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Original Article

Evolutionary factors and habitat filtering affect the pattern of Gerbillinae diversity

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Abstract

How ecological and evolutionary factors affect small mammal diversity in arid regions remains largely unknown. Here, we combined the largest phylogeny and occurrence dataset of Gerbillinae desert rodents to explore the underlying factors shaping present-day distribution patterns. In particular, we analyzed the relative contributions of ecological and evolutionary factors on their species diversity using a variety of models. Additionally, we inferred the ancestral range and possible dispersal scenarios and estimated the diversification rate of Gerbillinae. We found that Gerbillinae likely originated in the Horn of Africa in the Middle Miocene and then dispersed and diversified across arid regions in northern and southern Africa and western and central Asia, forming their current distribution pattern. Multiple ecological and evolutionary factors jointly determine the spatial pattern of Gerbillinae diversity, but evolutionary factors (evolutionary time and speciation rate) and habitat filtering were the most important in explaining the spatial variation in species richness. Our study enhances the understanding of the diversity patterns of small mammals in arid regions and highlights the importance of including evolutionary factors when interpreting the mechanisms underlying large-scale species diversity patterns.

Key words: arid regions, evolutionary time, Gerbillinae, habitat filtering, landcover, speciation rate.

The distribution of species diversity across the Earth's surface is characterized by pronounced heterogeneity. Although extensive research has been undertaken by biogeographers on large scales (Belmaker and Jetz 2015), biodiversity hotspots (Li et al. 2021), and across different natural gradients (latitude or altitude) (Kinlock et al. 2017; Quintero and Jetz 2018), less attention has been directed towards investigating the spatial pattern of species diversity in arid regions (Zhang et al. 2023). Arid regions, including hyper-arid, arid, and semi-arid, have traditionally been construed as harsh and barren landscapes (Ward 2016). Consequently, these regions have received far less attention than other biomes (e.g., forests and steppes), despite their substantial coverage, constituting approximately one-third of the Earth's terrestrial surface and harboring distinct biodiversity (Byrne et al. 2008; Durant et al. 2012; Zhang et al. 2023). As a result, species diversity patterns and their underlying mechanisms in arid regions have been poorly explored, which limits our understanding of the origin and evolution of the world's biodiversity. There is an urgent need for more research on the spatial patterns and influencing factors of species diversity in arid regions.

Understanding what determines the spatial patterns of species diversity is one of the greatest challenges in evolutionary biology and ecology (Pennisi 2005; Jin et al. 2021). Many factors have been proposed to explain the spatial variation of species diversity in different scales. For example, habitat heterogeneity shows particularly strong associations with species richness of terrestrial plants and animals (Stein et al. 2014), although contemporary climate determines the geographic distribution of European mammal diversity (Santos et al. 2020). A recent study found that Quaternary climate change is a major driver of species richness and rarity of mammals, birds, amphibians, and dragonflies across sub-Saharan Africa (Pinkert et al. 2020). However, prior studies exploring large-scale patterns have suggested that considering only the correlations between environmental variables and species richness may fail to fully understand how species richness was generated over time, as this requires incorporating evolutionary factors into the models (Wiens and Donoghue 2004; Cai et al. 2020).

From an evolutionary perspective, phylogenies combined with spatial data can be used to infer historical processes and ultimately the formation of contemporary patterns of biodiversity (Stevens 2006; Feijó et al. 2022a). Indeed, the spatial pattern of species diversity is ultimately generated by the processes of speciation, extinction, and dispersion

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on the evolutionary time scale (Wiens and Donoghue 2004; Shrestha et al. 2018; Feijó et al. 2022a). Two classic hypotheses, the time-for-speciation hypothesis (Stephens and Wiens 2003) and the diversification rate hypothesis (Mittelbach et al. 2007), have attracted widespread attention in studies explaining patterns of species diversity from an evolutionary perspective. The time-for-speciation hypothesis refers to the idea that the earlier an area is occupied by a lineage, the more species are likely to accumulate (Stephens and Wiens 2003). For example, a study by Wiens et al. (2011) found that climate, diversification rates, or morphological variation do not primarily account for the local patterns of treefrog species diversity, which is largely determined by the timing of colonization in each region. On the other hand, the diversification rate hypothesis assumes that high speciation rates or low extinction rates contribute to the accumulation of species diversity (Condamine et al. 2012). Scholl and Wiens (2016) provided an empirical case where most of the variation in richness among clades across the Tree of Life is due to variation in diversification rates. However, neither of these 2 hypotheses alone can fully explain the mechanisms underlying species diversity patterns.

A cumulative number of studies have attempted to combine ecological with evolutionary factors to explain species diversity patterns, such as in amphibians (Wiens et al. 2006), reptiles (Tejero-Cicuéndez et al. 2022), birds (Cai et al. 2020), and mammals (Belmaker and Jetz 2015). Nearly all of these studies revealed the importance of time-for-speciation effects in shaping species diversity patterns, except for reptiles. Analysis of global desert lizard diversity showed that the environment is the main factor shaping lizard diversity in different arid regions, although diversification rate and time-for-speciation hypotheses have less explanatory power (Tejero-Cicuéndez et al. 2022). These studies highlight the complexity of the mechanisms underlying species diversity patterns. Therefore, it is imperative to consider a broader range of potential factors, including both ecological and evolutionary factors, to arrive at a robust conclusion.

Species diversity in arid regions is primarily represented by animals that are highly adapted to arid environments with large populations but small sizes, such as rodents (Smith et al. 2010). Rodents have huge populations and long evolutionary histories, and their fossils are abundant and widespread, making them ideal groups for studying the formation mechanisms of diversity patterns in desert biota. Here, using one of the largest rodent subfamilies, Gerbillinae, we evaluated the relative importance of ecological and evolutionary factors in driving large-scale patterns of rodent diversity in arid regions. Gerbillinae is the second-largest subfamily (after Murinae) in the Muridae family of rodents and contains 14 genera and 102 species, which consist almost exclusively of arid-adapted species (Shenbrot et al. 2012; Burgin et al. 2018; Mammal Diversity Database 2023). They are an essential component of arid ecosystems in Africa and Eurasia and are widely distributed in deserts, semi-deserts, steppes, savannas, and other arid environments (Shenbrot and Krasnov 2001; Denys et al. 2017). However, to date, there have been no studies on the large-scale diversity pattern of Gerbillinae. Due to the lack of sufficient sampling and molecular data, previous evolutionary studies have mainly focused on phylogenetic reconstruction, divergence time estimation, and biogeographic history at long temporal scales (Chevret and Dobigny 2005; Abiadh et al. 2010; Ito et al. 2010; Granjon et al. 2012; Alhajeri et al. 2015; Ndiaye et al. 2016), whereas ecological studies have often investigated the species distribution dynamics at short temporal scales and ignored historical biogeography (Brown et al. 2000; Shenbrot et al. 2010). To disentangle the mechanisms driving the large-scale distribution of Gerbillinae species diversity, evolutionary, and ecological approaches should be used jointly.

Here, we reconstructed a robust phylogeny and estimated the divergence times for Gerbillinae species based on all available molecular data and newly generated sequences. Based on this robust phylogenetic framework, we investigated the role that historical biogeography, diversification rate, and ecological conservatism play in shaping the diversity patterns of Gerbillinae species. Finally, generalized linear, spatial simultaneous autoregressive, random forest, and structural equation models (SEMs) were used to investigate the factors influencing spatial diversity patterns in these groups. We aimed to address 2 main questions: (1) Where and when did Gerbillinae originate? and (2) What is the relative importance of ecological and evolutionary factors in shaping the patterns of Gerbillinae diversity? We predict that evolutionary factors may play a more important role than ecological factors in shaping the spatial pattern of Gerbillinae diversity. Given that Gerbillinae species are typical xeric animals (Denys et al. 2017), the insights gained from them could serve as a reference for other small mammals in arid regions.

Materials and Methods

Data collection

We compiled the distributions of Gerbillinae species from multiple sources, including the National Zoological Museum, Institute of Zoology of the Chinese Academy of Sciences, Beijing, China (IOZCAS), the Centre de Biologie pour la Gestion des Populations "CBGP - Small mammal Collection" (https://doi.org/10.15454/WWNUPO), Global Biodiversity Information Facility (GBIF, http://www.gbif.org/), African Mammalia website (http://projects.biodiversity.be/african-mammalia), published literature, and our fieldwork. These datasets were carefully assessed in ArcGIS 10.6 and erroneous and duplicated records were removed. To test the time-for-speciation hypothesis and the diversification rate hypothesis, we excluded species for which we did not have molecular data. Our final dataset included a total of 8059 unique distribution records from 66 species (Supplementary Table S1). Additionally, we obtained fossil records from the Fossilworks (http://www.fossilworks.org/), Paleobiology Database (https://paleobiodb.org/#/), and New and Old World Database of Fossil Mammals (https://nowdatabase.org/).

We retrieved sequences for all available Gerbillinae species from GenBank and combined them with 66 newly generated sequences (GenBank accession numbers: OQ423071-OQ423076, OQ507339-OQ507372, OR150475-OR150482, OR159306-OR159311, OR159338-OR159339, and OR166795-OR166804). A total of 9 genes, from 66 (65%) species of 13 genera of Gerbillinae and 4 species of the sister clade Deomyinae as outgroups, were used to reconstruct the phylogenetic relationships (Supplementary Table S2).To investigate the influence of morphological characteristics on the diversification of Gerbillinae, we analyzed 6 common morphological characteristics of Gerbillinae from the COMBINE database and previous studies (Alhajeri and Steppan 2018; Alhajeri et al. 2020; Soria et al. 2021): body mass, head-body length, tail length, hind-foot length, ear length, and bulla volume. To handle missing data, we estimated values through phylogenetic imputation using the R package "Rphylopars" (Goolsby et al. 2016), assuming a phylogenetic correlation among morphological characteristics.

To explore the effects of environmental and geographic factors on Gerbillinae diversity patterns, we collected 28 ecological variables, including 19 bioclimatic variables (Bio1-19) and one topographical layer (elevation) from WorldClim 2.0 (http://www.worldclim.org/) (Fick and Hijmans 2017). We also included the Climate Stability Index (CSI) variable from Herrando-Moraira et al. (2022) as it provides information on climate vulnerability from the Pliocene (3.3 Ma) to the present. CSI values range 0–1 (most to least stable) (Herrando-Moraira et al. 2022). Additionally, we gathered one energetic variable (the global Net Primary Productivity (NPP) from 1981 to 2018) (Wang et al. 2021) and 4 land-cover classes (consensus5-7, consensus11) (Tuanmu and Jetz 2014). We also included the annual potential evapotranspiration (PET) and aridity index (AI) (Trabucco and Zomer 2018). These variables were downloaded and processed at a resolution of 2.5 arc minutes. The choice of this coarser resolution was preferred due to the variety of methods used to record species occurrence (Feijó et al. 2022b). All variables were grouped into 4 categories: (a) historical climate (CSI), (b) contemporary climate (Bio1-19, AI, PET), (c) habitat heterogeneity (elevation and land covers), and (d) energetic variable (NPP).

Gerbillinae richness map

To estimate the spatial richness of Gerbillinae, we generated species distribution models (SDMs) for each species. Initially, for each of the 66 taxa, we compared a set of Maxent models using the "ENMevaluate' function implemented in the ENMeval 2.0 R package (Kass et al. 2021). These models varied in complexity, including regularization multipliers ranging from 0.5 to 6, in increments of 0.5, and 6 combinations of feature classes (L, LQ, LQH, LQHP, LQHPT, and H; where L = linear, Q = quadratic, P = product, T = threshold, H = hinge). We selected 11 less correlated ($r < 0.8$) climate predictors from the full set of 19 layers obtained from WorldClim. Additionally, we included elevation, PET, NPP, and the 4 land-cover classes (consensus5-7, consensus11) as environmental predictors based on Gerbillinae's habitat preference. The models" performance was tested by partitioning the localities into testing and training bins using the 'checkerboard2' method. For model training, 10,000 background points were randomly selected for model training from a buffer area that extended 5 km from the most marginal records. The best model was selected based on spatial cross-validation metrics using the AICc (Feijó et al. 2022b). Subsequently, we built models using the maximum entropy algorithm in MAXENT 3.4.1 (Phillips et al. 2006), and the area under the curve (AUC) was used to assess the accuracy of the modeling outcomes (Lobo et al. 2008). The logistic output of each species' best model, representing the probability of presence varies from 0 to 1, was used for direct comparison across models (Phillips and Dudik 2008). To mitigate overprediction in species-poor areas, we removed grid cells with suitability values lower than the maximum training sensitivity plus specificity threshold (Liu et al. 2013). Model performance well (AUC > 0.8) except for *Gerbillus hesperinus* (AUC = 0.5), probably because it had only had 2 distribution records, so we excluded it (Supplementary Table S3). The final SDM suitability outputs contains 65 species were then stacked to produce the Gerbillinae richness map (Feijó et al., 2022b), which was projected to a Behrmann equal-area cylindrical projection and divided into grid cells of 55 × 55 km. Gerbillinae richness map was visualized in ArcGIS 10.6. Based on Maxent output, we calculated the average species richness of each grid cell.

Phylogenetic analyses and divergence time estimation

To understand the evolutionary history of Gerbillinae, we first constructed a phylogenetic tree and estimated the divergence time between its component species. Phylogenetic relationships were inferred under maximum-likelihood (ML) method in IQ-TREE 1.6.8 (Nguyen et al. 2015) and Bayesian inference (BI) method in MRBAYES v3.2.6 (Ronquist et al. 2012). Divergence time estimation was performed using BEAST v2.6.4 (Bouckaert et al. 2019) with a relaxed clock and BD prior. The calibration points were obtained from fossil records and previous studies (Supplementary Methods and Supplementary Tables S4 and S5).

Ancestral range estimation and niche reconstruction

To investigate the origin and dispersal of Gerbillinae, we estimated its ancestral range using the R package "BioGeoBEARS" (Matzke 2013, 2014) in R v4.1.3 (R Core Team 2022). We defined 8 geographical regions based on the distribution of Gerbillinae: 1) Sub-Saharan Africa, 2) Horn of Africa, 3) Sahara, 4) Arabia, 5) Western Asia, 6) Southern Asia, 7) Central Asia, and 8) Eastern Asia. We tested 3 models provided by BioGeoBEARS, including the dispersal-extinction-cladogenesis model (DEC) (Ree and Smith 2008), the dispersal–vicariance model (DIVALIKE) (Ronquist 1997), and the BayArea model (BAYAREALIKE) (Landis et al. 2013). The maximum number of areas was set to 4. Models were ranked by the standard correction to Akaike's Information Criterion (AICc) (Anderson and Burnham 2004). Biogeographic stochastic mapping (BSM) was employed to calculate the number of dispersal events among the 8 geographic regions. Event frequencies were estimated by taking the mean and the SD of event counts from 100 BSMs.

To estimate the ancestral niches of Gerbillinae, we reconstructed the ancestral mean annual temperature (MAT) and aridity index (AI) using the residual maximum likelihood (REML) method (Felsenstein 1985) in the R package "ape" (Paradis and Schliep 2019). The MAT and AI of each species were calculated as the average of the values of all geographical units where the species was distributed.

Diversification rate estimation

To explore the temporal diversification of Gerbillinae species, we first investigated its diversification pattern by constructing a lineage through time (LTT) plot using the R package 'ape' (Paradis and Schliep 2019). In addition, we used Bayesian analysis of macroevolutionary mixtures (BAMM) (Rabosky 2014) to estimate diversification rates over time and identify potential rate shifts. We ran BAMM analysis using the time-calibrated phylogeny without outgroups obtained from the MCC tree. Two methods were used to ensure the robustness of our results to alternative analytical parameters. BAMM can account for non-random incomplete taxon sampling in diversification studies. There are 2 different ways to account for backbone topology if not completely sampled: by using the total sampling fraction across the whole group; or by using not a single global sampling probability, but a rather specified clade- or species-specific sampling probability (Rabosky, 2014). Because the percentage of sampled taxa varied considerably across the tree, we chose the latter method. BAMM was run for 10 million generations and sampled every 1,000 generations. Appropriate prior values were estimated using the setBAMMpriors function. Post-run analysis and visualization were performed using the R package "BAMMtools" (Rabosky et al. 2014). The initial 25% of samples were discarded as burn-in, and the remaining data were assessed for convergence using the R package "coda" (Plummer et al. 2006) to ensure that the effective sample size (ESS) values were above 200.

To investigate the effects of global paleo-temperature on Gerbillinae diversification, we used the R package "RPANDA" (Morlon et al. 2016) to fit a series of time- and temperature-dependent likelihood diversification models. Speciation and extinction dependences were modeed as all possible combinations of constant, linear, and exponential relationships as well as pure-birth models (Jin et al. 2021). We compared the likelihood supports, and the model with the smallest AICc value was selected as the best diversification model. The global paleotemperature data set was obtained from Sun et al. (2020).

Phylogenetic signal detection

Blomberg's K (Blomberg et al. 2003) and Pagel's λ (Pagel 1999) are 2 measures of phylogenetic signals. To test whether the ecological variables and morphological characteristics of Gerbillinae are phylogenetically constrained, Blomberg's K was calculated using the phylosignal function in the R "picante" package (Kembel et al. 2010), and Pagel's λ was estimated with 1,000 simulation replicates of trait data using phylosig function in the R package "phytools" (Revell 2011). $K = 0$ indicates that there is no phylogenetic signal in the trait, $K < 1$ indicates that there is a weak phylogenetic signal, whereas $K > 1$ indicates that there is strong phylogenetic signal. Pagel's λ varies continuously from 0 to 1, where $\lambda = 0$ indicates that there is no phylogenetic signal in the trait, λ close to 1 indicates that there is a strong phylogenetic signal, and the trait has evolved according to the Brownian motion model of evolution (Kamilar and Cooper 2013).

Evolutionary time and speciation rate

To estimate a proxy of the time that lineages have been present, we first obtained the time-calibrated branch lengths for all species included in the phylogeny with the R package "ape" (Paradis and Schliep 2019). This procedure was repeated for a set of 100 trees from the posterior probability distribution. Next, we extracted the values corresponding to the species assemblage of each grid and used the maximum branch length (MBL) of this species set (which represents the age of the oldest species assuming no extinction) as a simple relative estimate of its evolutionary time (García-Rodríguez et al. 2020). Although focused on recent and independent colonization events, this metric is a useful proxy for our primary aim of obtaining informative estimates of assemblage evolutionary time (García-Rodríguez et al. 2020).

To obtain speciation rates of Gerbillinae species, we estimated a proxy of mean species-specific rates of speciation with the DR metric (species-level lineage diversification rate); (Jetz et al. 2012) using a set of 100 trees from the posterior probability distribution. This metric, originally described as a metric of diversification, is a good measure of speciation (Title and Rabosky 2019), and here we used it in that context. The calculation of this metric considers the number of splitting events and the internode distances along the root-to-tip path of the phylogeny while giving greater weight to branches closer to the present (Jetz et al. 2012). Based on the tip speciation rates from the DR metric, we estimated the mean speciation rate for each grid based on their corresponding species assemblages.

Effect of evolutionary and ecological factors

For habitat heterogeneity variables, we considered all 12 landcover classes, which were simplified to landcover types that indicate how many landcover classes there are within each grid and we also calculated the range values of elevation within each grid cell to represent topographical heterogeneity. The values of other ecological variables were extracted as mean values within each 55 × 55 km grid cell. To investigate the underlying mechanisms of the diversity pattern of Gerbillinae, we used a generalized linear model (GLM) to examine the effects of evolutionary and ecological factors on species richness. The mean species richness was log-transformed to improve normality and linearity. All predictor variables were standardized (a mean of zero and a variance of one) to eliminate dimensional effects between variables before conducting multiple regression analyses. To remove multicollinear variables, we included predictor variables in the models only when the variance inflation factor (VIF) was less than 5. The VIF was calculated using the R package 'car' (Fox et al. 2012). We applied the dredge function in the R package "MuMIn" (Barton 2022) to select the best models, based on the lowest Akaike information criterion (AIC). The determined proportion of deviance explained by the GLM, or a pseudo-R2 value, was calculated using the Dsquared function in the R package 'modEvA' (Barbosa et al. 2021). We then built a spatial simultaneous autoregressive (SAR) model using the R package "spdep" to account for spatial autocorrelation (Kissling and Carl 2007). Then, a random forest model (RF) was used to rank the importance of the variables using the R package 'randomForest' (Liaw and Wiener 2002). However, a relationship between ecological variables and species richness may be explained by higher speciation rates (Wiens et al. 2011). Therefore, we estimate the direct and indirect influences of ecological and evolutionary factors on Gerbillinae species richness using a SEM. Before modeling, we first standardized each variable to allow for a direct comparison of the path coefficients (β) in the SEM (Algar et al. 2009). The total effect of a predictor on species richness is equal to the sum of direct and indirect effects. Indirect effects are estimated simply by multiplying the standardized paths involved (Cerezer et al. 2020). We constructed a SEM using the R package 'lavaan' (Rosseel 2012), and the significance of path coefficients was re-evaluated using the lavSpatialCorrect function (https://github.com/jebyrnes/spatial_correction_lavaan) to remove spatial autocorrelation impact. All statistical analyses were implemented in R v.4.1.3 (R Core Team 2022).

Results

Global pattern of Gerbillinae species diversity

The spatial pattern of Gerbillinae richness showed strong geographical variation with higher diversity in North Africa and West Asia in contrast to the lower diversity in South Asia (Figure 1). In particular, the highest species richness was found along the coastal areas of northern Africa, particularly in Egypt and Libya, followed by the Sahara-Sahel region. The lowest species richness region was found in India (Figure 1). Interestingly, typical desert regions (such as the Sahara Desert) do not contain the most Gerbillinae species.

Phylogeny and divergence time estimates

The BI and ML phylogenetic trees derived from the supermatrix dataset show similar topologies and clades with overall strong support (Supplementary Figure S1). Our results supported all genera in Gerbillinae but *Meriones*, which was found paraphyletic but with low support values for both the ML and BI trees. This result is consistent with previous studies that show that *Meriones tamariscinus* is closely related to *Rhombomys opimus* (Alhajeri et al. 2015). In addition, we also found that the phylogenetic relationship between mitochondrial and nuclear trees showed inconsistent topological results (Supplementary Figures S2 and S3). The differences occurred mainly in the positions of the genera *Pachyuromys*, *Desmodilliscus*, and *Taterillus* (Supplementary Figures S2 and S3). The nuclear gene tree topology was consistent with the super matrix dataset, whereas in the mitochondrial gene tree, *Pachyuromys* and *Desmodilliscus* were closer to *Ammodillus*, although with low support values. In addition, the mitochondrial tree recovered *Taterillus* as the sister lineage of the clade including *Gerbillus* and *Meriones* (Supplementary Figure S3).

The divergence between Gerbillinae and Deomyinae was estimated at 16.82 (19.36–14.48) Ma in the early Miocene and the basal split of Gerbillinae species was at 12.89 (14.35–11.51) Ma in the middle Miocene. All extant monotypic genera in Gerbillinae originated in the Miocene, whereas non-monotypic genera originated in the Pliocene, except for the genus *Gerbilliscus* (Supplementary Figure S4).

Ancestral range estimation and niche reconstruction

The AICc model selection supported the DEC model (LnL = −191.6, AICc = 387.5) (Supplementary Table S6). According to ancestral range estimation (Figure 2 and Supplementary Figure S5), Gerbillinae originated in Sub-Saharan Africa during the Middle Miocene. According to the results of biogeographic stochastic mapping (BSM), most biogeographical events can be explained by within-area speciation (65.9%) and dispersals (34.1%) (Supplementary Table S7). Many dispersals occurred between Sub-Saharan Africa and the Sahara as well as the Sahara and Arabia. The

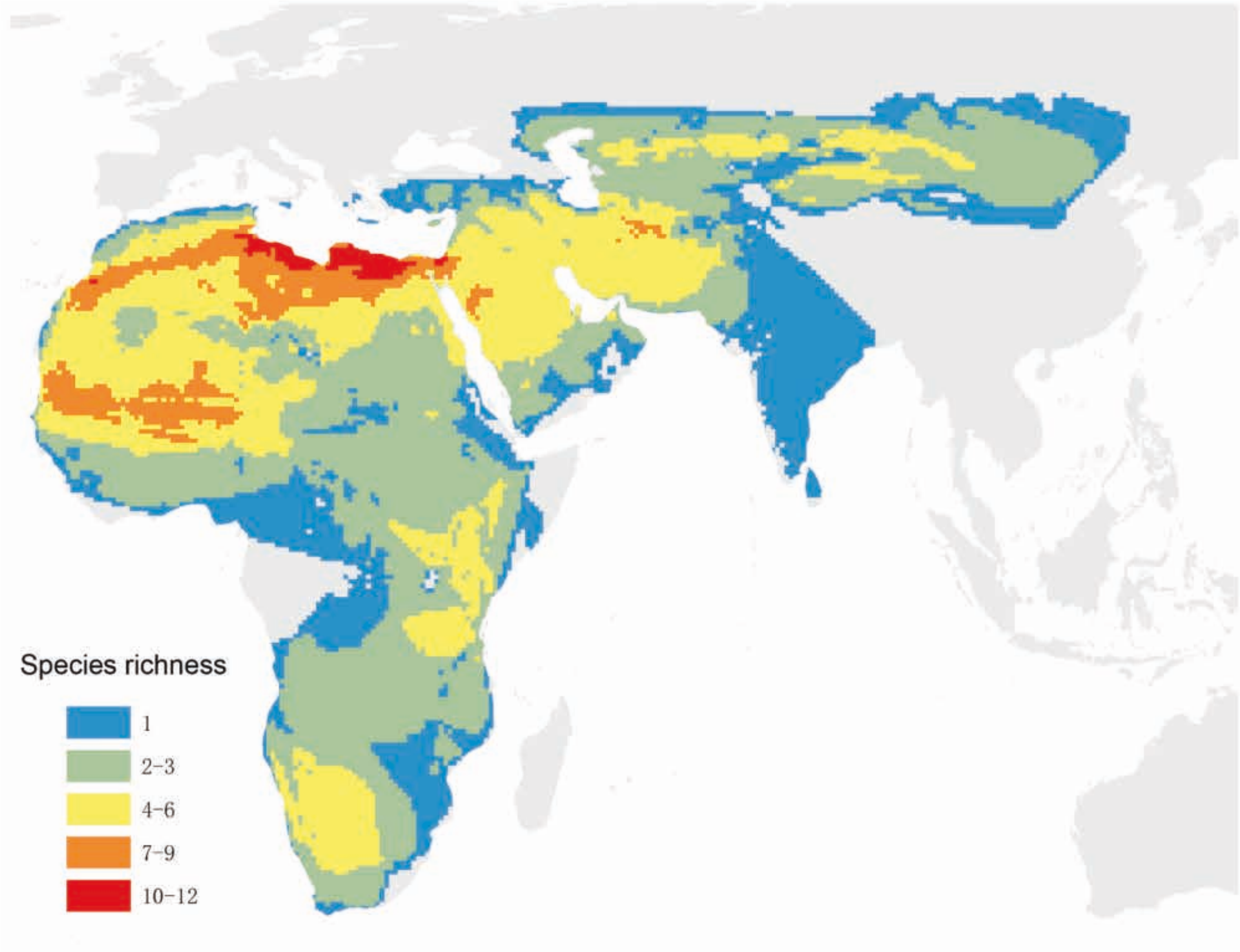

Figure 1. Gerbillinae species richness map across grid cells of 55 × 55 km based on species distribution models. Map in Behrmann projection. The continents map was obtained from the Resource and Environment Science and Data Center of the Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences.

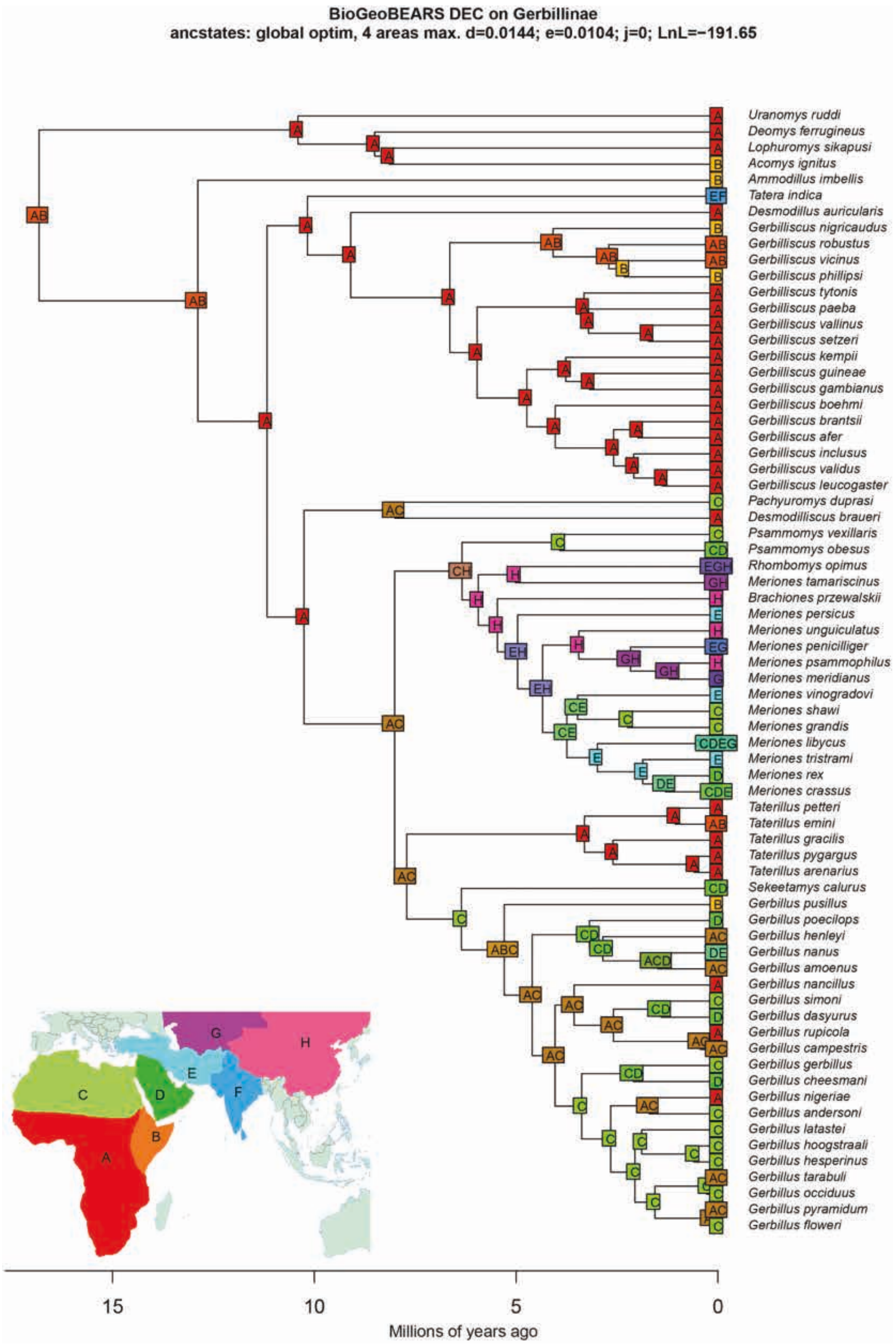

Figure 2. Ancestral areas of Gerbillinae estimated under the DEC model using BioGeoBEARS. Biogeographical regions: A, Sub-Saharan Africa; B, Horn of Africa; C, Sahara; D, Arabia; E, Western Asia; F, Southern Asia; G, Central Asia and H, Eastern Asia.

reconstructed ancestral niche based on the REML method suggested a hot and arid environment at most of the early nodes (Figure 3). MAT at the root node was reconstructed to be ~22.82 °C, and the reconstructed AI was ~1863.86.

Macroevolution rates estimates

The LTT plot showed that there is a remarkably constant rate of species accumulation from 12 to 2 Ma, and then a slight decline (Figure 4a). This result was similar to the Bayesian

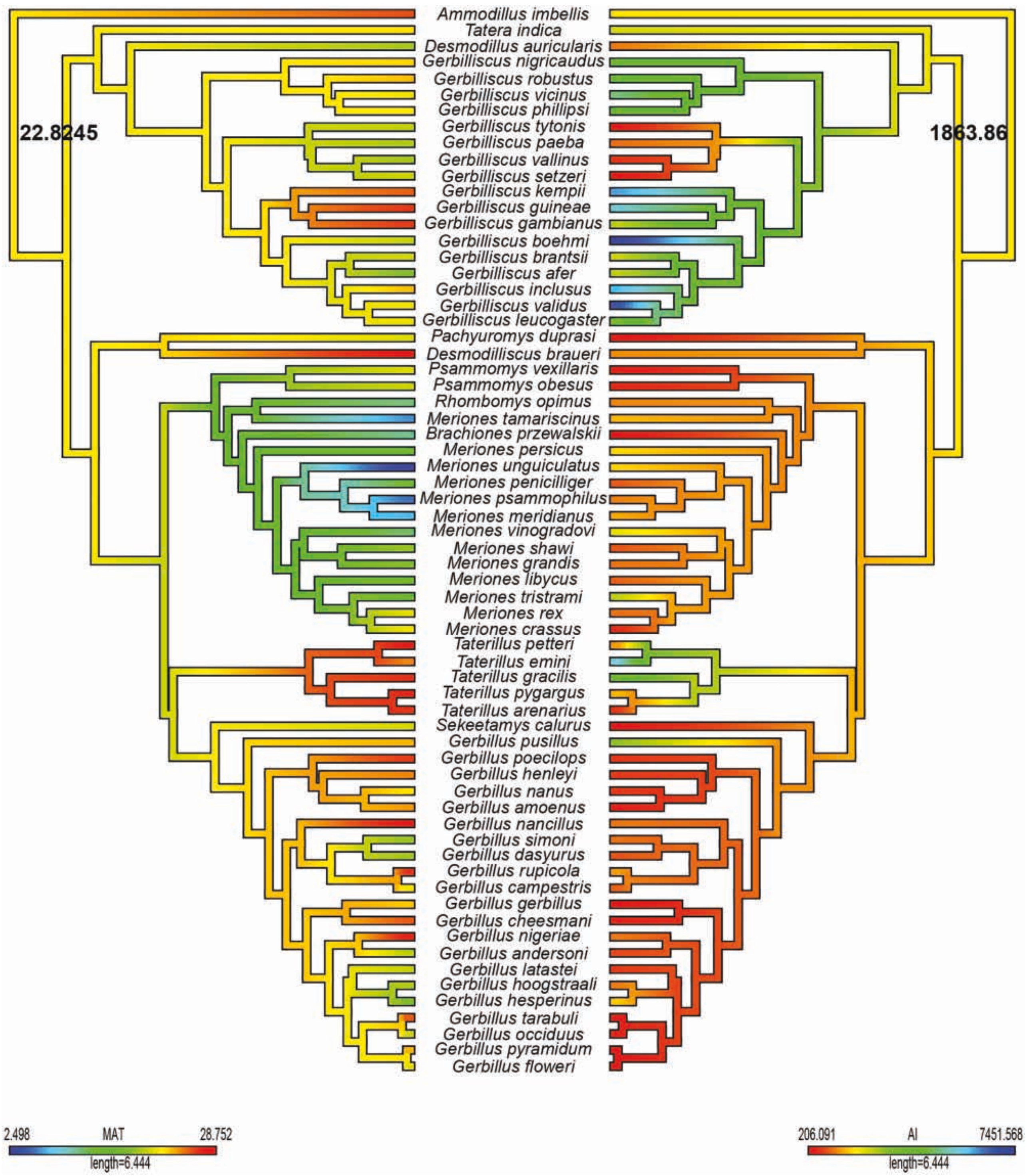

Figure 3. Results of ancestor climatic niche reconstruction. Left panel represents reconstructed ancestor values of mean annual temperature (MAT), right panel aridity index (AI). Warm colors represent hot and arid, cool colors represent cold and wet.

approach that showed a pattern of constant speciation rate over time, with no shift and only a slight decrease in the magnitude of speciation over time (Figure 4b and Supplementary Figure S6).

We also investigated the relationship between diversification rates and global paleotemperature by fitting likelihood models of time and temperature dependence in RPANDA. The linear speciation without extinction with temperature dependence was the best model (AICc = 304.0047) (Supplementary Tables S8 and S9), indicating that the diversification rate in Gerbillinae decreased as the paleotemperature decreased, which was consistent with the results of BAMM (Figure 4b,c).

Phylogenetic signals of niche and morphological

The results indicate that significant phylogenetic signals exist in morphological characteristics (Blomberg's $K = 1.058471$, $P = 0.001$, Pagel's $\lambda=0.757014$, $P < 0.001$) of Gerbillinae,

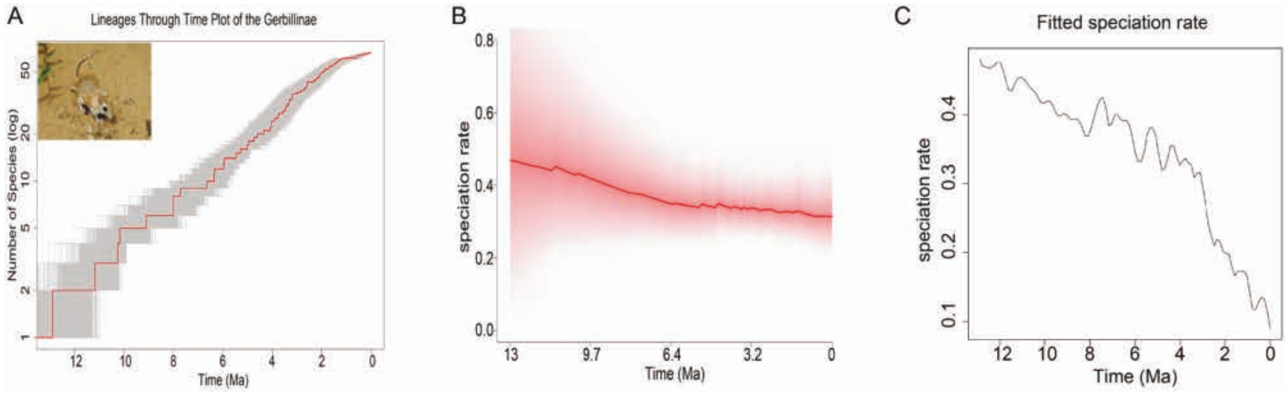

Figure 4. Results of diversification rate estimate byLTT, BAMM and RPANDA. (A) Lineages through time of Gerbillinae. (B) Speciation rate. (C) Speciation rate through temperature estimated by RPANDA. The picture at the top left of (A) is *Gerbillus occiduus* from Laurent Granjon.

whereas niche (Blomberg's $K = 0.5800498$, $P = 0.001$, Pagel's λ=0.42442, $P = 0.0104$) have a weak phylogenetic signal (Supplementary Table S10).

Evolutionary and ecological factors driving the Gerbillinae diversity pattern

The spatial pattern of Gerbillinae diversity was better explained by a combination of ecological variables and evolutionary factors (Supplementary Table S11). According to the results of the GLM, the species richness of Gerbillinae correlated with 7 variables ($R^2 = 0.3602$) (Figure 5a and Supplementary Table S12). Five ecological factors, including CSI, precipitation seasonality (Bio15), precipitation of coldest quarter (Bio19), landcover types, and altitude range, were negatively correlated with species richness. Two evolutionary factors, evolutionary time and speciation rate, were positively correlated with species richness. After considering spatial autocorrelation, neither Bio15 nor altitude range were significantly correlated with species diversity (Supplementary Table S12). Therefore, we excluded these 2 factors in subsequent random forest and SEM analyses. The result of the random forest model indicated that these variables together explained 86.54% of the variation in Gerbillinae species richness. Evolutionary time and speciation rate had higher explanatory power in the variation of species richness among grid cells (Figure 5b).

The SEM fitted the data well (SRMR < 0.08 and CFI > 0.90) and explained 34% of the variation in Gerbillinae species richness (Figure 5c). A strong and direct effect was also found for models using speciation rate as the predictor ($\beta = 0.41$, $P < 0.001$). Evolutionary time was the most important variable associated with the increase in Gerbillinae species richness through direct effect ($\beta = 0.60$, $P < 0.001$) and indirect effect (speciation rate mediated: $\beta = -0.324$ (-0.79×0.41), $P < 0.001$). Landcover types also had direct effect ($\beta = -0.39$, $P < 0.001$) and indirect effect (speciation rate mediated: $\beta = -0.103$ (-0.25×0.41), $P < 0.001$) on species richness. CSI had weak direct effect ($\beta = -0.06$, $P < 0.001$) and indirect effect (speciation rate mediated: $\beta = -0.041$ (-0.10×0.41), $P < 0.001$) on species richness. The direct effect of precipitation of coldest quarter on species richness was extremely weak and not significant (precipitation of coldest quarter: $\beta = -0.01$, $P = 0.088$). CSI ($\beta = -0.01$, $P = 0.421$) had extremely weak and no significant negative effect on evolutionary time.

Discussion

The origin and dispersal of Gerbillinae

Here, we provide the most complete phylogeny of the Gerbillinae to date by combining 4 mitochondrial and 5 nuclear genes, which is the first step needed for reconstructing the evolutionary and biogeographic histories of any group. Our ancestral range estimation shows that Gerbillinae likely originated in Sub-Saharan Africa and the Horn of Africa regions during the middle Miocene, but its more precise geographic origin is still an open question. The earliest fossil of Gerbillinae was found in the Lower Miocene fauna of Saudi Arabia as '*Gerbillidae indet*.' at about 16–23 Ma (Thomas et al. 1982; Whybrow 1987; Wessels 2009; Ndiaye et al. 2016). However, the morphology of the fossil material is incomplete, and it cannot be completely determined that it is a gerbil fossil. Except for this earliest fossil found in Saudi Arabia, other Gerbillinae fossils were found at about 11 Ma: *Gerbillidae indet*. in southern Africa (Wessels, 2009), *Protatera indet*. in Egypt (Mein and Pickford 2010), *Pseudomeriones* in Turkey (Koufos et al. 2009), and *Abudhabia baheensis* in China (Qiu et al. 2004). Previous studies have proposed that Gerbillinae originated in the Horn of Africa (Chevret and Dobigny 2005; Ndiaye et al. 2016; Kostin et al. 2022). Additionally, the reconstructed ancestral MAT and AI of Gerbillinae suggest the presence of ancestors in a hot and arid environment. Therefore, we agreed with the origin of Gerbillinae in the Horn of Africa and then dispersed across arid regions in Africa and Asia. This was the same as the result of a weak niche phylogenetic signal, indicating that the niche of Gerbillinae species may be relatively adaptive in the genetic and evolutionary sense, such that it does not retain the imprint of phylogenetic history (Rezende et al. 2004). The non-conservatism niche of Gerbillinae means that the species has left its ancestral niche and spread outward, resulting in the low richness of Gerbillinae in the Horn of Africa today. We inferred the potential diffusion route based on fossil records and the result of ancestral range estimation (Figure 6).

Based on our divergence time estimation, Gerbillinae species diverged from their sister taxon Deomyinae in the Early Miocene, but all extant genera (except genus *Psammomys* and *Taterillus*) originated in the Late Miocene to the Pliocene, and more than 90% of extant Gerbillinae species appeared after 6 Ma (Supplementary Figure S4) and diversified at a constant rate (Figure 4b). This pattern of diversification at

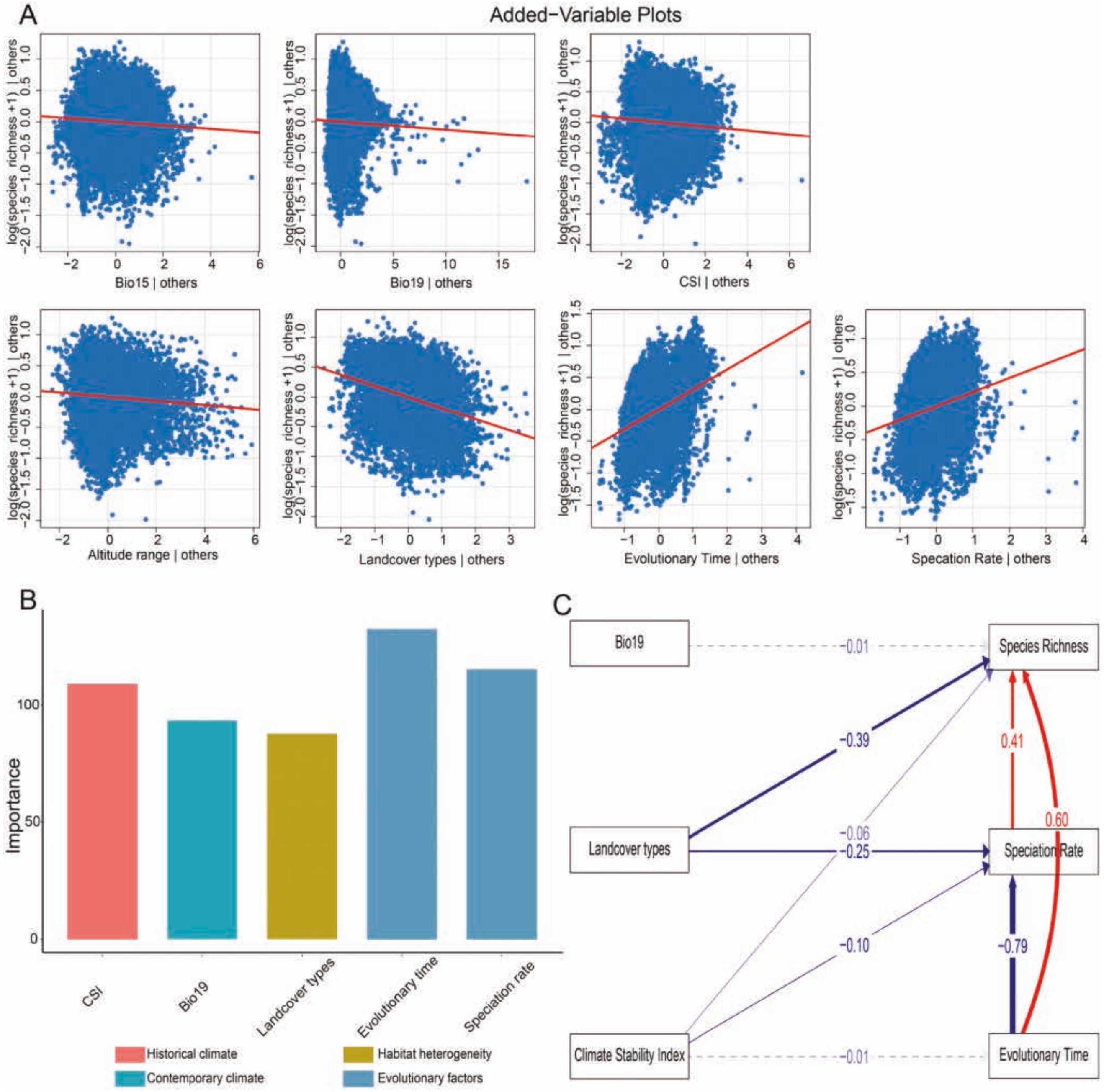

Figure 5. Determinants of Gerbillinae species diversity. (A) Relationships between predictor variables and log-transform species richness based on the generalized linear models across grid cells of 55 km × 55 km. (B) The relative importance of ecological and evolutionary factors for patterns of Gerbillinae species richness. (C) Direct and indirect effects of ecological factors on Gerbillinae species richness based on structural equation model (SEM). Numbers along the arrows (blue, negative; red, positive) represent the standardized path coefficient and the thickness of the line is proportional to coefficient strength. Solid and dashed arrows represent significant and non-significant path coefficients after taking spatial autocorrelation into account, respectively. Bio15, precipitation seasonality; Bio19, precipitation of coldest quarter; CSI, climate stability index; Altitude range, range values of altitude (max altitude—min altitude) in each grid; Landcover types, landcover classes in grid; Evolutionary time, maximum branch length of species set in each grid cell; Speciation rate, rate of speciation with the DR metric in each grid cell.

a constant rate has also been found in African Bufonidae (Liedtke et al. 2016). We uncovered a linear paleotemperature-dependent relationship associated with Gerbillinae diversification, indicating that the speciation rate gradually decreased with the climatic cooling along the late Neogene and Quaternary (Fortelius et al. 2014; Holbourn et al. 2018).

The result of ancestral region estimation indicated that Gerbillinae likely originated in the Horn of Africa in the Middle Miocene and then dispersed across arid regions in northern and southern Africa and western and central Asia, forming their current distribution pattern. We combined fossil data with climate change and tectonic activities since the middle Miocene to infer the potential diffusion route (Figure 6). The fossil genus *Protatera*, from the late Miocene of northern Africa, southwestern Europe, and southern Asia, was most similar to the extant genera *Desmodillus* and *Ammodillus* (Pavlinov 2008). The distribution of this extinct genus supported an initial dispersal of Gerbillinae taxa from the Horn

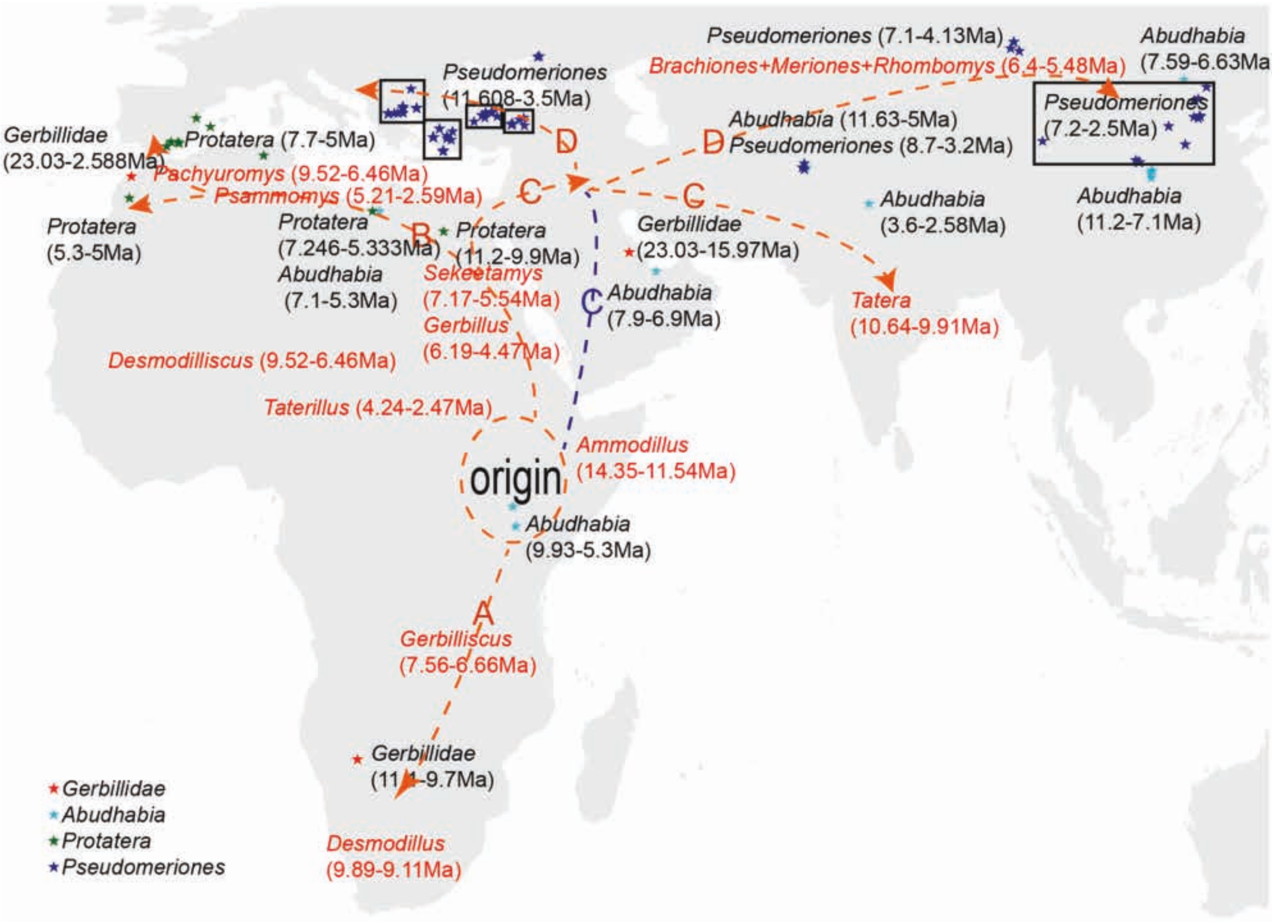

Figure 6. Map summarizing the inferred dispersal scenarios for Gerbillinae showing their origin and dispersal pathways. This figure shows 4 representative fossil genera (black) and 13 extant genera (red) that we used in Gerbillinae. According to the distribution of fossils and ancestral range reconstruction, we speculated that Gerbillinae had 4 main dispersal scenarios: dispersal scenario A is from the Horn of Africa to southern Africa; dispersal scenario B is from the Horn of Africa to northern Africa; dispersal scenario C and D are from the Horn of Africa to Eurasia, there were 2 potential pathways for the dispersal: the Bab-El-Mandeb strait south of the Red Sea and the Sinai route north of the Red Sea. The continents map was obtained from the Resource and Environment Science and Data Center of the Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences.

of Africa towards the northern ranges of the continent (Figure 6, dispersal scenarios B and C). The closure of the Strait of Bab-El-Mandeb and the establishment of a southern land bridge between Africa and Arabia during the Late Miocene (Bosworth et al. 2005; Portik and Papenfuss 2015), provided routes for terrestrial species dispersal to Asia (Figure 6, dispersal scenario C). In addition, the shrinkage of the Tethys Sea (Zhao et al. 2022) and the Messinian salinity crisis during the Late Miocene (Agustí et al. 2006; García-Alix et al. 2016), which provided a terrestrial environment suitable for arid-adapted species dispersal, have also likely facilitated the dispersal of Gerbillinae across both northern Africa and central Asia (Figure 6, dispersal scenarios B and C). The fossil genus *Abudhabia*, from the late Miocene to Pliocene of southern and central Asia, remarkably resembles the extant genus *Tatera* (Pavlinov, 2008), and may have originated in Pakistan in the late Miocene (Wessels, 2009). The fossil genus *Pseudomeriones*, from the late Miocene and Pliocene of Europe to southern and central Asia, is most similar to the extant tribe Rhombomyina (Pavlinov, 2008), and originated in Turkey in the late Miocene, and then dispersed to Greece and China (Suata-Alpaslan 2009; Vasileiadou and Sylvestrou 2009). The distribution of these 2 genera seems to support dispersal scenarios C and D (Figure 6). The intensification of aridification in Central Asia during the Late Miocene, caused by the final closure of the Tethys, and the rapid orogeny of the Qinghai-Tibetan Plateau–Himalayas (Miao et al. 2012; Spicer 2017; Feijó et al. 2022a), provided an opportunity for the dispersal of arid-adapted fauna to Central Asia (Figure 6, dispersal scenarios D). Consistently, Feijó et al. (2022) also show an increase in emigrations out of Western Asia by the mid-Miocene, pumping novel lineages mainly into Northern Asia, Europe, and Africa. Furthermore, the insolation-driven monsoon and Indo-Pacific Walker circulation drove aridification in Africa and Western Asia during the Plio-Pleistocene (Trauth et al. 2009; Ndiaye et al. 2016; Wang et al. 2016; van der Lubbe et al. 2021), leading to the expansion of desert habitats and ultimately boosting the diversification of Gerbillinae taxa in these areas. We found that the basal members of the radiation dispersed to all major regions currently occupied by extant species early in the clade's history, followed by in situ species accumulation, which is consistent with our BSM results that most biogeographical events can be explained by within-area speciation and dispersal.

To sum up, we suggested that Gerbillinae likely originated in the Horn of Africa and dispersed across Africa and Asia during the Late Miocene and Pliocene. Some ancient lineages of Gerbillinae may have dispersed to their current distribution shortly after the subfamily's origin, only to later become extinct. Consequently, extant species could be the outcome of an independent dispersion during the late Miocene and Pliocene periods, subsequently diversifying across arid regions in Africa and Eurasia, ultimately forming the present distribution pattern.

Spatial pattern of Gerbillinae diversity

We investigated the relative importance of ecological and evolutionary factors in shaping the diversity of small mammals in arid regions. Our results suggest that neither ecological nor evolutionary factors alone can well explain the spatial variation in global Gerbillinae diversity, and the combination of the 2 has a higher explanatory power for species richness. In addition, both the results of the random forest and SEM show that evolutionary factors play a more important role in shaping the spatial diversity pattern of Gerbillinae than ecological factors, which is consistent with our prediction. Our different analyses indicated that evolutionary time and speciation rate were significantly positively correlated with Gerbillinae species richness, which thus supports the time-for-speciation and diversification rate hypotheses. Previous studies have also shown that evolutionary factors (evolutionary time and speciation rate) are major determinants of species diversity (Wiens et al. 2006; Kozak and Wiens 2012; Scholl and Wiens 2016; Economo et al. 2018; Cai et al. 2020; Miller et al. 2021). For example, Cai et al. (2020) demonstrated that the global diversity patterns of babblers have predominantly been shaped by the time-for-speciation effect. We also found a signification negative correlation between evolutionary time and speciation rate, indicating that Gerbillinae has experienced a relatively stable environment and occupied stable ecological niches throughout its evolutionary history. Our results, together with previous findings, confirm that evolutionary factors as non-negligible factors when investigating the mechanisms underlying large-scale species diversity patterns.

In addition to evolutionary factors, large-scale species diversity patterns may be affected by ecological and geographic factors. The CSI, as an indicator of historical climate stability, was negatively correlated with species richness, indicating that the more stable the historical climate is, the higher the species richness of Gerbillinae is, which is consistent with the historical climate stability hypothesis (Pianka 1966). Previous studies also showed that Quaternary climate changes explain diversity among reptiles and amphibians (Araújo et al. 2008; Pinkert et al. 2020). Landcover types, used here as a proxy of habitat heterogeneity, directly influence species richness and show a negative correlation with it. This implies that Gerbillinae species tend to inhabit areas with similar land cover types, indicating they share a similar environmental niche. This is consistent with the niche evolution recorded in Gerbillinae and likely reflects its adaptation to different arid environments. According to these results, we consider habitat filtering the most crucial ecological mechanism driving Gerbillinae species diversity pattern. This could also explain the strong phylogenetic signal associated with morphological traits, as many species share phenotypic adaptations to survive in xeric environments. Our result is consistent with previous studies showing that habitat heterogeneity has a great impact on species diversity patterns in arid regions. For example, environmental heterogeneity promotes an uneven spatial distribution of gerbils (Gromov 2001) and relates to arid species diversity in outback Australia (Traill et al. 2013). Similarly, topographic heterogeneity is the strongest predictor for Arabian squamate species richness (Šmíd et al. 2021). Moreover, we also found landcover types had a significant negative effect on speciation rate. This may be derived from habitat fragmentation, which increased the species extinction rate (Kisel et al. 2011) because a greater number of landcover types means that there is more fragmentation.

In conclusion, we found that the highest species richness of Gerbillinae was found along the coastal areas of northern Africa, particularly in Egypt and Libya, followed by the Sahara-Sahel region. Based on the ancestral range models combined with the available fossil record, we discussed possible origin and dispersal scenarios for Gerbillinae. We hypothesized that they likely originated in the Horn of Africa during the Middle Miocene, and then dispersed and diversified across arid regions in Africa and Eurasia, forming their current distribution pattern. Our analyses demonstrated that both evolutionary and ecological factors played important roles in shaping the spatial pattern of Gerbillinae diversity. Notably, we found that evolutionary factors (evolutionary time and speciation rate) played stronger roles in shaping the spatial pattern of Gerbillinae diversity, followed by habitat filtering. It should be noted that the 66 species included in this study cover about 65% of all known species of Gerbillinae. Assuredly, we can expect to obtain a clearer view of the evolutionary history of Gerbillinae when molecular data of unexplored species (especially for African gerbils) becomes available in the future. With this information, we can further explore the phylogenetic diversity pattern of taxa and the mechanisms underlying it, which may differ from those generating the species richness pattern observed here. Our study emphasizes the importance of integrating evolutionary and ecological approaches to gain a comprehensive understanding of the mechanisms underlying large-scale species diversity patterns in global arid regions, where species are extremely vulnerable to global warming and therefore require immediate conservation and management actions.

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Authors' Contributions

Q.Y. designed the study program; Y.C., J.C. and Q.Y. conceived the ideas; Y.C., J.C., L.X., D.G., E.A., L.G. and Q.Y. collected the data; Y.C., J.C., Z.W., and A.F. carried out the statistical analyses; and all authors drafted the manuscript.

Conflict of Interest statement

The authors declare that they have no conflict of interest.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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