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Environmental and evolutionary factors jointly shape life-history trait diversity of terrestrial vertebrates across China

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ABSTRACT

Life-history traits represent evolutionary adaptations that mediate responses to external environments. Analyzing variation in these traits provides valuable insights into macroecological processes and supports the development of effective conservation and restoration strategies. However, large-scale biogeographic patterns in life-history trait diversity among terrestrial vertebrates remain insufficiently characterized, and the processes shaping these patterns are not well understood. This study integrated life-history and spatial distribution data for 2 334 terrestrial vertebrate species in China, including 398 amphibians, 211 reptiles, 541 mammals, and 1 184 birds, to evaluate spatial patterns of trait diversity and identify underlying drivers. Assemblages in South and Southwest China exhibited high species richness, substantial assemblage-level evolutionary distinctiveness, expanded trait volumes, and elevated trait densities compared to null expectations, indicating roles as both evolutionary museums and cradles. In contrast, assemblages on the Tibetan Plateau showed expanded trait volumes but low trait densities, reflecting niche expansion among limited taxa. These findings emphasize the importance of niche packing before assemblages reach environmental carrying limits. Assemblages with high evolutionary distinctiveness tended to display high trait volumes and low trait densities, suggesting a consistent relationship between phylogenetic structure and functional diversification. Among the four groups, amphibians showed the highest sensitivity to environmental variation, highlighting the need for focused conservation efforts. Overall, this study revealed pronounced spatial heterogeneity in trait diversity across China, shaped by species richness, evolutionary distinctiveness, and environmental variation, providing valuable insights for refining conservation priorities for terrestrial vertebrate taxa.

Keywords: Trait density; Trait variance; Evolutionary distinctiveness; Niche expansion; Cross-taxon congruence

INTRODUCTION

Species traits reflect evolutionary responses to environmental pressures, shaped by long-term interactions with both biotic and abiotic factors (Kelley et al., 2018). As such, they can serve as integrative indicators of species sensitivity to external disturbances, including climate change and anthropogenic impact (Nowakowski et al., 2017), while also encapsulating intrinsic phylogenetic relationships (Campos et al., 2019). Critically, linking organisms to their traits enables the distillation of complex community-level dynamics into measurable dimensions, facilitating improved predictions of species interactions with their biotic and abiotic environments, as well as their contributions to ecosystem functioning and stability (Cadotte, 2017; Etard et al., 2022; Gross et al., 2017).

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Consequently, trait-based approaches have become essential tools for advancing biogeographic and community ecological research, providing a robust framework for addressing pressing ecological challenges (de Bello et al., 2021; Ellis et al., 2021; Schleuning et al., 2023).

Life-history traits, such as clutch size, habitat preference, and breeding season, represent evolved characteristics that influence the allocation of resources toward survival and reproduction, thereby enhancing fitness under specific environmental conditions (Endler, 1986; Morrison & Hero, 2003). These traits play a critical role in shaping species distribution and abundance across environmental gradients (Sternberg & Kennard, 2013). For instance, mammal species with extended reproductive lifespans and higher breeding frequency are more likely to successfully colonize and persist in novel environments (Capellini et al., 2015). Unlike morphological and physiological characteristics, life-history traits tend to be less constrained by body size and typically vary within narrower ranges (Hallmann & Griebeler, 2020). For instance, raptors have been observed to breed earlier in urban environments than in rural ones, likely driven by differences in food abundance (Kettel et al., 2018). The integration of multiple life-history traits, often referred to as life-history strategies, provides a powerful framework for understanding how environmental and physiological constraints shape evolutionary outcomes over time (Healy et al., 2019). This highlights the importance of considering how different aspects of life history interact with external conditions to influence adaptive trajectories. However, despite their significance, life-history traits remain difficult to characterize, particularly in long-lived species inhabiting remote or inaccessible regions (Trochet et al., 2014), impeding progress in quantifying and understanding trait variance across taxa.

Advances in ecological data availability, including species traits, occurrence records, and climatic variables, have facilitated increasing efforts to characterize spatial gradients in life-history trait distributions and identify their underlying determinants (Bruelheide et al., 2018; Chen et al., 2023; Hao et al., 2021; Kopf et al., 2021; Liu et al., 2017; Pavanetto et al., 2024). Recent studies have revealed pronounced latitudinal trends, such as delayed reproductive onset and steeper reproductive scaling in polar marine fish compared to tropical fish (Álvarez-Noriega et al., 2023). Similarly, in hibernating mammals, warming temperatures have been linked to earlier emergence, larger litters, and increased interbout arousal frequency (Findlay-Robinson et al., 2023). In addition to environmental factors, phylogenetic constraints are another crucial driver in determining these traits (Comte & Olden, 2017; Lyu et al., 2021). For example, avian egg morphology, including asymmetry and ellipticity, exhibits remarkable taxonomic variation, displaying phylogenetically constrained patterns (Bańbura et al., 2018; Stoddard et al., 2017). These findings suggest that both evolutionary history and environmental context jointly influence trait diversity, although their relative contributions may vary across taxonomic groups. Despite this progress, prior investigations have primarily focused on individual traits or pairwise trait interactions (Bansal & Thaker, 2021). As a result, the biogeographic patterns of combined life-history traits across terrestrial vertebrates remain unclear. Such analyses are essential for predicting structural and functional shifts in ecological assemblages in response to ongoing climate change (Toussaint et al., 2021).

As a critical component of global biodiversity, terrestrial vertebrates play an essential role in maintaining ecosystem stability and functioning through direct consumption and nutrient cycling (Breviglieri & Romero, 2017; Hocking & Babbitt, 2014). Identifying the spatial organization of their life-history traits and the mechanisms driving observed patterns is key to understanding how evolutionary and environmental factors influence ecosystem functioning. In the present study, trait diversity was assessed across terrestrial vertebrate assemblages in China, a region harboring approximately 15% of global vertebrate species (Jiang et al., 2024). Specifically, biogeographic patterns of life-history trait diversity were mapped and regions exhibiting significantly high or low values relative to null expectations were identified. Finally, the relative influences of evolutionary distinctiveness and environmental heterogeneity on trait diversity patterns were quantified, providing a comprehensive framework for understanding trait-environment-evolution interactions in terrestrial vertebrate.

MATERIALS AND METHODS

Data collection

Data on life-history traits for four major groups of terrestrial vertebrates, including amphibians, reptiles, birds, and mammals, were primarily sourced from previously published studies (Ding et al., 2022; Song et al., 2022; Wang et al., 2021; Zhong et al., 2022). Trait selection was based on ecological relevance and data availability (Table 1). Intraspecific variability was excluded, as previous studies have shown it to be minimal relative to interspecific differences at broad spatial scales (Su et al., 2019; Toussaint et al., 2018). To address missing values in the trait dataset, trait imputation was conducted using the *missForest* package (Stekhoven & Bühlmann, 2012), incorporating phylogenetic structure through the inclusion of the first 10 phylogenetic eigenvectors in the trait matrix (Carmona et al., 2021; Penone et al., 2014). Phylogenetic data were sourced from established datasets for amphibians (Jetz & Pyron, 2018), reptiles (Tonini et al., 2016), mammals (Upham et al., 2019), and birds (Jetz et al., 2012). For species absent from the original phylogenies, placement was performed at the root of the corresponding genus using the "*add.species.to.genus*" function from the *phytools* package (Revell, 2012).

Following imputation, Gower functional distances were calculated among species within each taxonomic group based on centered and scaled trait values (Podani, 1999). Principal coordinates analysis (PCoA) was applied to the resulting functional distance matrices with the *ade4* package (Dray & Dufour, 2007). The quality of the reduced trait spaces was evaluated by calculating the absolute deviation between the trait-based distance and distance derived from PCoA-based space (Maire et al., 2015). The number of PCoA axes yielding the lowest deviation was retained for further analysis (Hahs et al., 2023). Specifically, six axes for amphibians, five for reptiles, three for mammals, and five for birds were used in subsequent trait diversity calculations.

Species distribution data

Species range data were primarily obtained from the spatial database of the International Union for Conservation of Nature (IUCN, https://www.iucnredlist.org/). To address taxonomic coverage gaps in the IUCN spatial database, additional occurrence records were integrated from the Global

Table 1 Life history traits of terrestrial vertebrate groups in the present study

Group	Trait	Completeness (%)
Amphibian (398)	Litter size	52.26
	Egg size	61.81
	Breeding season	78.89
	Breeding site	96.23
	Reproductive cycle	79.40
	Microhabitat preference of larva	97.74
	Habitat preference of adults	99.75
	Active time	51.51
	Parental care	86.18
	Fertilization type	82.41
Reptile (Squamata, 211)	Clutch size	64.93
	Reproductive mode	83.89
	Habitat type	89.10
	Active time	83.89
Mammal (541)	Sexual maturity	93.12
	Gestation length	95.01
	Litter size	95.87
	Litters per year	95.35
	Generation length	94.49
	Activity cycle	99.31
Bird (1 184)	Clutch size	88.51
	Egg size	92.23
	Egg volume	92.48
	Nest site	94.51
	Nest type	94.17
	Flocking status	90.54
	Migrant status	100.00

Biodiversity Information Facility (GBIF; https://www.gbif.org/), a widely recognized repository for species distribution data (Supplementary Table S1). Data quality control involved the removal of duplicate records and entries originating from institutes and museums using the "*dplyr*" and "*CoordinateCleaner*" packages, respectively. Only occurrence records labeled as "Human observation", "Machine observation", "Observation", and "Occurrence" were retained. For species with recent but spatially incomplete records, distribution information was supplemented by reviewing the original literature sources. Final species distribution data were rasterized into a uniform grid system with a spatial resolution of 0.5°×0.5° (approximately 50 km by 55 km) using ArcGIS v.10.8. Species presence-absence matrices were constructed for each grid cell, and species lists and richness were subsequently determined.

Environmental variable data

To assess the association between climate and spatial patterns of life-history trait diversity within species distribution ranges, nine climatic variables were selected based on previous studies (Supplementary Table S2; Mi et al., 2022, 2024). These variables encompassed four major environmental dimensions, including environmental energy, water availability, climate variability, and habitat suitability. Environmental energy was represented by mean annual temperature (MAT) and mean solar radiation (MSR); water availability by mean annual precipitation (MAP), mean relative humidity (MRH), and potential annual evapotranspiration (PAE); climate variability by temperature seasonality (TSE) and precipitation seasonality (PSE); and habitat suitability by the normalized difference vegetation index (NDVI) and habitat heterogeneity (HAH), the latter quantified as the difference between maximum and minimum altitude within each target cell (Luo et al., 2024). MAT, MSR, MAP, TSE, PSE, and elevation data were obtained from WorldClim (https://worldclim.org/; Fick & Hijmans, 2017). MRH and PET were sourced from CHELSA v1.2 (https://chelsa-climate.org/; Brun et al., 2024), while NDVI data were obtained from the Resource and Environment Science and Data Center (http://www.resdc.cn/; Gao et al., 2025). All environmental variables were spatially resampled and averaged to match the resolution of the geographic cells using ArcGIS v.10.8.

Statistical analyses

To quantify variation in life-history trait volume and density, two key metrics were employed: sum of variance and mean nearest-neighbor distance. These metrics were evaluated using the "*test.metric*" function in the *dispRity* package (Guillerme, 2018), which evaluates changes based on simulated species gains and losses. The sum of variance was used as a measure of trait volume (Guillerme et al., 2020), while mean nearest-neighbor distance measured trait packing density within functional ecospace (Guillerme, 2018). Evolutionary distinctiveness scores were captured for each species using taxonomic group-specific phylogenetic trees, implemented via the *'evlo.distinct'* function in the *picante* package (Kembel et al., 2010). For each community, scores were summed to provide a cumulative measure of evolutionary uniqueness.

For each grid cell, 1 000 random assemblages were generated using a null model in which species richness was held constant and species were randomly selected from the corresponding taxonomic species pool. Expected values for the sum of variance, mean nearest-neighbor distance, and cumulative evolutionary distinctiveness were derived from these simulations. Standardized effect sizes (SES) for each assemblage were calculated as follows:

$$SES = \frac{obs - mean_{null}}{sd_{null}} \quad (1)$$

where obs is the observed value, and $mean_{null}$ and sd_{null} are the mean and standard deviation derived from the 1 000 randomly generated assemblages. A positive SES indicates greater-than-expected functional or evolutionary diversity, while a negative SES denotes lower-than-expected values. Deviations were considered statistically significant when $|SES|>2$ (Hughes et al., 2022).

Generalized least squares (GLS) models were used to assess the associations between life-history trait disparity and environmental variables. Prior to modeling, Pearson correlation coefficients were calculated to identify collinearity among predictors. When pairs of variables exhibited strong correlation ($|r|>0.70$), only one variable was retained (Dormann et al., 2013). Based on these results (Supplementary Figure S1), MAT and MAP were selected for inclusion due to their known influence on terrestrial vertebrate distribution and diversity (Hu et al., 2021; Mi et al., 2022). Species richness and assemblage-level evolutionary distinctiveness were also included as predictor variables. All continuous predictors were log_{10}-transformed to normalize distributions, except for MAT and HAH, which included negative values. Both linear and quadratic terms were included to capture potential non-linear relationships. To correct for spatial autocorrelation, models were fitted with exponential, gaussian, or spherical correlation structures based on spatial information derived from the longitudinal and latitudinal centroids of grid cells. Model selection was guided by Akaike Information Criterion (AIC) scores, with the model yielding the lowest AIC value identified as the best fit (Supplementary Table S3). A ΔAIC threshold of 2 was used to differentiate competing models (Symonds & Moussalli, 2011). Variance inflation factor (VIF) values were calculated using the "*vif*" function in the *car* package (Fox & Weisberg, 2018), and predictors with VIF values exceeding 10 were removed to reduce multicollinearity (Supplementary Table S4). All statistical analyses were conducted in R v.4.2.1 (The R Core Team, 2022).

RESULTS

Geographical patterns of trait diversity

Trait diversity was evaluated for 2 334 terrestrial vertebrate species, including 398 amphibians, 211 reptiles, 541 mammals, and 1 184 birds. According to the Catalogue of Life China (The Biodiversity Committee of Chinese Academy of Sciences, 2024), the dataset represents 66.48% of all terrestrial vertebrate species distributed in China. Species richness across all groups was higher in the South (e.g., southern Yunnan mountain and Min-Guang coast subregions), Southwest (e.g., Southwest mountain subregion), and Central China (e.g., western mountains and plateau subregion), and lowest in the North, Northwest, and Tibetan Plateau regions (Figure 1). A similar spatial pattern was observed for assemblage-level evolutionary distinctiveness, which was concentrated in areas with high species richness across all taxa (Supplementary Figure S2A–D). After accounting for species richness, elevated levels of evolutionary distinctiveness remained most prominent in South China (Supplementary Figure S2E–H).

Trait diversity showed substantial spatial heterogeneity across taxonomic groups. In amphibians, high trait variance was concentrated along the margins of the western mountain and plateau subregion, reflecting occupation of a wide functional space (Figure 2A). Reptiles exhibited high trait variance in South (e.g., Min-Guang coast and southern Yunnan mountain subregion), Central, Southwest, and Northwest China (e.g., western desert subregion), as well as the Tibetan Plateau (Figure 2B). Trait variance in mammals and birds exhibited a similar pattern, with high values in Northwest China and the Tibetan Plateau (Figure 2C, D). Patterns of trait density revealed distinct regional clustering. Amphibian communities with low nearest-neighbor distances, indicating high trait density, were found in Central (e.g., western mountains and plateaus subregion), Southwest (e.g., southwest mountain subregion), and South China (Figure 3A). In contrast, reptile, mammal, and bird communities in areas surrounding the Tibetan Plateau exhibited high nearest-neighbor distances, indicating low trait density and increased functional divergence within assemblages (Figure 3B–D).

Trait diversity patterns derived from null models closely mirrored the observed distributions of both trait variance and density across all taxa (Figures 2E–H, 3E–H). Observed trait variance in mammals was consistently lower than expected, illustrating a narrower functional niche breadth. In contrast, amphibians, reptiles, and birds displayed trait variances comparable to null expectations (Supplementary Figure S3). In amphibians, elevated trait variance was notably concentrated along the edge of the western mountain and plateau subregions (Figure 2E). Reptile communities in South China (e.g., Min-Guang coast subregion) exhibited high trait variance, occupying a broader functional space relative to other regions (Figure 2F). Mammal and reptile assemblages

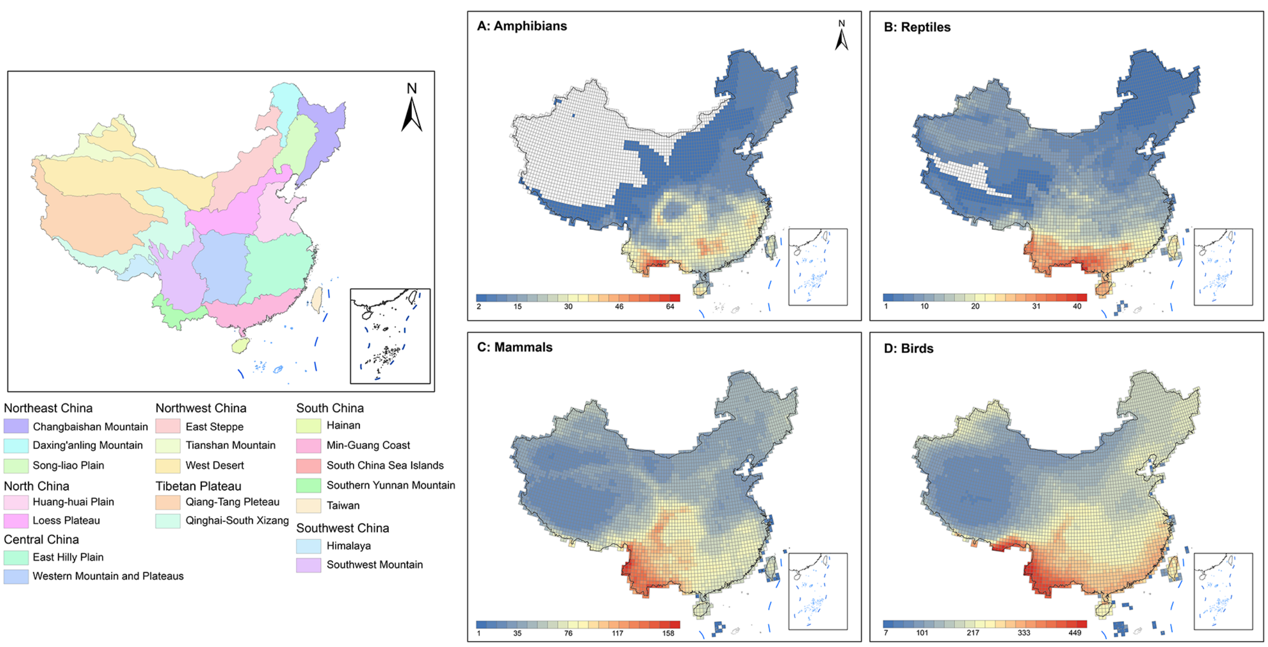

Figure 1 Biogeographic patterns of terrestrial vertebrate species richness across the study area

Spatial distribution of species richness is shown at a resolution of 0.5°×0.5° (approximately 50 km by 55 km). Zoogeographic regions are delineated based on Gao et al. (2017). All maps in this study use the Asia Lambert Conformal Conic projection, with approval (GS(2024)0650) from the Ministry of Natural Resources of China.

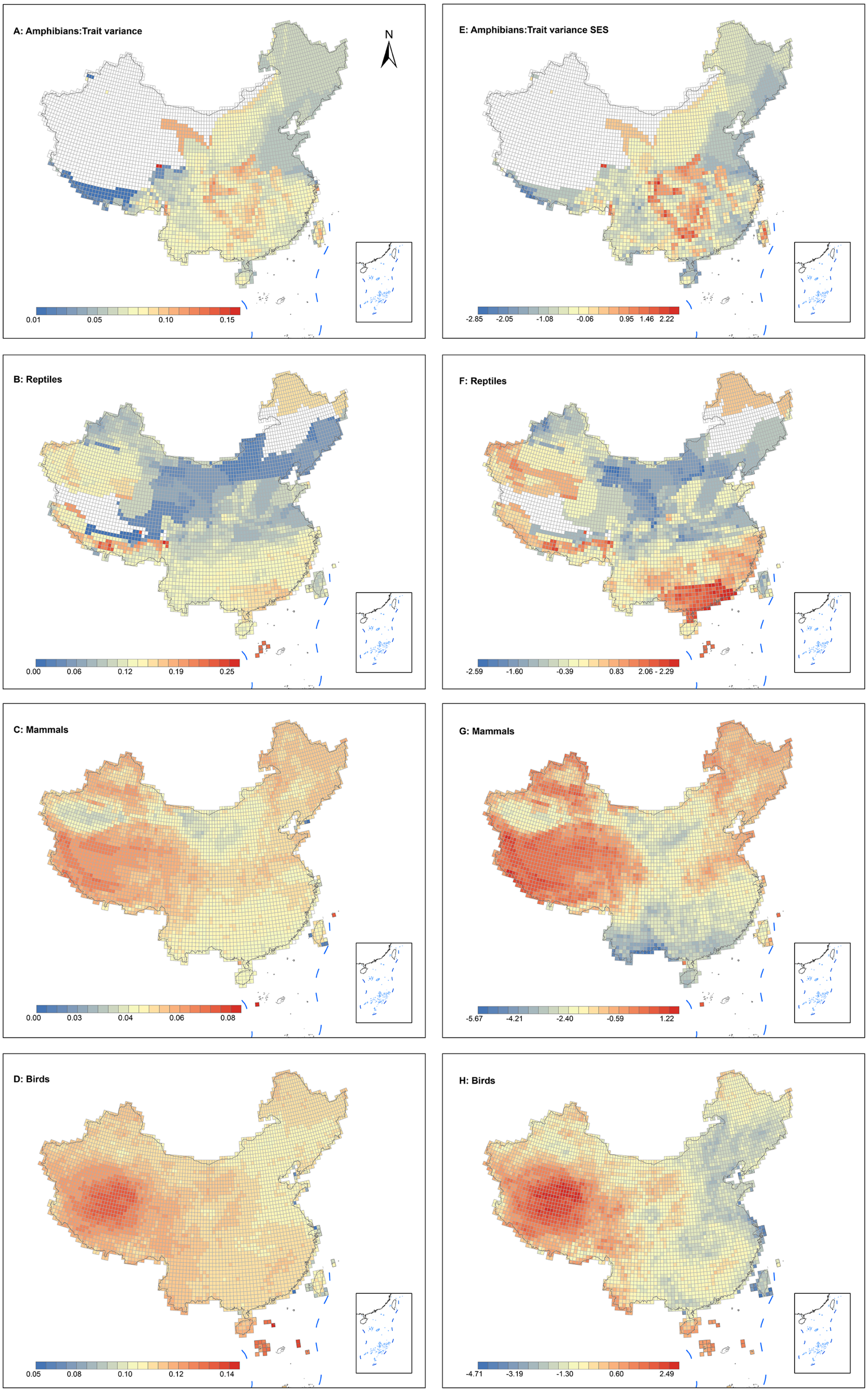

Figure 2 Biogeographic patterns of trait variance and standardized effect sizes (SES) in terrestrial vertebrates

Spatial distribution of trait variance and corresponding SES values for terrestrial vertebrates across the study area is shown at a resolution of 0.5°×0.5° (approximately 50 km by 55 km). High values of trait variance represent high trait volume and therefore high variation.

on the Tibetan Plateau exhibited high trait variance (Figure 2G, H). Trait density across all groups was consistently lower than expected under null models (Supplementary Figure S3), indicating that species were more functionally dispersed than anticipated based on species richness alone, with higher trait differentiation within assemblages. Low-density amphibian assemblages were concentrated in Central (e.g., western mountain and plateau subregions), Southwest (e.g., southwest mountain subregion), and South China (Figure 3E). For reptiles, mammals, and birds, assemblages surrounding the Tibetan Plateau and Northwest China showed elevated nearest-neighbor distances, reflecting low trait density and greater differentiation among trait combinations (Figure 3F–H).

Regions exhibiting exceptional trait diversity

Regions exhibiting exceptional trait diversity were identified based on significant SES values for trait variance and trait density across the four taxonomic groups. Most amphibian and reptile assemblages displayed trait diversity within the expected range, with SES values for both trait variance and density falling between −2 and 2 (Figure 4). However, several amphibian assemblages in South and Central China exhibited extremely high trait density despite trait variance remaining within expected limits (−2<trait variance SES<2, trait density SES<−2, Figure 4). Among reptiles, comparable patterns were observed in Central China, while multiple assemblages on the Tibetan Plateau demonstrated exceptionally low trait density (trait density SES>2, Figure 4). In mammals, most assemblages with significant SES values were characterized by smaller-than-expected trait volume (trait variance SES<−2, Figure 4). Some of these assemblages also showed increased trait density within this constrained functional space and were primarily located in the western desert and western mountain and plateau subregions (trait variance SES<−2 and trait density SES<−2, Figure 4). Conversely, assemblages along the margins of the Tibetan Plateau showed extremely low density (trait density SES>2, Figure 4). Bird assemblages on the Tibetan Plateau exhibited elevated trait variance with trait density near expected values, a pattern consistent with that observed in reptiles and mammals.

Determinants of trait diversity

Results from the GLS models revealed that trait variance SES was significantly associated with species richness and assemblage-level evolutionary distinctiveness SES in amphibians, mammals, and birds. In contrast, reptile trait variance was significantly correlated only with the assemblage evolutionary distinctiveness SES (Table 2). Among environmental determinants, nearly all selected factors were significantly related to amphibian trait variance, except for habitat heterogeneity. However, the specific response patterns varied (Figure 5; Table 2). In mammals and birds, trait variance SES exhibited a significant U-shaped response along the mean annual temperature gradient (Figure 5; Table 2). A similar U-shaped relationship was also observed for mammal trait variance SES in response to habitat heterogeneity (Figure 5; Table 2).

Trait density SES was significantly influenced by species richness and assemblage evolutionary distinctiveness SES in amphibians, reptiles, and mammals, whereas in birds, it was significantly correlated only with assemblage evolutionary distinctiveness SES (Table 3). In amphibians, trait density SES demonstrated a significant U-shaped response to both solar radiation and mean annual precipitation, and increased non-linearly with rising temperature seasonality (Figure 6; Table 3). Mammal trait density SES also followed a pronounced U-shaped pattern along the mean annual precipitation gradient, whereas bird trait density SES exhibited a noticeable hump-shaped relationship with temperature seasonality (Figure 6; Table 3).

DISCUSSION

This study integrated life-history traits and spatial distribution data for 2 334 terrestrial vertebrate species across China to assess biogeographic patterns of trait diversity within each major taxonomic group and to identify potential underlying drivers. The results revealed pronounced spatial heterogeneity in both taxonomic and trait diversity across zoogeographical regions and groups, primarily shaped by the interplay among species richness, evolutionary history, and environmental variation.

Geographical patterns of trait diversity

Tropical and subtropical regions of Southwest and South China supported communities with elevated species richness, high evolutionary distinctiveness, expanded trait volumes, and increased trait densities across all four vertebrate lineages. These regions contained assemblages composed of both evolutionarily ancient species with distinct life-history strategies and more recently diverged, closely related taxa exhibiting functional similarity. This pattern is consistent with previous research and supports the dual role of these regions as both evolutionary museums and cradles in China (Hu et al., 2021; Zhang et al., 2023, 2024). High trait density in these areas suggests that niche packing contributes substantially to trait diversity in tropical and subtropical regions, likely facilitated by favorable abiotic conditions such as high energy availability, abundant water resources, and stable food supplies (Pellissier et al., 2018). Amphibian trait diversity was particularly concentrated in mountainous areas surrounding the Sichuan Basin, Nanling Mountains, and Wuyi Mountains, a pattern distinct from the other three taxonomic groups. This distinct spatial pattern is consistent with prior studies highlighting these montane regions as biodiversity hotspots, enriched by both described and cryptic amphibian taxa. The restricted elevational extent of these systems limits opportunities for altitudinal range shifts in response to warming, further emphasizing the need for conservation (Xu et al., 2024; Zhang et al., 2023).

Regions exhibiting exceptional trait diversity

Niche expansion likely contributed to community structure on the Tibetan Plateau, as indicated by assemblages—especially of reptiles, mammals, and birds—that exhibited large trait volumes combined with lower trait density, despite supporting relatively few species (Pigot et al., 2016). The extreme climatic conditions of the region, including pronounced temperature fluctuations, act as a strong environmental filter, favoring species with specific adaptations while excluding ecological generalists (He et al., 2022). Simultaneously, environmental heterogeneity across the Tibetan Plateau facilitates the coexistence of functionally distinct species by enabling partitioning of limited resources (Karuno et al., 2023). These findings highlight the importance of prioritizing conservation efforts in this region, which supports uniquely adapted taxa under severe ecological constraints. However, further

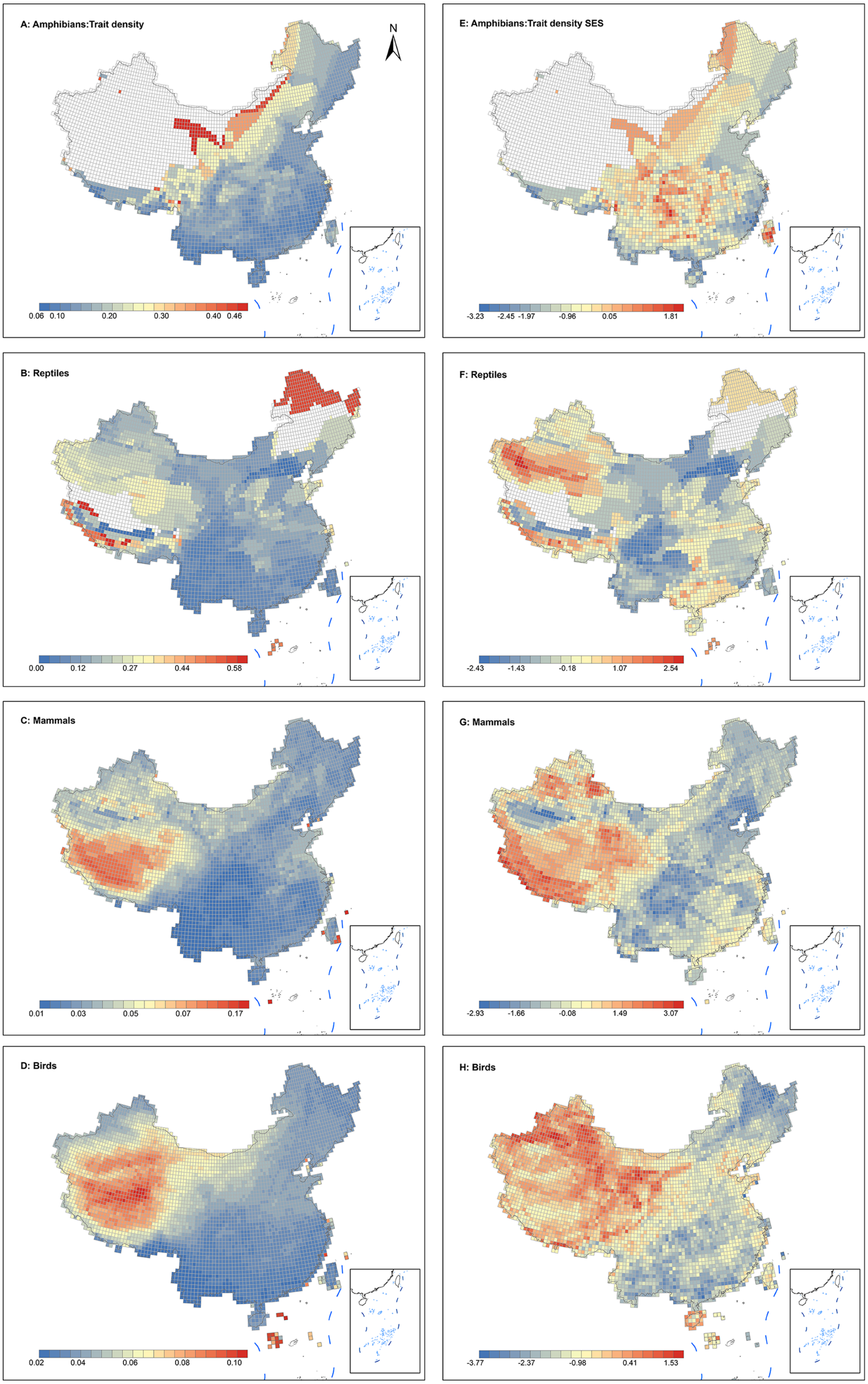

Figure 3 Biogeographic patterns of trait density and standardized effect sizes (SES) in terrestrial vertebrates

Spatial distribution of trait density and corresponding SES values for terrestrial vertebrates across the study area are shown at a resolution of 0.5°×0.5° (approximately 50 km by 55 km). High values of trait density represent high mean nearest-neighbor distances and therefore low density.

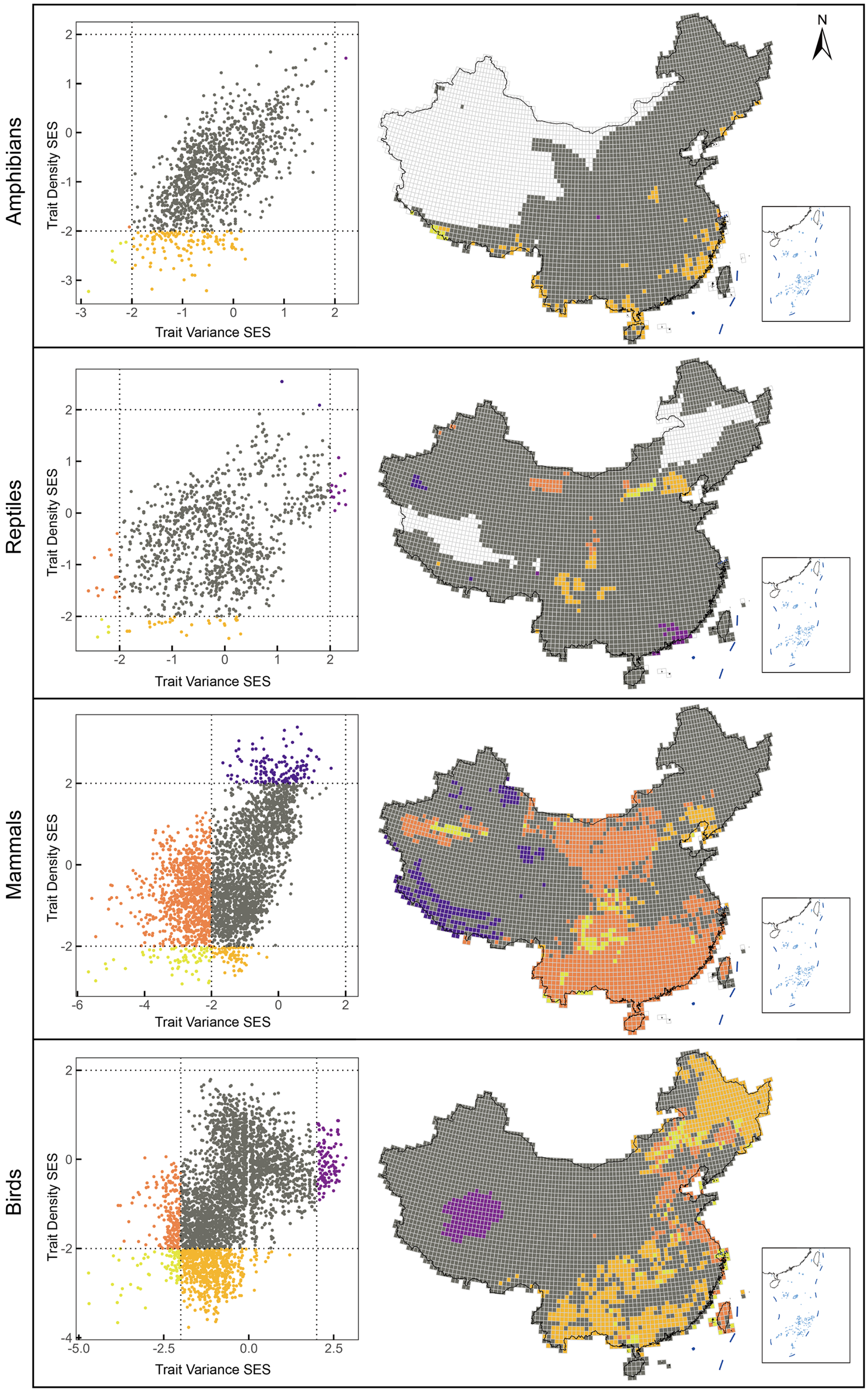

Figure 4 Regions exhibiting significant deviations in trait diversity standardized effect sizes (SES) for terrestrial vertebrates

Areas with significant deviations in SES for trait variance or density are shown at a resolution of 0.5°×0.5° (approximately 50 km by 55 km). Gray areas indicate no significant differences from null expectations.

Table 2 Best-fit multi-predictor GLS models of trait variance (sum of variance) SES for species pools

	Trait variance SES			
	Amphibian	Reptile	Mammal	Bird
Predicted variable	Parameter estimate (±SEM)			
Species richness	−3.558 (±0.194)***	−0.242 (±0.201)	1.766 (±0.414)***	−41.609 (±1.283)***
Species richness^2	1.811 (±0.103)***	−0.226 (±0.131)	−1.237 (±0.134)***	8.969 (±0.300)***
Assemblage ED SES	0.162 (±0.017)***	0.518 (±0.020)***	0.153 (±0.013)***	−0.104 (±0.012)***
Assemblage ED SES^2	0.117 (±0.011)***	0.027 (±0.008)**	−0.058 (±0.004)***	0036 (±0.004)***
Mean annual temperature	0.021 (±0.007)**	0.006 (±0.007)	−0.004 (±0.007)	−0.009 (±0.006)
Mean annual temperature^2	−0.012(± 0.000)*	<0.001	<0.001	<0.001
Mean solar radiation	−198.285 (±90.103)*	104.412 (±160.204)	262.761 (±181.067)	−13.039 (±151.417)
Mean solar radiation^2	23.622(±10.868)*	−12.414 (±19.283)	−32.157 (±21.789)	1.198 (±18.225)
Mean annual precipitation	−5.001 (±1.248)**	−0.745 (±0.675)	−2.770 (±0.766)***	−2.308 (±0.681)***
Mean annual precipitation^2	0.918(±0.236)**	0.081 (±0.151)	0.532 (±0172)**	0.453 (±0.53)**
Temperature seasonality	22.348 (±4.023)***	0.029 (±7.416)	7.370 (±8.507)	6.287 (±6.821)
Temperature seasonality^2	−3.689 (±0.689)***	−0.384 (±1.260)	−1.162 (±1.443)	−1.189 (±1.157)
Precipitation seasonality	−10.966 (±4.763)*	−6.235 (±4.267)	0.453 (±4.791)	−3.017 (±4.368)
Precipitation seasonality^2	2.794(±1.272)*	1.594 (±1.167)	0.016 (±1.311)	0.686 (±1.191)
Habit heterogeneity	<0.001	<0.001	<0.001**	<0.001
Habit heterogeneity^2	<0.001	<0.001	<0.001	<0.001

significance (: P<0.05; **: P<0.01; ***: P<0.001). All predicted variables were log-transformed, except mean annual temperature and habitat heterogeneity. Linear and quadratic terms for all predicted variable were included in the model (e.g., species richness/Species richness^2, etc).

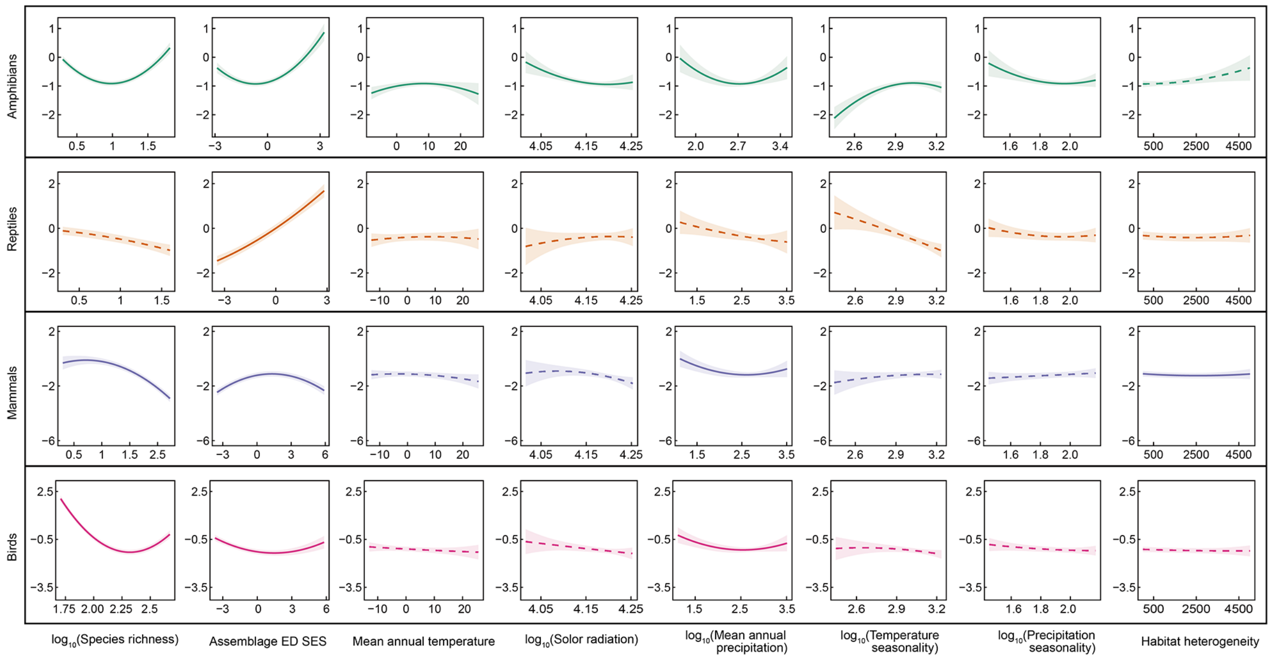

Figure 5 Effects of species richness, evolutionary distinctiveness, and environmental factors on trait variance SES

Predicted relationships between trait variance SES (sum of variance) and multiple predictors based on GLS models. Solid lines denote significant predictors; dotted lines denote non-significant ones. Shaded regions indicate 95% confidence intervals.

research is required to refine these observations, as the null model framework used in this study assumed uniform distribution ranges for all species across China. This simplification may introduce bias, particularly for narrowly distributed endemic species, and should be addressed in future analyses.

Determinants of trait diversity

Species richness is recognized as a primary determinant of trait diversity, with previous studies consistently reporting increases in both trait volume and density as species richness rises (Safi et al., 2011). The present results reinforce the significance of species richness, even after accounting for its influence through null model standardization. However, distinct patterns emerged across taxonomic groups. In reptiles and mammals, trait volume SES tended to decline with increasing species richness, while trait density SES exhibited a positive relationship along the same gradient. This pattern aligns with the concept of niche packing, wherein increasing species richness leads to tighter occupation of trait space before communities reach environmental saturation. Similar dynamics have been documented in other groups such as ferns (Aros-Mualin et al., 2021) and freshwater mussels

Table 3 Best-fit multi-predictor GLS models of trait density (mean nearest-neighbor distance) SES for species pools

	Trait density SES			
	Amphibian	Reptile	Mammal	Bird
Predicted variable	Parameter estimate (±SEM)			
Species richness	−3.267 (±0.223)***	1.868 (±0.243)***	8.229 (±0.589)***	1.463 (±1.615)
Species richness^2	1.212 (±0.119)***	−1.583 (±0.157)***	−3.111 (±0.191)***	−0.673 (±0.378)
Assemblage ED SES	0.058 (±0.020)**	0.420 (±0.024)***	0.178 (±0.018)***	−0.022 (±0.015)
Assemblage ED SES^2	−0.005 (±0.013)	0.030 (±0.011)**	−0.034(±0.005)***	0.100 (±0.005)***
Mean annual temperature	0.009 (±0.011)	0.010(±0.008)	−0.012(±0.011)	0.009 (±0.008)
Mean annual temperature^2	<0.001	<0.001	<0.001	<0.001
Mean solar radiation	−398.918 (±160.682)*	94.669(±179.195)	259.013(±243.908)	367.674(±199.821)
Mean solar radiation^2	47.831 (±19.375)*	−11.331 (±21.571)	−31.354(±29.352)	−44.073(±24.049)
Mean annual precipitation	−4.193 (±1.892)*	−0.833 (±0.782)	−3.811 (±1.056)***	−0.759(±0.880)
Mean annual precipitation^2	0.728 (±0.355)*	0.198 (±0.175)	0.695(±0.237)***	0.118(±0.197)
Temperature seasonality	19.056 (±7.085)**	−4.722 (±8.095)	2.849 (±11.247)	43.783(±9.110)***
Temperature seasonality^2	−3.096 (±1.213)**	0.740 (±1.375)	−0.817 (±1.907)	−7.496(±1.546)***
Precipitation seasonality	−10.195 (±7.230)	−4.085 (±5.010)	−2.521(±6.654)	−4.517 (±5.594)
Precipitation seasonality^2	2.438 (±1.944)	1.036 (±1.369)	0.742(±1.818)	1.064 (±1.523)
Habit heterogeneity	<0.001	<0.001	<0.001	<0.000
Habit heterogeneity^2	<0.001	<0.001	<0.001	<0.001

significance (: P<0.05; **: P<0.01; ***: P<0.001). All predicted variables were log-transformed, except mean annual temperature and habitat heterogeneity. Linear and quadratic terms for all predicted variable were included in the model (e.g., species richness/Species richness^2, etc).

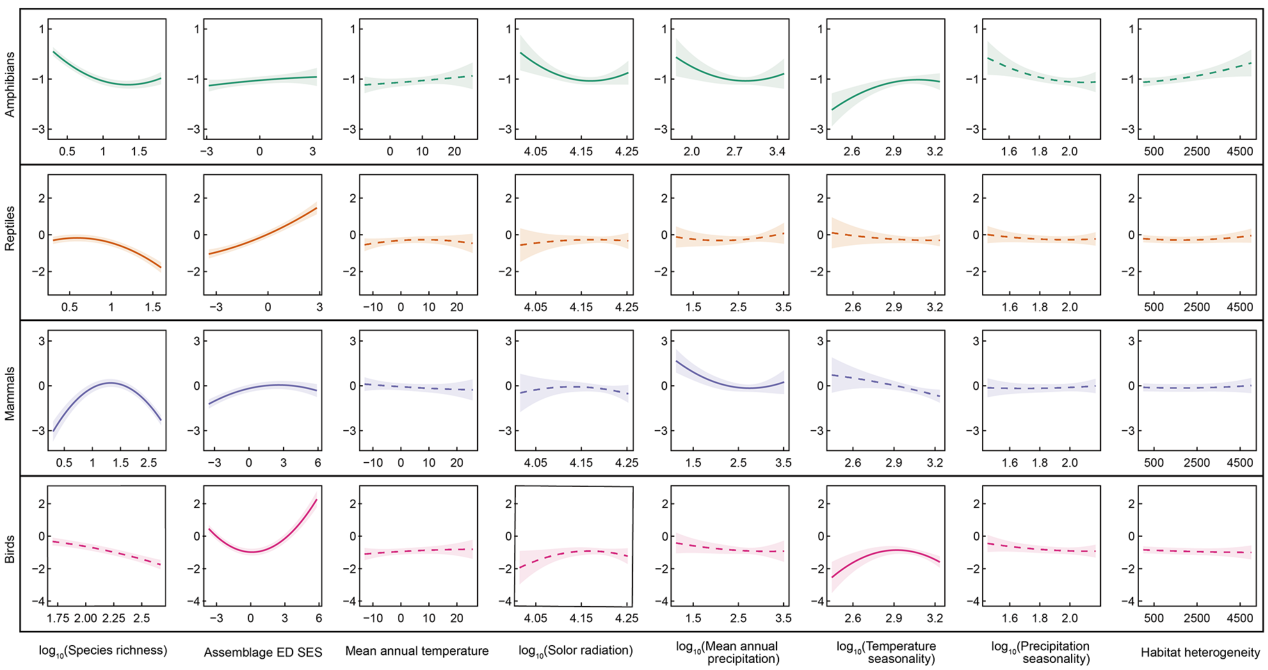

Figure 6 Effects of species richness, evolutionary distinctiveness, and environmental factors on trait density SES

Predicted relationships between trait density SES (mean nearest-neighbor distance) and multiple predictors based on GLS models. Solid lines denote significant predictors; dotted lines denote non-significant ones. Shaded regions indicate 95% confidence intervals.

(Sánchez González et al., 2023), suggesting a shift towards more structurally stable communities and reduced vulnerability to species invasions (Ghosh et al., 2024). In amphibians, trait volume SES increased significantly with species richness, while trait density SES declined. This divergent pattern suggests a transition from niche packing to niche expansion in highly diverse assemblages, likely driven by intensified competition for limited resources. Under such conditions, species may be compelled to exploit previously unoccupied regions of ecological space to minimize niche overlap (Costa-Pereira et al., 2019). In contrast, the observed reduction in trait density with increasing species richness in mammals reflects persistent niche overlap, indicating that functional redundancy remains high even in species-rich assemblages (Pellissier et al., 2018).

The pronounced role of evolutionary history in shaping trait diversity was strongly supported by the GLM results. Assemblages with greater-than-expected assemblage-level evolutionary distinctiveness exhibited expanded trait volume and reduced trait density across all taxonomic groups. This pattern aligns with previous global assessments of avian morphological diversity (Hughes et al., 2022), where communities composed of evolutionarily distinctive species, characterized by ancient speciation events and relatively few extant relatives, tend to occupy broad but sparsely filled trait spaces (Jetz et al., 2014). These findings reinforce the ecological link between phylogenetic structure and trait diversity. Diversification within sympatric lineages often involves a shift from generalist ancestral forms to more specialist descendants, effectively expanding functional space as lineages accumulate (Sjödin et al., 2018; Srivastava et al., 2012).

Beyond species richness and evolutionary history, key environmental variables also contributed to biogeographic variation in terrestrial vertebrate trait diversity. Across all taxa, regions characterized by adequate environmental energy, high water availability, and significant climatic variation supported assemblages with compact trait volumes and high trait density—patterns consistent with strong niche packing, typically observed in tropical regions (Pellissier et al., 2018). Amphibians demonstrated particularly strong environmental sensitivity compared to reptiles, mammals, and birds, likely due to physiological constrains and narrow habitat requirements (Alford, 2011; Alford et al., 2007). Unlike reptiles, which tolerate arid conditions, and endothermic vertebrates, which maintain thermal homeostasis, amphibians rely heavily on ambient moisture and temperature regimes, making them especially vulnerable to environmental fluctuations (Gouveia & Correia, 2016; Walls & Gabor, 2019). These physiological dependencies underscore the urgency of targeted conservation efforts for amphibians under accelerating climate change (Luedtke et al., 2023). In mammals, trait volume but not trait density demonstrated a significant U-shaped response to habitat heterogeneity. Flat landscapes likely support higher species numbers through spatial expansion of generalist species, while topographically complex regions promote ecological divergence by offering a mosaic of microhabitats suitable for species with distinct trait combinations (Chen et al., 2024; Sanders & Rahbek, 2012).

The observed spatial patterns of species and traits diversity likely reflect the multifaceted influences of environmental conditions on animal physiology, behavior, and life-history characteristics (Mi et al., 2022, 2024; Wang et al., 2024). Water availability, for example, plays a fundamental role in shaping vertebrate survival, particularly in taxa such as amphibians, for which water is not only vital for physiological processes but also essential for reproduction and developmental stages (Mi et al., 2022). Furthermore, other environmental factors, such as temperature variability and oxygen availability, exert strong selective pressures on species distributions (Murali et al., 2023) and adaptive trait evolution (Yan et al., 2022). In extreme environments, functional trait diversity is often closely associated with the intensity of environmental drivers. For instance, species inhabiting polar regions have independently evolved convergent traits that enhance survival under severe cold stress (Blix, 2016). Nevertheless, life-history trait variation across spatial gradients remains poorly understood, and further investigation into its geographic patterns and underlying drivers is essential for advancing ecological and evolutionary research.

In summary, the present study revealed that life-history trait diversity in terrestrial vertebrates is unevenly distributed across China, shaped by complex interplay among species richness, evolutionary history, and environmental factors. These findings have significant implications for conservation, particularly in tropical and subtropical regions and the Tibetan Plateau, where biodiversity is both abundant and unique. Crucially, the results highlight the value of integrating life-history traits into conservation assessment frameworks, offering a more integrative and functionally informed approach to species preservation. However, a key limitation of the present analysis lies in the incomplete alignment of trait and distribution data across species, which may introduce biases in taxonomic comparisons. Addressing this will require expansion of trait databases and occurrence records through long-term field surveys and standardized monitoring programs.

DATA AVAILABILITY

All data used in this study are available at figshare (https://figshare.com/s/2c8d2eb3ca2122ca9bfb). Species distribution data are available at https://www.iucnredlist.org/ and https://www.gbif.org/. Environmental variables used in the present study can be accessed from https://worldclim.org/, https://chelsa-climate.org/, and http://www.resdc.cn/.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

Z.J.S.: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Validation, Writing – original draft. B.J.S.: Conceptualization, Writing – review & editing; Y.P.W.: Conceptualization, Writing – review & editing; G.H.S.: Writing – review & editing; J.T.L.: Writing – review & editing; J.P.J.: Writing – review & editing; S.Q.S.: Supervision, Writing – review & editing. T.Z.: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing. All authors read and approved the final version of the manuscript.

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