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The Hengduan Mountains' Subsidiary ranges impacted the geographic distribution patterns of bats

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Abstract

The role of the Hengduan Mountains in biodiversity distribution is well-documented, but the impact of its subsidiary ranges on species distribution and evolution remains unclear. This study examined the Stoliczka's Asian Trident Bat (*Aselliscus stoliczkanus*) to assess how Pleistocene climatic changes and the uplift of these ranges influenced its distribution and evolution. Using species distribution models, morphometric data, and molecular genetic analysis, we identified shifts in the bat's distribution under different climatic scenarios and evaluated its morphological and genetic differentiation. We found a significant correlation between the bat's distribution and warmest quarter precipitation, with habitat suitability fluctuating in response to climatic changes. The subsidiary ranges facilitated morphological and genetic differentiation among bat populations and acted as barriers to dispersal. These findings underscore the critical role of the Hengduan Mountains' subsidiary ranges in shaping bat distribution and evolution, providing new insights into the effects of geological changes on small mammals in the region.

Keywords

bats – evolution – Pleistocene – subsidiary ranges of the Yunling Mountains – uplift of the Qinghai-Tibetan Plateau

Introduction

During the Pleistocene epoch of the Quaternary period, significant climatic and geological changes profoundly influenced the evolutionary history of flora and fauna (Hewitt, 2000; Ruedi & Castella, 2003; Hewitt, 2004; Ehlers & Gibbard, 2008; Wang et al., 2022). The active phase of the Himalayan orogeny at the end of the Pliocene and the beginning of the Pleistocene led to a significant uplift of the Tibetan Plateau, shaping its unique topographical features (Hongzhen & Xuanxue, 1995). This region, known as the "Roof of the World" and the "Third Pole," plays a central role in biogeography, influencing biodiversity and geographic distribution patterns (Shen et al., 2002; Qu et al., 2010). The Hengduan Mountains, as part of the southeastern Tibetan Plateau, are a key area for global biodiversity. This region hosts approximately 12,000 species of vascular plants across 1,500 genera (Qu et al., 2010). Recent geological and biological studies have highlighted the link between the uplift of the Tibetan Plateau, particularly the Hengduan Mountains, and accelerated species diversification, revealing a rich evolutionary history (Qu et al., 2010; Wang et al., 2022; Qin et al., 2023). Despite extensive research on the Hengduan Mountains' role in biodiversity distribution and evolution, the specific contributions of its subsidiary ranges to species distribution, differentiation, and dispersal amid climatic and geological changes remain unclear. Further research is needed to fully understand how the Hengduan Mountains and the Tibetan

Plateau influence species evolution and distribution patterns.

The Ailao and Wuliang Mountains, subsidiary ranges of the Hengduan Mountains in the southeast, are known as the Yunling Subsidiary Ranges (Li et al., 2011; Wen et al., 2016; Chen et al., 2018; Yuan, 2023). Spanning over 500 kilometers from Dali, China, to the Hoang Lien Mountains, Vietnam, these mountains average over 2000 meters in elevation, stretching northwest to southeast across northern Indochina (You et al., 2013). Their unique geographical position and altitude gradient create diverse ecological niches and habitats for animals (Gong et al., 2011; Liu, 2015; Hou et al., 2023). High-altitude areas support alpine ecosystems (Lipan et al., 2008), while low-altitude areas exhibit tropical or subtropical characteristics (Young et al., 1992; Liu et al., 2003). This gradient offers habitats from tropical rainforests to alpine meadows (Long et al., 1994; Lin Chen et al., 2010; Song et al., 2012), allowing animals to choose environments that meet their ecological needs (Wang et al., 2000; Haiqing Xu, 2005). The junction of the Yunling Subsidiary Ranges with the Indochina Peninsula forms a biogeographical crossroads. Many species from Indochina may migrate northward, while some East Asian species may move southward (Fan et al., 2022). This bidirectional dispersal enriches the species diversity within the Yunling Subsidiary Ranges (Gu et al., 2018; Fan et al., 2022), providing a unique backdrop for studying the impact of the Hengduan Mountains' subsidiary ranges on the distribution and evolution of animals.

Small mammals, especially bats and rodents, may be more affected by the ecological influences of the Yunling Subsidiary Ranges compared to larger mammals such as wolves (*Canis lupus*) (Chen et al., 2011; Wang et al., 2022 Doan et al., 2023). Bats, serving as pivotal model organisms, have their evolutionary history significantly driven by geological and climatic changes (Wei et al., 2010; Rebelo et al., 2012). Previous studies (Teeling et al., 2005; Ruedi et al., 2013; Yi & Latch, 2022) have highlighted that the flight capabilities of bats may facilitate gene flow across geographical regions, mitigating the effects of geological barriers. Moreover, there is a clear positive correlation between the migration capabilities of bats and their genetic fluidity (Stadelmann et al., 2007), with their ability to migrate long distances being a key factor for successful settlement in diverse ecosystems (Voigt & Lewanzik, 2011). Thus, selecting chiropteran species to explore how the Yunling Subsidiary Ranges affect the distribution and evolution of animals offers valuable insights, aiding our understanding of the impact of the Hengduan Mountains' subsidiary ranges on the geographical distribution of small mammals. This research is not only representative but also of universal value.

The Stoliczka's Asian Trident Bat (*Aselliscus stoliczkanus*), belonging to the Hipposideridae family, Aselliscus genus, serves as an ideal model for studying how the Yunling Subsidiary Ranges influence species' geographical distribution and evolution. According to the International Union for Conservation of Nature (IUCN) data from 2024, the distribution of the Stoliczka's Asian Trident Bat reaches its northernmost extent in the northern part of the Yunling Subsidiary Ranges, traversing the center of its distribution

area (IUCN, 2024). Currently, research on the phylogeographic structure and evolutionary history of this species remains scarce, posing challenges for its in-depth understanding and effective conservation (Smith et al., 2010; Guangping et al., 2021). We have employed a comprehensive approach, integrating species distribution models, morphological data, mitochondrial, and nuclear genetic methods, to delve into the geographical distribution patterns and evolutionary processes of the Stoliczka's Asian Trident Bat, analyzing the combined effects of Pleistocene climatic oscillations and the uplift of the Yunling Subsidiary Ranges on its distribution and evolution. Our hypothesis posits that climatic oscillations during the Pleistocene and the uplift of the Yunling Subsidiary Ranges have jointly shaped the geographical distribution patterns and evolutionary pathways of this species. Further research will contribute to validating this hypothesis and enhancing our understanding of biogeography and species evolution in the Qinghai-Tibetan Plateau.

Methods

The Yunling Subsidiary Ranges (fig. 1) are one of the world's biodiversity hotspots (Myers et al., 2000; Wen et al., 2016), with an annual average temperature of 11.0 °C and an annual average rainfall of 1,902 millimeters (You et al., 2013; Gu et al., 2018). The predominant forest vegetation in this area is moist evergreen broad-leaved forest (Liu, 2015). The study focuses on the Pleistocene, including four glacial events (fig. 1E), occurring approximately 800–1170, 500–720, 130–300, and 10–70 thousand years ago (Zheng et al., 2002). The timeline spans from the early Pleistocene (about 2.3 million years ago) to the recent era (1970–2000). The rapid uplift of the Qinghai-Tibetan Plateau, a major geological event in western China, occurred from the late Pliocene to the early Pleistocene (Hongzhen & Xuanxue, 1995).

Predicting species' potential distribution across different periods

The Stoliczka's Asian Trident Bat (*Aselliscus stoliczkanus*), an insectivorous cave-dwelling bat, is classified as a species of least concern (Tu et al., 2015; Zhang et al., 2016; IUCN, 2024). The distribution data for this study (fig. 1C) include field survey data from 2019 to 2023, as well as information from IUCN and NCBI (see supplementary table S1 for distribution data). Paleoclimatic data were derived from the CCSM4 climate model within the WorldClim 1.4 dataset (Hijmans et al., 2005). We employed the Biomod2 (Version: 4.2–4) ensemble model (Thuiller et al., 2009; R Corm Team, 2023) to estimate the impact of climatic oscillations on the species' distribution (detailed methodology in supplementary text S1, supplementary figs. S1–S2 and supplementary tables S2–S3). Using ArcGIS software (Version: 10.2.2), we calculated the area and proportion of highly suitable habitats (distribution probability ≥0.7) within East Asia for the current period, the Last Glacial Maximum (LGM), and the Mid-Holocene (MH) period.

Morphometric differentiation of Stoliczka's Asian Trident Bat

Mist nets were used to capture and measure 16 morphometric indices of the bats before releasing them back at the site of

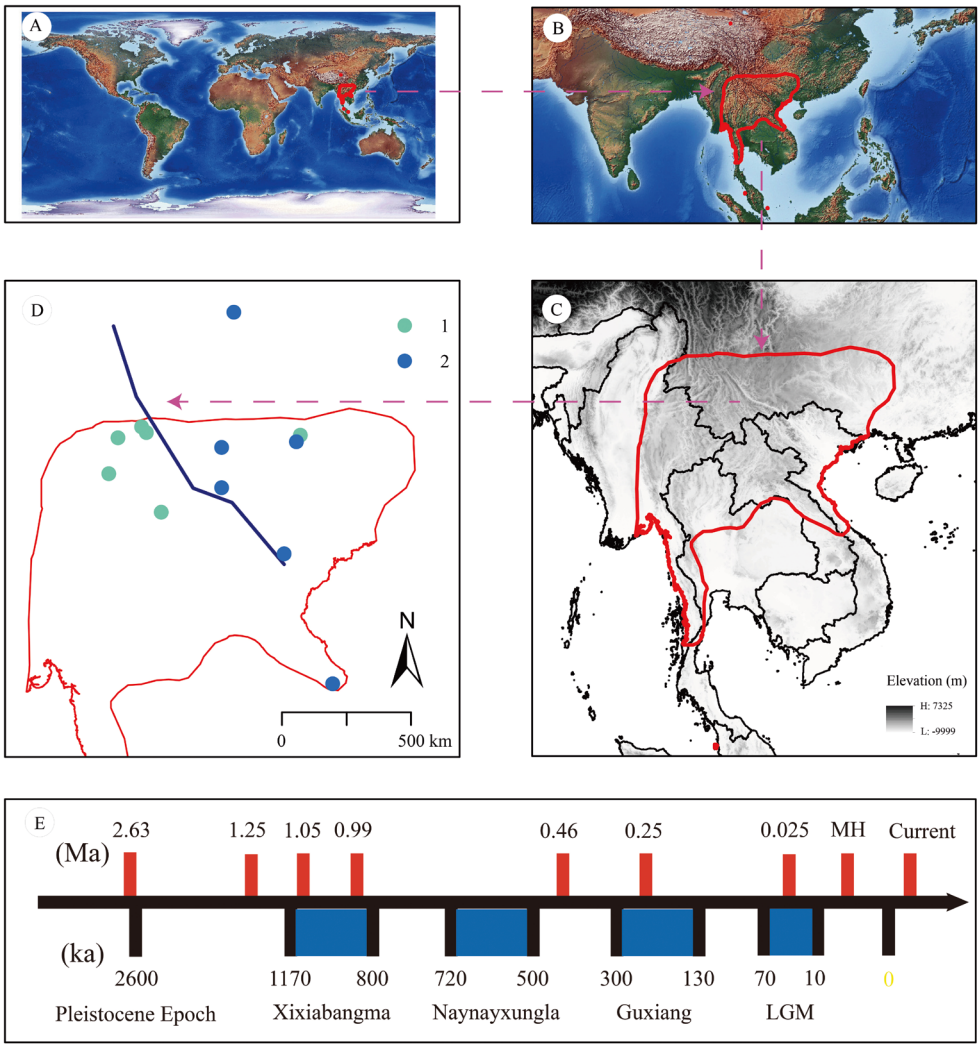


FIGURE 1 Study area and schematic representation of Stoliczka's Asian Trident Bat distribution sites. (A) shows a world map, where the red box indicates the global distribution of Stoliczka's Asian Trident Bat (source: IUCN). (B) displays the overview of the Qinghai-Tibetan Plateau and the Hengduan Mountains, with the red box also marking the distribution of Stoliczka's Asian Trident Bat. (C) illustrates the elevation data of the Yunling Subsidiary Ranges within the Hengduan Mountains and the main distribution areas of Stoliczka's Asian Trident Bat in this study area. (D) represents the Yunling Subsidiary Ranges with the collection sites and the locations of mitochondrial gene sequences, where 1 denotes the sites where Stoliczka's Asian Trident Bat was collected in this survey, and 2 refers to the location information of the Stoliczka's Asian Trident Bat mitochondrial gene data downloaded from NCBI. The red boxes in (A), (B), and (C) are consistent. The black lines in (D) serve as a schematic of the Yunling Subsidiary Ranges. (E) is a schematic of the study time range, including the Pleistocene starting from 2.6 Ma, through four glacial periods, up to the Current (1970–2000). The timeline above corresponds to the time points involved in this study, aligning with evidence from section 3.3.3 of the results.

capture. A small number of specimens were taken for skull preparation, measuring 18 indices (see supplementary tables S4–S6 for details). Principal Component Analysis (PCA) was employed for dimensionality reduction, and the first and second principal components were used for plotting; independent sample T-tests were conducted to analyze differences between categories. All fieldwork was carried out in accordance with the "Wildlife Protection Law of the People's Republic of China." All experiments involving live bats adhered to the guidelines of the American Society of Mammalogists (Gannon et al., 2007).

Genetic structure, divergence, and historical dynamics of the Stoliczka's Asian Trident Bat

Molecular phylogeographic methods have been extensively applied in related research (Newton et al., 1999). In this study, tissue samples from the wing membranes of 107 individuals were collected from six habitats in Yunnan and Guizhou provinces of China (fig. 2A) and released at the point of capture; the samples were preserved in 95% ethanol. A mitochondrial gene (*cyt b*) and two nuclear gene fragments (THY, SORBS2), along with seven microsatellite loci, were amplified using PCR from the extracted DNA samples (extraction methods detailed in supplementary text S2, supplementary table S7, supplementary figs. S3–S4).

Genetic structure

The haplotype diversity (h) and nucleotide diversity (π) of *cyt b*, THY, and SORBS2 were calculated using DNASP software (Version 6.12.03) (Rozas et al., 2017). For microsatellite data analysis, observed heterozygosity (HO) and expected heterozygosity (HE) were calculated using POPGENE 1.32 software (Nei, 1972). Genepop software (Rousset & Francois, 2008) was used to test each locus for Hardy-Weinberg equilibrium (HWE), linkage disequilibrium, and null allele frequency.

Phylogenetic trees of the *cyt b* sequence and combined nuclear genes (THY and SORBS2) were constructed using

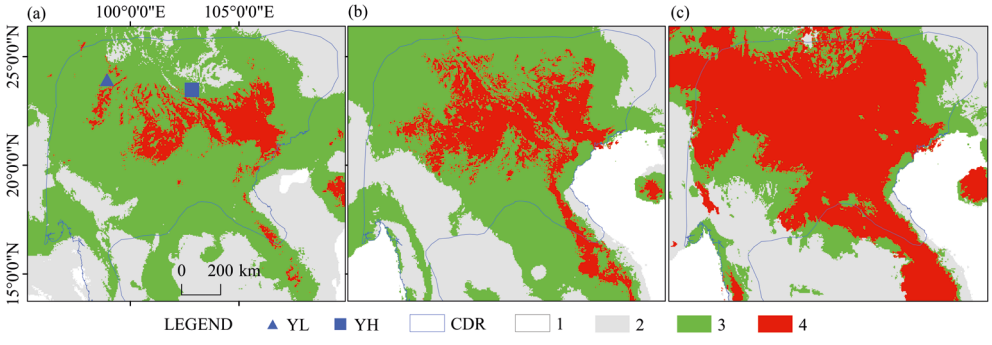


FIGURE 2 Potential distribution of Stoliczka's Asian Trident Bat (*Aselliscus stoliczkanus*) during the Last Glacial Maximum (A), the Mid-Holocene period (B), and the present (C). CDR: current distribution range. 1: Non-suitable area (distribution probability ≤0.15), 2: Low suitability area (0.15 < distribution probability ≤0.5), 3: Medium suitability area (0.5 < distribution probability ≤0.7), 4: High suitability area (distribution probability >0.7).

Maximum Likelihood (ML) and Bayesian Inference (BI) methods (methods detailed in supplementary text S2, supplementary table S7, supplementary figs. S3–S4). Median-joining networks of *cyt b* haplotypes and nuclear genes were constructed using Network 10.2 software (Bandelt et al., 1999). The population genetic structure of microsatellite data was analyzed using STRUCTURE 2.3.4 software (Pritchard et al., 2000), and the most likely number of clusters (K) was determined using the online tool Structure Harvester (https://taylor0.biology.ucla.edu/struct_harvest/).

Gene flow and genetic variation between lineages

The isolation with migration model (IMa2 algorithm) was applied to analyze mitochondrial and nuclear gene data to estimate gene flow among populations (methods detailed in supplementary text S2, supplementary table S7, supplementary figs. S3–S4). Based on the branches of the mtDNA *cyt b* phylogenetic tree, molecular variance analysis (AMOVA) (Excoffier et al., 1992) across lineages, between populations, and within populations was conducted using Arlequin 3.5 software (Pritchard et al., 2000; Excoffier & Lischer, 2010).

Population historical dynamics and timeframes

The time to the most recent common ancestor (TMRCA) of major lineages was estimated using BEAST 1.10.4 software (Suchard et al., 2018). The average substitution rate for *cyt b* was set at 0.013 substitutions per site per million years (Thong et al., 2012; Lin et al., 2014), with GTR+F+G4 as the optimal nucleotide substitution model. Tajima's D (Tajima, 1989)and Fu's Fs tests (Fu, 1997) were conducted using Arlequin 3.5. Population dynamics were assessed by constructing Bayesian skyline plots (BSP) in BEAST 1.10.4 (methods detailed in supplementary text S2, supplementary table S7, supplementary figs. S3–S4).

Results

The potential distribution patterns of Stoliczka's Asian Trident Bat at different periods

This section identifies a significant link between bat distribution and precipitation, with suitable habitats expanding from the LGM to the present. We collected data from 74 sites (supplementary table S1). The integrated model's AUC score was 0.98 (single model scores, see supplementary text S2, supplementary table S7, supplementary figs. S3–S4), with the most significant environmental factor affecting species distribution being Bio 18 (Precipitation of Warmest Quarter), contributing 32% (scores for other factors, see supplementary text S2, supplementary table S7, supplementary figs. S3–S4). During the LGM period, the area of high suitability habitats (probability ≥0.7) for the Stoliczka's Asian Trident Bat was approximately 491,027 km^2, representing 1% of the study region; the YL and YH populations were located at the northernmost extent of the bat's high suitability habitats (fig. 2A). Compared to the LGM, the high suitability habitat area during the Mid-Holocene (MH) increased nearly

threefold, to about 1,036,204 km^2 (fig. 2B), representing 3% of the study area. The current high suitability habitat area is approximately 3,424,398 km^2, accounting for 10% of the study area and marking an almost tenfold increase from the LGM period (fig. 2C).

Morphological differences among populations along the Subsidiary Ranges of the Yunling Mountains

This section shows significant morphological differences between bat populations on the eastern and western sides of the Yunling Subsidiary Ranges. We analyzed data from 53 morphometric measurements and 41 skull measurements (see supplementary tables S4–S6 for details). Significant morphological differences ($P < 0.05$) were found between populations on the eastern side of the Yunling Subsidiary Ranges, including YDWS, YB, and YL, and the population on the western side in GA (fig. 3 and supplementary tables S4–S6).

Molecular phylogeographic analysis

This section analyzes the genetic differentiation, gene flow, and population dynamics of Stoliczka's Asian Trident Bat, revealing significant genetic variation between eastern and western populations, minimal gene flow, and notable population declines over time.

Population differentiation along the Yunling Subsidiary Ranges

Genetic analysis was conducted on 107 individuals, with mitochondrial and nuclear haplotype sequences uploaded to NCBI (sequence numbers, see supplementary text S2, supplementary table S7, supplementary figs. S3–S4). Based on the mitochondrial *cyt b* gene, nucleotide diversity was significantly higher in the YL and YH populations than in other groups (supplementary text S2, supplementary table S7, supplementary figs. S3–S4), with haplotype networks and phylogenetic trees clearly distinguishing between the western (Clade A) and eastern (Clade B) sides of the Yunling Subsidiary Ranges. Nuclear genes (microsatellite clustering analysis, nuclear haplotype networks, and combined gene trees) did not show significant differentiation (supplementary text S2, supplementary table S7, supplementary figs. S3–S4).

Gene flow and genetic variation between lineages

IMa2 analysis revealed no significant gene flow among the studied populations of Stoliczka's Asian Trident Bat. The migration rates (2NM) between pairs of populations were low, with likelihood ratio tests yielding *P*-values greater than 0.05, indicating no significant level of gene flow.

Molecular variance analysis (AMOVA) grouped by eastern and western lineages showed extremely significant levels of variation at all three tested levels ($P < 0.01$), with genetic variation between the eastern and western sides of the Yunling Subsidiary Ranges reaching 75.33% (table 1).

Population dynamics and timeframes

The Stoliczka's Asian Trident Bat began to diverge into eastern and western lineages around 2.63 Ma; by 1.05 and 0.99 Ma, Clade B experienced intensified differentiation, forming distinct geographical populations in Vietnam, the Red River in mainland China, and Guizhou;

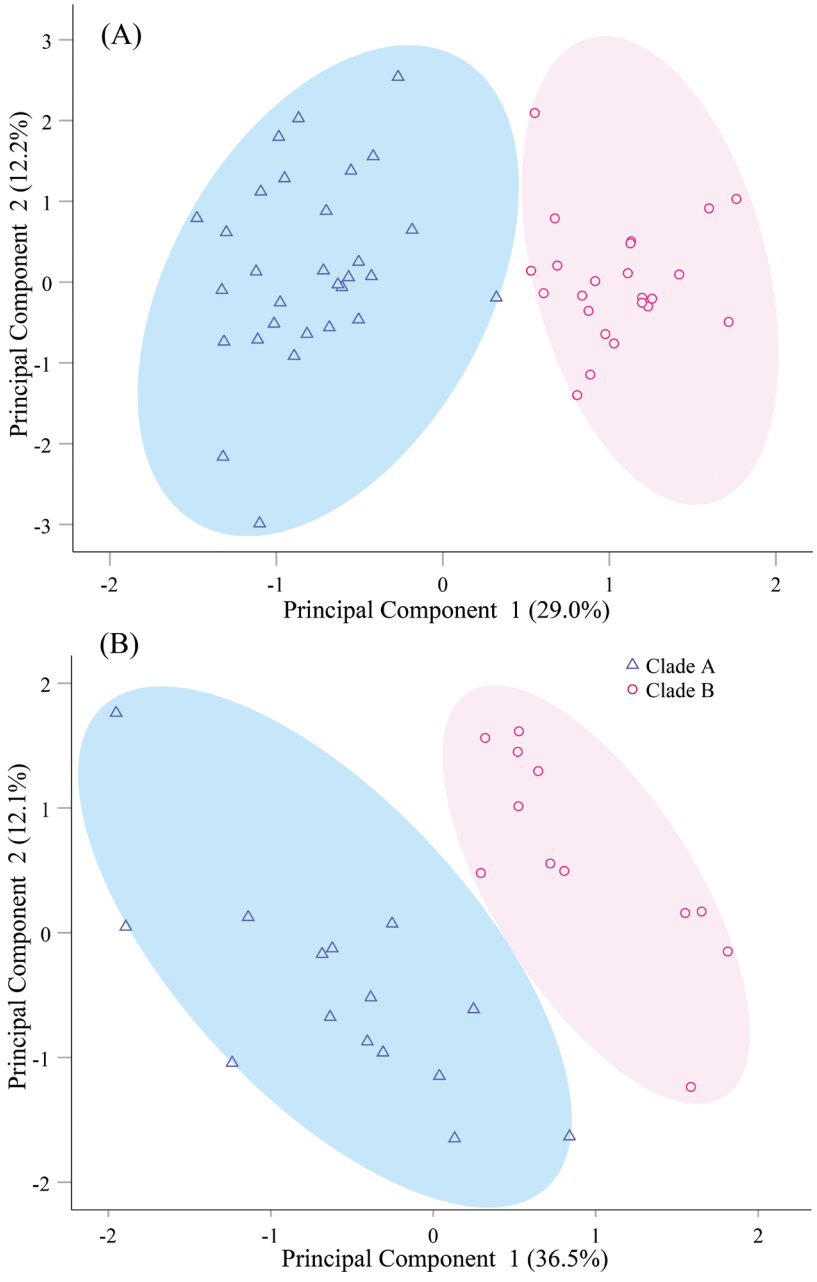


FIGURE 3 PCA analysis of morphometric data for Stoliczka's Asian Trident Bat (*Aselliscus stoliczkanus*). (A) is based on morphometric data, including 16 indices, and (B) is based on Skull data, comprising 18 indices (specific indices detailed in supplementary text S2, supplementary table S7, supplementary figs. S3–S4). Clade A refers to the lineage on the western side of the Yunling Subsidiary Ranges, while Clade B refers to the lineage on the eastern side of the Yunling Subsidiary Ranges.

TABLE 1 AMOVA of Stoliczka's Asian Trident Bat *cyt b* gene. The two different groups were clade A (YL, YB, YDWS, YDYB, YNPE and YK populations) and clade B (SC, GA, GQ, YH, YN1 and YN2 populations). A *P*-value less than 0.01 indicates that the probability of the percentage of variation occurring randomly is very low, suggesting a high likelihood that the percentage of variation is not random.

Source of variation	Variance	Sum of squares	Percentage of variation	Fixation indices
Among groups	1	875.749	75.33	F_{CT} : 0.7533 ($P < 0.01^{**}$)
Among populations	10	505.527	20.79	F_{SC} : 0.8426 ($P < 0.01^{**}$)
Within groups				
Within populations	118	121.539	3.88	F_{ST} : 0.9612 ($P < 0.01^{**}$)

Clade A began dispersing from 0.46 Ma (figs. 1E and 4C).

Tajima's D and Fu's Fs tests did not yield significantly negative values ($P > 0.05$), with mismatch distributions showing a multimodal pattern. The overall population of Stoliczka's Asian Trident Bat showed a sharp decline around 0.25 Ma; Clade A's effective population size notably decreased around 0.025 Ma; Clade B started to decrease gradually from 0.25 Ma (fig. 1E and supplementary text S2, supplementary table S7, supplementary figs. S3–S4).

Discussion

Pleistocene climate oscillations significantly influenced the geographic distribution patterns and evolutionary processes of Stoliczka's Asian Trident Bat

Analysis using the Biomod2 integrated model, based on 11 common models, revealed that Pleistocene climate oscillations significantly impacted the distribution range and area of Stoliczka's Asian Trident Bat. The alternating glacial and interglacial periods during the Pleistocene led to shifts between cold, dry climates and warm, humid conditions (Hiemstra, 2012), causing environmental changes across most of the Northern Hemisphere. During warm periods, increased river flow and lush vegetation contrasted with the significant reduction in suitable habitats for animals due to extensive ice coverage during cold periods (Hofreiter & Stewart, 2009; Axmanová et al., 2020). The area of potential high suitability habitats (probability ≥0.7) for the Stoliczka's Asian Trident Bat was at its smallest during the LGM, only one-tenth of the present-day area, suggesting a retreat in distribution areas towards the south due to cold climate impacts. With warming climates, the area of high suitability habitats showed a marked increase, a trend also confirmed in studies on the Hengduan Mountains' specific rodent group (*Niviventer andersoni*) (Chen et al., 2011; Deyan et al., 2017) and four perennial herb species, indicating the sensitive response of flora and

fauna in the Hengduan Mountains region to climate changes (Luo et al., 2016; Yao et al., 2020).

The distribution of Stoliczka's Asian Trident Bat was significantly correlated with precipitation during the warmest quarter. Below 500 mm of precipitation, bat distribution positively correlated with precipitation levels, possibly due to abundant food resources, especially during the breeding season, and favorable climatic conditions. Above 500mm, the distribution probability of the bat remained around 0.75 (supplementary text S1, supplementary figs. S1–S2 and supplementary tables S2–S3). The relationship between the bat's distribution and precipitation highlights complex interactions within ecosystems, understanding which is crucial not only for the conservation of bat populations and biodiversity but also for comprehending the mechanisms of climate change impacts on species distribution.

During the Last Glacial Maximum, the Lincang (YL) and Red River (YH) populations provided potential refugia for Stoliczka's Asian Trident Bat. The northernmost edge of its most suitable habitat lay near the Tropic of Cancer, with both the YL and YH populations located at this northern extremity. These locations, acting as refugia, might have harbored a more diverse genetic background, a notion supported by genetic diversity data (supplementary text S2, supplementary table S7, supplementary figs. S3–S4) indicating that these two populations had significantly higher genetic diversity compared to other groups. During the second interglacial period, phylogenetic trees showed dispersal from the western lineage's Lincang population towards the northern Dali population (fig. 4C), likely driven by warmer climates.

Phylogenetic tree divergence times revealed that Pleistocene climate oscillations significantly impacted the evolutionary history of Stoliczka's Asian Trident Bat. The harsh climates of the first glacial period reduced the likelihood of interpopulation exchanges (results section "Population dynamics and timeframes"), ultimately increasing the differentiation among eastern lineage populations (results section "Population dynamics and timeframes"). Historically, Stoliczka's Asian Trident Bat did not undergo significant population expansion (mismatch distribution results); instead, populations significantly declined during glacial periods, especially the third and fourth glaciations, as indicated by population trends (results section "Population dynamics and timeframes" and supplementary text S2, supplementary table S7, supplementary figs. S3–S4).

Our findings support the view that Pleistocene climate oscillations could lead to species declines. Climate oscillations during the Pleistocene might have caused habitat fragmentation, further leading to species fragmentation (Siegel et al., 2023). From the perspective of Stoliczka's Asian Trident Bat population sizes, intolerance to cold climates may have been a primary reason for species decline. However, suitable habitats (refugia) during glacial periods allowed for differentiation and accumulation of different gene pools (Hewitt, 2000; Hewitt, 2008), eventually leading to new species. While climate change might lead to local population or

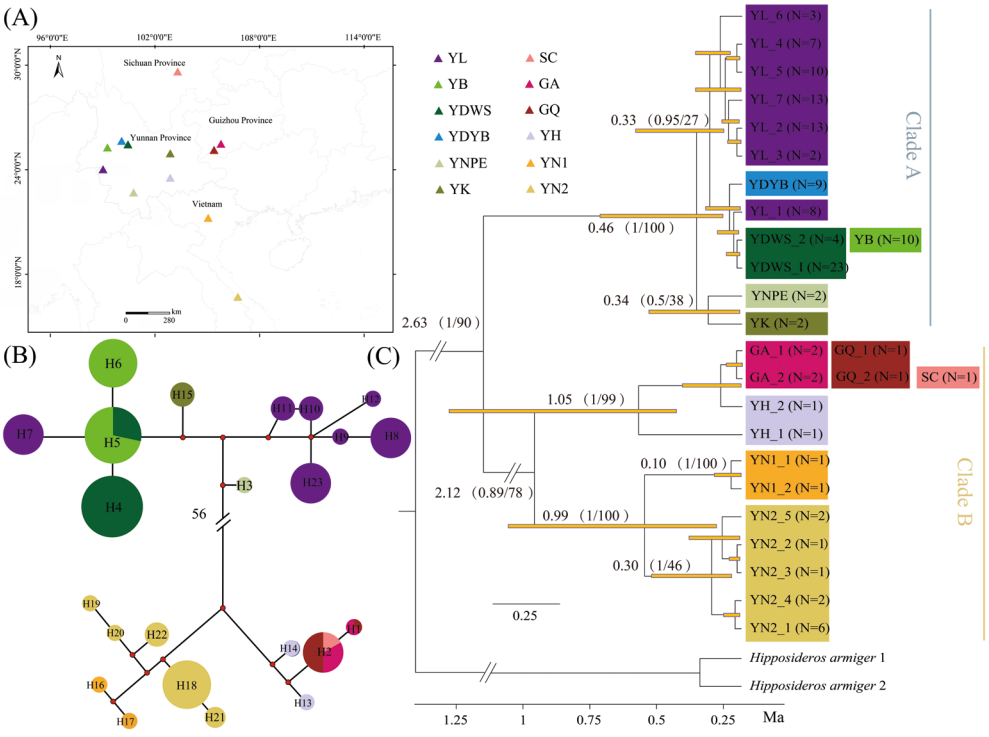


FIGURE 4 Sampling locations of Stoliczka's Asian Trident Bat (*Aselliscus stoliczkanus*), median-joining network, and ML tree based on *cyt b* sequences. (A) Collection sites for this study include YL (Lincang city, Yunnan Province), YB (Baoshan city, Yunnan Province), YDWS (Weishan county, Yunnan Province), YDYB (Yangbi county, Yunnan Province), YNPE (Pu'er city, Yunnan Province), YK (Kunming City, Yunnan Province), SC (Leshan city, Sichuan Province), GA (Anlong County, Guizhou Province), GQ (Qiandongnan Autonomous Prefecture, Guizhou Province), YH (Honghe Autonomous Prefecture, Yunnan Province), YN1 (Qingshan county, Vietnam), YN2 (Xianghua county, Vietnam). (B) Median-joining network constructed using mitochondrial haplotypes. Each circle corresponds to a haplotype, with size proportional to its overall frequency, and circle colors represent geographical locations. Numbers in the network denote mutational steps between haplotypes. The network illustrates shared haplotypes among YL, YB, and YDWS populations, suggesting the latter two populations result from direct dispersal. YH, GA, and SC populations also share haplotypes, implying similar dispersal origins. (C) Bayesian phylogenetic tree inferred from mitochondrial *cyt b* sequences. Numbers above or below branches represent the times to the most recent common ancestor (in million years, Ma); values in parentheses are Bayesian posterior probabilities and maximum likelihood bootstrap support values.

even species extinction, under these circumstances, climate change could be a significant positive factor in generating biodiversity, necessitating further evidence to comprehensively assess the positive or negative impacts of climate change on biodiversity.

The Yunling Subsidiary Ranges significantly influenced the geographic distribution patterns and evolutionary trajectories of Stoliczka's Asian Trident Bat

The two lineages of the Stoliczka's Asian Trident Bat were situated on either side

of the Yunling Subsidiary Ranges. This observation was supported by morphometric data, haplotype network diagrams, and phylogenetic trees. Although microsatellite data also suggested a bifurcation into two lineages, there remained shared ancestry between them, and the network diagrams and phylogenetic trees for the two nuclear genes did not show clear branches (supplementary text S2, supplementary table S7, supplementary figs. S3–S4), implying that the two lineages had not reached the level of species differentiation.

We hypothesized a strong correlation between the intraspecific differentiation of the Stoliczka's Asian Trident Bat and the uplift of the Yunling Subsidiary Ranges. No significant gene flow was observed between the two major lineages, and the differences between lineages were significantly greater than those within each lineage (table 1). The divergence times obtained from the phylogenetic trees revealed that, coinciding with the uplift of the Hengduan Mountains (2.63 million years ago), the Stoliczka's Asian Trident Bat began to differentiate into eastern and western directions. Therefore, compared to Pleistocene climate oscillations, we believed that the intraspecific differentiation of the bat was more closely related to the uplift of the Yunling Subsidiary Ranges.

The Yunling Subsidiary Ranges are not unrelated to the evolutionary history of small mammals, particularly Chiroptera. Zhang (2011) defined this line as the boundary between different subregions in the southwest, and our research provides strong evidence in support of this. Asia may be the center of origin for Chiroptera (Ruedi et al., 2013; W. et al., 2014), and the northward dispersal through the Indochina Peninsula to Europe and East Asia could be an important dispersal route. This route involves crossing the geographical barrier of the Yunling Subsidiary Ranges. Through this study, insights were provided into the evolution of the entire Chiroptera order and the impact of Quaternary environmental changes.

Two reasons could explain why sequences from the Kunming population (YK) on the eastern side of the Yunling Subsidiary Ranges were distinctly grouped with the western lineage (Clade A). The first reason might be that before the uplift of the Yunling Subsidiary Ranges, the Stoliczka's Asian Trident Bat had not differentiated into two distinct lineages, hence the Kunming population on the eastern side retained a genetic background closer to the western lineage. The second reason could be due to gene introgression, resulting in the capture of genes from the western population by the eastern population. Of course, the possibility of record errors cannot be ruled out. Future work will require more field surveys and additional genomic evidence to support these findings.

The role of climatic and geological events in shaping the geographic distribution patterns and evolutionary trajectories of species

The question of whether climatic factors or tectonic forces plays a dominant role in shaping species' distribution and evolutionary history intrigued researchers (Shi & Li, 1994). Our results indicated that both climate and tectonic factors significantly contributed to the geographic distribution patterns and evolutionary trajectories of the Stoliczka's Asian Trident Bat. Pleistocene climate oscillations primarily

influenced the bat's latitudinal distribution, while the Yunling Subsidiary Ranges, extending north to south, mainly affected its distribution on either side of the mountain (longitude). In terms of evolutionary history, the Yunling Subsidiary Ranges were crucial in delineating the divergence of the two lineages, whereas climatic fluctuations influenced the dispersion and differentiation processes within each lineage. It was important to note that during climatic oscillations, caves within the mountains provided potential refuges for the Stoliczka's Asian Trident Bat.

Overall, the uplift of the mountain ranges led to intraspecific differentiation, while climatic oscillations caused differentiation within lineages and a decline in population sizes. This aligned with findings from broader geographic studies in Europe and North America (Hewitt, 2004). Some research suggested that populations' responses to Pleistocene climate oscillations depended on their geographic locations (Antton, 2015), with topographical factors possibly playing a more significant role. The frozen Alps seemed to have been the initial barrier for species such as hedgehogs and oaks expanding northwards, and the Pyrenees also acted as a barrier for species like locusts, alders, and beeches. The Alps were relatively impermeable barriers to gene flow for bat lineages in the Apennines (Manuel et al., 2008).

Our study offered new insights into the impact of geological structures on Chiroptera and refined our understanding of how the Hengduan Mountains influenced the geographic distribution patterns and evolutionary processes of species. Previous research on Chiroptera primarily focused on land bridges, such as the Qiongzhou Strait of Hainan Island, the Taiwan Strait, and the Korean Strait (Yugo & Masaharu, 2021), without paying much attention to or discussing the impact of the Hengduan Mountains' subsidiary ranges. However, existing results also indirectly demonstrated the role of the Yunling Subsidiary Ranges in differentiation, such as significant genetic differentiation between the greater roundleaf bat populations in Baoshan (west side of the Yunling Subsidiary Ranges) and Jinning (east side of the Yunling Subsidiary Ranges) (Wei, 2013), and different branches between the greater horseshoe bat populations in Pu'er (west side of the Yunling Subsidiary Ranges) and Jinning (east side of the Yunling Subsidiary Ranges) (Xu et al., 2010). Therefore, the Yunling Subsidiary Ranges may have been an important geographical factor in the interspecific and intraspecific differentiation of Chiroptera in Asia, warranting further in-depth exploration (Fan et al., 2022).

Environmental heterogeneity was the "hand of God" in shaping biodiversity in the Hengduan Mountains region. This view was consistent with that of Yang and He (Yang & He, 2003), suggesting that habitat heterogeneity might benefit the formation of biodiversity. The uplift of the Hengduan Mountains' subsidiary ranges led to the differentiation of the Stoliczka's Asian Trident Bat into eastern and western lineages and hindered gene flow between them. Prolonged differentiation times further led to morphological changes, which might have deepened selective mating

choices (e.g., between the Guizhou snub-nosed monkey and the Sichuan snub-nosed monkey), ultimately leading to interspecific isolation (Hong et al., 2023). Future efforts should employ comprehensive methods to thoroughly examine the mechanisms by which environmental heterogeneity influences species formation and biodiversity.

Conclusion

The distribution patterns and evolutionary history of Stoliczka's Asian Trident Bat were influenced by Pleistocene climate oscillations and the uplift of the Yunling Subsidiary Ranges. Climate changes significantly impacted its distribution, with a positive correlation between its range and warmest quarter precipitation. The Yunling Subsidiary Ranges served as natural barriers, promoting significant morphological and genetic differentiation among populations. Our findings underscore the importance of climatic and geological factors in shaping biodiversity. Although climate change affected population sizes, geological structures played a crucial role in species differentiation and evolution. The uplift of the Yunling Subsidiary Ranges not only influenced intraspecific differentiation but also restricted gene flow between lineages. This study provides insights into how the Hengduan Mountains and the Qinghai-Tibetan Plateau have shaped Chiroptera distribution and evolution. Future studies should further analyze the mechanisms by which environmental heterogeneity influences species formation and biodiversity.

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Author contributions

Bu Yanzhen and Niu Hongxing designed the study; Liu Wei , Li Jing, He Jingying and Xu Guanbing performed the experiments; Wang Yanmei, Yang Yaping, Song Yiwen and Zhao Liming analyzed the data; Liu Wei wrote the manuscript.

Conflict of interest

The authors have no conflict of interest to declare.

Data availability

The datasets supporting the conclusions of this article have been archived in GenBank.

Ethics

All fieldwork was conducted in accordance with the Law of the People's Republic of China on the Protection of Wildlife. All experiments involving live bats followed the guidelines of the American Society of Mammalogists.

Supplementary material

Supplementary material is available online at:
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