

Cenozoic evolution of beta diversity and a Pleistocene emergence for modern mammal faunas in China

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Abstract

Aim: Historical changes in community structure underlie modern spatial diversity patterns, but few empirical studies have focused on the variation in the community composition of fossil assemblages at large spatio-temporal scales. We investigated how the spatial differentiation of mammal communities changed in China throughout the Cenozoic in response to tectonic uplift and palaeoclimatic changes and explore the timing of the emergence of the modern spatially structured faunas.

Location: China.

Time period: Cenozoic (from 65 Ma to the present).

Major taxa studied: Terrestrial mammals.

Methods: We used a compiled database of the distributions of fossils and extant mammals to compare the multiple-site beta diversity among families and genera within six time intervals of the Cenozoic using Sørensen dissimilarity (β_{sor}) and Simpson dissimilarity (β_{sim}). To investigate the timing of the emergence of the modern spatially structured faunas, we applied hierarchical clustering and non-metric multi-dimensional scaling ordination based on pairwise β_{sim} among seven zoogeographical regions for each time slice.

Results: The multiple-site beta diversity at the family level displayed hump-shaped changes during the Cenozoic, and it peaked in the Eocene and gradually decreased towards the present. However, the genus-level multiple-site beta diversity remained rather constant throughout the Cenozoic. Pronounced variations in the relationships among the zoogeographical regions were revealed in both the cluster analyses and the ordinations. The modern spatial structure of mammal faunas at the family level was broadly similar to those observed in the Pliocene and Pleistocene.

Main conclusions: The spatial differentiation of mammal faunas in China dates back to the Eocene and pre-dates the formation of modern topography and climate. Throughout the Cenozoic, the spatial structure of mammal faunas was reorganized by an interplay of the uplift of the Tibetan Plateau, the emergence of the monsoon system and global macroevolutionary processes. The modern relationships among zoogeographical regions at the family level were established in the Pleistocene.

KEYWORDS

beta diversity, China, fossil, hierarchical clustering, ordination, Tibetan Plateau, turnover, zoogeographical region

1 | INTRODUCTION

Understanding how contemporary biodiversity patterns are influenced by regional-scale processes that operate over evolutionary time-scales is a fundamental goal in biogeography (Mazel et al., 2017; Platnick & Nelson, 1978; Ricklefs, 2004). Beta diversity indicates the change in community composition across space (Whittaker, 1960) and represents a central concept in macroecology, biogeography and biodiversity conservation (Barton et al., 2013) and it is useful to studies on the changes in community structures in space and time (Anderson et al., 2011). Recent beta diversity studies on different taxa and in different regions (e.g., Alahuhta et al., 2017; Dobrovolski, Melo, Cassemiro, & Diniz-Filho, 2012; König, Weigelt, & Kreft, 2017; Mazel et al., 2017; Svenning, Fløjgaard, & Baselga, 2011) have advanced our knowledge on the mechanisms that shape modern diversity patterns. However, studies on beta diversity that focus on fossil assemblages across space and deep time are scarce (Darroch, Webb, Longrich, & Belmaker, 2014; Tomašových & Kidwell, 2009; Xing, Gandolfo, & Linder, 2015) and, consequently, the role of historical community changes in structuring modern biodiversity remains poorly understood (White, Ernest, Adler, Hurlbert, & Lyons, 2010).

For terrestrial environments at large spatial scales, two primary patterns of spatial beta diversity through time are expected: biotic differentiation or homogenization. First, spatial beta diversity may increase owing to mountain uplift and climatic differentiation. Mountain uplift creates barriers to species dispersal and promotes biotic differentiation via isolation and speciation (Badgley et al., 2017; Barton et al., 2013; Pisano et al., 2015). Climatic differentiation, in turn, increases environmental heterogeneity, filtering out those species that cannot survive in specific habitats (Xing et al., 2015). Second, spatial beta diversity may decrease because of biotic interchange; for example, the closure of the Isthmus of Panama in the Neogene and the emergence of the Beringian land bridges during the Quaternary glacial maxima provided considerable connections for biotic interchange (Bacon, et al., 2015; Cook et al., 2009). In such circumstances, dispersal or immigration can contribute to more shared species and lower the opportunity for lineage differentiation or speciation, resulting in increased community similarity (Olden & Rooney, 2006). Consequently, the current patterns of beta diversity and faunistic differentiation are proposed to be shaped by a combination of environmental filtering, historical differences and biotic interactions (Alahuhta et al., 2017; Daru, Elliott, Park, & Davies, 2017).

Using estimates of beta diversity, recent studies have explored the processes that drive the temporal changes in spatially structured biota in deep time (Mazel et al., 2017; Xing et al., 2015). So far, two methods have been used to address this issue. One method is to infer historical biotic changes by estimating beta diversity patterns along phylogenetic time-scales (e.g., Cowma, Parravicini, Kulbicki, & Floeter, 2017; Mazel et al., 2017); another method uses fossil collections (e.g., Graham et al., 1996; Xing et al., 2015). The former method, which is based on molecular phylogenetic data, provides a transparent taxonomic assignment and successive time slices of changes in beta diversity (Mazel et al., 2017),

shedding light on biodiversity changes in deep time (Daru et al., 2017). However, this approach is not without problems (Marshall, 2017), considering past extinctions and the potential for geographical range shifts (Silvestro et al., 2016). Palaeontological data, in contrast, represent a record of the composition of real communities (Kidwell & Flessa, 1995). When integrated with estimates of beta diversity, these data can offer an unprecedented opportunity for investigating the long-term dynamics of terrestrial faunas (Darroch et al., 2014; Graham et al., 1996). Although measures of beta diversity are difficult to apply to fossil collections because the temporal resolution is generally coarser or more variable than when applied to ecological datasets (Kidwell & Holland, 2002), the time-averaged nature of fossil records provides some advantages (Darroch et al., 2014; Tomašových & Kidwell, 2009). That is, time averaging can minimize the potential effects of short-term environmental fluctuations, allowing for investigations for the effects of processes operating over longer geological time-scales (Kidwell & Flessa, 1995; Tomašových & Kidwell, 2010).

China harbours varied climatic conditions ranging from the tropical to the boreal zone and from the humid zone in the south-east to arid climate in the north-west. China also shows a pronounced topographic heterogeneity, from lowlands to Mount Everest. These diverse environmental gradients give rise to many distinct faunas (He, Kreft, Gao, Wang, & Jiang, 2017). Recently, He et al. (2017) proposed 10 major zoogeographical regions of China based on distributions of extant species. For example, there is a lowland fauna adapted to warm and humid climates in the eastern part of China, a montane fauna adapted to high elevations in the Tibetan Plateau and a drought-tolerant fauna in Northwest China. Previous studies have argued that the historical changes in topography and climate (e.g., uplift of the Tibetan Plateau and glacial oscillations) strongly influenced the long-term changes in the local community composition and underpinned the modern faunistic differentiation of China (Figure 1; Lucas, 2001; Qiu & Li, 2005). However, until recently, few quantitative studies have assessed to what extent these processes shaped the current biodiversity patterns, particularly at a continental scale (He et al., 2017; Tsubamoto, Takai, & Egi, 2004; Wang, Meng, Ni, & Li, 2007). Recently, the collection of new fossils has intensified in China (Lucas, 2001), and fossil occurrences are increasingly available from large databases (e.g., Paleobiology Database; see also Uhen et al., 2013 for review), both of which provide an opportunity to investigate the development of zoogeographical regions in China.

Here, we studied mammals, one of the most suitable terrestrial model groups for historical biogeography owing to their good preservation and rich fossil record (Blois & Hadly, 2009). Based on a recently compiled database of mammal fossil collections and extant distributions, the aims of our study were as follows: (a) to explore the temporal changes in the spatial differentiation of mammal faunas in China during the Cenozoic; and (b) to determine when the modern spatial structure of mammal faunas formed. We placed these temporal changes within the context of geological and climatic events.

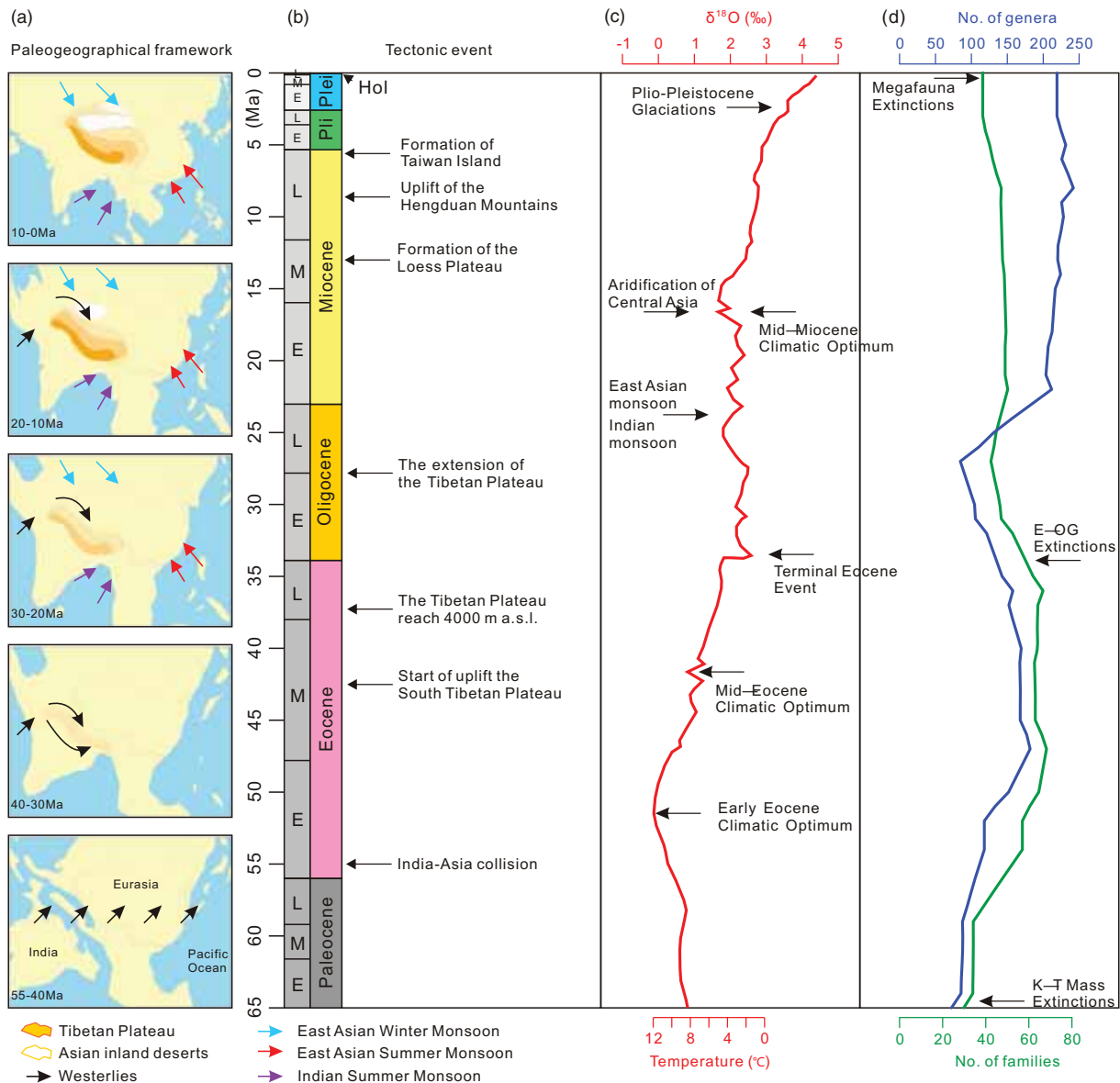


FIGURE 1 Palaeogeographical context and biotic events in China during the Cenozoic. (a) Maps of tectonic movements and major changes in atmospheric circulation. (b, c) Major tectonic events (b) and climatic events (c) during the Cenozoic that were compiled from Favre et al. (2015) and Renner (2016). The global average benthic $\delta^{18}\text{O}$ curve (red line) indicates the global ocean water temperatures and was modified from Zachos et al. (2001). (d) The overall mammal diversity (gamma diversity) of China was calculated by overlapping the range-through of taxa between first and last occurrences within each 1 Myr bin and smoothed by running mean values with a 5 Myr sliding window [Colour figure can be viewed at wileyonlinelibrary.com]

2 | MATERIALS AND METHODS

2.1 | Dataset

Fossil collections of terrestrial mammals in China from the Cenozoic were obtained from different databases: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing (IVPP; <http://www.ivpp.ac.cn/>); the Paleobiology Database (PBDB; <https://www.paleobiodb.org/>); the New and Old Worlds database (NOW; <https://www.helsinki.fi/science/now/>); and the Fossilworks database (<https://fossilworks.org/>) (all accessed on 27 September 2016). Estimates

of the age of mammal fossil occurrences were typically based on stratigraphic units, which commonly included temporal ranges (minimum and maximum ages) instead of a single age estimate (Silvestro et al., 2016). To avoid repeated sampling, we carefully reviewed the fossil assemblages, particularly the spatially closest localities. Furthermore, to minimize the effect of spatial variability in sampling, collections from the same period were regarded as a fauna once localities were within 0.1° of latitude and longitude (Darroch et al., 2014). Although species-level analyses are often used in studies of beta diversity (Darroch et al., 2014), we restricted our analyses to the family and genus levels for the purpose of a more comparable and

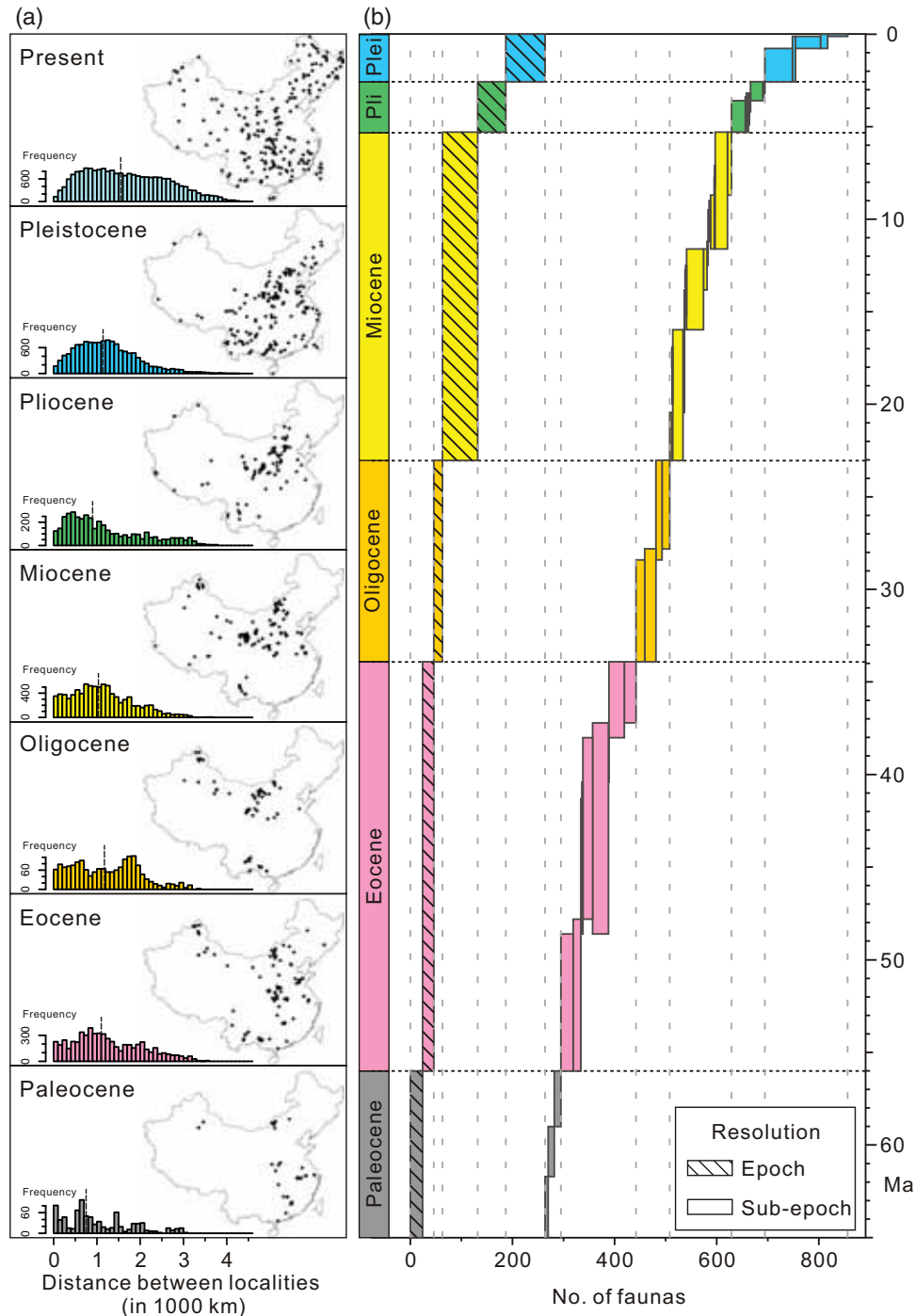


FIGURE 2 Spatial and temporal distribution of fossil collections during the Cenozoic and extant mammal samples in China. (a) Maps showing the sampling localities within six epochs (from the Palaeocene to the Pleistocene) and the present. The bar plots indicate the number of pairwise distances between localities during each time slice, and the dotted lines indicate the medians. (b) Temporal resolutions and distributions of each fauna during the Cenozoic except the present [Colour figure can be viewed at wileyonlinelibrary.com]

more complete sampling (Plotnick, Smith, & Lyons, 2016; Xing et al., 2015). We standardized the taxonomy according to the Paleobiology Database and excluded uncertain taxa with taxonomic modifications such as 'cf.' or '?' and those identified at only higher taxonomic levels (e.g., Carnivora Fam. indet.). We also excluded fossil assemblages with uncertain age estimates and bats, because of their poor preservation in the fossil record (Davis, 2005). The final fossil dataset

contained 4,708 mammal fossil occurrences from 856 faunas from 479 individual localities. These occurrences included 132 families and 871 genera (Figure 2; raw data are provided in Supporting Information Appendix S1).

To investigate the relationships between the historical and modern faunas, the modern faunas were mapped based on extant mammal records derived from a terrestrial vertebrate distribution

database of China that was originally compiled from a national survey, nature reserve reports and published literature (for details, see He et al., 2017; Supporting Information Appendix S1).

2.2 | Spatio-temporal bias in the fossil records

Biodiversity databases often contain strong geographical sampling bias, and this might lead to inaccurate results (Yang, Ma, & Kreft, 2013). In particular, palaeontological data (e.g., fossil records) are prone to bias, because they are usually subjected to differences in preservation rates among taxa and by time averaging and are unevenly

distributed in space and time (Figure 2; Behrensmeyer, Kidwell, & Gastaldo, 2000). First, older stratigraphic units, on average, preserve fewer fossil assemblages (Figure 2a; Villalobos, Carotenuto, Raia, & Diniz-Filho, 2016). Regarding the 856 faunas in our database, sampling varied from 55 faunas recorded in the Palaeocene to 239 faunas in the Pleistocene (Figure 2a; Supporting Information Appendix S2, Table S2.1). Second, the temporal resolution of the majority of fossil mammal collections in China was provided at only the epoch (264 faunas) or sub-epoch (592 faunas) level (Figure 2b). In addition, the duration of an epoch varied from 2.57 Myr (Pleistocene) to 22.1 Myr (Eocene), and the duration of a sub-epoch varied from 0.11 Myr (Late

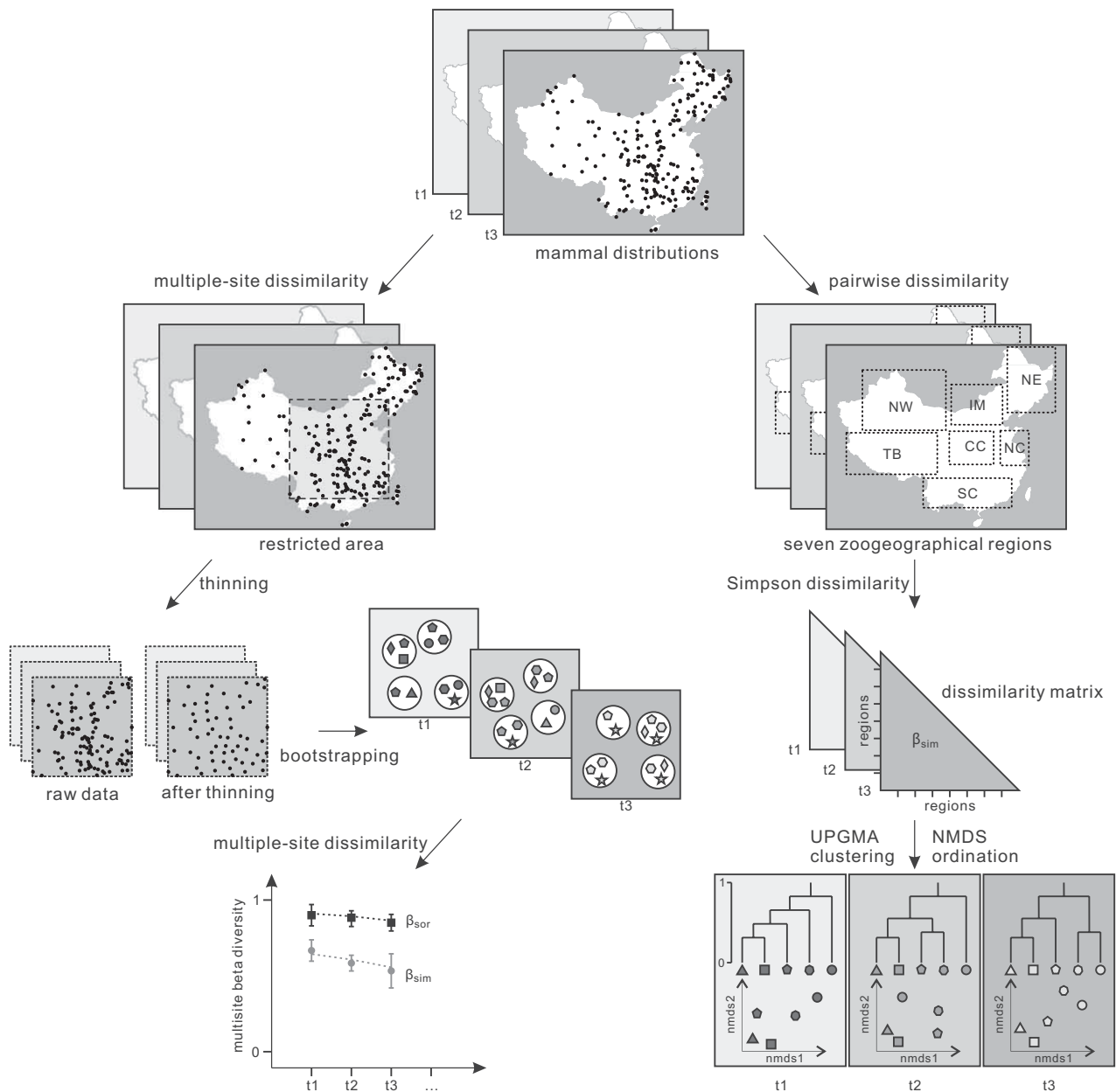


FIGURE 3 Conceptual diagram of the present study for analysing the spatio-temporal beta diversity of the Cenozoic mammal faunas in China. The multiple-site dissimilarities through time reveal the change in the overall spatial differentiation of mammal faunas, and the temporal changes of the pairwise dissimilarities mirror the variations in interrelationships among region pairs. Abbreviations: NMDS = non-metric multidimensional scaling; UPGMA = unweighted pair-group method using arithmetic averages

Pleistocene) to 10 Myr (Middle Eocene). Third, fossil collections are unevenly distributed in space (Figure 2a). Overall, the sampling intensity in Western China is relatively low, particularly on the Tibetan Plateau (Figure 2a). Accordingly, the between-sample geographical distances inevitably varied among different time intervals (Figure 2a); for example, the fossil localities in the Oligocene and Pliocene were, on average, more closely distributed, whereas the Eocene and Pleistocene showed relatively even distributions (Figure 2a). Together, uneven sampling in space and time might introduce a bias. Thus, in the following analyses, we began by evaluating the effects of scale in our fossil dataset and accounted for the sampling bias.

2.3 | Multiple-site beta diversity

To compare the variation in spatial differentiation throughout China through time, we calculated the multiple-site beta diversity of localities (Figure 3) using Sørensen dissimilarity (β_{sor}) and Simpson dissimilarity (β_{sim}) based on the presence and absence of families and genera. Multiple-site beta diversity indices were calculated using the 'betapart' package (Baselga & Orme, 2012) in R v. 3.2.3 (R Development Core Team, 2015). The β_{sor} index indicates total dissimilarity including species turnover and nestedness components, and the β_{sim} index represents only the turnover component and true taxa substitution between communities (Baselga, 2010). For the calculation of beta diversity, we excluded faunas with fewer than five taxa to avoid potential bias of small sample sizes (Davis, 2005). We applied four methods to standardize the sampling effort for estimates of beta diversity, particularly in terms of the time-averaged sampling (Tomašových & Kidwell, 2010), geographical extent of sampling (Barton et al., 2013) and between-sample geographical distance (Darroch & Wagner, 2015). First, we assigned each fossil record to one of six time intervals with relatively equal lengths: Palaeocene (65.0–56.0 Ma), early Eocene (56.0–47.8 Ma), middle–late Eocene (47.8–33.9 Ma), Oligocene (33.9–23.0 Ma), early–middle Miocene (23.0–11.6 Ma) and late Miocene–Pleistocene (11.6 Ma–11.8 Ka). The mean duration of these time intervals was 10.8 Myr (8.2–13.9 Myr). Second, we analysed the fossil collections at two different spatial extents, namely 2,200 km × 2,200 km (c. 20° × 20°) and 3,300 km × 3,300 km (c. 30° × 30°) (Supporting Information Appendix S2, Figure S2.1). Third, we used a 'thinning technique' to account for spatial autocorrelation (Darroch & Wagner, 2015) and the fact that faunistic dissimilarity generally increases with spatial distance (Supporting Information Appendix S2, Figure S2.2). We sub-sampled localities outside a minimum distance of 100 km (Supporting Information Appendix S2, Figure S2.3) and with 100 iterations. Finally, to account for the effect of the number of sites on the multiple-site beta diversity (Baselga, 2010), we randomly sampled five localities at both the family and genus level (based on the minimum number of localities among all periods). We repeated this sampling 100 times and then calculated the mean and standard deviation of the multiple-site beta diversity. We used locally weighted scatterplot smoothing (LOWESS) trend lines to visualize the overall trends in the spatial beta diversity. Given

that fossils in the late Miocene to Pleistocene period are relatively well sampled, the between-sample distances were much closer in that period than in any other periods (Supporting Information Appendix S2, Figure S2.2); thus, we repeated all analyses by sub-sampling localities within this period with a threshold of 500 km (Supporting Information Appendix S2, Figure S2.3). The results were consistent with those with a threshold of 100 km (Supporting Information Appendix S2, Figure S2.4); thus, we report only the results from the 100 km threshold in the main text.

2.4 | Pairwise beta diversity

Multiple-site beta diversity reveals the overall spatial differentiation of mammal faunas, whereas pairwise beta diversity mirrors the interrelationships between region pairs (Baselga, 2013). To investigate the timing of when the modern spatially structured faunas of China formed, we calculated pairwise beta diversity among the seven broad zoogeographical regions through time (Figure 3). In this procedure, we used only Simpson dissimilarity because this index is independent of nestedness, relatively insensitive to richness differences (Baselga, 2010) and has been used previously as a useful measure to study the pairwise beta diversity of fossil assemblages (Darroch et al., 2014; Xing et al., 2015). Moreover, we did not assign fossil records to time intervals with relatively equal durations. Instead, we performed analyses at the epoch level to capture the explicit timing of the emergence of the modern spatially structured faunas (Supporting Information Appendix S2, Table S2.2). Thus, we assigned all fossil records to one of six epochs: Palaeocene (65.0–56.0 Ma), Eocene (56.0–33.9 Ma), Oligocene (33.9–23.0 Ma), Miocene (23.0–5.33 Ma), Pliocene (5.33–2.58 Ma) and Pleistocene (2.58 Ma–11.8 Ka). To address the sampling bias, we assigned each mammal record to one of seven coarse-grained primary zoogeographical regions, namely, Northeast China, Inner Mongolia, Northwest China, North China, Central China, the Tibetan Plateau and South China (He et al., 2017). To assess the sample completeness of each region within an individual time period, we documented the spatio-temporal distributions of the fossil records (Supporting Information Appendix S2, Table S2.2) and calculated the incidence-based Chao2 estimator using the 'specpool' function in the 'vegan' R package (Oksanen et al., 2015). The estimators revealed that sampling completeness at the family level was higher than that at the genus level (Supporting Information Appendix S2, Table S2.3). Sampling completeness of the Pliocene was relatively low, and the standard deviation among regions during the Pliocene was large. The undersampled faunas included those of the Central China Palaeocene, Northeast China Eocene, the Tibetan Plateau Miocene, North China and Central China Pliocene, and Northwest China Pleistocene (Supporting Information Appendix S2, Tables S2.3 and S2.4). Although our database inevitably suffered from geographical bias in sampling intensity, time averaging and a coarse spatial resolution should strengthen the confidence in the fossil sample regarding the current availability and spatio-temporal precision of fossil collections (see Discussion below).

We performed non-metric multidimensional scaling (NMDS) and unweighted pair-group method using arithmetic averages (UPGMA) clustering based on the Simpson dissimilarity matrices among the seven regions (Kreft & Jetz, 2010). Different topologies and assignments of clusters in the UPGMA clustering reflected changes in the spatial structures of the mammal faunas. Finally, NMDS ordinations and UPGMA clusterings of regions for each of the seven periods (Palaeocene, Eocene, Oligocene, Miocene, Pliocene, Pleistocene and present) were produced. To maximize the comparability of the pairwise spatial beta diversity of mammal faunas among the seven time slices, region-epoch mammal faunas were plotted in a combined NMDS ordination (see also Supporting Information Appendix S2, Figures S2.5 and S2.6 for the seven individual ordinations). The UPGMA dendrograms were rotated to maximize accordance with the present-day clusters. To examine the temporal variations of the pairwise relationships among the seven regions, we used Mantel tests based on Spearman rank correlations to evaluate the variations of the pairs of β_{sim} matrices through time. Statistical significance was calculated with a Monte Carlo permutation test using 999 permutations.

3 | RESULTS

The family-level multiple-site β_{sor} and β_{sim} displayed general hump-shaped patterns during the Cenozoic at both 2,200 km \times 2,200 km and 3,300 km \times 3,300 km spatial extents (Figure 4). There was a notable increase in multiple-site beta diversity during the Palaeocene–Eocene period, followed by a decrease towards the Pleistocene (Figure 4). The genus-level multiple-site beta diversity showed a different trend. Although a slight increase also occurred in the Eocene, there was not a noticeable decreasing trend towards the Pleistocene (Figure 4). In general, the analyses at the 2,200 km \times 2,200 km and 3,300 km \times 3,300 km spatial extents showed similar trends. Unsurprisingly, the family-level multiple-site beta diversity values were consistently lower than the genus-level analogues ($p < .05$).

The UPGMA dendrograms for the seven time slices yielded striking differences in the topologies and assignments of zoogeographical regions (Figures 5 and 6), as evidenced by the Mantel tests on the pairwise faunistic dissimilarity matrices between time intervals (all Mantel correlations were not significant, $p > .05$; Supporting Information Appendix S2, Table S2.5). These results indicated that the spatial structure of the dissimilarities among these regions changed significantly through time. At the family level, for example, Northwest China was merged with South China in the Palaeocene and then clustered with the other parts of China (Figure 5a). In the Eocene, however, Northwest China first merged with Inner Mongolia, then grouped with Central China and South China and, finally, grouped with North China and Northeast China. During the Oligocene and Miocene, South China emerged as a separate group, showing significantly high dissimilarities to other regions (Figure 5a). During the Pliocene, China was notably divided into an eastern part (including South China and North China) and a

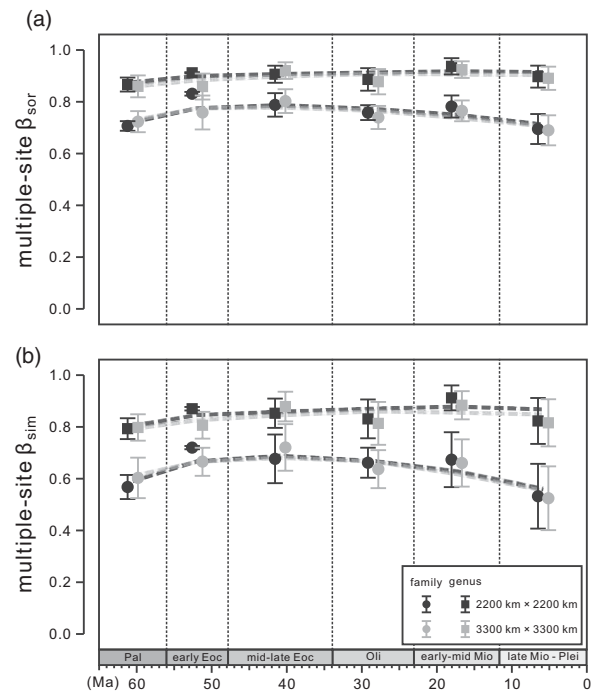


FIGURE 4 Multiple-site beta diversity of mammal faunas in different time intervals. Analyses were conducted using Sørensen dissimilarity (a) and Simpson dissimilarity (b) at the family (circles) and genus (squares) levels, at spatial extents of 2,200 km \times 2,200 km (black) and 3,300 km \times 3,300 km (grey), respectively. The trend lines are the best-fit locally weighted scatterplot smoothing (LOWESS) lines

western part. The recent relationships of the seven zoogeographical regions finally established in the Pleistocene when three major groups were identified: group 1 = the Tibetan Plateau; group 2 = Northwest China + Inner Mongolia + Northeast China; and group 3 = South China + Central China + North China (Figure 5a). That means that the boundary between groups 2 and 3 was largely similar to the Palaearctic–Oriental boundary, and group 1 identified the distinct fauna endemic to the Tibetan Plateau (compare Figure 5a with Supporting Information Appendix S2, Figure S2.7). The genus-level dendrograms were largely consistent with the family-level analogues, but some discrepancies emerged (compare Figures 5a and 6a). For example, in the Pliocene, Inner Mongolia was merged with North China, and Northwest China was first grouped with Central China (Figure 6a). The three major groups that were recognized at the family level in the Pleistocene were not strongly evident at the genus level (Figure 6a).

Notably, large shifts occurred in the relationships between the Tibetan Plateau and the other surrounding regions (Figures 5 and 6), shedding light on the origin and development of the highly endemic fauna on the Tibetan Plateau. In the Miocene, when the earliest mammal fossil faunas were recorded on the Tibetan Plateau, the plateau was merged with Inner Mongolia (Figures 5 and 6). During the Pliocene–Pleistocene, the Tibetan Plateau was generally recognized as a distinct group, except at the family level in the Pliocene (compare Figures 5a and 6a). In the present, although the relationships

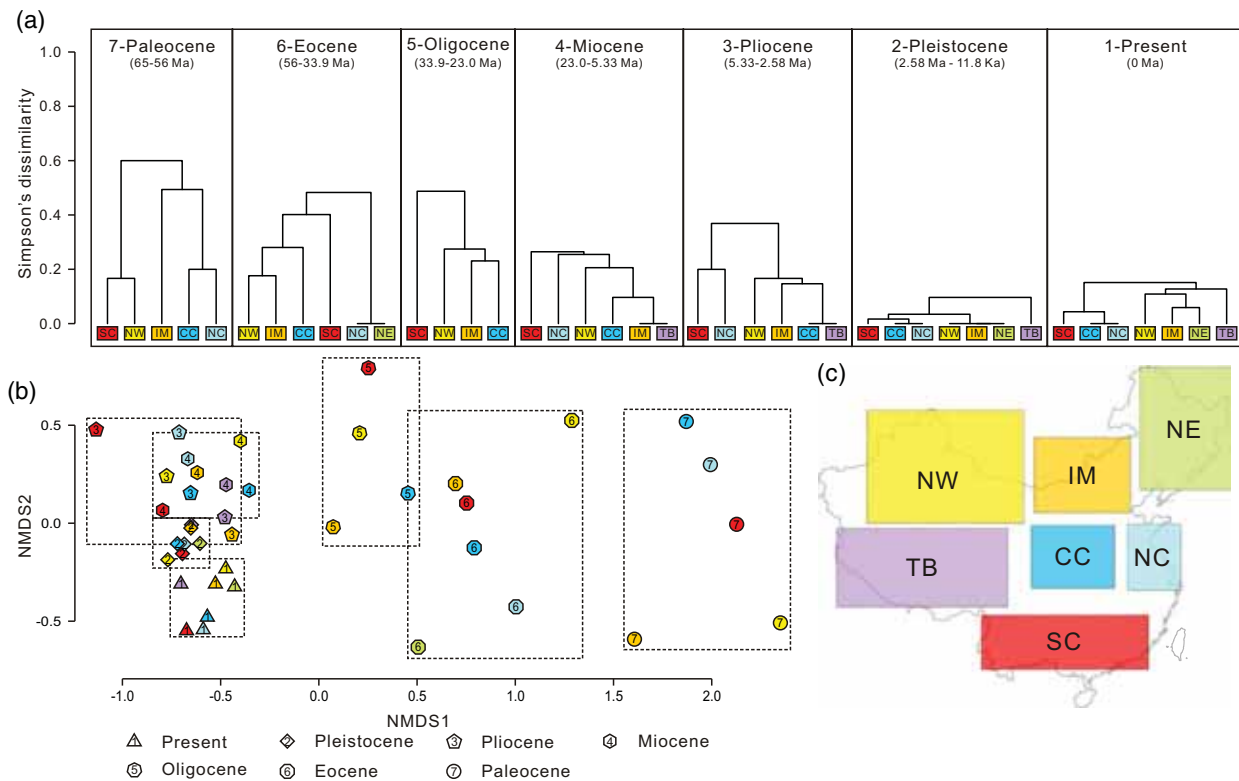


FIGURE 5 Changes in the spatial structure of the mammal communities of China during the Cenozoic at the family level. (a) Dendrograms from the unweighted pair-group method using arithmetic averages (UPGMA) hierarchical clustering of regional mammal lists during six epochs and the present. (b) Non-metric multidimensional scaling (NMDS) ordination based on the β_{sim} matrix of regional mammal assemblages (see also Supporting Information Appendix S2, Figure S2.5 for the seven individual ordinations). (c) Geographical division of the modern zoogeographical regions of China. Abbreviations: CC = Central China; IM = Inner Mongolia; NC = North China; NE = Northeast China; NW = Northwest China; SC = South China; TB = the Tibetan Plateau [Colour figure can be viewed at wileyonlinelibrary.com]

between the Tibetan Plateau and other regions were closer, the status of the Tibetan Plateau as a distinct group continued to be justified (Figures 5 and 6).

The NMDS ordinations generally represented similar interrelationships among regions through time, like the cluster analyses (Figures 5b and 6b). Interestingly, the family-level NMDS ordinations revealed that older faunas were more scattered in the ordination space than younger ones. Even after accounting for the varied durations by combining the faunas recorded during the Miocene to the present (c. 23.0 Myr), the faunas in the Palaeocene (c. 10 Myr) and Eocene (c. 22.1 Myr) still showed greater dispersion (Figure 5b), implying that the faunistic beta diversity among regions was larger in deeper time. Nevertheless, this pattern was much weaker at the genus level (Figure 6b), corroborating the multiple-site beta diversity results (Figure 4).

4 | DISCUSSION

In general, the overall β_{sor} and β_{sim} of mammal faunas increased from the Palaeocene to the Eocene. Afterwards, the family-level multiple-site beta diversity gradually decreased towards the present, whereas the multiple-site beta diversity at the genus level remained

relatively constant. The Cenozoic mammal faunas of China experienced pronounced changes in spatial structure, as indicated by the temporal differences in topologies and structures in the UPGMA and NMDS results. Notably, the modern relationships of the zoogeographical regions at the family level originated in the Pliocene and finally established in the Pleistocene.

4.1 | Effects of spatio-temporal sampling on beta diversity

The quality of the fossil collections is scale dependent and highly variable in taxonomic groups and in spatio-temporal resolutions (Kidwell & Holland, 2002). Accordingly, analyses based on palaeontological data inevitably suffer from effects of scale (McGill, Hadly, & Maurer, 2005), either in space or in time (Behrensmeyer et al., 2000). This calls for a careful assessment of the possible biases in the results.

Time averaging (i.e., the assignment of fossils to a time interval) may lump organisms together that never lived contemporaneously (Behrensmeyer et al., 2000). Although time averaging is almost always inevitable and common in palaeontological studies (Jernvall & Fortelius, 2004), it may affect measures of beta diversity (McGill et al., 2005; Tomašových, Dominici, Zuschin, & Merle, 2014). For

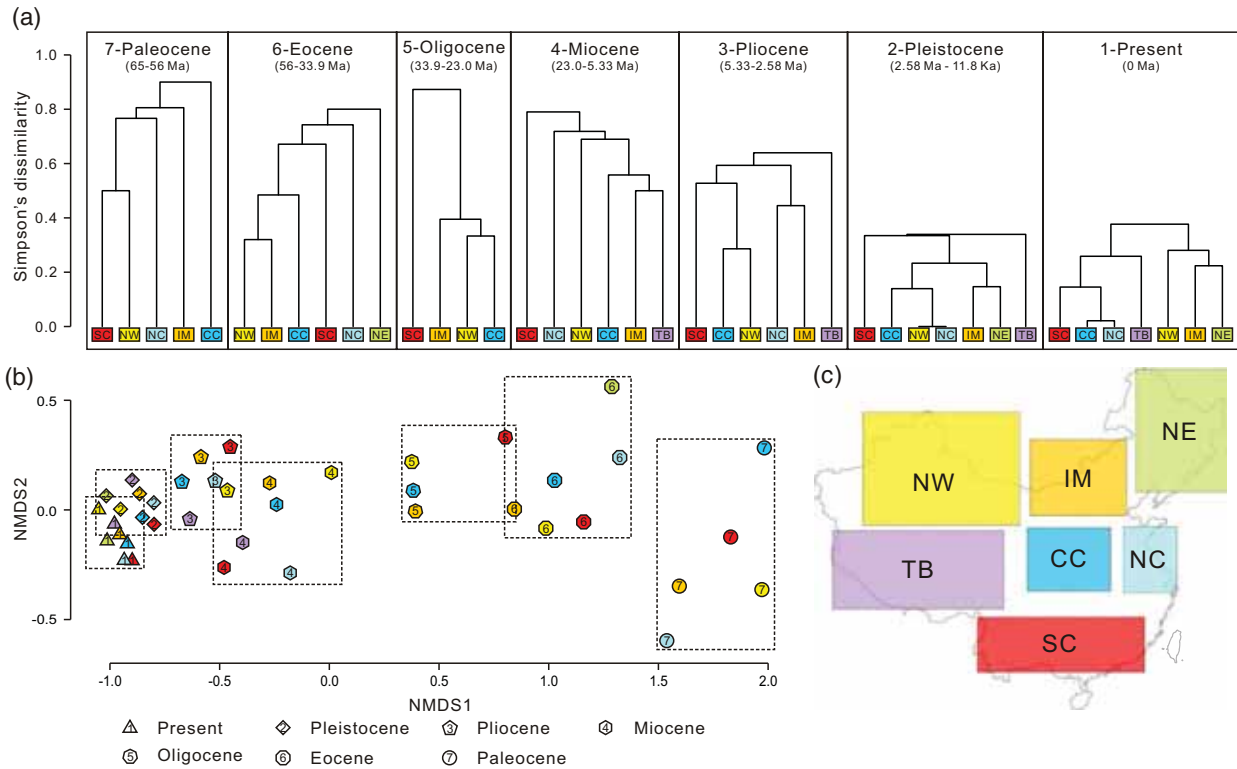


FIGURE 6 Changes in the spatial structure of the mammal communities of China during the Cenozoic at the genus level. (a) Dendrograms from the unweighted pair-group method using arithmetic averages (UPGMA) hierarchical clustering of regional mammal lists during six epochs and the present. (b) Non-metric multidimensional scaling (NMDS) ordination based on the β_{sim} matrix of regional mammal assemblages (see also Supporting Information Appendix S2, Figure S2.6 for the seven individual ordinations). (c) Geographical division of the modern zoogeographical regions of China. Abbreviations: CC = Central China; IM = Inner Mongolia; NC, North China; NE = Northeast China; NW = Northwest China; SC = South China; TB = the Tibetan Plateau [Colour figure can be viewed at wileyonlinelibrary.com]

instance, different time interval durations might introduce bias; with all other things being equal, longer time slices accumulate more species, resulting in lower beta diversity (Tomašových & Kidwell, 2010). In addition, time averaging might bias towards short-living and more abundant taxa (Behrensmeyer et al., 2000), thus concealing important faunistic turnover and biogeographical changes in deep time. However, as noted by Tomašových and Kidwell (2010), palaeontological time averaging can smooth out uninformative short-term fluctuations and is thus a desirable method for large-scale biogeographical analyses based on assemblages with similar temporal resolution. Therefore, measures of beta diversity that are derived from time-averaged fossil assemblages can provide unique insights into the historical variations of community composition (Darroch et al., 2014; Tomašových & Kidwell, 2009).

Second, an uneven spatio-temporal distribution of the fossil records can introduce additional bias (Davis, 2005). Incomplete taxonomic coverage might affect estimates of beta diversity, particularly when completeness varies in space and time (Darroch & Wagner, 2015). Older stratigraphic units tend to be preserved in fewer outcrops and over a smaller area than younger units (Villalobos et al., 2016), and this is also the case in our database (Figure 2; Supporting Information Appendix S2, Table S2.1). Furthermore, the lack of

useful fossil collections on the Tibetan Plateau (before the Miocene) and in Northeast China (before the Pleistocene) makes further interpretation of their palaeontological contexts challenging (Figure 2; Supporting Information Appendix S2, Figure S2.8). In addition, even if the fossils were well sampled, unbalanced between-sample geographical distances within regions and epochs (Supporting Information Appendix S2, Figure S2.9) potentially biases the beta diversity estimates (Darroch & Wagner, 2015). Specifically, when investigating the relationships of the seven broad zoogeographical regions, spatial averaging (i.e., coarser spatial grain) that neglects the differences in the between-sample geographical distances might conceal the real spatial beta diversity to some degree.

Finally, estimates of beta diversity at higher taxonomic levels have also been questioned (Hendricks, Saupe, Myers, Hermsen, & Allmon, 2014). Nonetheless, although species-level data are desirable in evolutionary studies (Hendricks et al., 2014), the recovery of past faunistic changes can be improved based on higher taxonomic levels (Benton, Wills, & Hitchin, 2000). Thus, families and genera are still regarded as effective taxonomic surrogates for palaeontological studies (Darroch et al., 2014; Tsubamoto et al., 2004) and for capturing large-scale patterns on a broad geological time-scale (Benton et al., 2000).

4.2 | Temporal changes in multiple-site beta diversity

Our results reveal that the spatial differentiation in China emerged much earlier than expected, as indicated by the multiple-site β_{SOR} and β_{SIM} at both the family and the genus level (Figure 4). The uplift of the Tibetan Plateau since c. 40 Ma (Renner, 2016) and the aridification in the northern part of China since c. 11 Ma (Figure 1a; Favre et al., 2015; Fortelius et al., 2002) are assumed to have created new habitats, prompted speciation by isolation and divergent adaptation and, ultimately, contributed to the zoogeographical differentiation of China (Li, et al., 2014; Qiu & Li, 2005). Recent phylogeographical studies are consistent with this hypothesis (Pisano et al., 2015; Zhang et al., 2006). However, our results provide palaeontological evidence that multiple-site beta diversity of mammal faunas towards the present was not higher at either the family level or the genus level (Figure 4), indicating that the mammal faunas of China did not witness deeper differentiation despite the pronounced tectonic movements and climatic changes. Instead, such a spatial differentiation probably dates back to the Eocene, when the modern topography and climate were not yet formed (Figure 4), and largely pre-dates the timing proposed by Qiu and Li (2005). This observation is consistent with the results of Du, Ma, Cheng, and Wu (1992), who provided evidence that the faunistic differentiations in China emerged among the Palaeogene mammal assemblages, which was probably caused by considerable archaic taxa and high endemism (Wang et al., 2007).

The family-level multiple-site beta diversity has decreased since the Eocene (Figure 4). This result indicated that despite the uplift of the Tibetan Plateau and the associated restructuring of the landscape, the terrestrial geographical barriers within China are not large enough (compared with straits or oceans) to hinder the biotic exchange of mammals (Li & Wang, 2015). In contrast, newly created habitat, in turn, might facilitate dispersal and, potentially, lead to the expansion of geographical ranges (Pisano et al., 2015; Yang, Dong, & Lei, 2009; for passerine birds, see also Päckert et al., 2012). Furthermore, during the Plio-Pleistocene glacial–interglacial cycles, mammals had to adapt to the climatic changes by shifting their geographical ranges (Norton, Jin, Wang, & Zhang, 2011). Therefore, the decrease of the family-level multiple-site beta diversity towards the present might result from the dispersal and biotic interchange driven by tectonic activity and climatic history (Blois & Hadly, 2009; Davies, Purvis, & Gittleman, 2009).

The genus-level multiple-site beta diversity, however, showed rather different trends, which remained relatively constant throughout the Cenozoic (Figure 4). These differences coincide with the changes in the family and genus gamma diversity (compare Figures 1d and 4). Although overall family diversity decreased in the Oligocene, genus diversity increased markedly (Figure 1d). This result implies that the genus-level diversification events in spatially separated faunas probably increased the multiple-site beta diversity and sustained the high spatial differentiation (Pisano et al., 2015). In China, for example, the uplift of the Tibetan Plateau created new

habitat for mammals that were migrating from the surrounding regions (Li & Wang, 2015; Li, Wang, Xie, & Yin, 2013), lowering the family-level beta diversity. However, more divergent genera and species endemic to the Tibetan Plateau (Yang et al., 2009) can result in a higher genus-level beta diversity.

4.3 | Temporal changes in spatially structured faunas

The spatial structure of mammal faunas was strikingly reorganized throughout the Cenozoic (Figures 5 and 6), and the modern relationships among the zoogeographical regions at the family level were established in the Pleistocene. The high faunistic similarity between Northwest China and South China in the Palaeocene is consistent with the palaeogeographical evidence that neither significant topographic barriers (Zhang, Xia, & Liang, 2002) nor climate divergence (Zhang, Wang, Guo, & Jiang, 2007) hindered faunistic interchange between these two regions (Figure 1a). Since the Eocene, there has been major faunistic reorganization (Figures 5 and 6) owing to the thorough replacement of archaic mammals (Figure 1d; Wang et al., 2007) and the final closure of the Tethys Ocean caused by the Indo-Asian collision (Figure 1a; Favre et al., 2015). From the Oligocene to Miocene period, South China consistently emerged as the most distinct region (Figures 5 and 6), and this is in line with the high endemism reported by Tsubamoto et al. (2004). However, in this period, the relationships among regions in the northern part of China changed considerably owing to pronounced topographic uplift and extensive climatic changes (Li et al., 2014). When the Tibetan Plateau reached 4,000 m a.s.l. in the late Eocene (c. 40 Ma; Renner, 2016), the aridification of Central Asia resulted in the significant environmental heterogeneity in the northern part of China (Figure 1a; Fortelius et al., 2002). Furthermore, in the context of global climatic changes (Zachos, Pagani, Sloan, Thomas, & Billups, 2001), the faunas that were adapted to warm and humid climates (e.g., perissodactyl-dominated faunas) in the northern part of China were replaced by open-steppe faunas (e.g., rodent/lagomorph-dominated faunas; Meng & McKenna, 1998; Pisano et al., 2015). Meanwhile, the emergence of the monsoon system (Sun & Wang, 2005) was proposed to intensify these faunistic changes (Li et al., 2014). In summary, the uplift of the Tibetan Plateau, emergence of the monsoon system and macroevolutionary processes during this period played vital roles in restructuring the mammal faunas of China. Notably, the assignments of the modern zoogeographical regions at the family level originated in the Pliocene and finally established in the Pleistocene (Figure 5). This result is supported by Li et al. (2014), who suggested that the initiated establishment of the current interrelationships among mammal faunas coincided with the formation of the modern Chinese environmental patterns at the end of the late Pliocene.

On the present-day Tibetan Plateau, a highly endemic fauna is characterized by adaptations to the harsh, high-elevation environmental conditions (He et al., 2017; Wang et al., 2015); however, the debate continues over the origin, development and zoogeographical position of this fauna (Yang et al., 2009). Our results

reveal that during the Miocene, when the earliest mammal fossils were recorded on the Tibetan Plateau, the plateau first clustered with Inner Mongolia at both the family and genus levels (Figures 5 and 6). This result is in line with Li and Wang (2015), who proposed that the moderate topographic gradient in the northern part of the Tibetan Plateau (Favre et al., 2015) probably provided opportunities for faunistic interchanges (Figure 1a; see also Li et al., 2013). During the Pliocene, the Tibetan Plateau first grouped with Central China at the family level, whereas at the genus level the plateau was highly distinct from the other parts of China (compare Figures 5 and 6). This result implied that the endemic fauna on the Tibetan Plateau emerged in the Pliocene, and some distinct genera were first recorded on the plateau, such as blue sheep (*Pseudois*) and several rodents (e.g., *Aepyosciurus* and *Himalayactaga*). Notably, this timing coincides highly with the speciation events of most of the species endemic to the plateau (Päckert et al., 2012; Yang et al., 2009) and the final extension of the uplift of the Tibetan Plateau (Figure 1a; Favre et al., 2015). Afterwards, the Tibetan Plateau was established as a distinct zoogeographical region in the Pleistocene (Figures 5 and 6).

5. | CONCLUSIONS

Our study develops the first quantitative spatio-temporal framework for the mammal faunas in China during the Cenozoic based on fossil records. Despite several data limitations, our results demonstrate that:

1. The overall spatial differentiation of mammal faunas emerged much earlier than expected, probably dating back to the Eocene, predating the formation of modern topography and climate.
2. The mammal faunas in China experienced considerable reorganization throughout the Cenozoic, most probably attributable to an interplay of the uplift of the Tibetan Plateau, emergence of the monsoon system and global macroevolutionary processes.
3. The modern spatially structured faunas at the family level originated in the Pliocene and finally established in the Pleistocene.

ACKNOWLEDGMENTS

We thank G. Z. Ma and X. Liu for valuable discussions and comments that substantially improved this manuscript. We are grateful to the handling editor S. K. Lyons and the three anonymous referees for their constructive comments that greatly improved the earlier version of this manuscript. We thank the hundreds of archaeologists for contributing to the fossil collections and thank the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing (<http://www.ivpp.ac.cn/>); the Paleobiology Database (<https://www.paleobiology.org/>); the New and Old Worlds database (<https://www.helsinki.fi/science/now/>); and the Fossilworks database (<https://fossilworks.org/>) for data accessibility. The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

H.J. and J.H. conceived the ideas; J.H., S.L. and Y.X. contributed the data; J.H., S.L. and H.J. analysed the data; and J.H., H.J. and H.K. led the writing.

DATA ACCESSIBILITY

The complete fossil collections and extant mammal records of China are included as Supporting Information Appendix S1. The Supporting Information, including occurrence data and community data, are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.n2tb31q>.

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BIOSKETCH

JIEKUN HE has completed his PhD in biogeography recently at School of Life Sciences, South China Normal University. This study was part of his doctoral program. He specifically focuses on distribution patterns of terrestrial vertebrates and gradients of biodiversity.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: He J, Kreft H, Lin S, Xu Y, Jiang H. Cenozoic evolution of beta diversity and a Pleistocene emergence for modern mammal faunas in China. *Global Ecol Biogeogr*. 2018;27:1326–1338. <https://doi.org/10.1111/geb.12800>