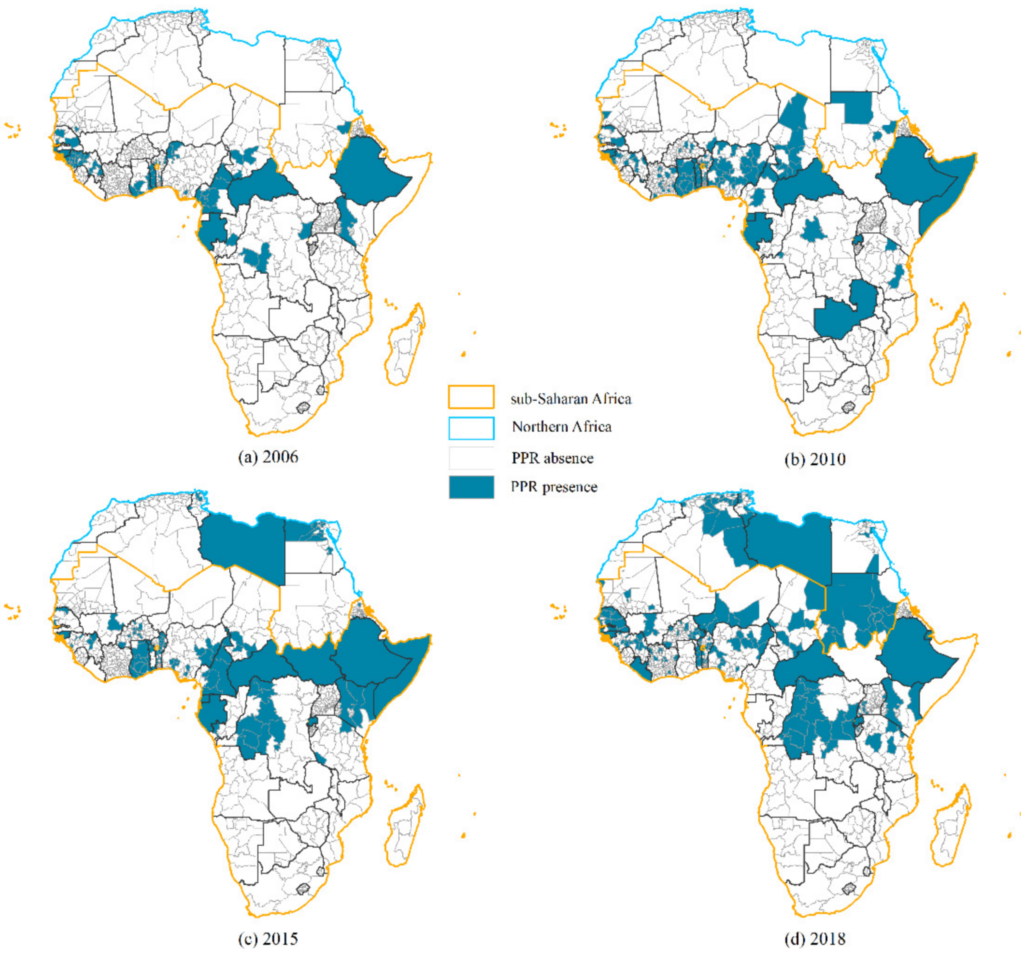

Figure 1. Spatial patterns of PPR occurrence in Africa in 2006 (**a**), 2010 (**b**), 2015, (**c**) and 2018 (**d**).

2.2. Data of Predictors

To explore the risk factors associated with PPR occurrence in sub-Saharan Africa and northern Africa, we considered a large set of predictors including livestock density, landscape factors, and climatic variables (Table 1).

Table 1. Description of predictors used in this analysis. X relates to the land cover class (for landscape variables).

Variables	Description of Data	Units
Biotic predictors		
Pig	Pig density	n/km^2
Goat	Goat density	n/km^2
Sheep	Sheep density	n/km^2
Cattle	Cattle density	n/km^2
Landscape predictors		
NP_X [1]	Number of patches of a land cover class X	-
PLAND_X [1]	Percentage of area of a land cover class X	-
ED_X [1]	Edge density of a land cover X at the region	-
TE_X [1]	Total edge length of a land cover X at the region	-
Elevation	Average elevation of each administrative area	km
People	Population density of each administrative area	n/km^2
Road	Total roads density of each administrative area	km/km^2
Climatic predictors		
premean	Annual mean precipitation	mm
tmean	Annual mean temperature	°C
BIO9	Mean temperature of driest quarter	°C
BIO10	Mean temperature of warmest quarter	°C
BIO11	Mean temperature of coldest quarter	°C
BIO17	Precipitation of driest quarter	mm
BIO18	Precipitation of warmest quarter	mm
BIO19	Precipitation of coldest quarter	mm

Note: [1] X—(2, 3, 8, 9, 10, 13 and 15); 2—evergreen broad-leaved forest; 3—deciduous broad-leaved forest; 8—shrub; 9—grassland; 10—sparse vegetation; 13—urban; 15—water body.

Domestic and wild small ruminants are the main host species of PPRV. Infected animals often show symptoms such as fever, diarrhea, pneumonia, stomatitis, and mucus secretion from the eyes and nose [32], which can transmit to other susceptible individuals through direct contact, water sharing, etc. [33]. Domestic goats and sheep are the primary host species of PPRV, with up to 100% morbidity and mortality in infected individuals [34]. Besides domestic goats and sheep, domestic pigs and cattle can also be infected by PPRV and even transmit PPRV to goats and sheep [35]. Previous studies have found that the number of these species can influence PPR risk at the herd level [18,19,36]. Thus, in this study, we calculated goat density, sheep density, pig density, and cattle density for each administrative area and tested their correlations with PPR occurrence on a regional scale.

As landscape structure can influence the spread of animal diseases by affecting the host movements and distributions [37], we here calculated a series of landscape predictors based on the global land cover maps from the European Space Agency CCI 300 m annual global land cover products. We focused on seven land cover classes (i.e., grassland, sparse vegetation, shrub, water body, deciduous broad-leaved forest, evergreen broad-leaved forest, and urban) that are closely associated with ruminant habitat selection and activity [38–40]. For each land cover class, we calculated the number of patches (NPs) and the percentage of area covered by a land cover class (PLAND) for each administrative area, as previous studies found that PPR was more likely to occur in grasslands, deciduous broad-leaved forests, shrub lands, and urban areas [28,29]. In addition, as habitat fragmentation can affect disease risk through the impacts on resource availability as well as animal movements and distributions [41], we also calculated the edge density (ED) and total edge length (TE) for each land cover class. These two metrics were used as the measures of habitat fragmentation, as fragmented landscapes usually contain high-density edges, defined as the total length of the boundary between the two habitat types per unit core area [42]. In addition, we also calculated the mean elevation as previous studies have found a correlation with PPR risk [26]. The mean population density (People) and road density (Road) were calculated as the measures for livestock trade activities [43].

In addition to landscape factors, we also included several climatic variables, as they can influence disease risk by affecting the pathogen survival, host behavior, and distributions [44–46]. Thus, in this study, we included the average annual temperature (premean) and the average annual precipitation (tmean). Moreover, studies have suggested that extreme climatic conditions, such as hot and humid summer [22] and low precipitation in the driest month [45], could promote PPR outbreaks; thus, we also included the mean temperature of the driest quarter (BIO9), the mean temperature of warmest quarter (BIO10), the mean temperature of coldest quarter (BIO11), the precipitation of driest quarter (BIO17), the precipitation of warmest quarter (BIO18), and the precipitation of coldest quarter (BIO19). These climatic variables were calculated based on the climatic data collected from WorldClim (https://worldclim.org, accessed on 1 December 2021). All data were processed in ArcGIS 10.5.

2.3. Statistical Analyses

We used generalized linear mixed models (GLMMs) with a binary response (logit link) to investigate the relationships between PPR occurrence and predictors. We included country and year as random factors to control for the variations between years and countries. Before performing GLMMs, we log-transformed density-related variables and then scaled all predictor variables to have a mean of zero and a standard deviation of one.

We first performed univariate regression analyses to examine the association of each predictor with PPR occurrence. Variables with a significant association ($p < 0.05$) were identified as potential risk factors, for which we evaluated the multi-collinearity by calculating the pairwise correlation coefficients (r). For highly correlated variables ($r > 0.7$), we only included the variable with the lowest p-value to construct multiple regression models. After constructing a full model with all remained potential risk factors, we performed backward selection based on the changed Akaike information criterion (AICc) value [47] to obtain the final regression model. For both univariate analyses and multiple regression analyses, the county area (AREA) was retained in the model to control for the effect of area size. All statistical analyses were conducted in R 4.2.0 with *lme4* [48] and *MuMIn* [49] packages.

3. Results

3.1. Univariate Regression Analyses

The univariate analysis for sub-Saharan Africa (Table 2) showed that PPR occurrence was positively correlated with pig density, goat density, sheep density, and population density (People). As regards the landscape predictors, PPR occurrence was positively correlated with the number (NP_13) and total edge length (TE_13) of urban patches, the patch number (NP_2) and total edge length (TE_2) of evergreen broad-leaved forest areas, and the percentage of deciduous broad-leaved forest areas (PLAND_3), while negatively associated with the patch number of grassland areas (NP_9). In addition, PPR occurrence was positively correlated with several climatic variables, namely the mean precipitation of the warmest quarter (BIO18), the mean temperature of the driest quarter (BIO9), and the mean temperature of the coldest quarter (BIO11).

In northern Africa, univariate analysis showed that PPR occurrence was positively correlated with pig density. In terms of the landscape predictors, PPR occurrence was positively correlated with the patch number (NP_2) and edge length (ED_2) of evergreen broad-leaved forest areas, the edge density (ED_9) and percentage of grassland areas (PLAND_9), and the patch number of urban areas (NP_13).

Table 2. Univariate regression results (standardized regression coefficient, b, and Z-statistics) for the predictors correlated with the PPR occurrence in sub-Saharan Africa and northern Africa.

Variables	Sub-Saharan Africa		Northern Africa	
	b	**Z-Value**	**b**	**Z-Value**
Biotic predictors				
Sheep density	0.145	2.80 **	0.179	1.36
Goat density	0.239	4.43 ***	0.205	1.72
Pig density	0.250	4.45 ***	0.249	2.34 *
People	0.222	2.98 **	0.394	1.63
Landscape predictors [1]				
NP_2	0.135	2.21 *	0.264	3.13 **
TE_2	0.130	2.31 *	0.188	2.16 *
PLAND_3	0.085	2.00 *	−0.105	−1.08
PLAND_9	−0.083	−1.73	0.441	3.03 **
NP_9	−0.141	−2.33 *	0.197	0.86
ED_9	−0.065	−1.37	0.382	2.67 **
NP_10	−0.074	−1.34	0.222	2.09 *
TE_10	−0.074	−1.42	0.193	2.00 *
NP_13	0.157	2.85 **	0.236	2.07 *
TE_13	0.162	3.67 ***	0.163	1.43
Climatic predictors [2]				
BIO9	0.152	2.51 *	0.113	1.20
BIO11	0.127	2.27 *	0.107	0.48
BIO18	0.176	3.02 **	−0.178	−0.91

Note: * $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$; [1] PLAND_X, percentage of area of a land cover class X; X, (2—evergreen broad-leaved forest; 3—deciduous broad-leaved forest; 9—grassland; 10—sparse vegetation; 13—urban); NP_X, number of patches of a land cover class X; TE_X, total edge length of a land cover X; ED_X, edge density of a land cover X; [2] BIO9, mean temperature of driest quarter; BIO1, -mean temperature of coldest quarter; BIO18, precipitation of warmest quarter.

3.2. Multiple Regression Analyses

The results of the final multiple regression model for sub-Saharan Africa (Table 3) showed that PPR occurrence was positively associated with pig density, goat density, the total edge length of urban areas (TE_13), the percentage of area covered by deciduous broad-leaved forest (PLAND_3), and the mean temperature in the driest quarter (BIO9), while negatively correlated with the patch number of grassland (NP_9). The AUC for the final model in sub-Saharan Africa was 0.701.

Table 3. Summary statistics (standardized regression coefficient b, Z-value, and *p*-value) for the predictors correlated with the PPR occurrence in multiple regression models in sub-Saharan Africa.

Variables	b	Z	*p*-Value
Pig density	0.131	2.19	0.028 *
Goat density	0.260	4.49	<0.001 ***
PLAND_3	0.093	2.12	0.034 *
NP_9	−0.134	−2.10	0.035 *
TE_13	0.143	3.08	0.002 **
BIO9	0.176	2.84	0.004 **
BIO18	0.109	1.76	0.077

Note: * $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$. BIO18, precipitation of warmest quarter; BIO9, mean temperature of driest quarter; NP_9, patch number of grassland; PLAND_3, percentage of area covered by deciduous broad-leaved forest; TE_13, total edge length of urban areas.

In northern Africa, the final model had an AUC value of 0.814. Three predictors, namely pig density, the patch numbers of evergreen broad-leaved forest (NP_2), and sparse vegetation (NP_10), showed positive correlations with PPR occurrence (Table 4).

Table 4. Summary statistics (standardized regression coefficient b, Z-value, and *p*-value) for the predictors correlated with the PPR occurrence in multiple regression models in northern Africa.

Variables	b	Z	*p*-Value
Pig density	0.316	2.81	0.005 **
NP_2	0.291	3.24	0.001 **
PLAND_9	0.308	1.92	0.055
NP_10	0.322	2.72	0.006 **

Note: ** $p < 0.01$. NP_2, patch number of evergreen broad-leaved forest; NP_10, patch number of sparse vegetation; PLAND_9, percentage of area covered by grassland.

4. Discussion

Landscape factors have been considered to affect infectious disease risk through their influence on pathogen survival, host movements, and distributions [2,41,46]. However, few studies considered the impacts of landscape factors, particularly habitat fragmentation and urbanization, on the risk of PPR occurrence. Moreover, previous risk analyses on PPR in Africa usually focused on sub-Saharan Africa, while neglecting northern Africa, where frequent animal trade and transboundary movements may promote the spread of PPR to other regions. Therefore, in this study, we explored and compared the risk factors, with a focus on landscape factors, associated with PPR occurrence in sub-Saharan and northern Africa. In general, our results showed that the risk factors for PPR occurrence in sub-Saharan and northern Africa were distinct, except for pig density, which, consistent with previous studies [35], was positively correlated with PPR occurrence in the two regions.

We showed that the total edge length of urban areas (TE_13) was positively associated with PPR occurrence risk in the sub-Saharan region. The increase in the total edge length of urban areas is often related to the expansion of urban areas. Africa, especially sub-Saharan Africa, is one of the fastest urbanizing regions in the world [50]. Informal livestock breeding is common in African cities. Urbanization comes with the intensification of livestock feeding and production systems, which can promote the interactions between animals and thus increase the risk of virus transmission [43,51]. In addition, with increasing urbanization, more and more wildlife habitats are occupied by humans, affecting wildlife distribution and density, the wildlife–livestock interface, as well as the environmental pollution caused by pathogens [41], all of which can largely alter the contact rates between hosts and pathogens. In fact, our univariate analyses also supported this notion, showing that the patch number of urban areas (NP_13) was positively associated with PPR occurrence in sub-Saharan Africa.

We also found that the percentages of area of deciduous broad-leaved forest (PLAND_3) and grassland (PLAND_9) showed, respectively, a positive correlation with PPR occurrence in sub-Saharan and northern Africa. A larger proportion of habitat area means more abundant food and space, which can attract more animals to gather, thereby increasing the contact rates between animals, leading to a high risk of infectious disease [28,29]. However, we showed that PPR occurrence was oppositely correlated with the numbers of habitat patches in the two regions, with positive associations with the numbers of sparse vegetation patches (NP_10) and evergreen broad-leaved forest patches (NP_2) in northern Africa, while negative associations with the number of grassland patches (NP_9) in the sub-Saharan region. An increase in the number of habitat patches is usually correlated with an increased degree of habitat fragmentation and decreased connectivity between patches, which could reduce the contact rates among animals, as animal herds may move less between patches. This might be the reason for the negative correlation between the patch number of grassland and PPR occurrence in sub-Saharan Africa.

In addition to reducing opportunities for connectivity or dispersal (reducing patch-to-patch contact), however, habitat loss and fragmentation can also promote the contact rates among animals within patches due to smaller patch sizes and/or resource aggregation, or increasing contact between wildlife and domestic animals due to increased marginal habitats, both of which can influence pathogen transmission by altering intra- and interspecies contact rates [41]. In fact, previous studies have shown that the net effect of habitat fragmentation on disease risk can be either positive or negative, depending on the relative importance of the processes involved in the effects of habitat fragmentation on pathogen transmission [52]. Compared with sub-Saharan Africa, resource availability for small ruminants in northern Africa is relatively poorer due to more severe climatic conditions [53,54]. The reduction in habitat area and lack of food resources caused by habitat fragmentation may make ruminants gather in limited suitable habitat spots and promote contact rates among animals. Meanwhile, the survival pressure of ruminants may also increase with increased habitat fragmentation, leading to a decline in herd immunity and an increase in disease infection. Therefore, the positive impact of habitat fragmentation on PPR transmission might be far less than its negative impact (by reducing animal movements) in northern Africa, resulting in positive correlations between PPR occurrence and the patch number of habitats (i.e., sparse vegetation and evergreen broad-leaved forest) in northern Africa.

In addition to landscape factors, we found that PPR occurrence in sub-Saharan Africa was also positively correlated with the mean temperature in the driest quarter (BIO9). PPRV can spread by sharing water sources and pastures. During dry seasons, animals are more likely to gather in pastures and water sources, increasing the contact rates among animals, which consequently increases the possibility of virus transmission. Meanwhile, animals usually travel long distances to find pastures and water sources during the dry and hot seasons when food and water availability were relatively low. This can increase the animals' survival pressure, which thus reduces the immunity of animals and increases the infection risk of the PPR [25,55].

We admit that it is generally difficult to draw conclusions from the correlative studies at such a large spatial scale, due to the difficulties of controlling for confounding factors [1]. In fact, there are several limitations in our analyses. For example, due to the passive reporting system applied by OIE, the disease data may not fully reflect the actual PPR occurrence in Africa. Furthermore, we did not include some important factors, such as the quality of the veterinary services or control measures applied, due to the lack of data. However, we included the country as the random factor in the analyses, which may partly control for the variation caused by these country-level factors. Finally, we used country-level boundaries based on UNSD to define sub-Saharan and northern Africa. Some countries, such as Niger, Chad, Mauritania, and Mali, that were classified as sub-Saharan countries in the analyses may also have Saharan zones, which may affect the precision of our analyses. However, the results generated by reanalyzing the subset data (excluding these four countries) were only slightly different.

Despite having these limitations, this study is among the first, to our knowledge, that tested and compared the effects of landscape factors on PPR occurrence at a regional scale in sub-Saharan and northern Africa and thus provides a good reference for understanding the impacts of urbanization and habitat fragmentation on PPR risk. Particularly, the positive effect of urbanization on PPR risk that we found suggested that the expansion of urban areas, together with the intensification of livestock breeding, can promote the risk of some livestock diseases. This result implies that, with the ongoing urbanization in Africa, it is necessary to strengthen the management of livestock in urban and peri-urban areas, which may help to prevent not only PPR but also other direct-transmitted livestock diseases. In addition, we found that the fragmentation of natural habitats was positively correlated with PPR risk in northern Africa with lower resource availability for livestock, which implies that protecting natural habitats and reducing habitat fragmentation might be useful, particularly for resource-poor regions, to avoid animal aggregation and prevent livestock diseases. However, in resource-rich areas, such as some fertile grasslands in sub-Saharan regions, fences could be used to reduce the contact rates and pathogen transmission between animal herds.

5. Conclusions

In this study, we investigated and compared the spatial patterns of PPR occurrence in sub-Saharan and northern Africa and explored the effects of landscape factors, as well as livestock density and climatic variables, on PPR occurrence. We demonstrated that the habitat-related risk factors for PPR occurrence in the two regions were distinct. Generally, the fragmentation of ruminant habitats showed a positive correlation with PPR occurrence in northern Africa, while a negative correlation in sub-Saharan Africa. In addition, urbanization was positively associated with PPR occurrence in sub-Saharan Africa. With the ongoing land use change, this study not only provides new insights into understanding the regional risk factors for PPR in Africa but also deepens our understanding of the effects of land use change and urbanization on animal disease risk.

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