

PALEONTOLOGY

Central Asian radiation of modern large-mammal faunas in Miocene

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Elucidating how modern faunas were established is crucial for understanding mammalian evolution in response to the Cenozoic global climatic and tectonic changes. However, complicated exchanges of faunas between continents in the Late Cenozoic have made it challenging to identify general patterns of faunal evolution and migration. We developed a method, faunal phylogenetic contribution, to quantify faunal relationships based on taxon distances in a supertree. Our results suggest Central Asia faunas exhibited two notable expansion phases: 19 to 16 million years (Ma) ago (pre-Tungurian surge) and 11 to 9 Ma ago (Bahean surge). The latter phase was directly correlated with formation of the modern large-mammalian faunas, driven by the ecomorphological revolution of local mammalian communities following a regional mass extinction, “the Central Asian Tortonian Crisis.” We propose that the rapid uplift of the Tibetan Plateau altered Central Asian hydrological system, promoting aridification and earlier development of open habitats, which in turn drove the adaptation of large mammals to prolonged environmental shifts.

INTRODUCTION

Tracing the origins of various modern mammalian clades through phylogenetic reconstruction has been increasingly researched (1); however, relatively few studies have investigated mammalian evolutionary trajectories at the fauna level. The rise and fall of mammalian clades and faunas were consistently linked to ecological niche turnover within ever-changed ecosystems (2), occurring against the backdrop of global climatic transformations during the Late Cenozoic (3). The establishment of modern faunas in the “northern continents (NCs),” encompassing Eurasia, Africa, and North America (Fig. 1A), holds particularly importance as these regions now harbor Earth’s most extensive ecosystems characterized by diverse large mammal faunas (4). Modern zoogeography partitions the NC into three principal regimes: Ethiopian (Arabia-Africa), Oriental (South and Southeast Asia, part of East Asia), and with the latter further subdivided into Nearctic (North America) and Palearctic (remaining Eurasian regions) provinces. However, the persistent Neogene connectivity between these continental masses facilitated extensive mammalian fauna exchanges (5), obscuring clear spatial-temporal patterns in species evolution and migration. This sustained faunal exchange has obscured the identification of biogeographic pattern formation thresholds in modern mammalian distributions.

Asia was regarded as “the East of Eden,” serving as a center of mammalian evolution during the Paleogene (6). It also played a crucial role in shaping modern faunas, termed the “Central Asian radiation center” by Kretzoi (7) during the Late Cenozoic. Two key factors influenced this process. First, the transition from a “warm house” to an “ice house” climate markedly pushed terrestrial biota to

more open ecosystems (8). Second, the rapid uplift of the Tibetan Plateau fundamentally altered the hydrological system of the pan-Third Pole region, triggering the long-term aridity of Central Asia (9, 10). This stepwise aridification promoted the emergence of local open environments, which acted as evolutionary hot spots for NC mammalian faunas. For example, previous studies reveal that an open-habitat-adapted mammalian fauna, comparable to modern African savanna communities, emerged in middle-latitude western Eurasia (11). However, studies of faunal succession in East and Central Asia remain preliminary, hindering our understanding of the underlying mechanism and dynamic process of mammalian evolution and dispersal at the faunal level. Quantitative analyses using big data at this scale are poised to reveal these evolutionary secrets.

To address these knowledge gaps, we conducted a spatiotemporal analysis of mammalian faunal evolution across the NCs over the past 23 million years (Ma). By integrating phylogenetic relationships with spatiotemporal occurrence data, we developed a method—the faunal phylogenetic contribution (FPC)—to quantify evolutionary connections between regional faunas. This approach enables systematic evaluation of how large mammalian communities across different regions contributed to the assembly of modern ecosystems over time.

RESULTS

In our FPC method, the quantitative relationships between any two faunas are calculated based on the average distances throughout all faunal members on a supertree incorporating branching time information. This supertree (Fig. 1, B and C, and data S1 to S5) included 1246 genera of large terrestrial mammals. These taxa spanned continents of NC (Eurasia, Africa, and North America) and dated back to the beginning of the Miocene (~23 Ma). For details, please see Materials and Methods and the Supplementary Materials.

To determine which region had contributed a greater influence on the succession and evolution of modern faunas, we divided NC into five regions based on their geographical positions and modern zoogeographical regimes: Europe and parts of West Asia (Iran and Türkiye), abbreviated as EU; North America (NA); Africa and Arabia (AF); South, Southeast Asia, the China coastal region, and Japan

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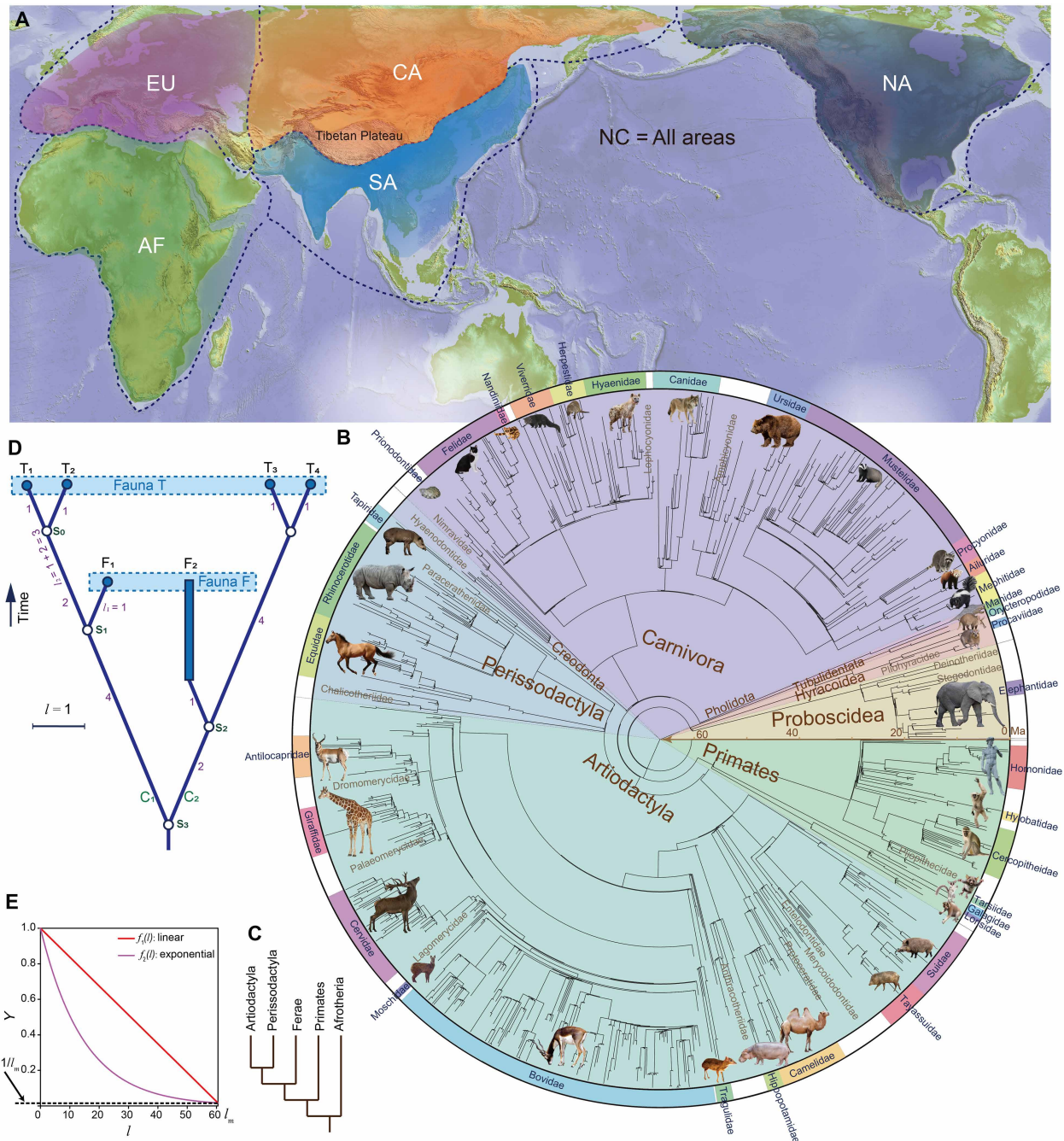


Fig. 1. Methods in this study. (A) Geographic subdivisions of “northern continents” (NCs), including EU (Europe, Iran, and Türkiye), pink; NA (North America), blue; AF (Africa and Arabia), dark green; SA (South Asia, Southeast Asia, southern China, China coastal region, and Japan), cyan; and CA (Central Asia, northern China, Mongolia, Asian part of Russia), red. (B) Supertree of large terrestrial mammals, which includes 1246 genera across Primates (109 gen.), Pholidota (4 gen.), Carnivora (394 gen.), Creodonta (13 gen.), Perissodactyla (115 gen.), Artiodactyla (537 gen.), Proboscidea (54 gen.), Hyracoidea (16 gen.), and Tubulidentata (4 gen.) in the Neogene and Quaternary (from 23.03 Ma to today). A hypothetic outgroup taxon, Hp1, living at 0 Ma was preset. Small icons indicate living representative taxa of the crown families. For the full dataset, see the Supplementary Materials. (C) Phylogenetic relationship of orders or superorders of the supertree, in which Ferae comprises [Pholidota (Creodonta Carnivora)], and Afrotheria is composed of [Tubulidentata (Hyracoidea Proboscidea)]. (D) Schematic figure for TPC and FPC calculation. For example, $TPC_{F1 \rightarrow T1} = f_1(l_1)f_2(l_2)$, where $l_1 = \text{length}(F1 \rightarrow S1) = 1$, $l_2 = 1 + \text{length}(S1 \rightarrow T1) = 3$, $f_1(l) = 1 + \frac{1-l}{l_m}$, $f_2(l) = \exp\left[-\frac{\ln(l_m)}{l_m}l\right]$ [see below (E)]. Here, l means distances between any two points on the

tree, and l_m is the root length of the supertree, whereas $FPC_{F \rightarrow T} = \frac{1}{8} \sum_{i=1}^2 \sum_{j=1}^4 TPC_{Fi \rightarrow Tj}$. (E) Function images of f_1 (linear function) and f_2 (exponential function) in the TPC calculation.

(SA); and northern China (including the Tibetan Plateau), Mongolia, the Asian part of Russia, and Central Asia (CA) (Fig. 1A). The time ranges of above 1246 taxa in the five regions, (Eu, NA, AF, SA, and CA) and NC were recorded (data S1).

To identify key periods for the formation of modern fauna during the Neogene, we subdivided the Neogene and Quaternary into a sliding time bins of 0.3 Ma with a resolution of 0.1 Ma. In each time bin, taxa from the six regions (EU, NA, AF, SA, CA, and NC) constituted six chronological faunal series (CFSs). We examined the FPCs of these CFSs to the modern NC fauna (Fig. 2A), generating six FPC curves. These curves revealed that CA exhibited greater contribution to the modern NC fauna than other regions, particularly during 20 to 8 Ma, forming two prominent peaks: one around 20 to 15 Ma, termed the pre-Tunggurian (the Chinese Land Mammal Age) surge, and another around 12 to 8 Ma, the Bahean surge. This indicates that CA faunas contributed more substantially than contemporary faunas from other regions in their phylogenetic contributions to the modern NC fauna. Before 20 Ma, the FPC curves of EU contribute more than other regions, this dominance ceased 20 to 19 Ma, possibly due to the formation of the “*Gomphotherium* Landbridge” (12) that facilitated large mammal exchanges between Eurasia and Africa. During 16 to 13 Ma, FPC curves from AF and SA exhibit marked increases coinciding with CA’s decline, indicating that warm-adapted mammalian faunas flourished in these regions during the Mid-Miocene Climatic Optimum and exerted enduring influences on extant faunal communities. The high contribution of EU fauna during 8 to 6 Ma correlates with the mammalian turnover event known as the Vallesian crisis at ~9.5 Ma (13), where forest habited fauna was replaced by the Pan-Eurasian Pikermi-Baode fauna, considered ancestral to modern savannah fauna in Africa (14). After 10 Ma, the FPC curves of EU and CA became similar, and EU faunas contributed more to modern NC fauna than faunas from CA and other regions. Moreover, a third small peak occurs around 5 to 4 Ma, the Zanda surge, corresponding to the “out of Tibet” scenario (15). Following the Zanda surge, the CA fauna contribution declined, suggesting that the Zanda fauna exhibited greater endemism in CA. Bootstrap resampling and right-tailed *t* tests confirmed that the high CA FPC values during the pre-Tunggurian and Bahean faunal surges are statistically robust ($P < 0.05$; Fig. 2, B and C).

To validate the robustness of our findings, we conducted comprehensive null model tests encompassing: (i) randomizing tree topologies at family and infraorder levels, (ii) perturbing node ages and taxon longevity distributions, (iii) subsampling taxa from NC or CA pools (with/without concurrent topology randomization), and (iv) collapsing taxa into higher hierarchies (family/subfamily/tribe). Critically, none of these perturbations altered the relative positions or statistically significant differences ($P < 0.05$) between FPC curves (figs. S1 to S16). This consistency across diverse null models underscores the methodological robustness of the FPC framework in capturing faunal provinciality patterns.

We also calculated the FPC curves between the six CFSs and the modern regional faunas of EU, NA, AF, SA, and CA (fig. S17). Similar to the FPC curves related to the modern NC fauna, CA substantially contributed to the model regional faunas more than other regions. Each region displayed similar FPC patterns, differing only in amplitude of FPC values. These results indicate pronounced faunal exchanges among Eurasia, Africa, and North America that ultimately shaped the modern NC faunas. As the FPC curves demonstrate, the

pre-Tunggurian and Bahean surges greatly contributed to both modern NC and regional faunas.

Further examinations were performed on the FPC curves from 11 to 9 Ma faunas in EU, NA, AF, SA, and CA relative to the subsequent Northern Hemisphere fauna series (NC CFS) (Fig. 2D). The results showed that the FPC curve of CA from 11 to 9 Ma, the Bahean fauna, consistently surpasses those of contemporary EU, NA, AF, and SA faunas. The contribution of the CA Bahean fauna to the subsequent NC CFS becomes more pronounced after mid-Pliocene (around 4 Ma). This trend was also evident in the FPC curves from 11 to 9 Ma faunas relative to regional fauna series, including those of EU, AF, SA, and NA (Fig. 2, E and F, and fig. S18). For example, the FPC curve of the CA Bahean fauna relative to the AF fauna series (AF CFS) surpasses that of the contemporary (11 to 9 Ma) AF faunas relative to AF CFS itself after ~7 to 4 Ma (Fig. 2E), indicating that descendants of the CA Bahean fauna gradually replaced African local faunas. This result statistically corroborates the hypothesis that the modern African Savannah fauna partially derived from the CA Bahean fauna (16). Similarly, the FPC curve of the CA Bahean fauna relative to the NA fauna series (NA CFS) surpasses that of 11 to 9 Ma NA fauna relative to NA CFS itself after ~2 Ma (Fig. 2F), highlighting substantial interconnections via the Bering Land Bridge since the Pleistocene. The results also reveal that, after the onset of the Ice Age at 2.6 Ma, Eurasia and North America united into a Holarctic zoogeographic regime, with the CA Bahean fauna serving as an important origin of the Holarctic fauna.

However, for the regional faunas of 8 to 6 Ma, FPC curves from EU relative to the subsequent global and regional CFSs were higher than those from CA (fig. S19). This indicates that, after 8 Ma, the European region became more important than Central Asia for global faunal succession. The “CA Bahean fauna” first evolved into the Pikermi-Baode fauna, which then spread to Africa (14), with some mammals also spread to North America (17).

DISCUSSION

To explore the underlying mechanisms for Central Asia playing as a Late Cenozoic radiation center for large mammals, we performed Bayesian birth-death process modeling based on our supertree. The results revealed a high peak in the extinction rate curve around 11 Ma (Fig. 3B), suggesting that this represents the largest extinction event of large terrestrial mammals in the Neogene. The origination rates also exhibited a small peak occurring at the same time (Fig. 3C), and these peaks around 11 Ma were not sensitive to the node branching ages (fig. S20). Furthermore, calculating superficial turnover rates based purely on fossil records indicates a substantial peak around 11 Ma in CA large mammals (Fig. 3D), indicating that CA region experienced a notable extinction/turnover event around 11 Ma (Fig. 3G and fig. S21), with only four large mammalian genera survived after Tunggurian. We termed this event the Central Asian Bahean Crisis (CABC). However, small mammals exhibited a less pronounced peak during the same period, likely due to their smaller body size limiting adaptive responses to extinction pressures (fig. S22).

The CABC event (~11 Ma) likely resulted from intensified mid-latitude aridity in Central Asia (18, 19). Global mid-latitude aridity during 12 to 10 Ma was a notable event driving the gradual transformation of forests into grasslands, fostering the development of more open ecosystems (20), particularly associated with the Mid-Miocene

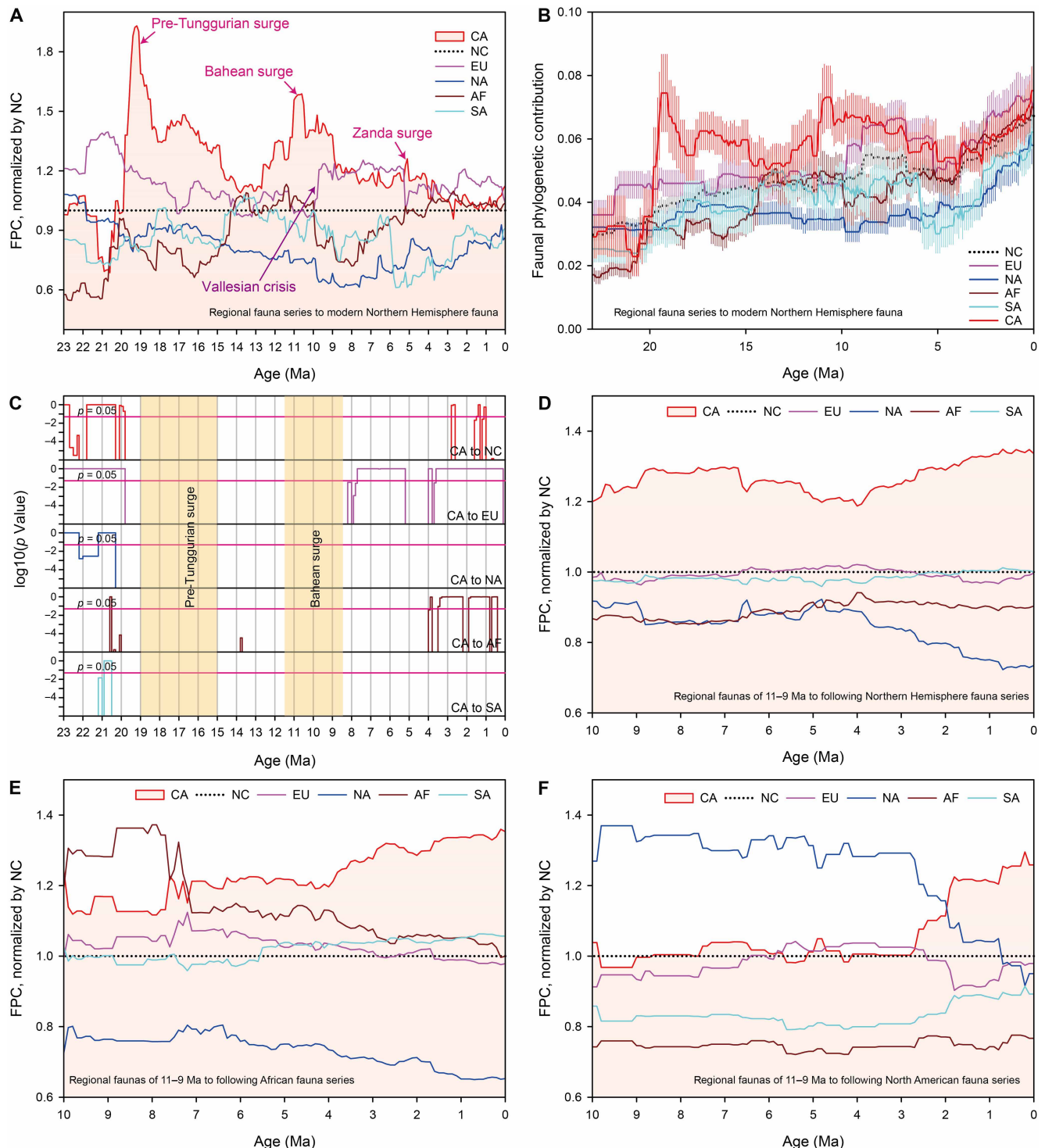


Fig. 2. Faunal relationships during the Late Cenozoic among the NCs. (A) FPC curves (normalized by the NC curve) from CFSs of the five areas relative to the modern NC fauna. Notably, the CA curve (red) shows three notable peaks: the pre-Tungurian, Bahean, and Zanda surges. Another important event, Vallesian crisis, is also marked. (B) Bootstrap analysis (1000 replicas) of FPC curves exhibits the means (solid lines) and SDs (error bars) of FPC curves. (C) Right-tailed T tests point-by-point of each time bin for Bootstrap curve of CA, respectively, to the Bootstrap curves of NC, EU, NA, AF, and SA, in the cases of (B). Note that the high significances for the CA Bootstrap curve that is larger than the other curves, particularly in the intervals of the pre-Tungurian and Bahean surges. (D) FPC curves (normalized by the NC curve) from the 11 to 9 Ma fauna of CA, EU, NA, AF, and SA relative to the subsequent NC CFS, showing the continuously high value of the CA curve (red). (E and F) FPC curves from the 11 to 9 Ma fauna of CA, EU, NA, AF, and SA relative to the subsequent CFSs of Africa-Arabia (E) and North America (F), showing that the CA curves (red) lastly surpass the local curves [surpassing AF after 7 to 4 Ma in (E) and surpassing NA after 2 Ma in (F)].

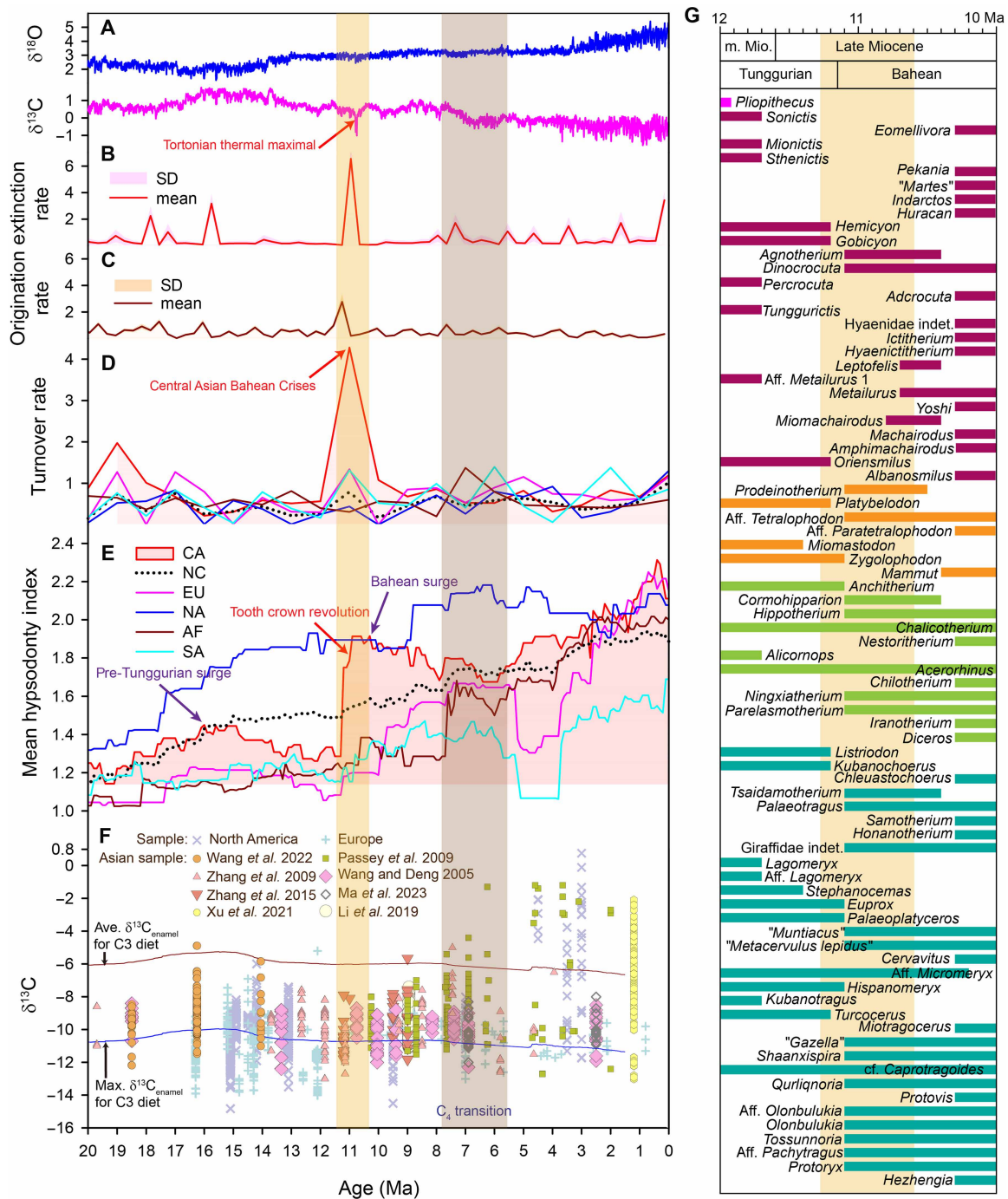


Fig. 3. Global and regional faunal turnover and ecomorphology revolution driven by global environment changes. (A) Global deep-sea $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopes curves, after (3), showing the strong negative shift of the $\delta^{13}\text{C}$ at ~11 Ma, which corresponded to the TTM event. (B and C) Extinction (B) and origination (C) rates of large terrestrial mammals in the Late Cenozoic simulated based on the supertree (Fig. 1B) using Bayesian birth and death process inference. Note that a steep peak of extinction occurs at ~11 Ma, possibly accompanied with the TTM event, and a small corresponding peak also occurs in the origination rate curve. (D) Faunal turnover rate (sum of extinction and origination rates) based on the fossil records in NC and five regions. Note that the largest faunal turnover event, the CABC, occurred at ~11 Ma. (E) Curves for the AHI in NC and five regions. Note that there are relatively high AHI values of CA compared with other Old World regions between 18 and 8 Ma. A particularly notable step occurred at the CABC, ~11 Ma, which indicated that the open environment promoted the presence of high-crowned taxa that occurred after CABC. (F) Integrative data for the mammalian tooth enamel $\delta^{13}\text{C}$ in the mid-latitude of the Northern Hemisphere. Note that the phase of tooth crown revolution in CA emerged at CABC event ahead of the C₄ transition event, and mammals of CA usually show higher $\delta^{13}\text{C}$ values than those of EU and NA before C₄ transition event. (G) Large-terrestrial mammalian faunal turnover at the Tunggurian/Bahean boundary; only four Tunggurian genera survived after the boundary (see also the larger time window in fig. S21). The yellow color denotes the potential influence range of the TTM event.

Climatic Transition (MMCT). Central Asia showed higher extinction than other regions, suggesting that MMCT was not the sole factor; the high uplift of the northern Tibetan Plateau likely intensified aridity (21, 22). In tooth enamel isotope records, the Kekemaideng (14.5 to 13.1 Ma) faunas of Junggar Basin show the higher $\delta^{13}\text{C}$ ranges compared with those from mid-latitude mammalian faunas of Europe, North America, and other Chinese regions. Similarly, the Tuosu Fauna (11.1 to 9.7 Ma) from Qaidam Basin shows elevated $\delta^{13}\text{C}$ range, indicating arid and open environments [Fig. 3F; data source: CA, after (23–30); EU, after (31–37); NA, after (38–40); biome boundaries after (41)]. The CABC event coincides with the Tortonian thermal maximum (TTM) (Fig. 3A) (3), which may further strengthen the local faunal turnover. However, the precise age of the CABC requires further calibration to verify causality between TTM and CABC.

We then calculated the averaged hypsodonty indices (AHIs) of large herbivores based on the CFS from EU, NA, AF, SA, and CA (Fig. 3E). Notably, NA consistently maintained the highest AHI values throughout the Neogene, primarily driven by diverse high-crowned groups such as horses, camelids, antilocaprids, and oreodonts (42). In the Old World, however, CA exhibited a curve with high AHI values from ~18 to 4 Ma, forming two peaks corresponding to the pre-Tungurian and Bahean surges. The Bahean surge showed a pronounced increase in AHI values around 11 Ma, even surpassing those of NA. AHI values are widely recognized as a proxy for open environments and aridity, at least in the Late Cenozoic of the Old World (19). This finding highlights a pivotal shift in tooth crown evolution among herbivores, strongly reflecting the adaptation of large terrestrial mammals to open environments well before the large-scale expansion of C_4 vegetation (Fig. 3, E and F). Fossil evidence, including early caprines from around 11 Ma in the Qaidam Basin—contemporaneous with the influx of *Hipparion* from North America—provides critical support for this event (43, 44). In addition, *Gazella*-like antelopes and crown cervids have also been documented in the same region (45). Thus, the adaptation of the CA large-mammalian fauna to open environments following the CABC likely served as a major driver for Late Cenozoic faunal succession and the establishment of modern zoogeographic patterns.

In conclusion, we present a comprehensive portrait of Late Cenozoic large terrestrial mammalian evolution and migration using FPC methods, and enable systematic faunal comparisons and evolutionary trajectory tracing. This approach demonstrates potential for exploring macroevolutionary patterns in biota, ecosystems, and zoogeography. Further analysis revealed that the CABC triggered the regional extinction in CA, subsequently driving a tooth crown revolution of mammals in Central Asia and shaping the CA Bahean fauna. This fauna likely represents the earliest iteration of modern mammalian assemblages. It first radiated to the Pikermi-Baode fauna across the mid-latitude of Eurasia. Approximately 4 Ma later, its descendants replaced indigenous taxa in Africa and South Asia, becoming dominant components of the Savannah fauna and profoundly restructuring the large-mammalian communities of the Ethiopian and Oriental regimes. Around 2 Ma, descendants of the Bahean fauna ultimately displaced native taxa in North America, forming the Holarctic large-mammal faunas. Collectively, our findings identify Central Asia as the evolutionary epicenter of Late Cenozoic terrestrial large mammals—a role previously underappreciated due to limited understanding of regional faunal succession. Intensified mid-latitude aridity in Central Asia, driven by the rapid uplift of the

Tibetan Plateau and the TTM event, created more open and arid environments than other Northern Hemisphere regions. This fostered long-term environmental adaptations in local large-mammal faunas, aligning with global Late Cenozoic cooling trends (8, 10, 46).

MATERIALS AND METHODS

We constructed a supertree for large terrestrial mammals of the Late Cenozoic (Fig. 1, B and C, and data S1 to S5), comprising 1246 genera from nine orders: Primates, Pholidota, Carnivora, Creodonta, Perissodactyla, Artiodactyla, Proboscidea, Hyracoidea, and Tubulidentata. These taxa spanned Eurasia, Africa, and North America, dating back to the beginning of the Miocene (~23 Ma). Data were sourced from the NOW (New and Old Worlds Database of fossil mammals) (47) and Deepbone (48) databases. The tree topology was established based on prior studies under a molecular evolution framework (see Supplementary Text), with branching times calibrated using a minimum branch length (MBL) (49) of 0.1 Ma. This MBL value was arbitrarily assigned to match the temporal resolution of this study. Sensitivity analyses confirm that MBL values below 1 Myr do not notably affect the results (see below).

For quantifying the relationships between two faunas, we developed a method: FPC. It shares the same underlying concept with the widely used method, mean pairwise distance (MPD) approach (50, 51), in phylogenetic community structure, as both are based on the distances between taxa on a phylogenetic tree. However, the primary distinction between our FPC and the MPD lies in how they consider the relationships between species. In MPD, the relationship between two species is determined solely by their distance on the phylogenetic tree (i.e., divergence time). However, in FPC, we also take into account the distances from each species to the split point (Fig. 1D and fig. S1). In the scenario of Fig. 1D, intuitively, F_1 had a closer phylogenetic relationship with the clade C_1 than F_2 did with the clade C_2 , because the distance from F_1 to T_1/T_2 (equaling to 4) is shorter than from F_2 to T_3/T_4 (F_2 represents an early-diverging lineage that persisted until the time of Fauna F). However, both F_1 and F_2 give equivalent MPD values to Fauna T (both equaling to 8). This occurs because although the distance from F_2 to T_3/T_4 is far, it is relatively close to T_1/T_2 , leading to an equalized MPD value. However, because F_1 and F_2 belong to widely separated lineages, the influence of F_1 on the lineage C_2 (and F_2 on the lineage C_1) should not be overemphasized.

In our FPC approach, distances between taxa are transformed into the (0, 1] interval, termed taxon phylogenetic contribution (TPC). For example, TPC from taxon F_1 to T_1 is calculated by the equation $\text{TPC}_{F_1 \rightarrow T_1} = f_1(l_1)f_2(l_2)$, where l_1 and l_2 represent the distance between F_1 to the split point S_1 , and S_1 to T_1 , respectively, and f_1 and f_2 are two monotone decreasing functions. If let $f_1 = f_2 = 1 - 0.1l$, a linear function, the TPC from F_1 to T_1 equals to $0.9 \times 0.7 = 0.63$. The FPC equals the mean of the pairwise TPC between members of the two faunas. In this example, the resulted FPC value for F_1 to Fauna T equals to $\frac{1}{4} \sum_{j=1}^4 \text{TPC}_{F_1 \rightarrow T_j} = \frac{0.63 + 0.63 + 0.15 + 0.15}{4} = 0.39$, whereas the FPC for F_2 to Fauna T is smaller, equaling to $\frac{1}{4} \sum_{j=1}^4 \text{TPC}_{F_2 \rightarrow T_j} = \frac{0.45 + 0.45 + 0.21 + 0.21}{4} = 0.33$. This approach effectively reduces the weight of the relationship between F_1 and the distant lineage (lineage C_2) and aligns with our intuitive understanding of phylogenetic trees. For the fauna F to T, the $\text{FPC}_{F \rightarrow T} = \frac{1}{8} \sum_{i=1}^2 \sum_{j=1}^4 \text{TPC}_{F_i \rightarrow T_j}$.

In this article, we set $f_1(l) = 1 + \frac{1-l}{l_m}l$ and $f_2(l) = \exp\left[-\frac{\ln(l_m)}{l_m}l\right]$, where l_m is the root length of the supertree (Fig. 1E). Here, we use an exponential function for the f_2 , which further diminishes the weight of distant lineages in the FPC calculation (for detail explanation, please see the Supplementary Materials). With the FPC method, quantitative relationships between any two faunas are calculated on the basis of the average TPC throughout all faunal member pairs on a supertree. The FPCs were calculated using MATLAB R2023b (code S1) with detailed descriptions, including sensitive tests of FPC (figs. S2 to S16), provided in the Supplementary Materials and Dryad [<https://doi.org/10.5061/dryad.31zcrjdwz>; (52)].

Generation and extinction rates based on the supertree were estimated using the fossilized birth-death model in BEAST 2.7.6 (codes S2 to S5), and superficial faunal turnover rates were inferred with the R package paleotree (code S6). The AHI of Primates, Perissodactyla, Artiodactyla, Proboscidea, and Hyracoidea were also derived from the NOW (47) and Deepbone (48) databases. For further details, please refer to the Supplementary Materials.

Supplementary Materials

The PDF file includes:

Supplementary Text
Figs. S1 to S22
Legends for data S1 to S7
Legends for codes S1 to S6
References

Other Supplementary Material for this manuscript includes the following:

Data S1 to S7
Codes S1 to S6

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Central Asian radiation of modern large-mammal faunas in Miocene

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