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Macroscale patterns of rodent herbivory damage and underlying mechanisms in forests of China

Fengqun Meng^{1,2,3*}

Abstract

Background Understanding the macroscale patterns of rodent herbivory damage and their driving factors are essential for effective rodent management. This study examines how climatic factors and human activities influence the large-scale spatial distribution of rodent herbivory damage in forests of China.

Results I utilized a unique long-term province-level dataset of rodent damage in China to map its extent across the country. A generalized linear mixed model was employed to analyze the relationship between rodent damage, and climatic variables, and human population density (HPD). The results reveal a clear spatial pattern of rodent herbivory damage in China's forests, primarily driven by HPD and precipitation of the warmest quarter, with a secondary influence of diurnal temperature range. These three variables explained approximately 58% of the variation in the geographic pattern of rodent herbivory damage in China's forests. Specifically, rodent damage was negatively correlated with both precipitation of the warmest quarter and HPD. Higher precipitation during the warmest quarter (often as rainstorms) probably exacerbates rodent mortality through flooding their burrows and imposing thermal stress, while higher HPD probably increases predation pressure, further lowering rodent populations. Additionally, rodent damage was positively related to diurnal temperature range, likely because greater diurnal temperature fluctuations impose greater thermal stress on their predator, thereby enhancing rodent survival. Consequently, regions in northwestern China that are arid, experience high diurnal temperature fluctuations and have low human populations, are particularly vulnerable to severe rodent damage. In contrast, southern and southeastern China, with higher precipitation, milder temperature fluctuations, and denser human populations, experience significantly lower rodent damage.

Conclusion The findings suggest that the combination of precipitation during the warmest quarter, diurnal temperature range, and HPD can serve as effective indicators of rodent pest severity in forests. This underscores the need for proactive surveillance and management in arid regions with high diurnal temperature fluctuations and low population densities worldwide.

Keywords Climate, Forest, Human population density, Rodent pest, Spatial pattern, Precipitation

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Introduction

Ecologists are increasingly tasked with addressing the causes and consequences of environmental problems at large scales, driven by societal demands for effective management policies [1–3]. For example, global analyses of threatened species patterns show that both land and marine species are concentrated in regions of high human pressure, such as Southeast Asia and the northern oceans [4]. These findings are critical for prioritizing conservation efforts. However, documenting ecological patterns and processes on a macroscale is challenging, as such data-intensive studies often require data that cannot be fully collected.

Rodents are a prime example of vertebrate pests impacting forests worldwide, both in the Northern [5] and Southern Hemispheres [6]. Although omnivores, rodents primarily feed on tree roots, bark, and vascular tissues, which can lead to tree mortality or reduced growth [7], causing billions in economic losses annually [6, 8, 9]. For instance, voles in Germany cause over £6.83 million in losses per year [8], and an outbreak in Finland in 2005 resulted in the destruction of 8.5 million tree seedlings over 5,400 ha [9]. Thus, identifying regions prone to severe rodent herbivory and understanding the mechanisms behind these patterns is essential for effective management.

While many studies on rodent pests focus on their ecological and economic impacts [10], less is known about the macroscale spatial patterns of rodent herbivory and their driving factors. It is well-documented that herbivory damage on a large scale is influenced by macroclimatic factors [11–13]. Examples include a latitudinal decrease in folivory damage in *Nothofagus pumilio* forests driven by temperature and precipitation, greater elephant damage to savanna trees in drier regions of Africa, and a reduction in folivory damage in *Betula pubescens* with increasing latitude linked to July temperatures [11–13]. These macroclimatic drivers likely influence the spatial distribution of rodent herbivory by directly affecting rodent survival and reproduction, as well as indirectly impacting plant production and food availability [14, 15].

Temperature, especially in spring and winter, is crucial for regulating rodent populations, as spring temperatures influence plant growth, while winter temperatures directly affect rodent survival. Specifically, warmer spring temperatures may promote plant growth [15] and trigger earlier reproduction in rodents [16], leading to higher rodent densities. Colder winter temperatures can reduce survival due to increased energy demands [17]. Precipitation, particularly in spring and summer, is also vital for regulating rodent populations, as spring precipitation influence plant growth, while summer precipitation directly affect rodent survival. Specifically, high summer precipitation can negatively affect rodents by flooding their

burrows [15, 18, 19] or reducing breeding success due to thermal stress [20]. In contrast, high spring precipitation may promote rodent growth by enhancing plant growth and extending the growing season [21, 22]. Despite these potential relationships between climate and rodent populations, the spatial variation in rodent herbivory damage remains poorly understood. I hypothesize that specific climatic factors—particularly spring and winter temperatures, as well as spring and summer precipitation—play key roles in shaping rodent herbivory patterns. Specifically, I expect that higher spring temperature and precipitation, along with higher winter temperature, will increase rodent densities and thus their herbivory damage, while higher summer precipitation will reduce rodent densities and thus their herbivory damage.

Human activities, which shape almost all ecosystems, have also significantly altered global macroecological patterns [23–26]. However, previous studies have not quantitatively assessed these impacts on rodent herbivory damage. A wide range of human activities, including lethal actions (e.g., hunting and retaliatory persecution), nonlethal actions (e.g., hiking and resource extraction), and infrastructure development (e.g., urbanization, road construction, and agriculture), pose different levels of risk or benefits to rodent populations [22, 24]. These human activities influence rodent herbivory damage in two primary ways: directly through their effects on herbivore survival and indirectly through impacts on food resources. On one hand, humans act as ‘super predators’ [27], negatively affecting rodent populations by directly killing them or inducing fear. Rodent control is common worldwide due to their detrimental effects on ecosystems and human health [6, 10, 28]. Additionally, rodents can perceive human predation risk [29], creating a trade-off between foraging and the risk of predation, as suggested by optimal foraging theory [30]. On the other hand, human activities can positively affect rodent populations by increasing anthropogenic resources [26]. For example, in human-disturbed environments, such as agricultural or peri-urban areas, rodents often thrive due to food waste and other anthropogenic resources [31, 32]. However, in forests, where anthropogenic resources are scarce due to intensive use for fuel, fodder and timber collection, human activities may exert more direct pressure on rodent populations, potentially reducing herbivory damage. While these human impacts are not always directly linked to high-density human populations, human population density (HPD) can be a more reliable macro-scale indicator than direct threats (e.g., habitat loss or hunting), or benefits (e.g., food availability), which are often difficult to measure accurately in a consistent manner across regions and biomes. As a result, HPD is one of the most effective and commonly used metrics to summarize the broader human impacts on mammal species across

large spatial scales [33, 34]. Thus, I hypothesize that human activities negatively impact rodent populations and their damage in forest ecosystems, suggesting that higher population densities will correlate with reduced rodent herbivory.

In China, forest ecosystems have experienced significant rodent herbivory, with rodents damaging approximately 1.6 million ha of forest annually [35]. China's vast climate diversity, ranging from tropical to temperate zones and from humid to arid regions, supports a variety of forest ecosystems [36]. This diversity offers a unique opportunity to examine how climatic factors influence rodent herbivory patterns. Additionally, China's population density shows a clear west-east gradient, with a high population density on the east side of the Hu Huanyong Line and sparse population in the west [37]. This gradient allows for the assessment of human activity impacts on rodent herbivory at large scales.

To test the above hypotheses, I collected a 16-year province-level dataset of rodent herbivory damage in China (2003–2018) from official sources. I mapped the spatial pattern of rodent herbivory damage and used generalized linear mixed models (GLMM) to analyze the contributions of climate and human activities (as represented by HPD) to this variation. To account for spatial autocorrelation, I applied an eigenvector-based spatial filtering approach.

Materials and methods

Rodent damage data

I compiled a province-level database on rodent herbivory damage to forest trees in China, utilizing data from the national rodent pest monitoring network maintained by the Ministry of Forestry. This network mandates county-level Forest Pest Management and Quarantine Stations to collect annual rodent damage data according to the standardized protocol DB13/T 886–2007 [38]. This study included rodent species from the order Rodentia (Mammalia) and the family Ochotonidae (Mammalia: Lagomorpha), as detailed in Table S1 in supplementary materials. Data collection occurred twice a year, in April–May and September–October.

According to the Regulations on the Management of National Forestry Pest Monitoring and Forecasting Sites, a total of 993 county-level monitoring and forecasting sites have established across China, covering all types of forest ecosystems and pest-prone areas in China. At each site (i.e., county), 30 standard plots (1 hm² each) across the county were selected for monitoring. These plots are located within zonal forest ecosystems, typically in state-owned farms, nature reserves, and national forest parks. Each plot contained 10 quadrats (~30 m × 30 m) for detailed assessments of rodent damage. Within each quadrat, the number of trees damaged by rodents

(indicated by bark or root gnawing) was recorded alongside the total number of trees. A quadrat was classified as damaged if $\geq 3\%$ of the trees showed damage. The damage rate was calculated by dividing the total area of damage in each plot by the plot area (1 hm²). The damaged area for each county was then derived by multiplying the damage rate by the county's forest area. The province-level dataset on rodent damage was acquired from official Chinese sources (see Table S2 in the supplementary materials for the online data access links).

To determine the extent of rodent damage for each province, I calculated the ratio of damaged area to total forest area. I sourced forest area data from official Chinese websites (see Table S2 in the supplementary materials for the online data access links). The dataset comprised 31 provinces spanning from 2003 to 2018.

Climate data

I obtained daily temperature and precipitation data for China from NOAA's Global Summary of the Day network for the years 2003–2018 (see Table S2 in the supplementary materials for the online data access links). For each monitoring county, the daily temperature and precipitation data were extrapolated from the NOAA weather station located within the monitoring county, where there is generally one such weather station within the county. If no station is available within the county, data were obtained from the nearest weather station. Based on daily temperature and precipitation data, I derived 19 commonly used bioclimatic variables (Bio1–Bio19; see Table S3 for definitions) for each weather station, following the methodology of O'Donnell & Ignizio [39]. The county-level bioclimatic variable data were then averaged to obtain provincial-level bioclimatic variable values.

I assessed the collinearity between bioclimatic variables using pairwise Pearson's correlation coefficients, considering an absolute correlation coefficient ≥ 0.7 as indicative of strong collinearity. The analysis revealed significant multicollinearity among the bioclimatic variables (see Fig. S1 in supplementary materials for details). I then performed variable selection based on collinearity intensity and predictive capacity. First, I conducted generalized linear mixed models (GLMMs) incorporating all 19 bioclimatic variables, with year as a random factor, to assess the significance of the partial regression coefficients. Variables with a P -value < 0.05 were retained, while those with a P -value > 0.05 were excluded. As a result, four variables were selected during this process: mean diurnal temperature range (Bio2), precipitation of wettest month (Bio13), precipitation seasonality (Bio15) and precipitation of warmest quarter (Bio18) (see Table S3 in supplementary materials). Random forest variable significance analysis [40] was further performed on these four variables to confirm their importance and

significance. Consistent with the GLMM results, the random forest analysis also identified these variables as significantly important predictors (Fig. S2 in supplementary materials). Next, I performed a multiple stepwise regression to refine the model further. The model's fit was assessed using the Bayesian Information Criterion (BIC) and the R^2 . Variables were removed if their exclusion led to a decrease in BIC without significantly reducing R^2 . After this step, two variables were retained: Bio2 and Bio18 (see Table S4 in supplementary materials). Further analysis confirmed that there was no collinearity between Bio2 and Bio18 (Pearson's $r = -0.43$). Therefore, Bio2 and Bio18 were selected for the final model. These results were further supported by partial correlations, as detailed in the supplementary materials (Table S3 & S4).

HPD data

Human activities were represented by HPD, which I acquired from open sources (see Table S2 in the supplementary materials for the online data access links). HPD values were aggregated at the provincial level.

Spatial pattern of rodent herbivory damage and its determinants

I employed a generalized linear mixed model (GLMM) with year as a random factor to examine the relationships between rodent herbivory damage and the explanatory variables (i.e., Bio2, Bio18 and HPD). To account for spatial autocorrelation, I utilized an eigenvector-based spatial filtering approach [25, 41]. Spatial filters were computed based on a spatial weight matrix, where elements were set to 1 for provinces sharing a border and 0 otherwise, following the first-order rook contiguity rule [42]. Using principal coordinate analysis, I extracted 18 eigenvectors with positive eigenvalues from the spatial weight matrix. These eigenvectors were incorporated as explanatory variables in the GLMM. I assessed the significance of the partial regression coefficients, retaining 11 significant eigenvectors (see Table S5 in supplementary materials).

Ultimately, Bio2, Bio18, HPD, and the selected 11 spatial filters (to correct for spatial autocorrelation) served as explanatory variables in the final GLMM. I calculated standardized regression coefficients and partial R^2 to evaluate the relative importance of Bio2, Bio18 and HPD. To enhance linearity and normality of the model residuals, Bio2, Bio18, and HPD were transformed using \log_{10} or $\log_{10}(1+x)$ transformations (the latter for cases with zero values). All statistical analyses were performed in R version 3.4.3.

Results

The GLMM analysis revealed that results with and without spatial autocorrelation correction were consistent (see Table S6 in supplementary materials). With spatial correction, Bio2, Bio18, and HPD together explained approximately 58% of the variation in rodent herbivory damage patterns. Among these, HPD and Bio18 emerged as the primary contributors, accounting for 32.6% and 17.9% of the overall variation, respectively (Fig. 1A). Both HPD and Bio18 had significant negative effects on rodent damage, with damage decreasing as HPD (Fig. 1B) and Bio18 (Fig. 1C) increased. In addition to the dominant influence of HPD and Bio18, Bio2 also had a notable positive effect on rodent damage (Fig. 1D), contributing 7% to the overall variation (Fig. 1A).

As a result, rodent herbivory damage in the forests of China displayed a clear spatial pattern over the study period (Fig. 2A). Damage levels were highest in northwestern, northern, and northeastern China, regions characterized by lower human population densities (Fig. 2A, B), lower precipitation during the warmest quarter (Fig. 2A, C), and higher diurnal temperature ranges (Fig. 2A, D). In contrast, southern and southeastern China, where population densities were higher (Fig. 2A, B), precipitation during the warmest quarter was greater (Fig. 2A, C), and diurnal temperature ranges were lower (Fig. 2A, D), experienced significantly lower damage. Notably, no rodent herbivory damage was observed in several provinces, including Beijing, Tianjin, Shandong, Henan, Jiangsu, Shanghai, and Guangdong. Additionally, several provinces, including Anhui, Zhejiang, Fujian, Jiangxi, Guangxi, and Hainan experienced extremely low levels of rodent herbivory, with the extent of rodent damage being less than 0.02%. No significant interannual fluctuations were observed, and spatial patterns remained consistent throughout the study period (Fig. S3 in supplementary materials).

Discussion

The results reveal a clear spatial pattern of rodent herbivory damage in China's forests, primarily driven by HPD and precipitation during the warmest quarter, with a secondary influence of diurnal temperature range. Specifically, I found significant negative correlations between precipitation of the warmest quarter and HPD, and rodent herbivory damage, and a significant positive correlation between diurnal temperature range and rodent herbivory damage. These findings suggest that rodent damage is most pronounced in arid regions with high diurnal temperature fluctuations and sparse human populations.

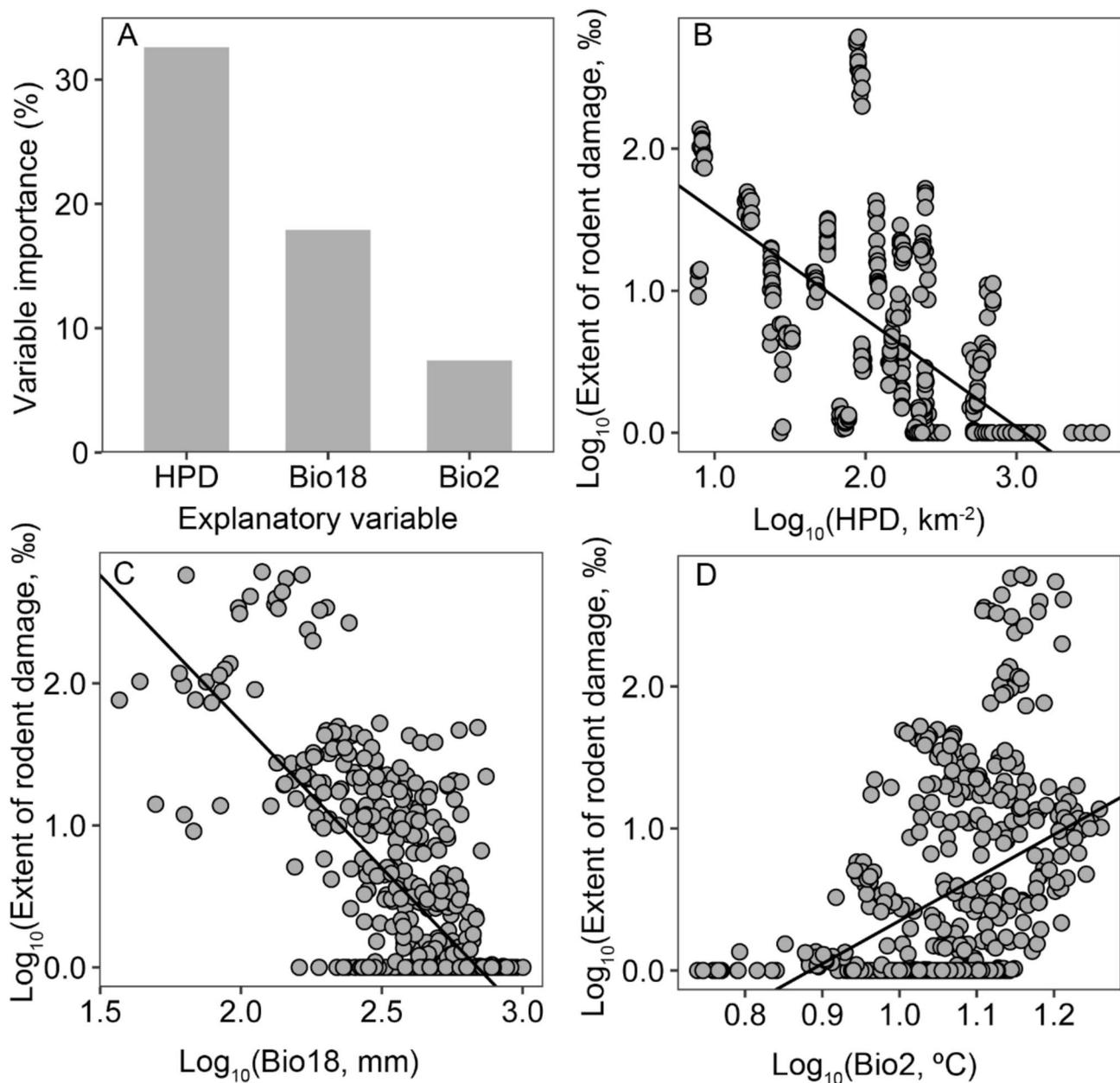


Fig. 1 (A) The fraction of the variation in the extent of rodent damage in forests of China explained by climatic variables and human population density (HPD), and the relationships between the extent of rodent damage in forests of China and (B) HPD, (C) Bio18 (precipitation of warmest quarter), and (D) Bio2 (annual mean diurnal range). Each data point represents the annual value for each province from 2003 to 2018

The effect of climate on rodent herbivory damage

Consistent with the hypothesis, rodent herbivory damage in forests of China was negatively correlated with precipitation of warmest quarter (generally occurring in the summer from June to August in China). This finding aligns with the results of Kalcounis-Rueppell et al. [43] and Marini et al. [44], who observed a negative effect of precipitation on rodent abundance, as well as with the results of Lima et al. [45], who identified summer precipitation—primarily resulting from localized thunderstorms—as the key driver of population fluctuations in

small rodents. Previous studies actually show both negative and positive effects of precipitation on rodent abundance. For example, Ventura-Rojas et al. [22] reviewed the impact of precipitation on rodent populations, showing that rodent abundance generally increases with precipitation, but decreases with precipitation when rainfall primarily consists of heavy rainstorms. These contradictory effects likely arise from the relative importance of direct effects of precipitation, such as mortality from flooding or reduced breeding success due to thermal stress [20, 21, 46], versus indirect effects of precipitation,

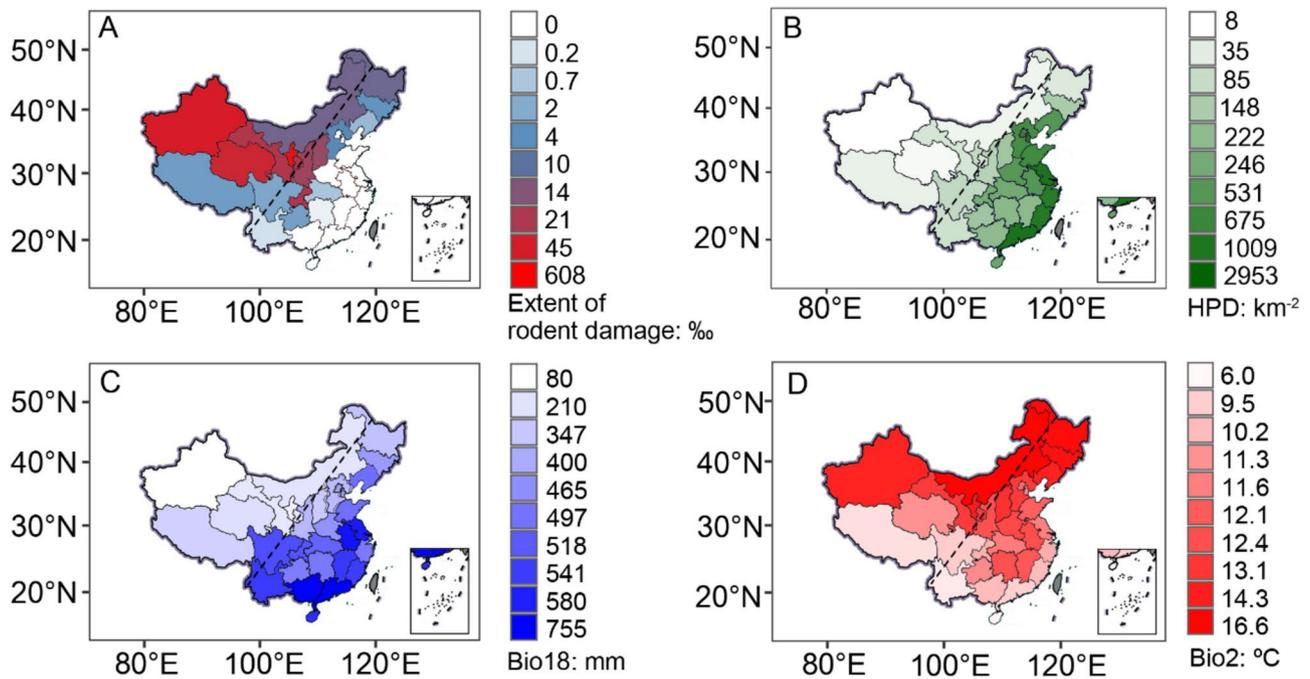


Fig. 2 Spatial patterns of (A) the annual extent of rodent damage in forests of China, (B) HPD (human population density), (C) Bio18 (precipitation of warmest quarter), and (D) Bio2 (mean temperature diurnal range) calculated over 2003 to 2018. Provinces without data are shown in gray. Dashed line: Hu Huanyong line

such as increases in primary productivity [21, 22], on rodent populations. In this study, the negative effect of summer precipitation on rodent damage is likely due to the direct effects of frequent summer rainstorms on rodent survival and breeding. The spatial variations in rainstorms across China probably shape the macroscale patterns of rodent herbivory damage observed in the country’s forests. In China, summer precipitation contributes to 40–60% of the total annual rainfall, with a significant portion falling as rainstorms [47]. Southern and southeastern provinces experience particularly frequent summer rainstorms, which contributes more than 20% of the total annual precipitation [47]. The high frequency of summer rainstorms in these regions likely increase rodent mortality due to burrow inundation. For example, coastal provinces such as Hainan, Guangdong, Fujian, Zhejiang, Jiangsu, and Shanghai, which are regularly affected by typhoon-driven summer precipitation, show exceptionally low levels of rodent herbivory (below 0.02%). Additionally, the combination of heavy summer precipitation and extremely high ambient temperatures may impair evaporative cooling, potentially suppressing reproduction during the breeding seasons from late March to early October [38]. Supporting this, Redhead [20] found that the wet season was too stressful for rodent breeding, causing dusky rats in monsoonal Australia to cease reproduction. This may explain why provinces with limited typhoon activity, such as Guangxi, Anhui, Yunnan, and Jiangxi, display also remarkably low

levels of rodent herbivory, as they experience very high summer precipitation (over 550 mm). In contrast, northwestern, northern, and northeastern provinces receive markedly less precipitation and fewer rainstorms, with rainstorms contributing less than 5% of the total annual precipitation [47]. This probably reduces flood-related mortality risks. Additionally, rodents in these regions are exposed to favorable climatic conditions during the summer, enabling them to grow faster and breed for longer periods each year, which may also contribute to increased tree damage. Furthermore, drought-prone northern ecosystems may also experience exacerbated damage, as rodents increasingly consume roots and bark for hydration during water scarcity [7].

In addition to the dominant role of precipitation of warmest quarter, this study also highlights the significant influence of diurnal temperature range on rodent damage, emphasizing the importance of temperature fluctuation. In general, large daily temperature fluctuations are detrimental to most animals’ growth, which in turn affects their abundances. However, rodents can mitigate the impact of such temperature fluctuations by becoming diurnal and sheltering in burrows, which provide more stable temperatures compared to the harsher conditions faced by their natural enemies (e.g., mustelids, weasels, and stoats). Consequently, rodents in northwestern, northern, and northeastern China—regions with greater diurnal temperature fluctuations—face lower predation risk and cause more damage, as their predators

endure greater thermal stress and have lower populations. In contrast, rodents in the southern and southeastern regions, where diurnal temperature fluctuations are smaller, experience higher predation pressure, resulting in less damage, as their predators face less thermal stress and have higher populations.

However, I found no relationships between rodent damage and spring temperature, spring precipitation, or winter temperature. This contrasts with previous studies in arid and semi-arid ecosystems [21, 48], which suggest that climatic factors mediate rodent populations mainly by influencing grass growth during the growing season. In these water-limited environments, increased precipitation enhances grass growth, providing food and shelter [49], thus promoting rodent populations [50, 51]. For instance, high precipitation has been linked to rodent population surges in the Simpson Desert [48] and parts of South America [52]. However, in forest ecosystems, the variety of microhabitats, such as roots and trunks, provides sufficient shelter and food sources, which may reduce the importance of grass growth and help explain the findings in this study. The results also diverge from previous studies in temperate and boreal forests [17, 53, 54], where winter climatic factors were found to significantly impact regional rodent outbreak risks. In those biomes, cold, snowy winters enhance rodent survival by providing stable environments and predator protection due to the snow cover [54, 55]. In China, which features a wide climatic range from snow-rich temperate zones to tropical areas, decreased winter temperatures may reduce rodent populations in tropical and sub-tropical regions due to increased energy demands for thermoregulation [17]. Conversely, in temperate regions, reduced winter temperatures may lead to increased rodent populations due to enhanced snow cover [55]. Thus, winter temperature may significantly shape rodent herbivory patterns within climatic zones but not across them.

Notably, climatic factors may also influence rodent herbivory damage indirectly through their influence on vegetation types. China's vast climate diversity supports a variety of forest ecosystems. The warmer, wetter southern and southeastern regions of China are home to biodiverse, multi-layered evergreen forests, while the colder, drier northwestern, northern, and northeastern regions are characterized by less diverse, mono-layered deciduous forests [36]. Previous studies have identified three key vegetation parameters that influence rodent abundances and thus their herbivory damage: stratification complexity, tree species diversity, and leaf habits. Specifically, rodent abundances are positively correlated with a higher abundance of evergreen trees and a higher tree diversity, likely due to increased food availability [56, 57]. However, rodent abundances tend to exhibit negative relationships with structural complexity, as multi-layered

forests probably harbor a higher presence of predators [58]. This suggests potential counterbalancing mechanisms across China's forest types. Southern forests may provide favorable conditions due to their perennial foliage and high tree diversity, while their complex vertical structure may limit rodent populations. In contrast, the simplified structure of northern forests may enhance rodent abundance, but this advantage could be reduced by seasonal leaf loss and lower tree diversity. Further research is needed to quantify the relative importance of these vegetation parameters in shaping rodent populations, to better understand the net vegetation-mediated effects on rodent herbivory patterns across diverse forest ecosystems.

The effect of HPD on rodent herbivory damage

In line with the hypothesis, I also observed a negative correlation between HPD and rodent herbivory damage, suggesting that human presence probably reduces rodent populations, thereby lowering associated damage. Supporting this, Newbold et al. [24], in their analysis of 208 mammal species across the world's tropical and subtropical forests, demonstrated a significant decline in the likelihood of mammal occurrence as HPD increased. Localized studies have also shown a decline in rodent abundance as human presence intensifies [59, 60]. Such a negative impact of human presence on rodent populations is generally ascribed to the direct effects of humans as apex predators [24, 61]. In this study, humans, as apex predators, likely exert their influence on rodent populations in several ways. First, routine control measures (including hunting and habitat management) were implemented nationwide following rodent damage assessments to suppress the rapid growth of rodent population [38]. These measures often result in significant population declines regardless of HPD, and may not affect spatial variations in rodent damage. Second, rodent control is not only routinely carried out but also practiced at the individual level. Humans have a low tolerance for pest rodents, and opportunistic killing by individuals seems to be widespread, leading to HPD-dependent reductions in rodent populations. For instance, a survey of 597 farmers in Weifang, Shandong province, China, revealed that 80.7% were aware of the negative impacts of rodents, and 63.3% implemented control measures upon the appearance of rodent pests [62]. As such, in densely populated regions, rodents are more likely to be observed and targeted for opportunistic killing, while sightings and killings are less frequent in sparsely populated areas. As in this study, when more people surround a forest, rodents are more likely to be noticed and threatened by direct killing. Rodents do not respect boundaries and often move between forests and nearby villages, farms, and agricultural lands [28]. Therefore, controlling rodent

populations in neighboring villages and agricultural areas may help reduce their abundances in adjacent forests. Third, the trade-off between foraging and predation risk [30], as predicted by optimal foraging theory, may also lead to HPD-dependent reductions in rodent populations, because higher HPD indicates greater predation pressure and thus lower energy intake and reproductive success [27]. These negative effects of human presence likely explain the observed biogeographic patterns: rodent damage was concentrated in the sparsely populated northwestern China, whereas it was less prevalent in the densely populated southeastern China. More specifically, the most densely populated provinces in China, such as Shanghai (2,952 people per km²), Tianjin (1,051 people per km²), Beijing (741 people per km²), Henan (521 people per km²), Jiangsu (1,050 people per km²), and Guangdong (1,189 people per km²), reported no rodent damage happen during the study periods. In contrast, the sparsely populated northwestern China (including Qinghai, Xinjiang, Gansu, Ningxia, and Inner Mongolia), with an average population density of 39 people per km², experienced the highest rodent damage, with an average damage extent of 80%.

Uncertainty and perspectives

There are several caveats in the interpretation of the findings in this study. First, the underlying mechanisms remain speculative due to the coarse spatial resolution of province-level monitoring data, which lack site-specific details. Second, other factors, such as topography, soil properties, and water availability, may also significantly influence rodent damage, yet these factors are difficult to measure accurately and consistently at a broad, coarse scale. Third, due to data constraints, this study simplifies seasonal rodent damage into interannual data. However, rodent damage patterns are likely to vary seasonally, as rodents may exhibit different feeding behaviors (e.g., root vs. leaf consumption) depending on seasonal variations in plant growth cycles and food availability. Future research should focus on higher-resolution spatial data (e.g., regional or local scales) and time-series analyses (e.g., quarterly or monthly) to better capture seasonal fluctuations in rodent herbivory and to elucidate the underlying mechanisms.

Nevertheless, these findings indicate that HPD, along with two bioclimatic variables (Bio2 and Bio18), which are easily measurable and routinely collected worldwide, account for approximately 58% of the variation in the geographic pattern of rodent herbivory damage in China's forests. Higher HPD is likely to increase predation pressure on rodents, thereby reducing rodent populations. Additionally, increased precipitation during the warmest quarter (often as rainstorms) may decrease rodent survival by flooding burrows or imposing thermal

stress. Conversely, greater diurnal temperature fluctuations could enhance rodent survival by imposing greater thermal stress on their predators. Consequently, areas in northwestern China that are arid, experience high diurnal temperature fluctuations, and have sparse human populations, are particularly vulnerable to severe rodent damage, making them priority regions for proactive rodent management. In contrast, areas in the southern and southeastern China, which are characterized by higher precipitation, lower diurnal temperature fluctuations, and higher human populations, tend to experience significantly lower level of rodent damage. However, in the context of global climate change, the risk of rodent pests in northwestern China, and likely throughout China, is projected to decrease. This is attributed to expected reductions in diurnal temperature ranges, along with increases in extreme rainfall events and overall precipitation, particularly in equatorial and high-latitude regions [63]. These findings are applicable to other arid areas with high diurnal temperature fluctuations and low population densities globally, emphasizing the need for preemptive rodent surveillance and management.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s12862-025-02383-x>.

Supplementary Material 1

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Author contributions

F.M. design of the work; F.M. the acquisition, analysis, interpretation of data; F.M. have drafted the work or substantively revised it.

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Data availability

The datasets supporting the conclusions of this article are included within the article and its additional file.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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References

- Clark JS, Carpenter SR, Barber M, Collins S, Dobson A, Foley JA, et al. Ecological forecasts: an emerging imperative. *Science*. 2001;293(5530):657–60.
- Peters D, Bestelmeyer B, Knapp A. Perspectives on global change theory. In: Scheiner S, MR W, editors. *The theory of ecology*. Chicago, IL: University of Chicago Press; 2011.
- Liu J, Hull V, Batistella M, DeFries R, Dietz T, Fu F, et al. Framing sustainability in a telecoupled world. *Ecol Soc*. 2013;18(2):26.
- Schipper J, Chanson JS, Chiozza F, Cox NA, Hoffmann M, Katariya V, et al. The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science*. 2008;322(5899):225–30.
- Jacob J, Tkadlec E. Rodent outbreaks in Europe: dynamics and damage. In: Singleton GR, Belmain SR, Brown PR, Hardy B, editors. *Rodent outbreaks: ecology and impacts*. Los Baños, Philippines: International Rice Research Institute; 2010. pp. 207–23.
- Elliott G, Kemp J. Large-scale pest control in new Zealand Beech forests. *Ecol Manag Restor*. 2016;17(3):200–9.
- Baxter R, Hansson L. Bark consumption by small rodents in the Northern and Southern hemispheres. *Mamm Rev*. 2001;31(1):47–59.
- Imholt C, Reil D, Plasil P, Roediger K, Jacob J. Long-term population patterns of rodents and associated damage in German forestry. *PEST Manag Sci*. 2017;73(2):332–40.
- Huitu O, Kiljunen N, Korpimäki E, Koskela E, Mappes T, Pietiäinen H, et al. Density-dependent vole damage in silviculture and associated economic losses at a nationwide scale. *Ecol Manage*. 2009;258(7):1219–24.
- Capizzi D, Bertolino S, Mortelliti A. Rating the rat: global patterns and research priorities in impacts and management of rodent pests. *Mamm Rev*. 2014;44(2):148–62.
- Asner GP, Levick SR. Landscape-scale effects of herbivores on treefall in African savannas. *Ecol Lett*. 2012;15(11):1211–7.
- Garibaldi LA, Kitzberger T, Ruggiero A. Latitudinal decrease in folivory within *Nothofagus pumilio* forests: dual effect of climate on insect density and leaf traits? *Glob Ecol Biogeogr*. 2011;20(4):609–19.
- Kozlov MV. Losses of Birch foliage due to insect herbivory along geographical gradients in Europe: a climate-driven pattern? *Clim Change*. 2008;87(1):107–17.
- Jacob J. Response of small rodents to manipulations of vegetation height in agro-ecosystems. *Integr Zool*. 2008;3(1):3–10.
- Jiang G, Liu J, Xu L, Yu G, He H, Zhang Z. Climate warming increases biodiversity of small rodents by favoring rare or less abundant species in a grassland ecosystem. 2013;162–74.
- Negus NC, Pinter AJ. Reproductive responses of *Microtus montanus* to plants and plant extracts in the diet. *J Mammal*. 1966;47(4):596–601.
- Jackson DM, Trayhurn P, Speakman JR. Associations between energetics and over-winter survival in the short-tailed field vole *Microtus agrestis*. *J Anim Ecol*. 2001;70(4):633–40.
- Zhang Z, Pech R, Davis S, Shi D, Wan X, Zhong W. Extrinsic and intrinsic factors determine the eruptive dynamics of Brandt's voles *Microtus brandti* in inner Mongolia, China. *Oikos*. 2003;100(2):299–310.
- Yan C, Xu L, Xu T, Cao X, Wang F, Wang S, et al. Agricultural irrigation mediates climatic effects and density dependence in population dynamics of Chinese striped hamster in North China plain. *J Anim Ecol*. 2013;82(2):334–44.
- Redhead TD. On the demography of *Rattus sordidus colletti* in monsoonal Australia. *Aust J Ecol*. 1979;4(1):15–36.
- Brown JH, Ernest SKM. Rain and rodents: complex dynamics of desert consumers: although water is the primary limiting resource in desert ecosystems, the relationship between rodent population dynamics and precipitation is complex and nonlinear. *Bioscience*. 2002;52(11):979–87.
- Ventura-Rojas PD, González-Romero A, Moreno CE, Sosa VJ. Effect of rainfall, temperature and climate change on the ecology of the rodents of arid zones: a review. *Mamm Rev*. 2025;55:e12372.
- Heffernan JB, Soranno PA, Angilletta MJ Jr, Buckley LB, Gruner DS, Keitt TH, et al. Macrosystems ecology: Understanding ecological patterns and processes at continental scales. *Front Ecol Environ*. 2014;12(1):5–14.
- Newbold T, Hudson LN, Phillips HRP, Hill SLL, Contu S, Lysenko I, et al. A global model of the response of tropical and sub-tropical forest biodiversity to anthropogenic pressures. *P Roy Soc B-Biol Sci*. 2014;281:20141371.
- Xu W-B, Svenning J-C, Chen G-K, Zhang M-G, Huang J-H, Chen B, et al. Human activities have opposing effects on distributions of narrow-ranged and widespread plant species in China. *Proc Natl Acad Sci USA*. 2019;116(52):26674–81.
- Tucker MA, Santini L, Carbone C, Mueller T. Mammal population densities at a global scale are higher in human-modified areas. *Ecography*. 2021;44:1–13.
- Darimont CT, Fox CH, Bryan HM, Reimchen TE. The unique ecology of human predators. *Science*. 2015;349(6250):858–60.
- Singleton GR. *Rodent outbreaks: ecology and impacts*. Los Baños, Philippines: International Rice Research Institute; 2010.
- Ebensperger LA, Wallem PK. Grouping increases the ability of the social rodent, *Octodon degus*, to detect predators when using exposed microhabitats. *Oikos*. 2002;98(3):491–7.
- Stephens DW, Krebs JR. *Foraging theory*. Princeton, NJ: Princeton University Press; 2019.
- de la Peña NM, Butet A, Delettre Y, Paillat G, Morant P, Le Du L, et al. Response of the small mammal community to changes in Western French agricultural landscapes. *Landsc Ecol*. 2003;18(3):265–78.
- Witmer G, Proulx G. Rodent outbreaks in North America. Rodent outbreaks: ecology and impacts. In: Singleton GR, Belmain SR, Brown PR, Hardy B, editors. *Rodent outbreaks: ecology and impacts*. Los Baños, Philippines: International Rice Research Institute; 2010. p. 253.
- Luck GW. A review of the relationships between human population density and biodiversity. *Biol Rev*. 2007;82(4):607–45.
- Cardillo M, Purvis A, Sechrest W, Gittleman JL, Bielby J, Mace GM. Human population density and extinction risk in the world's carnivores. *Plos Biol*. 2004;2(7):909–14.
- National Forestry and Grassland Administration. *China forestry and grassland statistical yearbook*. 2018.
- Xue J. *Forest ecology*. Beijing: China Forestry Publishing House; 2017.
- Chen M, Gong Y, Li Y, Lu D, Zhang H. Population distribution and urbanization on both sides of the Hu Huanyong line: answering the Premier's question. *J Geogr Sci*. 2016;26(11):1593–610.
- Hou J, et al. Technical specification for forecasting and controlling forest rodents (DB13/T 886–2007). Administration of Quality and Technology Supervision of Hebei Province; 2007.
- O'Donnell M, Ignizio D. Bioclimatic predictors for supporting ecological applications in the conterminous united States (No. 691). US Geological Survey; 2012.
- Archer E. rFPermute: estimate permutation p-values for random forest importance metrics. R Packag version 1.5.2. 2016.
- Diniz-Filho JAF, Bini LM. Modelling geographical patterns in species richness using eigenvector-based spatial filters. *Glob Ecol Biogeogr*. 2005;14(2):177–85.
- Patuelli R, Griffith DA, Tiefelsdorf M, et al. Spatial filtering and eigenvector stability: Space-Time models for German unemployment data. *Int Reg Sci Rev*. 2011;34:253–80.
- Kalcounis-Rueppell MC, Millar JS, Herdman EJ. Beating the odds: effects of weather on a short-season population of deer mice. *Can J Zool*. 2002;80(9):1594–601.
- Marini G, Arnoldi D, Rizzoli A, Tagliapietra V. Estimating rodent population abundance using early climatic predictors. *Eur J Wildl Res*. 2023;69(2):36.
- Lima M, Ernest SKM, Brown JH, Belgrano A, Stenseth NC. Chihuahuan desert kangaroo rats: nonlinear effects of population dynamics, competition, and rainfall. *Ecology*. 2008;89(9):2594–603.
- Jiang G, Zhao T, Liu J, Xu L, Yu G, He H, et al. Effects of ENSO-linked climate and vegetation on population dynamics of sympatric rodent species in semiarid grasslands of inner Mongolia, China. 2011;691:678–91.
- Huang C, Zhang S, Dong L, Wang Z, Li L, Cui L. Spatial and Temporal variabilities of rainstorms over China under climate change. *J Geogr Sci*. 2021;31(4):479–96.
- Letnic M, Dickman CR. The responses of small mammals to patches regenerating after fire and rainfall in the Simpson desert, central Australia. *Austral Ecol*. 2005;30(1):24–39.
- Hoffmann A, Zeller U. Influence of variations in land use intensity on species diversity and abundance of small mammals in the Nama Karoo, Namibia. *Belg J Zool*. 2005;135(1):91–6.
- Dickman CR, Mahon PS, Masters P, Gibson DF. Long-term dynamics of rodent populations in arid Australia: the influence of rainfall. *Wildl Res*. 1999;26(4):389–403.
- Lima M, Stenseth NC, Jaksic FM. Food web structure and climate effects on the dynamics of small mammals and owls in semi-arid Chile. *Ecol Lett*. 2002;5(2):273–84.
- Jaksic FM, Lima M. Myths and facts on Ratadas: bamboo blooms, rainfall peaks and rodent outbreaks in South America. *AUSTRAL Ecol*. 2003;28(3):237–51.

53. Imholt C, Esther A, Perner J, Jacob J. Identification of weather parameters related to regional population outbreak risk of common voles (*Microtus arvalis*) in Eastern Germany. *Wildl Res.* 2011;38(7):551–9.
54. Šipoš J, Suchomel J, Purchart L, Kindlmann P. Main determinants of rodent population fluctuations in managed central European temperate lowland forests. *Mammal Res.* 2017;62(3):283–95.
55. McCafferty DJ, Moncrieff JB, Taylor IR. Winter microclimate of field voles (*Microtus agrestis*) in SW Scotland. *J Therm Biol.* 2003;28(5):397–401.
56. Moura MC, Grelle CEV, Bergallo HG. How does sampling protocol affect the richness and abundance of small mammals recorded in tropical forest? An example from the Atlantic forest, Brazil. *Biol Conserv.* 2008;3(2):51–8.
57. Madden H, Van Andel T, Miller J, Stech M, Verdel K, Eggermont E. Vegetation associations and relative abundance of rodents on St. Eustatius, Caribbean Netherlands. *Glob Ecol Conserv.* 2019;20:e00743.
58. Morales-Díaz SP, Alvarez-Añorve MY, Zamora-Espinoza ME, Dirzo R, Oyama K, Avila-Cabadilla LD. Rodent community responses to vegetation and landscape changes in early successional stages of tropical dry forest. *Ecol Manage.* 2019;433:633–44.
59. Langton SD, Cowan DP, Meyer AN. The occurrence of commensal rodents in dwellings as revealed by the 1996 english house condition survey. *J Appl Ecol.* 2001;38(4):699–709.
60. Panti-May JA, Hernández-Betancourt S, Ruiz-Piña H, Medina-Peralta S. Abundance and population parameters of commensal rodents present in rural households in Yucatan, Mexico. *Int Biodeterior Biodegradation.* 2012;66(1):77–81.
61. Woodroffe R. Predators and people: using human densities to interpret declines of large carnivores. *Animal conservation forum.* Cambridge University Press; 2000. pp. 165–73.
62. Li L, Fan J, Liu G, Sun J. An investigation of the awareness of rodent control and prevention among rural residents in Weifang City, Shandong Province, in 2016. *Chin J Vector Biol Control.* 2019;30:350–3.
63. IPCC. Summary for policymakers. In: Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S, Caud N, Zhou B, editors. *Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change.* Cambridge: Cambridge University Press; 2021.

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