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RESEARCH PAPER

Geographical patterns and determinants of insect biodiversity in China

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Insects play important roles in the maintenance of ecosystem functioning and the provision of livelihoods for millions of people. However, compared with terrestrial vertebrates and angiosperms, such as the giant panda, crested ibis, and the metasequoia, insect conservation has not attracted enough attention, and a basic understanding of the geographical biodiversity patterns for major components of insects in China is lacking. Herein, we investigated the geographical distribution of insect biodiversity across multiple dimensions (taxonomic, genetic, and phylogenetic diversity) based on the spatial distribution and molecular DNA sequencing data of insects. Our analysis included 18 orders, 360 families, 5,275 genera, and 14,115 species of insects. The results revealed that Southwestern and Southeastern China harbored higher insect biodiversity and numerous older lineages, representing a museum, whereas regions located in Northwestern China harbored lower insect biodiversity and younger lineages, serving as an evolutionary cradle. We also observed that mean annual temperature and precipitation had significantly positive effects, whereas altitude had significantly negative effects on insect biodiversity in most cases. Moreover, cultivated vegetation harbored the highest insect taxonomic and phylogenetic diversity, and needleleaf and broadleaf mixed forests harbored the highest insect genetic diversity. These results indicated that human activities may positively contribute to insect spatial diversity on a regional scale. Our study fills a knowledge gap in insect spatial diversity in China. These findings could help guide national-level conservation plans and the post-2020 biodiversity conservation framework.

insect spatial patterns | multiple dimensions | driving factors | vegetation types

INTRODUCTION

Exploring macroscale biodiversity patterns from species diversity to genetic diversity and phylogenetic diversity is vital for maximizing overall biodiversity (Cardinale et al., 2012; Oliver et al., 2015). The accumulation of spatial distribution and molecular DNA sequencing data on numerous species over the past two decades has facilitated large-scale spatial distribution assessments of various taxa across multiple dimensions of biodiversity (Fan et al., 2022; Gheyret et al., 2020; Hu et al., 2021; Huang et al., 2023; Lu et al., 2018; Miraldo et al., 2016; Roberts et al., 2002; Sun et al., 2021; Wang et al., 2023; Zhang et al., 2023). These advances have expanded our knowledge of the underlying mechanisms that affect species biodiversity and have provided valuable information for determining conservation priority areas (Brum et al., 2017; Mi et al., 2023). However, current studies have focused on the spatial patterns of biodiversity in vascular plants or terrestrial vertebrates, and insect geographical patterns, which play a fundamental role in the functioning of the biosphere (Stork, 2018), remain largely unexplored due to the lack of systematic compilation of long-term observational data for most insects.

Approximately 970,905 insect species inhabit the world, constituting 65% of the total number of described animal species (1,501,609) (Bánki et al., 2023). Insects play a crucial role in human life. Some beneficial insects support the livelihoods of millions of people, ranging from silk production to beekeeping, helping pollinate a range of agricultural products (Kawahara et al., 2021) and serving as a source of nutrition for humans and livestock (Hazarika and Kalita, 2023; van Huis and Gasco, 2023). Some harmful insects feed on crops, causing damage and greatly affecting agricultural production (Zogli et al., 2020). These insects are pests that need to be controlled. Moreover, insect biodiversity is critical for the maintenance of ecosystem services (Weisser and Siemann, 2004), including pollination (Peña-Kairath et al., 2023) and nutrient cycling (Belovsky and Slade, 2000). However, globally, 76% of insect species are inadequately represented in protected areas (Chowdhury et al., 2023). Thus, there is an urgent need for strategies to ensure the maintenance of current levels of insect biodiversity. Current studies have focused on the insect biodiversity patterns of some well-studied taxa (Kass et al., 2022; Orr et al., 2021). However, a basic understanding of the geographical patterns for major insect components is lacking, which restricts the conservation of insect biodiversity. Moreover, previous studies have predicted that plant community diversity plays a crucial role in determining arthropod species diversity (Moreira et al., 2016). Although the evolutionary relationship between insects and plants has been explored (Benton et al., 2022), a comparison of insect geographical biodiversity patterns across different vegetation types at a national scale has yet to be investigated.

China is a country of mega-biodiversity with a very rich insect fauna. The number of insect species in China is estimated to account for 10% of the total described global insect species, and many rare and primitive insect species only exist in China (You, 1997). Here, using the distribution information of insect species, we estimated the distribution ranges of 14,115 species and performed a large-scale assessment of the spatial distribution of insect biodiversity using stacked species distribution models (SSDMs). The aims of our study were as follows: (i) explore the geographical distribution patterns of different insect taxa across multiple dimensions of biodiversity, (ii) evaluate the effects of abiotic and biotic factors on the multiple dimensions of insect biodiversity, and (iii) compare the insect geographical distribution biodiversity patterns across different vegetation types. Our study will provide valuable insights into the geographical patterns and factors affecting insect species biodiversity in China, and the findings can help guide national-level conservation plans and fulfill the post-2020 biodiversity framework.

RESULTS

Geographical patterns of insect species richness

Our original species distribution dataset included 919,222 raw occurrence records. Following data correction, georeferencing the coordinates, filtering record errors, and data integration and deduplication, 467,958 unique georeferenced records remained for the subsequent analysis. The georeferenced records for different insect species were plotted on a map of China, and the results indicated that the density of insect georeferenced records in Southern China was far greater than that in Northwestern China (Figure S1 in Supporting Information). The relative paucity of georeferenced insect records in Northwest China cannot be attributed to insufficient sample collection, as several official scientific expeditions have been conducted in this region since 1956, which have collected numerous insect samples from the provinces in Northwestern China (Table S1 in Supporting Information).

We selected species with more than five occurrence records to predict the distribution range of Chinese insects. These data covered 18 orders, 360 families, 5,275 genera, and 14,115 species (Figure 1A). The SSDM results indicated that the performance of the analyzed species was good, with area under the curve (AUC) values for the majority of the models >0.8 (Figure 1B). Moreover, we also evaluated the effect of environmental factors on insect distribution. The results showed that land cover (LC) and human population density (HPD) were the two most critical factors in predicting the distribution of insects (Figure 1C).

To obtain the geographical map of insect species richness, we divided the map of China into 50 km×50 km grid cells and calculated the species richness of each grid cell by summing the unique species located there. The results showed that high species richness predominantly occurred in Southwestern and Southeastern China, whereas the regions with low species richness were concentrated in Northwestern China (Figure 1D). Moreover, some mountainous areas (Taihang Mountains and Yanshan Mountains) located in Northeast China possessed high insect species richness. To reveal the geographical distribution of the insect groups of interest, we evaluated the geographical species richness patterns of five orders (Lepidoptera, Coleoptera, Hemiptera, Hymenoptera, and Diptera), which are most abundant and representative of modern insects in China and collectively comprise more than 1,000 species in this study (Figure S2A–E in Supporting Information). The results showed that the species richness patterns for the five insect orders were similar to those of all studied insect species.

Geographical patterns of insect genetic diversity

The species-level genetic diversity for Chinese insects was surveyed based on 76,425 mitochondrial cytochrome oxidase subunit I (Co1) sequences obtained from the NCBI and BOLD databases. After matching with the distribution data, the dataset used to assess the geographical pattern of genetic diversity included 2,775 insect species. To reduce the contribution of widespread species to the overall mean genetic diversity of each grid cell, we used the weighted genetic diversity of each grid cell to reveal the geographical patterns of insect genetic diversity. The results showed that the regions located in Southern China, particularly in the Yungui Plateau, the Hengduan Mountains, the Wuling Mountains, and Hainan Island, exhibited higher genetic diversity. Additionally, some regions located in the Altai Mountains and the Hulunbuir Plateau exhibited relatively high genetic diversity (Figure 2A). We also evaluated the geographical patterns of the five insect orders. The results showed different geographical genetic diversity patterns among the insect taxa. Specifically, regions located in Southeastern China exhibited higher genetic diversity for Lepidoptera, Hemiptera, Hymenoptera, and Diptera; regions located in Southwestern China possessed higher genetic diversity for Hymenoptera and Coleoptera; regions located in the Altai Mountains possessed higher genetic diversity for Lepidoptera, Coleoptera, and Hymenoptera; and regions located in the Hulunbuir Plateau harbored higher genetic diversity for Hemiptera and Hymenoptera (Figure 2B–F).

Geographical patterns of insect phylogenetic diversity

The phylogenetic diversity of Chinese insects was surveyed based on a newly constructed phylogenetic tree using coding sequences of three mitochondrial protein-coding genes (Cytb, Co1, and Nd1) and one mitochondrial ribosomal gene (12S-rRNA). After matching with the distribution data, 4,755 insect species were used to assess phylogenetic diversity (Figure 3A). A distribution map of insect phylogenetic diversity was obtained by calculating the phylogenetic diversity of insect species within each cell. Mapping the phylogenetic diversity values of all insect taxa revealed a transition belt that coincided with the Hu Huanyong Line (Hu, 1935), which divides China into the densely populated southeast and the sparsely populated northwest region (Figure 3B). These findings were also observed in the phylogenetic diversity analysis of angiosperm flora in China (Lu et al., 2018; Ye et al., 2023), suggesting a coevolutionary relationship between insects and plants. Considering that species richness is positively correlated with phylogenetic diversity, we calculated the standard effective size (SES) of phylogenetic diversity (SES-PD), which controls the effect of species richness, to identify the

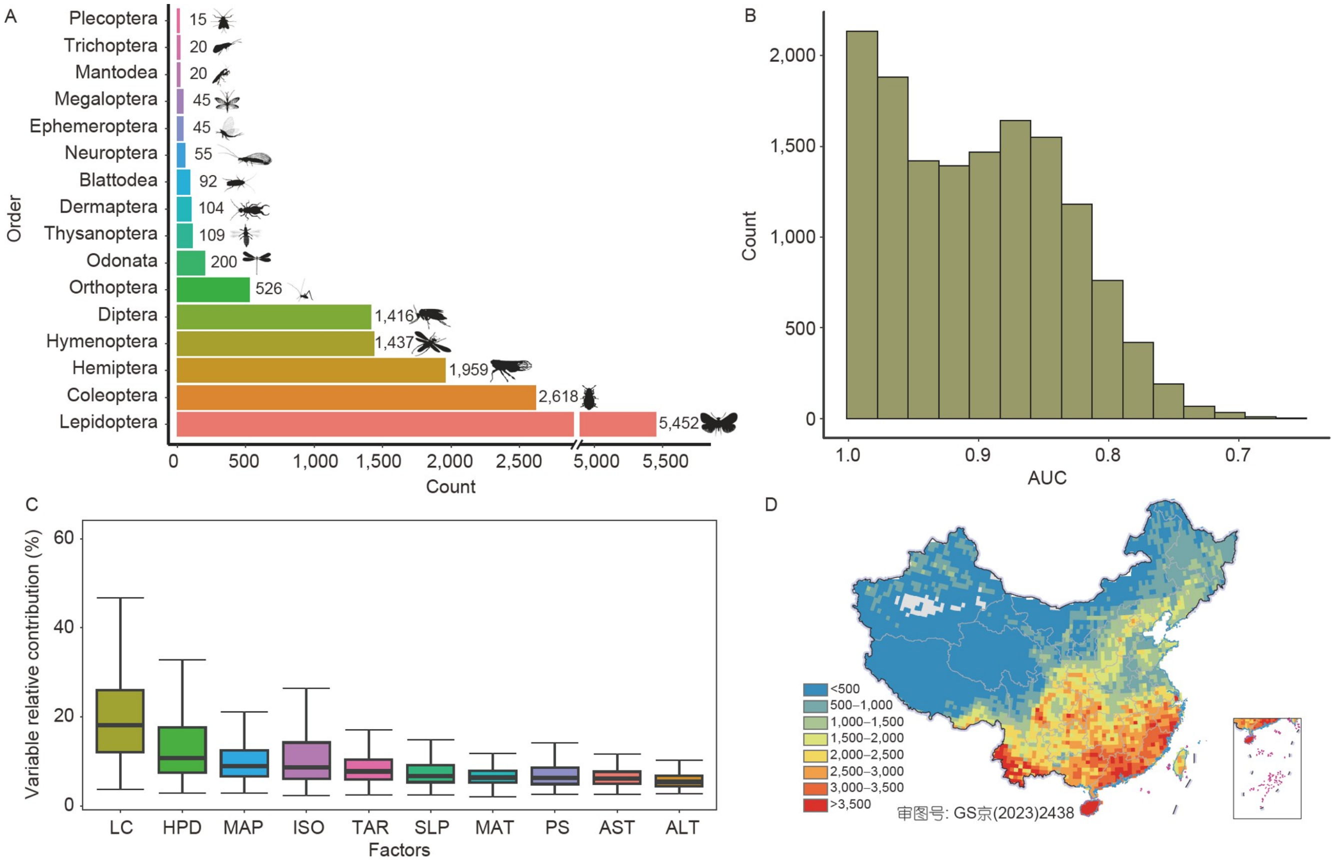

Figure 1. Number of species used to predict the distribution range, the AUC values for modeling, and the contribution of factors and spatial distribution of species richness for Chinese insect species. A, Number of insect orders used to predict the distribution range of Chinese insects. The orders are shown from the least (top) to the most (bottom); only orders with more than five species are displayed. B, Frequency distribution histogram of AUCs for SSDM modeling. C, Contribution of abiotic and biotic factors to the distribution of Chinese insect species. MAP, mean annual precipitation; ISO, isothermality; TAR, temperature annual range; SLP, slope; MAT, mean annual temperature; PS, precipitation seasonality; ASP, aspect; ALT, altitude. D, The spatial distribution pattern measured by the number of species. Species illustrations were taken from http://phylopic.org/ and are available for use with a Public Domain license under the Attribution-ShareAlike 3.0 Unported license.

neo-hotspot and paleo-hotspot regions (Procheş et al., 2006). The results revealed that regions with high SES-PD scores were mainly located in Southeastern China, suggesting that these regions are home to ancestral lineages and serve as a museum. In contrast, areas with lower SES-PD values were located in Northwestern China (Figure 3C), indicating that these areas are centers of recent insect speciation events and serve as an evolutionary cradle. Moreover, we evaluated phylogenetic diversity (Figure S3A–E in Supporting Information) and SES-PD (Figure S4A–E in Supporting Information) for the five insect orders. The results showed that the geographical distribution patterns of phylogenetic diversity for the five insect taxa were similar to those of all studied insect species.

Factors affecting the patterns of insect biodiversity

We performed spatially explicit generalized linear mixed modeling (spaGLMM) to evaluate the effects of abiotic (mean annual temperature (MAT), isothermality (ISO), temperature annual range (TAR), mean annual precipitation (MAP), precipitation seasonality (PS), altitude (ALT), slope (SLP), and aspect (ASP)) and biotic factors (HPD and LC) on the biodiversity patterns for all studied species and five orders. The results showed that most of the insect biodiversity could be well predicted by these factors. Specifically, MAT, MAP, SLP, and HPD had positive effects, whereas ALT, ISO, TAR, and PS had negative effects on insect species richness and phylogenetic diversity in most cases. Additionally, MAT and MAP had positive effects, whereas HPD had negative effects on the geographical pattern of insect genetic diversity (Figure 4; Table S2 in Supporting Information).

Comparison of insect biodiversity across different vegetation types

We developed a framework to compare the currently inventoried multidimensional insect biodiversity across different vegetation types. The findings indicated that areas of cultivated vegetation exhibited a high level of insect species richness and phylogenetic diversity (Figure 5A and C), suggesting that the human-modified cultivated vegetation harbored numerous insect species and ancient insect lineages. The areas of needleleaf and broadleaf mixed forests possessed the highest insect genetic diversity (Figure 5B), indicating that this vegetation type harbors insect species with high evolutionary potential.

DISCUSSION

Insects play important roles in maintaining biodiversity. However, only a few studies have focused on the geographical patterns of insect biodiversity compared with those of vertebrates

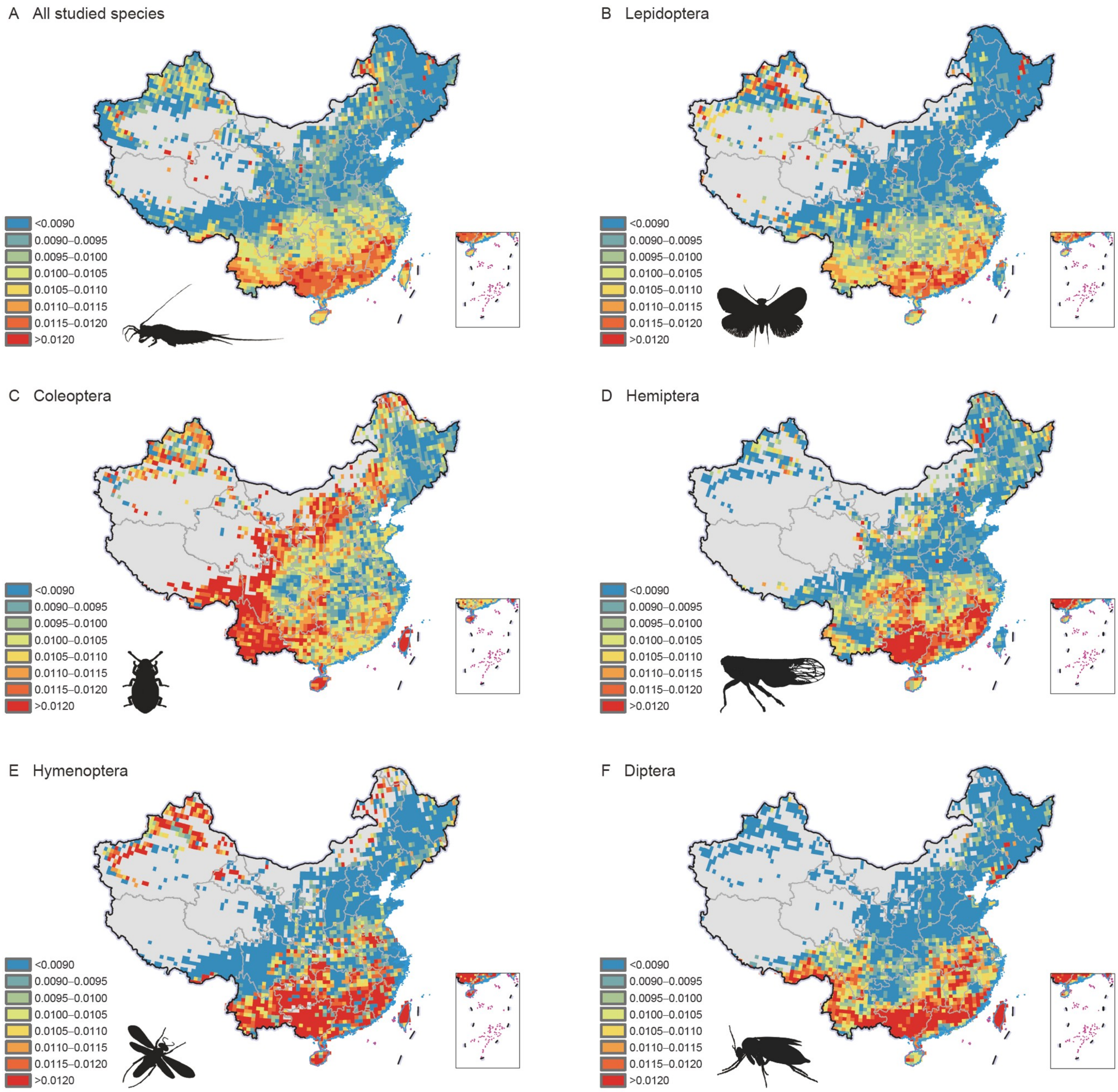

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Figure 2. Spatial distribution of genetic diversity of Chinese insect species, encompassing all studied species and five orders (A) all studied species. (B) Lepidoptera, (C) Coleoptera, (D) Hemiptera, (E) Hymenoptera, and (F) Diptera. Species illustrations are similar to those in Figure 1.

and plants. The insect biodiversity patterns are poorly understood, including basic questions, such as which areas contain the most insect species and which regions harbor the insect species with the oldest evolutionary history. Herein, we compiled a dataset of insects that contains the most comprehensive distribution data from different sources. We further investigated the geographical patterns of insect biodiversity across multiple dimensions in China based on this dataset. Our results revealed that the insects in mountainous areas exhibited high biodiversity across multiple dimensions. Previous studies have proposed that mountainous areas hold more than half of the global biodiversity due to the diverse climate conditions and heterogeneous habitats (Rahbek et al., 2019). We further demonstrated that mountainous areas are essential for preserving insect biodiversity. In addition, the results of this study demonstrated that insects in Southwestern and Southeastern China harbored high biodiversity, indicating that these regions may act as museums in the evolution of insect biodiversity (Kohler et al., 2010). The East Asian monsoon makes the region warmer and wetter (Molnar et al., 2010), which may provide conditions for speciation and high insect diversity in the region. Previous studies identified that Southwestern and Southeastern China also harbored high biodiversity for terrestrial vertebrates (Hu et al., 2021) and angiosperms (Lu et al., 2018). These results do not suggest that the diversity of terrestrial vertebrates and angiosperms correlates with the diversity of insects, as detailed relationships among

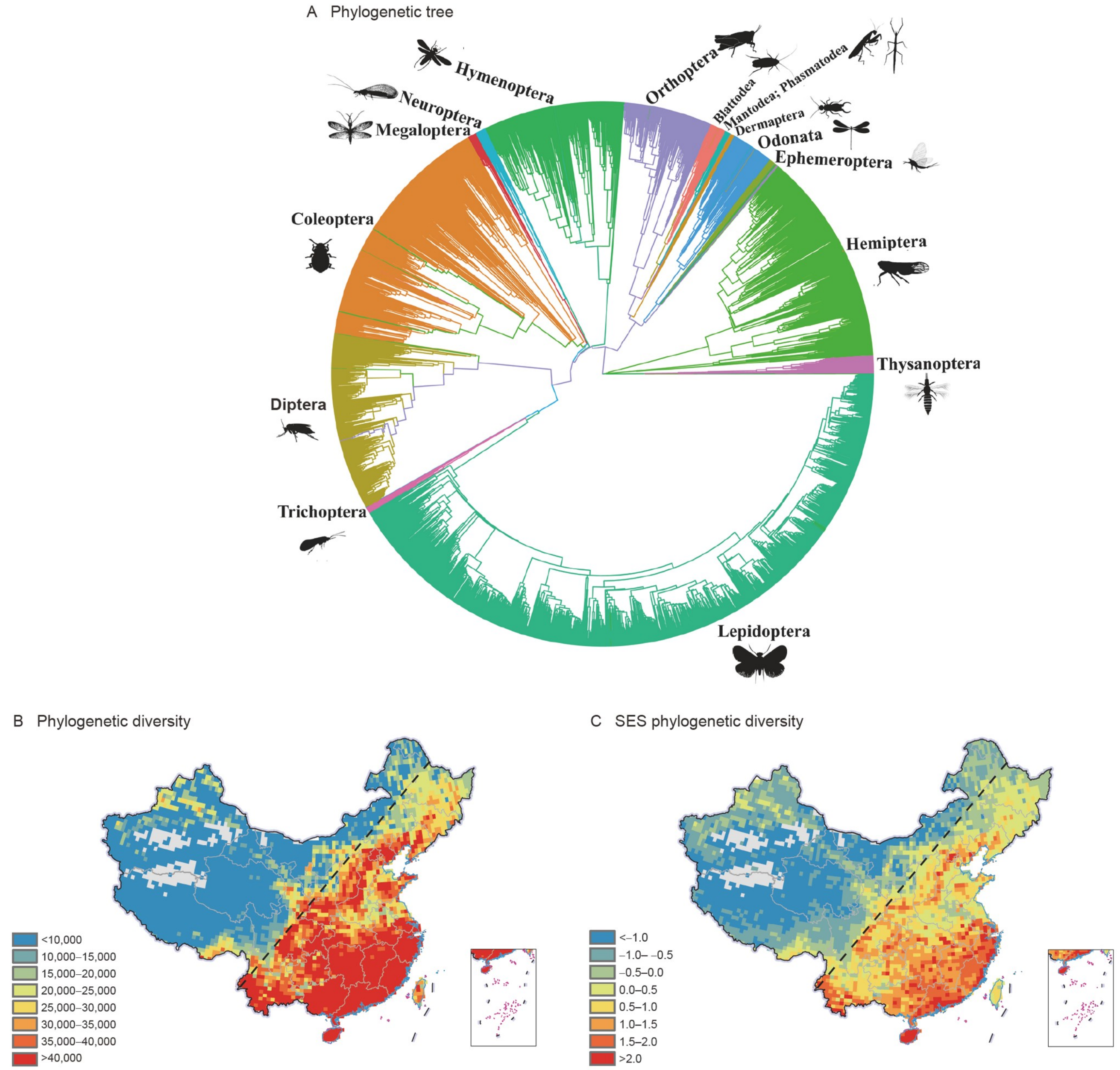

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Figure 3. Phylogenetic tree for Chinese insect species and the patterns of phylogenetic diversity. A, Dated phylogenetic tree of Chinese insect species based on four mitochondrial genes (Cytb, Co1, 12S-rRNA, and ND1). B, Spatial distribution patterns of PD measured by species divergence time. The dashed line is the Hu Huanyong Line. C, Spatial distribution patterns of SES phylogenetic diversity for Chinese insect species. The dashed line is the Hu Huanyong Line. Species illustrations are similar to those in Figure 1.

these three groups need further investigation. In contrast, our results indicated that the region in Northwest China, which is characterized by arid and semi-arid climates with low MAT, MAP, and high TAR (Hou et al., 2023), harbored relatively low insect biodiversity. These results were supported by the spaGLMM analyses, which revealed that MAT and MAP had significantly positive effects, whereas TAR had a significantly negative effect on insect biodiversity in most cases.

We investigated the effects of abiotic factors on insect biodiversity patterns in China and discovered that the patterns are influenced by MAP and altitude. The MAP, which represents environmental energy and water availability, had a significant positive effect on insect biodiversity. This result indicates that suitable precipitation may regulate insect species diversity, as stated by the "water-energy dynamic hypothesis" (O'Brien, 1998). In contrast, altitude had a significant negative effect on insect biodiversity. Higher elevation means lower oxygen content as well as extremely low temperatures, which strains the energy requirements of most insects.

Human activities have a negative impact on the biodiversity of vertebrates (Hu et al., 2021). However, we observed that HPD had a significant positive effect on insect taxa and phylogenetic diversity. Moreover, cultivated vegetation harbored the highest insect species richness and phylogenetic diversity. Thus, we hypothesized that domestication, cultivation, and transportation of plants could potentially enhance habitat heterogeneity for insects (Auffret et al., 2014), leading to an expansion of non-native insect species, thereby resulting in increased insect

Figure 4. SpaMM model results show the effect of abiotic and biotic factors on Chinese insect multidimensional biodiversity. Red circles indicate positively significant effects; blue circles indicate negatively significant effects; and blank circles indicate insignificant effects.

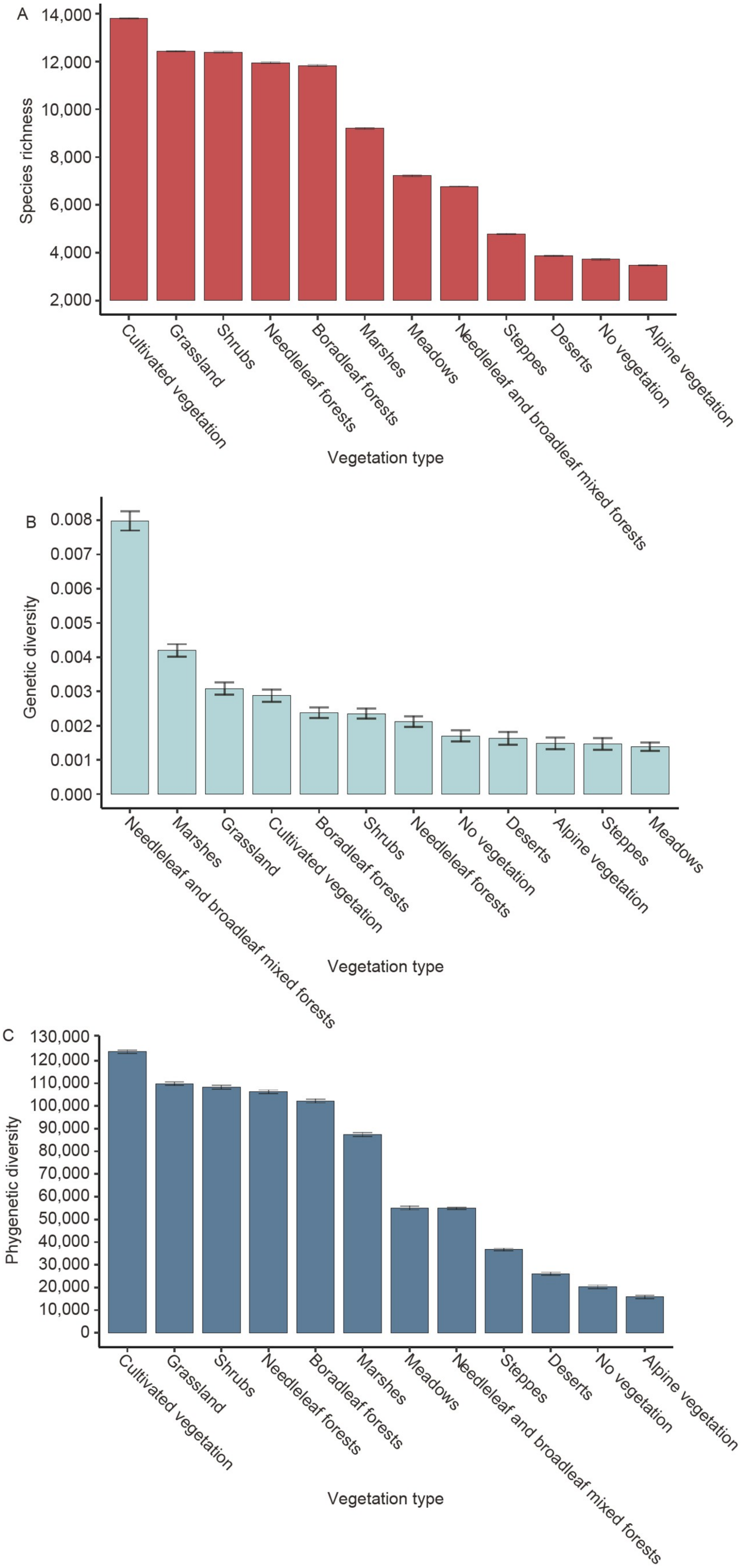

Figure 5. Comparison of insect biodiversity across different vegetation types. (A) Species richness, (B) genetic diversity, and (C) phylogenetic diversity.

taxonomic diversity. Moreover, human-induced changes in the landscape generate novel habitats, providing opportunities for expanding insect species. For example, cultivated habitats, typically composed of crops, provide flowers and fruits for insects. Additionally, cultivated habitats are consistently situated in close proximity to forested habitats and human-made structures, which offer ecological opportunities (e.g., food sources, living space, and habitats for various developmental stages) for insect taxa and simultaneously support a diverse array of ecosystem services for human society. Furthermore, insect species may have adapted to new stressors, food, and threats in urban and suburban environments, enabling them to thrive in close proximity to humans (Hunter, 2007). These results do not imply that human activities increase insect biodiversity across all dimensions. In fact, our study indicated that HPD has a negative effect on the genetic diversity of insects in China, suggesting that human activities may harm the evolutionary potential of insects. We hypothesized that the expansion of non-native insect species may lead to a decrease in genetic diversity through the loss of genetically distinct populations, loss of genes, and hybridization of non-native species with native species.

Our findings provide valuable insight into expanding protected areas in future conservation planning in China. The Chinese government proposed ambitious ecological red lines (ERLs) in 2011 to protect rare and endangered species and their habitats (Gao, 2019; Xu et al., 2018). Although the priority areas (PAs) under the ERLs include more than 30% of the total land, 90% of the critical ecosystem, and 74% of wild plants and animals (Liu, 2022), conservation of insect biodiversity has been neglected. We recommend that the future expansion of PAs should consider insect biodiversity so that proactive measures can be taken to reduce insect biodiversity loss. Our results provide useful information for the systematic expansion of PAs, and insect biodiversity hotspot regions could be designated as new PAs in future conservation plans. Although most of the widely distributed insect species were included in our analysis, numerous rare and narrow-range insect species were not included as they do not have sufficient occurrence records available. Moreover, the distribution maps of threatened and specific species were not included due to the lack of a threat category for insects. Therefore, to better conserve insect biodiversity, scientists and managers should perform more long-term professional surveys that are harmless to insects in more regions.

MATERIALS AND METHODS

Species distribution data compilation and cleaning

The distribution of Chinese insect species was obtained from the Global Biodiversity Information Network Database (GBIF, www.gbif.org; accessed in November 2022) and the National Animal Collection Resource Center (NACRC, http://museum.ioz.ac.cn/index.html; accessed in November 2022). As species occurrence data are typically fraught with errors and missing fields, we adopted a strict protocol to filter the data from these two databases before it was used in subsequent analysis. First, we used the following criteria to filter the occurrence data from GBIF: (i) coordinates with no valid species names were removed, (ii) coordinates with no latitude and longitude were removed, (iii) coordinates from unknown sources or not verified by GRSciColl (Grosjean et al., 2022) were removed, and (iv) coordinates with a precision radius >100 km were excluded. Then, we filtered the NACRC occurrence data using the following criteria: we excluded (i) fossils, as we were interested in recent distributions, and (ii) geographic names with very large zones and used the locations of the local administration to represent a few locations from small zones. The cleaned geographic names were converted into georeferenced occurrence points via the Baidu Geocoding API using the REmap package (https://github.com/lchiffon/REmap). Finally, we integrated the cleaned insect occurrence data from the two databases and removed duplicate records, obtaining a total of 467,958 records for subsequent analysis. To further ensure the reliability of the dataset, we manually checked and validated all insect taxa information with expert guidance. Previous studies suggested that the performance of SSDMs depends on the sample size of the species distribution (Wisz et al., 2008). Therefore, we excluded species with fewer than six distribution records from our analysis. Finally, 14,115 species were included in subsequent analyses.

Collection of environmental, land use, and human population data

The 1970–2000 climate data with a spatial resolution of 30 s (ca. 1 km×1 km at the equator) were obtained from WorldClim (version 2.1; http://www.worldclim.org). A total of 19 variables were obtained, which primarily represented the annual trends or extreme factors of temperature and precipitation. As some of the variables were highly correlated, Pearson correlation coefficients were calculated; if two variables were highly correlated ($r>0.8$), only one was retained. Finally, five climate variables remained, including MAT, ISO, TAR, MAP, and PS. In addition, we also included ALT, SLP, AST, LC, and HPD to reflect the influence of the terrain and human activities. The ALT, SLP, and AST data were obtained from the Geospatial Data Cloud Platform of the Chinese Academy of Sciences Computer Network Information Center (http://www.gscloud.cn). The slope angle was sine transformed, and the absolute value was determined after subtracting 180° from the AST. To build the effect of land use, we used the European Space Agency Climate Change Initiative (ESA CCI) land use and cover map. The original 37 classes from the ESA CCI were reclassified into 10 major classes, including coniferous forests, broadleaf forests, shrub lands, grasslands, croplands, urban areas, wetlands, bare areas, rock, and ice and water bodies. The data on HPD in China in 2000 were derived from the Resource and Environment Science and Data Center (https://www.resdc.cn/doi/doi.aspx?DOIid=32).

Species potential distribution based on SSDMs

We used the stacked SDM package "ssdm" in R software to predict the potential distribution of insect species in China. The SSDM assembles several single SDMs to eliminate biases and uncertainties from different algorithms and to obtain more robust results and insights (Schmitt et al., 2017). Five modeling algorithms were selected, including the generalized linear model (Williams et al., 2009), the generalized additive model (Guisan et al., 2002), random forest (Mi et al., 2017), maximum entropy (Beaumont et al., 2005), and support vector machine (Drake et al., 2006). The distribution data of each species were randomly partitioned into training (70%) and testing (30%) datasets, which were used to calibrate and evaluate the performance of the models using the area under the receiver operating characteristic curve. This process was repeated ten times to calculate the mean AUC value. The performance of the models was evaluated based on the AUC value, and the models with an overall AUC<0.6 were dropped. As different modeling algorithms perform differently, the results of the models were ensembled by an unweighted mean to obtain the final distribution of each species.

To eliminate the effect of area on the estimation of species richness, we divided the map of China into 50 km×50 km grid cells and transformed the distribution maps of the insect species into this grid map. We filtered the grid cells along the border and coast, where the area accounted for <50% of the total area. The map of China used in this study was from the Resource and Environment Science and Data Center (www.resdc.cn/data.aspx?DATAID=200). The species richness of each cell was calculated by summing the number of unique species located in the cell.

Estimation of insect genetic diversity

We used the mitochondrial Co1 to estimate the genetic diversity of insect species in China. The Co1 coding sequences were from GenBank (www.ncbi.nlm.nih.gov/genbank) and the BOLD databases (www.boldsystems.org). The following steps were used to collect the available sequences. We searched and downloaded the sequences from the GenBank database using the rules "(CO1[All Fields] OR "COX1" [All Fields] OR "COI" [All Fields] OR "COXI" [All Fields] OR "cytochrome oxidase subunit 1" [All Fields]) AND (species Latin name [Organism])." Then, we used the application-platform interface (http://www.boldsystems.org/index.php/resources/api) to directly obtain the insect Co1 sequences from the BOLD database. The union sequences from the two databases were extracted and integrated based on the sequence header. Finally, we filtered the genes whose coding sequence length was <300 bp and the species with fewer than four sequences. In addition, species with a coefficient of variation value >3 were filtered in the subsequent analysis.

We performed sequence alignment analysis for each species using MUSCLE software (Edgar, 2004) with the default parameters. Then, we selected pairwise alignments whose sequence overlaps were >60% and sequence differences were <10% to calculate genetic diversity. We calculated the genetic diversity of each species using the equation proposed by Miraldo et al. (2016) as follows:

$$GD = \frac{1}{\binom{n}{2}} \sum_{i=1}^{n-1} \sum_{j=i+1}^{n} \frac{k_{ij}}{m_{ij}},$$

where k_{ij} is the number of different nucleotides between sequence i and sequence j, m_{ij} is the length of shared bases between sequence i and sequence j, and $\binom{n}{2}$ is the number of pairwise comparisons. The community-wide genetic diversity of each grid cell was calculated as follows:

$$GD_Q = \frac{\sum_{i=1}^{S_Q} GD_i}{S_Q},$$

where GD_i is the overall genetic diversity computed for a specific species i by considering all sequences available from the entire habitat. Furthermore, we calculated an inverse range size-weighted GD_Q because large-range species could strongly determine the overall genetic diversity of a specific grid cell (Rabosky et al., 2018). The calculation form was given as follows:

$$GD_Q = \frac{\sum_{i=1}^{S_Q} \frac{1}{Y_i} GD_i}{\sum_{i=1}^{S_Q} \frac{1}{Y_i}} = \sum_{i=1}^{S_Q} w_i GD_i,$$

where $w_i = \frac{1}{Y_i} \Big/ \sum_{i=1}^{S_Q} \frac{1}{Y_i}$. Additionally, to reduce the potential impact of species-deficient regions on our analyses, we filtered out grid cells with fewer than five species in the subsequent analysis.

Estimation of insect phylogenetic diversity

Four mitochondrial genes (Cytb, Co1, 12S-rRNA, and Nd1) were used to construct the insect phylogenetic tree. We used the following steps to obtain the coding sequences of the three protein-coding genes (Cytb, Co1, and Nd1) and the 12S-rRNA sequence. All available mitochondrial reference genomes for insect species were downloaded from the GenBank database, and the corresponding sequences were extracted. For those remaining species without available mitochondrial genomes, the corresponding sequences were directly downloaded from GenBank using the species' Latin name and the corresponding gene name. In particular, the coding sequences for the mitochondrial gene Co1 in the BOLD database were collected. Finally, we excluded the short genes with lengths <300 bp and used the sequences with lengths similar to that of the corresponding gene to construct the phylogenetic tree.

We constructed a phylogenetic tree of insects in China using the following steps. First, the coding sequences of each gene were aligned using MAFFT software with default parameters (Katoh et al., 2002). Then, SequenceMatrix software (Vaidya et al., 2011) was used to construct a supermatrix with gaps regarded as missing data based on the aligned results of the four genes. Finally, the insect phylogenetic tree of insect species was constructed using IQ-tree (Minh et al., 2020) with 1,000 ultrafast bootstrap replicates. The species Allacma fusca and Allonychiurus kimi from the Collembola were used as outgroups. TreePL software (Smith and O'Meara, 2012) was used to date the divergence times of Chinese insects based on the newly constructed phylogenetic tree. A total of 272 available divergence times from TimeTree (Hedges et al., 2015) were selected as calibration points for the dating analysis (Table S3 in Supporting Information).

Faith's phylogenetic diversity and SES-PD were calculated using the "phyloregion" package in R software (Daru et al., 2020) based on the phylogenetic tree and the insect species distribution data. Phylogenetic diversity was calculated by summing the divergence times of all insect species surveyed within a grid. The SES-PD was calculated because phylogenetic diversity is always significantly correlated with species richness (Brum et al., 2017). Specifically, we obtained a null distribution of expected phylogenetic diversity values by shuffling the insect taxa labels across the tips of the phylogenetic tree 1,000 times. The SES-PD was calculated by dividing the difference between the observed and expected phylogenetic diversity values by the standard deviation of the null distribution.

Factors affecting spatial biodiversity patterns

We used a spatial generalized linear mixed model implemented in the "spaMM" package from R software (Nipperess and Matsen, 2013) to explore the abiotic factors MAT, ISO, TAR, MAP, PS, ALT, SLP, and ASP, as well as the biotic factors HPD and LC on different Chinese insect taxa. The value of the center point of the grid cell was used as the value of the variable. For the modeling results of spaMM analysis, we conducted a Student's t-test on the t-value obtained from the modeling results, and a variable was considered to have a significant effect on the levels of insect biodiversity when the P-value was <0.05.

Comparison of multifaceted insect biodiversity across different vegetation types

We compared the multidimensional biodiversity levels from different vegetation types with areas of varying sizes. However, we could not directly compare the observed biodiversity levels, as different vegetation types provide different sizes of ecological spaces for maintaining the survival of species. Therefore, we developed a rarefaction framework to compare the currently inventoried multidimensional insect biodiversity levels across different vegetation types. Details on the rarefaction models are provided in the Supplemental Information.

Compliance and ethics

The author(s) declare that they have no conflict of interest. All data needed to evaluate the conclusions in the paper are present in the paper and the supplementary materials. The code reported in this paper has been deposited in the GitHub database (https://github.com/fanhuizhong).

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Supporting information

The supporting information is available online at https://doi.org/10.1007/s11427-023-2483-0. The supporting materials are published as submitted, without typesetting or editing. The responsibility for scientific accuracy and content remains entirely with the authors.

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