Distribution patterns and drivers of non-endemic and endemic rodent species in China

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Abstract

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Distribution patterns and drivers of non-endemic and endemic rodent species in China

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Abstract

Species distribution patterns are essential for the conservation of biodiversity. The aim of this study was to evaluate the influence of multiple ecological hypotheses on the spatial patterns of rodent species richness in China. First, we divided the geographic region of China into 80 × 80 km^2 grid cells and mapped the distribution ranges of the 237 rodent species. Rodent taxa were separated into three response variables based on their distribution: (a) all species, (b) non-endemic species, and (c) endemic species. The predictors were divided into four factor sets: (a) energy-water, (b) climatic seasonality, (c) habitat heterogeneity, and (d) human factors, which were used to represent four different ecological hypotheses. We then performed multiple regression analysis (OLS), spatial autoregressive models (SAR), and variation partitioning analyses to determine the effects of predictors on the spatial patterns of rodent species. The Hengduan Mountains

and surrounding mountains in southwest China showed the highest species richness and endemism. Habitat heterogeneity is the most important factor explaining the species richness distribution patterns across all species and non-endemic species. Endemic species richness patterns are most susceptible to seasonal changes in climate and least affected by human factors. The effects of energy and water on the three response variables showed consistent levels of importance.

1 Introduction

Large-scale spatial distribution patterns of species richness and their formation mechanisms are central to ecology and biogeography. It is also the basic scale for measuring regional diversity and the basis for constructing evolutionary and ecological models and conservation strategies (Gotelli & Colwell, 2001; Jenkins, Pimm & Joppa, 2013; D'Antraccoli et al., 2019). The prediction of species ranges can usually be achieved in three ways: collection or surveyed species distribution record points, expert mapping of species distributions, and the ranges inferred from species distribution models (Guisan & Thuiller, 2005). At present, species distribution models (SDM) are frequently used in studies on species distribution prediction because of their relative flexibility and better discriminatory and predictive power. SDM can use the relationship between species distribution points and local environmental variables to predict the potential distribution areas of species (Zhang et al., 2019; Abdulwahab, Hammill & Hawkins, 2022; Sanczuk et al., 2022). China is a vast territory, and covering all biological surveys is challenging. Therefore, SDM can guide future field surveys to a certain extent, provide references for further exploration and discovery of species distribution, and provide a scientific basis for the formulation of species protection measures (Nguyen & Leung, 2022). Among the simulation methods of various distribution models, the maximum entropy model uses environmental variables and species distribution sites to calculate constraints in the case of a small sample size. It explores the possible distribution of maximum entropy under this constraint to predict the habitat suitability of species in the study area, resulting in better simulation results than other models (Wang et al., 2021).

How the interactions of the modern environment, evolutionary history, and ecological processes shape the patterns of species richness remains an interesting but controversial issue in biogeography. Ecologists have been trying to determine the effects of various environmental variables on the distribution and diversity of organisms in different ecological regions. The factors determining richness patterns are critical for understanding the structure and dynamics of organisms in an area (Holt et al., 2018). Species are not randomly distributed over the land surface; rather, their distribution patterns are based on climate, topography, and anthropogenic influences in recent decades (Li et al., 2015; Xu et al., 2019). Consequently, various theories and hypotheses have been developed to explain how geographical patterns of species richness are formed.

The energy-water hypothesis is the most common and discussed hypothesis for explaining species richness patterns (Hawkins et al., 2003; Pandey et al., 2020). This hypothesis states that the availability of energy and water determines the total plant resources that control biological activity and that total plant resources, in turn, determine changes in biodiversity (Jimenez-Alfaro et al., 2016). Second, habitat heterogeneity, another form of environmental variation that affects the production and maintenance of diversity, is considered one of the most important factors controlling species richness gradients. Increased space and shelter and opportunities for isolation and adaptation enhance species coexistence, persistence, and diversification (Stein, Gerstner & Kreft, 2014; Stein et al., 2015). Third, seasonal changes in climate and unsystematic changes in daily maximum and minimum temperatures increase organisms' tolerance levels by altering their thermal environments, enabling them to become geographically widespread (Mi et al., 2022). Finally, human-induced environmental changes, such as habitat fragmentation, land-use changes, and disturbances, can lead to habitat loss for species (Li et al., 2015; Xu et al., 2019). These hypotheses explore the main factors influencing species richness formation based on different influencing factors.

Some studies have tested a single hypothesis (Sun et al., 2020), whereas others have tested multiple hypotheses (Gebauer et al., 2018; Ding et al., 2019; Pandey et al., 2020). A single variable or hypothesis is limited in

its interpretation of species richness distribution patterns because it is a multiple-complex phenomenon that determines species richness distribution patterns. Thus, multiple modeling approaches are best suited for quantifying the contribution of various hypotheses to spatial richness distribution patterns. In the context of global biodiversity loss and concomitant climate change, attempts have been made to determine the relationships between species populations and their determinants (Xu et al., 2019; Pandey et al., 2020; Sun et al., 2020). Some studies have explained the distribution patterns of the regional richness of rodents in China (Zhou, Ma & Ye, 2002; Xing, Zhou & Ma, 2008) but have not considered the mechanisms that determine richness patterns. Chi et al. (2020, 2021) studied the distribution pattern of terrestrial mammal abundance in China and its relationship with environmental factors. Such studies include rodents in mammals, which inevitably do not fully consider their distribution pattern, resulting in studies that do not fully reflect the distribution pattern of rodents. Moreover, few studies have been on the richness distribution patterns of endemic and non-endemic rodent groups in China. Endemic species are those found only in specific locations or regions, not anywhere else in the world. They are usually restricted to a limited geographic range, with small ranges and population sizes, and sometimes with low genetic diversity and specific habitat requirements (Myers et al., 2000; Isik, 2011). Multiscale drivers and geographic distribution patterns of endemic species are also important topics in conservation biogeography because these species are particularly vulnerable to climate change and habitat degradation (Wu et al., 2016). It has been shown that there is a lack of consistency between all species richness or non-endemic species richness and endemic species richness (Orme et al., 2005; Lamoreux et al., 2006). Areas with high species richness may have many endemic species but not necessarily coherent patterns (Vetaas & Grytnes, 2002).

Therefore, we attempted to explore the geographic distribution pattern of rodents (Rodentia and Lagomorpha) in China. We divided rodent species into endemic and non-endemic species and assumed that the factors affecting endemic and non-endemic species distribution are different. We investigated the relative importance of energy-water, climatic seasonality, habitat heterogeneity, and human factors that may contribute to the distribution patterns of rodents in China. The main objectives of this research were to (1) explore the distribution pattern of rodents and their endemic and non-endemic species and (2) assess the explanatory power of energy-water, habitat heterogeneity, climate seasonality, and human factors for rodent distribution patterns in China.

2 Materials and methods

2.1 Study area

The study encompassed all of China's land mass, including Taiwan and Hainan Island, but excluded the surrounding oceans and islets. Chinese mammalian fauna belongs to the Palearctic and Oriental realms, which can be further subdivided into seven biogeographic subregions (i.e., northeast China, north China, Inner Mongolia-Xinjiang region, Qinghai-Tibet region, southwest China, central China, and south China). These ecogeographic zones have high species diversity and many endemic animal species, including rodents. The present study divided the Chinese territory into a grid system of 80×80 km^2 to eliminate the influence of spatial scale or area on species distribution patterns. Grids with less than 75% of the complete grid included in the study area were removed to prevent the incomplete grids in the coastline and boundary areas from affecting the subsequent statistical analysis. A total of 1672 grids were obtained.

2.2 Distribution pattern calculation

We compiled a database of rodent species distribution in China. Species distribution data were obtained mainly from the following sources: 1) the research results of Zhou et al. (2002) and Xing et al. (2008); 2) National Zoological Museum of China, NZMC; 3) Global Biodiversity Information Facility (GBIF); and 4) distribution and collection records available in books or literature (Jiang et al., 2015; Ge et al., 2018; Liu et al., 2019; Li et al., 2019; Cheng et al., 2021; Jackson et al., 2022). After removing null values, offset values, and redundant data from the distribution records, 237 species of rodents in two orders were included in the analysis of this study. There were 67 endemic and 170 non-endemic species (Jiang et al., 2015; Wei et al., 2021) (Table S1).

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MaxEnt (v3.4.1) was used for ecological niche modeling (ENM) of potential rodent habitat areas in China. Considering that the MaxEnt model requires at least five different coordinate values for each species to produce more accurate results, six points were used as the minimum criteria for calculating species distribution in this study. The potential habitats of 210 rodent species with six or more distribution points were simulated using ENM to determine the potential species richness of rodents in China. Based on the characteristics of distribution data and rodent habits, 26 environmental variables were selected. The five categories of predictors were climate, topography, vegetation, soil, and human activity intensity (Table S2). Chinese administrative vector boundaries were obtained from the Data Center for Resources and Environmental Sciences at the Chinese Academy of Sciences (RESDC) (http://www.resdc.cn) and converted to 1 km^{2}resolution.

The correlation of environmental variables was detected using the ENMTools (Warren et al., 2021) package in R 4.0.5 (http://www.r-project.org). The variables that were not highly correlated ($r < 0.7$) were used in the model prediction to reduce the complexity of the model (Table S2). The percentage of random test data was set to 25%, 10 sub-models were generated using the bootstrap function of the MaxEnt model, and the average of the output of the 10 sub-models on each image element was calculated as the final prediction result of the species. Because each species has a different degree of tolerance to the environment, the suitable habitat threshold for each species was divided based on the critical value of the available distribution records. The growth suitability at each sampling point was extracted from the plot of the calculated growth suitability. The standard deviation σ and mean value μ were calculated according to the theory of normal distribution, μ-σ was selected as the threshold value, transforming the species distribution probability maps into 0/1 binary distribution maps. The model accuracy was evaluated using receiver operating characteristic (ROC) curves. The area enclosed by the ROC curve and horizontal axis is the AUC value (Hanley & McNeil, 1982), which can be used to measure the strengths and weaknesses of the model. For species with predicted AUC values less than 0.8, the MaxEnt model was optimized using the ENMeveal package in R (Muscarella et al., 2014), and the model was run again.

The distribution ranges for the 27 species with less than six recorded distribution points defaults to the grids where the distribution points were located. The distribution range layer was converted into a 0/1 binary distribution map. Finally, the binary distribution map of 237 species was superimposed on the grid map, and the number of species appearing in a single grid was counted to obtain the species richness distribution map.

2.3 Analysis of influencing factors of the species richness pattern

2.3.1 Environment variables

Based on previous studies and the four hypotheses, we selected 12 environmental predictors in four categories to evaluate the hypotheses explaining the distribution pattern of rodent species richness in China. The hypotheses and their associated variables are

1. Energy-water: the availability of energy and water can be measured using many indicators, such as temperature, precipitation, and solar radiation (Pandey et al., 2020). We selected annual mean temperature (MAT), annual precipitation (DVL), potential evapotranspiration (PET), and actual evapotranspiration (AET) as substitute variables. We extracted MAT and DVL from the World-Clim (https://worldclim.org/) database as measures of temperature and water effectiveness variables, PET and AET were obtained from the Global Land Evaporation Amsterdam Model (GLEAM) (https://www.gleam.eu/).
2. Habitat heterogeneity: the mean elevation (MELV), elevation range (ELR), and the number of vegetation types (VEG) within a single grid, the most commonly used predictors to represent information on habitat heterogeneity, were selected as habitat heterogeneity factors. These values were obtained from the RESDC.
3. Climate seasonality: temperature seasonality (TES), annual temperature range (ART), and precipitation seasonality (PRS) were used as proxies for short-term climate seasonality. All factors were

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obtained from the WorldClim database download.

4. Human factors: we used the human impact index (HII) and human footprint index (HFI) as proxy variables representing human-induced effects. The HII and HFI data were downloaded from the archives of the Wildlife Conservation Society (http://sedac.ciesin.colum bia.edu/data/).

2.3.2 Data analysis

Species richness was defined as the number of species in each cell grid. Species richness data usually show non-normal distribution. The species richness data were square root transformed before regression analysis to avoid the impact of skewed data distribution on statistical analysis. We used a simple regression analysis of all species richness, non-endemic species richness, and endemic species richness for each environmental variable to explore the potential mechanisms of individual factors in explaining the distribution patterns of species richness.

To evaluate the relative importance of the predictive variables, we separated the environmental factors into four distinct predictor sets based on our main research objectives: (a) energy-water (EW), (b) climatic seasonality (CS), (c) habitat heterogeneity (HH), and (d) human factors (HE). Because all predictors were highly correlated, we eliminated collinearity by performing a principal component analysis (PCA) in each prediction set. The squared term of the predictor variable was included in the principal component analysis, considering the nonlinear relationship between the response variable and environmental factors. We extracted the first two principal components of each prediction set, which accounted for 94% of energy-water, 87% of habitat heterogeneity, 99% of climatic seasonality, and 99% of human factors (Table S3).

To make the model coefficients comparable, the principal components extracted from all factor sets were standardized (standard deviation = 1 and mean = 0). Multiple linear regression used ordinary least squares (OLS) to determine the most appropriate predictors that explain the richness of the three response variables. We followed the variable backward selection method to identify the optimal model. The optimal linear regression model was determined using the stepAIC function in R in combination with the Akaike Information Criterion (AIC). Variance inflation factors (VIF) were used to test for multicollinearity between predictor variables, and we selected predictors with VIF < 5 (Dormann et al., 2013) (Table S4). Because spatial autocorrelation affects the explanatory power of regression models, the spatial autocorrelation of the residuals of multiple regression models was assessed using Moran's I method. Because the residuals of the multiple regression models all had significant spatial autocorrelation ($p < 0.001$), the spatial linear simultaneous autoregressive error model (SAR) was further developed using the predictor variables from the optimal model. The explanatory power of the predictor variables for species richness was measured using Pseudo-R^2 (the square of the correlation coefficient between the predicted and actual values of the model for the non-spatial component) (Kissling & Carl, 2007). The relative importance between the predictor variables was also compared using standard regression coefficients.

Finally, we performed variance partitioning to assess the pure effects of the predictor variables and their joint contributions to better explain the distribution patterns of species richness. Wayne diagrams were used to show various factor sets' pure and shared effects.

Statistical analysis for this study was performed in R 4.0.5 (http://www. r-project.org). The "psych" package was used for principal component analysis, the "MASS" package for optimal model selection, the "vegan" package for variance partitioning, and the "spedep" package for spatial autoregressive model building.

3 Results

3.1 Species richness patterns of all species of rodents

Rodents are widely distributed in China and are recorded in almost every grid; however, their spatial distribution is uneven. All species (n = 237) of rodents occurred in 1665 grids, and the species richness in each grid was between 0 and 84 (mean: 31.39 ± 16.51 SD) species (Figure 1a; Table S5). The highest abundance of rodent species in China was found in the subtropical and tropical regions of the oriental realm, with the Hengduan Mountains being the most abundant region, followed by the Qilian Mountains

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and Tianshan Mountains regions. In addition, Taiwan and Hainan Island also have high species richness. The species richness was the lowest in the Qinghai-Tibet Plateau and Tarim Basin regions, with only a few species in most grids.

The simple regression results showed that, when considering the effect of individual factors, all species richness was highly significantly correlated with each environmental factor ($p < 0.001$). The two most relevant variables were VEG and AET (Figure 2a, b; Table S6).

Regarding the relationship between the predictor set and all species richness, the best model was explained by a set of five variables (EW1+CS1+HH1+HE1+HE2). The multiple regression model (OLS) explained 71% of the total variation in rodent species richness. Due to the removal of the effect of spatial autocorrelation by the spatial autoregressive model (SAR), the degree of explanation was reduced to 64% (Table 1). As shown in Table 1, the importance of each variable in explaining the species richness pattern varied slightly across the regression models, but the difference was not significant. Both the regression models showed that HH1 and HE1 were the most important predictors. The variance partitioning results showed that the four predictor sets explained 71.7% of the variance in the total species richness. The habitat heterogeneity predictor set explained 48.94% of the variation in all species richness patterns, followed by human factors (42.30%), energy-water (28.79%), and climatic seasonality (18.30%) (Figure 3a, b; Table S7)

3.2 Patterns of non-endemic species richness

Non-endemic species (n = 170) accounted for 71.7% of all species and were found in 1,659 grids. Their distribution in each grid ranges from 0–58 (mean: 25.65 ± 12.06 SD) species (Figure 1b; Table S5). The species richness distribution pattern of non-endemic species was similar to that of all rodent species. The Southern Hengduan Mountains, Qilian Mountains, Tianshan Mountains, and Altai Mountains had high non-endemic species richness. Similar to all species, species richness was low in the Tibetan Plateau and Tarim Basin regions.

The analysis of non-endemic species richness and individual environmental factors showed that VEG and AET had the greatest impact on the non-endemic species richness pattern. This result was the same for all the species (Figure 2c, d; Table S6).

The best model for predicting non-endemic species richness comprised three predictor sets of five variables (EW1+ HH1+ HH2+ HE1+ HE2). OLS and SAR explained 70% and 61% of the non-endemic species richness (Table 1), respectively. As with the results for all species, both regression models showed that HH1 and HE1 were the most important predictors. However, OLS showed that, in addition to the two factors mentioned above, EW1 is equally important. In variance partitioning, all four predictor sets explained 70.10% of the variance in defining the richness patterns of non-endemic species. Non-endemic species richness was significantly correlated with the habitat heterogeneity predictor set, explaining 51.21% of the variation. This was followed by human factors (50.42%), the energy-water predictor set (27.67%), and the climate seasonality predictor set (13.14%) (Figure 3a, c; Table S7).

3.3 Patterns of endemic species richness

Endemic (n = 67) species were found in 1430 grids, approximately 28.27% of all species. Endemic species richness in each grid ranged from 0–33 (mean: 5.75 ± 6.54 SD) species (Figure 1c; Table S5). The distribution of endemic species is mainly concentrated in the Hengduan Mountains and the surrounding areas. However, their distribution in the north is rare, and only a few endemic species have adapted to high-latitude environments.

Unlike all species and non-endemic species, when a single factor acted, TES and ART had the highest effect on endemic species richness (Figure 2e, f; Table S6).

Finally, regarding the relationship between the distribution pattern of endemic species richness and predictor sets, the best prediction model contained seven variables (EW1+EW2+CS1+CS2+HH1+HE1+HE2). OLS and SAR explained 65% and 53% of the total variation. The importance of the variables in explaining the

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endemic species richness pattern differed significantly between the two regression models (Table 1). In OLS, CS1 dominates overwhelmingly and is positively correlated with CS2. However, HH1 and CS1 were equally important and negatively correlated with CS2 in SAR. In variance partitioning, 65.58% of the variance was explained by the four predictor sets. The largest variation in endemic species richness was the total effect of the climatic seasonal predictor set, explaining 45.89% of the variation. The habitat heterogeneity set and energy-water predictor sets explained 32.44% and 15.14% of the variation in the endemic species richness pattern, respectively. The human factor predictor set explained the lowest variance (6.03%) (Figure 3a, d; Table S7).

4 Discussion

Species richness, including that of rodents, is characterized by spatial heterogeneity (Gaston, 2000). The results of this study indicate that there is a wide variety of rodents, including endemic species, in the Hengduan Mountains and surrounding areas of Southwest China. The Hengduan Mountain area is considered an ecological corridor between the Palaearctic and Oriental realms, connecting the northern and southern fauna. It is an important center for the origin of species (Wu et al., 2016). This may explain why southwest China has the highest level of endemism. Southwest China is rich in plant resources and has a complex topography and a high degree of habitat heterogeneity. The area's climate ranges from tropical to temperate and is dominated by high temperatures and abundant precipitation (Liu et al., 2015; Shrestha et al., 2017). These findings may contribute to the diversity of rodents in China. In comparison, the extreme climatic conditions of the Qinghai-Tibet Plateau, Tarim Basin, and northern China may limit the distribution of species intolerant to climatic factors (Hu et al., 2017; Ding et al., 2019). The results show that the border areas of China's Yunnan, Sichuan, and Tibet autonomous regions, especially the Qionglai, Yunling, Minshan, and Gaoligong mountain systems in the Hengduan Mountains, have the highest richness values of all studied areas due to their diverse topography, hydrothermal conditions, and habitats. The distribution pattern of rodent species richness may be explained by a combination of habitat heterogeneity, climate seasonality, energy-water, and human factors (Figure 3).

The close relationship between species richness and habitat heterogeneity and the variance partitioning results showed that habitat heterogeneity is the most influential predictor variable for describing the species richness of all and non-endemic rodent species in China. It is also an important factor in the richness distribution pattern of endemic species. Habitat heterogeneity is considered the most critical factor in shaping biological distribution patterns. Habitat variation creates a microhabitat for species reproduction by creating dramatic changes in climate and habitat differentiation on a small scale, enabling species to coexist locally (Carmignotto et al., 2022). Southwest China has a variety of hydrothermal conditions and habitats that result from a combination of topographic changes caused by elevation differentiation (Huang et al., 2011; Liu et al., 2015). As a result, the site had the highest richness values for rodent species. In this study, we used the elevation range as one of the main predictors of habitat heterogeneity, arguably the best indicator of topographic variation. Meanwhile, southwest China is also the richest region in terms of plant species (Shrestha et al., 2017; Dakhil et al., 2019; Sun et al., 2020; Pandey et al., 2020). Abundant plant resources provide a large amount of food for rodents and a suitable shelter for unfavorable climatic conditions (Barreto, et al., 2019). In addition, the Qinghai-Tibet Plateau's uplift has profoundly changed the geomorphology of mainland China, mountains, ravines, and canyons, resulting in huge mountain height differences. Quaternary ice sheet intrusion drives rodent migration from higher to lower elevations, and the cyclical effects of warming cause rodents to return to higher elevations (Barreto et al., 2019). Faunas that cannot migrate can only adapt to the differentiation of low- and medium-altitude environments, thus causing high endemic species richness in rodents. In addition, highly heterogeneous tropical and subtropical mountain ranges may be cradles of biodiversity and thus dominate in terms of species richness and concentrations of endemic species with narrow distributions.

The results showed that climatic seasonality is the dominant factor in the distribution patterns of endemic species of rodents in China. Conversely, it explained the least of all the species and non-endemic species richness patterns. This suggested that seasonal temperature changes have a profound effect on endemic species

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richness (Penjor et al., 2022). Previous research has also identified a significant role of climate seasonality in maintaining patterns of species richness in endemic species of small mammals (Amori et al., 2011; Wu et al., 2013; Hu et al., 2017). The temperature in China fluctuates widely, with more extreme temperatures in the north than in the south. This might be an important factor in northern China's restricted distribution of endemic species. Our findings support the theory of tropical niche conservation and the inability of endemic rodent species to adapt to northern environments. Their ability to migrate from south to north is consistent with our findings (Romdal et al., 2013). This seasonality in southwest China creates stable climatic conditions for endemic species to survive under harsh conditions. Araújo et al. (2008) and Dakhil et al. (2019) reported the significant role of climate stability during the warmest season of the Quaternary glaciation. Climatic stability is an ecological indicator of the range stability of subtropical fauna in the high-altitude regions of southwest China, including the eastern Tibetan Plateau (Thuiller, 2004; Huang et al., 2011). Due to climate variability and the unsystematic variation in daily maximum and minimum temperatures, modifying the thermal environment experienced by rodents to increase the body's tolerance level enables them to be widely distributed geographically.

Our results also revealed the importance of anthropogenic variables in the distribution patterns of total and non-endemic species. However, its effect on endemic species richness was minimal. Thus, it can be expected that anthropogenic activities will significantly impact the distribution of rodents. Anthropogenic activities can drive the contraction and expansion of species. Many species have lost significant areas of distribution owing to increased land use and other human activities (Ceballos & Ehrlich, 2002; Di Marco & Santini, 2015). Human activities have also contributed to the range expansion of many other species, and many regional native species have experienced increased range through human-mediated dispersal and the ability to thrive in anthropogenic landscapes (Li et al., 2015). However, endemic species have more specialized habitat requirements, are concentrated in specific geographic areas, and may deviate ecologically from a wide range of species (Tomašových & Jablonski, 2016). Therefore, the anthropogenic impact on rodent endemics is limited. However, endemic species are confined to limited areas, and their habitats are often fragile and highly susceptible to reduction or even disappearance by external factors. Therefore, we cannot ignore human-interference scenarios. In southwest China, anthropogenic disturbances, such as natural resource exploitation, tourism, and land use change, are gradually increasing, accelerating the impact of human activities on wildlife. Therefore, protecting this center of species richness and endemism is a big challenge.

On a large scale, energy-water did not have a significant direct relationship with the distribution pattern of rodent species richness in China. This finding differs slightly from Hu et al. (2017) and Wu et al. (2013) at the local scale. The spatial pattern of species richness and the importance of biotic and abiotic predictor variables in influencing species richness may depend to a large extent on the spatial scale of the sampling unit (Qian & Kissling, 2010). In some cases, species richness patterns and potential drivers can be reasonably explained by ecological requirements and the evolutionary history of species grouping (Wu et al., 2013). Rodents are phytophagous or omnivorous; therefore, the pattern of species richness may be more closely related to plant species richness (Hawkins & Pausas, 2004). At a large spatial scale, the direct impact of energy-water on plants is often more significant (Zhang et al., 2015). Although the effect of energy-water on the distribution pattern of rodent species richness is not very significant at large scales, on a smaller scale, rodent dispersal behavior is temperature oriented, and species may spread more rapidly when temperature changes (Wu et al., 2013). Therefore, temperature and precipitation may strongly influence rodent species richness at a regional scale.

In summary, we against using all species or non-endemic species richness as proxies for endemic species richness. This is consistent with the results of previous studies (Orme et al., 2005; Isik, 2011). The reasons for the formation of endemic and widespread species differ. Endemic species formation is often closely related to environmental and anthropogenic changes. Some endemic species may have been widely distributed; however, due to climate change during the geological and historical period, their habitats have shrunk or even disappeared, forcing them to confine their distribution to a narrow range; or newly evolved species have not yet spread to a larger geographic area; or destruction of the environment limits their ranges. In

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addition, we found that the reasons for determining the distribution of non-endemic and endemic species richness differed.

Although this study contributes to a more nuanced understanding of rodent species richness patterns and their drivers in China, it has several limitations. For example, there are 271 species of rodents in China (Wei et al., 2021), however, only the 237 species with relatively complete data were analyzed in this study, which does not provide a complete picture of the distribution pattern of rodents in China. The variables used in MaxEnt partially overlap with the factors involved in the regression model, which will inevitably affect the regression results. In addition, the species distribution model assumes that species distribution is influenced only by environmental variables, without interactions between organisms and biological dispersal constraints. In practice, species distribution is also influenced by biological factors such as competition, predation, and disease. A more sophisticated and integrated SDM for species range prediction is required to consider these factors, which is an important direction for future model development (Kearney & Porter, 2009).

5 Conclusion

This study investigated the spatial patterns of rodent species richness in China and possible interpretations of the results based on multiple environmental and human factors. This study found that the highest species richness values of non-endemic and endemic species of rodents in China were in and around the Hengduan Mountains in southwest China. The lowest number of rodent-endemic species was in the Qinghai-Tibet Plateau and northern China. Habitat heterogeneity was the most effective variable to reflect changes in the potential distribution of all rodents and non-endemic species, as well as species richness in China. Endemic species richness patterns are most vulnerable to seasonal changes in climate, they are least influenced by human factors, and the effect of energy-water on the three response variables showed a consistent level of importance.

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Table

Table 1 Results of multiple linear regression (OLS) and spatial autoregressive model (SAR) analysis of rodent species richness

Variable	All species OLS	All species SAR	Non-endemic OLS	Non-endemic SAR	Endemic OLS	Endemic SAR
EW1	0.15***	0.011	0.23***	0.017*	-0.16***	-0.025**
EW2	–	–	–	–	-0.13***	-0.018*
CS1	-0.18***	-0.032***	–	–	-0.73***	-0.080***
CS2	–	–	–	–	-0.08***	0.0062
HH1	0.55***	0.19***	0.43***	0.18***	0.36***	0.11***
HH2	–	–	-0.12***	-0.0038	–	–
HE1	0.40***	0.070***	0.38***	0.084***	0.14***	0.017*

HE2	-0.12***	-0.018**	-0.11***	-0.0067	-0.10***	-0.026***
AIC	2687.71	411.79	2745.89	695.88	2997.49	392.16
R^2	0.71	0.64	0.70	0.61	0.65	0.53
Moran's I	0.69***	0.068***	0.67***	0.07***	0.75***	0.02

EW, CS, HH, and HE refer to variables based on the first two axes of the PCA using the energy-water, climatic seasonality, habitat heterogeneity, and human factors variables, respectively. Moran's I is the Moran's index of the regression model residuals. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Figure legends

Figure 1 Spatial distribution of rodent species in China across all (a), non-endemic (b), and endemic (c) species.

Figure 2 Relationship between all, non-endemic, and endemic species richness and the most relevant environmental variables. VEG = Vegetation Types, AET = Actual Evapotranspiration, TES = Temperature Seasonality, ART = Temperature Annual Range. Shaded area shows 95% confidence interval.

Figure 3 Results of variance partitioning explained by environmental variables. (a) Schematic diagram of variance partitioning, each letter in the figure represents a part of the variance partitioning analysis. Results of variance partitioning for (b) all species, (c) non-endemic species and (d) endemic species.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

CONFLICT OF INTEREST

All authors state that there is no conflict of interest.

AUTHOR CONTRIBUTION

Lei Meng: Data curation (lead); Formal analysis (equal); Methodology (equal); Visualization (equal); Writing-original draft (lead); Writing-review & editing (lead).

Lizhi Zhou: Conceptualization (lead); Resources (lead); Supervision (equal); Visualization (equal); Writing-review & editing (equal).

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