RESEARCH PAPER

Understanding historical and current patterns of species richness of babblers along a 5000-m subtropical elevational gradient

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ABSTRACT

Aim To understand the causes of historical and current elevational richness patterns of Leiothrichinae babblers, a diverse and mostly endemic group of birds.

Location A 5000-m elevational gradient in the Hengduan Mountains, China.

Methods By means of a dated phylogenetic tree and reconstructed ancestral states, we estimated elevation-specific diversification rate, applied a new method to estimate colonization frequency and age and, for the first time, modelled historical species richness patterns that take account of temporal patterns of palaeo-temperature. As explanations for current richness patterns, we assessed area, geometric constraints, temperature, precipitation, seasonality and productivity.

Results The current elevational pattern of species richness is a hump-shaped curve with a peak at about 1000–2500 m. The reconstructed palaeopatterns of species richness suggest that babblers, as a clade, first occupied the Hengduan Mountains at low to mid-elevations, although the method of ancestral state reconstruction cannot conclusively reject origins outside the current elevational distribution of the group. Diversification rates varied little along the elevational gradient, and thus cannot explain the richness pattern, but historical colonization frequency and colonization age were highly correlated with present-day species richness. Seasonality and productivity had greater power than area and geometric constraints in explaining the present-day richness pattern of babblers along the elevational gradient.

Conclusions Historical and modern factors have both played important roles in shaping species richness patterns. Reconstructed historical richness patterns suggest that babblers first diversified in the Hengduan Mountains at low to mid elevations, but richness patterns almost certainly shifted substantially under changing climates of the past 10 Myr. The current richness patterns of babblers are associated with seasonality and productivity, but they are also a product of historical evolutionary and ecological dynamics. The methods we introduce for assessing historical colonization rates and past patterns of richness offer promise for understanding other elevational richness gradients.

Keywords

Biogeographical reconstruction, colonization age, colonization frequency, diversification rate, geometric constraints, Hengduan Mountains, historical biogeography, Leiothrichinae, niche conservatism, productivity.

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INTRODUCTION

Like the latitudinal gradient in species richness, elevational gradients in richness are globally ubiquitous but occur at a much smaller spatial scale at a vastly greater level of natural replication and vary more widely in pattern (Lomolino, 2001; Rahbek, 2005; McCain, 2009; Wu *et al.*, 2013b). For these reasons, a growing body of research is focusing on the utility of elevational gradients as tools for uncovering the mechanisms and constraints that shape both patterns of biodiversity and the functioning of ecosystems (Lomolino, 2001; Rahbek, 2005; Nogues-Bravo *et al.*, 2008; McCain, 2009; Kozak & Wiens, 2010; Wu *et al.*, 2013a). Furthermore, because many of the world's biodiversity hotspots are associated with montane regions, understanding the underlying mechanisms of montane diversity patterns is of crucial importance in biogeography, biodiversity and conservation research (Fjeldså *et al.*, 2012). Different elevational richness patterns and explanations have been reported for different taxa, for example plants (Wang *et al.*, 2007), insects (Brehm *et al.*, 2007), small mammals (Wu *et al.*, 2013a), birds (Wu *et al.*, 2013b) and reptiles (McCain, 2010), whereas our understanding of the underlying mechanisms shaping such patterns is in many ways still in its infancy and in some respects controversial (Lomolino, 2001; Rahbek, 2005; Sanders & Rahbek, 2012; Wu *et al.*, 2013a). Previous studies of patterns of elevational diversity have often tested either ecological hypotheses or historical hypotheses separately, but rarely both.

Among the historical hypotheses suggested to account for patterns of species richness, the diversification rate hypothesis proposes that regional richness is positively correlated with the net diversification rate of lineages in the region (Moritz *et al.*, 2000; Mittelbach *et al.*, 2007; Escarguel *et al.*, 2008; Wiens *et al.*, 2009). One variant of this hypothesis, known as the 'montane species pump' or 'montane cradle' hypothesis, proposes that the elevational richness gradient is determined by the species diversification rate (Smith *et al.*, 2007; Fjeldså *et al.*, 2012). Another variant, known as the 'montane museum' hypothesis (Smith *et al.*, 2007; Wiens *et al.*, 2007; Li *et al.*, 2009), proposes that a longer time (age) since colonization will allow more species to come into being (i.e. the time-for-speciation effect); thus species richness is positively correlated with colonization age in a region (Wiens *et al.*, 2009). The niche conservatism hypothesis (Wiens & Donoghue, 2004), which has focused primarily on latitude, needs to be tested in elevational studies (Cadena *et al.*, 2012). The most frequently cited present-day factors explaining spatial variation in species richness include climate, productivity, area and geometric constraints (mid-domain effect; MDE) (Colwell & Lees, 2000; Currie *et al.*, 2004; Rahbek, 2005; Koh *et al.*, 2006; Nogues-Bravo *et al.*, 2008; Rowe, 2009; Wu *et al.*, 2013a). However, the roles of these current ecological factors are still, in many respects, controversial.

In short, the relative roles of historical and modern factors and their interactions are badly in need of further assessment and analysis using improved methods and novel analyses. Moreover, the ecological requirements and dispersal history of species clades vary greatly, even among closely related taxa, and species composition often differs substantially between nearby regions. Here, based on a new phylogeny and improved methods, we investigate current and reconstructed historical biogeographical patterns and their causes for members of a species-rich avian clade in the poorly studied Asian subtropical region.

METHODS

Study area and taxon

The Hengduan Mountains (22.0–32.0° N, 98.0–104.0° E), one of the world's 25 hotspots of biodiversity and endemism (Myers *et al.*, 2000), have a very high species richness of birds (about 925 species; Wu *et al.*, 2013a). This region is thought to be the centre of distribution of the Leiothrichinae babblers (MacKinnon *et al.*, 2000; Yang *et al.*, 2004; Luo *et al.*, 2009), which we will refer to simply as babblers. The region is characterized by a series of parallel mountain ranges and rivers running north to south (Fig. S1 in Supporting Information), with a sharp elevational differentiation from approximately 70 to 7556 m, offering an exceptionally long gradient for elevational diversity research (Wu *et al.*, 2013b).

Phylogeny, current and ancestral ranges, and diversification rates of clades

The Leiothrichinae babblers are the most diverse species group within the family Timaliidae, and nearly a third of them (29 species) are endemic to the Hengduan Mountains. For the aims of this study we required a dated phylogeny for the Hengduan babblers. Because many of the Hengduan species are not included in any published phylogeny, we developed our own phylogenetic hypothesis based on the mitochondrial genes *Cytb* and *ND2*, using GenBank data for 38 species and new data for eight additional Hengduan babbler species. Seven of the 53 extant Hengduan species could not be included for lack of material. To date the tree, we included two Taiwan endemic babbler species and estimated the oldest divergence time based on the Pliocene emergence of the island of Taiwan (Appendix S1).

The elevational distributions of all the Hengduan babblers were compiled from primary-level museum records and observational records, supplemented with information from the specialized literature (Appendix S2). We used the highest and lowest elevational records for each species as its estimated elevational range limits (range interpolation). Species richness for the 46 sequenced babblers was calculated based on the number of interpolated ranges occurring in each 100-m elevational band (e.g. 100–199.9 m) from 100 to 5000 m above sea level.

We used the maximum likelihood (ML) phylogenetic tree (Kozak & Wiens, 2010) and the squared parsimony method in Mesquite 2.75 (Maddison & Maddison, 2011) to reconstruct the elevational range size and range midpoint of each ancestral

species. We analysed the relationship between the diversification rates of 10 principal babbler clades and their elevational positions (Appendix S1).

Colonization age and colonization frequency

Geographical gradients in species richness ultimately arise from three biological processes: speciation, extinction and dispersal (Wiens & Donoghue, 2004). Compared with speciation and extinction, dispersal processes have a more rapid and obvious influence on geographical richness patterns, because dispersal occurs on much shorter time-scales than speciation and extinction and is reversible and repeatable. Therefore, colonization of nearby elevational bands along the elevational gradient should be estimated for each species when estimating times of colonization for elevational bands, instead of considering only range midpoints.

Rather than applying the methods used by Wiens et al. (2009) and Kozak & Wiens (2010) to test the time-for-speciation hypothesis, we developed a novel and explicitly mechanistic method to incorporate the possible role of dispersal between nearby regions based on reconstructed elevational ranges. In previous studies, reconstructed elevational midpoints of clades were first sorted by elevational bands. Then, either (1) the oldest colonization age among all clades inferred to have been present in that elevational band or (2) the sum of colonization ages for all such clades was used to test the time-for-speciation hypothesis. However, because colonization (dispersal) of a species along the elevation gradient can be rapid and frequent, and elevational distributions of some reconstructed clades are broad, a clade will often not have been limited to the elevational band of its elevational range midpoint. Therefore, the previous methods, in neglecting the role of colonization of nearby elevational bands, may underestimate the age of colonization (first, summed and averaged) for these bands,

To overcome this limitation, we estimated the possible presence of each ancestral clade in elevational bands based not only on its reconstructed elevational midpoint (as in previous methods) but also on its reconstructed elevational range size. The elevational domain was divided into 10 bands (0–499 m, 500–999 m, . . . , 4500–5000 m), then the colonization age of each clade in each elevational band was calculated, based on the reconstructed range and midpoint of each clade. For example, suppose that the elevational distribution of one ancestral species was estimated as 1000–2000 m at 2.5 Ma, and the distribution of another ancestral species was estimated as 1500–2500 m at 1.3 Ma. For the elevational band at 1500–2000 m, the oldest colonization age should be 2.5 Ma, the summed colonization age should be 3.8 Ma (2.5 + 1.3) and the average colonization age should be 1.9 Ma (3.8/2).

We calculated the oldest age, summed age and average age of colonization in each elevational band using this new method (which we call colonization based on reconstructed range size and location, CRRL). This method offers not only a more sensitive test of the relationship between richness and colonization age along elevational gradients, but also helps us to calculate colonization frequency and reconstruct historical richness patterns. Colonization frequency is the total number of both ancestral and extant babbler species that occupied each of the 10 elevational bands at any time during the past 12 Myr, the estimated age of the clade. For comparability with previous studies and methods, we also calculated the oldest age of the clade and the summed age of clades in each elevational band, based on range midpoints, following the methods used by Wiens et al. (2009).

Reconstructing historical species richness patterns

Because today's species richness pattern is derived from patterns in the past, understanding richness patterns of the past would allow us to explore how the elevational richness pattern of these babblers may have developed. Based on the reconstructed ancestral states for the ML phylogenetic tree (Appendix S2) and the divergence time of each clade, we combined two approaches to understand and estimate the patterns of species richness at 10, 8, 6, 4 and 2 Ma and the Last Glacial Maximum (20 ka). The first method, which aims to reveal the effects of lineage diversification and evolutionary shifts in thermal tolerance, takes no account of deviations of palaeotemperatures from current temperatures at each elevation. The second, novel, method reflects not only diversification and evolution of thermal tolerance but also estimated palaeotemperature patterns.

For example, for the first method, to reconstruct the babbler richness pattern for 8 Ma, we recorded the estimated elevational distribution midpoint and range size of each branch represented on the ML tree at 8 Ma (Fig. 1). Only the reconstructed elevational midpoint and range of the crown node of those branches that occurred at 8 Ma were used to reconstruct the ancestral richness pattern. If a particular divergence node happened to be located on the 8 Ma time cutting line, only the reconstructed midpoint and range value of the node itself, but not the two daughter branches, were recorded. Richness patterns were calculated following the same methods for each time step.

Palaeoclimate, especially palaeotemperature, is certain to have influenced the elevational distribution of ancestral species and therefore shaped ancestral richness patterns in relation to elevation. During the warming and cooling phases of global climatic oscillations, thermal zones have moved up and down mountains. Assuming that babbler thermal tolerances (fundamental niche breadth for temperature) evolved more slowly than the climate changed, these shifts in thermal zones would probably have imposed significant changes on elevational range locations (the elevations of midpoints). At the same time, under the same assumption of slow evolutionary change, thermal zone shifts would have had relatively little effect on elevational range size (in metres of elevation), as long as the domain boundaries did not truncate ranges (Colwell & Rangel, 2010).

For the second method, on the assumption that thermal niches are conserved and ranges are in equilibrium with climate, we used palaeotemperature data (Zachos et al., 2001; Lisiecki & Raymo, 2005; Weijers et al., 2007) and images created by Robert
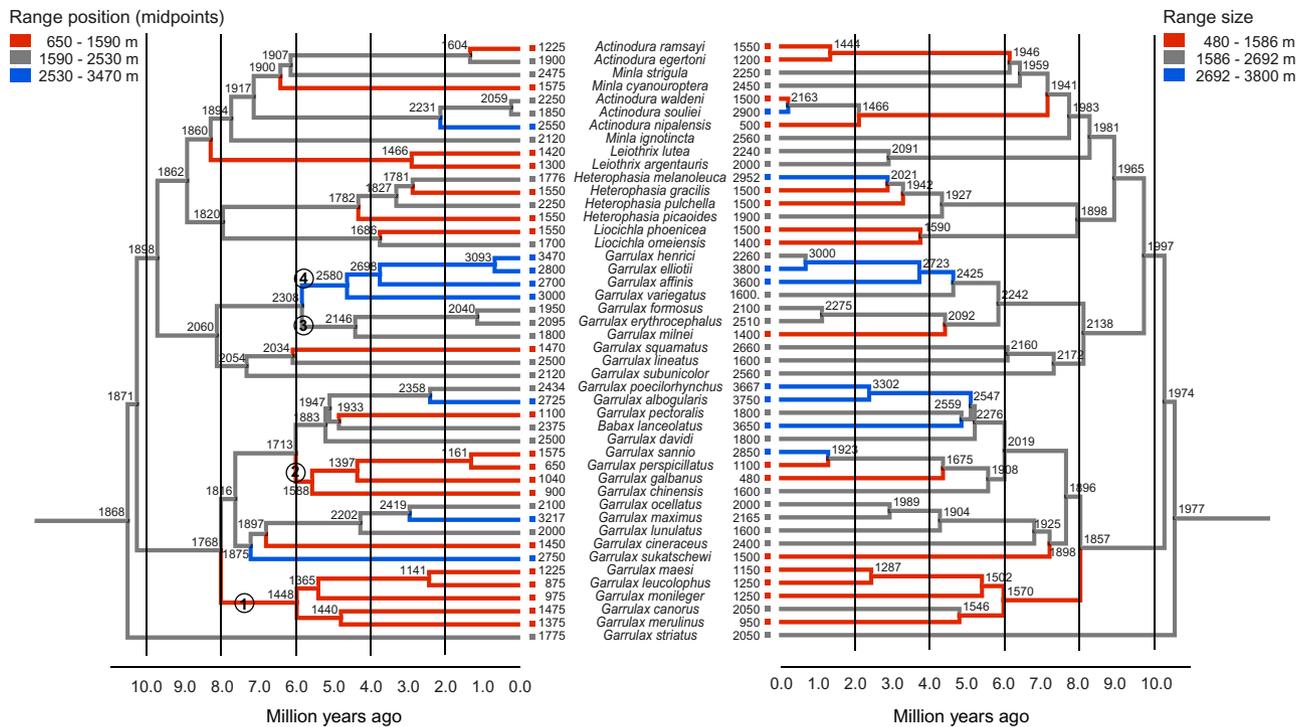
Figure 1 Estimated ancestral states (midpoint and range of elevational distribution) of babblers based on the ML (maximum likelihood) tree, without taking palaeotemperatures into account. The midpoint tree is on the left and the range size tree on the right. Numbers near the nodes are the estimated values of midpoint and range for ancestors based on parsimony reconstruction, treating elevational distributions as character states. The colours of the branches indicate the midpoint class (left) range-size class (right) of extant taxa and their inferred ancestors. Branch lengths are coordinated with the estimated ages of lineages based on Bayesian divergence–time estimation. Outgroup taxa are not shown.

A. Rohde at http://www.globalwarmingart.com to adjust the estimated historical richness patterns inferred in by the first method. Based on the modern lapse rate (−0.42 °C/100 m) in the Hengduan Mountains (Wu *et al.*, 2013b), a 1 °C change in temperature would force a 238-m change in elevational range position along the elevational gradient. Using this relation, we adjusted the range position (midpoint) of each ancestral species for each divergence time (10, 8, 6, 4 and 2 Ma and the LGM) based on the global palaeotemperature estimate for that divergence time (approximately +2, +2, +1, 0, −3 and −5 °C, respectively, compared with present-day temperature). Although local palaeotemperature regimes would of course be preferable, and other ancient ecological factors such as precipitation (Tingley *et al.*, 2012), seasonality (Wu *et al.*, 2013b), non-analogue climates, species interactions and local refugia may well have influenced ancient species richness patterns, data were not available.

The historical richness patterns were plotted using the empirical richness option in RangeModel 5 (Colwell, 2008) based on the reconstructed range midpoints and range sizes for clades. At the lowest palaeotemperatures, 2 Ma (−3 °C) and at the LGM (−5 °C), some reconstructed ranges extended below sea level. In these cases, truncated range sizes and adjusted midpoints were computed.

Ecological explanations for present-day richness

Following the methods and using the dataset of Wu *et al.* (2013b), current ecological factors in each 100-m elevational band ($n = 49$), from 100 to 5000 m were computed or tabulated from available records including: area, richness predicted under pure geometric constraints, mean annual temperature, annual precipitation, annual temperature range (the difference between mean January and mean July temperature, a measure of seasonality), normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI). The potential of these candidate explanatory factors to account for the current elevational pattern of richness was formally assessed in a multivariate, model-selection context. Methods are described in Appendix S1 and in Wu *et al.* (2013b).

RESULTS

Dated phylogenetic trees and ancestral state reconstruction

The dated phylogenetic ML tree based on two time calibrations appears in Fig. S3. (Alternative phylogenetic analyses are shown in Figs S4–S6.) The geological and molecular time calibrations
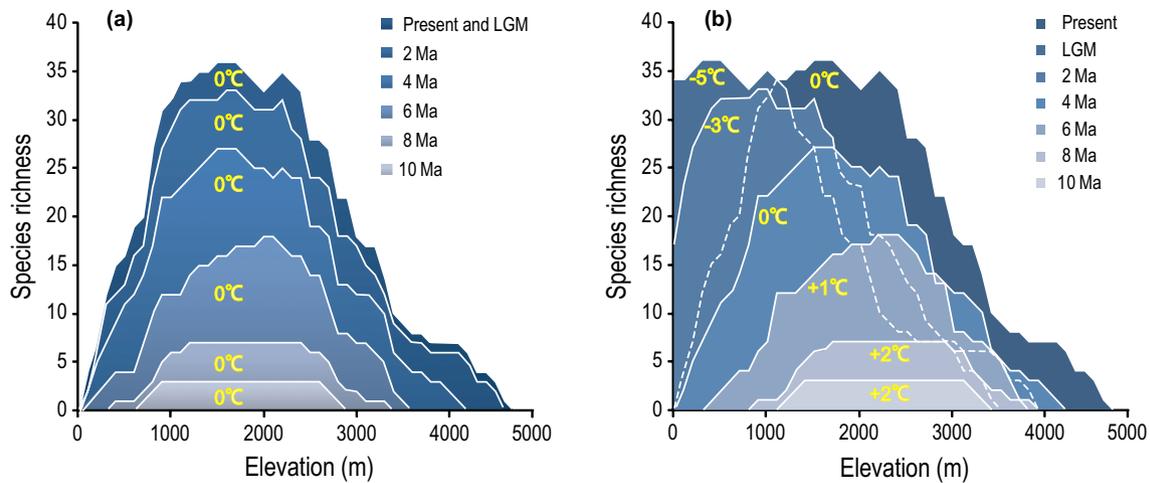
Figure 2 Reconstructed species richness patterns of babblers during the past 10 Myr under two scenarios. (a) Richness patterns taking only diversification and evolution of temperature tolerance into account. (b) Species richness patterns of babblers taking diversification, evolution of temperature tolerance and palaeotemperatures into account. The temperatures with '+' and '−' indicate the estimated temperature difference from current temperatures.

yielded concordant results when the divergence time estimation was run separately, using one time calibration to infer the other. The earliest ancestral species of Hengduan babblers appeared about 10–12 Ma, and the most recent speciation event happened about 0.2 Ma. Speciation rate peaked about 4–6 Ma, according to the dated ML tree (Fig. S7).

The current elevational richness pattern of the 46 babblers is a hump-shaped curve with the peak at about 1000–2500 m (Fig. 2). The ancestral state reconstruction based on the ML tree and divergence time appears in Fig. 1. The estimated midpoint of the elevational distribution for most of the oldest ancestral clades occurred at low to mid elevations (1768–2060 m). Taking into account that reconstructed ancestral elevational range sizes were about 2000 m for basal species, the lower elevation limits of these species map at about 700–1000 m elevation, suggesting that the ancestors of babblers first appeared at lower elevations on the 5000-m gradient. Subsequently, the lowest elevations and, later, the higher elevations (Fig. 1) were occupied by descendant species, according to this analysis. Two clades (clade ① and ② in Fig. 1) diversified principally at lower elevations, one clade (clade ③ in Fig. 1) mostly at mid elevations and one clade (clade ④ in Fig. 1) primarily at high elevations. The estimated elevational range for the oldest clades indicated that ancestral babblers had an intermediate elevational range size (about 1600–2700 m) and that range size evolved to larger and smaller sizes over time (Fig. 1). Methodological constraints that may affect these inferences are considered in the Discussion.

Diversification rate

The diversification rate and the average elevational midpoint of babbler clades were not significantly correlated (Fig. S8). The diversification rates estimated by assuming three different extinction rates ($E = 0$, 0.45, and 0.9), using the crown age of each clade, were quite similar at all elevations. The results from

using stem ages and crown ages were similar. Neither method demonstrated any significant variation in diversification rate among elevations (Figs S8 & S9, Table S3).

Colonization age and colonization frequency

Colonization age, estimated by our new method, and species richness of babblers in each elevational band are shown in Table S4. Linear regressions between colonization age and richness in each elevational band are plotted in Fig. 3 for the three alternative methods we investigated. Summed age of colonization was slightly more explanatory ($r^2 = 0.94$, $P < 0.01$) than oldest age of colonization ($r^2 = 0.80$, $P < 0.01$) or average age of colonization ($r^2 = 0.87$, $P < 0.01$). The linear regression analyses between richness and colonization age using methods from Wiens *et al.* (2009) are shown in Fig. S10 in Appendix S2.

Using our new CRRL method, both species richness and colonization frequency peaked at mid elevations (1000–2500 m; Table S4). Among elevational bands, richness was very highly correlated with the colonization frequency ($r^2 = 0.953$, $P < 0.01$; Fig. 4).

Reconstruction of historical species richness patterns

The reconstructed historical richness patterns for babbler species are shown in Fig. 2. On the left (Fig. 2a), the figure shows the estimated historical build-up of richness patterns over the past 10 Myr, assuming present-day temperatures at each elevation at all times in the past. We know, of course, that this is a false assumption, but this plot illustrates the pure effect of diversification and thermal niche shifts during the history of the clade. On the right (Fig. 2b), the figure shows the estimated historical richness patterns of babblers, taking into account not only diversification and historical shifts in the thermal niche (as in Fig. 2a) but also approximate global palaeotemperature
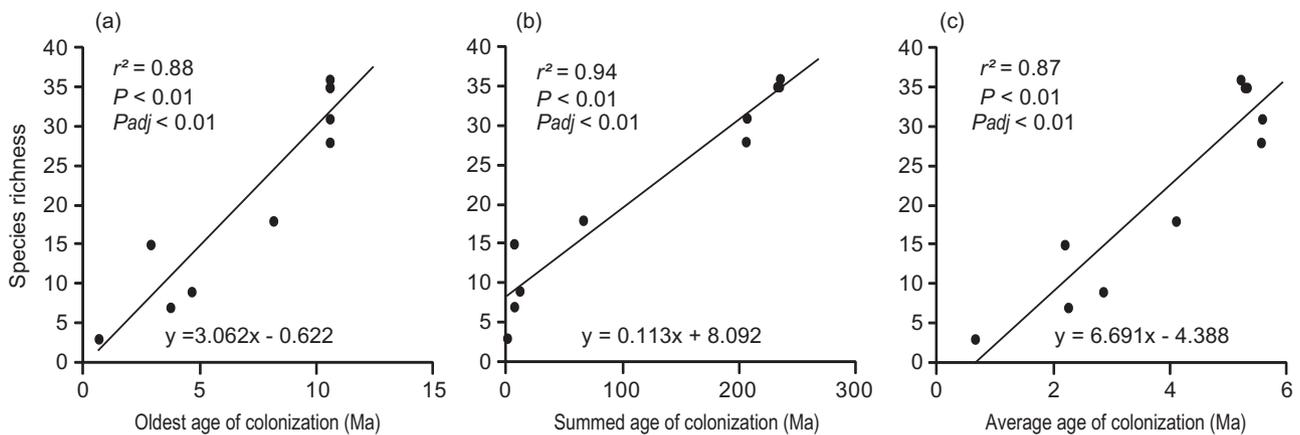
Figure 3 Relationship between the three measures of colonization age and species richness over the past 12 Myr, using the new method (colonization based on reconstructed range size and location, CRRL) developed for this study.
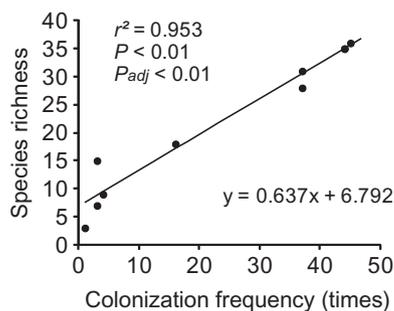

Figure 4 Relationship between species richness and colonization frequency along the elevational gradient over the past 12 Myr.

patterns. The reconstructed elevational midpoints and range sizes used in the two different methods appear in Tables S5 & S6 in Appendix S2. Species richness of babblers increased conspicuously at mid elevations, but at a slower rate at low and high elevations, from 8 Ma to the present. Although the height of the richness peak increases and its shape changes during diversification (Fig. 2a), the peak also shifts significantly upslope at 6 Ma, and back downslope subsequently, as a result of aggregated changes in thermal niche (Kolmogorov–Smirnov tests on successive patterns; $P < 0.05$ after Šídák adjustment for multiple comparisons). The elevational shift of the peaks and patterns becomes far more substantial when palaeotemperatures are also taken into account (Fig. 2b). During the cold of the early Pleistocene (2 Ma), and especially during the LGM, the downslope shift of the richness pattern of babblers approached a monotonically decreasing elevational pattern. Significantly, although the elevational ranges of 34 species were truncated at sea level during the LGM, all retained some portion of their ranges on the gradient.

Simple and multiple regression between species richness and ecological factors

Pearson correlation coefficients among the six selected explanatory variables and simple linear regressions between the richness

of babblers and each of these explanatory variables are shown in Tables S7 & S8 in Appendix S2. Table S9 compares multiple ordinary least squares (OLS) and conditional autoregressive (CAR) regression results. Annual temperature range (seasonality) emerged as the strongest explanatory factor (negative) in the OLS and CAR models for babbler species richness, and productivity was the second most important explanatory factor (positive). Geometric constraints and area had relatively smaller influences on the richness pattern of babblers over the whole elevational gradient. Model averaging and best model selection regression results with the four explanatory variables are also consistent with the OLS and CAR multiple regression results (Table S9).

DISCUSSION

Elevational species richness pattern and phylogeny of the babblers

The hump-shaped pattern of babbler species richness along the elevational gradient in the Hengduan Mountains (Fig. 2) is consistent with previous studies for plants, reptiles, fishes, birds and small mammals in the region, where a hump-shaped pattern of species richness has been found to be virtually universal (Fu *et al.*, 2007; Wang *et al.*, 2007; Li *et al.*, 2009; Wu *et al.*, 2013b, 2013a). Qualitatively, this pattern from subtropical Asia is also consistent with many studies on birds carried out elsewhere (Rahbek, 2005; McCain, 2009).

Using phylogenetic information to study species richness patterns illuminates the historical process by which these patterns develop over time. In this study, phylogenetic analyses using three methods based on two mitochondrial genes supported the result that the genus *Garrulax* is paraphyletic in the present taxonomic system, consistent with previous systematic studies based on both mitochondrial and nuclear genes (Gelang *et al.*, 2009; Luo *et al.*, 2009; Moyle *et al.*, 2012). The speciation rate peaked at about 4–6 Ma (Fig. S7), indicating that babblers may have undergone significant speciation events during a period in

which the climate was relatively stable in the Hengduan Mountains (An *et al.*, 2001). Our results demonstrate that lowland forest babblers diverged earlier than tree line and alpine montane babblers, in support of the conclusion in a previous phylogeographic study in Himalaya and East Asia (Päckert *et al.*, 2012) that the lowland forest birds tend to represent older groups and high montane birds younger groups.

Reconstruction of historical patterns of species richness along the elevational gradient

Here, for elevational distributions, we treated range position (as indicated by range midpoint) and range size (in metres of elevation) as character states of species to reconstruct their ancestral states, based on a phylogenetic hypothesis. Our reconstruction of historical richness patterns along the elevational gradient informs our understanding of how the species richness pattern originated and changed over time. When diversification and evolution of thermal tolerance, but not palaeoenvironment, were taken into account, reconstructed historical richness peaks, in relation to elevation, appeared to have been little changed in location throughout the evolutionary history of the babblers, although some significant shifts in the pattern do appear (Fig. 2a). In contrast, when the influence of palaeotemperature was included in our reconstructions, richness patterns shifted very substantially along the elevational gradient, with many species restricted to the lowlands, with truncated elevational ranges, during colder episodes such as the early Pleistocene (2 Ma) and the LGM (Fig. 2b).

Parsimony-based methods applied to the reconstruction of ancestral range positions and range sizes, however, have an intrinsic constraint that limits inferences about the past geography of any clade. In fact, for any quantitative character, unless fossil data are available, reconstructed ancestral states are weighted averages of that character as expressed by other taxa in the phylogeny (Martins & Hansen, 1997). A weighted average can never lie outside the scope of the underlying variants. For elevational range midpoints, this means that reconstructed range locations of basal species (holding environmental temperature constant, as in Fig. 2a) cannot lie below the lowest or above the highest elevational midpoint of extant species. In the present case, taking range sizes into account, present-day babblers on the Hengduan gradient covered virtually the entire elevational gradient (Fig. 2), so this constraint may perhaps be assumed to have minimal influence on our inferences, but it must nonetheless be acknowledged. Moreover, other poorly understood historical processes (elevational climate history, interaction between species, random or non-random species dispersal and partially expressed fundamental niches) also complicate the estimation of ancestral distributions.

When and how the Qinghai-Tibet Plateau, including the Hengduan Mountains, was uplifted and reached its current height is highly controversial (Harrison *et al.*, 1992; Li & Fang, 1998; Zheng *et al.*, 2002; Wu *et al.*, 2007). Although species range shifts can occur very quickly along elevational gradients, compared with the pace of geological change (e.g. mountain

uplift or pediplanation), elevational ranges probably changed little during periods when palaeoclimate was relatively stable. The climate of the Hengduan Mountain region is thought to have been warm since the early phase of uplift of the Qinghai-Tibet Plateau (about 38–45 Ma) and wet since the Asian monsoon climate began (8–10 Ma) (Liu, 1999; An *et al.*, 2001; Zheng *et al.*, 2002). If our estimates of ancestral elevational ranges, based on phylogeny, are sufficiently accurate, thermal niches have been relatively conserved and the palaeoclimate estimates are relatively reliable, the reconstructed elevational distribution of babblers (the lower range limit of the highest species) suggests that the Hengduan Mountains reached at least 1627 m in height by 8 Ma and 2200 m by 4 Ma (Fig. 2).

Historical hypotheses

Using a new and more sensitive method (CRRL), we found that babbler species richness is strongly correlated with colonization frequency and the summed age of colonization along the elevational gradient. Despite applying different methods, our findings are consisted with previous studies on the 'montane museum' hypothesis (Wiens *et al.*, 2007, 2009; Li *et al.*, 2009; Kozak & Wiens, 2010). But in contrast with the previous approach, CRRL has the following advantages: (1) it takes into account possible rapid colonization along the elevational gradient for each species and is thus more realistic; (2) the summed age of species occurring in each elevational band is more accurate than when estimated from only the reconstructed midpoints; (3) the new method makes it possible to calculate colonization frequency in different elevational bands; and (4) it does not require a logarithmic transformation for the two correlated variables, so that the correlation between richness and colonization age becomes easier to understand and interpret (Figs 3 & S10).

Summed age of colonization under CRRL is a composite measure of both colonization age and colonization frequency. It is essentially the total number of colonizations, where each colonization event is weighted according to how long ago it occurred. Although colonization frequency and the summed age of colonization have different ecological meanings, both measures were highly correlated with species richness (Figs 3 & 4) and strongly intercorrelated ($r = 0.998$, $P < 0.01$). Colonization frequency responds to dispersal, a relatively rapid ecological process that can substantially change the richness pattern by increasing or decreasing the number of species in a band, no matter how the diversification rate changes over time. In contrast, colonization age, especially the oldest colonization age, would have little influence on species richness if the diversification rate varies much over time. Therefore, colonization frequency, or the summed age of colonization using the CRRL method, should be a better indicator of the change of species richness as a result of rapid dispersal events.

Using the methods of Wiens *et al.* (2007, 2009), our results suggested that the diversification rate was very similar in all elevational bands (Figs. S7 & S8) and thus cannot be the principal underlying cause of the species richness pattern, which

peaks at intermediate elevations. This finding is consistent with most previous studies for other taxa (Wiens *et al.*, 2007, 2009; Escarguel *et al.*, 2008; Li *et al.*, 2009). In contrast, the diversification rate was reported to play an important role in explaining elevational richness patterns of the Middle American tree frogs (Smith *et al.*, 2007). Moreover, because our results represent a relatively narrowly defined taxonomic group, they may not be representative for avian diversity in the whole region. Clearly, to fully test the diversification rate hypothesis, new methods and studies covering more taxa and regions are needed.

Ecological hypotheses

Although area and geometric constraints had relatively weak explanatory power in multivariate analyses (Table S9), the simple correlation coefficients of observed richness against area and against randomly predicted richness under geometric constraints were both high (Table S8). The richness of babblers at mid-elevation surpassed the maximum theoretical value of species richness under geometric constraints and shifted to lower elevations, indicating that species richness at mid elevations was driven by both ecological and historical factors (Fig. S11). Although neither area nor geometric constraints were, statistically, among the most important explanatory factors for the current richness pattern of babblers along the elevational gradient, it would be prudent not to completely exclude their possible influence on species richness, especially in a historical context.

We found that annual temperature range (seasonality) played a greater role than other environmental factors in shaping the richness pattern of babblers along the elevational gradient (Table S9) consistent with previous studies (Hurlbert & Haskell, 2003; Wu *et al.*, 2013b). Both temperature and precipitation are high at low elevations, but the richness of babblers does not peak at low elevations. This discordance demonstrates that temperature and precipitation are not the definitive factors in shaping the pattern of babbler species richness. According to the theory of niche conservatism, limited climatic tolerances play an important role in restricting species dispersal and thus help to explain why species richness is high in regions with stable climate and low in regions with highly variable and extreme climates (Wiens & Donoghue, 2004; Wiens & Graham, 2005). The strong negative correlation between seasonal temperature range and species richness of babblers supports the niche conservatism hypothesis along the elevational gradient. Other ecological processes (e.g. complex vegetation structure and diverse habitats) may also contribute to the peak of species richness at mid elevations.

Species richness, as an important characteristic of ecosystems, reflects the complexity and amounts of energy and material transfer in an ecosystem, suggesting that species richness may be positively correlated with productivity. EVI played a statistically more explanatory role in shaping the richness pattern of babblers when other environmental factors were taken into account (Table S9). However, unlike EVI, species richness of babblers does not peak at low elevations, indicating that the richness of

babblers at low elevations may be constrained by other ecological (e.g. area and geometric constraints) or unknown historical factors there (Fig. S12).

CONCLUSIONS

Our analyses demonstrated that both historical and present-day factors have played important roles in shaping the elevational pattern of species richness of the Hengduan babblers. But the roles of these factors were quite different at different elevations, suggesting that different underlying mechanisms and their interactions may influence species richness at different elevations. Differential diversification rates appear not to have contributed to the elevational pattern of richness, whereas differing colonization frequency and colonization age (time) at different elevations explained the current richness pattern well. Historical reconstructions showed that the elevational pattern of species richness is likely to have shifted substantially under the influence of climate change. A small annual temperature range and higher EVI had greater explanatory power than area and geometric constraints in accounting for the current richness pattern. Integrated analyses using both historical and ecological factors are needed to achieve a comprehensive understanding of the pattern of diversity.

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Additional references may be found at the end of Appendices S1–S3 at [http://onlinelibrary.wiley.com/doi/10.1111/geb.12197/suppinfo].

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Supplementary methods.
Appendix S2 Supplementary tables and figures.
Appendix S3 Supplementary literature cited.

BIOSKETCH

Yongjie Wu is currently a PhD candidate in the Institute of Zoology, Chinese Academy of Sciences. His research is mainly focused on community ecology, macroecology, biogeography and evolutionary biology. In particular, he is interested in understanding the relative roles of historical and present-day factors in determining patterns of biodiversity on different spatial and temporal scales, as well as the response of diversity patterns to climate change.

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