

Article

Energy Availability Factors Drive the Geographical Pattern of Tenebrionidae (Coleoptera) in the Arid and Semiarid Areas of China

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Abstract: Species richness is regarded as the core index of biogeography. Estimating the correlation between species richness and modern environmental factors will be of great significance for species conservation. The arid and semiarid areas of China present serious desertification, but there are rich biodiversity resources of high value. In this study, we evaluated species diversity, species richness, and the correlation between species richness and modern environmental factors using the species of Tenebrionidae in arid and semiarid areas of China, which will provide basic data for species conservation. The species richness was measured using $1^{\circ} \times 1^{\circ}$ grid cells, and its determinants were explored based on generalized linear models (GLMs) and random forest models. A total of 696 species, belonging to 125 genera of 38 tribes and 7 subfamilies, were recorded in the study area. The non-uniform species richness pattern was presented, with more species in Altai, Tianshan, Nyenchen Thanglha and Helan Mountains. The species richness was affected by a variety of environmental factors. The variables representing energy availability and climate stability had stronger explanatory power, especially the annual mean temperature (BIO1) and the mean temperature of warmest quarter (BIO10). In contrast, water availability and habitat heterogeneity have relatively little correlation with species richness.

Keywords: Tenebrionidae; species richness; environmental factors; annual mean temperature; the mean temperature of warmest quarter; arid and semiarid areas of China



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1. Introduction

The arid and semiarid regions of China are located on the northwest side of the 400 mm isohyet (Figure 1), accounting for about half of the country's total area [1,2]. They have a dry climate and a complex geological environment, with mountains, basins, plateaus, and other landforms [2,3]. For example, the Tianshan Mountains, one of the great mountain ranges of Central Asia, are located there, covering two-thirds of the total length of the entire mountain system [4–6]. Helan Mountain is another famous mountain there, known as the green island in the desert [7,8]. The Qinghai-Tibet Plateau (QTP), as the highest plateau in the world, is an important faunistic component there and has a unique ecological environment and climatic conditions [9–12]. These areas not only have vast land with economic development potential, but also rich biodiversity resources with abundant value [13–22].

The arid and semiarid areas have a large mass of deserts in China [23,24]. Incidentally, disastrous climate often occurs in the arid and semiarid areas, which affects the sustainable development of economy and the regional and even global environment [25–27]. Global warming has led to the expansion of arid areas around the world, which may threaten the ecological security of arid and semiarid areas in China [13,28–30]. Insects compose the largest group of organisms in the world, and they perform a critical role in the maintenance of the ecosystem [31,32]. According to statistics, at least 30,000 species of insects have been reported in the arid and semiarid areas [33–82]. However, environmental changes,

such as precipitation and temperature, have forced some species to change their habitats and even affected their diversity, thereby greatly affecting the health of ecosystems in this area [32,83,84]. Therefore, the studies on insect diversity, distribution patterns and environmental influences on insect richness in arid and semiarid areas of China will be of great significance for ecological security and socio-economic development [85–91].

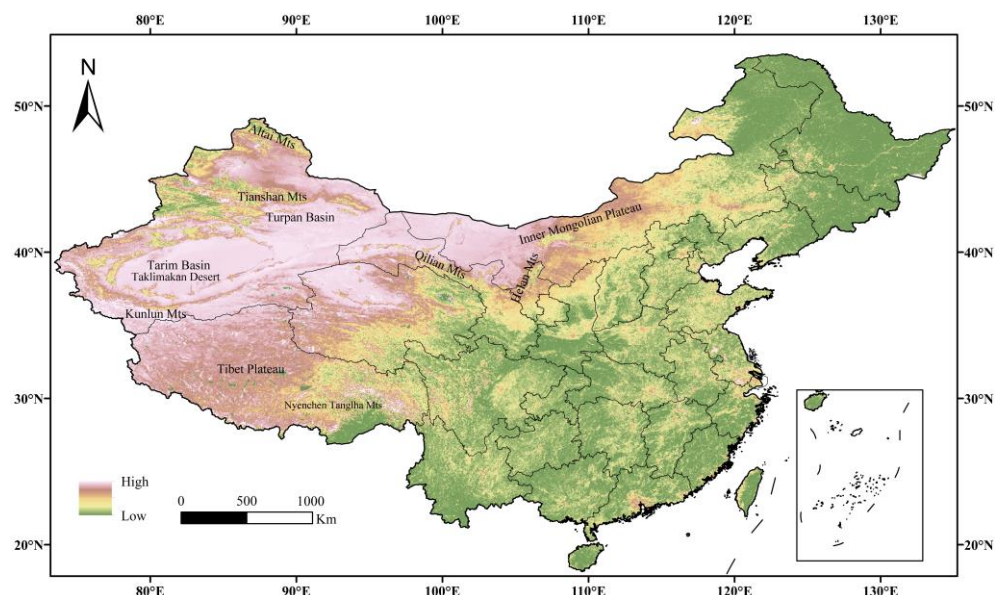


Figure 1. The map of drought levels in China is shown through a map of normalized difference vegetation index (NDVI).

Tenebrionidae is one of the largest beetle families, with about 35,000 species widely distributed in the world [92]. The tenebrionid beetles have a high species diversity due to their high adaptability to different habitats [93–95]. Unlike other insects, they exhibit an unusually high species diversity in the arid and semiarid areas, so they are always considered one of the indicator insects in these areas [96–98]. Simultaneously, the taxonomy of this beetle group, which is the basis of relevant geographical analysis [99], has been well studied. At present, 232 species of Tenebrionidae have been recorded in Inner Mongolia, 157 in the Ningxia region, and more than 2000 in the Qinghai-Xizang Plateau [62,100,101]. However, the total number of Tenebrionidae species in the arid and semiarid areas of China remains unknown. In addition, we do not know how the species richness is affected by environmental factors, and whether the species of Tenebrionidae will be greatly affected under a global warming scenario, although many taxonomic, molecular, and diversity studies have been published [102–104]. Thus, further research on the distribution pattern of Tenebrionidae will help to deepen our understanding of this beetle group in the arid and semiarid areas of China, which is of great significance for the development of biodiversity conservation plans [105].

Species richness is an essential index in the field of ecology and biogeography, which is a classic topic regarding distribution patterns [106–108]. A few studies have used species richness as a measure to explore species evolution and provide insights into biodiversity conservation [109–111]. The research on the influence of environmental factors on species diversity is also a trendy topic [106,112]. Most studies show that species richness is influenced by multiple environmental factors, although the ranking of importance of each variable is controversial [11,32,113–115]. Several hypotheses have been proposed to explain the mechanism of species diversity patterns, such as the ambient energy hypothesis, the water–energy dynamic hypothesis, the habitat heterogeneity hypothesis, and the freezing tolerance hypothesis (or tropical conservatism hypothesis) [116–120]. In the arid and semi-

arid areas of China, which hypothesis can explain the mechanism of species richness of Tenebrionidae remains to be tested.

To explore the relationship between species richness and environmental factors, many models are usually used for fitting [18,121]. The generalized linear models (GLMs) have been widely used, which have proved to be very useful tools for studying insect groups [122,123]. This model is an extension of the traditional linear model, which no longer requires continuous and normal dependent variables [124,125]. However, it requires that each independent variable and dependent variable must be linear [124]. Incidentally, the random forest model is a classifier used for classification and regression, which constructs a prediction model by sampling objects and variables [126,127]. It has many advantages, including the ability to measure the relative importance of variables to classification at the same time, using %IncMSE (increase in mean squared error) and IncNodePurity (increase in node purity) indexes [127]. The %IncMSE is detected by randomly assigning a value to each prediction variable to test the importance of the variable. If the prediction variable is more important, the model prediction error will increase after its value is randomly replaced [128]. The IncNodePurity is measured by the sum of squares of residuals [129]. In both indexes, the greater the value, the greater the importance of the variable; however, there are certain differences in the ranking of the two indexes [121]. Although the random forest model has strong universality, its results are often inaccurate when analyzing data with partial effect relationships [130,131]. Therefore, in this study, we used GLMs and random forest model to further clarify the influence of contemporary environmental factors on the species richness of Tenebrionidae in arid and semiarid areas of China, in order to establish a more comprehensive and accurate evaluation system.

Above all, in this study, the distribution data information of Tenebrionidae were collected in arid and semiarid areas of China, and the GLMs and random forest models were used to fit the species richness with contemporary environmental factors, aiming to: (1) summarize the species diversity of Tenebrionidae; (2) explore the diversity pattern and species richness center; and (3) estimate the correlation between the current environment and species richness.

2. Materials and Methods

2.1. Distribution Data

A total of 3610 distribution records of 696 species of Tenebrionidae in arid and semiarid areas of China were collected. The geographical distribution database was established for species of Tenebrionidae in arid and semiarid areas of China. Geographical information was collected mainly from publications [96,132–141], academic dissertations [94,97,101,139,142–147], specimens collection information (the Museum of Hebei University, China), and iNaturalist (<https://www.inaturalist.org/> (accessed on 15 July 2022)). Records with clear latitude and longitude information were used directly, while imprecise geographic records were corrected using Google Maps. Some provincial-level distribution information was excluded due to the large distribution range. Ultimately, the geographical distribution information of 550 species (3464 distribution records) was used in the subsequent analysis.

2.2. Environmental Variables

A total of 21 environmental variables were used to explore the impact of environmental factors on species diversity of Tenebrionidae in arid and semiarid areas of China [11,25,113,148,149]. The energy availability was represented by annual mean temperature (BIO1), mean diurnal range (mean of monthly (max temp–min temp)) (BIO2), isothermality (BIO2/BIO7) ($\times 100$) (BIO3), max temperature of warmest month (BIO5), min temperature of coldest month (BIO6), mean temperature of wettest quarter (BIO8), mean temperature of driest quarter (BIO9), mean temperature of warmest quarter (BIO10), and mean temperature of coldest quarter (BIO11). The water availability was represented by annual precipitation (BIO12), precipitation of wettest month (BIO13), precipitation of driest

month (BIO14), precipitation of wettest quarter (BIO16), precipitation of driest quarter (BIO17), precipitation of warmest quarter (BIO18), and precipitation of coldest quarter (BIO19). The climate stability was represented by temperature seasonality (standard deviation \times 100) (BIO4), temperature annual range (BIO5–BIO6) (BIO7) and precipitation seasonality (coefficient of variation) (BIO15) [11]. Habitat heterogeneity was represented by normalized difference vegetation index (NDVI) (1 km² resolution; data come from the Environment and Ecology Scientific Data Center of western China, National Natural Science Foundation, China <http://westdc.westgis.ac.cn> (accessed on 10 October 2022)) and elevation range (ELE). The nineteen bioclimatic variables in the global circulation model were downloaded from the WorldClim website (<http://www.worldclim.org> (accessed on 10 October 2022)) with a resolution of 2.5 min [150]. Elevation data were obtained at the WorldClim website with the resolution of 30 s.

2.3. Statistical Analysis

The geographic information database was imported into ArcGIS 10.2 (ESRI, Inc., Redlands, CA, USA). The presence (1) or absence (0) matrix was constructed for each species in 1° \times 1° grid cells, and 297 grids were found to have data distribution. The species accumulation curve was generated using the software EstimateS v9.1 [151]. Linear regression was used to assess the integrity of species richness within each grid, following previous methods [152,153].

GLMs were used to simulate the relationship between species richness and environmental factors [32,115,154]. The overdispersion in data was explained by GLMs with quasi-Poisson errors [155]. The explanatory power of each variable was estimated using the adjusted R^2_{adj} (%), which was calculated as follows: $R^2_{adj} (\%) = 100 \times (1 - (\text{residuals deviance}/\text{model DF})/(\text{species richness deviance}/\text{residuals DF}))$. To avoid the spatial autocorrelations inflating type I error, the modified *t*-test was used to determine the significance levels.

The random forest model was used to assess the relative importance of all variables for comparison with the GLMs results [11,18,32], since it was able to deal with nonlinear relationships between the variables [32,156,157]. The values of the relative importance of each environmental factor were obtained using R 4.2.1 (<http://www.r-project.org/> (accessed on 24 October 2022)), defined under the %IncMSE and IncNodePurity standard.

3. Results

3.1. Species Diversity

A total of 696 species, belonging to 125 genera of 38 tribes and 7 subfamilies, were recorded in arid and semiarid areas of China (Table S1). Among them, Blaptinae had the largest number of species (285 species, accounting for 40.9% of the total number), followed by Pimeliinae (246 species, 35.3%). At the generic level, the highest proportion was found in *Blaps* (61 species) and *Anatolica* (44 species), which accounted for 8.8% and 6.3% of all species, respectively. Some genera had only one species each in this area, such as *Mesomorphus*, *Mesomorphus*, *Pseudognaptorina*, *Thaumatoblaps*, *Hypsosoma*, etc.

3.2. Species Richness Pattern

In this study, species accumulation curves showed that sampling was adequate, and the data integrity was 86.3% (bootstrap mean approximately 643) (Figure 2A). The ratio of observed species richness to the expected by the linear regression models for each grid size was >64.2% (Figure 2B).

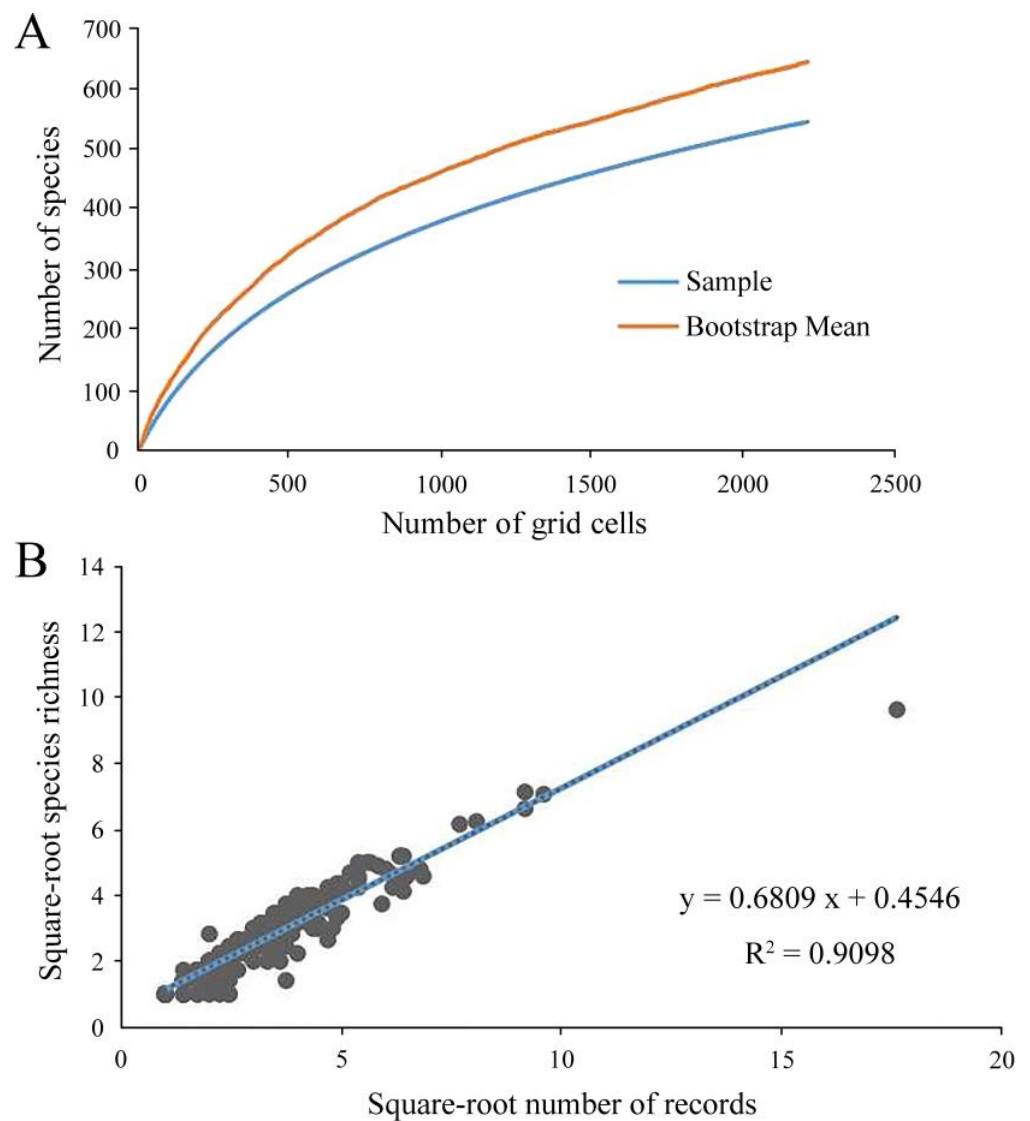


Figure 2. (A) Species accumulation curves for Tenebrionidae in arid and semiarid areas of China; (B) Linear regression ($y = 0.6809x + 0.4546$) for the number of records and species richness in the 1° grid size.

The species distribution of Tenebrionidae was relatively wide in the studied area. The species richness was higher in the Altai, Tianshan, Nyenchen Thanglha and Helan Mountains, but species were rarely distributed in the Tarim Basin, the Kunlun Mountains and the Turpan Basin (Figure 3).

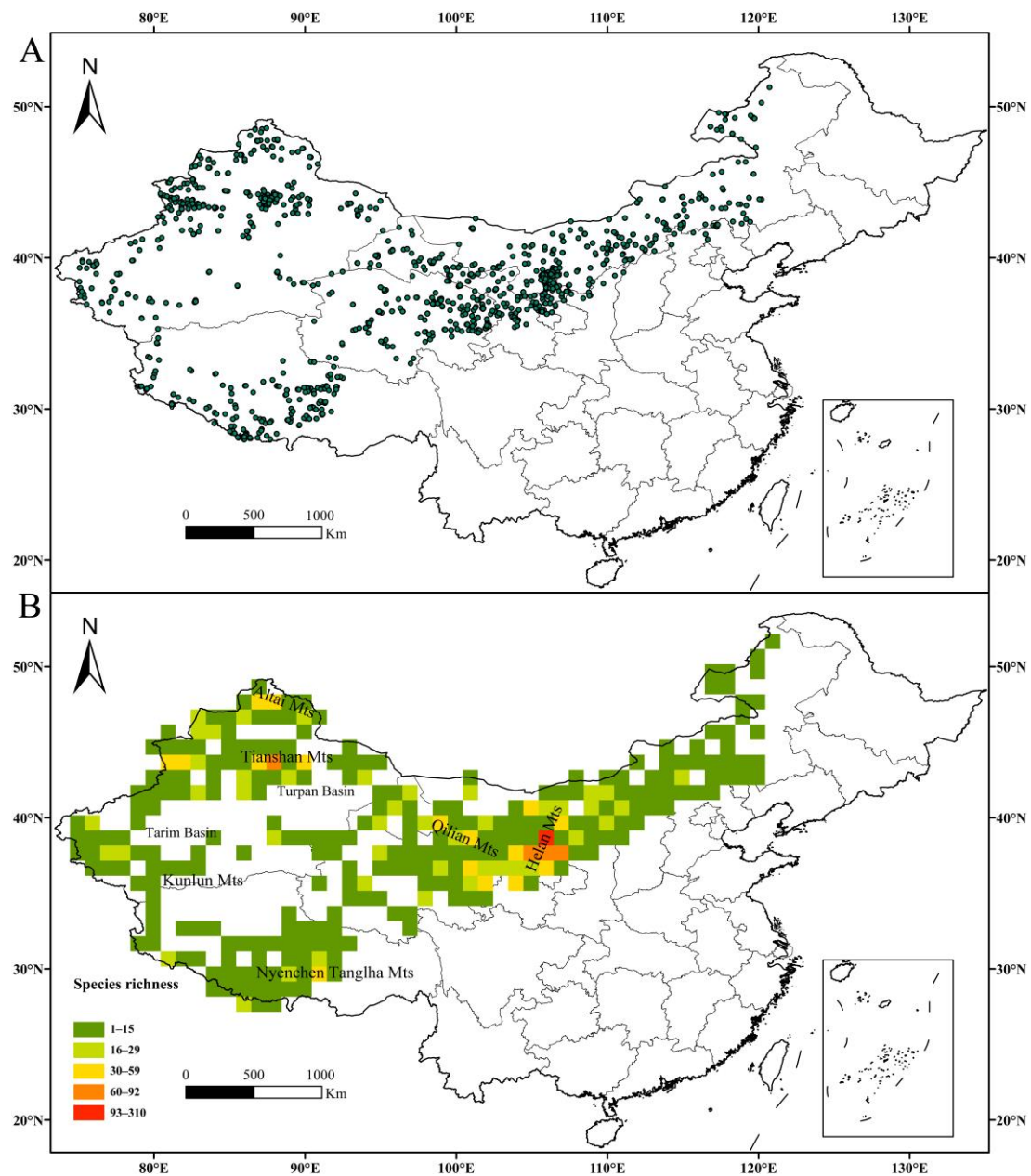


Figure 3. (A) Distribution records and (B) species richness patterns in 1° grid size of Tenebrionidae in arid and semiarid areas of China.

3.3. Relationships between Species Richness and Environmental Factors

The results of GLMs analysis showed that species richness of Tenebrionidae was affected by a variety of environmental variables (Table 1). Energy availability has the strongest explanatory power, followed by climate stability, compared with variables representing water availability and habitat heterogeneity (Table 1). Specifically, annual mean temperature (BIO1), mean temperature of warmest quarter (BIO10) and max temperature of warmest month (BIO5) accounted for 10.93% ($p < 0.001$), 9.68% ($p < 0.001$) and 9.27% ($p < 0.001$), respectively. Mean temperature of wettest quarter (BIO8), min temperature of coldest month (BIO6), mean temperature of coldest quarter (BIO11) and mean temperature of driest quarter (BIO9) explained 8.41% ($p < 0.001$), 7.89% ($p < 0.001$), 6.62% ($p < 0.001$), and 2.49% ($p = 0.037$), respectively. All of the seven variables above were positively correlated with species richness, except isothermality (BIO3) ($R^2_{\text{adj}} = 3.67$, $p = 0.011$) and mean diurnal range (BIO2) ($R^2_{\text{adj}} = 0.44$, $p > 0.1$), which also represented energy availability.

Among the variables representing climate stability, temperature annual range (BIO7) and temperature seasonality (BIO4) represented 2.80% ($p = 0.028$) and 2.50% ($p = 0.039$) explanatory power, respectively, and were positively correlated with species richness, while precipitation seasonality (BIO15) was not a significant factor, showing negative correlation and weak explanatory power. Some variables representing water availability and habitat heterogeneity had weak explanatory power ($R^2_{adj} < 2$), and were not significant predictors of species richness (Figure 4, Table 1).

Table 1. The generalized linear models (GLMs) used to evaluate the explanatory power of each environmental variable for species richness (R^2_{adj} , %).

	Environmental Variables	R^2_{adj}	p
Energy Availability	BIO1	10.93 (+) ***	<0.001
	BIO2	0.44 (−)	0.648
	BIO3	3.67 (−) **	0.011
	BIO5	9.27 (+) ***	<0.001
	BIO6	7.89 (+) ***	<0.001
	BIO8	8.41 (+) ***	<0.001
	BIO9	2.49 (+) **	0.037
	BIO10	9.68 (+) ***	<0.001
	BIO11	6.62 (+) ***	<0.001
	BIO12	0.79 (−)	0.345
Water Availability	BIO13	0.49 (−)	0.589
	BIO14	0.70 (−)	0.411
	BIO16	0.78 (−)	0.354
	BIO17	0.81 (−)	0.351
	BIO18	0.84 (−)	0.325
	BIO19	1.35 (−)	0.184
	BIO4	2.50 (+) **	0.039
Climate Stability	BIO7	2.80 (+) **	0.028
	BIO15	0.57 (−)	0.502
Habitat Heterogeneity	ELE	1.24 (−)	0.188
	NDVI	0.34 (−)	0.956

** $p < 0.05$; *** $p < 0.001$.

The results of the random forest method showed that there are some differences in the order of relative importance between the two indicators. In %IncMSE (Figure 5A), the first four variables affecting species richness were mean temperature of wettest quarter (BIO8), annual mean temperature (BIO1), temperature annual range (BIO7), and max temperature of warmest month (BIO5), which belong to energy availability and climate stability. Correspondingly, the top are water availability, energy availability and habitat heterogeneity in IncNodePurity (Figure 5B).

The overall analysis results showed that species richness of Tenebrionidae in arid and semiarid areas of China was affected by different factors. Inductively, energy availability and climate stability were the most important influencing factors.

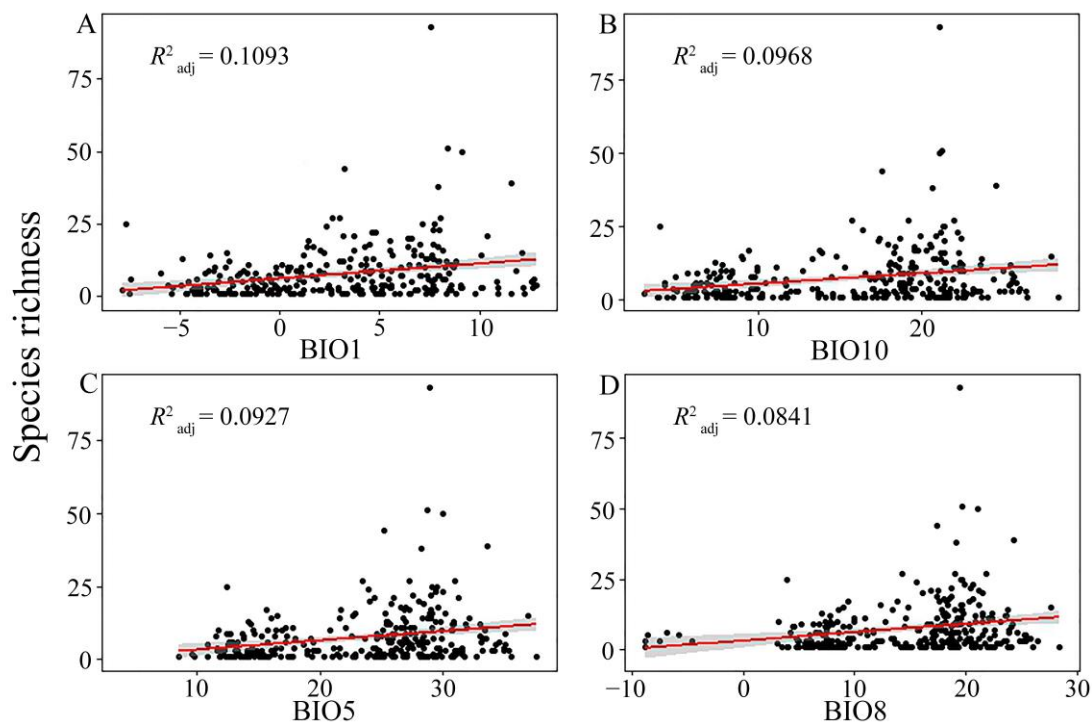


Figure 4. Relationship between species richness and the top four correlation variables based on the generalized linear models (GLMs). (A) BIO1, annual mean temperature; (B) BIO10, mean temperature of warmest quarter; (C) BIO5, max temperature of warmest month; (D) BIO8, mean temperature of wettest quarter.

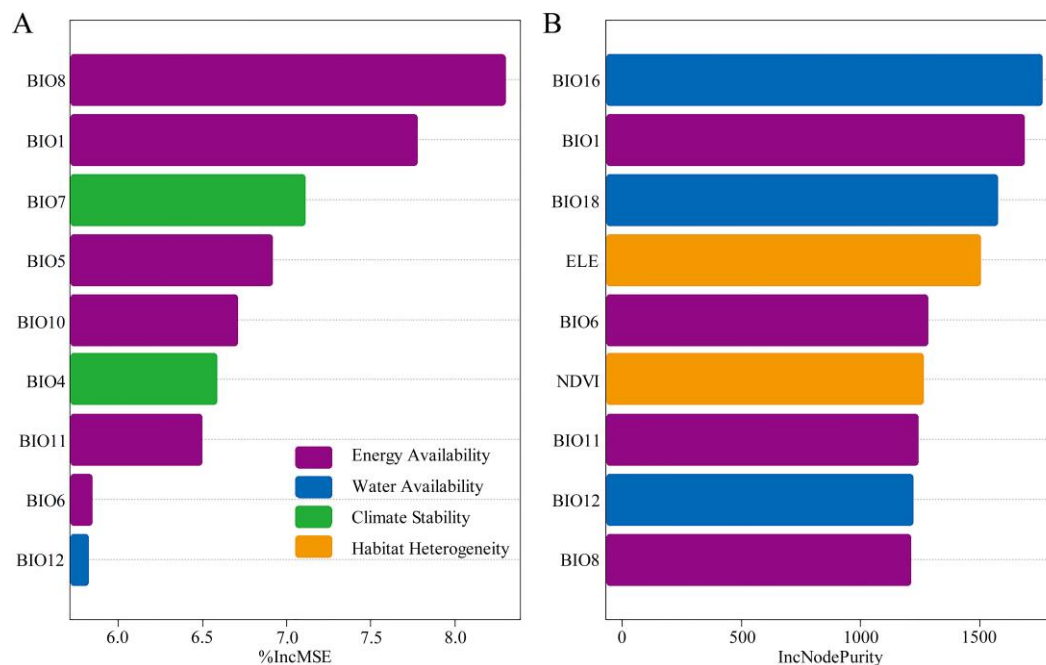


Figure 5. The importance of variables for species richness based on the random forest model by using (A) %IncMSE and (B) IncNodePurity.

4. Discussion

4.1. Species Diversity Pattern and Richness Centers

In general, the species richness centers of Tenebrionidae in arid and semiarid areas of China were located in the Altai, Tianshan, Nyenchen Thanglha and Helan Mountains. This is consistent with reports of plants [158], birds [159], and other insects [11,149,153,160].

The Altai Mountains are in the northern part of Xinjiang and run northwest to southeast [161,162]. They first appeared during the Caledonian movement and developed in the late neotectonics movement, with obvious continental climate characteristics [161,163]. The mountains have become a rainy area in Xinjiang due to their uplifting effect and are considered an important center of biodiversity [164].

The Tianshan Mountains have been strongly transformed by the remote effects of the Indo-Eurasian plate collision [165,166]. The Tianshan Mountain in China is the eastern part of the whole mountain system, which is the climatic divide between the northern and southern Xinjiang [167,168]. The different height gradients have created different geographical environments, which have provided varying conditions for the evolution of species [169,170].

The Nyenchen Thanglha Mountain is in the central and southern part of the QTP, which is the boundary between the sub-frigid zone and the temperate zone of plateau [171,172]. The Nyenchen Thanglha Mountain has been uplifting since the Middle Pleistocene, which is a response to the uplift of the QTP [173]. Elevations above 5000 m reduce the possibility of species exchange but provide a basis for new species to emerge [174,175].

The Helan Mountain, located at the boundary between temperate grassland and desert is strongly pressed by the northeastern margin of the QTP and becomes the last ecological barrier in northwest China [176,177]. The precipitation has obvious vertical differentiation phenomenon, and the vegetation has obvious change in the vertical zone, which is considered as a treasure house of mountain biodiversity with a complete vertical zone spectrum in the arid area [178–180].

The complex terrain of mountains often creates resistance to mass movement of species but it also facilitates the formation of new species [175,181]. The stable climates, diverse habitats and complex geological environment are generally considered major determinants of high biodiversity of species [105,182–184].

The four species richness centers revealed in this paper were all located in mountainous areas, which was consistent with the climate stability hypothesis [185]. The stable climate and the complex topography of the mountain region have led to the richness of the habitats of a series of species, which provides a favorable condition for high species richness [105,184]. Simultaneously, the adaptive evolution of the species in arid and semi-arid regions made it widely distributed in the study area [93,186,187]. However, due to the harsh environment and technical limitations, we cannot enter the hinterland of the desert and the uninhabited area in the QTP for collection. In addition, eastern Tibet, which is rich in biological resources, was not included in this study area [188,189].

4.2. Determinants of Variation in Species Richness

Species richness patterns are influenced by a combination of factors [190]. The results showed that energy availability had the strongest explanatory power for species richness, followed by climate stability.

Among the factors of energy availability, annual mean temperature (BIO1) has the strongest explanatory power. Higher temperatures produce favorable climatic conditions, which are conducive to the formation of new species and provide favorable conditions for species to evolve [32,191,192]. Other environmental factors representing energy availability also showed a strong influence on species richness, including BIO10, BIO5, BIO8, BIO6, BIO11 and BIO9. They may be related to temperature affecting the dispersal rate of species, which is consistent with the tropical conservatism hypothesis [120]. Simultaneously, some studies have shown that energy availability has a strong influence on species richness of plants [120,193], birds [194] and insects [11].

Climate stability influences biogeographic distribution to a great extent [11,32]. Temperature annual range (BIO7) and temperature seasonality (BIO4) had a positive correlation with and significant impact on species richness, and BIO7 ranked third in importance according to %IncMSE criteria. These results indicate that a stable climate is more suitable for the survival and evolution of the species of Tenebrionidae, because a stable climate

is conducive to the increase in ecological niches [195]. This is consistent with the climate stability hypothesis, which suggests that a stable climate will increase the species richness of an area [185].

Compared with energy availability and climate stability, water availability has weaker explanatory power. However, under the IncNodePurity standard, the importance ranking of the variable representing water availability was relatively high. This suggests that species richness patterns may be affected by both water and energy factors, which is consistent with the water–energy dynamics hypothesis [196].

Incidentally, habitat heterogeneity has a weak impact on species richness. This may be closely related to omnivores of the tenebrionid species and their high adaptability to special environments. In the hinterland of the QTP, it is very high in altitude, cold and dry with little vegetation [197]. The adaptive evolution of the Tenebrionidae is mainly toward the direction of resisting adverse ecological environment [198]. The main manifestations are dark body color and amplified elytron, and the lifestyle is usually terrestrial and clustered [93,198]. Meanwhile, the legs of ground active species are obviously elongated, while the legs of underground active species are obviously shortened [198]. In the low-altitude and bald desert, the adaptability of the Tenebrionidae is mainly reflected in the former amplified elytron combination, hind wing involution, the formation of the sub-elytral cavity, the variable legs, a well-developed tarsus, the activity of day and night, suspended animation and self-defense [93]. These features allow these species to overcome environmental resistance by storing water in their bodies and reducing the amount of ground they touch [93,94]. These changes in morphology, biology, and behavior improved the adaptation of tenebrionid beetles to the environment, so their distribution patterns are less restricted by vegetation and altitude.

5. Conclusions

In conclusion, this study is the first to investigate the species diversity, the species richness, and the impact of current environment on species richness of Tenebrionidae in arid and semiarid regions of China. A total of 696 species, belonging to 125 genera of 38 tribes and 7 subfamilies, were recorded in arid and semiarid areas of China. The non-uniform species richness pattern was presented, with more species in the Altai, Tianshan, Nyenchen Thanglha and Helan Mountains. The impact of current environmental variables on species richness was complex, among which variables representing energy availability and climate stability showed a strong influence. However, species richness may be influenced by both historical and current environments. We suggest further studies on the mechanisms underlying the species richness of Tenebrionidae in China, especially on its impact on endemic species in the context of historical climate. Targeted conservation programs will be proposed in the future to protect endemic species.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15010018/s1>, Table S1: A list of the species of Tenebrionidae in arid and semiarid areas of China; Table S2: Geographical distribution information on the species of Tenebrionidae in arid and semiarid areas of China.

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