# Species Diversity and Conservation of Typhlocybinae (Heteroptera: Cicadellidae) in China[1]

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**Abstract** Species diversity is undergoing rapid reductions globally. Identifying the causes underlying species diversity patterns and biodiversity hotspots is critical for developing conservation strategies. In this study, the 4,594 occurrence records of 854 Typhlocybinae (Heteroptera: Cicadellidae) species in China were used to investigate the factors affecting species richness and endemism patterns as well as identify species diversity hotspots to establish their conservation status. Generalized linear models and hierarchical partitioning were used to assess the effects of 6 environmental factors on species richness and endemism. Species diversity hotspots were obtained by integrating the 10 grids with highest levels of species richness and endemism; the conservation status of these hotspots was assessed via gap analysis. We found that species richness and endemism distribution of Typhlocybinae in China were heterogeneous, mainly concentrated in southern and central areas. The results also showed that plants were the most important environmental factors affecting species richness and endemism patterns, followed by niche conservatism. The 10 hotspots were identified; however, they were not fully protected by the existing nature reserves. This study highlights the importance of plants and niche conservatism in shaping species richness and endemism patterns of Typhlocybinae. Moreover, establishment of new nature reserves in hotspot areas with a conservation gap is required.

**Key Words** conservation gap, endemism, biodiversity hotspots, species richness, Typhlocybinae

Species richness and endemism are important species diversity indices and have frequently been found to vary greatly among different regions (Bystriakova et al. 2018, Gaston 2000, López-Pujol et al. 2011, Li et al. 2017, Stevenson et al. 2013, Zhao et al. 2021a). Identifying the factors affecting species richness and endemism patterns is one of the main goals of ecology and conservation (Gaston 2003, Liu et al. 2017, Ricklefs 2004). Numerous studies have reported that different types of factors influence the patterns of species richness and endemism (Diniz-Filho et al. 2013, Fine 2015, Hawkins and Porter 2003, Qian et al. 2007). These factors can be grouped into evolutionary (e.g., niche conservatism) and ecological (e.g., temperature, water availability, topographic heterogeneity). However, despite the emergence of theoretical advancement and a growing number of studies in the last few decades, there is no consensus on the relative importance of different types of factors in explaining species richness and

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endemism patterns (Wang et al. 2011, Wang et al. 2017), especially for insects. It is generally recognized that the spatial patterns in species richness and endemism are jointly driven by different types of factors, some of which play a vital role (Lyu et al. 2020, Yan et al. 2013, Zhao et al. 2020a).

To effectively protect species, conservationists frequently focus on species diversity hotspots (regions where species diversity is extremely high) (Huang et al. 2016, Marchese 2015, Zhang et al. 2021, Zhao et al. 2023) because this maximizes the use of limited conservation resources. Several species diversity indices have been used to identify biodiversity hotspots, such as endemism, total species, and threatened species (Chi et al. 2017, Myers et al. 2000, Noroozi et al. 2019a, Zhang et al. 2015). Identifying hotspots based on different species diversity indices is required if different types of species are to be protected. Establishment of protected areas is considered to be the most effective measure for protecting species (Grenyer et al. 2006, Primack 2014). Unfortunately, using gap analysis, a large number of studies have shown that the existing protected areas are not effective in protecting biodiversity hotspots, especially in a country like China where there is an extremely rich species diversity (Chi et al. 2017, Huang et al. 2016, Liu et al. 2018, Qin et al. 2019). Therefore, finding conservation gap areas within biodiversity hotspots and establishing completely protected areas within those areas are essential for the current conservation strategies.

The family Cicadellidae comprises by far the largest family in the Hemiptera in terms of species number. The members of this family are ideal for investigating grassland ecology and conservation, evaluating the conservation status of sites, monitoring environmental change, and studying the biogeography (Biedermann et al. 2005, Hamilton et al. 2010, Nielson and Knight 2000, Nielson et al. 2000, Trivellone et al. 2012). The Typhlocybinae has the second largest number of species and is the most evolved subfamily in the family Cicadellidae, with its members having a short body length (2–4 mm) (Lin et al. 2021). The members of Typhlocybinae mainly feed on leaf parenchymal cell contents of various plants, such as trees, shrubs, and herbaceous plants (Yan et al. 2022, Yuan et al. 2014). The Typhlocybinae occupy diverse ecological niches and are distributed worldwide. China is one of the countries with the largest number of Typhlocybinae species, accounting for approximately 17% of the total global species count. A previous study identified endemism centers and explored the factors that drive the congruence between species richness and endemism patterns (Yuan et al. 2014). Unfortunately, this study had some shortcomings. For example, it only quantitatively analyzed the effects of precipitation and temperature on species diversity patterns and did not assess the conservation status of species. Therefore, the driving factors of species diversity patterns and conservation status of the subfamily Typhlocybinae need to be further investigated.

In this study, using distributed data of the subfamily Typhlocybinae in China, we aimed to explore the main driving factors that shape species richness and endemism patterns and assess the conservation status of species diversity hotspots.

## Materials and Methods

**Species distribution data.** We collected 4,594 occurrence records of 854 Typhlocybinae species in China based on the study of Li et al. (2021), published references, and the Global Biodiversity Information Facility (https://www.gbif.org).

**Table 1. Six environment data categories and their related environmental variables.**

| Categories | Environmental variables |
|---|---|
| Temperature | Mean annual temperature (MAT) |
| | Annual potential evapotranspiration (PET) |
| Niche conservatism | Mean temperature of coldest quarter (MTCQ) |
| Water availability | Mean annual precipitation (MAP) |
| | Annual actual evapotranspiration (AET) |
| Plants | Deciduous broadleaf trees (DBT) |
| | Evergreen broadleaf trees (EBT) |
| | Herbaceous vegetation (HV) |
| | Shrubs (SH) |
| Habitat heterogeneity | Elevation range (ER) |
| | Slope (SP) |
| | Range of the MAT (MATR)<br>Range of the MAP (MAPR) |
| Historical climate change | MAT change since the last glacial maximum (MATC) |
| | MAP change since the last glacial maximum (MAPC) |

A 100 × 100-km grid size was used to map species richness and endemism patterns due to its appropriateness for richness–environment relationship assessment and resolution of the occurrence records. In a 100 × 100-km grid, species richness is indicated by the species number, and endemism is measured by weighted endemism, based on equation (1) (Linder 2001).

$$\text{Weighted endemism} = \sum 1/M_{\mathrm{i}} \tag{1}$$

where $M_{\mathrm{i}}$ is the number of grids occupied by each species.

**Environmental data.** Fifteen environmental variables were grouped into 6 categories (Table 1): (1) temperature: mean annual temperature (MAT) and annual potential evapotranspiration (PET); (2) niche conservatism: mean temperature of coldest quarter (MTCQ); (3) water availability: mean annual precipitation (MAP) and annual actual evapotranspiration (AET); (4) plants: deciduous broadleaf trees (DBT), evergreen broadleaf trees (EBT), herbaceous vegetation (HV), and shrubs (SH); (5) habitat heterogeneity: elevation range (ER), slope (SP), range of MAT (MATR), and range of MAP (MAPR); and (6) historical climate change: MAT change since the last glacial maximum (MATC) and MAP change since the last glacial maximum (MAPC). ER, MATR, and MATR are the differences between the maximum and minimum values in the 100 × 100-km grid. MATC and MAPC in the 100 × 100-km grid was defined as the absolute value of the differences in MAT and MAP between modern and last glacial maximum (LGM), respectively, and were calculated using the following equation (2):

$$\text{MATC} = |\text{modern}_{\text{MAT}} - \text{LGM}_{\text{MAT}}| \text{ and } \text{MAPC} = |\text{modern}_{\text{MAP}} - \text{LGM}_{\text{MAP}}| \quad (2)$$

The remaining variables in the 100 × 100-km grid were calculated as the averages of the pixels within that grid using ArcGIS 10.7 (Esri, Redlands, CA).

PET and AET at 30 arc-seconds were downloaded from the CGIAR-CSI database (http://www.cgiar-csi.org). Four environment variables from plants were obtained from global 1-km consensus land-cover data created by Tuanmu and Jetz (2014). Other related environment data were obtained from the WorldClim database (http://www.worldclim.org) with a spatial resolution of 30 arc-seconds (except for MAT and MAP in the LGM at 2.5 min).

**Data analysis.** Assessing geographical sampling bias is the first step in macroecological pattern analyses and inferences, and the regions with a high degree of sampling bias should be excluded (Yang et al. 2013). Therefore, an ordinary least squares (OLS) model using the squared-root transformed number of records as a predictor variable and squared-root transformed numbers of richness as a response variable was developed for a 100 × 100-km grid size. Grids with observed richness $<70\%$ of the expected richness obtained from the OLS model were excluded from the analyses (Romo and García-Barros 2010, Sánchez-Fernández et al. 2008, Zhao et al. 2023). We used generalized linear models (GLMs) with quasi-Poisson residuals to analyze the relationships between species richness/endemism and each environment variable. The modified t-tests were used to assess the significance of OLS and GLMs (Dutilleul et al. 1993). Moreover, we performed hierarchical partitioning to assess the relative roles of each environmental variable and determine the key environmental categories influencing species richness and endemism. Hierarchical partitioning can identify the most likely causal factors and effectively alleviate collinearity (Chevan and Sutherland 1991, Olea et al. 2010). However, its use is not recommended when the number of explanatory variables is $>9$ (Olea et al. 2010). To overcome this challenge, we excluded the insignificant variables in GLMs and the lowest $R^2$ value variables until the number of environment variables was 9. The relative role of each environment variable was determined based on its independent effects. All analyses were performed using R package 4.2.1 with the lm and glm functions and hier.part and SpatialPack packages.

We selected the top 10 grids with highest species richness and endemism as species richness and endemism hotspot areas, respectively (Noroozi et al. 2019b). These grids were then integrated to obtain species diversity hotspots. Gap analysis was used to assess the conservation status of the species diversity hotspots. In particular, the species diversity hotspot layer was overlaid with the nature reserves layer, and the conservation gap was determined as the hotspot grids with a nature reserve coverage of $<10\%$ of the grid area (Xu et al. 2017). The map of the nature reserve was obtained from the National Earth System Science Data Center (http://www.geodata.cn/) and Protected Planet (https://www.protectedplanet.net).

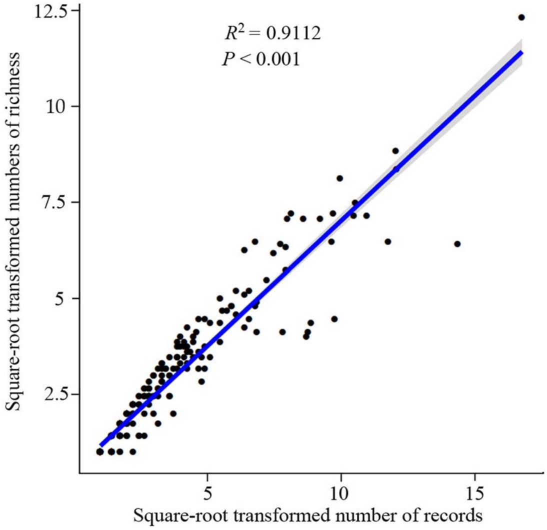

**Fig. 1. Ordinary least squares models (OLS) (y = 0.652x + 0.503) for the number of records and species richness.**

## Results

**Species diversity patterns.** Based on the constructed OLS model (Fig. 1), 13 grids were under-sampled and, therefore, these grids were removed. Overall, the species richness and endemism distribution of Typhlocybinae in China was heterogeneous. In particular, species richness and endemism were concentrated in southern and central China and was lower in northern China (Fig. 2a, b).

**Species richness–environment relationships.** Results of GLMs show that PET, DBT, and MAPC were not significant for species richness. HV and MATC were negatively associated with species richness (Table 2). The other environmental variables were positively correlated with species richness (Table 2). Furthermore, PET, DBT, HV, MATC, and MAPC were not significant for weighted endemism (Table 2). The remaining environmental variables were positively associated with weighted endemism (Table 2).

Hierarchical partitioning revealed the effects of environmental variables of different categories on species richness and weighted endemism (Fig. 3a, b). Plants (EBT) had the greatest influence on species richness and weighted endemism, followed by niche conservatism (MTCQ) (Fig. 3a, b). The next most important environment variables for species richness and weighted endemism were temperature (MAT) and habitat heterogeneity (ER) (Fig. 3a, b). Water availability (MAP and AET) had little effect on species richness and weighted endemism. Historical climate change also exerted a low effect on species richness (MATC) (Fig. 3b).

**Species diversity hotspots and conservation.** Based on the hotspot analysis, 10 species diversity hotspots located in central and southern China were identified (Fig. 4): south Yunnan (No. 1), northwest Yunnan (No. 2), central Sichuan

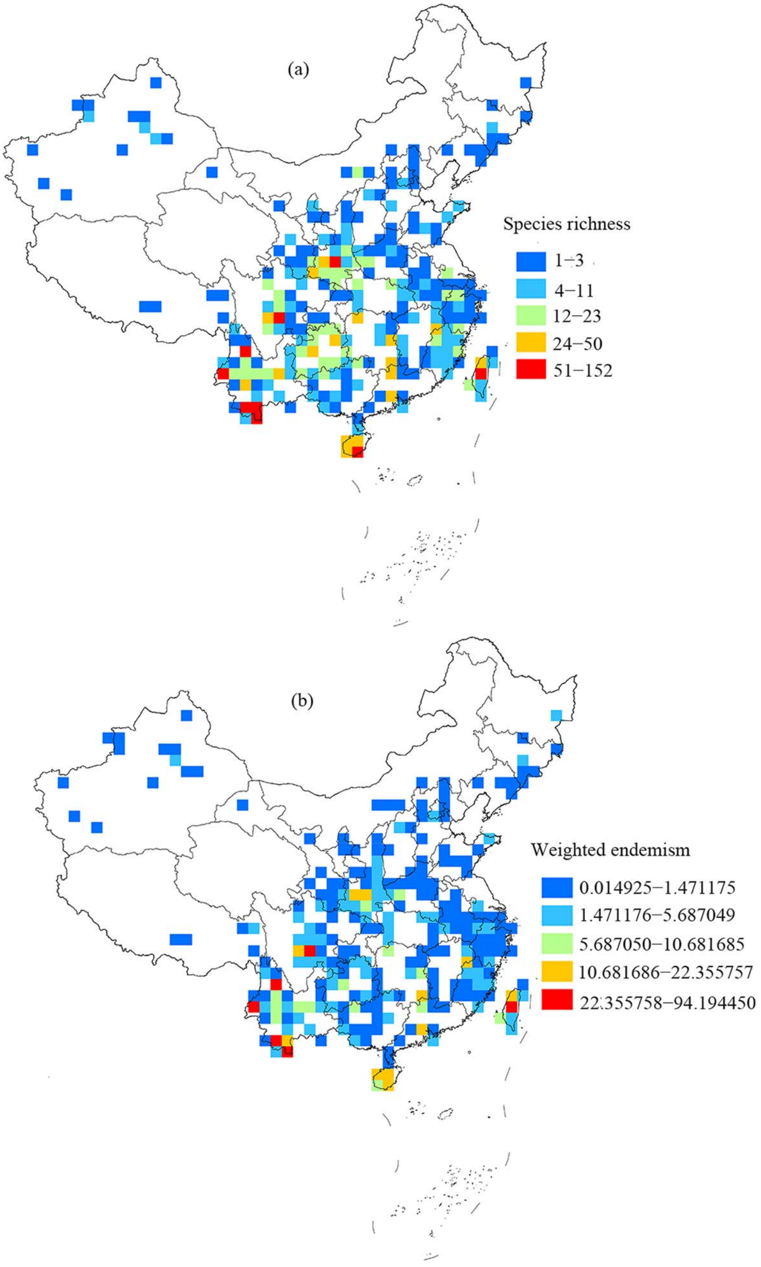

**Fig. 2. Patterns of species richness (a) and weighted endemism (b) of Typhlocybinae in China.**

**Table 2. Relationship between species richness/weighted endemism and each environmental variable obtained from GLMs.**

| Environmental Variables | Species Richness | | Weighted Endemism | |
|---|---|---|---|---|
| | *r* | $R^2$ (%) | *R* | $R^2$ (%) |
| MAT | 0.079** | 10.61 | 0.102* | 10.34 |
| PET | 0 ns | 0 | 0 ns | 0.57 |
| MTCQ | 0.073** | 19.10 | 0.101** | 21.07 |
| MAP | 0.000** | 9.26 | 0** | 11.54 |
| AET | 0.001** | 12.26 | 0.002* | 10.51 |
| DBT | 0.019 ns | 0.61 | 0.026 ns | 0.76 |
| EBT | 0.035** | 18.91 | 0.048** | 26.22 |
| HV | −0.026* | 5.92 | −0.026 ns | 3.76 |
| SH | 0.105** | 19.05 | 0.128** | 18.28 |
| ER | 0** | 5.79 | 0** | 8.47 |
| SP | 0.1** | 7.13 | 0.138** | 9.24 |
| MATR | 0.047** | 4.44 | 0.073** | 7.25 |
| MAPR | 0** | 9.26 | 0** | 11.54 |
| MATC | −0.267* | 10.74 | −0.234 ns | 5.21 |
| MAPC | −0.001 ns | 0.58 | −0 ns | 0.22 |

* $P < 0.1$; ** $P < 0.05$; ns, not significant.

(No. 3), Qinling Mountains (No. 4), eastern Yungui Plateau (No. 5), eastern Hunan (No. 6), eastern Wuyi Mountains (No. 7), Taiwan Island (No. 8), southern Guangdong (No. 9), and Hainan Island (No. 10). Furthermore, the gap analysis showed that the grids of the hotspots were not effectively covered by the existing nature reserves, i.e., there were conservation gaps (Fig. 4).

## Discussion

The findings of the present study indicated that plants are the most important environmental variables affecting species richness and endemism of Typhlocybinae in China. This result is reasonable, considering that Typhlocybinae are herbivorous insects. Plants can influence the species diversity of Typhlocybinae by providing them with food sources and different habitats (Yuan et al. 2014). Although a previous study stated that plants play an important role in driving the species diversity patterns of Typhlocybinae in China, it failed to test this quantitatively. The results of the present study provide a strong statistical answer (Fig. 3) and, thus, indicate that the plant variable must be considered when investigating the key causes of species diversity patterns of Typhlocybinae within a region. Several studies have claimed

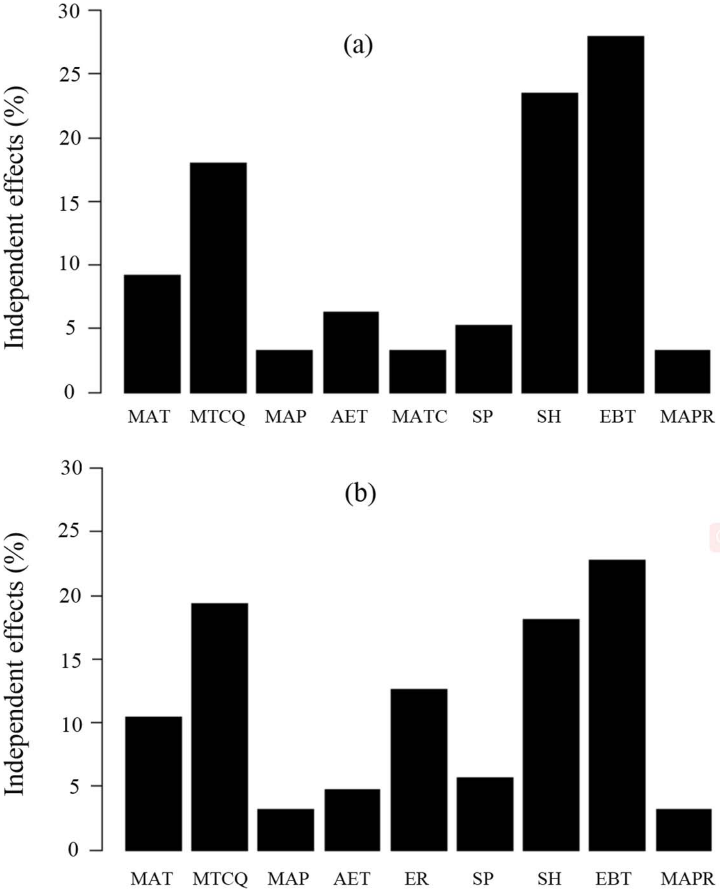

**Fig. 3. Independent effects of each environmental variable for species richness (a) and weighted endemism (b).**

that the distribution of vegetation in China will shift under the influence of climate change (Wang et al. 2017, Weng and Zhou 2006, Zhao and Wu 2014). In this case, it can be expected that the species diversity patterns of Typhlocybinae may also shift in the future accordingly.

The relationship between species diversity and modern climate reflects the impact of the evolutionary history on species distribution patterns (Ricklefs 2006, Rohde 1992). The niche conservatism hypothesis claims that species tend to retain the niche of their ancestors, making it difficult to evolve in response to new physiological tolerances (e.g., winter coldness) (Harrison and Grace 2007, Wiens 2004, Wiens et al. 2010). If the climate conditions in a region differ greatly from the ancestral niche of the clade, the species diversity in the region is reduced due to the limited colonization caused by niche conservatism. Accordingly, the species diversity was high in a region where climatic conditions were similar to those of the ancestral niche (Wiens 2004, Wiens et al. 2010). A recent study showed that

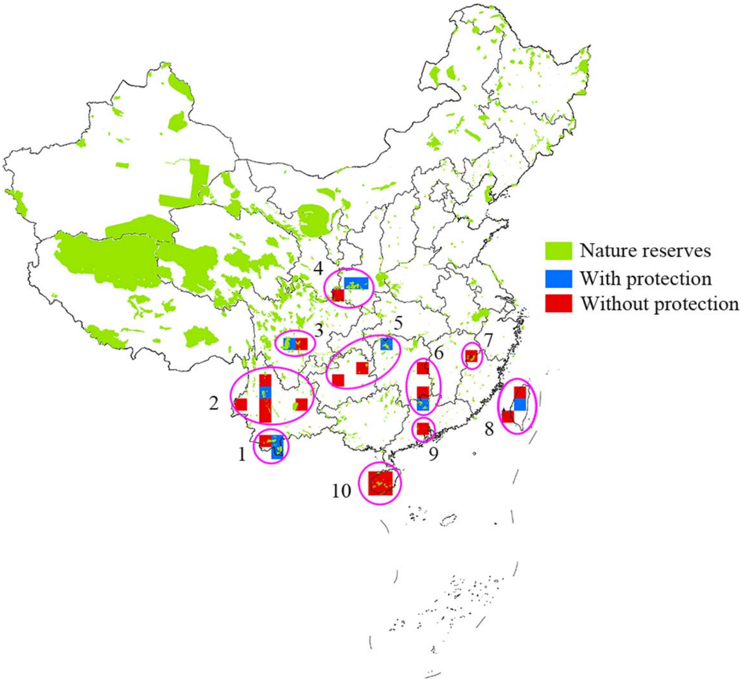

**Fig. 4. Species diversity hotspots and conservation status.**

Typhlocybinae originated during the middle Cretaceous period (Yan et al. 2022), and the temperature during this period was high, indicating that this group is suitable for living in tropical climate conditions. Therefore, from the viewpoint of the niche conservatism hypothesis, southern China, where the temperature in winter is higher, had a higher Typhlocybinae species richness and endemism than northern China, where the temperature in winter is lower (Fig. 2).

Numerous studies have found that temperature is closely related to the formation of species diversity patterns, with high species diversity observed in high temperature regions (Chen et al. 2011, Luo et al. 2012, Qian 2010, Qian and Xiao 2012). This result is consistent with the findings of the present study. Temperature affects species diversity by affecting physiological activities (Wang et al. 2009). China's topography is complex, with towering mountains, basins of various sizes, undulating plateaus and hills, and fertile plains (Meng et al. 2008). Furthermore, it is characterized by a wide range of climate variation (Qian 2013). However, our study found that, although habitat heterogeneity was positively related to species richness and endemism of Typhlocybinae, it was not a dominant factor. The relative importance of temperature and water availability in the formation of species diversity patterns has been widely discussed over the past few decades, but no consistent results have been obtained (Chen et al. 2011, Liu et al. 2022, Lü et al. 2018, Xu et al. 2016). Our study indicated that temperature was more important than water availability for species richness and endemism patterns of Typhlocybinae in China. This is likely related to the fact that these insects are terrestrial organisms. A previous study declared that historical climate change dominated the diversity patterns of planthoppers in China (Zhao et al. 2020b) Nevertheless, our study found that historical climate change had a low impact on the Typhlocybinae species richness. This difference shows that, even within the same region, the dominant factor may vary between groups in shaping the species diversity patterns.

A large number of events (e.g., climate change and habitat loss) have resulted in a significant decrease in the number of insects at many different places worldwide (Cardoso et al. 2020, Dicks et al. 2021, Van Klink et al. 2020, Wagner et al. 2021), which has prompted conservationists to pay greater attention to the conservation of insects. In China, the number of insects far exceeds that of plants, but the corresponding conservation research is less than that of plants. Identifying species diversity hotspots is extremely important for insect conservation because they provide a cost-effective conservation solution. The 10 species diversity hotspots of Typhlocybinae obtained in our study host high species richness and endemism. Therefore, these hotspots should be given priority for conservation. Unfortunately, 20 out of a total of 29 (68.96%) hotspot grids were not effectively covered by the existing nature reserves, thereby showing significant conservation gaps and indicating that the Typhlocybinae are not effectively protected. Furthermore, it was found that each hotspot had a different degree of conservation gap. For example, all grids belonging to Hainan are not covered by the existing nature reserves. One of the three grids in southern Yunnan was not covered by the existing nature reserves. Given that the protected areas are a key tool to protect species, establishment of nature reserves in conservation gap areas is urgently required for effective conservation of Typhlocybinae. Consistent with our results, previous studies have also found significant conservation gaps in other insect taxa in China, such as true bugs (Jiang et al. 2022). These results imply that China's nature reserves may not be adequately protecting insects, and further research is required to confirm this in the future.

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## References Cited

**Biedermann, R., R. Achtziger, H. Nicke and A.J.A. Stewart. 2005.** Conservation of grassland leafhoppers: a brief review. J. Insect Conserv. 9: 229−243.

**Bystriakova, N., T. Griswold, J.S. Ascher and M. Kuhlmann. 2017.** Key environmental determinants of global and regional richness and endemism patterns for a wild bee subfamily. Biodivers. Conserv. 27: 287−309.

**Cardoso, P., P.S. Barton, K. Birkhofer, F. Chichorro, C. Deacon, T. Fartmann, C.S. Fukushima, R. Gaigher, J.C. Habel and C.A. Hallmann. 2020.** Scientists' warning to humanity on insect extinctions. Biol. Conserv. 242: 108426.

**Chen, S.B., G.M. Jiang, Z.Y. Ouyang, W.H. Xu and Y. Xiao. 2011.** Relative importance of water, energy, and heterogeneity in determining regional pteridophyte and seed plant richness in China. J. Syst. Evol. 49: 95−107.

**Chevan, A. and M. Sutherland. 1991.** Hierarchical partitioning. Am. Stat. 45: 90–96.

**Chi, X.L., Z.J. Zhang, X.T. Xu, X.B. Zhang, Z.P. Zhao, Y.N. Liu, Q.G. Wang, H. Wang, Y. Li and G. Yang. 2017.** Threatened medicinal plants in China: Distributions and conservation priorities. Biol. Conserv. 210: 89−95.

**Dicks, L.V., T.D. Breeze, H.T. Ngo, D. Senapathi, J. An, M.A. Aizen, P. Basu, D. Buchori, L. Galetto, L. Garibaldi, B. Gemmill-Herren, B.G. Howlett, V. L. Imperatriz-Fonseca, S.D. Johnson, A. Kovács-Hostyánszki, Y.J. Kwon, H.M.G. Lattorff, T. Lungharwo, C.L. Seymour, A.J. Vanbergen and S.G. Potts. 2021.** A global-scale expert assessment of drivers and risks associated with pollinator decline. Nat. Ecol. Evol. 5: 1453−1461.

**Diniz-Filho, J.A.F., S. Ceccarelli, W. Hasperué, J. Rabinovich, S.R. Leather and J.M. Lobo. 2013.** Geographical patterns of Triatominae (Heteroptera: Reduviidae) richness and distribution in the Western Hemisphere. Insect Conserv. Diver. 6: 704−714.

**Dutilleul, P., P. Clifford, S. Richardson and D. Hemon. 1993.** Modifying the t test for assessing the correlation between two spatial processes. Biometrics 49: 305–314.

**Fine, P.V.A. 2015.** Ecological and evolutionary drivers of geographic variation in species diversity. Annu. Rev. Ecol. Evol. S. 46: 369−392.

**Gaston, K.J. 2000.** Global patterns in biodiversity. Nature 405: 220−227.

**Gaston, K.J. 2003.** The Structure and Dynamics of Geographic Ranges. Oxford Univ. Press, Oxford, UK.

**Grenyer, R., C.D. Orme, S.F. Jackson, G.H. Thomas, R.G. Davies and T.J. Davies. 2006.** Global distribution and conservation of rare and threatened vertebrates. Nature 444: 93–96.

**Hamilton, K.A. and R.F. Whitcomb. 2010.** Leafhoppers (Homoptera: Cicadellidae): A major family adapted to grassland habitats, Pg. 169–197. *In* Shorthouse, J.D. and K.D. Floate (eds.), Arthropods of Canadian Grasslands. Biological Survey of Canada, Yukon, Canada.

**Harrison, S. and J.B. Grace. 2007.** Biogeographic affinity helps explain productivity-richness relationships at regional and local scales. Am. Nat. 170: 5–15.

**Hawkins, B.A. and E.E. Porter. 2003.** Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. Glob. Ecol. Biogeogr. 12: 475−481.

**Huang, J.H., J.H. Huang, C.R. Liu, J.L. Zhang, X.H. Lu and K.P. Ma. 2016.** Diversity hotspots and conservation gaps for the Chinese endemic seed flora. Biol. Conserv. 198: 104−112.

**Jiang, K., X. Dong, J.Q. Zhang, Z. Ye, H.J. Xue, G.P. Zhu and W.J. Bu. 2022.** Diversity and conservation of endemic true bugs for four family groups in China. Divers. Distrib. 28: 2824−2837.

**Li, J.J., Q. Li, Y. Wu, L. Ye, H. Liu, J.F. Wei and X.L. Huang. 2021.** Mountains act as museums and cradles for hemipteran insects in China: Evidence from patterns of richness and phylogenetic structure. Global Ecol. Biogeogr. 30: 1070−1085.

**Li, Y., J. Chen, L.Y. Jiang and G.X. Qiao. 2017.** Islands conserve high species richness and areas of endemism of Hormaphidinae aphids. Curr. Zool. 63: 623−632.

**Lin, S., M. Huang and Y. Zhang. 2021.** Structural features and phylogenetic implications of 11 new mitogenomes of Typhlocybinae (Hemiptera: Cicadellidae). Insects 12: 678.

**Linder, H.P. 2001.** Plant diversity and endemism in sub-Saharan tropical Africa. J. Biogeogr. 28: 169−182.

**Liu, B., M. Zhang, W.R. Bussmann, H.M. Liu, Y.Y. Liu, Y.D. Peng, K.L. Zu, Y.M. Zhao, Z.B. Liu and S.X. Yu. 2018.** Species richness and conservation gap analysis of karst areas: A case study of vascular plants from Guizhou, China. Glob. Ecol. Conserv. 16: e00460.

**Liu, L., X.T. Xu, L. Zhang, Y.Q. Li, N. Shrestha, D.M. Neves, Q.G. Wang, H. Chang, X.Y. Su, Y.P. Liu, J.Y. Wu, D. Dimitrov, Z.H. Wang, J.Q. Liu and K.P. Ma. 2022.** Global patterns of species richness of the Holarctic alpine herb Saxifraga: the role of temperature and habitat heterogeneity. J. Plant Ecol. 15: 237−252.

**Liu, Y.P., Z.H. Shen, Q.G. Wang, X.Y. Su, W.J. Zhang, N. Shrestha, X.T. Xu and Z.H. Wang. 2017.** Determinants of richness patterns differ between rare and common species: implications for Gesneriaceae conservation in China. Divers. Distrib. 23: 235−246.

**López-Pujol, J., F.M. Zhang, H.Q. Sun, T.S. Ying and S. Ge. 2011.** Centres of plant endemism in China: places for survival or for speciation? J. Biogeogr. 38: 1267−1280.

**Lü, L.S., H.Y. Cai, Y. Yang, Z.H. Wang and H. Zeng. 2018.** Geographic patterns and environmental determinants of gymnosperm species diversity in China. Biodivers. Sci. 26: 1133–1146.

**Luo, Z.H., S.H. Tang, C.W. Li, H.X. Fang, H.J. Hu, J. Yang, J.J. Ding and Z.G. Jiang. 2012.** Environmental effects on vertebrate species richness: testing the energy, environmental stability and habitat heterogeneity hypotheses. PLoS One 7: e35514.

**Lyu, Y.M., X.P. Wang and J.C. Luo. 2020.** Geographic patterns of insect diversity across China's nature reserves: The roles of niche conservatism and range overlapping. Ecol. Evol. 10: 3305−3317.

**Marchese, C. 2015.** Biodiversity hotspots: A shortcut for a more complicated concept. Glob. Ecol. Conserv. 3: 297−309.

**Meng, K., S.Q. Li and R.W. Murphy. 2008.** Biogeographical patterns of Chinese spiders (Arachnida: Araneae) based on a parsimony analysis of endemicity. J. Biogeogr. 35: 1241–1249.

**Myers, N., R.A., Mittermeier, C.G. Mittermeier, G.A. da Fonseca and J. Kent. 2000.** Biodiversity hotspots for conservation priorities. Nature 403: 853−858.

**Nielson, M.W. and W.J. Knight. 2000.** Distributional patterns and possible origin of leafhoppers (Homoptera, Cicadellidae). Revta. Bras. Zool. 17: 81−156.

**Nielson, M.W., W.J. Knight and Y. Zhang. 2000.** Distributional patterns and possible origins of the tribes and genera of Coelidiinae (Homoptera, Membracoidea, Cicadellidae). Revta. Bras. Zool. 17: 915−940.

**Noroozi, J., A. Naqinezhad, A. Talebi, M. Doostmohammadi, C. Plutzar, S.B. Rumpf, Z. Asgarpour and G.M. Schneeweiss. 2019a.** Hotspots of vascular plant endemism in a global biodiversity hotspot in Southwest Asia suffer from significant conservation gaps. Biol. Conserv. 237: 299−307.

**Noroozi, J., G. Zare, M. Sherafati, M. Mahmoodi, D. Moser, Z. Asgarpour and G.M. Schneeweiss. 2019b.** Patterns of endemism in Turkey, the meeting point of three global biodiversity hotspots, based on three diverse families of vascular plants. Front. Ecol. Evol. 7: 159.

**Olea, P.P., P. Mateo-Tomás and Á.de Frutos. 2010.** Estimating and modelling bias of the hierarchical partitioning public-domain software: implications in environmental management and conservation. PLoS One 5: e11698.

**Primack, R.B. 2014.** Essentials of Conservation Biology, 5th Ed. Sinauer Associates, Sunderland, MA.

**Qian, H. 2010.** Environment–richness relationships for mammals, birds, reptiles, and amphibians at global and regional scales. Ecol. Res. 25: 629−637.

**Qian, H. 2013.** Environmental determinants of woody plant diversity at a regional scale in China. PLoS One 8: e75832.

**Qian, H., P.S. White and J.S. Song. 2007.** Effects of regional vs. ecological factors on plant species richness: an intercontinental analysis. Ecology 88: 1440−1453.

**Qian, H. and M. Xiao. 2012.** Global patterns of the beta diversity–energy relationship in terrestrial vertebrates. Acta Oecol. 39: 67−71.

**Qin, F., T.T. Xue, X.D. Yang, W.D. Zhang, J.Y. Wu, Y.F. Huang, G. Khan and S.X. Yu. 2022.** Conservation status of threatened land plants in China and priority sites for better conservation targets: distribution patterns and conservation gap analysis. Biodivers. Conserv. 31: 2063−2082.

**Ricklefs, R.E. 2004.** A comprehensive framework for global patterns in biodiversity. Ecol. Lett. 7: 1–15.

**Ricklefs, R.E. 2006.** Evolutionary diversification and the origin of the diversity-environment relationship. Ecology 87: S3–S13.

**Rohde, K. 1992.** Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65: 514–527.

**Romo, H. and E. García-Barros. 2010.** Biogeographic regions of the Iberian Peninsula: butterflies as biogeographical indicators. J. Zool. 282: 180–190.

**Sánchez-Fernández, D., J.M. Lobo, P. Abellán, I. Ribera and A. Millán. 2008.** Bias in freshwater biodiversity sampling: the case of Iberian water beetles. Divers. Distrib. 14: 754–762.

**Stevenson, L.A., C.E. González-Orozco, N. Knerr, D.C. Cargill and J.T. Miller. 2013.** Species richness and endemism of Australian bryophytes. J. Bryol. 34: 101−107.

**Trivellone, V., L.P. Paltrinieri, M. Jermini and M. Moretti. 2012.** Management pressure drives leafhopper communities in vineyards in Southern Switzerland. Insect Conserv. Diver. 5: 75−85.

**Tuanmu, M.N. and W. Jetz. 2014.** A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. Glob. Ecol. Biogeogr. 23: 1031−1045.

**Van Klink, R., D.E. Bowler, K.B. Gongalsky, A.B. Swengel, A. Gentile and J.M. Chase. 2020.** Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. Science 368: 417−420.

**Wagner, D.L., E.M. Grames, M.L. Forister, M.R. Berenbaum and D. Stopak. 2021.** Insect decline in the Anthropocene: Death by a thousand cuts. Proc. Nat. Acad. Sci. 118: e2023989118.

**Wang, Q.G., X.Y. Su, N. Shrestha, Y.P. Liu, S.Y. Wang, X.Y. Xu and Z.H. Wang. 2017.** Historical factors shaped species diversity and composition of Salix in eastern Asia. Sci. Rep. 7: 1−10.

**Wang, S.Y., X.T. Xu, N. Shrestha, N.E. Zimmermann, Z.Y. Tang and Z.H. Wang. 2017.** Response of spatial vegetation distribution in China to climate changes since the Last Glacial Maximum (LGM). PLoS One 12: e0175742.

**Wang, Z.H., J.Y. Fang, Z.Y. Tang and X. Lin. 2011.** Patterns, determinants and models of woody plant diversity in China. P. Roy. Soc. B-Biol. Sci. 278: 2122−2132.

**Wang, Z.H., Z.Y. Tang and J.Y. Fang. 2009.** The species-energy hypothesis as a mechanism for species richness patterns. Biodivers. Sci. 17: 613–624.

**Weng, E.S. and G.S. Zhou. 2006.** Modeling distribution changes of vegetation in China under future climate change. Environ. Model. Assess. 11: 45−58.

**Wiens, J.J., D.D. Ackerly, A.P. Allen, B.L. Anacker, L.B. Buckley, H.V. Cornell, E.L. Damschen, T.J. Davies, J.A. Grytnes and S.P. Harrison. 2010.** Niche conservatism as an emerging principle in ecology and conservation biology. Ecol. Lett. 13: 1310–1324.

**Wiens, J.J. and M.J. Donoghue 2004.** Historical biogeography, ecology and species richness. Trends Ecol. Evol. 19: 639–644.

**Xu, X.T., Z.H. Wang, C. Rahbek, N.J. Sanders and J.Y. Fang. 2016.** Geographical variation in the importance of water and energy for oak diversity. J. Biogeogr. 43: 279−288.

**Xu, Y., Z.H. Shen, L.X. Ying, Z.H. Wang, J.H. Huang, R.G. Zang and Y.X. Jiang. 2017.** Hotspot analyses indicate significant conservation gaps for evergreen broadleaved woody plants in China. Sci. Rep. 7: 1859.

**Yan, B., C.H. Dietrich, X.F. Yu, M. Jiao, R.H. Dai and M.F. Yang. 2022.** Mitogenomic phylogeny of Typhlocybinae (Hemiptera: Cicadellidae) reveals homoplasy in tribal diagnostic morphological traits. Ecol. Evol. 12: e8982.

**Yan, Y.J., X. Yang and Z.Y. Tang. 2013.** Patterns of species diversity and phylogenetic structure of vascular plants on the Qinghai-Tibetan Plateau. Ecol. Evol. 3: 4584−4595.

**Yang, W.J., K.P. Ma and H. Kreft. 2013.** Geographical sampling bias in a large distributional database and its effects on species richness–environment models. J. Biogeogr. 40: 1415–1426.

**Yuan, S. 2013.** Research on the distribution pattern of Chinese Typhlocybinae and its formation mechanism. Chinese Academy of Sciences, Beijing, China.

**Yuan, S., M. Huang, X.S. Wang, L.Q. Ji and Y.L. Zhang. 2014.** Centers of endemism and diversity patterns for Typhlocybinae leafhoppers (Hemiptera: Cicadellidae: Typhlocybinae) in China. Insect Sci. 21: 523–536.

**Zhang, Y.B., G.Y. Wang, H.F. Zhuang, L.H. Wang, J.L. Innes and K.P. Ma. 2021.** Integrating hotspots for endemic, threatened and rare species supports the identification of priority areas for vascular plants in SW China. Forest Ecol. Manag. 484: 118952.

**Zhang, Z.J., J.S. He, J.S. Li and Z.Y. Tang. 2015.** Distribution and conservation of threatened plants in China. Biol. Conserv. 192: 454–460.

**Zhao, D. and S. Wu. 2014.** Responses of vegetation distribution to climate change in China. Theor. Appl. Climatol. 117: 15–28.

**Zhao, Z.X., B.C. Jin, Z.X. Zhou, L. Yang, J.K. Long and X.S. Chen. 2020a.** Determinants of Delphacidae richness and endemism in China. Ecol. Entomol. 45: 1396–1407.

**Zhao, Z.X., L. Yang, J.K. Long, Z.M. Chang, Z.X. Zhou, Y. Zhi, L.J. Yang, H.X. Li, Y.J. Sui, N. Gong, X.Y. Wang and X.S. Chen. 2020b.** Testing seven hypotheses to determine what explains the current planthopper (Fulgoridae) geographical and species richness patterns in China. Insects 11: 892.

**Zhao, Z.Z., L. Yang, J.K. Long, Z.M. Chang, Z.X. Zhou, Y. Zhi, L.J. Yang, H.X. Li, Y.J. Sui, N. Gong, X.Y. Wang and X.S. Chen. 2021.** Endemism patterns of planthoppers (Fulgoridae) in China. Front. Ecol. Evol. 6: 683722.

**Zhao, Z.X., X.L. Feng, Y.B. Zhang, Y.J. Wang and Z.X. Zhou. 2023.** Species diversity, hotspot congruence, and conservation of North American damselflies (Odonata: Zygoptera). Front. Ecol. Evol. 10: 1087866.