

## ECOLOGY

# Spatial patterns and conservation of genetic and phylogenetic diversity of wildlife in China

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Genetic diversity and phylogenetic diversity reflect the evolutionary potential and history of species, respectively. However, the levels and spatial patterns of genetic and phylogenetic diversity of wildlife at the regional scale have largely remained unclear. Here, we performed meta-analyses of genetic diversity in Chinese terrestrial vertebrates based on three genetic markers and investigated their phylogenetic diversity based on a dated phylogenetic tree of 2461 species. We detected strong positive spatial correlations among mitochondrial DNA-based genetic diversity, phylogenetic diversity, and species richness. Moreover, the terrestrial vertebrates harbored higher genetic and phylogenetic diversity in South China and Southwest China than in other regions. Last, climatic factors (precipitation and temperature) had significant positive effects while altitude and human population density had significant negative impacts on levels of mitochondrial DNA-based genetic diversity in most cases. Our findings will help guide national-level genetic diversity conservation plans and a post-2020 biodiversity conservation framework.

## INTRODUCTION

Biodiversity loss and conservation are among the most concerning global issues. The Convention on Biological Diversity (CBD) was established to develop national strategies for the conservation and sustainable use of biological diversity. An endangerment status assessment of worldwide vertebrates showed that approximately 20% of vertebrates have become threatened (1). In China, the situation is even worse: 21.4% of vertebrates are threatened, including 43.1% of amphibians, 29.7% of reptiles, 26.4% of mammals, 20.4% of fishes, and 10.6% of birds (2). Thus, it is urgent to protect biodiversity regionally and globally. As the most fundamental dimension of biodiversity, genetic diversity is a key basis for species survival and ecosystem functions (3). Higher genetic diversity means higher evolutionary potential and a greater ability to respond to environmental changes (4). An increasing number of studies have shown that genetic factors play a critical role in species endangerment and extinction (5–7). Thus, assessment and protection of genetic diversity are becoming essential and high-priority strategies for biodiversity conservation (4). However, under the current CBD framework, the goal proposed for genetic diversity focuses mainly on the conservation of farmed and domestic animals and cultivated plants and neglects that of wild animals and plants, which would overlook genetic erosion and harm the evolutionary potential of wildlife (8). Therefore, to better conserve the genetic diversity of wildlife, it is

necessary to assess genetic diversity at regional and global scales for use in the scientific designs of natural protected areas and biodiversity conservation strategies. Miraldo *et al.* (9) presented the first global distribution of genetic diversity for mammals and amphibians using mitochondrial cytochrome b (Cytb) and cytochrome oxidase subunit I (Co1) gene sequences. However, the grid cell size (~150,000 km<sup>2</sup>) that they used was so large that it was difficult to determine the national- or regional-level pattern of genetic diversity in detail, including in China.

Phylogenetic diversity is the sum of phylogenetic branch lengths for all of the species in an area (10). Phylogenetic diversity measures the time scale of species evolution and reflects the evolutionary history of species (11), which contributes to the selection of biodiversity conservation priority areas (12–14). Higher phylogenetic diversity excluding the effect of taxonomic richness indicates a higher proportion of distantly related and anciently diverged taxa (11, 15). Previous studies have shown that regions with higher phylogenetic diversity may not necessarily have higher species diversity, which would result in neglecting the conservation of the regions (11, 16). In this case, the conservation of older evolutionary lineages might be neglected. Thus, monitoring the level and spatial distribution of phylogenetic diversity is also important for effective conservation of biodiversity.

China is one of the countries with the richest biodiversity in the world, harboring more than 3000 terrestrial vertebrates (2). In recent years, with the development of molecular genetics, genetic diversity of many species has been assessed and numerous DNA sequences have been accumulated. In this study, we focus on the patterns of genetic and phylogenetic diversity in Chinese terrestrial vertebrates, using meta-analyses of a large published dataset and a robust dated phylogenetic tree as well as species distribution. We aim to (i) reveal whether positive spatial correlation existed among species richness, genetic diversity, and phylogenetic diversity; (ii) identify hotspot regions of high genetic diversity and high phylogenetic diversity; and (iii) explore the influences of abiotic (precipitation, temperature, and altitude) and biotic (human population) factors on the levels of

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genetic and phylogenetic diversity. We found that, on the whole, species richness predicted phylogenetic diversity and mitochondrial DNA-based genetic diversity in a positive direction, and higher phylogenetic diversity predicted higher genetic diversity. We identified that the terrestrial vertebrates in South China and Southwest China harbored higher genetic and phylogenetic diversity than in other regions, and central South China was identified as an “evolutionary museum,” while the Hengduan Mountains was identified as an “evolutionary cradle.” We also revealed that both mean annual precipitation and temperature had significant positive effects, while altitude and human population density had significant negative impacts on levels of mitochondrial DNA-based genetic diversity in most cases. Our findings provide insights into the spatial patterns and influencing factors of genetic and phylogenetic diversity at a regional scale.

## RESULTS

### Estimation of genetic and phylogenetic diversity

We surveyed the population-level genetic diversity data of Chinese terrestrial vertebrates (mammals, birds, reptiles, and amphibians) based on three molecular markers (mitochondrial *Cytb* gene sequence, mitochondrial D-loop sequence, and nuclear microsatellites). A total of 287 terrestrial vertebrate species (103 mammals, 59 birds, 31 reptiles, and 94 amphibians) were assessed for population-level genetic diversity with at least one molecular marker, accounting for 9.3% of the 3075 terrestrial vertebrates distributed in China (figs. S1 to S4 and tables S1 to S9). Two unbiased genetic diversity indices, nucleotide diversity ( $\pi$ ) for the *Cytb* and D-loop sequences and expected heterozygosity ( $H_E$ ) for microsatellite, were used as measures of population-level genetic diversity. In this study, the *Cytb*-, D-loop-, and microsatellite-based genetic diversity measures were analyzed separately (tables S1 to S9). Furthermore, the species-level genetic diversity for three genetic markers was obtained by averaging the population-level genetic diversity values (tables S10 to S12).

The species-level phylogenetic diversity of Chinese terrestrial vertebrates was surveyed on the basis of the coding sequences of five mitochondrial genes (*Cytb*, *Co1*, *Nd1*, *12S rRNA*, and *16S rRNA*). A total of 2461 terrestrial vertebrates were assessed for phylogenetic diversity with at least one available mitochondrial gene sequence, accounting for 80% of the Chinese terrestrial vertebrates (figs. S5 to S7 and table S13). On the basis of a constructed maximum likelihood phylogenetic tree and 391 available divergence times from the TimeTree database (table S14), we estimated the divergence times of these vertebrates. The results showed that the amphibians first diverged from the fishes and then the reptiles evolved from the amphibians. Both the mammals and birds evolved from the reptiles, with the mammals diverging first. These results are consistent with the general conclusion about the divergence order of the terrestrial groups (17). In this study, we used divergence time as the measure of phylogenetic diversity for further analysis.

### Spatial correlation between genetic diversity, phylogenetic diversity, and species richness

We first divided the map of China into  $0.5^\circ \times 0.5^\circ$  (~50 km by 55 km) grid cells and then calculated the species richness, genetic diversity, and phylogenetic diversity within each grid cell. The spatial correlation tests showed that the genetic diversity measures based on mitochondrial *Cytb* and D-loop sequences were significantly correlated

[correlation coefficient ( $r$ ) = 0.385,  $P$  = 0.012]. However, no significant correlation was observed for *Cytb* versus microsatellites ( $r$  = 0.128,  $P$  = 0.475) and for D-loop versus microsatellites ( $r$  = 0.084,  $P$  = 0.463) (fig. S8 and table S15). The inconsistencies in spatial correlations among the three genetic markers were most likely due to different measure rationales (nucleotide diversity versus expected heterozygosity) and evolutionary rates (slowly versus rapidly evolving). The differences in correlation among the different markers were similar to that of Miraldo *et al.* (9).

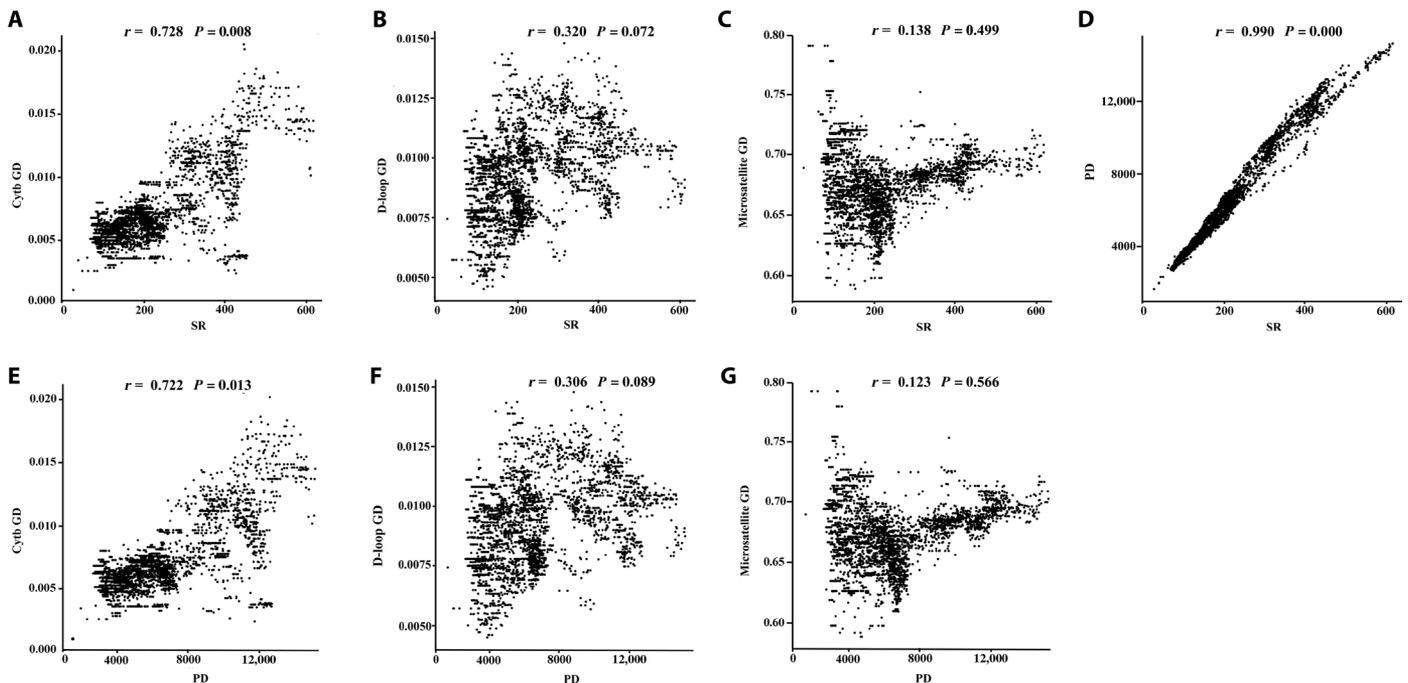
The tests for spatial correlations between genetic diversity and species richness revealed a significant positive correlation for *Cytb* genetic diversity ( $r$  = 0.728,  $P$  = 0.008), and a marginally significant correlation for D-loop genetic diversity ( $r$  = 0.320,  $P$  = 0.072) (Fig. 1, A and B). These results were consistent with those of global terrestrial mammals (18) and global marine and freshwater fishes (19). However, a nonsignificant correlation for microsatellite genetic diversity ( $r$  = 0.138,  $P$  = 0.499) was detected (Fig. 1C and table S15), which was similar to AFLP marker-based genetic diversity assessment of alpine plant communities (20). The differences in correlation showed that the widely discussed correlation relationship between genetic and species diversity was genetic marker dependent.

The tests for spatial correlations between genetic diversity and phylogenetic diversity showed a significant positive correlation for *Cytb* ( $r$  = 0.722,  $P$  = 0.013) and a marginally significant positive correlation for D-loop ( $r$  = 0.306,  $P$  = 0.089) (Fig. 1, E and F). The results were similar to those of global terrestrial mammals (18). However, the correlation was not significant for microsatellites ( $r$  = 0.123,  $P$  = 0.566) (Fig. 1G and table S15). In addition, we selected a set of abundant terrestrial vertebrate species with a threatened status rank of LC (Least-Concern) (table S16) and tested the spatial correlations between genetic and phylogenetic diversity. The results were similar to those for all the terrestrial vertebrates (table S17).

A significant positive correlation was detected between phylogenetic diversity and species richness ( $r$  = 0.99,  $P$  < 0.001) (Fig. 1D and table S15), implying that the regions with high species richness often had high phylogenetic diversity. The significant positive correlation pattern between phylogenetic diversity and species richness may be common, as shown in different large-scale analyses focusing on birds, mammals, and angiosperms (16, 18, 21).

### Patterns of genetic diversity across zoogeographical regions and provinces

It is generally accepted that China's zoogeographical regionalization is divided into the Palaearctic and Oriental realms, including seven zoogeographical regions (22, 23). The Palaearctic realm includes the Northeast China, North China, Inner Mongolia-Xinjiang, and Qinghai-Tibet Plateau regions, while the Oriental realm consists of the Southwest China, Central China, and South China regions. We mapped the genetic diversity data onto the zoogeographical region map of China using a grid size of  $0.5^\circ \times 0.5^\circ$ . Overall, the terrestrial vertebrates distributed in the Oriental realm had higher genetic diversity than those in the Palaearctic realm for all three markers (Fig. 2, A to C; fig. S9; and table S18). In the case of zoogeographical regions, the vertebrates in South China harbored the highest genetic diversity for *Cytb* and microsatellites, suggesting a hotspot region of genetic diversity, whereas those in North China had the lowest genetic diversity for D-loop and microsatellites (table S18). In addition, the Southwest China and west Central China harbored relatively high genetic diversity. The spatial pattern of species richness across



**Fig. 1. The spatial correlation tests between GD, PD, and SR. (A to C)** Correlation tests between species richness (SR) and Cytb-, D-loop-, and microsatellite-based genetic diversity (GD). **(D)** Correlation test between SR and phylogenetic diversity (PD). **(E to G)** Correlation tests between PD and Cytb-, D-loop-, and microsatellite-based GD.

the Palaearctic and Oriental realms was similar to that of genetic diversity (Fig. 2D). However, within the zoogeographical regions, the spatial patterns of species richness were somewhat different from those of genetic diversity. The South China region had the highest species richness, whereas the Qinghai-Tibet Plateau and Inner Mongolia-Xinjiang regions harbored the lowest species richness (Fig. 2D). These results suggest that regions with low species richness do not necessarily have low genetic diversity, such as the Qinghai-Tibet Plateau, which should be given more conservation attention. To determine the possible effects of different sample sizes of the grid cells, we examined the frequency distribution of the proportion of species with surveyed genetic diversity data in the grid cells based on the classification of seven zoogeographical regions and found similar frequency distributions on the whole across the seven regions (figs. S10 to S12).

The province-level distributions of genetic diversity based on the three markers demonstrated similar patterns on the whole (figs. S13 and S14). The terrestrial vertebrates distributed in Yunnan, Guangxi, Sichuan, and Guizhou provinces harbored the highest genetic diversity. In contrast, the terrestrial vertebrates distributed in Shanxi, Shandong, Hebei, Liaoning, Jilin, Heilongjiang, and part of Xinjiang had lower genetic diversity. The terrestrial vertebrates in Qinghai and Tibet had intermediate genetic diversity. These results could help guide province-level conservation plans for genetic diversity.

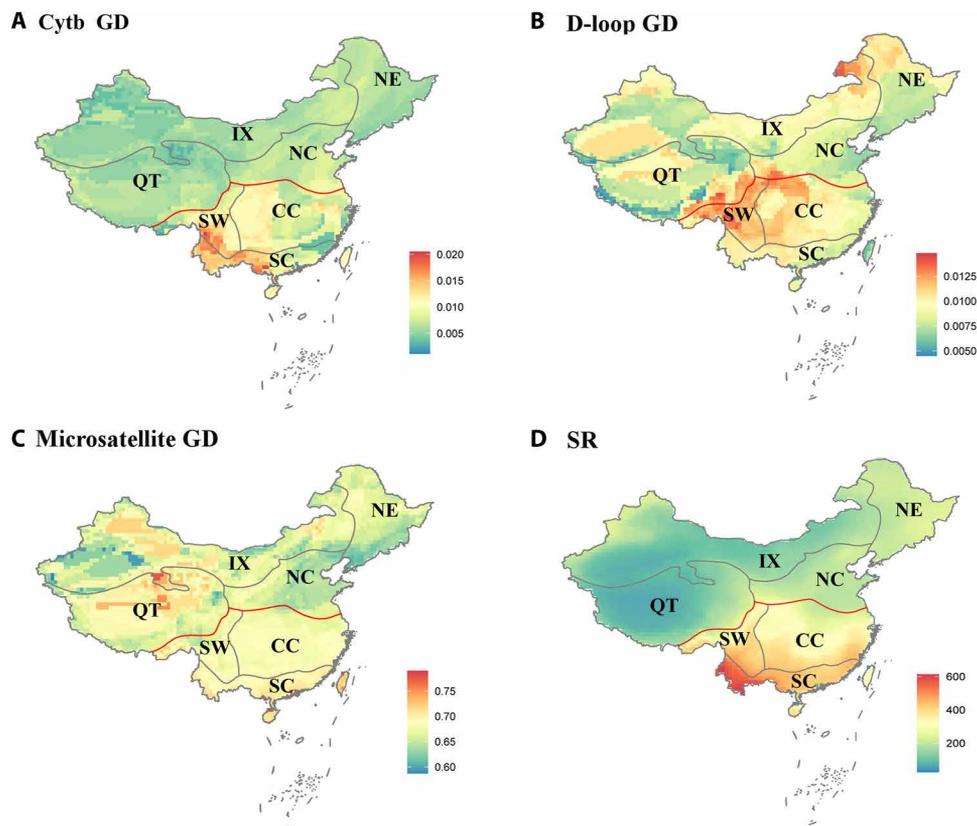
### Patterns of phylogenetic diversity across zoogeographical regions and provinces

The terrestrial vertebrates in the Oriental realm had significantly higher phylogenetic diversity ( $PD = 10,390.25 \pm 2029.43$ ) than those in the Palaearctic realm ( $PD = 4942.60 \pm 1402.09$ ) (Fig. 3, A and B). The terrestrial vertebrates in South China harbored the highest phylogenetic diversity ( $PD = 12,327.46 \pm 2111.27$ ), and those in Central China and Southwest China had the second highest phylogenetic

diversity. The terrestrial vertebrates on the Qinghai-Tibet Plateau had the lowest phylogenetic diversity ( $PD = 3936.66 \pm 1162.35$ ) (Fig. 3B and table S18). The province-level distribution of phylogenetic diversity showed a clear pattern, in which the terrestrial vertebrates in south China had notably higher phylogenetic diversity than those in north China (fig. S15). Specifically, the vertebrates in Yunnan and Guangxi provinces had the highest phylogenetic diversity, and those in Tibet, Xinjiang, and Qinghai had the lowest phylogenetic diversity (fig. S15). These results could help guide province-level conservation plans for phylogenetic diversity.

### Divergence pattern between phylogenetic diversity and species richness

As shown by the correlation analysis above, the phylogenetic diversity pattern was highly correlated with the species richness pattern (Fig. 1D). To control for the confounding effect of species richness, we detected areas with significantly higher or lower phylogenetic diversity than expected using a randomization method. The result showed that significantly higher phylogenetic diversity occurred in the central South China region, mainly including Hainan and Guangxi provinces, suggesting that these areas harbored many older terrestrial vertebrate lineages, serving as an evolutionary museum (Fig. 3C and fig. S16) (9). This result is similar to that for the phylogenetic diversity of genus-level angiosperms in China, in which the top 5% highest phylogenetic diversity and standard effective size of phylogenetic diversity were mainly located in Guangdong, Guangxi, Guizhou, and Hainan provinces (15). These results suggested that the above areas are phylogenetic diversity hotspots not only for terrestrial vertebrates but also for angiosperms in China, which deserve more conservation efforts. In contrast, significantly lower phylogenetic diversity occurred in the Southwest China region, i.e., the Hengduan Mountains, suggesting that these areas were the



**Fig. 2. Spatial patterns of GD and SR across seven zoogeographical regions of China.** Northeast China (NE), North China (NC), Inner Mongolia-Xinjiang (IX), Qinghai-Tibet Plateau (QT), Southwest China (SW), Central China (CC), and South China (SC). The red line indicates the boundary between the Palaearctic and Oriental realms. (A and B) Spatial patterns of Cytb- and D-loop-based GDs, measured by nucleotide diversity. (C) Spatial pattern of microsatellite-based GD measured by expected heterozygosity. (D) Spatial pattern of SR measured by number of species.

centers of recent speciation events and thus contained many younger lineages, serving as an evolutionary cradle (Fig. 3C and fig. S16) (15, 24). This divergence pattern is similar to that of a study on global terrestrial birds (16).

### Factors affecting the patterns of genetic and phylogenetic diversity

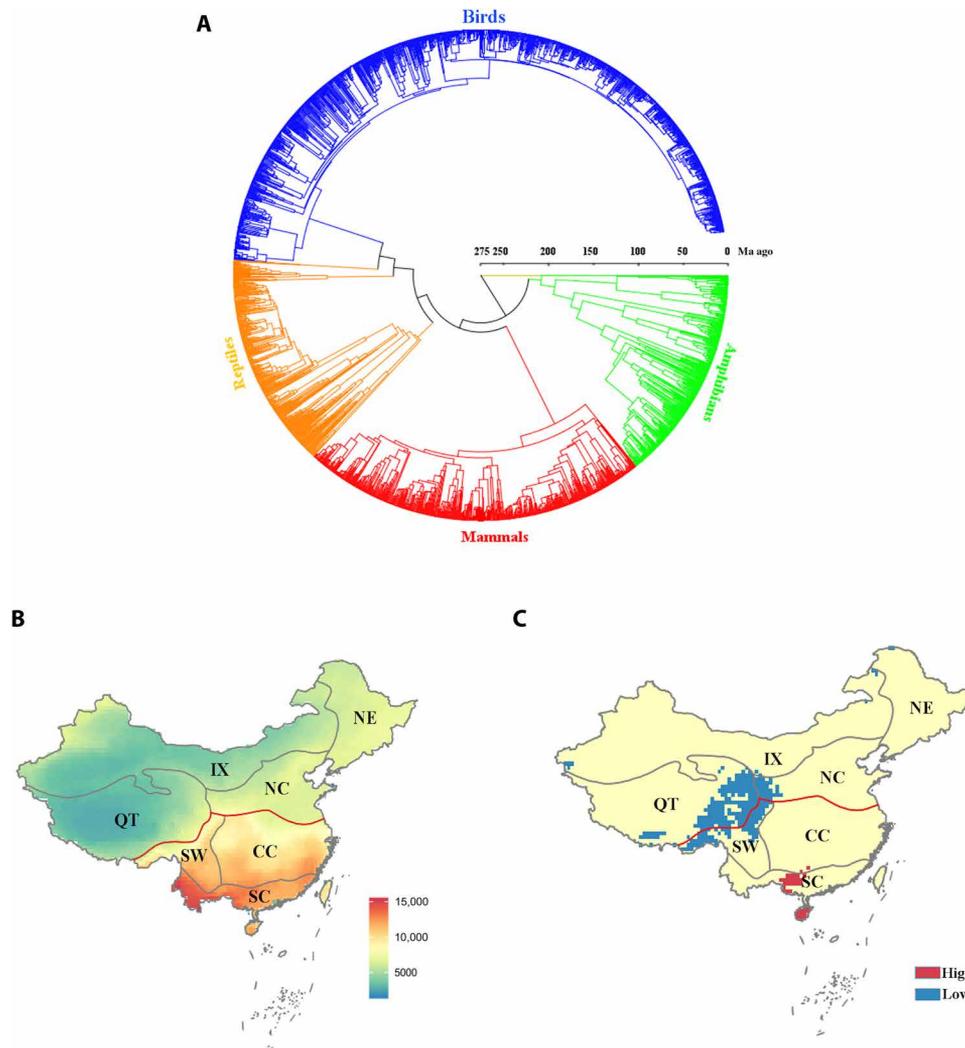
The above correlation results showed that the mitochondrial DNA-based genetic diversity was strongly correlated with species richness. Therefore, to reveal the effects of abiotic and biotic factors on genetic diversity, we performed the semi-part spatially explicit generalized linear mixed modeling (spaGLMM) analysis by regressing genetic diversity against species richness and then using the residuals of models to evaluate the effects of abiotic (mean annual precipitation, mean annual temperature, and altitude) and biotic (human population density) factors. The results showed that most of the genetic diversity measures were well predicted by these factors (Table 1). In detail, mean annual precipitation had a significant positive effect on Cytb-based genetic diversity; mean annual temperature had a significant positive effect on D-loop-based genetic diversity; and altitude and human population density had significant negative impacts on Cytb- and D-loop-based genetic diversity (Table 1). In addition, the spaGLMM analysis with the species richness included as an explanatory variable gave similar results to the semi-part spaGLMM analysis (table S19). Because the relationships between most of the

factors and microsatellite-based genetic diversity were different from theoretically expected, here we did not discuss microsatellite-related results.

Because the phylogenetic diversity was very strongly correlated with species richness, we also performed the semi-part spaGLMM analysis for phylogenetic diversity. The results showed that the above abiotic and biotic factors had no significant impacts on phylogenetic diversity (Table 1), suggesting that the species richness had a much higher effect on phylogenetic diversity compared to other factors. To test this, we performed the spaGLMM analysis with species richness as an independent variable. The results showed that the importance of species richness was far more than those of other factors, indicating that phylogenetic diversity was mainly affected by species richness (table S19).

### DISCUSSION

This is the first study to assess the correlation between genetic diversity and phylogenetic diversity for all the terrestrial vertebrate groups at a large spatial scale. The findings revealed a significant correlation between genetic and phylogenetic diversity for Cytb-based genetic diversity measure and a marginally significant correlation for D-loop-based measure at a grid cell scale, demonstrating the important role of phylogenetic diversity in predicting level of genetic diversity. In addition, we also found a significant positive correlation



**Fig. 3. Phylogenetic tree of Chinese terrestrial vertebrates and patterns of PD across zoogeographical regions.** (A) A dated phylogenetic tree of Chinese terrestrial vertebrates based on five mitochondrial genes (Cytb, Co1, Nd1, 12S rRNA, and 16S rRNA). Ma, million years. (B) Spatial pattern of PD measured by species divergence time. The red line indicates the boundary between the Palearctic and Oriental realms. (C) Areas with significantly higher or lower PD after controlling for the confounding effect of SR. The red line indicates the boundary between the Palearctic and Oriental realms.

between genetic diversity and species richness for Cytb-based genetic diversity measure and a marginally significant correlation for D-loop-based measure. However, no significant correlations were detected between genetic diversity and phylogenetic diversity (or species richness) for microsatellite-based measure, suggesting that these correlations are genetic marker dependent.

Our study is also the first region-level survey and assessment of the genetic and phylogenetic diversity of Chinese terrestrial vertebrates that demonstrated the spatial distribution pattern of diversity and identified the regions of high and low genetic/phylogenetic diversity. The spatial patterns showed that the terrestrial vertebrates in South China and Southwest China harbored not only higher genetic diversity but also higher phylogenetic diversity, highlighting the high conservation priority for these hotspot regions. We also identified key areas with significantly higher or lower phylogenetic diversity after controlling for the effects of species richness and discerned the “evolutionary museum and cradle” for Chinese terrestrial

vertebrates. In particular, we found inconsistencies among the regions in terms of genetic and species diversity. Although the terrestrial vertebrates on the Qinghai-Tibet Plateau had the lowest species richness, they had intermediate genetic diversity, possibly because of less human activity and heterogeneous abiotic effects in this region. The terrestrial vertebrates in North China and Northeast China, which are exposed to more human activity and located in north further in latitude, harbored intermediate species richness but lower genetic diversity. These results were supported by the semi-part spaGLMM analyses, which revealed that abiotic (precipitation, temperature, and altitude) and biotic factors (human population) played important roles in the spatial patterns of genetic diversity.

We investigated the effects of abiotic and biotic factors driving the spatial patterns of genetic and phylogenetic diversity at a grid cell scale. On the whole, the effects of these factors on Cytb- and D-loop-based genetic diversity were consistent with ecological and evolutionary expectations. Mean annual precipitation and temperature

**Table 1. Results of semi-part spaGLMMs that used the residuals to evaluate the impacts of other abiotic and biotic factors on genetic diversity (GD) or phylogenetic diversity (PD) after controlling for the effect of species richness.** MAP, mean annual precipitation; MAT, mean annual temperature; ALT, mean altitude; HPD, human population density.

Factors	Cytb GD			D-loop GD		
	Estimate	cond.SE	t value	Estimate	cond.SE	t value
Intercept	$1.31 \times 10^{-5}$	$4.47 \times 10^{-5}$	0.2934	$7.03 \times 10^{-5}$	$4.47 \times 10^{-5}$	1.571
MAP	$1.58 \times 10^{-7*}$	$4.41 \times 10^{-8}$	3.5891	$-1.30 \times 10^{-7*}$	$4.41 \times 10^{-8}$	-2.9572
MAT	$-7.97 \times 10^{-6*}$	$3.59 \times 10^{-6}$	-2.2215	$9.64 \times 10^{-6*}$	$3.59 \times 10^{-6}$	2.6876
ALT	$-1.84 \times 10^{-8*}$	$1.43 \times 10^{-8}$	-1.2855	$-1.39 \times 10^{-8*}$	$1.43 \times 10^{-8}$	-0.9722
HPD	$-1.43 \times 10^{-7*}$	$5.53 \times 10^{-8}$	-2.5941	$-2.15 \times 10^{-7*}$	$5.53 \times 10^{-8}$	-3.8951
Factors	Microsatellite GD			PD		
	Estimate	cond.SE	t value	Estimate	cond.SE	t value
Intercept	$-1.44 \times 10^{-5}$	$4.47 \times 10^{-5}$	-0.322	$1.19 \times 10^{-3}$	$1.88 \times 10^{-3}$	0.63023
MAP	$-3.43 \times 10^{-8*}$	$4.41 \times 10^{-8}$	-0.7787	$-4.02 \times 10^{-7}$	$1.90 \times 10^{-6}$	-0.21105
MAT	$3.18 \times 10^{-6*}$	$3.59 \times 10^{-6}$	0.8872	$-5.03 \times 10^{-5}$	$1.55 \times 10^{-4}$	-0.32458
ALT	$6.52 \times 10^{-9*}$	$1.43 \times 10^{-8}$	0.4566	$-3.58 \times 10^{-7}$	$6.16 \times 10^{-7}$	-0.58035
HPD	$1.91 \times 10^{-8*}$	$5.53 \times 10^{-8}$	0.3449	$1.35 \times 10^{-7}$	$2.39 \times 10^{-6}$	0.05671

\*Confidence intervals of the estimated coefficients significantly deviated from zero.

had significant positive effects on genetic diversity, because higher precipitation and temperature most likely provide more suitable conditions for species survival, population expansion, and speciation. In contrast, altitude had significant negative impacts on genetic diversity, because higher elevation means harsher living conditions especially for terrestrial vertebrates. For biotic factor, human population density had significant negative impacts on genetic diversity, because higher density means more human activities and more possible interference with wildlife and their habitats.

Our study summarizes the findings of genetic/phylogenetic diversity studies, revealing the basic background of genetic resources in Chinese terrestrial vertebrates, which could facilitate genetic resource protection under the CBD framework and guide future genetic/phylogenetic diversity research and conservation. In addition, compared with the total number of Chinese terrestrial vertebrates, the number of species with surveyed genetic diversity data is relatively small. To better conserve genetic diversity, scientists and managers should cooperate to perform genetic diversity surveys for more species, especially those with an unclear genetic status. Furthermore, the genetic and phylogenetic diversity of freshwater and marine vertebrates should be surveyed and assessed to protect gradually decreasing aquatic genetic resources. Last, our study is the first to use nuclear microsatellite markers to assess large-scale genetic diversity pattern and explore the relationship between genetic and phylogenetic diversity. However, it is worth noting that microsatellite-based correlation and model analyses produced different results from those based on mitochondrial DNA, which cautions us to carefully interpret results from different genetic markers.

## MATERIALS AND METHODS

### Data collection and estimation of genetic diversity

We retrieved published literatures of population-level genetic diversity studies from public academic databases. For the English literature,

we searched the Web of Science database (<http://apps.webofknowledge.com/>) using the search rule TS = (“species Latin name” OR “species English name”) AND TS = genetic diversity AND TS = population. For the Chinese literature, we searched the CNKI database ([www.cnki.net](http://www.cnki.net)), CQVIP database ([www.cqvip.com](http://www.cqvip.com)), and Chinese Science Citation Database (<http://sciencechina.cn>) using the search rule species Latin name AND genetic diversity. Then, to search the literature as comprehensively as possible, we searched only the species Latin name again for species without related references or with few related references.

We screened the retrieved literature following several steps. First, we used only the literature about wild animal studies and discarded the literature studying captive populations. Second, we focused on population-level studies based on microsatellite, mitochondrial Cytb, or D-loop markers. These three markers have been widely used in population genetics and phylogeographic studies of vertebrates. For microsatellite-based studies, we extracted the expected heterozygosity ( $H_E$ ) values for each population of species as the measure of microsatellite genetic diversity.  $H_E$  is an unbiased measure and thus insensitive to small sample sizes (25). For mitochondrial Cytb gene and D-loop sequence-based studies, we extracted Nei's nucleotide diversity ( $\pi$ ) values for each population of species as the measure of Cytb or D-loop genetic diversity (26).  $\pi$  is also unbiased and thus insensitive to small sample sizes (26). If the same population had more than one  $H_E$  or  $\pi$  from different references, we used the mean value as the genetic diversity measure of this population. Last, on the basis of population-level genetic diversity data, we estimated species-level genetic diversity by averaging the population-level genetic diversity values (9). Mean genetic diversity metric has been widely applied in large-scale studies (9, 18, 19).

In total, we compiled a dataset of 287 terrestrial vertebrates, which included 103 mammals, 59 birds, 31 reptiles, and 94 amphibians, accounting for 15.6, 4.1, 6.7, and 18.6% of the respective total numbers of species (figs. S1 and S2). Overall, the assessment proportions for

genetic diversity of mammals and amphibians were higher than those of birds and reptiles, with the proportion of birds being the lowest. The number of terrestrial vertebrate species with population-level genetic diversity data based on microsatellite marker ( $n = 151$ ) was higher than those based on Cytb gene ( $n = 142$ ) and D-loop ( $n = 105$ ), accounting for 4.9, 4.6, and 3.4% of the 3075 Chinese terrestrial vertebrates, respectively (figs. S3 and S4).

### Data collection and estimation of phylogenetic diversity

Sequences of five mitochondrial genes (Cytb, Co1, 12S rRNA, 16S rRNA, and Nd1) were used to reconstruct the phylogeny of Chinese terrestrial vertebrates. The sequences of the five mitochondrial genes were searched in GenBank with the following steps. First, the available mitochondrial reference genomes were downloaded, and the corresponding coding sequences of these genes were extracted. Then, the available coding sequences for the remaining species were directly downloaded from GenBank using the species Latin name and gene name. If more than one sequence was available for the same locus of a species, the sequence with a length similar to that of the corresponding gene was selected. Last, the short genes whose coding sequence length was <300 base pairs were discarded from the dataset. After these steps, we compiled a total of 2461 species including 573 mammals, 1170 birds, 359 reptiles, and 359 amphibians, representing 87.0, 81.0, 77.2, and 71.0% of the respective total numbers of species. Our dataset covered 46 orders, 204 families, and 847 genera. For each gene, the coding sequences of 973 species were extracted from their mitochondrial genomes, while others were directly downloaded from the GenBank database. The numbers of species with Cytb and Co1 sequences were higher than those with Nd1, 12S rRNA, and 16S rRNA sequences (fig. S7).

The coding sequences of each gene were concatenated and aligned by MAFFT (27) with default parameters, and the poorly aligned sites at the beginning and the end were trimmed. Then, the aligned sequences of these five genes were imported into SequenceMatrix software (28) to construct a supermatrix with the gaps treated as missing data. A phylogenetic analysis was performed on this supermatrix using the maximum likelihood method implemented in RAxML 8.2.12 (29) with the ASC\_GTRGAMMA model and 1000 bootstrap replicates. Each gene was treated as a partition, and the zebrafish was used as outgroup. On the basis of this phylogenetic tree, we used the penalized likelihood method implemented in treePL (30) to date the divergence times of these vertebrates. A total of 391 available divergence times from TimeTree (31) were selected as calibration points for the dating analysis (table S14). The “prime” option and “through” analysis were implemented with optimal parameters.

On the basis of our dated phylogenetic tree and species distribution data, we calculated Faith’s phylogenetic diversity of Chinese terrestrial vertebrates using the “picante” package (32) in R, as widely used in phylogenetic diversity studies (33). In this study, we used divergence time as the measure of phylogenetic diversity of each species.

### Collection of species distribution, climate, altitude, and human population density data

The distributional ranges of terrestrial vertebrate species (including mammals, amphibians, reptiles, and birds) were derived from the IUCN spatial database ([www.iucnredlist.org/resources/spatial-data-download](http://www.iucnredlist.org/resources/spatial-data-download)). The range of each species was originally in a vectorized shapefile format and was rasterized into a grid system with a  $0.5^\circ \times 0.5^\circ$  resolution (~50 km by 55 km). We double-checked the rasterized maps

to confirm that they matched the original vectorized distributional range maps. The resultant rasterized map of each species was always conservative relative to the original vectorized map, as many margins of species’ fragmented distributions might not have been recorded as the presence of the species in our  $0.5^\circ \times 0.5^\circ$  grid cells. This is because the areas of these margins were too small in the corresponding grid cells. The map of China used in this study was from Resource and Environment Science and Data Center ([www.resdc.cn/data.aspx?DATAID=200](http://www.resdc.cn/data.aspx?DATAID=200)). The Latin name of each species was checked to avoid potential synonyms. In total, our gridded distribution database included the occurrence records for 1941 species. After matching with the genetic and phylogenetic data, the final distribution dataset used for the diversity assessment included a total of 180 species for the genetic diversity analysis and 1685 species for the phylogenetic diversity analysis.

Climate data with a 2.5’ spatial resolution were collected from the WorldClim database (<https://worldclim.org/>). We used the two most important climatic variables, mean annual temperature and mean annual precipitation that were calculated for the climate data from 1970 to 2000, as predictors of spatial patterns of genetic and phylogenetic diversity of terrestrial vertebrates in China. Human population density in 2010 in China (in persons per square kilometer) was derived from the Gridded Population of the World collection (<https://sedac.ciesin.columbia.edu/data/collection/gpw-v4>). Digital elevation data with a 2.5’ spatial resolution in China were originally derived from the NASA Shuttle Radar Topographic Mission and downloadable from the WorldClim database. Because we mapped the genetic and phylogenetic diversity using a grid cell size of  $0.5^\circ \times 0.5^\circ$  for each variable (including altitude), we took the average of all values within each grid cell as the variable’s value for the grid cell.

### Spatial correlation tests between genetic diversity, phylogenetic diversity, and species richness

In many cases in which biodiversity data are collected associated with spatial information (e.g., sampling location coordinates), conventional correlation tests are not valid because the assumption of total independence of samples is violated. For spatial biodiversity data, neighboring locations can present similar biodiversity features (e.g., genetic diversity or phylogenetic diversity as investigated here), which is a phenomenon known as spatial autocorrelation, resulting in non-independent association of biodiversity information between neighboring locations. To this end, conventional correlation tests can be misleading. To cope with this issue, we used a modified  $t$  test to account for spatial autocorrelation (34, 35) when testing the spatial associations between genetic diversity, phylogenetic diversity, and species richness. The test is based on the adjustment of the sample correlation coefficient between the two spatially correlated quantities and requires the estimation of an effective sample size (degrees of freedom).

We performed spatial correlation tests between genetic diversity based on different markers, between genetic diversity and species richness, between genetic diversity and phylogenetic diversity, and between phylogenetic diversity and species richness. In addition, we selected a set of abundant terrestrial vertebrate species with a threatened status rank of LC (2) to further explore the relationship between genetic diversity and phylogenetic diversity. The set of abundant terrestrial vertebrates included 39 species for Cytb, 25 species for D-loop, and 45 species for microsatellite (table S16). We performed the correlation analyses for Cytb-, D-loop-, and microsatellite-based genetic diversity separately.

## Spatial patterns of species, genetic, and phylogenetic diversity

We divided the map of China into  $0.5^\circ \times 0.5^\circ$  grid cells using R software. Then, we mapped the spatial distributional patterns of species richness, genetic diversity, and phylogenetic diversity based on the diversity values calculated for each grid cell. For species richness, we summed the total number of species occurring in the grid cell. For genetic diversity, we summed the genetic diversity values of each species present within the grid cell and divided the total value by the number of species surveyed in the grid cell, as used in (9). For phylogenetic diversity, we summed the divergence times of all species surveyed within the grid cell following the definition of Faith's phylogenetic diversity (10, 15).

## Detection of divergent areas between phylogenetic diversity and species richness

To detect grid cells with significantly higher or lower phylogenetic diversity than expected controlling for the confounding effect of species richness, we used a randomization protocol (36). In detail, we first computed the phylogenetic diversity for each grid cell and divided this value by the species richness found in the cell. Then, we used a random swapping algorithm to randomize the species-site binary matrix while fixing the species richness of each grid cell and the range size of each species. The randomization procedure was repeated 1000 times, and the following effective size of phylogenetic diversity-species richness was computed

$$Z_{PD} = \frac{\text{Obs}_{PD} - \text{Mean}(\text{Rand}_{PD})}{\text{SD}(\text{Rand}_{PD})}$$

where  $\text{Obs}_{PD}$  is the observed phylogenetic diversity-species richness ratio for each grid cell.  $\text{Rand}_{PD}$  represents the random phylogenetic diversity-species richness ratio calculated for each grid cell derived from the randomized species-site matrix.  $\text{Mean}(\text{Rand}_{PD})$  and  $\text{SD}(\text{Rand}_{PD})$  denote the mean and standard deviation of the 1000 random phylogenetic diversity-species richness ratio values, respectively.  $Z_{PD}$  approximately followed a standard normal distribution; as such, at the significance level of 0.05, a grid cell was identified as having statistically significantly high phylogenetic diversity given the associated species richness if  $Z_{PD} > 1.96$ . Conversely, a grid cell was identified as having statistically significantly low phylogenetic diversity given the associated species richness if  $Z_{PD} < -1.96$ .

## Factors that may affect spatial patterns of genetic and phylogenetic diversity

Species richness might have strong associations with genetic and phylogenetic diversity (37, 38). To explore the effects of factors affecting the spatial patterns of genetic and phylogenetic diversity of Chinese terrestrial vertebrates, we performed a semi-part spaGLMM implemented in the spaMM package (39) in the R environment (40), in which the influence of species richness on genetic or phylogenetic diversity was explicitly partialled out. To do so, we firstly constructed a spaGLMM model in which species richness is the only explanatory variable of genetic or phylogenetic diversity and then we used the residuals of this model for evaluating the impacts of other abiotic and biotic factors on genetic or phylogenetic diversity. In addition, to assess the effect of species richness on genetic and phylogenetic diversity, we also performed the spaGLMM analyses with the species richness as an explanatory variable as well as other factors.

For all the above spaGLMM analyses, a correlation matrix according to the Matérn correlation function was assumed and fitted on the basis of the longitude and latitude information of the center point of each grid cell when fitting the mixed model. The Matérn correlation function, containing a scale parameter and a smoothness parameter, is widely applied to model spatial correlation by including exponential and squared exponential models as special cases (41, 42). For the modeling results of semi-part spaMM analyses, when the confidence interval of the estimated coefficient for an explanatory variable was significantly deviated from zero, the variable was considered to have a significant effect on levels of genetic or phylogenetic diversity.

## SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/7/4/eabd5725/DC1>

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