

Urbanization influences hemorrhagic fever with renal syndrome transmission: 34-year evidence from China's national surveillance

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ABSTRACT

Background: Mainland China accounts for over 90 % of the global hemorrhagic fever with renal syndrome (HFRS) cases, yet quantitative relationships between climate, urbanization and transmission dynamics remain poorly understood across national scales.

Methods: We analyzed 34 years of HFRS surveillance data (1985–2018) from 31 provincial-level administrative divisions in China to examine the associations with climatic variables, socioeconomic indicators, and land use types using Bayesian nonlinear mixed-effects models. Dominance analysis was conducted to quantify the relative importance of each predictor. Additionally, linear mixed-effects and generalized additive models were implemented for comparative and validation purposes.

Findings: Annual HFRS incidence declined sharply from a peak of 10.99 cases/10⁵ in 1986 to fewer than 0.98 cases/10⁵ after 2010, with the top four highest annual averaged HFRS incidence cases reported at the provinces of Heilongjiang, Shandong, Shaanxi and Zhejiang. Bayesian models demonstrated excellent predictive performance ($R^2 = 0.8722$ and 0.8592 for early/late periods, i.e., 1985–2004 and 2005–2018, respectively). Before 2005, impervious surfaces, population and wetlands emerged as the top three dominant transmission predictors. After 2005, however, the key predictors shifted, with wetlands, the Palmer Drought Severity Index (PDSI), and impervious surfaces having the highest relative importance.

Interpretation: The quantification of urbanization is provided through impervious surface expansion and wetlands changes, which represent the primary predictors of HFRS

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transmission in China, likely operating through rodent habitat modification and altered human-wildlife contact patterns. The emerging wetland influence suggests that environmental policies are reshaping disease dynamics. Our findings support urbanization-targeted prevention strategies across the Western Pacific region and highlight integrating land use surveillance into regional infectious disease monitoring systems.

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1. Introduction

Hemorrhagic fever with renal syndrome (HFRS) poses a significant public health challenge, representing a substantial disease burden across mainland China (Bai et al., 2019; He et al., 2023; Zhang et al., 2014). This zoonotic disease, primarily transmitted through hantaviruses carried by rodents, presents a spectrum of clinical manifestations ranging from fever to life-threatening complications, including renal failure and hemorrhage (Chen, 1999; Song, 1999; Zou et al., 2016). Between 1950 and 2018, mainland China reported over 1.66 million HFRS cases, with persistent transmission across multiple provinces (He et al., 2023; Xiao et al., 2014).

China's rapid socio-economic development contributes to urbanization rates, population density, land use types, healthcare infrastructure, and socio-cultural behaviors (He et al., 2018, 2019a; Liu, Liu, et al., 2024; Tian et al., 2018; Wang et al., 2022, 2024; Xiao, Tong, Gao, & et al, 2018; Zhu et al., 2022). These factors intricately shape the vulnerability of communities to HFRS by influencing human-rodent interactions, housing conditions, access to healthcare services, and compliance with preventive measures. On the other hand, environmental factors, such as temperature, precipitation, humidity, and other climatic variables, also exert significant influence in the transmission of vector-borne and zoonotic diseases (He, Christakos, et al., 2019; Wang et al., 2022; Zhu et al., 2022). Therefore, elucidating the key factors driving HFRS transmission has become increasingly important for developing effective disease prevention and control strategies.

From an ecological/epidemiological perspective, the reproductive dynamics of virus hosts directly determine the abundance of two major viruses: *Hantaan* virus and *Seoul* virus. Optimal temperature and precipitation conditions create favorable habitats and enhance primary food production for rodents, particularly in grassland and shrub ecosystems, as well as in areas with adequate river runoff and water availability (Li et al., 2024; Tian et al., 2017; Wang et al., 2023; Xiang et al., 2018). Moreover, the humidity influences the rodent activity and virus infectivity (Xiao et al., 2013a). Therefore, changes in climate patterns can alter the geographical distribution of rodent populations, leading to shifts in disease prevalence and the emergence of new epidemic trend. Furthermore, climatic factors can also influence human behavior and activities, such as outdoor recreational pursuits and agricultural practices, which consequently modify the risk of HFRS transmission and exposure pathways (Hansen et al., 2015; Ramankutty et al., 2006; Xiao et al., 2014).

Regarding the socio-economic development, educational, economic and medical conditions demonstrate significant effects on HFRS infections, as early warning systems, healthcare accessibility and timely treatment are crucial for preventing disease transmission (Wang et al., 2022; Xiao et al., 2014). Moreover, given that larger populations correlate with higher probabilities of HFRS infection, the human population also plays an important role in the HFRS transmission (Ge et al., 2016; Tian et al., 2018; Xiao, Tong, Huang, & et al, 2018). Last but not least, alterations in land use patterns not only significantly impact the ecological and climatic environments of both rodents and human populations, but also serve as important indicators of underlying socio-economic development levels, indicating the dynamics of ecological niche of rodent and human (Li et al., 2023a; Zhu et al., 2022). For instance, agricultural land, forested areas, and urban development have been identified as key determinants of HFRS incidence patterns in Shaoyang City, China (Xiao, Tong, Huang, & et al, 2018). Hence, China, with its vast geographical expanse and significant heterogeneity in climatic, socio-economic, and land use characteristics, offers exceptional opportunities for comprehensive HFRS research.

During the past decades, various methodologies were implemented to detect the major impact factors of HFRS in China. He et al. used a quasi-Poisson regression with a distributed lag non-linear model (DLNM) to quantify the relationship between HFRS and four factors, including temperature, rainfall, relative humidity and normalized difference vegetation index, in 109 counties of China, and found that HFRS was sensitive to temperature (He, Wang, et al., 2019). A similar DLNM analysis was conducted in 151 cities of China concluding that low temperature positively influences the long-term HFRS incidence (Luo et al., 2024). However, these studies only focused on the impact of climatic factors on HFRS. As for the socio-economic factors, Wen et al. utilized age-period-cohort model, Bayesian space-time hierarchy model and optimal parameters-based geographical detector model were employed to investigate the disease incidence trends, spatiotemporal heterogeneity and contribution of impact factors, respectively, and it was found that GDP/capita and relative humidity are the major factors in hot spot and warm spot regions (Wen et al., 2024). However, the land use was not considered in a large spatiotemporal scale study.

Further, wavelet coherency analysis together with the Bayesian maximum entropy (BME) method and the gradient boost machine framework were used to study the association between HFRS and global climate change in eastern China and detect the dominant geographical factors. The results showed that locations, grassland and woodland have the highest

impacts on HFRS-climate associations (He et al., 2018). Nevertheless, the land use types in this framework functioned primarily as contextual factors to elucidate the mechanisms underlying HFRS-climate associations, rather than serving as direct predictors in the HFRS estimation model.

In an effort to address these critical knowledge gaps, the present study undertakes a comprehensive, nationwide analysis of HFRS transmission dynamics across mainland China over 34 years (1985–2018). Employing a robust multi-model framework, including Bayesian nonlinear and dominance analysis, we aim to build an accurate HFRS estimation model by including land use, climatic, and socio-economic factors as predictors, and quantify their relative contributions to HFRS incidence.

2. Materials and methods

2.1. Data collection

Annually reported HFRS cases from 1985 to 2018 were collected from the China Information System for Disease Control and Prevention, covering 31 provincial-level administrative divisions in mainland China.

Eight relevant climatic variables were considered in this study including: near-surface downward shortwave radiation (SRAD), the palmer drought severity index (PDSI), soil moisture (SOIL), maximum temperature (TMAX), minimum temperature (TMIN), precipitation (PRE), water vapor partial pressure in air (VAP), and wind speed (WS), which together characterize atmospheric energy input, moisture availability, thermal extremes, and dynamic atmospheric conditions. They were downloaded from the Climatology Lab (<https://www.climatologylab.org/terraclimate.html>), and were spatially averaged at the provincial level for each time point.

In addition, several socio-economic factors were considered. Population (POP) and Gross Domestic Product (GDP) at each province were collected from the Statistical Yearbook of China, reflecting human density and potential exposure to HFRS risk, and serving as an indicator of economic development and living standards, respectively. Specifically, the factor POP includes the urban population and village population during the period from 2005 to 2018. GDP per capita reflects long-term economic growth and associated improvements in infrastructure and public health capacity (Endrei et al., 2018; Niu et al., 2021). We calculated GDP per capita and used it as an additional variable for further analysis. Land use and land cover (LULC) data (Yang & Huang, 2021) with spatial resolution of 30 m were downloaded from Zenodo (<https://zenodo.org/records/12779975>), and they divided land cover into 9 types, including cropland (LULC1), forest (LULC2), shrub (LULC3), grassland (LULC4), water (LULC5), snow/ice (LULC6), barren (LULC7), impervious surfaces (LULC8), and wetland (LULC9). These land cover types influence rodent habitats, human exposure patterns, and overall disease transmission dynamics. The proportion of each land cover type in each province were further calculated.

2.2. Statistical analysis

To investigate the association between environmental variables and HFRS incidence (cases/10⁵ population), we employed a comprehensive multi-model analytical framework comprising spatiotemporal clustering, Bayesian mixed-effect modeling, sensitivity analyses, and dominance analysis.

2.2.1. Spatiotemporal cluster determination

In light of the diverse regional patterns of HFRS transmission, HFRS incidence series were utilized to determine spatiotemporal clusters for further analysis. Specifically, a spatiotemporal distance matrix D was designed as Eq. (1),

$$D_{ij} = \sqrt{D_{Lon_{ij}}^2 + D_{Lat_{ij}}^2 + D_{Series_{ij}}^2}, \quad (1)$$

where D_{ij} denotes the comprehensive distance between Province i and j ; $D_{Lon_{ij}}$ and $D_{Lat_{ij}}$ represent the standardized absolute differences in longitude and latitude between the two provinces, respectively; $D_{Series_{ij}}$ represents the standardized HFRS time series distance between the two provinces, which was computed using the dynamic time warping (DTW) method implemented in the R DTW package. Subsequently, the partitioning around medoids (PAM) method was applied to identify clusters of HFRS time series patterns across different provinces using the R cluster package. The number of clusters was determined to be 6.

2.2.2. Bayesian nonlinear mixed-effects model and dominance analysis

To address multicollinearity among the environmental and socio-economic factors under consideration, a backward stepwise multiple linear regression model was employed to characterize the relationship between HFRS incidence and the predictor variables, retaining only those with variance inflation factors (VIF) less than 3. The selected variables were subsequently incorporated into a Bayesian nonlinear mixed-effects model to account for both fixed and random effects in the relationship between environmental and socio-economic factors and HFRS incidence, as Eq. (2) shows,

$$y = \beta_0 + \sum_{i=0}^n \beta_i s(x_i) + r_c + r_{cp} + e, \quad (2)$$

where y denotes the HFRS incidence; β_0 and β_i denote the intercept and slope coefficients; x_i denote the predictor variables; $s(\cdot)$ represents the spline nonlinear function; r_{cp} and r_c denote the random effects for specific province nested in the cluster and for specific cluster, respectively; e represents the residual error. For Bayesian inferences and estimation of the unknown parameters in Eq. (2), the model was fitted using the Monte Carlo sampler Stan by using the R cmdstanr package. Due to inconsistencies in population data across the entire study period, the Bayesian modeling analysis was conducted in two distinct phases: 1985–2004 and 2005–2018.

Dominance analysis was employed to quantify the relative importance of each predictor variable (Budescu, 1993). The main procedure is as following: fit the models with and without specific predictor variable x_i , and obtain the averaged difference between the coefficients of determination, i.e., ΔR^2 , which accounts for the relative importance.

For comparison and robustness validation purposes, linear mixed-effects model (LMM) and generalized additive model (GAM) were developed with the same data, and with identical dominance analysis procedures applied to ensure methodological consistency.

3. Results

3.1. Spatiotemporal characteristics of HFRS and the corresponding clusters

As Fig. 1(a) shows, the temporal trend of HFRS incidence from 1985 to 2018 demonstrates a pronounced declining pattern. The HFRS incidence peaked dramatically in 1986 reaching 10.99 cases/10⁵, and then experienced a sharp decline to around 3.63 cases/10⁵ by the late 1980s. The trend exhibits notable fluctuations during the 1990s, with secondary peaks occurring in 1995, reaching 5.22 cases/10⁵. However, these fluctuations occur within an overall downward trajectory. From 2000 onwards, the decline becomes more consistent and stabilized, HFRS decreasing steadily from approximately 3.00 cases/10⁵ to reach a plateau of around 0.71 cases/10⁵ by 2010. After that, HFRS cases remained relatively stable, varying between 0.49 cases/10⁵ and 0.98 cases/10⁵ annually.

The spatial distribution pattern of annual averaged HFRS incidence during 1985–2018 (Fig. 1(b)) reveals distinct regional correlations. Heilongjiang Province reported the highest HFRS incidence, followed by the Shandong, Shaanxi, and Zhejiang provinces. A clear geographic gradient emerges, with western regions demonstrating consistently low incidence, while southern provinces exhibit intermediate incidence levels.

The spatial clusters of HFRS cases for the periods 1985–2004 and 2005–2018 are presented in Fig. 2. The analysis reveals that areas with similar HFRS transmission patterns are spatially clustered together. By comparing the two cluster maps of Fig. 2(a) and (b), the latter period (Fig. 2(b)) presents some discrete provinces in the same cluster, such as Yunnan Province in the southwest part of China, indicating a more complex variation than the former one (Fig. 2(a)).

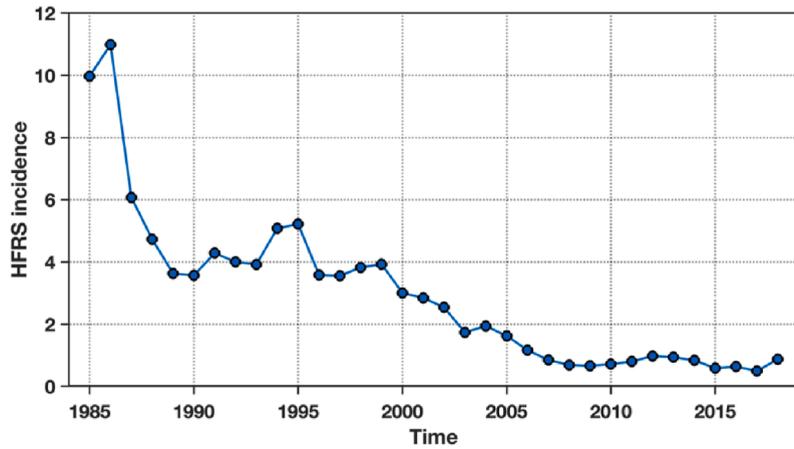
3.2. Bayesian nonlinear mixed-effects model

Through stepwise multiple linear regression with multicollinearity diagnostics, the final models incorporated twelve predictor variables for each period. The 1985–2004 model included: GDP/person, POP, VAP, WS, PDSI, SRAD, LULC2, LULC3, LULC5, LULC7, LULC8, and LULC9. The 2005–2018 model contained: GDP/person, POP, WS, PDSI, SOIL, SRAD, LULC2, LULC3, LULC5, LULC6, LULC8, and LULC9. Further, the coefficients of determinant (R^2) for the two models were 0.37 and 0.54, respectively.

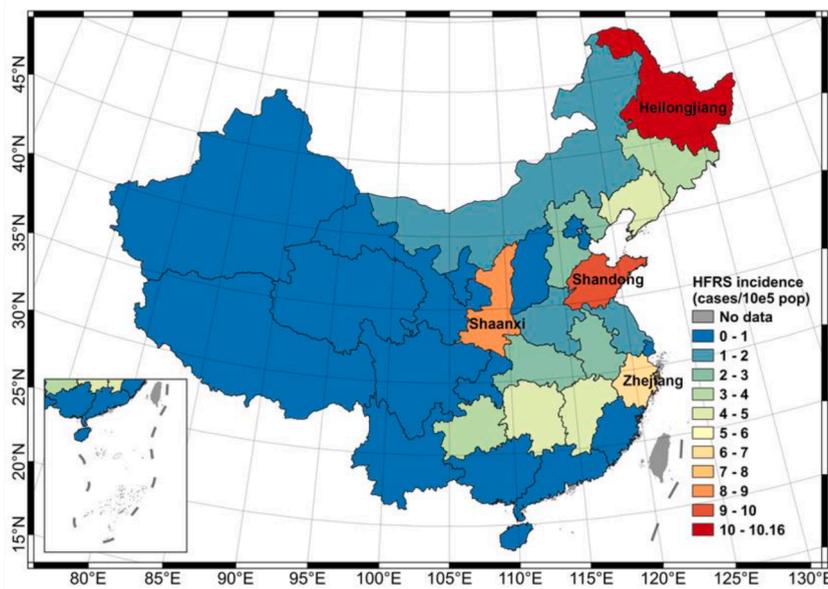
Subsequently, the corresponding variables along with the clustering results were utilized in developing a Bayesian nonlinear mixed-effects model. The results for both time periods are presented in Fig. 3, while the relative importance of the input variables is illustrated in Fig. 4. The results demonstrate that Bayesian nonlinear mixed-effects models exhibit superior performance, achieving R^2 values of 0.8722 and 0.8592 for the periods 1985–2004 and 2005–2018, respectively. These results substantially outperform the corresponding LMM with R^2 values of 0.7182 and 0.8213 for the two periods, and GAM with R^2 values of 0.8111 and 0.8183 for the two periods, as illustrated in Fig. S1 and S4.

Moreover, the leave-one-out cross-validation (LOOCV) demonstrated that the Bayesian nonlinear mixed-effects model yielded the lowest prediction error among the three models (Table 1). Dominance analysis revealed that impervious surfaces (LULC8), population and wetlands (LULC9) are the top three primary variables influencing HFRS transmission during the period 1985–2004. In contrast, during the period 2005–2018, wetlands, the Palmer Drought Severity Index (PDSI), and impervious surfaces are the most influential variables.

As illustrated in Fig. 5, the partial dependence trends of most variables vary between the two time periods, with the exception of PDSI. Additionally, the trends for POP, LULC3, LULC5, LULC8, and LULC9 exhibit greater fluctuations in the previous period than in the latter period. Specifically, wetlands (LULC9) exhibit markedly different patterns between the two periods: during 1985–2004, an increasing-then-decreasing dependence pattern is observed, whereas the 2005–2018 period demonstrates a consistently positive dependence. The partial dependence of impervious surface (LULC8) exhibits a slower rate of increase in the latter period than in the previous one. Regarding population, a decreasing trend with



(a)



(b)

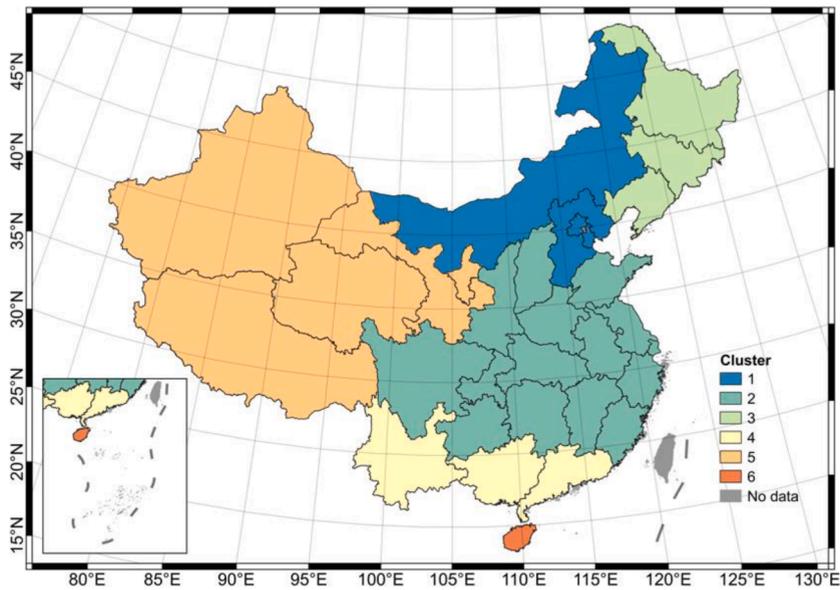
Fig. 1. The (a) temporal and (b) spatial pattern of annual HFRS incidence in China during the period 1985–2018.

fluctuations is found in the earlier period, while a decreasing-increasing trend is detected in the latter period. Furthermore, wind speed (WS) displays contrasting dependence trends between the two temporal periods.

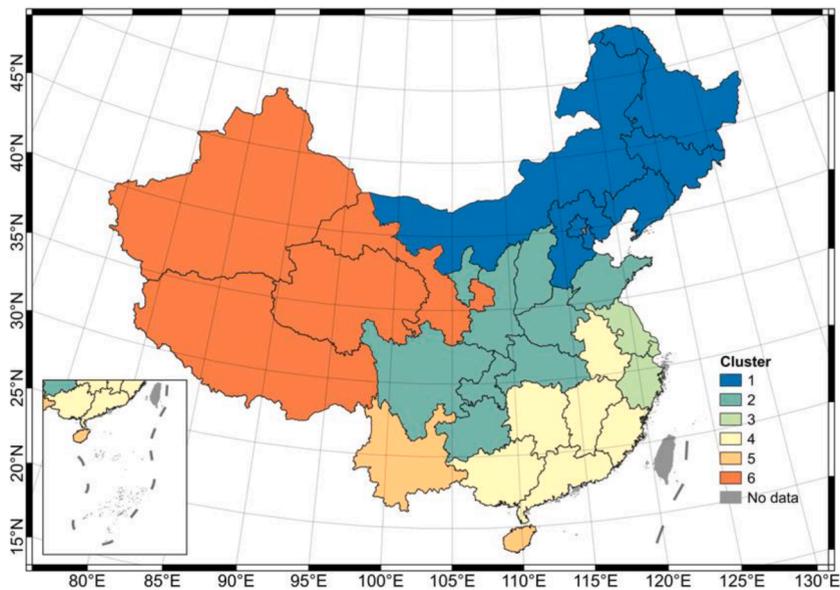
4. Discussion

The present nationwide study investigates the evolving relationships between socio-economic, climatic and land use factors with HFRS incidence across mainland China over a 34-year period. By integrating Bayesian nonlinear mixed-effects with dominance analysis, our findings reveal urbanization as the primary driver of HFRS transmission dynamics in China, with impervious surface and wetlands consistently dominating disease patterns across two distinct developmental periods. These findings provide quantitative evidence of urbanization's fundamental contribution in shaping zoonotic disease transmission at the national scale.

The expansion of impervious surfaces consistently emerged as one of the top three primary predictors for HFRS transmission throughout both the initial (1985–2004) and later (2005–2018) periods. China's total impervious surface area reached 209,950 km² in 2017, reflecting a three-fold increase since 1990 (Gong et al., 2019). The sustained positive



(a)



(b)

Fig. 2. The spatial clusters of HFERS incidence in China during the periods (a) 1985–2004 and (b) 2005–2018.

association in this study is mechanistically aligned with the observation that urbanization intensifies HFERS risk by increasing the ecological niche-overlap between humans and rodents (Despommier et al., 2006; Hassell et al., 2017; Li et al., 2023b). As a reflecting indicator for urbanization levels, the impervious surfaces can modify rodent habitats, leading to increased population densities in fragmented edge habitats, while the expansion of built-up areas can elevate human-rodent contact, particularly at urban-rural interfaces. Changes in impervious surfaces may also alter local ecological dynamics, such as disrupting predator-prey interactions and resource availability, which indirectly influences hantavirus transmission (Tian et al., 2018; Xiao, Tong, Huang, & et al, 2018; Zhu et al., 2023). Moreover, our Bayesian nonlinear mixed-effects model and GAM results revealed complex non-linear relationships, suggesting that the impervious surfaces-HFERS association follows an increasing-decreasing pattern where moderate urban development increases risk, while intensive

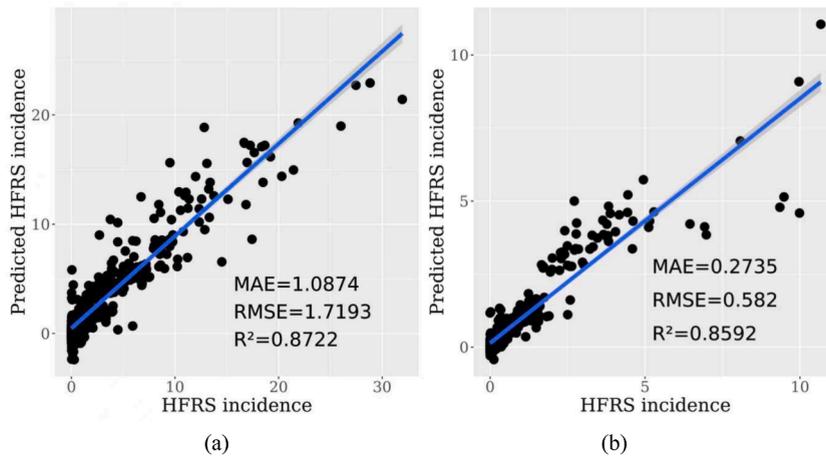


Fig. 3. The performance of Bayesian nonlinear mixed-effects model in predicting the HFRS incidence in China during the periods (a) 1985–2004 and (b) 2005–2018.

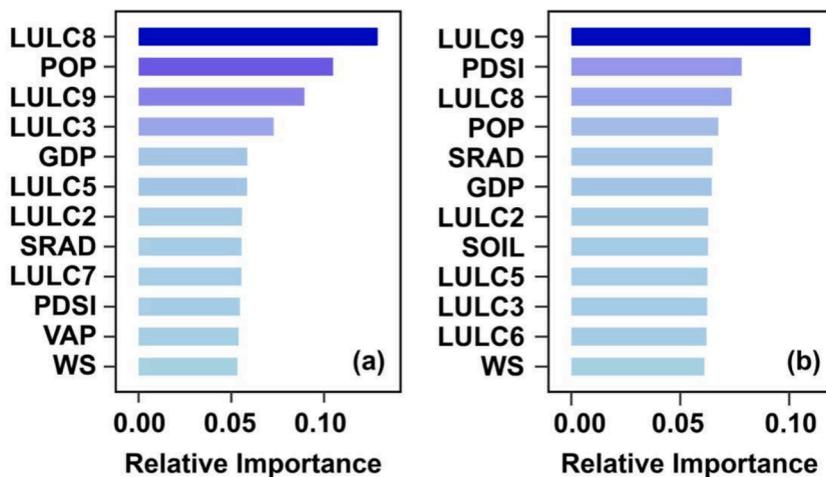


Fig. 4. The relative importance of the considered variables in the Bayesian nonlinear mixed-effects model during the periods (a) 1985–2004 and (b) 2005–2018. POP, GDP, SRAD, PDSI, VAP, WS, LULC2, LULC3, LULC5, LULC6, LULC7, LULC8, LULC9 represent population, gross domestic product per person, near-surface downward shortwave radiation, the palmer drought severity index, water vapor partial pressure in air, wind speed, forest, shrub, water, snow/ice, barren, impervious surfaces and wetland, respectively.

urbanization may eventually reduce transmission through complete habitat transformation and improved public health infrastructure (Fig. 5a and S6).

The rise of wetlands as a major factor of HFRS spread during 2005–2018 suggested a potential association between environmental policy and landscape-level ecological shifts. The shift in the wetland is closely linked to the Chinese government’s intensified efforts in wetland conservation after 2005. Since joining the Ramsar Convention in 1992, China had gradually increased its commitment to wetland protection, but a pivotal phase began in 2005. Between 2005 and 2010, the government implemented a range of effective measures, including the restoration of degraded wetlands, the establishment of protected areas, and the enactment of relevant legislation and regulation (Liu, Lin, et al., 2024; Sun et al., 2015). The restored wetlands may have created biodiversity and new ecological niches for rodent reservoirs while simultaneously altering human exposure patterns through changed agricultural and recreational activities around wetland areas. This policy-epidemiology nexus demonstrates how large-scale environmental interventions can have unintended consequences for zoonotic disease transmission, requiring integrated approaches to environmental and public health.

Taking into consideration that China’s urban population grew dramatically from 170 million in 1978 to 670 million in 2010 (Chen et al., 2013), the well-established association between population density and HFRS dynamics reveals an unprecedented human-environment coupling that is recognized as a major driver challenging public health in China, particularly by altering the transmission ecology of zoonotic diseases like HFRS (Li et al., 2023b). During the first period (1985–2004), the population increased while HFRS showed a fluctuating declining trend, forming multiple “inverted U-

Table 1
Leave-one-out cross validation results of the three models.

Models	1985–2004		2005–2018	
	Mean absolute error	Root mean squared error	Mean absolute error	Root mean squared error
Bayesian nonlinear mixed-effects model	1.4078	2.3244	0.3429	0.7382
Generalized additive model	1.7335	2.8614	0.4108	0.8759
Linear mixed-effects model	2.0355	4.0259	0.3828	0.8118

shaped” waves. This pattern may reflect the combined effects of urbanization and population density: moderate increases in rural populations and movement toward peri-urban areas could have temporarily elevated human-rodent contact, whereas subsequent urban consolidation and improvements in living conditions reduced exposure risk. In the second period (2005–2018), HFRS exhibited a rising trend following earlier declines, consistent with population stabilization and new migration patterns that reshaped human exposure at urban-rural interfaces. These observations suggest that demographic shifts, including rural-to-urban migration and regional population redistribution, modulate the temporal dynamics of HFRS by altering the intensity and spatial distribution of human-rodent interaction.

Moreover, we observed that climatic variables such as the palmer drought severity index (PDSI), exhibited higher relative importance after 2005 than before 2005. The relationship between PDSI and HFRS exhibited a slight pattern, initially declining before increasing, highlighting the role of environmental stressors and weather patterns in modulating disease spread. This pattern suggests that HFRS transmission is lowest under moderate climatic conditions but increases under both severe drought (indicated by low/negative PDSI values) and excessive wetness (indicated by high/positive PDSI values). The extreme drought conditions, exert an immense survival pressure on the rodents that forces them to invade human homes in search of food and water (Douglas et al., 2021). At the same time, the dry and dusty environment makes it easier for the virus to become airborne and be inhaled (Douglas et al., 2021; Xiao et al., 2013b). On the other hand, the HFRS increase under excessive wetness conditions could be attributed to an increase in vegetation and water sources, which enhances food availability. This, in turn, likely leads to an increase in rodent populations and their breeding success (Tian et al., 2015; Wan et al., 2022).

Additionally, a negative trend in SRAD after 2005 could imply that higher solar radiation might directly or indirectly reduce hantavirus viability in the environment, or alter rodent behavior, potentially driving them into less human-frequented areas or reducing their reproductive capacity (Joshi et al., 2017).

These complex relationships of HFRS with climatic stressors underscore the multifaceted role of environmental factors in modulating disease spread. While direct analyses of PDSI or SRAD on HFRS may be limited, these findings align with the epidemiological understanding that climatic factors like mean temperature, wind speed, precipitation (which are integrated into drought indices like PDSI) and solar radiation at a 4-month lag in influence vector-borne and rodent-borne diseases (Li et al., 2024; Luo et al., 2022; Wang et al., 2023).

However, the period 2005–2018 revealed important shifts in these relationships between population, impervious surfaces and wetland and HFRS. This transition could be attributed to several factors, including the dramatic changes in China's socio-economic development and urbanization. In particular, China underwent significant structural changes post-2005, which encompassed rapid urbanization, increased industrialization and migration from rural to urban areas. This has likely altered human-environment interactions, including changes in land use patterns that may affect rodent populations and their interactions with humans (Tian et al., 2018; Wang et al., 2022). Additionally, climate change has likely played a role in altering regional climate patterns, exacerbating the frequency and intensity of extreme weather events, which can further influence HFRS transmission dynamics. The shift in the relationship between land use and HFRS incidence after 2005 could also be indicative of the growing influence of environmental policies and interventions. For example, the Chinese government has been increasingly investing in urban planning, green spaces, and the management of rodent populations in cities since the mid-2000s. Such measures might have mitigated the risk of HFRS transmission in urban areas by reducing the abundance of rodent reservoirs, which are critical to the disease's spread. However, the increasing of urbanizing and population density may also raise the health risk (Poel et al., 2012; Tian et al., 2018).

The comparative GAM modeling confirms the robustness of our findings. The GAM analysis, which also accounts for non-linear relationships, revealed similar curves in variables such as POP, PDSI, SRAD, shrub, impervious surfaces and wetland. Several of them present fluctuations further highlighting the complex interactions between environmental factors and disease dynamics. Consistent with recent studies demonstrating comprehensive non-linear relationships between HFRS and meteorological factors (Luo et al., 2024; Zhang et al., 2022), our GAM model further revealed the presence of non-linear associations of HFRS with forest and water areas. These findings underline the importance of considering non-linear relationships when modeling complex epidemiological processes.

Several limitations should be acknowledged when interpreting our findings. First, the ecological study design precludes direct causal inference, as associations observed at the provincial level may not necessarily reflect individual-level risk factors or causal physical mechanisms. Second, the spatial resolution of provincial-level data may mask important sub-provincial heterogeneity in disease transmission, particularly given the geographic and demographic diversity in the different provinces of China. The observed associations between impervious surfaces or wetlands and HFRS may be partially

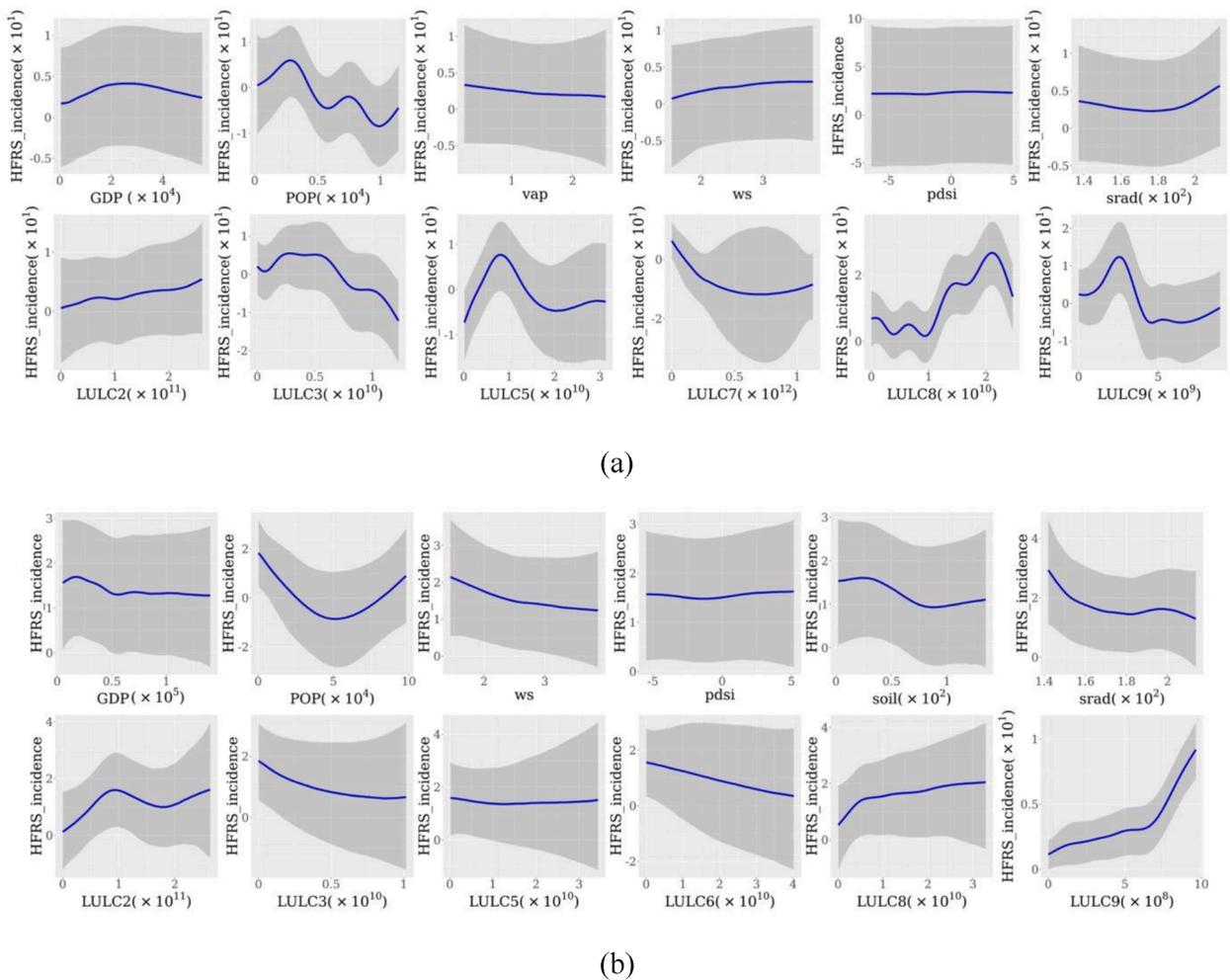


Fig. 5. The partial dependence of the considered variables in the Bayesian nonlinear mixed-effects model during the periods (a) 1985–2004 and (b) 2005–2018. POP, GDP, SRAD, PDSI, VAP, WS, LULC2, LULC3, LULC5, LULC6, LULC7, LULC8, LULC9 represent population, gross domestic product per person, near-surface downward shortwave radiation, the palmer drought severity index, water vapor partial pressure in air, wind speed, forest, shrub, water, snow/ice, barren, impervious surfaces and wetland, respectively.

confounded by some unmeasured variables such as rodent control programs, healthcare access or occupational exposures, which vary across regions and over time. Third, potential temporal inconsistencies in surveillance quality and reporting completeness across the 34-year study period could influence trend interpretations, despite China's generally robust infectious disease monitoring system. In our view, it is imperative to incorporate more advanced mathematical models and methods into HFRS research to address quantitatively these dynamic complexities (Sun et al., 2022, 2025). Finally, while our land use types provide comprehensive coverage, they may not capture specific habitat characteristics most relevant to rodent reservoir ecology, such as agricultural practices within broader land use types.

5. Conclusion

Our study highlights the evolving nature of the relationship between environmental, socio-economic and land use factors and HFRS transmission in China. The findings suggest that while urbanization and land use changes, particularly the expansion of impervious surfaces and wetland, have been important impact factors of HFRS, shifts in socio-economic conditions, climate patterns, and government interventions after 2005 have altered these dynamics. The dynamics in impervious surface areas, PDSI, and wetland areas in the post-2005 period may be indicative of changing patterns of human-rodent interactions driven by urbanization, migration, and climate change.

This study contributes to the understanding of HFRS epidemiology in mainland China and emphasizes the need for integrated public health strategies that consider environmental and socio-economic factors. Our findings also highlight the importance of continuous monitoring and the need for adaptive strategies in response to ongoing changes in climate and

land use. Future research should (a) integrate finer spatial resolution, individual-level exposure data, and information on local public health interventions to explore the impact of specific policy interventions on HFRS, and (b) consider additional factors such as healthcare access and human behavior, which may further clarify causal pathways and shape disease dynamics.

CRediT authorship contribution statement

Junyu He: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Yanding Wang:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Xiaopeng Xu:** Visualization, Validation, Investigation, Formal analysis. **George Christakos:** Writing – review & editing, Methodology. **Danjie Zhang:** Writing – review & editing. **Yuanyong Xu:** Writing – review & editing. **Qjulan Chen:** Writing – review & editing. **Wenyi Zhang:** Writing – review & editing, Data curation, Conceptualization.

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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.

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Appendix A. Supplementary data

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