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Patterns and drivers of zoogeographical regions of terrestrial vertebrates in China

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ABSTRACT

Aim Zoogeographical regionalizations have recently seen a revived interest, which has provided new insights into biogeographical patterns. However, few quantitative studies have focused on zoogeographical regions of China. Here, we analyse zoogeographical regions for terrestrial vertebrates in China and how these regions relate to environmental and geological drivers and evaluate levels of cross-taxon congruence.

Location China.

Methods We applied hierarchical clustering and non-metric multidimensional scaling ordination to β_{sim} dissimilarity matrices to delineate zoogeographical regions of China, based on the species distribution of 2102 terrestrial vertebrates in 50 × 50 km grid cells. We used generalized linear models and deviance partitioning to investigate the roles of current climate, past climate change, vegetation and geological processes in shaping the zoogeographical regions. Finally, we used Mantel and Kruskal–Wallis tests to evaluate the levels of cross-taxon congruence.

Results Cluster analyses revealed 10 major zoogeographical regions: South China, the Yungui Plateau, Taiwan, North China, Northeast China, the Inner Mongolia Plateau, Northwest China, the Longzhong Plateau, the Tibetan Plateau and East Himalaya. In contrast to previous regionalizations, a major split was identified by clustering grid cell assemblages and dividing the eastern and western parts of China, followed by the northern part of China. Deviance partitioning showed that current climate and geological processes explained most of the deviance both jointly and independently. Congruence in species composition of endotherms and ectotherms was surprisingly low.

Main conclusions We propose new zoogeographical regions for China based on our quantitative methods. In contrast to previous regionalizations, we consider Central China as a part of South China and identify the Longzhong Plateau and Taiwan as independent regions. While our results strongly support the notion of a broad biogeographical transition zone in East Asia, they also suggest a major south–north-oriented Palearctic–Oriental boundary in China.

Keywords

bioregionalization, China, fauna, Oriental, Palearctic, species composition, terrestrial vertebrate, transition zone

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INTRODUCTION

Biogeographical regions are useful for understanding the origin of and relationship between distinct fauna, for exploring species distributions in space and time and in

providing a spatial framework for questions regarding biogeography, evolutionary ecology and conservation (Morrone, 2009; Kreft & Jetz, 2010). The study of biogeographical regions has a rich history (Sclater, 1858; Wallace, 1876), and with increasing availability of species distribution data,

taxonomic and phylogenetic information, and novel multi-variate algorithms (Kreft & Jetz, 2010; Carstensen *et al.*, 2012; Holt *et al.*, 2013; Vilhena & Antonelli, 2015), it has experienced a revived interest in recent years. Recent studies of biogeographical regionalization have covered continental to global scales and focused on different taxonomic groups (Kreft & Jetz, 2010; Rueda *et al.*, 2010, 2013; Linder *et al.*, 2012; Procheş & Ramdhani, 2012; Holt *et al.*, 2013; Hattab *et al.*, 2015).

Although bioregionalization has witnessed an innovation at the continental to global extents and provided fresh perspectives in global biogeography (Kreft & Jetz, 2010; Holt *et al.*, 2013; Vilhena & Antonelli, 2015), delineating the zoogeographical regions of China and other broad transition zones has proved to be challenging (Kreft & Jetz, 2013). China extends from the tropical to the boreal zone and shows a pronounced longitudinal gradient in precipitation from rain forests in the south-east to the Gobi desert in the north-west. China also shows a great geological complexity. For instance, the phased uplift of the Tibetan Plateau caused significant changes in climate, topography and faunistic composition since the late Eocene (*c.* 38 Ma; Favre *et al.*, 2015; Renner, 2016). Particularly during the Pleistocene (*c.* 2.6 Ma to 11.7 ka), eastern China served as a bidirectional faunistic migration corridor with episodic and repeated interchange between Palaeartic and Oriental faunas (Norton *et al.*, 2011). In response to climatic oscillation, species were pushed southward during glacial periods and expanded northward during warmer interglacial periods (Zhang *et al.*, 2000). This resulted in gradual species turnover from south to north and formed a broad faunistic transition zone (Zhang, 1999; Procheş & Ramdhani, 2012). Such diverse environmental gradients and its intricate geological history make China one of the most zoogeographically complex regions in the world (Procheş & Ramdhani, 2012; Holt *et al.*, 2013; Kreft & Jetz, 2013).

Traditionally, China has been divided into seven broad zoogeographical regions: Northeast China, North China, Northwest China, the Tibetan Plateau, Central China, Southwest China and South China (Zhang, 1999; Fig. 1a). Most previous zoogeographical schemes were based on expert opinions (Cheng & Chang, 1956; Zhang & Zhao, 1978; Zhang, 1998). Recently, the number of quantitative zoogeographical studies of China has increased rapidly, but most of these have been lineage-specific (Xie *et al.*, 2004; Chen & Bi, 2007; Päckert *et al.*, 2012), used coarse grain sizes (Xiang *et al.*, 2004; Heiser & Schmitt, 2013), or focussed on the local scale (Chen *et al.*, 2008). Studies have been based on diverse area sizes and operational geographical units (e.g. physiographical regions), varying taxa and different methods, resulting in ongoing disagreement. Consequently, a quantitative national-scale investigation based on fine resolution data for several lineages of terrestrial vertebrates is needed to understand and update the zoogeographical regions of China.

Global zoogeographical regionalizations traditionally divided China into the Palaeartic and Oriental realms

(Sclater, 1858; Wallace, 1876; Cox, 2001; Kreft & Jetz, 2010; Morrone, 2015). Wallace (1876) placed the Palaeartic–Oriental boundary at *c.* 30° N, and most expert-based schemes followed this proposition with only slight modifications (Zhang, 1999; Cox, 2001; Fig. 1b). Using comprehensive mammal distribution data and clustering algorithms, Kreft & Jetz (2010) suggested a more northern placement of this boundary at *c.* 40° N (see also Rueda *et al.*, 2013), whereas Procheş & Ramdhani (2012) suggested that a much more southern location (at *c.* 20° N). Most recently, by integrating species distributions and phylogenetic information, Holt *et al.* (2013) proposed a new ‘Sino-Japanese’ realm to lie between *c.* 25° N and 40° N in East Asia (including most of eastern China, the Tibetan Plateau and Japan). In sum, there is considerable disagreement among previous studies (Fig. 1b), and the location of the East Asian boundary between the Palaeartic and Oriental realms has oscillated *c.* 2000 km from *c.* 20° N to 40° N.

Here, we used the quantitative framework described in Kreft & Jetz (2010) to identify zoogeographical regions for China based on a large species dataset of terrestrial vertebrates and specifically investigated the location of the Palaeartic–Oriental boundary. We used multiple regression analyses to investigate the current and historical environmental drivers shaping zoogeographical regions. Finally, we evaluated the level of cross-taxon congruence.

MATERIALS AND METHODS

Species distribution data

Species distributions of terrestrial vertebrates (amphibians, reptiles, birds and mammals) for the 2499 counties of China (based on a 1 : 250,000 national digitized database updated in 2002 with a median range size of 1780 km² and 5% and 95% quartiles of 252 km² and 12,771 km², respectively) were compiled from (1) The First National Terrestrial Animal Survey database (11,165 species records) and 76 Nature Reserve Reports (13,918 species records), both of which were obtained from the State Forestry Administration and (2) books on fauna published before 2012 (72,853 species records), including Fauna of China (20 issues of 28 volumes for terrestrial vertebrates), as well as national and regional atlases and books (a full reference list is provided in Appendix S1 in the Supporting Information). In total, we included 97,936 species–county records in this study. We excluded all bats (120 species) because of incomplete distribution information as well as all birds with only wintering ranges in China (156 species) because their migratory behaviour is of limited usefulness for regionalization (Rueda *et al.*, 2013). This resulted in a total of 2102 species for analysis, including 329 amphibians, 361 reptiles, 1008 birds and 404 mammals (see Appendix S2: Table S1 for details). Additionally, combining the species distributions in each genus and family produced higher taxonomic rank analyses.



Figure 1 Maps of previous studies of zoogeographical regions in China. (a) Seven zoogeographical regions are labelled and were redrawn from Zhang (1999). The thick black lines and black lines indicate the boundaries of realms and regions, respectively. (b) Different boundaries between the Palearctic and Oriental realms at a global scale. Maps are in Lambert conformal conic projection.

To avoid area effects on species records, especially for the large counties in western China, we transformed county-level distributions to grid cells for analyses. First, we generated equal-area grid cells of 50×50 km using a Lambert conformal conic map projection. Then, we implemented a simple habitat model to eliminate unlikely species presences in grid cells based on the consistency of the actual environment and empirical knowledge of species habitat preferences (e.g. suitable vegetation and elevation limits) (compare Rondinini *et al.*, 2011; see Appendix S3 for details). We excluded all grid cells with $< 50\%$ land area and < 5 species to minimize the influence of unequal sampling area and low species numbers (Krefl & Jetz, 2010), leaving a total of 3595 grid cells for analyses. To evaluate the sample completeness of our

database, we conducted an incidence-based Chao2 estimate to extrapolate the actual species richness of each grid cell based on a 200×200 km species pool (Soberón *et al.*, 2007) and mapped the ratio of recorded species to estimated species (Appendix S2: Fig. S1).

Species turnover

We used Simpson's dissimilarity index (β_{sim}) to quantify pairwise dissimilarity among grid cells (Krefl & Jetz, 2010; Leprieur & Oikonomou, 2014). We chose β_{sim} because of its robustness to differences in species richness and because it only quantifies the species turnover component of beta diversity (Baselga, 2010), two desirable properties in

bioregionalization (Kreft & Jetz, 2010). The β_{sim} index calculates the species dissimilarity distance between two grid cells as follows:

$$\beta_{\text{sim}} = 1 - \frac{a}{\min(b, c) + a}$$

where a is the number of shared species and b and c are the number of species unique to each grid cell. β_{sim} ranges from 0 to 1, with smaller values indicating lower dissimilarity.

Cluster analysis

We applied unweighted pair-group method using arithmetic averages (UPGMA) hierarchical clustering to the dissimilarity matrix. UPGMA produces a dendrogram displaying the hierarchical relationships of all grid cells and has been shown to consistently perform best in global-scale biogeographical regionalization (Kreft & Jetz, 2010). We assessed the performance of UPGMA in transferring the dissimilarity matrices into dendrograms using cophenetic correlation coefficients. Three UPGMA results were produced and compared using (1) grid-based species (genus/family) assemblages; (2) regional taxa lists of the grid-based outputs; and (3) weighted dissimilarity matrices relative to the species numbers (0.35 for amphibians, 0.30 for reptiles, 0.10 for birds and 0.25 for mammals).

To compare our results to previous studies and to test for levels of cross-taxon congruence, we used three criteria in choosing a suitable cut-off point in the dendrograms: (1) regions should not be disjunct; (2) the number of regions should vary between 6 and 10, following Zhang (1999); and (3) the number of regions should perform best with sum-of-squares (Krzanowski & Lai, 1988).

Ordination analysis

Non-metric multidimensional scaling (NMDS) was performed to investigate whether a zoogeographical transition zone exists in eastern China. Grid cells in the NMDS ordination plots were coloured based on UPGMA cluster membership to visualize the relative distance between zoogeographical regions. Additionally, we plotted external environmental factors as vectors onto NMDS plots (González-Orozco *et al.*, 2013) to detect underlying relationships between faunistic dissimilarity and dominant environmental gradients. We used stress values to assess the fit between the NMDS and the original dissimilarity matrix. Stress values ranged from 0 to 1, with smaller values indicating better NMDS results. Finally, the NMDS results were rotated and rescaled to maximize comparability with geography.

Environmental variables

We investigated four main categories of predictor variables that potentially determine zoogeographical regions: (1) current climate (Buckley & Jetz, 2008), (2) past climate change

(Dobrovolski *et al.*, 2012), (3) vegetation (Mac Nally *et al.*, 2004) and (4) geological processes (Badgley, 2010). Current climatic predictors included mean annual temperature (°C; MAT), mean annual precipitation (mm; PRE), temperature seasonality (°C; TS) and precipitation seasonality (%; PS). The average climatic conditions for each grid cell were derived from the WorldClim dataset (~1 × 1 km resolution; Hijmans *et al.*, 2005; <http://www.worldclim.org>). Past climate change predictors included temperature change (°C, TC) and precipitation change (°C, PC), which were calculated according to the standard deviation of four climate periods: Current (1950–2000), Last Interglacial (LIG; ~120,000–140,000 yr BP), Last Glacial Maximum (LGM; ~21,000 yr BP) and Mid-Holocene (~6000 yr BP). Dominant vegetation types were sourced from the vegetation map of China (Zhang *et al.*, 2007; Appendix S2: Fig. S2). Topographic predictors, including mean elevation (m, ELE) and elevation range (m, ELER), were derived from digital elevation data (~90 × 90 m resolution) downloaded from the Consortium for Spatial Information (<http://www.cgiar-csi.org/data/srtm-90m-digital-elevation-database-v4-1>). Tectonic plates (TEC) were obtained from Kusky *et al.* (2007) (Appendix S2: Fig. S3) and were digitized using a geographical information system (ArcInfo version 9.3., ESRI, 2008). These data resulted in eight continuous and two categorical variables.

Among the 28 pairwise Pearson correlations of the eight continuous predictors (Appendix S2: Table S2), only two (MAT and PRE; MAT and ELE) were above the commonly used threshold of $|r| = 0.7$ (Dormann *et al.*, 2013). Additionally, we selected predictors based on the Akaike information criterion (AIC) and R^2 values that were not affected by collinearity (Burnham & Anderson, 2002; Cohen *et al.*, 2003). All continuous variables were standardized to have a mean of zero and a variance of one.

Drivers of zoogeographical regions

We used generalized linear models (GLMs) with multinomial logit-link functions to model UPGMA group membership as a multinomial response variable (Rueda *et al.*, 2010). Models including all possible combinations of the 10 variables were calculated and model selection was based on corrected Akaike's information criterion (AICc) scores (Johnson & Omland, 2004). We selected the best model according to the commonly accepted criterion of $\Delta\text{AICc} < 2$ (Burnham & Anderson, 2002). Next, we used deviance partitioning to identify the amount of independent and joint deviance explained by each predictor (Rueda *et al.*, 2010). Only predictors retained in the best models were included.

Cross-taxon congruence

To evaluate the level of cross-taxon congruence, we first carried out separate clustering analyses for the four individual lineages to visualize spatial patterns. Next, we used Mantel

tests (Mantel, 1967) to calculate the correlation coefficients (r_m) for pairs of dissimilarity matrices (β_{sim}). Statistical significance was calculated with a Mantel Carlo permutation test using 999 permutations. We used Kruskal–Wallis tests to test for differences in geographical range sizes among the four lineages which may cause differences in biogeographical regionalizations. The geographical range size was measured as the latitudinal extent and the longitudinal extent occupied by each species (Gaston, 1996).

All analyses were conducted in R version 3.1.2 (R Development Core Team, 2015), using the packages ‘vegan’ (Oksanen *et al.*, 2015), ‘betapart’ (Baselga *et al.*, 2013), ‘NbClust’ (Charad *et al.*, 2014), ‘nnet’ (Venables & Ripley, 2002), ‘MuMIn’ (Bartoń, 2016) and ‘ecodist’ (Goslee & Urban, 2007).

RESULTS

Zoogeographical regions

The UPGMA clustering of grid-based species assemblages yielded 10 major zoogeographical regions for China (Fig. 2a, b): South China, the Yungui Plateau, Taiwan, North China, Northeast China, the Inner Mongolia Plateau, Northwest China, the Longzhong Plateau, the Tibetan Plateau and East Himalaya. A high cophenetic correlation coefficient ($r > 0.8$) indicated good agreement between cluster assignments and the original β_{sim} matrix. The grid cell assemblages of the 10 major zoogeographical regions included a range of β_{sim} values of *c.* 0.93–0.67 (Fig. 2a,b). The boundary between the traditionally accepted Palearctic and Oriental realms in eastern China (*c.* 30° N) emerged at a height of *c.* 0.84 in the dendrogram (Fig. 2a: node 6). Taiwan merged with the nearby mainland at *c.* 0.91 (Fig. 2a: node 8) and the regions of western China and eastern China merged last at *c.* 0.93

(Fig. 2a: node 9). Two small clusters, coloured with grey and nested among South China and North China, were excluded from further discussion.

Clustered regions were also separated in the NMDS (Fig. 2c). The stress value of 0.17 indicated relatively good projection of the dissimilarity matrix into the two-dimensional ordination space. The change in faunistic composition in western China was discontinuous: Northwest China, the Tibetan Plateau, the Longzhong Plateau and East Himalaya were distinctly separated from each other (Fig. 2b,c). Conversely, there was a gradual transition in faunistic composition in eastern China. In particular, grid cells belonging to North China largely overlapped with grid cells belonging to Northeast China and South China.

The UPGMA clustering of grid cell assemblages based on a higher taxonomic level showed some differences. At the family level, only four large clusters were identified, but the major separation between western China and eastern China remained valid (Fig. 3a). At the genus level, clustering showed geographical patterns similar to those at the species level with two exceptions: the Longzhong Plateau and East Himalaya merged and the Yungui Plateau and South China merged at the genus level (compare Fig. 3b with Fig. 2b), yielding eight major regions.

Drivers of zoogeographical regions

When relating environmental factors to the NMDS ordination, mean annual precipitation, temperature seasonality and mean elevation emerged as the most important factors (Fig. 2c). The vector for PRE separated grid cells located in Southeast China, where the climate was strongly monsoonal with high precipitation from grid cells in the very dry environment of Northwest China. Alpine environments in the

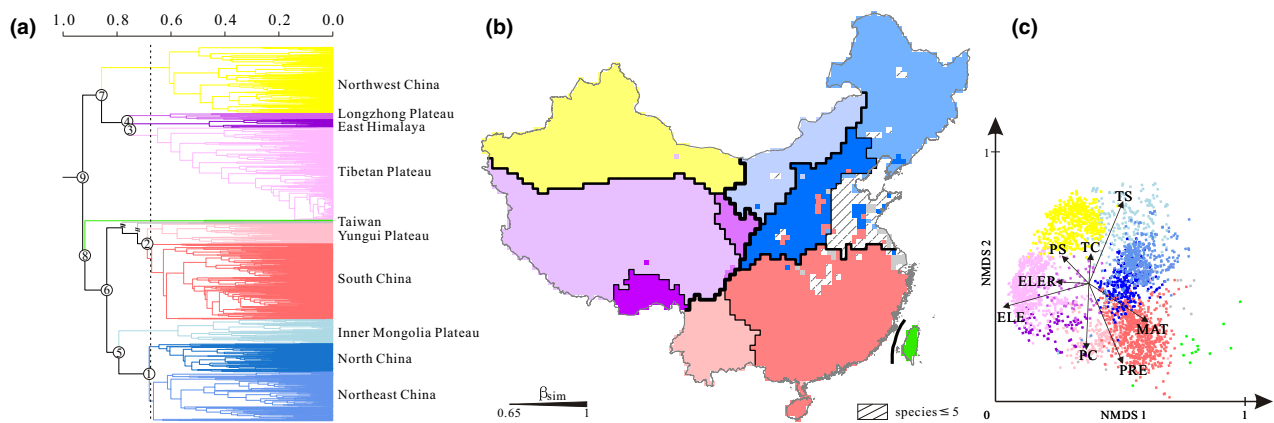


Figure 2 Zoogeographical regionalization for the terrestrial vertebrates of China. (a) Dendrogram from UPGMA hierarchical clustering of grid-based species assemblages. The phenon line indicates the cut-off location and nine main nodes are labelled in sequence. The cophenetic correlation coefficient is 0.82. (b) Map showing the results from UPGMA clustering on a 50 × 50 km grid. The map is in Lambert conformal conic projection. (c) NMDS ordination based on the β_{sim} dissimilarity matrix of grid cell assemblages and the stress value is 0.17. The grid cells with less than five species are not shown in the ordination. The NMDS result is rotated and rescaled to maximize consistency with geography. Eight continuous environmental variables are fitted to interpret the ordination. All variables in this analysis are highly significant ($P < 0.001$).

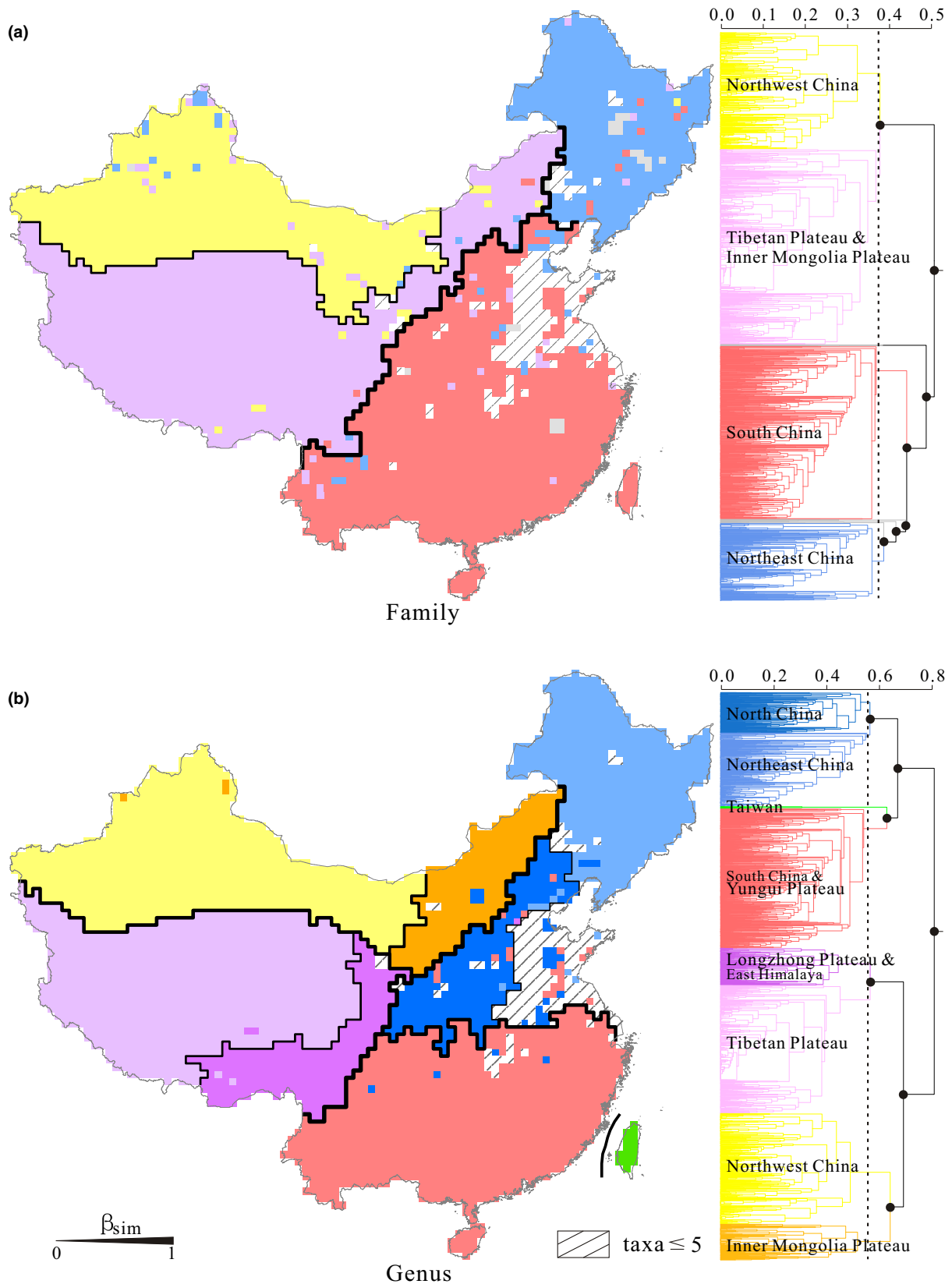


Figure 3 Dendrograms and maps of UPGMA clustering for terrestrial vertebrates at the (a) family and (b) genus levels. Cophenetic correlation coefficients for cluster analyses are 0.50 for the family level and 0.73 for the genus level. The maps are based on a 50×50 km grid and are in Lambert conformal conic projection.

Tibetan Plateau were characterized by positive mean elevation vectors and elevation range vectors.

In single-predictor GLMs (Table 1), factors reflecting vegetation types explained the highest amounts of deviance (57%). Geological processes ranked high in explaining deviance, with tectonic plates ranking second (55% of the deviance explained) and mean elevation ranking fourth (42% of the deviance explained). Current climate, which included temperature seasonality, mean annual precipitation and mean annual temperature, also explained large amounts of the deviance (45%, 40% and 39%, respectively). When all ten factors were considered in multiple regression GLMs (Table 1, Appendix S2: Table S3), the best model ($\Delta AICc < 7$; Akaike weight = 0.98) explained 90% of the deviance and included all predictors except vegetation types, mean annual temperature and precipitation change.

According to the deviance partitioning analysis (Fig. 4), geological processes accounted for most of the deviance explained independently (8.3%) followed by current climate (7.1%). These two groups of predictors also jointly explained the highest percentage of deviance (61.0%). Past climate change explained only 0.8% of deviance independently and 7.6% of deviance jointly with current climate and geological processes.

Cross-taxon congruence

Mantel tests on the β_{sim} matrices showed the highest correlation between mammals and birds ($r_m = 0.74, P < 0.001$), followed by mammals and reptiles ($r_m = 0.71, P < 0.001$), and

Table 1 Results from generalized linear models investigating the effects of current climate, past climate change, vegetation and geological processes on zoogeographical regions in China.

Variables	Best model	Variable importance	R ²
Mean annual temperature	–	0.02	0.39
Mean annual precipitation	+	1	0.40
Temperature seasonality	+	1	0.45
Precipitation seasonality	+	1	0.18
Temperature change	+	1	0.14
Precipitation change	–	<0.01	0.22
Vegetation types	–	<0.01	0.57
Mean elevation	+	1	0.42
Elevation range	+	0.98	0.09
Tectonic elements	+	1	0.55
AICc	1671.7	–	–
Akaike weight	0.98	–	–
R ² _{model}	0.90	–	–

‘+’ indicates variables included in the best model ($\Delta AICc \leq 2$); AICc is Akaike’s information criterion corrected for a small sample size; Akaike weight is the probability of one model being in favoured over alternative models; R²_{model} is the deviance explained by the best model; Variable importance is the relative importance of each variable calculated by the sum of the Akaike weight of models including them; R² is the deviance explained by each factor in single-predictor models.

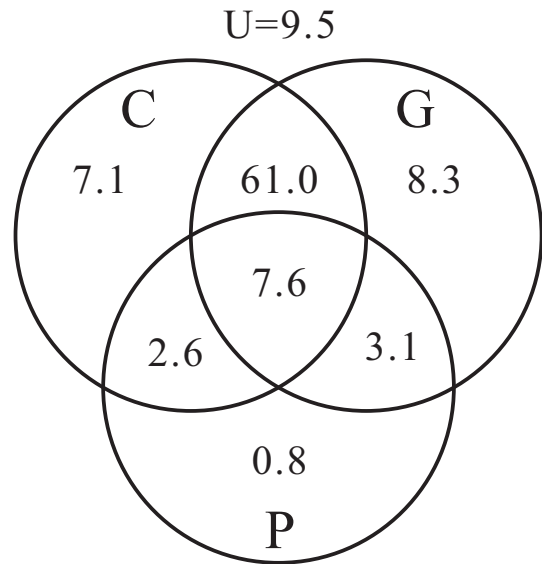


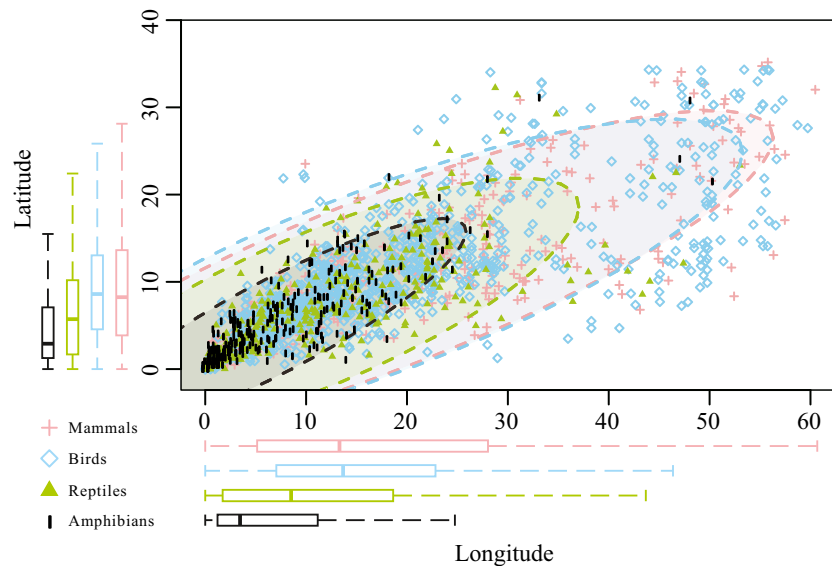
Figure 4 Partitioned deviances of the three main categories used in investigating the assignment of the zoogeographical regions. Predictors are derived from the best model in GLMs: C (current climate: mean annual precipitation + precipitation seasonality + temperature seasonality); G (geological processes: mean elevation + elevation range + tectonic elements); P (past climate change: temperature change); U (unexplained).

the lowest correlation between mammals and amphibians ($r_m = 0.58, P < 0.001$; Table 2). When controlling for spatial autocorrelation (geographical distance), the pairwise partial correlation coefficients were weaker yet highly significant ($P < 0.001$). The combined dissimilarity matrix corresponded strongly to mammals and birds (both $r_m = 0.91$) and represented all four lineages well (all $r_m > 0.75, P < 0.001$). The four vertebrate lineages showed significant differences in range size (Kruskal–Wallis test, $P < 0.001$; Fig. 5). Mammals and birds occupied relatively larger spatial extents (the medians were 13.4 longitudes, 8.3 latitudes for mammals and 13.4 longitudes, 8.7 latitudes for birds) than reptiles and amphibians (the medians were 8.4 longitudes, 5.8 latitudes for reptiles and 3.5 longitudes, 2.9 latitudes for amphibians). Moreover, the dendrograms and maps of the four individual groups yielded noteworthy differences in the topologies and assignments of zoogeographical regions (see

Table 2 Mantel correlation coefficients (r_m) among pairs of taxa measured by Mantel (above diagonal) and partial Mantel (below diagonal) tests based on β_{sim} matrices. Spatial autocorrelation was accounted for in the partial Mantel test by including a geographical distance matrix. All tests were highly significant ($P < 0.001$).

	Combined	Mammals	Birds	Reptiles	Amphibians
Combined	–	0.91	0.91	0.81	0.76
Mammals	0.86	–	0.74	0.71	0.58
Birds	0.86	0.62	–	0.66	0.63
Reptiles	0.70	0.56	0.47	–	0.60
Amphibians	0.68	0.43	0.51	0.44	–

Figure 5 Species geographical range sizes for each lineage in China. Geographical range size is estimated as the latitudinal extents and longitudinal extents occupied by each species. Ellipses indicate 95% confidence intervals. Vertical and horizontal box-and-whisker plots stand for the latitudinal extents and longitudinal extents occupied by the four groups. Outliers are not shown. The range sizes (i.e. latitudinal extents and longitudinal extents) between endotherms and ectotherms are significantly different (Kruskal–Wallis test, $P < 0.001$).



Appendix S2: Fig. S4 for details). The dendrograms of mammals and birds divided China into a western part and an eastern part, whereas the dendrograms of reptiles split the Tibetan Plateau and the dendrograms of amphibians spilt Taiwan from the rest of China. Reptiles and amphibians tended to have more divided regions in the tropical–subtropical zone, but the configurations of regions for mammals and birds were more balanced.

DISCUSSION

Zoogeographical regions

The zoogeographical regions revealed by UPGMA clustering (Fig. 2b) were largely consistent with the expert-based scheme of Zhang (1999) (Fig. 1a). For example, Northeast China and North China matched well with Zhang (1999), and Northwest China and the Inner Mongolia Plateau combined coincided with Zhang's Northwest China region (compare Fig. 2b to Fig. 1a). However, some discrepancies emerged. First, we did not find support for a distinction between South China and Central China (Fig. 1a, Fig. 2), and the UPGMA only identified a single South China region (Fig. 2). This finding was consistent with other mammalian studies claiming that the boundary between Central China and South China is not significant and that Central China is best considered as part of a larger South China region (Xiang *et al.*, 2004). Second, Taiwan was previously regarded as a subregion of South China (Fig. 1a; Zhang, 1999). However, UPGMA clustering identified Taiwan as a distinct region due to the island's unique fauna and high levels of endemism (Lei *et al.*, 2007; Fig. 2a,b). The distinct position of Taiwan was detected for the combined dataset, for each individual vertebrate group, and occurred at the species and genus levels (Figs 2 & 3b; Appendix S2: Fig. S4). Although the relationships between Taiwan and South China were closer at the genus level, the status of Taiwan as a distinct region

appears to be justified. High avian endemism for Taiwan has been reported before (Lei *et al.*, 2003), and recent phylogenetic studies on birds provide evidence that a considerable number of Taiwanese endemic species originated from Indochina rather than from the nearby mainland (Wang *et al.*, 2013; Chen *et al.*, 2015), supporting Taiwan as a distinct region. Third, and also unexpectedly, the Longzhong Plateau, which was not previously regarded as a distinct region, was clearly separated from the Tibetan Plateau in hierarchical clustering (Fig. 2). Even at the genus level, the combined Longzhong Plateau and East Himalaya regions were identified (Fig. 3b), indicating distinct fauna from surrounding regions. This distinction occurred because the Longzhong Plateau region is located at the point of convergence of lineages from the north–south and east–west and is characterized by a uniquely mixed species composition instead of high levels of endemism (Appendix S2: Table S4). Such an area may also be considered a transition zone (Ferro & Morrone, 2014; Morrone, 2015), but following the classical regionalization system, we regard the Longzhong Plateau as an independent region.

Noteworthy, some differences emerged when contrasting the three UPGMA results produced by the grid cells (Fig. 2a), regional lists (Appendix S2: Fig. S6a) and weighted dissimilarity matrix (Appendix S2: Fig. S6b). For instance, the Yungui Plateau recognized in the grid-based analysis was divided into three parts in the weighted dissimilarity matrix analysis (Appendix S2: Fig. S6b). Due to greater weights for amphibians and reptiles, species turnover in the combined weighted dissimilarity matrix produced sharper changes between tropical and mountainous areas and resulted in unbalanced assignments of zoogeographical regions (temperate regions were much bigger than tropical regions). Therefore, unless dealing with a specific question related to the impact of weighted species numbers or weighted species occurrences on bioregionalization, the traditionally accepted grid-based approach without weights is preferable (Linder

et al., 2012). Furthermore, the Yungui Plateau had a closer affinity to South China in the grid-based result, whereas in the analysis based on regional lists, the Yungui Plateau was closer to East Himalaya. This may be attributed to the fact that zoogeographical regions based on whole regional lists share more linking species than single grid cells (Kreft & Jetz, 2010). Although there were inevitably discrepancies among the different approaches, the assignments of the main zoogeographical regions were consistent. The most important boundary, at *c.* 105° E, first split western China and eastern China, followed by the latitudinal boundary at *c.* 30° E, which split eastern China into South China and North China. Next, western China was separated into Northwest China, the Tibetan Plateau and East Himalaya. Taiwan was identified consistently in all approaches. We, therefore, advocate the grid-based scheme because of its objective operational geographical units (Kreft & Jetz, 2010) and equal weight for each individual species (Linder *et al.*, 2012).

Palaeartic-Oriental boundary

East Asia is a region with complex interchange between tropical Oriental and temperate Palaeartic faunas (Procheş & Ramdhani, 2012; Morrone, 2015). Thus, establishing a discrete boundary between these two realms is very difficult and has resulted in many different proposals owing to differences in methods, taxa, taxonomic ranks, grain sizes or spatial extents (Wallace, 1876; Hoffmann, 2001; Kreft & Jetz, 2010; Heiser & Schmitt, 2013; Holt *et al.*, 2013). According to our results, however, the traditionally accepted boundary at *c.* 30° N only emerged at $\beta_{\text{sim}} = c. 0.84$, whereas the boundary between western and eastern China emerged at $\beta_{\text{sim}} = c. 0.93$ and was located at *c.* 105° E, indicating that northern and southern China had smaller dissimilarity than western and eastern China (Fig. 2a). A strong east–west separation was also supported at a higher taxonomic rank (Fig. 3). This situation may be attributed to the interchange between northern and southern fauna caused by unstable climate change in eastern China during the Pleistocene period (Norton *et al.*, 2011). However, due to the elevational barrier of the Tibetan Plateau and the very dry environment of Northwest China, species dissimilarity between eastern China and western China is greater. Therefore, as hierarchical clustering first distinguished eastern China and western China (Fig. 2a,b), we suggest that the Palaeartic-Oriental boundary in China is more likely to be of north–south orientation than the traditionally accepted east–west orientation. This finding is generally consistent with the global scheme proposed by Kreft & Jetz (2010) (compare Fig. 2 and Fig. 3 to Fig. 1).

Drivers of zoogeographical regions

Current climate emerged as a major determinant of zoogeographical regions in general and as a determinant of the strong east–west differentiation in particular. These results

were consistent with previous findings by Wang *et al.* (2012) who found that environmental effects determined longitudinal patterns of woody plants in China. Because of its pronounced aridity, Northwest China is inhabited mainly by drought-tolerant species, and the Tibetan Plateau is characterized by a fauna adapted to high altitudes, excessive drought, severe coldness and low oxygen levels (Yin, 1994). South China, in contrast, harbours numerous arboreal vertebrate species that are confined to the subtropical zone, which reaches its limit at $\sim 30^\circ \text{N}$ in eastern China (Zhang, 1999).

Our results also highlight a strong role of geological processes in shaping zoogeographical regions. For instance, although environmental conditions in Taiwan are similar to those in the nearby mainland (Appendix S2: Fig. S5), Taiwan was clearly identified as a distinct region due to the geographical isolation caused by its island setting. Tectonic plate membership, as a surrogate for historical effects (Keith *et al.*, 2013), had high R^2 value in our single-predictor models and, together with the two elevation-related variables, independently explained the highest deviance in the multi-predictor GLMs (Table 1, Fig. 4). Tectonic plates and continent boundaries are important in understanding the underlying relationships between geological events and the formation of zoogeographical regions (Wallace, 1876; Kreft & Jetz, 2010), but their effect on geological history at the regional scale is less clear. Our faunistic regions showed a good match to geological elements in China. For example, the border of the Tibetan Plateau region was strikingly similar to the borders of the Alpine–Himalaya orogen, the Songpan Ganzi orogen and the Central China orogen. South China matched the Yangtze Craton and the Cathaysia Craton, and North China matched to the North China Craton (Kusky *et al.*, 2007; compare Fig. 2b to Appendix S2: Fig. S3).

Cross-taxon congruence

Congruence between endotherms and ectotherms was relatively low and the individual UPGMA dendrograms showed considerable differences (Table 2; Appendix S2: Fig. S4). These patterns may be attributed to different basic underlying traits, particularly sensitivity to environmental conditions (Buckley & Jetz, 2007), range size and dispersal ability (Rueda *et al.*, 2010; Fig. 5). Ectotherms are assumed to have higher sensitivity to climatic conditions (Buckley & Jetz, 2007) and lower dispersal ability (Fig. 5). Therefore, zoogeographical regions based on ectotherms tended to be smaller in tropical–subtropical and mountainous areas (e.g. the Yungui Plateau) and tended to be bigger in temperate and flat areas (e.g. Northwest China) (Appendix S2: Fig. S4; compare Chen & Bi, 2007). Mammals and birds, in contrast, have larger ranges (Pimm *et al.*, 2014) and were less influenced by the environment. Consequently, changes in species composition were more gradual (Appendix S2: Table S4). Together, these results explain the low congruence between endotherms and ectotherms. Interestingly, the regionalization for mammals generally corresponded most closely to the combined

regionalization (compare Appendix S2: Fig. S4a to Fig. 2b; Table 2), supporting the use of mammals as a model group for zoogeographical regionalization (Wallace, 1876; Hagmeier & Stults, 1964; Smith, 1983; Heikinheimo *et al.*, 2007; Kreft & Jetz, 2010; Escalante *et al.*, 2013).

Potential caveats

Our study has several limitations. First, grid cells with less than five species (particularly for amphibians and reptiles) caused by either ecologically restricted environments or deficient sampling would bias our results. Distributions derived from field surveys and faunistic books were also prone to spatial differences in sampling effort (compare Meyer *et al.*, 2015). In particular, vertebrates sampling was incomplete in southeastern China and the North China Plain (Yang *et al.*, 2013) due to the low collection intensity (Appendix S2: Fig. S1). The robustness of the simple habitat model that converted county-level records into grid cells also represented a potential problem. Fine-scale mapping of species distributions in China is a challenging and ongoing mission (Yang *et al.*, 2013), but despite these shortcomings, our study was the first to use a grid-based database consisting of nearly all terrestrial vertebrates to delineate zoogeographical regions of China. Second, similarity measures might fail to reveal historical relationships among zoogeographical regions (Escalante *et al.*, 2013), meaning that regions obtained by cluster analyses lack evolutionary support. For historical biogeography, analyses under the criterion of endemism (e.g. parsimony analysis of endemism and endemism analysis) should be used (Morrone, 2015). It should be noted that to understand the current spatial patterns of biodiversity in China, we defined a biogeographical region as a regional species pool with a maximum internal similarity and with maximum differences compared with other regions (Kreft & Jetz, 2010; Linder *et al.*, 2012). From this point of view, biogeographical regionalizations based on species (genus/family) similarity proved to be valid (Cox, 2010; Kreft & Jetz, 2010; Procheş & Ramdhani, 2012). Finally, from a methodological point of view, although hierarchical clustering is an effective tool for bioregionalization, it has an inherent limitation in dealing with transition zones (Kreft & Jetz, 2013). Refining and combining different approaches, such as clustering (Kreft & Jetz, 2010), ordination (Williams *et al.*, 1999) and network analyses (Vilhena & Antonelli, 2015), are promising for future studies.

CONCLUSIONS

Biogeographical regionalizations, based on detailed species distributions from different lineages and multivariate techniques, provide new insights into biogeography and put biogeography on a quantitative footing. Here, we used a quantitative framework and proposed an updated scheme for the zoogeographical regions of China, a country with outstanding vertebrate diversity.

Our study yielded four main results: (1) In contrast to previous studies, we found support for Central China being a part of South China, and the Longzhong Plateau and Taiwan were identified as two new regions. (2) Overall, our results provide ample support for a broad biogeographical transition zone in East Asia and provide a fresh, regional perspective suggesting that the Palaeartic–Oriental boundary inside China has a more strongly south–north orientation rather than the conventionally accepted east–west orientation. (3) The zoogeographical regions for China are significantly influenced by complex interplay between topography, geological context and current climate. (4) Although the configurations of zoogeographical regions for the four lineages showed some discrepancies, our scheme held up well for each group.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Data source of species distributions.

Appendix S2 Additional information of analyses.

Appendix S3 Framework of habitat suitability model.

BIOSKETCH

Jiekun He is a PhD student with interests in biogeography and biodiversity. He specifically focuses on distribution patterns of terrestrial vertebrate and gradients of biodiversity.

Author contribution: H.K. and J.H. conceived the ideas for this study; H.J., E.G., Z.W. and J.H. contributed the data; J.H., H.K. and H.J. analysed the data; and J.H., H.K. and H.J. led the writing.

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