

Influence of Last Glacial Maximum legacies on functional diversity and community assembly of extant Chinese terrestrial vertebrates

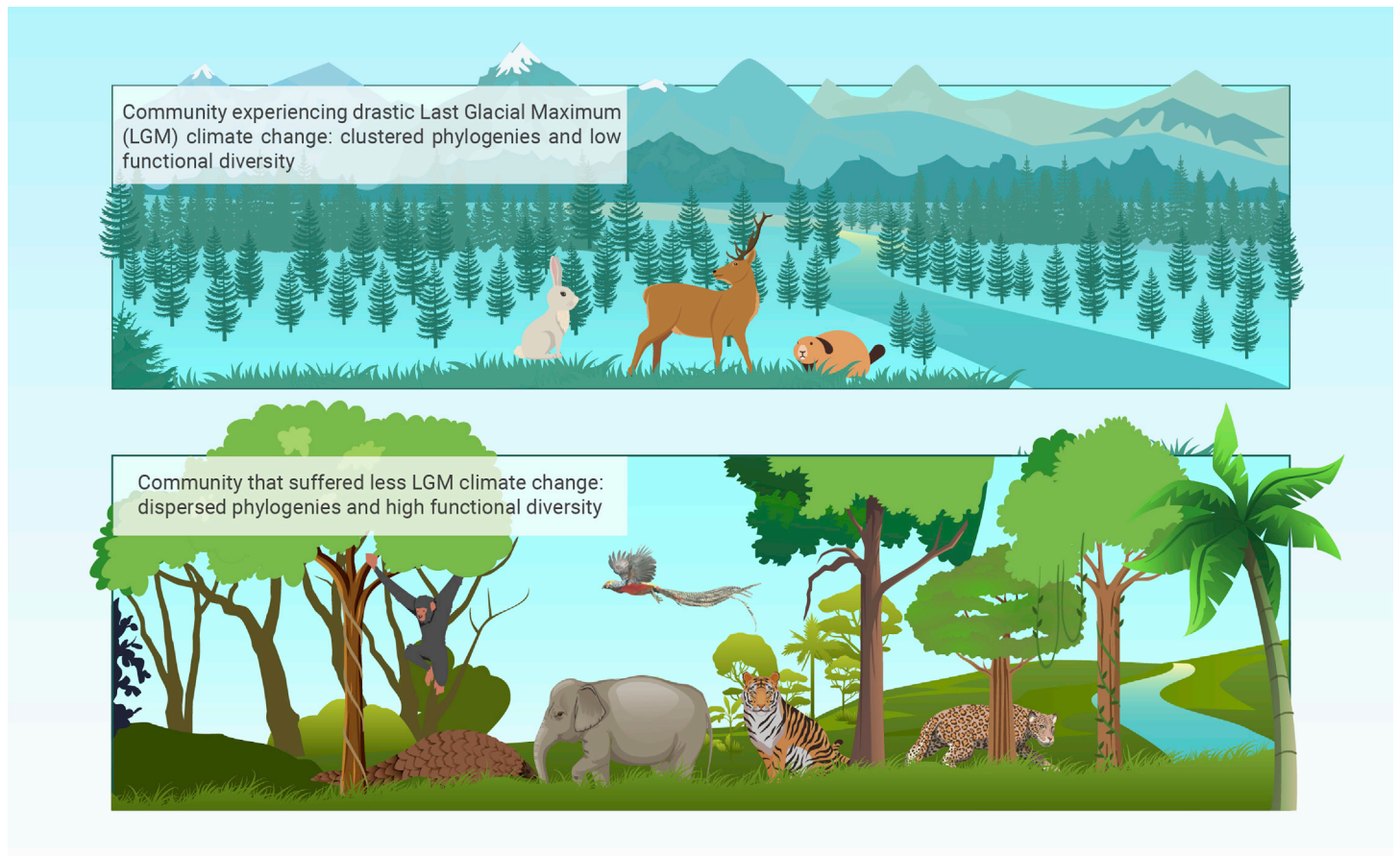
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GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- LGM climate shapes contemporary phylogenetic structure and functional diversity.
- LGM climate drives the dominance of “fast” species in mammal communities.
- Habitat filtering and dispersal limitation lead to the LGM legacies on biodiversity.



Influence of Last Glacial Maximum legacies on functional diversity and community assembly of extant Chinese terrestrial vertebrates

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Contemporary biodiversity patterns are shaped by not only modern climate but also factors such as past climate fluctuations. Investigating the relative degree of paleoclimate legacy could help us understand the formation of current biodiversity patterns. However, an assessment of this issue in China is lacking. Here, we investigated the phylogenetic structure and functional diversity patterns of Chinese terrestrial vertebrates. We found that Southern China harbored higher functional richness, while Northern and Western China were more phylogenetically clustered with higher functional divergence and evenness, indicating environmental filtering effects. Moreover, we found that drastic Last Glacial Maximum climate changes were positively related to phylogenetic clustering, lower functional richness, and higher functional divergence and evenness, although this effect varied among different taxonomic groups. We further found that mammal communities experiencing more drastic Last Glacial Maximum temperature changes were characterized by “faster” life-history trait values. Our findings provide new evidence of the paleoclimate change legacies influencing contemporary biodiversity patterns that will help guide national-level conservation plans.

INTRODUCTION

Biodiversity has undergone significant loss during the ongoing Anthropocene. Investigating the driving factors of modern biodiversity patterns will help us cope with the dramatic decline of biodiversity. Modern climate has been identified as one of the most dominant factors underlying specific biodiversity patterns.¹ However, increasing studies have suggested that Quaternary glacial–interglacial oscillations may have also played an important role in shaping contemporary biodiversity patterns via the environmental filtering effect.² Regional extinction caused by paleoclimate change and dispersal limitation in species recolonization could lead to paleoclimate legacies on contemporary biodiversity patterns.² Previous studies found that Quaternary glacial–interglacial climate changes had driven species endemism,³ community phylogenetic and functional structures,^{4–7} and the spatial turnover component of phylo- β diversity at the continental scale,⁸ highlighting the necessity for exploring the influence of paleoclimate legacies on contemporary biodiversity. In addition, the impact of prehistorical anthropogenic interference on shaping present biodiversity patterns is usually overlooked, although it was related to the recent extinction of megafauna.⁹

In contrast to other biological attributes such as taxonomic and phylogenetic dimensions, functional traits directly mediate the interaction between organisms and ecosystems. Understanding this interaction will inform us as to how communities respond to environmental changes. Although the concept of functional diversity was initially developed in plant ecology, it has been increasingly adopted in different organisms, including bacteria,¹⁰ corals,¹¹ invertebrates,⁵ fishes,¹² birds,¹³ and mammals.¹⁴ A quantification of community functional diversity can provide new perspectives on a variety of ecological questions, including community assembly mechanisms,¹⁵ ecosystem functioning,¹⁶ and biodiversity responses to global change¹⁷ that can guide conservation efforts.¹⁸ In addition, recent studies have highlighted the importance of the “fast–slow” traits continuum for understanding community response to disturbance. Species can be assigned to different positions in the fast–slow trait continuum according to their resource uptake rates and growth.¹⁹ Specifically, fast species are characterized by a high rate of resource uptake and growth manifested as smaller body size, larger clutch size, a shorter lifespan, and higher growth rates, resulting in susceptibility to environmental stress but a concomitantly higher recovery rate after

disturbance, whereas slow species are the opposite,²⁰ exhibiting strong resistance to disturbance.

China harbors more than 3000 terrestrial vertebrates across diverse ecosystems and thus has become one of the countries with the richest biodiversity. The Quaternary glacial–interglacial climate changes in China differed from those in North America and Europe.²¹ During the Last Glacial Maximum (LGM; ~22 000 years ago), most of the existing glaciers were found on the Qinghai–Tibetan plateau in China, whereas much of the area of North America and Europe was covered by glaciers. However, imprints of Quaternary glacial–interglacial climate changes on terrestrial vertebrate biodiversity across the country are poorly understood.

The aim of this study is to explore the relative influence of the LGM and modern climate factors (precipitation and temperature) on the contemporary biodiversity patterns of Chinese terrestrial vertebrates. Based on a combined dataset comprising the phylogenies and functional traits, the phylogenetic and functional diversity patterns of Chinese terrestrial vertebrates were revealed via two phylogenetic metrics (the net relatedness index [NRI] and nearest taxon index [NTI]) and three functional metrics (functional richness [FRic], functional divergence [FDiv], and functional evenness [FEve]). Then, we predicted biodiversity patterns based on LGM climate change, modern climate, elevation range, and prehistorical human population density (10 000 BC) across different taxonomic groups using spatial mixed-effects models. We tested the hypothesis that LGM climate change shaped the contemporary biodiversity patterns with the following predictions: (P1) LGM climate change may have resulted in clustering of phylogenetic structure, lower FRic, and higher FDiv and FEve due to the habitat filtering. (P2) LGM climate change may have had less impact on birds and a stronger impact on amphibians due to their contrasting dispersal abilities. We further investigated how LGM temperature changes affected the functional structure of communities. We predicted that communities that experienced drastic LGM climate changes were dominated by fast species because of their higher recovery rate after the LGM. These results will provide valuable insights into the role of past climate change in the formation of today's biodiversity and thus offer guidance for conserving the diverse organisms of East Asia.

RESULTS

Phylogenetic structures across different taxonomic groups

We constructed a time-calibrated phylogenetic tree of 2430 species (466 amphibians, 211 lizards, 1177 birds, and 576 mammals) (Figure S2), including 154 threatened amphibians, 19 threatened lizards, 71 threatened birds, and 77 threatened mammals (Figure S3). Most of our traits showed a strong phylogenetic signal (Table S2), suggesting that the habitat filtering may have led to a clustered phylogeny through the selection of specific traits. Based on the constructed phylogenetic tree, the NRI and NTI for amphibians, lizards, birds, and mammals were calculated. We identified several hotspots of phylogenetic clustering and dispersion after mapping the NRI and NTI patterns. The NRI was the highest in Southern China for amphibians, in Northeast China for lizards, in Southwest China and Southeast Tibet for birds, and in Southeast Tibet for mammals (Figure S4), indicating that the phylogenetic structures of communities within these regions were more clustered. The NTI values for amphibians, lizards, birds, and mammals were consistently higher in Northern and Western China, implying that communities within these regions were more phylogenetically clustered (Figure S5). The discrepancy between the NRI and NTI patterns implied that the habitat filtering, manifesting as phylogenetic clustering, varied across different taxonomic groups and regions.

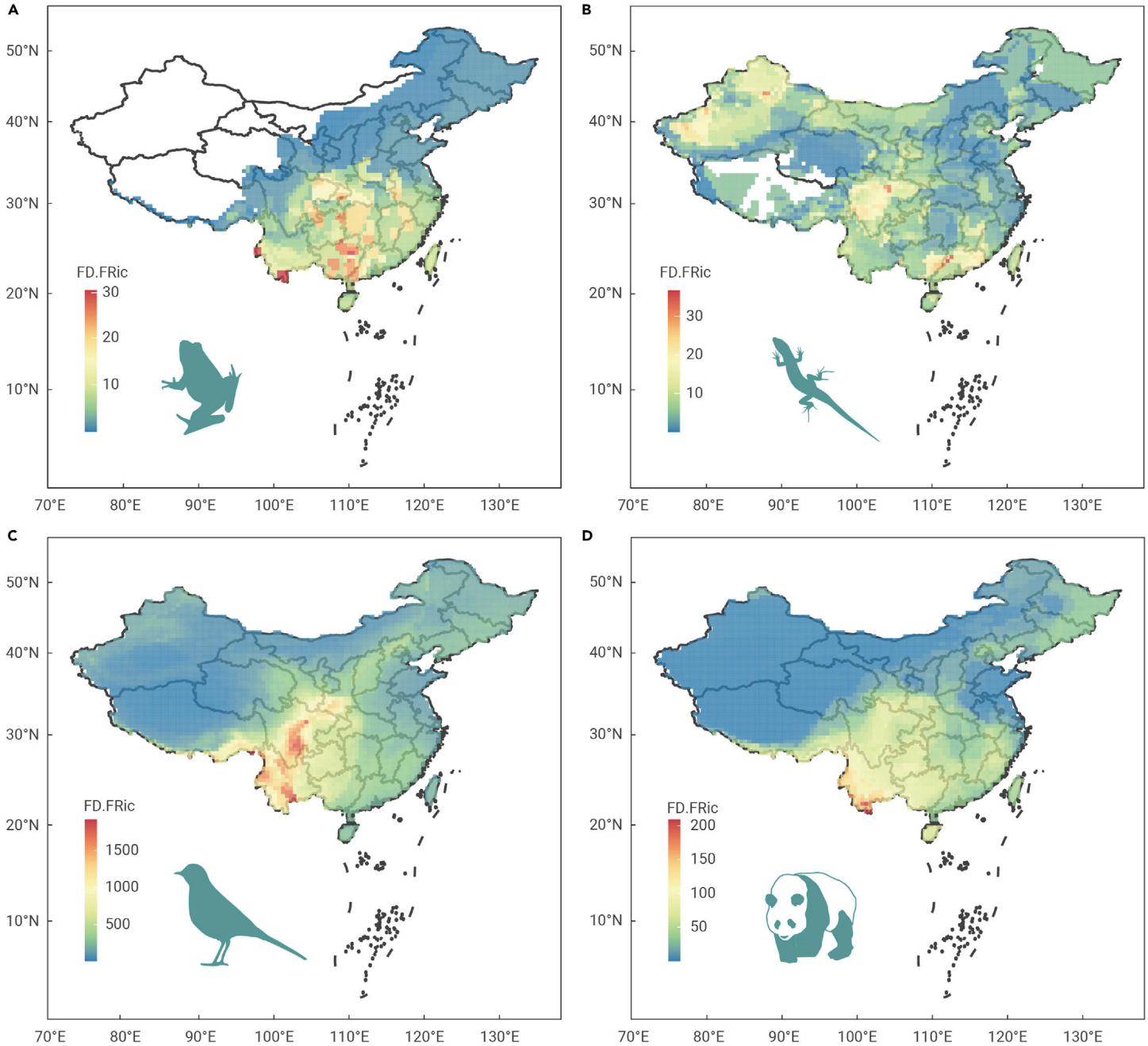


Figure 1. Functional richness patterns of vertebrate taxa Amphibians (A), lizards (B), birds (C), and mammals (D). Maps were based on the standard map GS(2020)4619 from the Ministry of Natural Resources, and vertebrate illustrations were obtained from PhyloPic (<http://phylopic.org/>), the same as in the other figure legends.

Functional diversity patterns across different taxonomic groups

We compiled a functional trait dataset of 2263 species, including 320 amphibians, 212 lizards, 1180 birds, and 551 mammals, from published datasets. We found that functional richness—the volume of niche space occupied by species in the community—was higher in Southern China for all vertebrates, especially in Yunnan for amphibians, Xinjiang for lizards, and Southwest China for birds and mammals, suggesting that these areas supported rich niches for vertebrates (Figure 1). In addition, for amphibians, we identified three *Bombina* species (*B. microdeladigitata*, *B. lichuanensis*, *B. fortinuptialis*) as well as *Limnonectes liui*, *Zhangixalus wui*, *Gracixalus jinxiuensis*, *Pseudohynobius flavomaculatus*, and *Paramesotriton fuzhongensis* as the most functionally distinct species in the functional richness hotspots. Moreover, we identified four species, *Eremias buechneri*, *Tenuidactylus dadunensis*, *Teratoscincus roborowskii*, and *Plestiodon tunganus*, as the most functionally distinct species in the functional richness hotspots of lizards. As for birds, *Tragopan blythii*, *Arborophila rufipectus*, *Liocichla omeiensis*, and *Schoeniparus variegaticeps* were identified

as the most functionally distinct native species in the functional hotspots. Four gibbon species (*Hoolock tianxing*, *Nomascus leucogenys*, *N. concolor*, and *Hylobates lar*) as well as *Elephas maximus*, *Capricornis rubidus*, *Axis porcinus*, *Trachypithecus shortridgei*, *Rhinopithecus strykeri*, *Manis javanica*, and *Nycticebus pygmaeus* were identified as the most functionally distinct mammal species in the hotspots, indicating that these threatened species played an important role in local ecosystem functioning and thus needed priority in conservation.

The extent to which species spread across the occupied community trait space, measured as FDiv, was higher in Central China for amphibians, in Western and Northeast China for lizards, in West Tibetan plateau and North China for birds, and in Western China for mammals (Figure 2), suggesting that communities in these regions have a higher degree of niche differentiation. The regularity component, or evenness in functional diversity, was also higher in Northern and Western China for all vertebrates, except for birds, for which the FEve was higher in Eastern China, suggesting the effective utilization of the resources available to a given niche space in these areas (Figure 3).

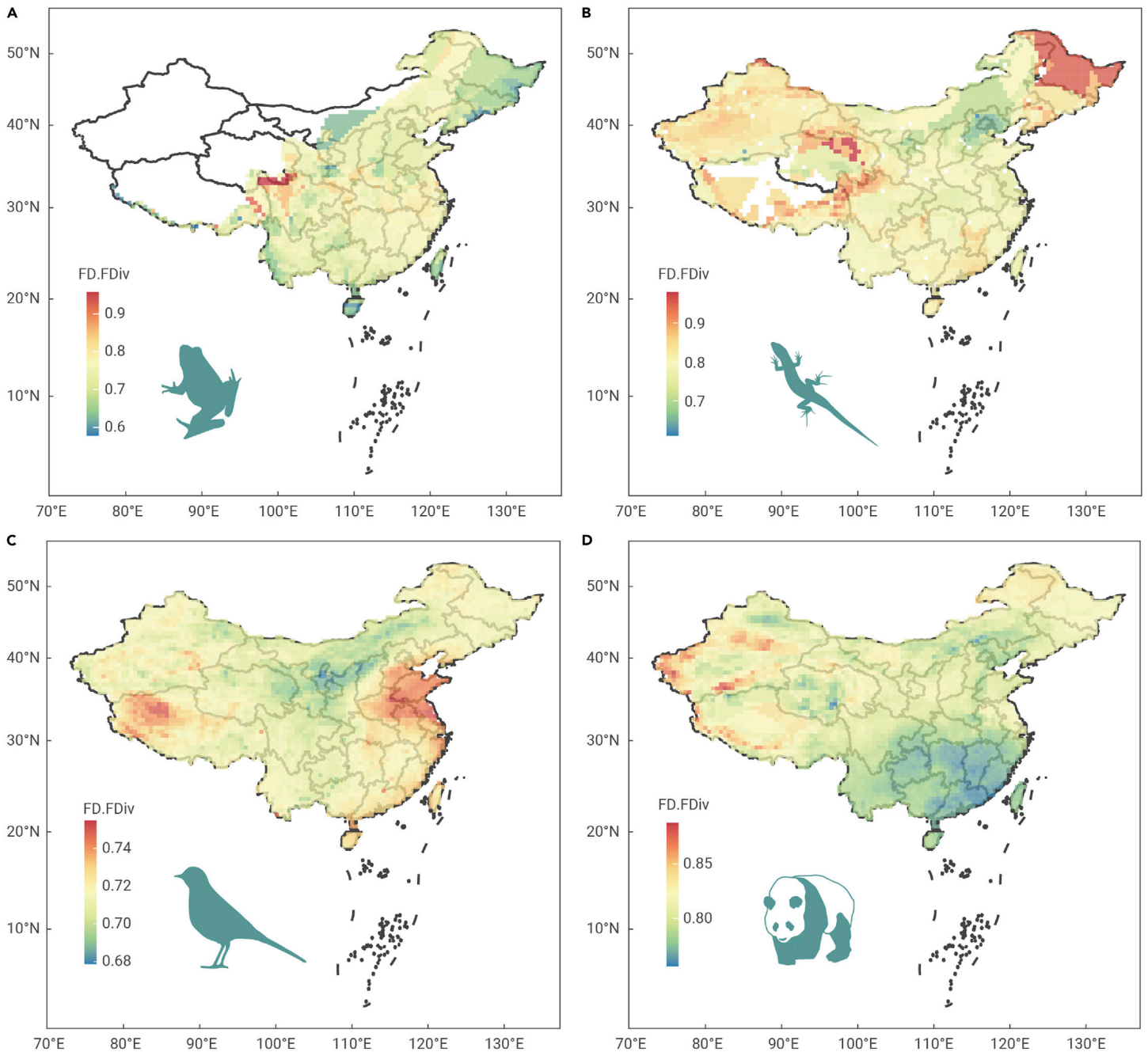


Figure 2. Functional divergence patterns of vertebrate taxa Amphibians (A), lizards (B), birds (C), and mammals (D).

LGM climate changes drove phylogenetic clustering and functional diversity patterns

We used spatial mixed-effects models to predict grid-cell-based community phylogenetic and functional diversity from the modern annual temperature and precipitation, the temperature and precipitation changes from the LGM, the elevation range, and the prehistorical human population density (10 000 BC). Our results showed that the impact of modern and paleoclimate factors varied among different taxonomic groups (Figure 4). Specifically, LGM climate changes had little impact on the NRI for all vertebrates, except for amphibians, where there was a negative relationship between LGM temperature changes and the NRI. However, LGM temperature changes were positively related to the NTI for lizards, birds, and mammals, whereas LGM precipitation changes only had a positive impact on the NTI for birds.

Regarding functional diversity, among all the significant effects, both LGM temperature and precipitation changes had negative impacts on FRic, while the modern climate and elevation range had positive impacts, suggesting that higher

temperature and precipitation and more undulating terrain supported more diverse niches. We also found that FDiv increased with LGM temperature changes for lizards and mammals but decreased with LGM precipitation changes for amphibians. The magnitude of LGM temperature changes was positively related to FEve for lizards, birds, and mammals, while LGM precipitation changes were negatively related to evenness for amphibians. The significant effect of LGM temperature and precipitation changes supported prediction P1 except for the NRI, FDiv, and FEve of amphibians. Prehistorical human population density showed little influence on any of the patterns except for the NTI of lizards.

Impacts of LGM temperature changes on community traits

We explored whether there was a fast–slow life-history trait continuum for birds and mammals because of their abundant life-history traits data, and we tested the relationship between life-history traits and LGM temperature changes. We identified two main axes of bird life-history traits. The first principal component (PC1) and PC2 explained 57.5% and 15.7% of the total variation among

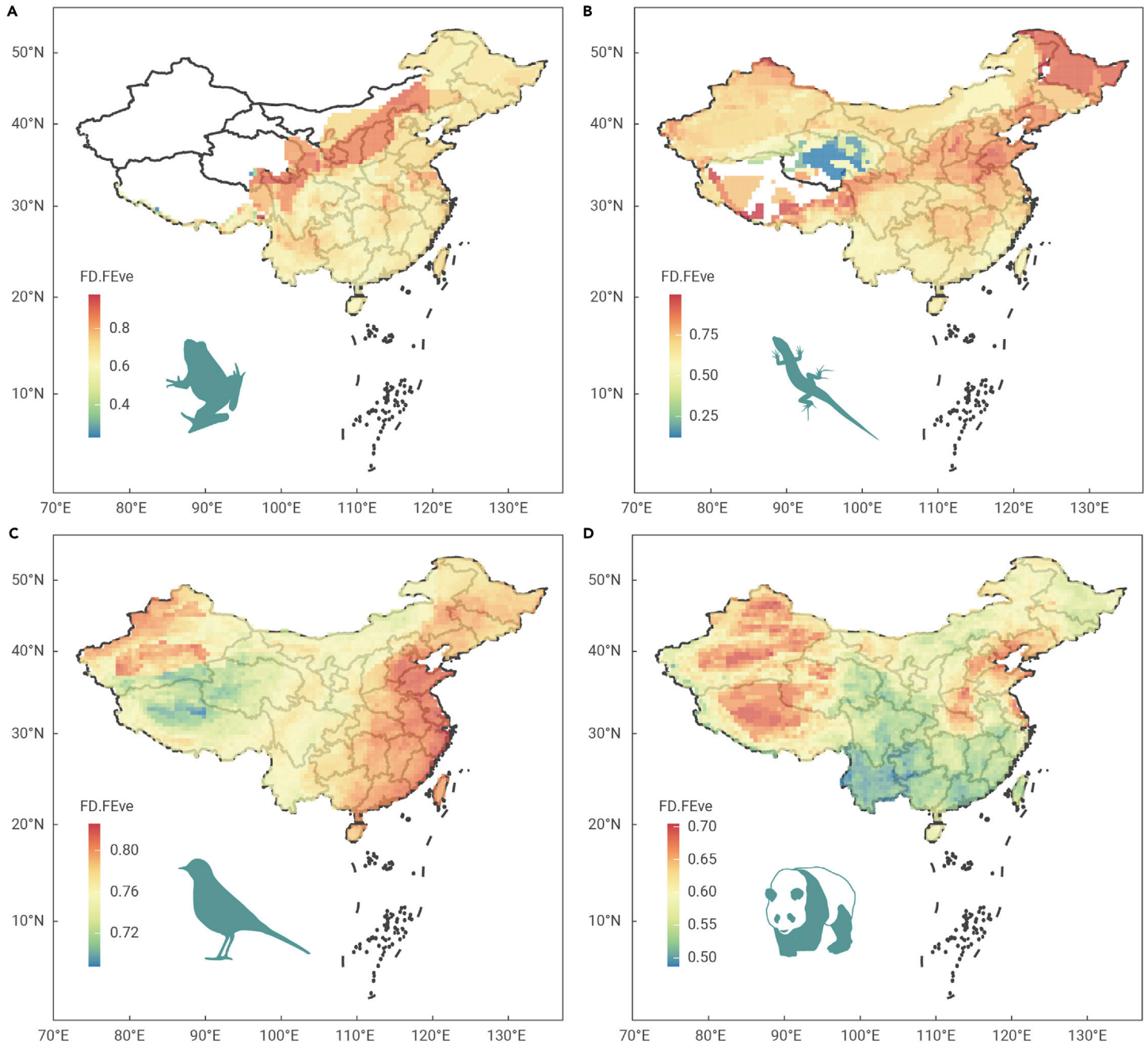


Figure 3. Functional evenness patterns of vertebrate taxa Amphibians (A), lizards (B), birds (C), and mammals (D).

all life-history traits (Table S3), respectively. Specifically, a larger value of PC1 corresponded to bird species characterized by larger body size and mass, a longer lifespan, and precocial offspring. The second axis was largely a function of clutch size, with a larger PC2 value meaning a larger clutch size. Clutch size was set apart from other life-history traits, suggesting that there was not a fast–slow life-history trait continuum for birds. Our model indicated a positive relationship between the first and second axes and LGM temperature changes, implying that communities that experienced drastic LGM temperature changes were dominated by birds that had larger body size and mass, a longer lifespan, larger clutch size, and precocial offspring (Figure 5).

As for mammals, PC1 explained 66.5% of the total variance among all life-history traits (Table S4). The correlation between life-history traits and PC1 suggested a fast–slow continuum in life history. A larger PC1 value corresponded to slow species characterized by larger body mass and a longer lifespan, female maturation timing, gestation length, interbirth interval, and generation length, as well as later weaning age and smaller litter size. We found a negative relationship between PC1 and LGM temperature changes, indicating that mammal commu-

nities that experienced drastic LGM temperature changes were dominated by fast mammal species (Figure 5).

DISCUSSION

Our results suggested that communities that experienced drastic LGM temperature changes would be more phylogenetically clustered. This pattern held for lizards, birds, and mammals in the case of the NTI, indicating the effect of environmental filtering caused by LGM temperature changes. An exception was amphibians, whose NRI decreased with the magnitude of LGM temperature changes. The NRI takes the average phylogenetic distance among all species into account and reflects a deeper phylogenetic history of the community than the NTI. Compared with other taxonomic groups, amphibians have a longer speciation history (eg, *Ichthyophis bannanicus* split from other extant amphibian lineages 223 Mya ago) (Figure S2) and thus may be less affected by more recent LGM climate changes. By contrast, the higher temperature in Southern China may have facilitated the speciation of amphibians, resulting in a higher NRI value.^{22,23}

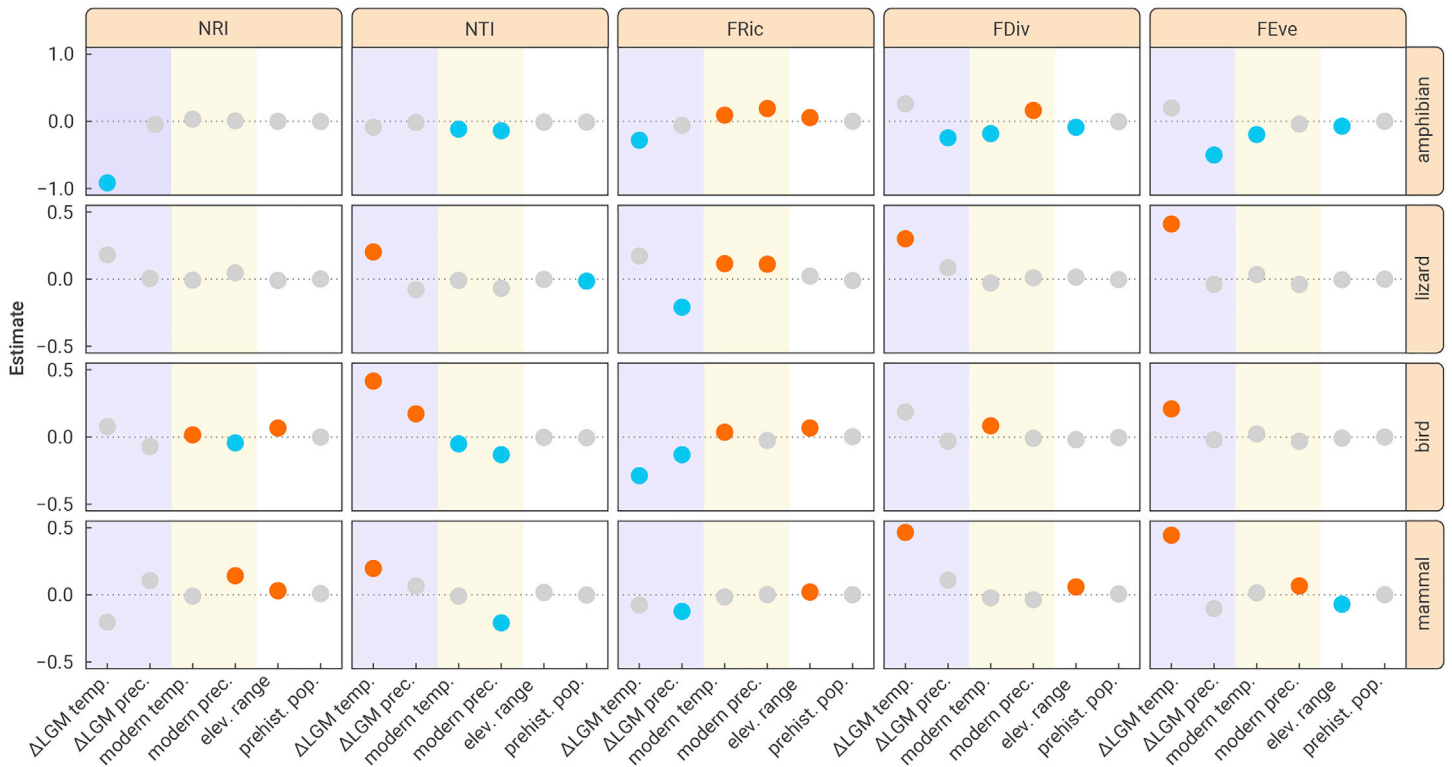


Figure 4. Coefficients of the spaMM model results show the effect of LGM climate changes, modern climate, elevation range, and prehistorical human population density on the functional diversity and phylogenetic structure of Chinese terrestrial vertebrates. Δ LGM temp., LGM temperature changes; Δ LGM prec., LGM precipitation changes. Red indicates positively significant coefficients, blue indicates negatively significant coefficients, and gray indicates an insignificant effect.

Our analyses suggested that LGM climate changes had a significant impact on community functional diversity, partially conforming to our prediction P1. In detail, the negative impact of LGM climate changes on FRic indicated the filtering effect of past climate on species trait space that would have led to the loss of species that took advantage of some environmental conditions before the LGM. The FDiv and FEve results indicated a more dispersed and regular distribution of organisms in trait space with increasing LGM climate changes, demonstrating greater competition and/or extreme adaptation to more harsh habitats during the LGM.²⁴ However, LGM climate changes had little impact on the FDiv of birds; this conformed to our prediction P2 that birds might recover from LGM climate changes due to their strong dispersal ability. In addition, amphibians' FDiv and FEve were negatively related to LGM precipitation changes but were unrelated to LGM temperature changes, suggesting that precipitation had a stronger influence on amphibians than temperature because of their dependence on water for reproduction. LGM precipitation changes could have had a harsh influence on amphibians, resulting in weaker adaptation and competition between surviving species, thus leading to low FDiv and FEve. Elevation range also had a significant effect on functional diversity, suggesting that undulating terrain may have buffered LGM climate changes and harbored diverse habitats, thus preserving some special functional traits. After taking prehistorical anthropogenic interference (measured as the population density of 10 000 BC) into consideration, we found little influence on diversity patterns except for the NTI of lizards. This result indicated that the prehistorical human population density did not shape the biodiversity patterns across the entire country, although it had driven large-sized mammals such as gibbons and elephants to local extinction and reduced the functional diversity of these regions.⁹

We explored the filtering effect of LGM temperature changes on the first two main dimensions of the community functional trait spaces of birds and mammals. We found that communities that were more severely affected by LGM temperature changes were characterized by faster life-history trait values. However, this pattern was only found in mammal communities, not in bird communities, probably due to the resistance of birds to paleoclimate changes due to their strong dispersal ability. This result suggested that fast species, manifested

as smaller body size, larger clutch size, a short lifespan, and higher growth rates, could recover from environmental filtering more easily and thus might have become dominant in mammal communities.

Our study is the first to investigate the functional diversity patterns of Chinese terrestrial vertebrates, and our results could serve to identify areas of conservation priority beyond the criteria of species richness and phylogenetic diversity. Our analyses identified several functional richness hotspots and native species that were most functionally distinct, and the results can be used to guide conservation policy. For example, northern Guangxi Province was identified as a functional richness hotspot for amphibians, indicating the presence of rich and valuable habitats in the area. In addition, the lagging effect of LGM climate changes on today's biodiversity patterns suggests that the influence of climate change could be long-lasting and may cause future extinction debts. Urgent action should be taken to relieve the pressure of climate change on biodiversity. For instance, the conservation network of protected areas should be improved to provide stepping stones for animal migration in response to climate change.²⁵ Refuges such as primitive mountains could also play an important role for organisms in confronting climate change due to the complex terrain, and thus they need to be well protected.

However, there are still some gaps in this study. Data shortages in the functional traits of some species, especially amphibians and reptiles, should be investigated in future studies. Such fundamental data could also serve to investigate the speciation process and endangerment mechanisms. In addition, although prioritizing phylogenetic diversity sometimes captures functional diversity unreliably because of incomplete trait datasets, ecologists commonly believe that functional metrics such as richness, divergence, and regularity provide another unique perspective for biodiversity research.²⁶ Thus, we call for stronger efforts to build a more complete trait database covering different taxonomic groups.

MATERIALS AND METHODS

See [supplemental information](#) for details.

DATA AND MATERIALS AVAILABILITY

All data needed to evaluate the conclusions in the paper are present in the paper and/or the [supplemental information](#). Scripts and the datasets necessary to

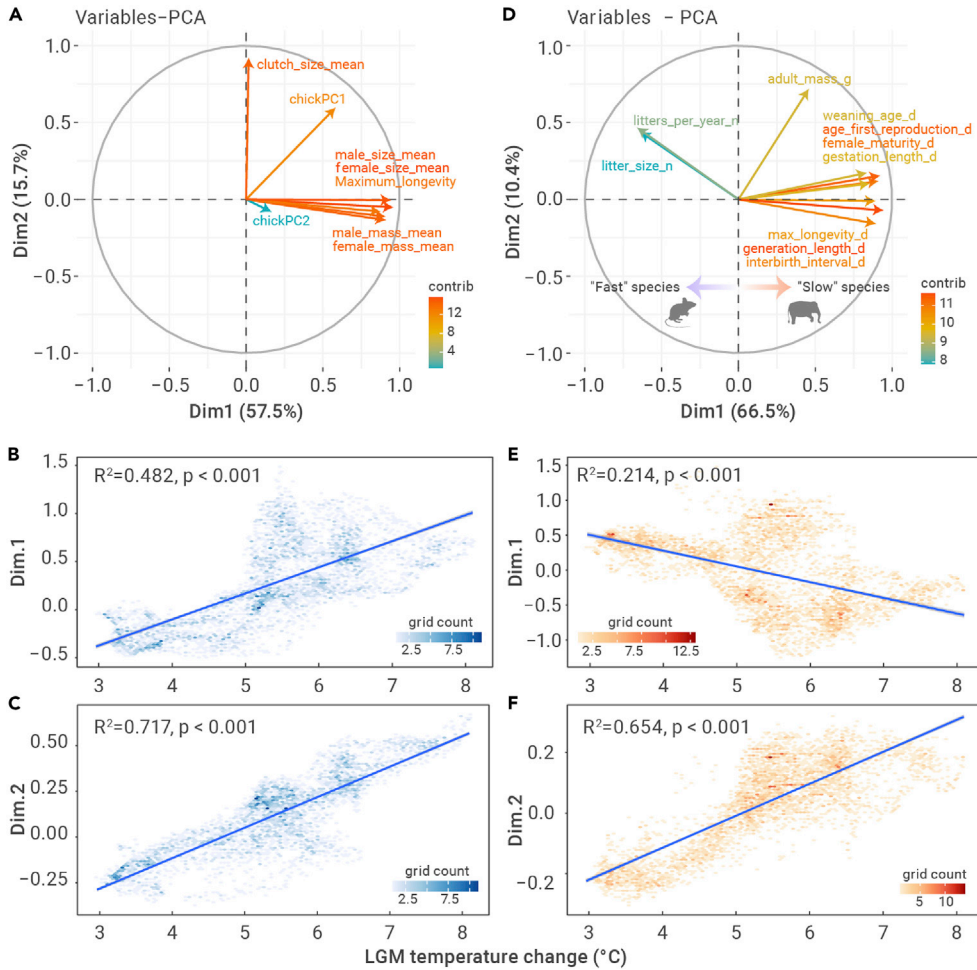


Figure 5. Effect of LGM temperature changes on the community weighted traits mean value (A and D) The principal-component analysis graph of the life-history traits of avian (A) and mammal (D) species. Traits that are closer to each other are more correlated. Positive x and y axes values mean a positive relationship between traits and dimensions. The color of arrows indicates the contribution of traits to dimensions. (B, C, E, and F) The linear model results between LGM temperature changes and life-history trait principal-component analysis dimensions of avian (B and C) and mammal (E and F) species, with the R-Squared (R^2) and p value of each linear model shown in the panels. The value of "grid count" means the number of grid-cell-based communities within the hexagons.

run the analysis are available in the github repository (<https://github.com/Huangmp1996/paleocliamte>).

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AUTHOR CONTRIBUTIONS

F.W. designed research. M.H., G.H., and H.F. performed research. All authors participated in the writing of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

SUPPLEMENTAL INFORMATION

It can be found online at <https://doi.org/10.1016/j.xinn.2023.100379>.

LEAD CONTACT WEBSITE

http://sourcedb.ioz.cas.cn/zw/zjrc/200907/t20090716_2088462.html.