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The role of evolutionary time, diversification rates and dispersal in determining the global diversity of a large radiation of passerine birds

Tianlong Cai^{1,2,3} | Shimiao Shao¹ | Jonathan D. Kennedy^{3,4} | Per Alström^{1,5}  |
Robert G. Moyle⁶ | Yanhua Qu¹ | Fumin Lei^{1,2,7}  | Jon Fjeldså³

¹Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing, China

²College of Life Sciences, University of Chinese Academy of Sciences, Beijing, China

³Center for Macroecology, Evolution and Climate, GLOBE Institute, University of Copenhagen, Copenhagen, Denmark

⁴Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK

⁵Department of Ecology and Genetics, Animal Ecology, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden

⁶Department of Ecology and Evolutionary Biology and Biodiversity Institute, University of Kansas, Lawrence, KS, USA

⁷Center for Excellence in Animal Evolution and Genetics, Chinese Academy of Sciences, Kunming, China

Correspondence

Fumin Lei, Key Laboratory of the Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China.
Email: leifm@ioz.com

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Abstract

Aim: Variation in species diversity among different geographical areas may result from differences in speciation and extinction rates, immigration and time for diversification. An area with high species diversity may be the result of a high net diversification rate, multiple immigration events from adjacent regions, and a long time available for the accumulation of species (known as the 'time-for-speciation effect'). Here, we examine the relative importance of the three aforementioned processes in shaping the geographical diversity patterns of a large radiation of passerine birds.

Location: Global.

Taxon: Babblers (Aves: Passeriformes).

Methods: Using a comprehensive phylogeny of extant species (~90% sampled) and distributions of the world's babblers, we reconstructed their biogeographical history and analysed the diversification dynamics. We examined how species richness correlates with the timing of regional colonization, the number of immigration events and the rate of speciation within all 13 geographical distribution regions.

Results: We found that babblers likely originated in the Sino-Himalayan Mountains (SHM) in the early Miocene, suggesting a long time for diversification and species accumulation within the SHM. Regression analyses showed the regional diversity of babblers can be well explained by the timing of the first colonization within of these areas, while differences in rates of speciation or immigration have far weaker effects. Nonetheless, the rapid speciation of *Zosterops* during the Pleistocene has accounted for the increased diversification and accumulation of species in the oceanic islands.

Main Conclusions: Our results suggest that the global diversity patterns of babblers have predominantly been shaped by the time-for-speciation effect. Our findings also support an origin centred in tropical and subtropical parts of the SHM, with a cradle of recent diversification in the oceanic islands of the Indo-Pacific and Indian Ocean regions, which provides new insights into the generation of global biodiversity hotspots.

Tianlong Cai and Shimiao Shao have contributed equally.

KEYWORDS

biogeography, dispersal, diversification rate, explosive radiation, oceanic islands, Sino-Himalayan Mountains, time-for-speciation effect

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1 | INTRODUCTION

Species richness patterns vary widely across the earth's surface, and understanding the mechanisms underlying this pattern has remained a challenge for biologists and biogeographers since the early 19th century. In general, areas with the highest species richness are mainly restricted to tropical and subtropical moist forests, for example, the tropical Amazon and Andes, the Afrotropical Region, the Indo-Pacific Region and the Sino-Himalayan Mountains (SHM) (Fjelds , Bowie, & Rahbek, 2012; Francis & Currie, 2003; Rahbek & Graves, 2001). The uneven distribution of global biodiversity has been extensively analysed in plant and vertebrate study systems, and it has been shown that climatic and topographic variables explain 60%–80% of the variance in these patterns (Francis & Currie, 2003; Rahbek & Graves, 2001). However, correlations of this nature do not explain how richness was generated over time, as this requires congruent analysis of distributional and phylogenetic data (Wiens & Donoghue, 2004). From an evolutionary perspective, areas that maintain large numbers of species may result from high rates of net diversification rates (speciation minus extinction rates; the 'diversification rate hypothesis') (Rohde, 1992; Mittelbach et al., 2007) and/or immigration from adjacent regions (the 'multiple immigration hypothesis') (Johansson et al., 2007; MacArthur & Wilson, 2001; P ckert et al., 2012; Chazot et al., 2016). If speciation, extinction and immigration rates are generally constant across time and space, the number of species in a region could also be regulated by the amount of time that taxa have been present ('time-for-speciation effect') (Jetz & Fine, 2012; Stephens & Wiens, 2003).

The diversification rate hypothesis focuses on how speciation and extinction rates may differ between regions (Stenseth, 1984). For example, high speciation rates ('evolutionary cradle') and/or low extinction rates ('evolutionary museum') (Stebbins, 1974; Stenseth, 1984) can lead to rapid accumulation of species within a region. The multiple immigration hypothesis emphasizes dispersal and the influence of repeated immigration for the accumulation of lineages within assemblages that may subsequently radiate (Chazot et al., 2016; Johansson et al., 2007; MacArthur & Wilson, 2001; P ckert et al., 2012). According to this hypothesis, areas with high rates of immigration generally have available ecological opportunities and/or stable climates, providing more niches for diversification and refuges for escaping the negative consequences of climatic changes (Fjelds  et al., 2012; Price et al., 2014; Hoorn, Perrigo, & Antonelli, 2018). Lastly, the time-for-speciation effect predicts that species-rich regions represent ancestral areas, or those that were colonized by lineages early in their history, have more time for speciation and species accumulation (Jetz & Fine, 2012; Stephens & Wiens, 2003). The different processes that enable the build-up of species diversity hotspots are not mutually

exclusive, and potentially act in concert. However, few studies (e.g., Cai et al., 2018; Chazot et al., 2016) have integrated all processes to explain diversity patterns on a large scale, in part due to the lack of comprehensive phylogenies available for widely distributed groups.

'Babblers' (Aves: Passeriformes) provide an ideal system for testing hypotheses on the processes leading to the build-up of diversity. It is a large group comprising seven families (Cai et al., 2019), representing 7% of global passerine birds species, which are mainly associated with the understorey of evergreen forest or thicket habitats, although especially *Zosterops* also occur within the canopy. The highest diversity of babblers is found in the SHM, with lower diversity in other parts of the world (Figure 1). The heightened species diversity of babblers in the SHM could be generated through three processes. First, accelerated allopatric speciation related to the formation of landscape barriers due to mountain building, as has been suggested to be the main driver of the high diversity in the SHM in plants (Wen, Zhang, Nie, Zhong, & Sun, 2014; Xing & Ree, 2017) and birds (Qu et al., 2014; Wu et al., 2014; Liu et al., 2016). Under this scenario, diversification rates should be higher in the SHM than in other regions because of the extensive uplift of the SHM due to the formation of the Qinghai-Tibetan Plateau (QTP), which is particularly notable in the past 5–10 million years (Favre et al., 2015). Second, the diversity of babblers in the SHM may be the result of multiple immigration events from adjacent regions followed by subsequent allopatric diversification. This scenario has been postulated as a major driver for the build-up of diversity patterns of birds in the Himalayas (Cai et al., 2018; Johansson et al., 2007; P ckert et al., 2012), although Price et al. (2014) concluded that colonization along the Himalayas is currently limited due to competitive exclusion. Immigration into the SHM could also be facilitated by the ecological opportunities generated by mountain building and subsequent climate fluctuation during the past 10 million years (Favre et al., 2015). If true, immigration rates would be higher from adjacent regions into the SHM than in the opposite direction. Third, the higher diversity of babblers in the SHM than in other regions might be the result of longer periods of time for diversification and accumulation of species in the SHM than elsewhere. Under this scenario, it can be predicted that babblers first originated in the SHM and subsequently colonized other regions (Fjelds , 2013). Taken together, the lower diversity of babblers outside the SHM could be due to lower diversification rate, limited immigration and shorter evolutionary time for diversification.

In this study, we aim to evaluate the role of evolutionary time, diversification rates and immigration on shaping the geographical distribution patterns of babbler diversity. To achieve this, we used a near-complete, time calibrated phylogeny and distribution maps of

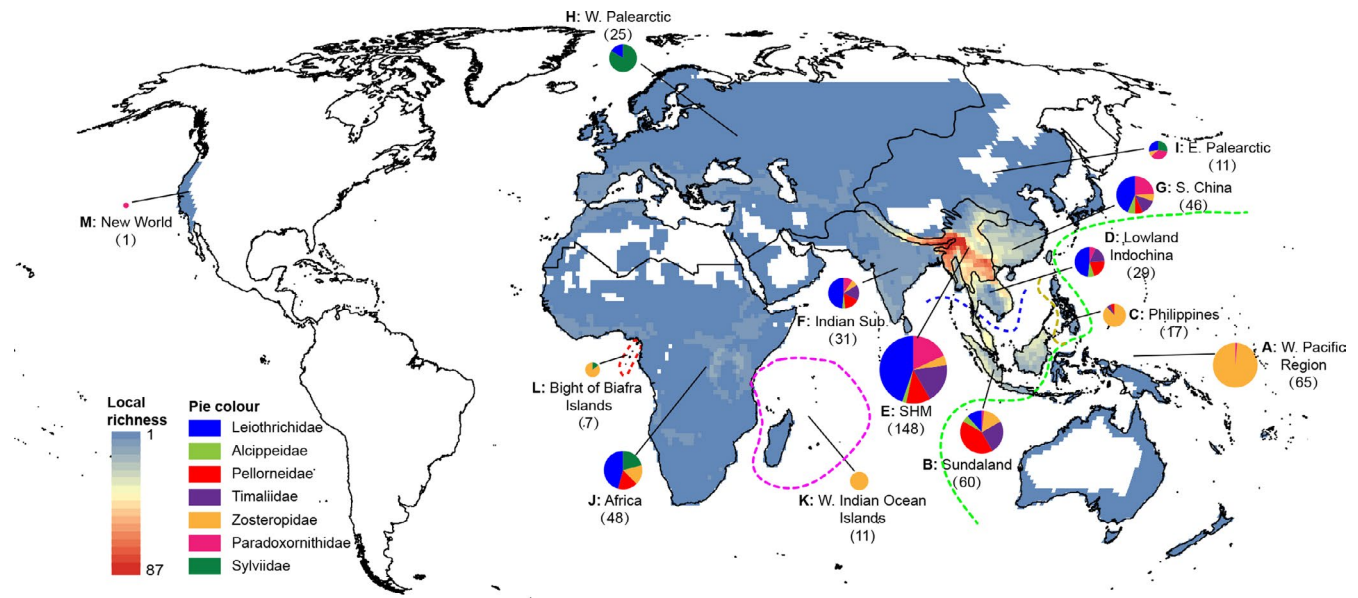


FIGURE 1 Global species richness map of babblers. Grid cells ($0.5^\circ \times 0.5^\circ$) with red colours have a higher richness, whereas blue colours indicate lower richness. Pie charts show regional richness in the 13 geographical regions. The sizes of pies are proportional to the number of species. The seven families of babblers are indicated by different colours. Species distributions are from BirdLife International & Handbook of the Birds of the World (2016)

the world's babblers as a basis for inferring ancestral geographical areas. Based on the results of this analysis, we estimated the timing of the first colonization and the number of immigration events in each region. We then examined diversification dynamics through time and among regions. Lastly, we compared the relative predictive power of evolutionary time, speciation rate and the number of immigration events upon explaining the regional species diversity of babblers.

2 | MATERIALS AND METHODS

2.1 | Taxonomy and phylogeny

We used the taxonomy and phylogeny of babblers generated by Cai et al. (2019), based on 402 ingroup and 108 outgroup taxa (106 proposed closest relatives of the group), inferred from 12 genes. The phylogeny strongly supported seven families (Sylviidae, Paradoxornithidae, Zosteropidae, Timaliidae, Pellorneidae, Leiothrichidae and Alcippeidae) and 64 genera within the babblers. According to these results, babblers split from their closest relatives in the early Miocene (Figure S1.1, see Appendix S1).

2.2 | Distribution maps and species richness

The species distribution maps used in this study were downloaded from BirdLife International and Handbook of the Birds of the World (2016). We manually checked and adjusted the distributions based on occurrence points from online databases, primary literatures

and museum collections (see Appendix S2). We only used breeding ranges in our analyses. To estimate richness patterns, we divided our study area into grid cells with a spatial resolution of 0.5 geographical degrees. By overlaying all the range maps, we summed the number of species in each grid cell. If a species range overlapped <50% of the area of a grid, we defined this species as absent from that grid. We also estimated the regional richness in 13 geographical regions (A–M; Figure 1). These geographical regions were identified loosely follow the classic biogeographical realms, zoogeographical boundaries and areas of montane forest (details and references see Appendix S2).

2.3 | Inferring ancestral areas

We used the package 'BioGeoBEARS', version 1.1.2 (Matzke, 2014) in R 3.6.0 (R Core Team, 2019) to infer ancestral geographical ranges based on an analysis of the 13 regions defined (Figure 1). Species were assigned to one or more of these geographical regions according to their breeding distributions. For some species whose distributions spanned two or more regions, a regional assignment was made only for the regions that covered >25% of the species' total range. We included the majority of the closely related outgroup taxa in the analyses to improve the accuracy by which the area of the most recent common ancestor of babblers could be determined. The model parameters and ancestral state probabilities at each node were estimated using BioGeoBEARS (Matzke, 2014). In addition to three primary models implemented in BioGeoBEARS (DEC, DIVA and BayArea), we included an additional parameter to each model (DEC+j, DIVA+j and BayArea+j),



which allowed for 'founder event' speciation (Matzke, 2014). We did not choose the best-fitting model based on the likelihood and Akaike Information Criterion (AIC) values due to conceptual and statistical problems suggested by a recent study (Ree & Sanmartín, 2018). Instead, we estimate whether the model fit the data by taking the geographical traits of tips into consideration. For babblers, some lineages (especially white-eyes) are endemic in islands (del Hoyo, Elliott & Christie, 2007), in which new lineages could be directly established by colonizations without intermediate existence of a widespread ancestor (Clark et al., 2008; Matzke, 2014). Thus, we preferred models with parameter 'j' to account for 'founder event' or 'jump dispersal' in the historical biogeographical analyses (Matzke, 2014). The results of these analyses were summarized by plotting the states with probabilities greater than 30% at each node.

2.4 | Analyses of diversification rate changes among lineages

We used BAMM v.2.5.0 (Rabosky, Donnellan, Grundler, & Lovette, 2014) to model speciation and extinction rates through time and how these rates varied among lineages. This method has recently been criticized for being overly sensitive to the prior on the 'number of shifts' (Moore, Höhna, May, Rannala, & Huelsenbeck, 2016). Thus, we evaluated the effect of this prior (1, 2, 5, 10, 20 and 50) on the posterior distribution of the shifts, but ultimately found this made little impact upon our final results (Figure S1.2 see Appendix S1). We used a prior value of 1 for the expected number of shifts in our results presented in the main text. Other prior variables were set using the 'setBAMMpriors' function in the BAMMtools package (Rabosky, Grundler, et al., 2014). We ran the analysis for 50 million generations, sampling the Markov chain Monte Carlo (MCMC) chain every 1,000 generations. We used the non-random incomplete taxa sampling method (Rabosky, Grundler, et al., 2014) to incorporate missing species into our analyses because almost half of the missing species belonged to Zosteropidae. The phylogenetic placement of the missing species was inferred using the taxonomic information provided in Cai et al. (2019). The first 25% of the generations from the BAMM output were discarded as a burn-in. The rate shift configurations on the phylogeny and the rate variation through time plots were summarized using 'BAMMtools' (Rabosky, Grundler, et al., 2014).

2.5 | Diversification rate changes among geographical regions

We used the regional lineage-through-time (LTT) plot to visualize the accumulation of lineages through time across the different geographical regions (Mahler, Revell, Glor, & Losos, 2010). In the regional LTT plots, the geographical state and lineage diversity at each node in the phylogeny were estimated using maximum likelihood ancestral reconstruction (Mahler et al., 2010). Then, the ancestral

states and log-transformed lineage diversity of each node were plotted against time, to allow a visualization of how lineages accumulate in each geographical region through time. Due to the ambiguity of the reconstructed states at the internal nodes when analysing the 13 regions, we reduced the total number of regions when analysed by merging different areas/regions as follows: (1) islands (A + C + K + L, and some archipelagos adjacent to Sundaland; Australia was merged into islands because Australia has only a single white-eye species); (2) the lowlands of Indochina-Sundaland (B + D); (3) the SHM (E); (4) the Indian subcontinent (F); (5) South China (G); (6) the Palearctic and North America (H + I + M) and (7) the mainland of sub-Saharan Africa (J).

To test whether rates of diversification and colonization differ between the SHM and other regions, we estimated speciation, extinction and dispersal rates among these areas using the Geographic State Speciation and Extinction (GeoSSE) model (Goldberg, Lancaster, & Ree, 2011). Species were classified into SHM/non-SHM based on their current breeding distributions. The GeoSSE model includes three parameters: speciation rate (s), extinction rate (x) and dispersal rate (d) for the SHM (s_A , x_A and d_A) or the non-SHM areas (s_B , x_B and d_B) and between two states (s_{AB} , x_{AB} and d_{AB}). We first tested a full model that allowed the seven parameters to vary freely. Then, we compared this full model with nine sub-models, where one or more parameters were set to be equal between the regions (Table S3.1 see Appendix S3). We used the AIC to select the best model. To account for model uncertainty, we also sampled the posterior probability (PP) distribution of the parameters for the best model using 10,000 generations of MCMC samples. These analyses were conducted in the R package 'diversitree' (FitzJohn, 2012).

2.6 | The influence of evolutionary time, immigration and speciation rate

To examine which factors predict the geographical diversity of babblers worldwide, we used univariate and multiple regressions to examine how regional richness correlate with the timing of first colonization, the number of immigration events and the speciation rate in the 13 geographical regions. The timing of the first colonization and the number of immigration events in each region were estimated using the ancestral states with the highest probability at each node inferred from the results of BioGeoBEARS (Matzke, 2014). The first colonization time in a given geographical region was defined as the crown age of the clade that first occupied that region following previous studies (Stephens & Wiens, 2003; Wiens, Pyron, & Moen, 2011). If only a single species was present within a region, we arbitrarily used half of the age from when the species split from its closest relative. A colonization event was identified if the descendant lineage was determined to be distributed in a new region, compared to its most recent common ancestor. For example, if the ancestral state of a lineage is A and one of its descendants presently occurs in AB, we can identify that a colonization event occurred to region B. The speciation rate in each region was estimated using the average tip rates of all

the species present estimated from BAMM (Rabosky, Grundler, et al., 2014). We did not use net diversification rate in this analysis because tip rates metrics are more reliable estimators of speciation rates than net diversification rates (Title & Rabosky, 2019).

3 | RESULTS

3.1 | Geographical patterns of species richness

The distribution of the species richness of babblers shows substantial geographical variation (Figure 1). Six families are represented in five of the regions: SHM (E), Sundaland (B), Indian Subcontinent (F), Lowland Indochina (D) and South China (G). In contrast, the West Pacific (A), Philippines (C), Western Palearctic (H), West Indian Ocean Islands (K), Bight of Biafra Islands (L) and New World (M) have only one to three families. Sylviidae is mainly distributed in the Palearctic (H, I) and Africa (J). Zosteropidae is the predominant group on oceanic islands, especially the Philippines, Western Pacific Region, Western Indian Ocean Islands and the Bight of Biafra Islands. The other babbler lineages are mostly distributed in the southeastern parts of Asia (B, D, E, F and G), with Leiothrichidae making up almost 50% of the diversity on the continental areas D, E, F and G, and in Africa. Pellorneidae is the most diverse group in Sundaland but also occurs from the Eastern Palearctic to Africa. The Paradoxornithidae are mainly distributed in the SHM and South China, but the group also includes the single North American (M) babbler species, whereas the Timaliidae is most diverse in the SHM and Sundaland. Regionally, the SHM has the highest overall species diversity (148 species). At the grid cell scale, babblers reach their highest species diversity in the SHM, particularly in the eastern Himalayas–western Yunnan (up to 87 species in a single grid cell).

3.2 | The biogeographical history of babblers

The biogeographical reconstruction analyses based on six models implemented in BioGeoBEARS (Matzke, 2014) show very similar patterns (Figure 2, and Figures S1.3–S1.7 in Appendix S1). Results from the DEC model suggest that the highest PP for the ancestral area of babblers was the SHM (PP = 55%), but ancestral babblers may also have been widespread in the SHM and the Western Palearctic (EH, PP = 35%). BayArea model found babblers likely originated in the SHM (PP = 0.45) or the SHM–Sundaland (BE, PP = 0.44). The remaining four models (DEC+j, DIVA, DIVA+j, BayArea+j) strongly supported (PP = 70%–99%) the SHM to be the ancestral areas of the group. Models accounting for jump dispersal events were generally favoured over those that did not (Table S3.2 in Appendix S3). Despite that recent results by Ree and Sanmartín (2018) revealed potential flaws with their implementation, it seems reasonable to take founder events speciation into account for some islands endemic lineages of babblers. Three models with founder events yield similar results. In

the following text, we present our results based on DIVA+j model which was largely in agreement with the estimations of ancestral ranges of the DEC+j and BayArea+j models.

The results suggest multiple dispersal events of babblers from the SHM to other regions (Figure S1.8 Appendix S1). The group first dispersed out of the SHM to the Western Palearctic in the early Miocene, with a subsequent split between the Sylviidae and Paradoxornithidae, and two independent dispersals to Africa within Sylviidae. Dispersals to South China, the Eastern Palearctic and North America also occurred among Paradoxornithidae, with the remaining taxa mainly diversifying within the SHM. Within Zosteropidae, the early splits took place in the SHM in the mid-Miocene, with dispersal to the Philippines sometime during the latter half of the Miocene. Colonization of Sundaland and the Western Indo-Pacific island regions also occurred in the late Miocene. Then, a long-distance dispersal led Zosteropidae to become distributed within the Western Indian Ocean islands, Africa's 'sky islands' and the Bight of Biafra Islands by the early Pleistocene. Regarding Timaliidae, there were several independent dispersal events to Sundaland, starting in the mid-Miocene, with several subsequent back-colonizations, as well as further dispersals to South China, Lowland Indochina, the Indian Subcontinent and the Philippines. Pellorneidae underwent dispersal to Sundaland during the early Miocene, with multiple back-colonizations of the Asian mainland, as well as a single dispersal to Africa, accompanied by subsequent diversification in these regions. The branch leading to Alcippeidae split from the remaining lineages in the early Miocene, but the extant species did not start to diversify until the late Miocene, again with the most likely ancestral distribution in the SHM, and subsequent colonization of other areas. Leiothrichidae diversified mainly within the SHM, with an early dispersal to Lowland Indochina in the mid-Miocene, and multiple subsequent colonizations of other areas including at least two independent dispersals to the Indian Subcontinent and two to Africa, resulting in the origination of the genera *Argya*, and *Turdoides*.

3.3 | Diversification dynamics among lineages

The results of the BAMM analysis strongly supported a single rate shift (Figure S1.2a see Appendix S1) on the branch leading to the clade that includes *Tephrozosterops* and *Zosterops* (Figure 3a, and Figure S1.9 see Appendix S1). The overall rate through time plot considering all babblers suggests an initially high rate of speciation that gradually decreased over time until the end of the Pliocene, followed by a marked increase at 2.5 Ma (Figure 3b). Analyses of each family separately indicated that this increased rate were associated solely with the radiation of Zosteropidae (Figure 3e), while all other families showed patterns of a gradual decline in the rate of speciation through time (Figure 3c,d,f–i). When we excluded *Zosterops* from these analyses (Figure 3j), we observed a significant decline in the background rate of speciation among all babblers towards the present (Figure 3k).

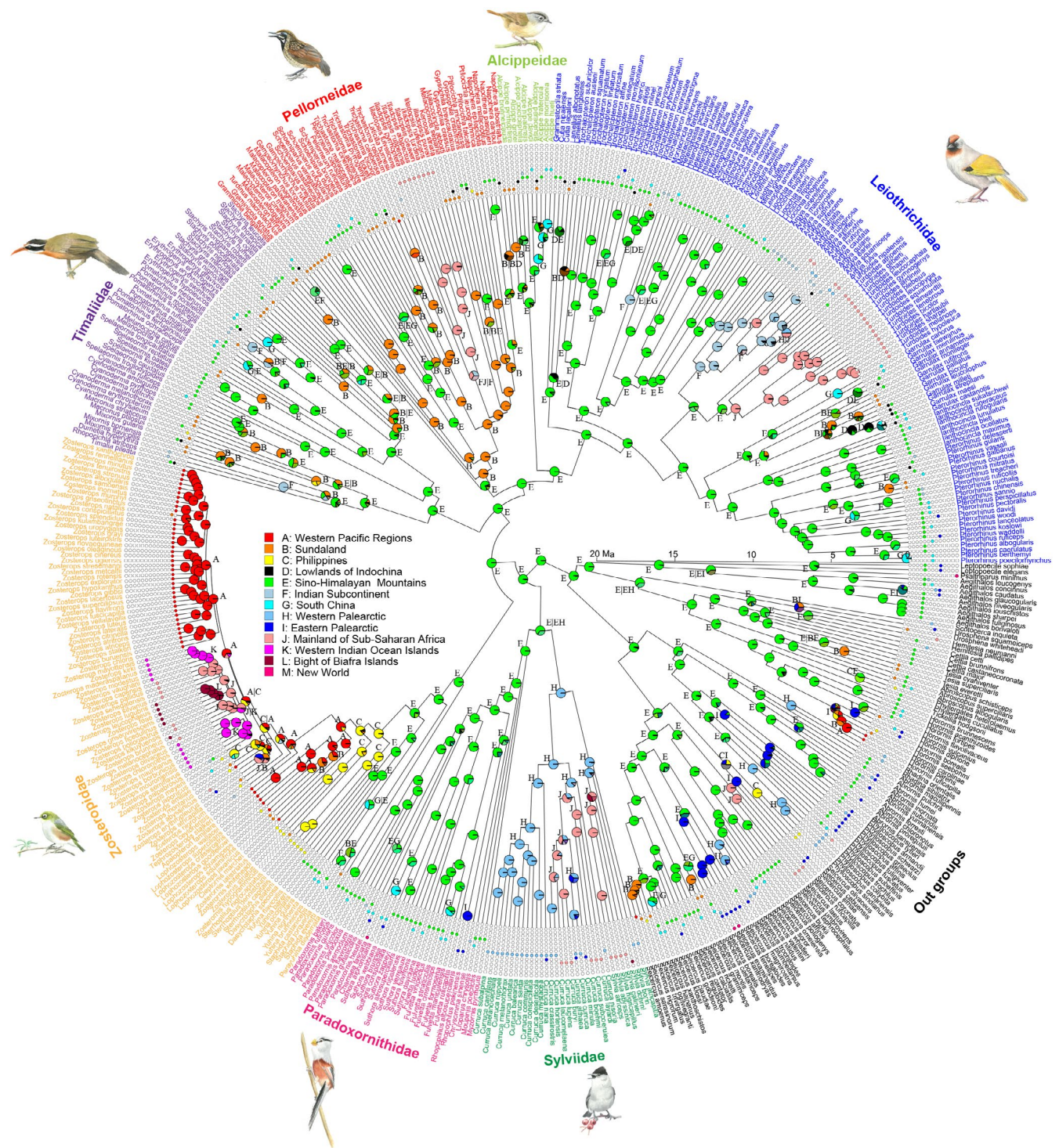


FIGURE 2 Ancestral reconstruction of babblers computed using the DIVA+j model in BioGeoBEARS (Matzke, 2014). The text and pie charts at the nodes indicate the ancestral regional states with probability greater than 30% (text in the left side of ‘|’ is state with the highest probability). Letters A–M correspond to the 13 geographical regions in Figure 1 and Table 1. Illustrations of birds by J.F.

3.4 | Diversification dynamics among geographical regions

The regional LTT plots revealed different patterns of lineage accumulation in mainlands and islands, and a longer presence in mainland areas compared to islands (Figure 4a). In mainland areas, rapid

cladogenesis first began in the SHM during the early Miocene, followed by a gradual slowdown in diversification rates towards the present. The lineages began to accumulate in non-SHM mainland areas later than in the SHM, following multiple dispersals from this area. The insular assemblages first began to accumulate species following the expansion of Zosteropidae to islands at the boundary of

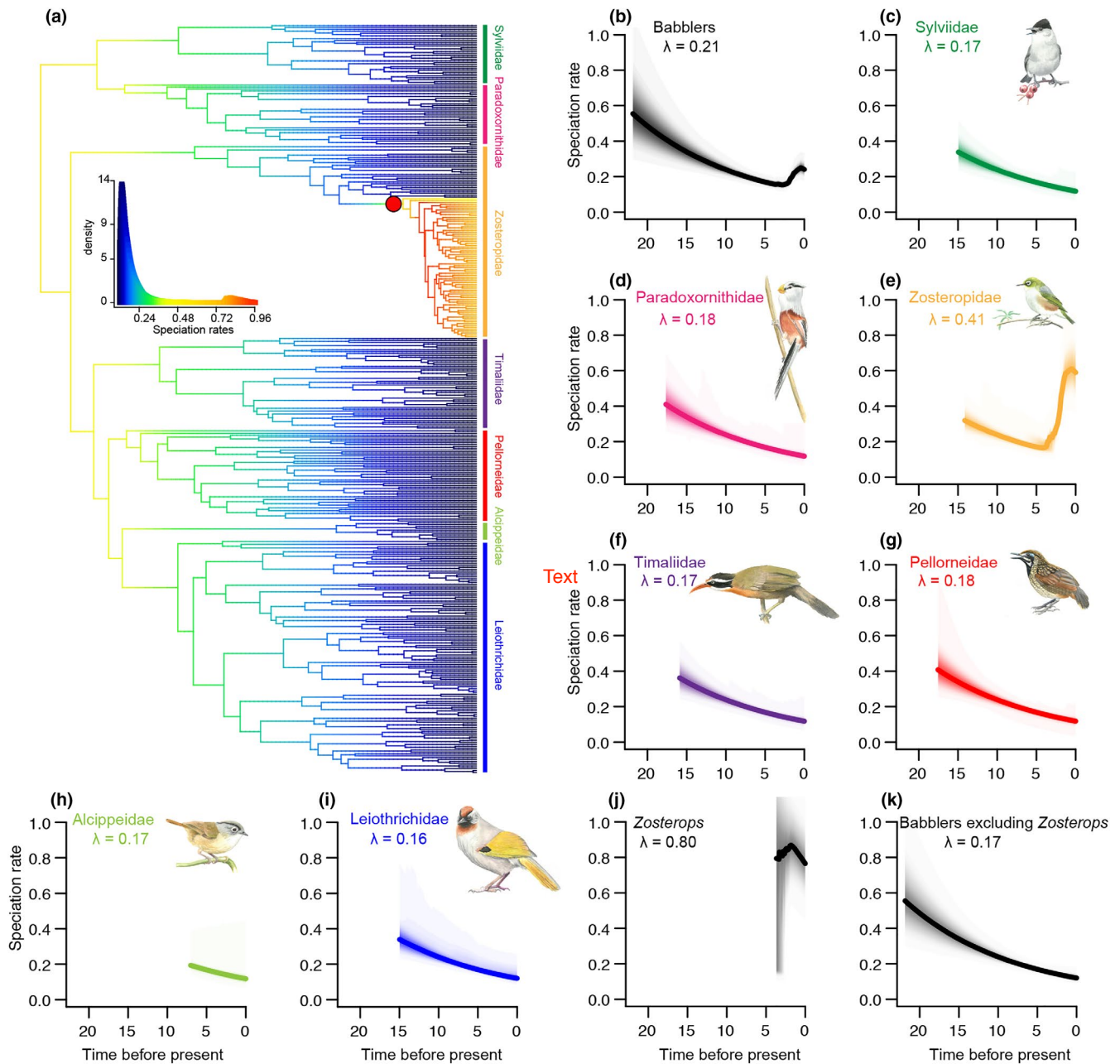


FIGURE 3 The BAMB phylo-rate plot and plots of the babblers' speciation rates over time. (a) BAMB phylo-rate plot showing speciation rates along each branch of babblers. Cool colours represent slow rates; warm colours represent fast rates. The red dot along the branch leading to the clade including genera *Tephrozosterops* and *Zosterops* shows the most likely position of an inferred rate shift. Speciation rates are shown for (b) all babblers, (c) Sylviidae, (d) Paradoxornithidae, (e) Zosteropidae, (f) Timaliidae, (g) Pellorneidae, (h) Alcippeidae, (i) Leiothrichidae, (j) genus *Zosterops*, (k) all babblers excluded genus *Zosterops*. Illustrations of birds by J.F.

the Pacific Region in the late Miocene. Initially, species accumulation in the islands increased at a constant rate, before a slight slow-down during the Pliocene and subsequently a rapid increase in the Pleistocene. The timing of this increase corresponds to a period of repeated global sea level changes (Figure 4b) (Miller et al., 2005).

The GeoSSE results showed that the equal extinction rate model ($x_A = x_B$, $s_A \neq s_B$, $d_A \neq d_B$) had the lowest AIC and can be considered the best-fitting model (Table S3.1 see Appendix S3). Therefore, we sampled the PP distribution of the parameters for this model

using MCMC. The results indicated significant variation in the diversification patterns between the different geographical regions (Figure 5). The non-SHM areas were characterized by higher speciation rates than the SHM. When the explosive radiation group of insular *Zosterops* was excluded from the analyses, the speciation rates showed no difference between the SHM and the non-SHM areas. Both analyses show that the immigration rates were significantly higher from the SHM to non-SHM areas, than in the reverse direction.

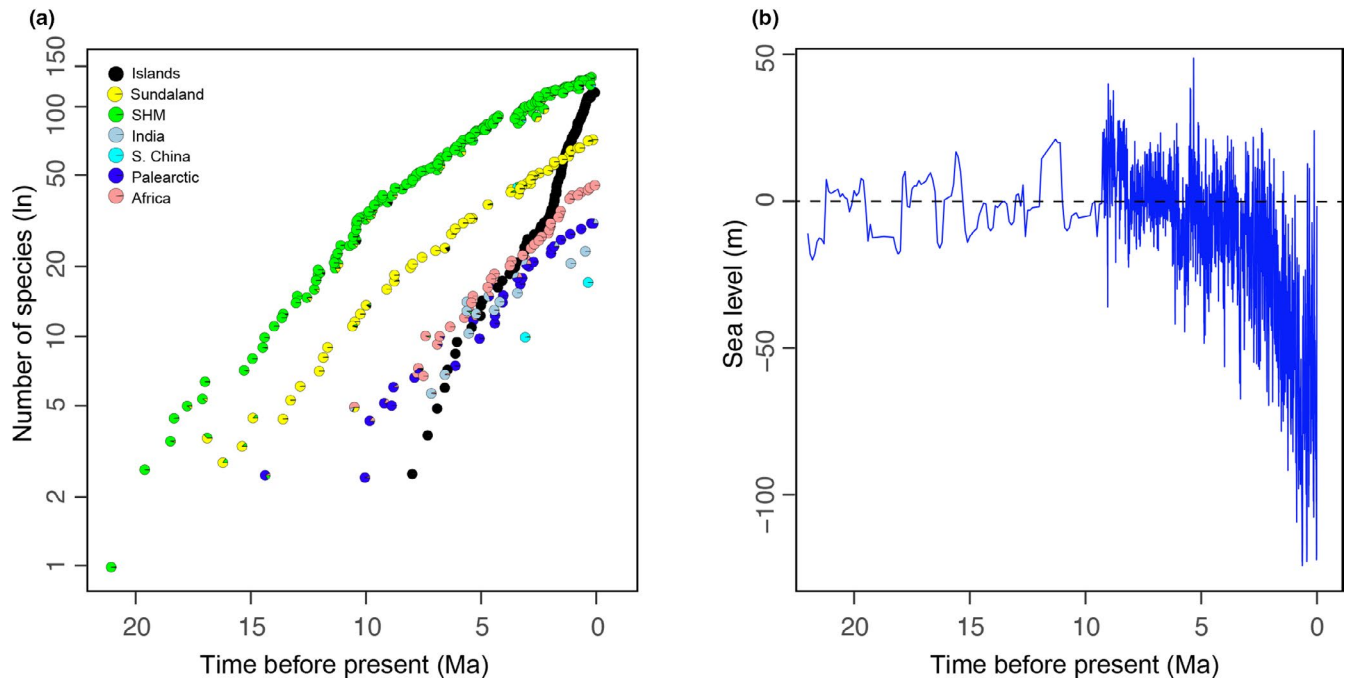


FIGURE 4 Regional lineage-through-time (LTT) plots show the lineage accumulation of babblers in seven geographical regions in the global scale (a) as well as the global sea level changes through time (b). Estimated global sea level was from Miller et al. (2005)

3.5 | Effects of evolutionary time, immigration and speciation rate

Table 1 shows the regional species richness, the time of the first colonization, the number of immigration events and the average speciation rate in the 13 major geographical regions. The results of the univariate regressions indicate that the regional species richness could be well explained by the first time of colonization (Figure 6a; $r^2 = .36$; $p < .05$). In contrast, richness was not significantly related to the number of immigration events (Figure 6b; $r^2 = .30$; $p = .06$) or the speciation rate (Figure 6c; $r^2 = 0$; $p = .97$). These results remain robust after a single outlier (region M) is removed from this analysis (evolutionary time: $r^2 = .59$, $p < .01$; immigration events: $r^2 = .11$, $p = .24$; speciation rate: $r^2 = .17$, $p = .18$). The multiple regressions suggest that the three predictors can together explain 76% of the variance in regional richness (Figure 6d). However, the explanatory power is predominantly driven by the timing of the first regional colonization because the number of immigration events and the average speciation rate were not significant in these models.

4 | DISCUSSION

In this study, we used phylogenetic comparative methods to understand the drivers of babblers diversity at the global scale. Our results revealed that the timing of the first regional colonization was the major factor in explaining regional richness. The high diversity of babblers in the SHM was better explained by the long time available for the accumulation of species in this region since the early Miocene, rather than by high speciation rates or repeated immigrations.

4.1 | The origin and dispersal of babblers

The biogeographical history of babblers has not been comprehensively examined by previous studies, some of which have focused on only one lineage among them, such as laughingthrushes (Luo, Qu, Han, Li, & Lei, 2009; Päckert et al., 2012), parrotbills (Liu et al., 2016) and the Old World warblers (Voelker & Light, 2011). However, there remains a lack of consensus with regards to the geographical origin of babblers. With the first comprehensive sampling of babblers including 183 species, Moyle, Andersen, Oliveros, Steinheimer, and Reddy (2012) suggested an origin in mainland Asia for most babbler lineages (Sylviidae and Paradoxornithidae not included). Our ancestral state reconstructions based on a near-complete phylogeny indicate that babblers most likely originated in the SHM in the early Miocene, as already suggested by Fjeldså (2013).

After their origination, the early radiation of babblers was characterized by in situ diversification and formation of six major lineages within the SHM in the early to mid-Miocene. During this period, the southern parts of the QTP likely reached an elevation comparable to that of the present day, resulting in the formation of the Asian monsoon and a diverse set of habitats within the SHM (Favre et al., 2015; Miao, Herrmann, Wu, Yan, & Yang, 2012). The ancestor of babblers presumably acquired ecological and behavioural adaptations to different habitats and climate regimes, followed by differentiation in niches along elevational gradients in the Sino-Himalayas and subsequent colonization throughout south-eastern Asia and elsewhere (Päckert et al., 2012). This dispersal pattern has not been reported in earlier studies of birds in this region. For example, pheasants (Cai et al., 2018), leaf warblers (Johansson et al.,

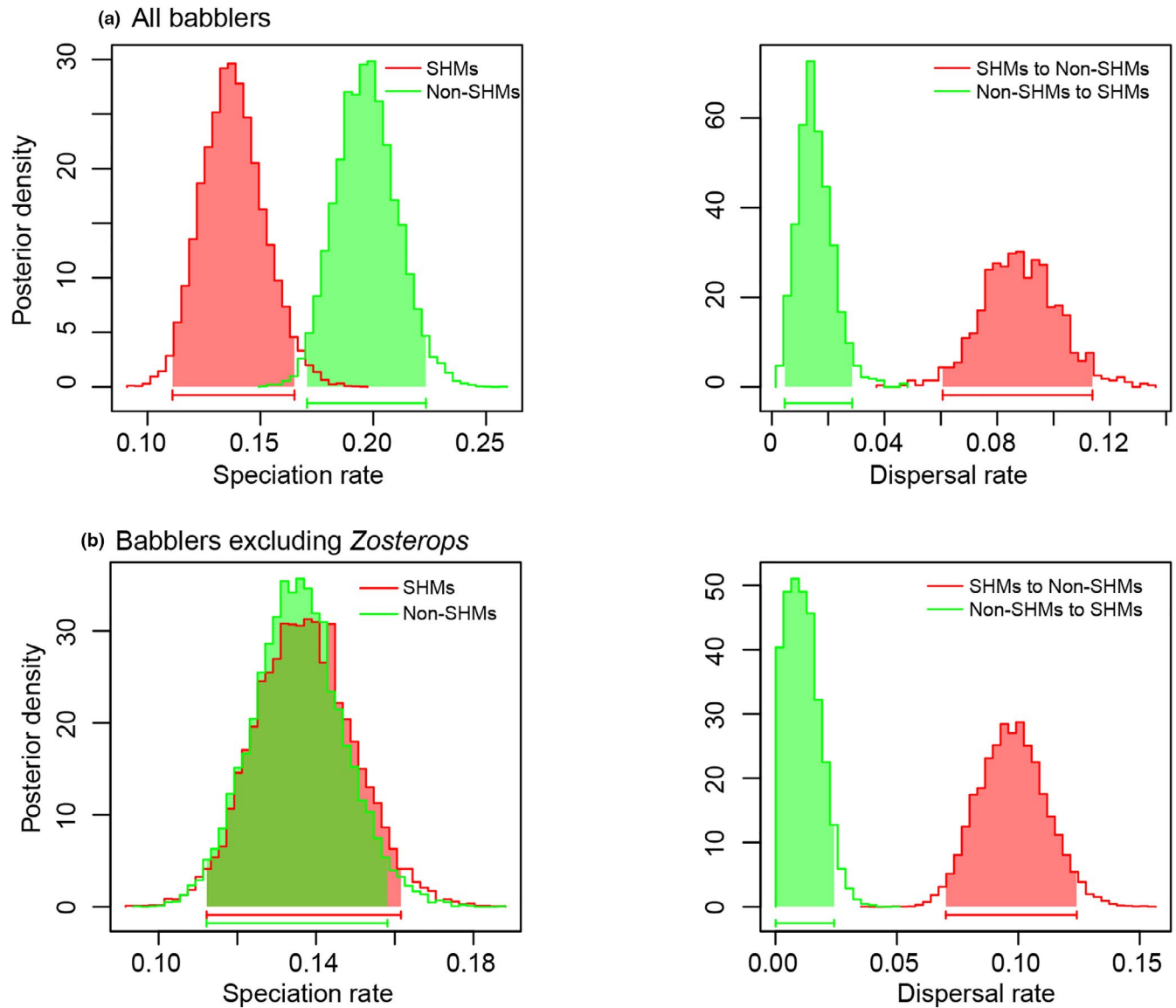


FIGURE 5 The speciation and dispersal rates in the Sino-Himalayan Mountains (the SHM) versus the non-SHM for (a) all babblers and (b) babblers excluding *Zosterops*. The probability density plots are based on 10,000 Markov chain Monte Carlo (MCMC) samples of the equal extinction rate model under Geographic State Speciation and Extinction (GeosSE)

2007) and long-tailed tits (Päckert et al., 2012) are all suggested to have had origins outside of the SHM before colonizing the region. Moreover, Price et al. (2014) concluded, based on a study of all 358 species of songbirds that occur in the eastern Himalayas, that this community 'has been assembled largely by immigration from outside, with ecological differences either generated in situ, or before invasion'.

4.2 | The role of evolutionary time

Our results suggest that the species richness within each major region is correlated with the timing of their first colonization, in agreement with the predictions of the time-for-speciation effect (Stephens & Wiens, 2003). This hypothesis has been suggested to

explain latitudinal and elevational gradients in species richness, especially for reptiles and amphibians (Jetz & Fine, 2012; Stephens & Wiens, 2003; Wiens et al., 2011). Our support for the time-for-speciation effect for shaping the geographical diversity of babblers in the SHM is unsurprising because the region is considered a relatively old mountain region and can provide suitable habitats for the ancestor of babblers. The QTP was formed by the collision of the Indian and Eurasian plates 50–55 Ma and probably reached a height of 4,000 m by 40 Ma (Favre et al., 2015). The uplift of the QTP and the resulting formation of the Asian Monsoon created a warm and wet climate in the southern and eastern margins of the QTP (e.g. SHM) (Favre et al., 2015). This region was characterized by a stable climate (Deng, Li, Vasconcelos, Cohen, & Kusky, 2014; Favre et al., 2015) as many of the deep valleys along the margins of the large highlands would be places of atmospheric inversions, where cold air would sink down

TABLE 1 Properties of the 13 regions including the number of colonization events, the timing of the first colonization, overall species richness and average speciation rate for the babblers in the global scale

Label	Region	Overall species richness	Number of colonization events	Time for the first colonization (Ma)	Speciation rate
A	W. Pacific	65	5	6.88	0.78
B	Sundaland	60	21	16.84	0.19
C	Philippines	17	6	8.34	0.28
D	Lowland of Indochina	29	17	4.94	0.24
E	SHM	148	16	21.86	0.22
F	Indian Subcontinent	31	15	10.94	0.24
G	South China	46	35	4.44	0.27
H	W. Palearctic	25	6	14.95	0.25
I	E. Palearctic	11	10	0.30	0.25
J	Africa	48	8	10.94	0.36
K	W. Indian Ocean Islands	11	2	1.96	0.88
L	Bight of Biafra Islands	7	3	1.18	0.80
M	New World	1	1	5.78	0.08

into the valleys at night, creating distinct mist zones that would maintain high humidity and cloud forest (Fjelds  et al., 2012). It has been suggested that part of northern Indochina has been covered by broadleaf forests since the Miocene (Deng et al., 2014), which would provide suitable habitats for subalpine taxa. Within babblers, three of the families contain species in monospecific genera that are endemic to the SHM (*Myzornis pyrrhous*, *Moupinia poecilotis*, *Lioparus chrysotis*, *Parayuhina diademata* and *Grammatoptila striata*), and whose origins can be traced back to the early/mid-Miocene (12.5–18 Ma) (Figure 2). Accordingly, it seems that the SHM allowed species accumulation over much longer periods in comparison to climatically unstable regions in boreal and lowland areas. Of course, we also need to consider the birth–death processes if the time-for-speciation effect is truly responsible for the high species richness in the SHM. Under the constant birth–death model, if the speciation rate is greater than the extinction rate, the number of species is expected to grow exponentially through time. In that sense, applied to a specific geographical area the expectations are similar to the time-for-speciation hypothesis. However, if extinction rates are higher than speciation, there will be a decline in the number of overall species through time in the birth–death model.

4.3 | The role of repeated colonization

We found that the non-SHM regions with high diversity were colonized repeatedly, followed by significant in situ diversification, particularly in the lowlands of Indochina, South China, Sundaland and India. In these instances, species diversity has mainly accumulated following multiple immigrations from the SHM (Table 1). In addition, some African and Western Palearctic lineages were established by long-distance immigrations from Southeast Asia, such as the genera *Curruca*, *Sylvia*, *Illadopsis*, *Turdoides* and *Zosterops* (Figure 2). The

important role of colonizing new geographical areas for subsequent diversification has been demonstrated in several recent studies (Johansson et al., 2007; P ckert et al., 2012; Liu et al., 2016; Cai et al., 2018; Chazot et al., 2016; but see Kennedy et al., 2017). It has been suggested that the high diversity in tropical and subtropical mountains has been shaped mainly by the immigration of species from adjacent lowlands or more northern areas (Hoorn et al., 2018). Several studies on birds within the SHM have also suggested the critical role of immigration in the build-up of diversity hotspots (Cai et al., 2018; Johansson et al., 2007; Liu et al., 2016; P ckert et al., 2012; Price et al., 2014). However, our study suggests that the diversity of babblers in the SHM was not predominantly caused by immigration events because the GeoSSE analysis also indicated that the immigration rate was higher from the SHM to non-SHM areas than the reverse scenario (Figure 5). This was further supported by the results of the linear regressions, which suggests that regional species richness is not well explained by the number of colonization events (Figure 6b).

4.4 | The role of diversification rate variation

The results suggest that regional species richness is not correlated with the mean speciation rate of the species present in these areas (Figure 6). Our lack of support for the diversification rate hypothesis is somewhat unexpected given that many studies have suggested that the SHM have played a central role in the build-up of species diversity (Cai et al., 2018; Liu et al., 2016; Wen et al., 2014; Xing & Ree, 2017), such that this region functioned both as a cradle of diversification and as a museum where old lineages could accumulate. These double roles may reflect the topographic complexity of the montane region, with ecological stratification and environmental heterogeneity, promoting vicariance while also

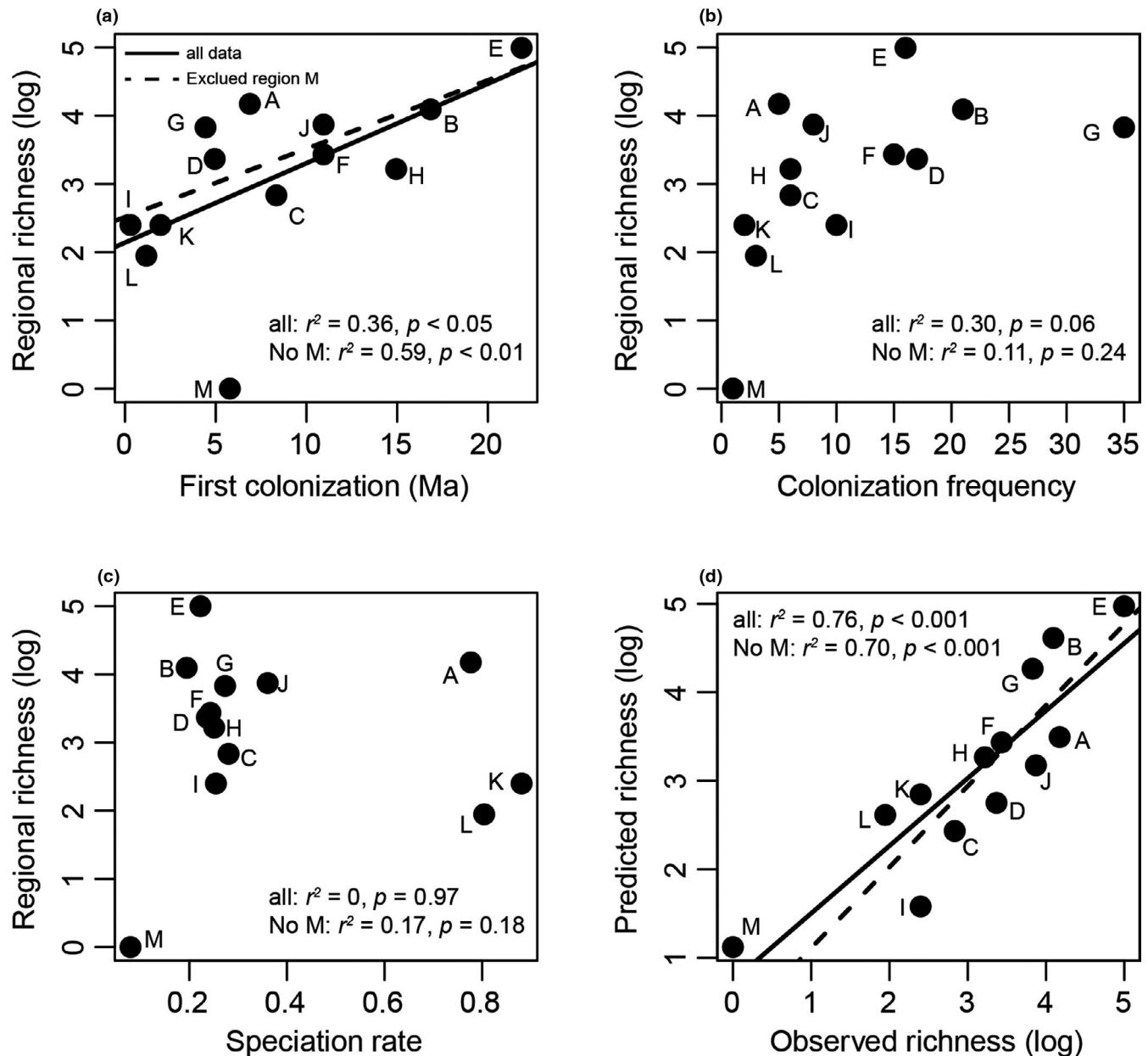


FIGURE 6 The relationship between regional species richness and (a) the timing of first regional colonization, (b) the number of colonization events and (c) the speciation rate for babblers in the global scale. The relationship between the observed richness and predicted richness which was estimated by the first colonization time, the number of colonization events and speciation rate in the multiple regressions (d). Letters A–M correspond to the 13 geographical regions listed in Figures 1 and 2 and Table 1

maintaining multiple niches in the distinct ecological zones (Favre et al., 2015; Fjeldsø et al., 2012). Although the western and southern areas of the QTP reached their current elevations by the mid-Miocene, it is generally believed that its south eastern marginal regions (e.g. Hengduan Mountains) underwent dramatic uplift from approximately 10 Ma to present (Favre et al., 2015). Physical barriers and climatic fluctuations are likely to have contributed to allopatric or parapatric speciation by facilitating geographical isolation and restricting gene flow among populations, promoting the radiation of SHM lineages (Qu et al., 2014; Xing & Ree, 2017). However, the regional LTT plots and diversification dynamic analyses suggest that diversification rates gradually decreased towards

the present for the major lineages in the SHM. Recent studies of passerine birds in the SHM have also suggested a gradual slow-down in diversification rates (Kennedy et al., 2012; Liu et al., 2016; Price et al., 2014), and Price et al. (2014) and Kennedy et al. (2012) concluded, based on an analysis of all Himalayan songbirds, that competition for niche space limits species accumulation, and ecological competition for resources ultimately constrains speciation rates.

As the previous studies mentioned (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012; Moyle, Filardi, Smith, & Diamond, 2009), we found the accelerated speciation of Zosteropidae in the Pleistocene drive the rapid accumulation of species on oceanic islands. Many previous

studies have documented cases of increased rates of diversification among animals and plants on oceanic islands during the Pleistocene (Moyle et al., 2009; Irestedt et al., 2013; Andersen, McCullough, Mauck, Smith, & Moyle, 2018), indicating similar evolutionary causes. Due to the lack of major eco-morphological differences among most of the species of Zosteropidae (del Hoyo et al., 2007), we reject adaptive radiation as an explanation for their high speciation rates (Mayr & Diamond, 2001; Moyle et al., 2009). Most members of *Zosterops* are endemic to small islands, and we therefore speculate that peripatric isolation during expansion across island chains is the main driver of their rapid diversification (Mayr & Diamond, 2001; Sheldon, Lim, & Moyle, 2015). We found that the period of rapid diversification of Zosteropidae coincides with a period of repeated sea level fluctuations in the late Pliocene–Pleistocene. During this period, global sea levels drastically and repeatedly changed as a consequence of global cooling and warming throughout glacial cycles (Zachos, Pagani, Sloan, Thomas, & Billups, 2001), resulting in the sea level being at least 100 m below today's level during the glacial maxima (Miller et al., 2005; figure 4b). Lowering of sea levels would lead to exposure of extensive new areas of flat lowland habitats where mangroves and coastal forest vegetation would rapidly spread, providing an ideal habitat for social and dispersive birds such as *Zosterops* (Figure S1.10 see Appendix S1) (Mayr & Diamond, 2001; Sheldon et al., 2015).

Lineage-specific life-history traits (e.g. rapid evolutionary shifts in dispersal ability) might have promoted the rapid speciation of Zosteropidae (Moyle et al., 2009). The strong dispersal ability of *Zosterops* has been shown by previous studies documenting dispersal over 300–1500 km from the source population during the past 2–3 centuries (Clegg et al., 2002; Diamond, Pimm, Gilpin, & LeCroy, 1989). An increased dispersal capacity could have been aided by evolutionary changes in habitat preference, as the phylogenetically isolated yuhinas lineages are birds preferring montane bamboo and thicket vegetation, while in *Zosterops*, there was a shift to the canopies of lowland forests (which was not paralleled by other babbler families) (del Hoyo et al., 2007). As social living canopy birds with high vagility, Zosteropidae could successfully colonize new areas by group dispersal from the mainland or nearby large islands, and establish populations (Mayr & Diamond, 2001). Once a new habitat was successfully occupied, *Zosterops* lineages appear to reduce their dispersal ability considerably, as indicated by the strong population structure at small spatial scales (Bertrand et al., 2014). Subsequent sea level rises accompanied the evolutionary losses of dispersal ability (Mayr & Diamond, 2001; Moyle et al., 2009) led local populations to become isolated as single-island endemics, mostly inhabiting montane forests. In addition, the short generation time, indicated by the higher rates of substitutions and gene duplication than found in other birds (Cornetti et al., 2015), could also facilitate the rapid speciation of *Zosterops*. Together, we hypothesize these processes caused rapid speciation with a fourfold higher rate of speciation in *Zosterops* compared to other babblers.

In conclusion, our results indicate that babblers likely originated in the SHM in the early Miocene, and gradually built up high

species diversity in this region. The timing of the first colonization is a strong predictor of the regional richness within these regions, while the explanatory power of immigrations and speciation rate are relatively weak. Thus, the global diversity patterns of babblers appear to be predominantly regulated by the evolutionary time in each major region. Nonetheless, repeated sea level changes during the Pleistocene probably led to intensive speciation in the dispersive and canopy-dwelling genus *Zosterops* which is known as a 'great speciator' on the oceanic archipelagos. This study underlines that tropical and subtropical mountains (e.g. SHM) may act as a role of origin centre to accumulate higher species richness, while oceanic islands promote rapid speciation among passerine birds.

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DATA AVAILABILITY STATEMENT

A near-complete phylogeny with divergence times of babblers is available from the Dryad Digital Repository (DOI: <https://doi.org/10.5061/dryad.905qfttgp>). All species distribution maps can be freely downloaded from BirdLife International (<http://www.birdlife.org>). You can download the latest version because the range maps of babblers are not updated in recent.

ORCID

Per Alström  <https://orcid.org/0000-0001-7182-2763>

Fumin Lei  <https://orcid.org/0000-0001-9920-8167>

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BIOSKETCHES

Tianlong Cai studies the macroecology and biogeography of birds, and the mechanisms that shape species richness gradients in mountains.

Shimiao Shao is interested in macroevolution. Her work focuses on patterns of lineage diversification and phenotypic evolution and how these processes influence one other.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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