

Miocene uplift and monsoon intensification coincided with avian diversification in the Himalaya-Hengduan Mountains

Running Title: Avian diversification in Himalaya-Hengduan Mountains

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Abstract

Mountains are well recognized for their exceptional high biodiversity, with rich aggregations of small-ranged species forming centers of endemism. The Himalaya-Hengduan Mountains adjacent to the Qinghai-Xizang Plateau, represent two of the world's largest and most diverse temperate mountain systems, both categorized as global biodiversity hotspots. Previous studies have underscored its global importance in biodiversity conservation and the influence of environmental drivers on its current distribution patterns. However, a comprehensive understanding of avian assemblage dynamics over time in these regions remains elusive. In this study, we used the most up-to-date avian tree and reconstructed historical biogeographical models for 5392 species of 58 families, representing groups with distinct dispersal abilities, to examine the temporal patterns and avifaunal assembly mode (*in situ* speciation vs colonization) in these mountain systems, as well as their influence on the surrounding avifauna. We further estimate net diversification rates and compare them with palaeo-reconstructed East Asian summer monsoon precipitation trajectories. Our results revealed that modern avian assemblage in the Himalaya-Hengduan Mountains primarily began at the early-Oligocene and experienced rapid diversification during the Miocene, broadly overlapping with the inferred timing of the mountain uplift and the intensification of monsoon climates. *In situ* speciation has consistently remained the dominant driver of avian accumulation, but the speciation-colonization ratio varied across major clades and was associated with species' dispersal ability. Our findings suggest that the Himalaya-Hengduan Mountains acted as a cradle for bird diversification, potentially

56 driven by mountain uplift and the intensification of the Asian monsoon during the
57 Neogene.

58 **Key words:** Orogeny; Diversification; Bird assemblage; Dispersal; *In situ* speciation

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uncorrected proof

INTRODUCTION

Species are unevenly distributed across the world, forming scattered clusters of high concentration, as in many mountain regions (Gaston 2000, Myers et al. 2000, Marchese 2015). Investigating biota assembly patterns in these global biodiversity hotspots has long been a central focus on biogeography and biodiversity conservation. Numerous studies show that deterministic processes, often dictated by environmental changes (Coelho et al. 2023, Martínez-Núñez et al. 2023), and stochastic processes, such as dispersal (Quintero & Jetz 2018, Peña et al. 2024, Zhang et al. 2025), account for regional species composition and distribution patterns, but correlations of this nature do not fully elucidate the temporal emergence of species richness. From an evolutionary standpoint, species richness can accumulate through three primary ways, including speciation within a given region (Losos & Ricklefs 2009, McGuire et al. 2014, Kuhnhäuser et al. 2025), multiple colonization from other regions (de Bruyn et al. 2014, Reeve et al. 2023), and the long-term preservation of lineages across evolutionary timescales (Stephens & Wiens 2003, García-Andrade et al. 2021). Integrating these processes with paleogeological events and paleoclimatic changes can provide deeper insights into the temporal dynamics of biodiversity hotspot formation (Igea & Tanentzap 2019, Feijó et al. 2022, Smiley et al. 2024).

Mountains are renowned for their high biodiversity and endemism (Fjeldså et al. 2012, Rahbek et al. 2019a, Rahbek et al. 2019b). Persistent orogenic activities generated marked vertical environmental heterogeneity and climatic variability, creating towering peaks and steep valleys that act as significant barriers to species

dispersal, thereby accelerating speciation (Hoorn et al. 2013, Xing & Ree 2017, Rahbek et al. 2019a, Marder et al. 2025). Among the global biodiversity hotspots, the mountains surrounding the Qinghai-Xizang Plateau, particularly the Himalaya-Hengduan Mountains, stand out as one of the most biologically rich regions in the Northern Hemisphere (Lei et al. 2015, Wang et al. 2022, Liu et al. 2025) (Figure 1). They possess distinct geological histories and uplift stages, and are surrounded by varied vegetation types (Spicer et al. 2021). Recent studies indicated that the uplift of the Himalayas initiated in the early Eocene but underwent rapid rise during the Miocene, attaining an average elevation of 5 000 m (Ding et al. 2017, Lai et al. 2025). On the other hand, fossil and tectonic evidence have indicated that the Hengduan Mountains reached its near-modern elevations earlier, during the early Oligocene, and continued to experience deformation from the late Oligocene to the early Miocene (Su et al. 2019). Following these uplift events, the towering mountain ranges and high-standing plateau acted as formidable topographic barriers that intercepted prevailing westerlies and reconfigured atmospheric circulation. This orographic blocking intensified land-sea thermal contrasts and strengthened seasonal wind reversals, thereby establishing and progressively amplifying the modern Asian monsoon system (Boos & Kuang 2010). The resulting intensification of summer precipitation and increased climatic seasonality profoundly altered regional hydrothermal regimes and seasonality (Spicer 2017), further amplifying environmental heterogeneity and niche diversification. Together, these geological and climatic drivers generated a complex mosaic of elevations, slopes and vegetation zones that serve as a spatial template for montane biodiversity.

Furthermore, these mountain regions are thought to play a distinct role in Asian biota evolution. They act as both a cradle and a museum, facilitating *in situ* radiation while simultaneously accumulating lineages derived from elsewhere (Martens et al. 2011, Liu et al. 2016, Cai et al. 2018, Feijó et al. 2022).

Despite the well-recognized role of the Himalaya-Hengduan Mountains in driving species diversification (Xing & Ree 2017, Lu et al. 2025), recent advances in integrating comprehensive phylogenies and accurate species distribution data have provided deeper insights into the biota assembly of these mountain ranges (Perrigo et al. 2019). Large-scale study on alpine flora suggest that the Himalaya-Hengduan Mountains functioned primarily as a cradle of diversification, with Oligocene-Miocene orogeny and monsoon intensification driving extensive *in situ* speciation (Ding et al. 2020). In contrast, studies on Asian mammals indicate a stronger role of colonization from adjacent regions, with the Himalaya-Hengduan Mountains acting as an immigration center over evolutionary timescales (Feijó et al. 2022). Whether birds conform to the cradle pattern observed in plants, the immigration pattern observed in mammals, or a distinct trajectory remains unresolved. Existing avian studies in the Himalaya-Hengduan Mountains have been largely confined to one or a few families, yielding seemingly inconsistent conclusions. For instance, Johansson et al. (2007) found that warblers (*Phylloscopus*) primarily colonized the Himalayas from Central China and Southeast Asia rather than undergoing extensive *in situ* radiation. Conversely, babblers experienced extensive *in situ* speciation in the Himalaya-Hengduan Mountains, followed by subsequent colonization into Southeast Asia and the Pacific Islands (Cai et

al. 2020). While Päckert et al. (2020) integrated five passerine clades and identified bidirectional exchanges, the lack of a comprehensive analysis encompassing the entire regional avifauna makes it difficult to determine which process dominates the build-up of this biodiversity hotspot.

The observed discrepancies among avian clades may be not random but are fundamentally mediated by functional traits (especially related to dispersal ability) that dictate how lineages interact with the complex landscape in the Himalaya-Hengduan Mountains. For example, species with weaker flight are more prone to geographic isolation by mountain barriers and thus may exhibit higher *in situ* speciation rates, whereas strong fliers experience recurrent gene flow that can either suppress speciation or facilitate rapid colonization across ranges (Claramunt et al. 2025). Body mass serves as a crucial proxy for an organism's ecological niche breadth and metabolic constraints. Small-bodied lineages often exhibit narrower niches and more restricted ranges, potentially accelerating divergence in the heterogeneous mountain environment (Fourcade & Alhajer 2023), whereas larger-bodied taxa may have a greater ability to cross biogeographic barriers and facilitate colonization (Nicolai & Matzke 2019). Despite these clear theoretical expectations, whether functional traits actually predict the relative contributions of *in situ* speciation and colonization across avian families in the Himalaya-Hengduan Mountains remains untested. Therefore, it is essential to conduct a comprehensive and integrated approach to understand avian evolution on this complex region and compare differences among groups with varying dispersal ability.

In this study, we tested two hypotheses to explore the dominant mode of avifaunal

assembly in the Himalaya-Hengduan Mountains and whether the relative contributions of *in situ* speciation and colonization vary among lineages in a trait-dependent manner. First, considering the extreme topographic relief and "sky island" configuration of the Himalaya-Hengduan Mountains, we predict that the regional avifauna primarily represents an evolutionary cradle, with *in situ* speciation dominating the accumulation of bird diversity over time. Second, given that species differ markedly in their capacity to traverse such geographic barriers, we further predict that taxa with weak dispersal ability are expected to exhibit higher *in situ* speciation ratios in the Himalaya-Hengduan Mountains, whereas taxa with strong dispersal ability should show greater colonization propensity. Furthermore, we evaluated whether the inferred timing of diversification shifts coincides with Miocene mountain uplift and the intensification of the Asian monsoon, thereby assessing the potential role of these geoclimatic drivers in shaping the tempo of avian assembly.

MATERIALS AND METHODS

Data collection

At the family level, we compiled all avian lineages distributed in the Himalaya-Hengduan Mountains, excluding shorebirds because of their dependence on wetland habitats, encompassing 58 families. The Himalaya harbors approximately 842 breeding bird species (Hu et al. 2022), and the Hengduan Mountains harbor approximately 734 breeding bird species (Zhang et al. 2025). Our study includes 777 species from this region. For each of these 58 families, we extracted all globally distributed member

species (5,392 species in total) from a recently published, comprehensive avian phylogenetic tree (McTavish et al. 2025). This global sampling is necessary because historical biogeographic inference requires a complete distribution matrix across all defined regions, enabling accurate reconstruction of ancestral distributions.

Definition of biogeographic regions

Drawing on the biogeographic regionalization approach of Cai et al. (2020) and Feijó et al. (2022), We tested two alternative regionalization schemes: one treating the Himalayas and Hengduan Mountains as distinct biogeographic units, and another merging them into a single region. Because these two adjacent mountain systems share a high proportion of co-distributed avian species, the optimal models frequently reconstructed ancestral ranges that united both regions, and the reconstructed trends of *in situ* speciation events were nearly identical between the two regions (Supplementary Figure S1). We therefore adopted the scheme treating the Himalaya and Hengduan Mountains as a single biogeographic unit for all subsequent analyses. Following this scheme, the Asian continent was split into six regions based largely on primary habitat types and geological history: Qinghai-Xizang Plateau, Himalaya-Hengduan Mountains, eastern Asia, southern Asia, western Asia, and northern Asia (Supplementary Figure S2). Southern Asia is characterized by its modern tropical forests, and includes southern China, India, Southeast Asia, and the Malay Archipelago. eastern Asia represents the temperate broadleaf and coniferous forests in the eastern Palearctic realm. Northern Asia is predominantly composed of lowland deserts and temperate grasslands, with its southern boundary adjacent to the Qinghai-Xizang Plateau, northern border contiguous

with Europe, and western flank separated by the biodiversity hotspot mountains of Central Asia. Western Asia exemplifies a typical desert environment, including the Arabian Peninsula and most West Asian countries. The delineation of the Qinghai-Xizang Plateau and Himalaya-Hengduan Mountains follows the definition of Liu et al. (2022). This categorization aims to recognize the distinct avifauna across Asia and to reflect the distinct geological, ecological and evolutionary history of the continent, while balancing model complexity and computational limitations (Feijó et al. 2022). In addition, we categorized non-Asian lineages into four geographical regions: the Americas, Europe, Africa, and Oceania (Supplementary Table S1).

Ancestral range reconstruction

Species distribution layers were sourced from BirdLife International (<http://datazone.birdlife.org/species/requestdis>). We followed the general practice in avian biogeographic studies by incorporating only breeding ranges or year-round activity ranges into the analyses (Cai et al. 2020). Species were assigned to one or more of 10 geographical regions according to their breeding distributions (Appendix S1). To minimize the inclusion of marginally distributed species, we considered a species to be present in a region when at least 20% of its range was contained within that area. Although this approach reduces the number of species per region, it more accurately reflects the core avian assemblage of each region (Feijó et al. 2022). For example, several bird species typically included as part of the Himalayan and Hengduan fauna, such as *Pellorneum tickelli*, and *Pterorhinus nuchalis* are predominantly lowland tropical forest species from southern Asia and so they were not categorized as montane

species. Additionally, we manually refined species distributions within the Himalaya-Hengduan Mountains using occurrence records from eBird (<http://ebird.org/>), Global Biodiversity Information Facility (GBIF, <http://www.gbif.org/>), and China Bird Report (<http://www.birdreport.cn>). A total of 30 species had their regional assignments adjusted. Although their BirdLife range polygons placed them at the marginal areas in the Himalaya-Hengduan Mountains, multiple different occurrence records confirmed their presence in the core positions of this region.

We reconstructed the ancestral ranges of the 58 families using the “BioGeoBEARS” package (Matzke 2014) in R 4.2 (R Core Team 2022). For each family, we tested six biogeographic models to infer the probabilities of ancestral states at each node on the phylogenetic tree implemented in BioGeoBEARS: dispersal-extinction-cladogenesis (DEC), likelihood-version of dispersal-vicariance analysis (DIVALIKE), likelihood-version of BayArea (BAYERLIKE), and these three models with founder-event speciation (+j). The optimal model was selected based on the Akaike Information Criterion (AIC) (Supplementary Table S2). To mitigate the impact of ancestral range reconstruction uncertainties, we employed 1 000 biogeographic stochastic mappings (BSM) using the parameters of the best-fitted model for each family to estimate the frequency of each biogeographic event. These results were used to estimate the number and timing of biogeographic events contributing to the avian assembly of the Himalaya-Hengduan Mountains (Dupin et al. 2017, Magalhaes et al. 2021). For each scenario, we counted the mean number of *in situ* speciation, vicariance, sympatric-subset speciation, founder-event speciation and dispersal events for every

two million years. Specifically, *in situ* speciation refers to ancestor and descendent occur in a single region. Vicariance occurs when one descendant lineage inherits part of the ancestral range and the other inherits the remaining part. Sympatric-subset speciation is a process where one descendant species inherits the original ancestral widespread range, and the other descendant species inherits only a subset of the ancestral range. Founder-event speciation is a situation where a descendant species occupies a new area to the ancestral range (Matzke 2014). When one or more new areas are incorporated into the species range, shifts recorded along the branches of the phylogenetic tree represent dispersal events. When calculating dispersal events, if a descendant occupies multiple new regions, we compute one event of dispersal for each region involved. We used the average values to represent the frequency of biogeographic events over time for each family and assessed the directionality of dispersals between regions. Moreover, we used the *e.divisive* function from the “*ecp*” R package to identify inflection points for each BSM replicate in diversification events through time (James & Matteson 2014). The inflection points represent significant shifts in the diversification trajectories, reflecting an acceleration or reduction in temporal diversification rates.

Analyses of net diversification rate

Diversification dynamics of each family were inferred with BAMM v.2.5.0 (Rabosky et al. 2014a). Priors were estimated with the *setBAMMpriors* function in the “BAMMtools” package (Rabosky et al. 2014b). The MCMC chain was run for 10 million generations, sampling every 1 000 generations. The first 25% of samples were

discarded as burn-in. We examined the convergence of the parameters of the MCMC chains and the effective sample size (ESS). Posterior distributions of rate-shift configurations and temporal rate trajectories were summarised with BAMMtools (Rabosky et al. 2014b). Following the method of Dore et al. (2025), we further estimated net diversification rates through time for the all Himalaya-Hengduan avifauna. After discarding burn-in, we randomly sampled 1 000 posterior evolutionary scenarios for each family and calculated the median net diversification rates along branches. Net diversification rates were then aggregated by biogeographic regions according to the membership assignments obtained from the BSM simulations. Subsequently, we performed cross-correlation function (CCF) analysis between the time series of net diversification rates and the East Asian summer monsoon precipitation proxy, to evaluate whether changes in monsoon precipitation preceded, lagged behind, or were contemporaneous with shifts in net diversification.

Diversification modes of families and influencing factors

To assess the dispersal differences between different families, we obtained the hand-wing index (HWI) and body mass data from publicly available databases (Tobias et al. 2022). The hand-wing index is commonly used as a proxy for flight ability in birds, with a higher index suggesting potentially stronger dispersal ability (Sheard et al. 2020). Larger-bodied species may also dispersal more easily to other regions due to their greater resilience against environmental changes (Van Bocxlaer et al. 2010). In addition to these traits, we incorporated several other indices that may influence species dispersal capacity, including functional dispersion index, ecological specialization

index (ESI), elevational range, and migratory behavior (see Supplementary Information for details in Appendix S1; Supplementary Table S3). HWI, body mass, and elevational range were ln-transformed to reduce the influence of right-skewness and extreme values. For each family, we calculated the mean values of species distributed within the Himalaya-Hengduan Mountains for subsequent analyses (Supplementary Table S4). Three families (Indicatoridae, Podargidae, and Tytonidae) were excluded because they only have one species in the Himalaya-Hengduan Mountains.

To quantify the diversification mode of each family we computed the ratio of *in situ* speciation events to immigration events inferred from 1 000 BSM analysis. This ratio was subsequently ln-transformed to avoid infinite estimates. Because lineages that occupied a region for longer periods may have more evolutionary time to accumulate *in situ* speciation (Stephens & Wiens 2003), we also extracted the earliest colonization time of each lineage in the Himalaya-Hengduan Mountains from the best-fitted biogeographic reconstruction. The earliest colonization time was included as a covariate in subsequent analyses. Subsequently, after detecting no significant phylogenetic signal, we employed generalized linear model to examine the relationships between diversification patterns and the above explanatory variables. Prior to model fitting, we assessed multicollinearity among predictors using variance inflation factors (VIF); all VIF values were below 2, indicating negligible collinearity among variables. We used a backward stepwise model selection approach to evaluated all possible candidate models and selected the optimal one based on the Akaike Information Criterion (AIC) (Supplementary Table S5). The best-supported model

included HWI, body mass, and colonization time as variables and individual effects of variables were calculated using the “glmm.hp” R package (Lai et al. 2022, Lai et al. 2023).

To evaluate the impact of HWI and body mass on the diversification dynamics of birds in the Himalaya-Hengduan Mountains, we first classified regional lineages into upper and lower trait quartiles based on family-level HWI or body mass distributions. At 0.1 million years ago (Ma) intervals, we extracted 1 000 posterior samples of net diversification rates for each time slice. These samples were partitioned into paired rate vectors corresponding to the top 25% and bottom 25% trait groups, allowing us to test for rate differences between high- and low-trait assemblages at every temporal point. Differences in net diversification rates between these groups were tested independently for every time slice with a Bayesian two-sample t-test, yielding Bayes factors (BF) as evidence metrics. $BF > 10$ and $BF > 100$ were interpreted as strong and extreme evidence, respectively.

RESULTS

Reconstructing the biogeographic histories of the 58 families shed light on the processes driving the avian assemblages in the Himalaya-Hengduan Mountains (Appendix S2). The modern avian assemblages began to form during the early Oligocene (Figure 2A). During the Miocene, the number of diversification events rapidly increased, and this high rate of diversification events persisted through the late Pliocene. We identified significant increases in *in situ* speciation at 21.0 Ma (95%

confidence interval is 20-24 Ma) and 10.8 Ma (95% confidence interval is 10-12 Ma) (Figure 2A). In parallel, we integrated posterior samples of net diversification rates estimated from BAMM with branch-specific occupancy histories generated through biogeographic stochastic mapping. The net diversification rates of Himalaya-Hengduan avian assemblages began to increase in the late Oligocene, peaking at approximately 12 Ma before declining gradually toward the present (Figure 3). Although the trajectory of net diversification rates temporally overlapped with the intensification period of the Asian summer monsoon, cross-correlation function analysis (allowing lags from -2 to 2 Ma) did not detect a statistically significant correlation between the two time series (Supplementary Table S6).

When comparing the dominant process driving bird assembly, the average number of *in situ* speciation events was 930.70 (56.1%), whereas the average number of immigration events was 397.31 (24.0%) (Figure 2B). *In situ* speciation was also the predominant factor throughout most of the evolutionary history of the group (Figure 2A). In addition to *in situ* speciation and immigration, sympatric-subset speciation has also played significant roles in the evolution of birds in the Himalaya-Hengduan Mountains (14.5% of total events) (Figure 2B). Sympatric-subset speciation primarily originated from ancestral species that occupied the southern Asia and Himalaya-Hengduan Mountains, with one descendant still inherited the original ancestral widespread range (52.1%), and the other descendant diversifying within Himalaya-Hengduan Mountains (17.7%) (Supplementary Figure S3). By comparison, vicariance events accounted for only a small proportion (5.4% of total events) (Figure 2B). Most

of them were due to the splitting of a binary ancestral area into two, primarily occurring between Europe and Himalaya-Hengduan Mountains, southern Asia and Himalaya-Hengduan Mountains, and Africa and Himalaya-Hengduan Mountains (Supplementary Figure S4). Notably, both sympatric-subset speciation and vicariance increased sharply from mid-Miocene to Pliocene, supporting the strong diversification trend during this period.

Family-level comparisons revealed that 27 families exhibited higher levels of *in situ* speciation than dispersal events within the Himalaya-Hengduan Mountains, representing a predominant mode of lineage accumulation (Figure 4C). These families mostly include groups in the lower quantile of HWI (Figure 4A), such as Timaliidae, Leiotrichidae (Appendix 2). For the remaining 28 families, colonization was the dominant factor in explaining present-day species diversity in Himalaya-Hengduan Mountains. Representatives such as Hirundinidae and Caprimulgidae are known to exhibit long-distance dispersal ability and broad ranges. Generalized linear model analyses revealed that HWI exerted a significant negative effect on diversification patterns ($R^2 = 0.4947$, individual contribution = 40.63%, Table 1), indicating that families with smaller HWI were more likely to undergo within-region radiation. Body mass had weak effect on diversification mode, with 19.08% individual contribution (Figure 4B; Table 1). Bayesian t-tests applied to each time slice revealed significantly higher net diversification rates for families with low HWI than families with high HWI (Figure 5A; Supplementary Table S7). Families with low body mass also exhibited higher net diversification rates before 6.3 Ma compared with families with high body

mass, but this difference became non-significant thereafter (Figure 5B; Supplementary Table S8).

We further observed similar number of immigration (401.67) and emigration events (377.52) in the Himalaya-Hengduan Mountains, suggesting that these regions served not only as important accumulation centers but also as significant sources of lineages for surrounding areas. Overall, the avifauna in the Himalaya-Hengduan Mountains was largely shaped by colonization from southern Asia, accounting for 65.1% of all immigration events (Figure 6B). Immigration from southern Asia began in the late Oligocene and grew progressively over time (Figure 6A). Colonization from other regions occurred later, primarily during the Miocene. In addition, the Himalaya-Hengduan Mountains were crucial contributors to the modern fauna of Asian birds, characterized by significant emigration from these regions to their surroundings. The largest proportion of emigrants was directed toward southern Asia (25.6%), followed by eastern Asia (22.9%) (Figure 6B).

DISCUSSION

Integrating phylogenetic, distributional, functional, and paleoclimatic data to interpret the formation mechanisms of biodiversity has become an important trend in evolutionary ecology. Our study based on a comprehensive phylogenetic framework, covering a wider range of taxa and incorporating geographical distribution data and continent-scale historical biogeographic analysis, reveals the spatiotemporal coupling patterns driving bird diversity in the Himalaya-Hengduan Mountains. In addition, by

exploring trends across different clades, we provide both an overall and specific taxa perspective in explaining the underlying mechanism of mountain hotspots formation and the influences of the surrounding regions. Our study reveals that *in situ* speciation dominated the bird evolutionary history in Himalaya-Hengduan Mountains, supporting the region as an evolutionary cradle. Correspondingly, colonization played a major role in families with higher dispersal ability, consistent with our trait-dependent prediction. The burst of avian diversity in Himalaya-Hengduan Mountains was synchronous with the uplift of mountains and the intensification of the Asian monsoon climate. Species exchange between mountain regions and surrounding areas had a significant impact on the present-day assemblage of birds in Asia.

Bird assembly through time in Himalaya-Hengduan Mountains

By analyzing the species diversification (diversification events and net diversification rates) through time, we identified clear signatures of lineage diversification that is timely congruent with periods of intensified orogeny and Asian monsoon climate. *In situ* speciation in the Himalaya-Hengduan Mountains dates back to the 34 Ma, early than the rapid uplift stage of Himalayas (Ding et al. 2017, Su et al. 2019). During Miocene, the number of diversification events and net diversification rates in these mountain systems increased rapidly. In particular, we identified a significant upward inflection point of *in situ* diversification during mid-Miocene, coinciding with rapid orogenic events when Himalaya-Hengduan Mountains approached their contemporary elevations (Ding et al. 2017). This finding is consistent with recent studies on mammals, amphibians, and reptiles in these two mountain

systems surrounding the Qinghai-Xizang Plateau (Xu et al. 2021, Feijó et al. 2022), revealing shared species diversification trends across the major vertebrate groups during the Miocene, a period of intense tectonism in Asia (Wang et al. 2025). The progressive uplift of the Himalayas and the Qinghai-Xizang Plateau altered land-sea thermal contrasts, thereby modifying atmospheric circulation and potentially intensifying the Asian monsoon and associated precipitation (Boos & Kuang 2010, Spicer 2017, Farnsworth et al. 2019, Wan et al. 2025). We detected a second, marked upturn in lineage accumulation within the Himalaya-Hengduan avifauna during this phase. However, cross-correlation function analysis did not detect a significant correlation between the net diversification rates and the Asian summer monsoon precipitation, suggesting that the influence of the monsoon on regional biodiversity is likely indirect and synergistic with the many other important geological and climatic changes that occurred during the Miocene (Spicer et al. 2020). Furthermore, glacial oscillations during the Pleistocene likely further driven population divergence (Song et al. 2009, Lei et al. 2015). During warm and humid interglacial periods, the upward shift of vegetation zones led to population fragmentation and genetic divergence. Conversely, as temperatures dropped during glacial periods, the downward movement of vegetation zones forced secondary contacts among populations, resulting in founder effects, disruptive selection, and trait displacement, thus further promoting allopatric speciation (Rahbek et al. 2019a).

Our findings have also revealed a rapid increase in avian sympatric-subset speciation and vicariance since Miocene, mirroring the pattern detected in Asian

mammals (Feijó et al. 2022), although vicariant speciation has played only a minor role. The orogeny not only provides numerous niches that facilitated *in situ* speciation and colonization, but also create the conditions for isolation and divergence through the high mountains and deep valleys (Qu et al. 2014, Perrigo et al. 2019). Particularly at the junction between the eastern Himalayas and the Hengduan Mountains, the snow-capped mountains have been considered as the primary barrier to species dispersal (Tietze et al. 2013, Lei et al. 2015, Li et al. 2019). Given the extensive overlap in avian species composition between the Himalaya and the Hengduan Mountains, we treated these two regions as a single biogeographic unit in our analyses, thereby hindering intrinsic patterns within each mountain. Nevertheless, numerous population genetic studies have provided evidence for this phenomenon (Dong et al. 2020b, Jiao et al. 2024). Studies based on genomic data indicate a high degree of population divergence in these areas, suggesting that speciation processes are likely ongoing (Dong et al. 2020a), and in some cases, divergence of different populations have reached to a level beyond the typical within-species variation (Zhang et al. 2019). These discoveries may lead to taxonomic revisions that could cause us to overlook certain biogeographic events. Future work incorporating independent biogeographic models for the Himalaya and the Hengduan Mountains, along with dense taxon sampling and genomic data, will be essential to reveal the distinct diversification events hidden within each range.

Dominant mode of bird assembly

In situ speciation events in the Himalaya-Hengduan Mountains are higher than colonization events, highlighting their role as cradles of avifauna. This contrasts sharply

with findings from mammals in Asia, where the colonization rate is three and six times than *in situ* speciation in the two mountain systems (Feijó et al. 2022). This conclusion seems counterintuitive, given that birds appear to possess a greater dispersal ability than mammals (He et al. 2022). However, many narrowly-range montane birds have strong dependency on habitat types and struggle to adapt to new environments. The high habitat heterogeneity along elevational gradients brought about by mountain uplift can accelerate their divergence, promoting *in situ* diversification (Fjeldså et al. 2012, Hughes & Atchison 2015). Our findings are also not fully consistent with prior studies on avian communities in the Himalayas or Hengduan Mountains that reported colonization as the primarily mode of species accumulation. (Martens et al. 2011, Lu et al. 2025). This discrepancy likely reflects the broader taxonomic coverage applied in this study, covering much of the bird diversity in Himalaya-Hengduan Mountains.

When exploring family-specific patterns, we found colonization as the dominant mechanism for some specific taxa, aligning with findings from previous studies (Johansson et al. 2007, Liu et al. 2016). These differences among taxa could be explained by their first colonization time and dispersal ability. Specifically, lineages that colonized the Himalaya-Hengduan Mountains early have a longer window for *in situ* accumulation, a pattern already documented in babblers (Cai et al., 2020). Late colonists, in contrast, encounter increasingly saturated montane niches that suppressed speciation (Price et al. 2014), leaving their modern diversity largely dependent on continued immigration. On the other hand, species traits may significantly influence their historical biogeography (Weil et al. 2023). Large body size has been associated

with successful dispersal (Nicolai & Matzke 2019, Weil et al. 2022), but our analyses do not provide strong support for this expectation for birds in the Himalayas-Hengduan Mountains. Instead, our results show that diversification patterns are strongly associated with flight capability: families with weak flight capability exhibit higher *in situ* diversification ratio and net diversification rates. Birds with high dispersal ability are likely to occupy larger geographic areas, a pattern that may hinder *in situ* speciation within any single region because high dispersal probability can disrupt the development of local adaptation or reproductive isolation (Claramunt et al. 2025). These patterns are reflected in our results that shows families with the highest HWI exhibited the highest colonization-speciation ratio.

While our family-level reconstructions capture broad-scale temporal dynamics of speciation and colonization across the entire Himalaya-Hengduan Mountains region, we acknowledge that they do not resolve fine-scale spatial heterogeneity. Recent spatial phylogenetic studies have shown that within mountain ranges, different elevations may play distinct roles. High elevation regions may exhibit higher diversification rates than lowlands, acting as cradles of neo-endemism, whereas lowlands may harbor more ancient lineages and serve as museums of paleo-endemism (van Els et al. 2021, Zhang et al. 2021). Future studies that integrate spatial phylogenetic tools with temporal frameworks could further elucidate how avian diversification patterns vary along the elevational gradient in the Himalaya-Hengduan Mountains.

Avifauna dispersal across Asian regions and surrounding continents

The dynamics of immigration and emigration are major components besides speciation and extinction in building and sustaining regional biodiversity (Wiens & Donoghue 2004). Päckert et al. (2020) found the immigration/emigration ratio in the Himalaya-Hengduan Mountains shaped the modern distribution patterns of five passerine Asian clades. Leveraging a much broader dataset, we have confirmed that species exchange between mountain regions and surrounding areas have significantly impacted the distribution pattern of birds in Asia. Generally, regions with high biodiversity are likely to contribute new lineages to areas with lower biodiversity (Feijó et al. 2022, Dore et al. 2025). Consequently, southern Asia, being the richest region, has provided the highest numbers of colonization into the Himalaya-Hengduan Mountains. These colonization events can be traced back to early Oligocene, exerting a profound influence on the local species pool. In contrast, the colonization from these two regions into southern Asia is much less frequent. The Himalaya-Hengduan Mountains exhibit higher colonization patterns towards the east compared to the west and north. Similar colonization trends were also recovered for mammals (Feijó et al. 2022). With the aridification of Western and Northern Asia during the early Miocene, the avian biota there became markedly different from those in the subtropical forests, and the vast habitat variation may have hindered the colonization of mountain species into Western and Northern Asia. Consequently, colonization towards eastern Asia appears more feasible. This region is characterized by extensive temperate forests influenced by the Asian monsoon, with more food and niches provided by the warm and wet environment (He et al. 2024). This eastward colonization trend is further

exemplified by the fauna of Taiwan Island, where phylogenetic and ancestral range reconstructions demonstrate that endemic lineages predominantly originated from the Eastern Himalayas during the Pliocene, rather than from adjacent South China (He et al. 2018). This pattern highlights how the warm and humid monsoon-driven environments of eastern Asia facilitate successful colonization and subsequent diversification of montane species.

CONCLUSION

Miocene orogeny coupled with the prevailing Asian monsoon climate collectively leaves a profound signature in the buildup of bird and other vertebrate groups in the Himalaya-Hengduan biodiversity hotspots. Our findings uncover that the assembly of bird communities in the Himalaya-Hengduan Mountains is dominated by *in situ* speciation as the primary mode, but this pattern exhibits significant variation among different families, primarily regulated by their dispersal capabilities and colonization history. Moreover, colonization remains a significant process, particularly since the Pliocene, where southern Asia emerges as the primary source for this global biodiversity conservation hotspot, which has also been impacting the fauna formation of other Asian areas. Our study revealed that Himalaya-Hengduan Mountains are important center of species diversification for birds and acted as pump of new lineages to other Asian regions.

DATA AVAILABILITY

All underlying data are presented in the Supplementary Tables and Appendix S1-S2. The phylogeny tree file can be downloaded from McTavish et al. (2025). The traits data can be downloaded from publicly available databases (Tobias et al. 2022, Şekercioğlu et al. 2025). We used the script provided by Magalhaes et al. (2021) to perform biogeographic stochastic maps over a sample of trees. The script of estimating the net diversification rate of a single region is provided by Doré et al. (2025).

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

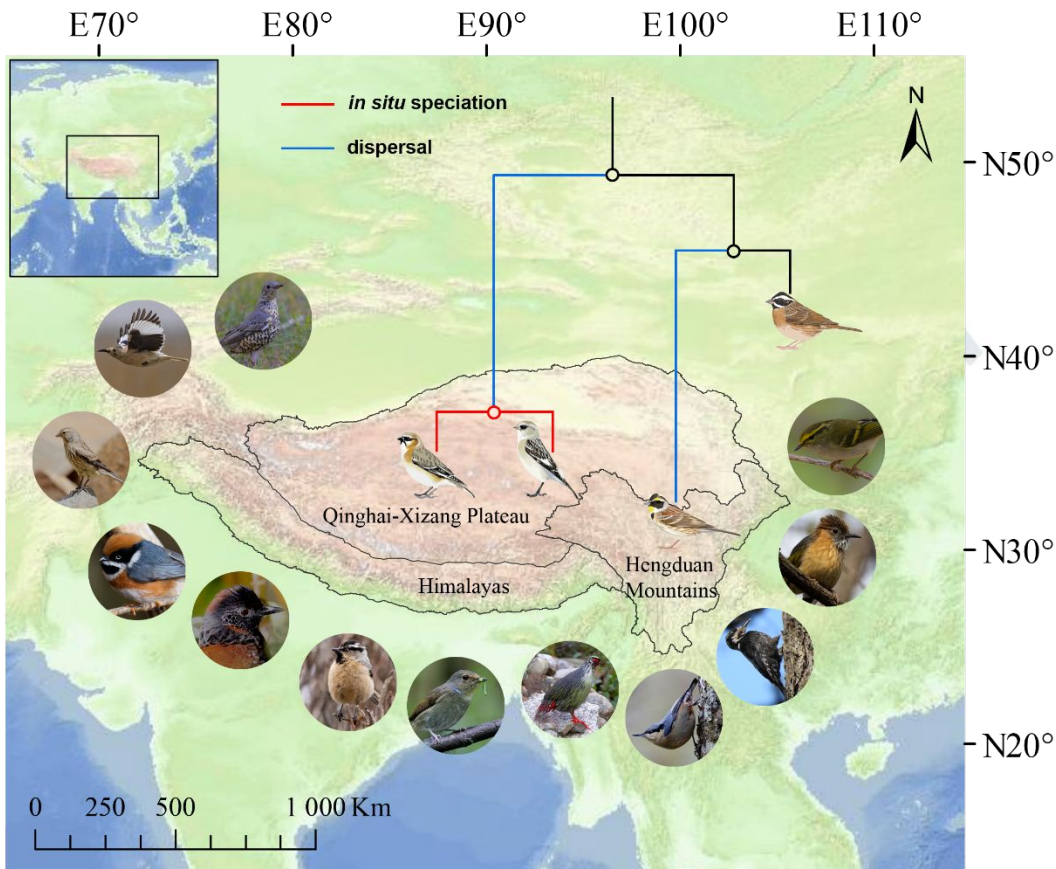
AUTHORS' CONTRIBUTIONS

FL, KZ and AF conceived the ideas; KZ, AF, TC and LW collected and organized the data; KZ, AF, TC and HW analyzed the data; KZ and QZ made the figures; KZ, AF and TC prepared the writing; and all authors revised and approved the manuscript.

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559 **Figures and legends**



561 Figure 1. Topographic map of the Qinghai-Xizang Plateau, Himalayas and Hengduan Mountains.
562 Inset images show representatives of part families that we analyzed (clockwise from top left:
563 Phylloscopidae, Pycnonotidae, Picidae, Sittidae, Phasianidae, Muscicapidae, Paridae,
564 Leiothrichidae, Aegithalidae, Fringillidae, Corvidae, Turdidae). The phylogenetic tree represents
565 two diversification events.

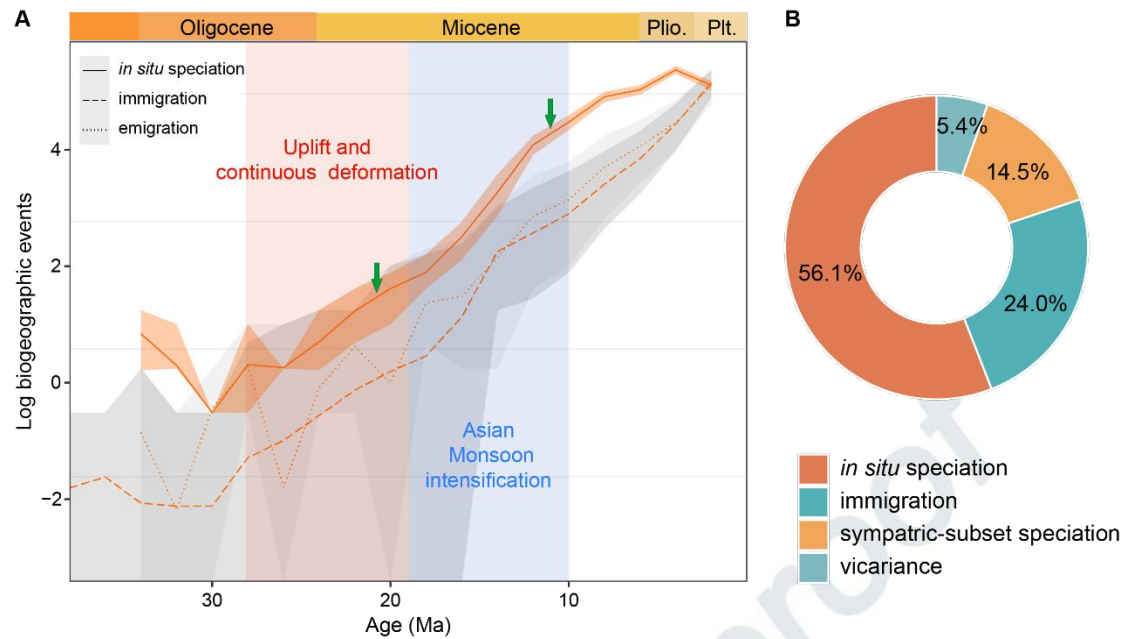


Figure 2. Temporal dynamics and relative contributions of biogeographic processes in shaping avifauna of the Himalaya-Hengduan Mountains. A: Temporal trends of *in situ* speciation, immigration, and emigration in the Himalaya-Hengduan Mountains averaged over 1 000 biogeographic scenarios and clustered by 2-Ma bins. Shaded region indicates 5–95% quantile intervals. The green arrow indicates the inflection points. B: Proportion of the major biogeographic events in the buildup of modern avifauna in Himalaya-Hengduan Mountains.

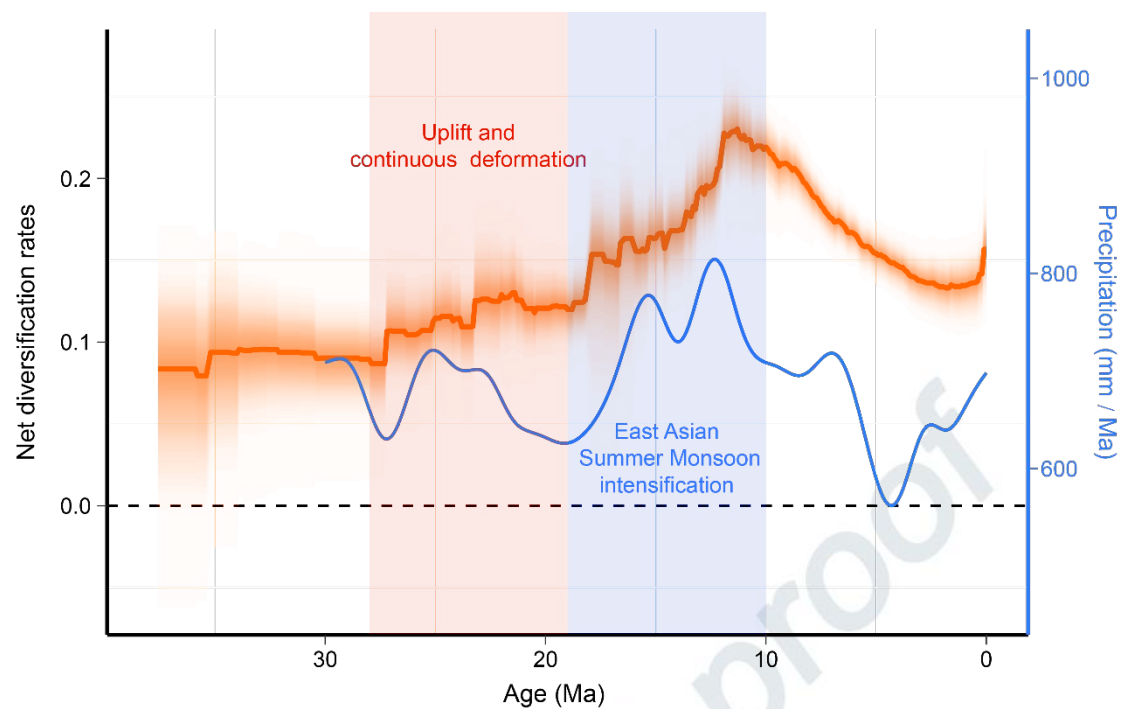


Figure 3. Comparison between net diversification rate in the Himalaya-Hengduan region and East Asian summer monsoon precipitation. The orange curve depicts the net diversification rate in the Himalaya-Hengduan region, extracted from 1 000 posterior samples of a BAMM analysis. Lineages were assigned to bioregions according to their posterior probability of presence in each region, estimated from 1 000 Biogeographic Stochastic Mapping (BSM) simulations. The shadow represents the credible interval. The blue curve shows East Asian summer monsoon precipitation based on kaolinite/illite at IODP Site U1501 (Wan et al. 2025).

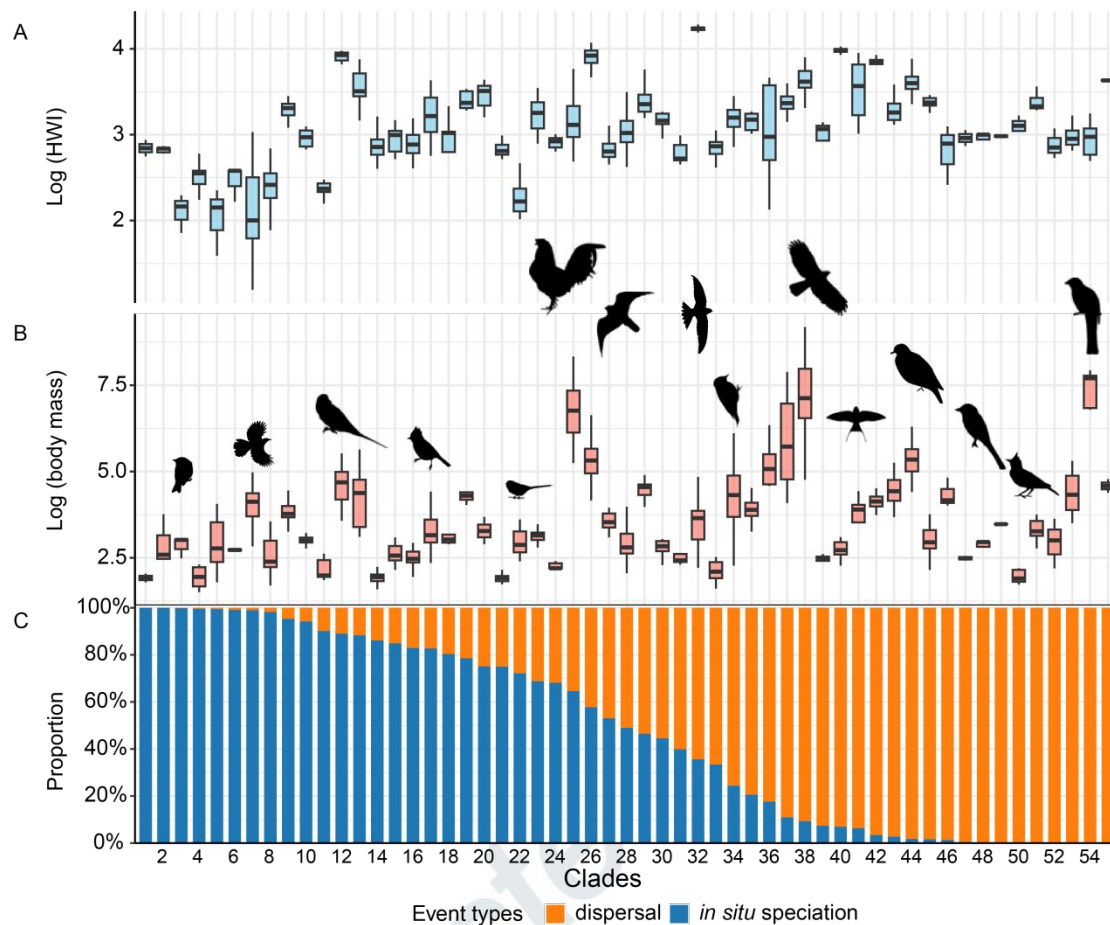


Figure 4. Morphological traits and diversification mode of different avian clades in the Himalaya-Hengduan Mountains. A: Hand-wing index (HWI) of different clades in the Himalaya-Hengduan Mountains. B: Body mass of different clades in the Himalaya-Hengduan Mountains. C: The proportion of *in situ* speciation and dispersal events of different clades in the Himalaya-Hengduan Mountains. Silhouette images (from left to right: Vireonidae, Leiotrichidae, Psittaculidae, Fringillidae, Pellorneidae, Phasianidae, Falconidae, Apodidae, Picidae, Accipitridae, Hirundinidae, Columbidae, Monarchidae, Alaudidae, Trogonidae) were adapted from an online open database (PhyloPic, <http://phylopic.org>) without restrictions on reuse (CC0 1.0). Each clade and its corresponding family can be found in Appendix S2.

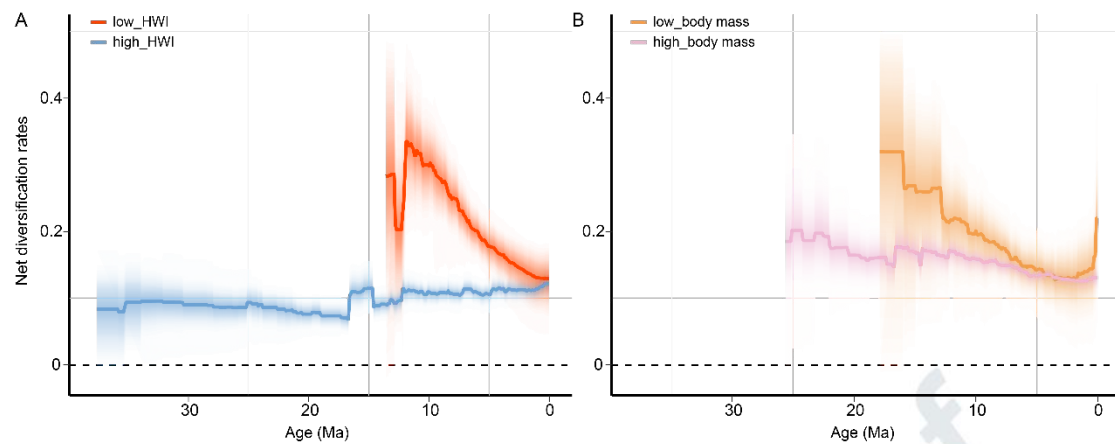


Figure 5. Comparison of net diversification rates between avian families with low versus high morphological traits. A: Net diversification rates of families with low versus high hand-wing index. B: Net diversification rates of families with low versus high body mass. The families were partitioned into low and high hand-wing index and body mass based on the top 25% and bottom 25% quantiles for each trait.

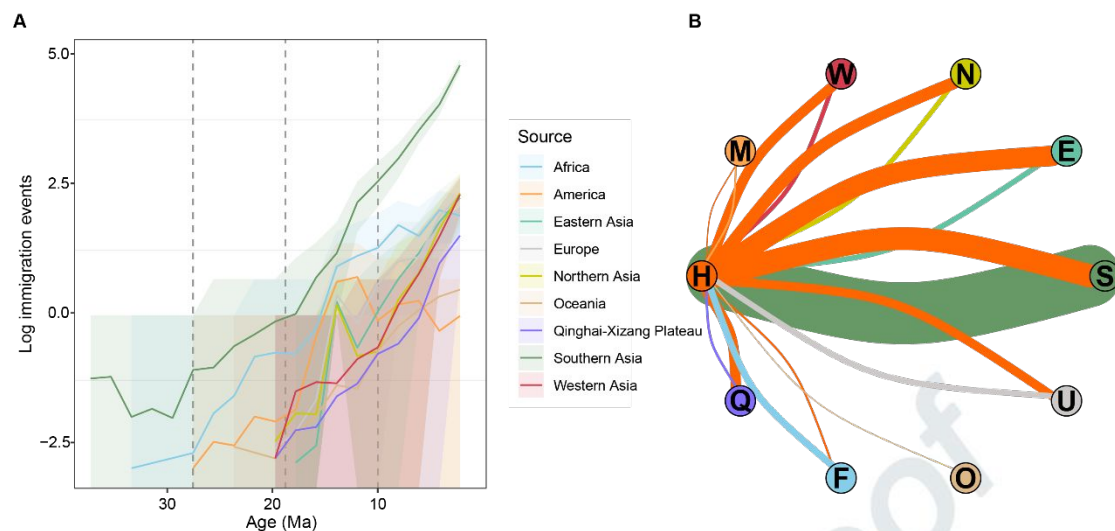


Figure 6. Historical dispersal dynamics between the Himalaya-Hengduan Mountains and adjacent regions. A: The number of immigration events through time toward the Himalaya-Hengduan Mountains averaged over 1 000 biogeographic scenarios and clustered by 2-Ma bins per region. Shaded region indicates 5–95% quantile intervals. B: Proportion of historical dispersions between the Himalaya-Hengduan Mountains and other regions based on the average of 1 000 range reconstruction scenarios. Color of lines relates to the source region and line thickness is proportional to the number of dispersal events. Only connections involving above 50th quantiles are shown. S, southern Asia; E, eastern Asia; N, northern Asia; W, western Asia; H, Himalaya-Hengduan Mountains; Q, Qinghai-Xizang Plateau; F, Africa; M, America; O, Oceania; U, Europe.

Table 1. Results of generalized linear model addressing the effects of body mass, hand-wing index (HWI), and the earliest colonization time on diversification patterns (proportion of *in situ* speciation events) for Himalaya-Hengduan avian clades.

Variables	Estimate	Std. Error	Pr(> t)	Individual contribution	Percentage
(Intercept)	5.4155	1.3824	0.0003		
Mean body mass	-0.4416	0.1766	0.0156	0.0944	19.08%
Mean HWI	-1.6895	0.4727	0.0008	0.2010	40.63%
Colonization time	0.1442	0.0310	0.0000	0.1993	40.29%
R ²				0.4947	100%

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标题

喜马拉雅-横断山脉鸟类多样化与中新世隆升及季风增强同步

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摘要

山区以其极高的生物多样性而著称, 包括大量分布范围狭窄的特有物种。毗邻青藏高原的喜马拉雅-横断山脉是世界上面积最大、多样性最高的两个温带山地系统, 均被列为全球生物多样性热点地区。先前的研究已强调其在全球生物多样性保护中的重要性, 并揭示了环境驱动因素对其当前分布格局的影响。然而, 目前仍然缺乏对这些地区鸟类类群在时间尺度上的动态变化的全面认识。在本研究中, 我们利用最新的鸟类系统发育树, 重建了 58 科 5392 种鸟类 (这些物种代表了具有不同扩散能力的类群) 的历史生物地理学模型, 旨在探究这些山地系统中鸟类群落形成的时间趋势及其构建模式 (即原位物种形成与定殖), 以及它们对周边鸟类区系的影响。我们还进一步估算了净多样化速率, 并将其与基于古气候重建的东亚夏季风降水轨迹进行比较。研究结果表明, 喜马拉雅-横断山脉的现代鸟类类群主要始于渐新世早期, 并在中新世经历了快速多样化, 这一过程大致与推

断的山脉隆升和季风气候增强的时间重叠。原位物种形成始终是鸟类物种积累的主要驱动力，但不同科之间的物种形成-拓殖比例存在差异，且与其扩散能力相关。这些结果表明，喜马拉雅-横断山脉可能是鸟类多样化的摇篮，其驱动因素与新近纪的山脉隆升和亚洲季风的增强存在联系。

关键词：造山运动；多样化；鸟类区系；扩散；原位物种形成