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What makes the Sino-Himalayan mountains the major diversity hotspots for pheasants?

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Abstract

Aim: The Sino-Himalayas have higher species richness than adjacent regions, making them a global biodiversity hotspot. Various mechanisms, including ecological constraints, energetic constraints, diversification rate (DivRate) variation, time-for-speciation effect and multiple colonizations, have been posited to explain this pattern. We used pheasants (Aves: Phasianidae) as a model group to test these hypotheses and to understand the ecological and evolutionary processes that have generated the extraordinary diversity in these mountains.

Location: Sino-Himalayas and adjacent regions.

Taxon: Pheasants.

Methods: Using distribution maps predicted by species distribution models (SDMs) and a time-calibrated phylogeny for pheasants, we examined the relationships between species richness and predictors including net primary productivity (NPP), niche diversity (NicheDiv), DivRate, evolutionary time (EvolTime) and colonization frequency using Pearson's correlations and structural equation modelling (SEM). We reconstructed ancestral ranges at nodes and examined basal/derived species patterns to reveal the mechanisms underlying species richness gradients in the Sino-Himalayas.

Results: We found that ancestral pheasants originated in Africa in the early Oligocene (~33 Ma), and then colonized the Sino-Himalayan mountains and other regions. In the Sino-Himalayas, species richness was strongly related to DivRate, NPP, NicheDiv and colonization frequency, but weakly correlated with EvolTime. The direct effects of NicheDiv and DivRate on richness were stronger than NPP and EvolTime. NPP indirectly influenced species richness via DivRate, but its effect on richness via NicheDiv was relatively weak.

Main conclusions: Higher species diversity in the Sino-Himalayas was generated by both ecological and evolutionary mechanisms. An increase in available niches, rapid diversifications and multiple colonizations was found to be key direct processes for the build-up of the diversity hotspots of pheasants in the Sino-Himalayan mountains. Productivity had an important but indirect effect on species richness, which worked through increased DivRate. Our study offers new insights on species accumulation in the Sino-Himalayas and provides a useful model for understanding other biodiversity hotspots.

KEYWORDS

diversification rate, energetic constraints, mountains, multiple colonizations, niche diversity, Sino-Himalayas, time-for-speciation effect

1 | INTRODUCTION

Tropical and subtropical mountains harbour more species than adjacent lowlands on the global scale, and understanding mechanisms underlying this pattern is a challenge for ecologists and biogeographers (Ding, Yuan, Geng, Koh, & Lee, 2006; Fjeldså, Bowie, & Rahbek, 2012; Fjeldså & Rahbek, 2006; Jetz & Rahbek, 2002; Jetz, Rahbek, & Colwell, 2004; Rahbek et al., 2007; Ruggiero & Hawkins, 2008). Continental-scale analyses have suggested that contemporary climate models alone cannot explain this pattern (Jetz & Rahbek, 2002). Subsequent studies have revealed that they only explain the spatial richness patterns of wide-ranging species (Fjeldså & Rahbek, 2006; Jetz & Rahbek, 2002; Rahbek et al., 2007), while the richness patterns of narrowly ranging species in mountains are better predicted by topography, geometric constraint and the evolutionary history of lineages adapted to specific local conditions in the highlands (Fjeldså & Rahbek, 2006; Jetz et al., 2004; Rahbek et al., 2007). Therefore, it is necessary to integrate both ecological and evolutionary processes to fully understand the spatial variation in species richness in mountains in comparison with that in the adjacent lowlands (Fjeldså et al., 2012).

Several hypotheses have been proposed to explain spatial richness patterns in mountains based on ecological or evolutionary processes (Table 1). Under the ecological constraints hypothesis, the availability of niches (habitats or ecological zones) regulates species richness in a given region (Chesson, 2000; Rabosky, 2009). In a constrained ecological space, intense interactions and competition for restricted niches limit lineages diversification and species coexistence, resulting in slowdowns in species accumulation (Moen & Morlon, 2014; Rabosky, 2009). Thus, if diversity is constrained by ecological space, we would expect more species-rich clades to colonize mountains because the topographic heterogeneity in mountains provides more ecological space. The energetic constraints hypothesis emphasizes resource availability, reflecting the influence of productivity on the number of individuals in assemblages (Evans, Warren, & Gaston, 2005). Areas with a high productivity can sustain more individuals, which increases the probability of species survival, enabling the species to maintain a larger population with a lower extinction rate, consequently contributing to the total species richness in such areas (Currie et al., 2004; Evans et al., 2005; Wright, 1983).

However, ecological and energetic factors cannot directly change the number of species in a region without the direct roles of speciation, extinction and dispersal processes (Wiens & Donoghue, 2004). Therefore, a greater number of species in mountains could be explained by the higher diversification rate (DivRate) (the DivRate hypothesis), available time for evolution within the area (the timefor-speciation effect) (Smith, de Oca, Reeder, & Wiens, 2007; Wiens, Parra-Olea, García-París, & Wake, 2007) and the higher colonization frequency into mountains from adjacent regions (the multiple colonizations hypothesis) (Johansson et al., 2007; Päckert et al., 2012). Under the DivRate hypothesis, higher DivRate in mountains due to prominent topological features and stable local climate contributed to accumulating species faster than in adjacent lowlands (Smith et al., 2007; Wiens et al., 2007). The time-for-speciation effect (Stephens & Wiens, 2003), emphasizing evolutionary time (EvolTime) of lineages in a region, predicts that species prefer to colonize humid mountain forest habitats and then stay there longer than in the lowlands, allowing lineages to have sufficient time to arise and accumulate (Smith et al., 2007; Wiens et al., 2007). Finally, multiple colonizations from adjacent regions enable more lineages to occupy

	TABLE 1	Hypotheses and	the mechanisms	that explain hig	h biodiversity	in mountains
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Hypothesis	Mechanism	Prediction
Ecological constraints hypothesis	Lineage accumulation slows with decrease of available ecological spaces (Moen & Morlon, 2014). More available niches can facilitate species coexistence and support more species (Chesson, 2000; Rabosky, 2009)	Richness is positively related to niche diversity
Energetic constraints hypothesis	Habitats with high productivity provide more available sources and sustain more individuals and viable populations, increasing the survival probability and decreasing extinction risks of species (Currie et al., 2004; Evans et al., 2005; Wright, 1983)	Richness is positively related to energetic predictors (i.e. temperature, precipitation and productivity)
Diversification rate hypothesis	High diversification rate (high speciation or low extinction) in mountains results in rapid accumulating in diversity (Smith et al., 2007; Wiens et al., 2007)	Richness is positively related to net diversification rate
Time-for- speciation effect	Areas are colonized earlier by lineages allowing the greater evolutionary time to accumulate higher diversity (Stephens & Wiens, 2003)	Richness is positively related to evolutionary time
Multiple colonizations hypothesis	Higher diversity in mountains results from multiple colonizations of lineages from adjacent regions (Favre et al., 2015; Johansson et al., 2007; Päckert et al., 2012)	Richness is positively related to frequency of colonizations into mountains

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the montane habitats and then diversify there (Johansson et al., 2007; Päckert et al., 2012).

The Sino-Himalayas span the southern and eastern margins of the Qinghai-Tibet Plateau (QTP), the Mountains of Southwest China and Indochina (Figure 1a). It was formed by the collision of the Indian Plate with the Eurasian Plate and may have already reached its greatest height in the Eocene (Favre et al., 2015; Renner, 2016). This region covers three global biodiversity hotspots (Figure 1a) (Marchese, 2015). Some studies have shown that the high diversity in the Sino-Himalayas is well explained by topographic heterogeneity and productivity (Ding et al., 2006; Wu et al., 2013; Zhang et al., 2016). Others have attempted to relate diversity to species diversification, EvolTime and colonizations into the mountain habitat by lineages (Johansson et al., 2007; Kennedy et al., 2012; Leneveu, Chichvarkhin, & Wahlberg, 2009; Päckert et al., 2012). However, only few studies have integrated ecological and historical processes to explain the species richness in the Sino-Himalayas due to lack of data and suitable groups (Price et al., 2014; Wu et al., 2014). Pheasants (Aves: Phasianidae) provide an ideal taxon to examine the ecology and evolutionary mechanisms underlying the species richness patterns in the Sino-Himalayas. It is a diverse group of 183 species distributed around the world, but especially concentrated in the Southeast Asia (Gill & Donsker, 2015). Pheasants are primarily ground-dwelling birds with relatively weak volant abilities and many species inhabit montane landscapes, making them a good model for montane biogeographic studies.

In this study, we aim to compare the roles of ecological and evolutionary processes (Table 1) underlying the species richness gradient in the Sino-Himalayas using pheasants as a model system. To achieve this, we estimated a time-calibrated phylogeny and species distribution maps, collected functional traits of species, as well as climate data. We integrated these data to quantify species richness and predictors and to reconstruct the biogeographic history of pheasants and then tested five key biogeographic hypotheses (Table 1). Primarily, we asked three questions as follow: (1) What is the role of each mechanism in generating species richness gradient in the Sino-Himalayas? (2) How were the direct and indirect effects of ecological and evolutionary processes on species richness? (3) Did the effects of ecological processes on species richness ultimately depend on how they influence evolutionary and biogeographic pro-

2 | MATERIALS AND METHODS

2.1 | Study area

cesses?

We defined a cell with 0.5 arc-min resolution as mountainous if the elevation difference between it and any of its eight adjacent cells exceeded 200 m (Körner, Paulsen, & Spehn, 2011). We also included a buffer region of approximately 200 km around mountains extending to the adjacent lowlands to ensure that the elevational temperature gradient on a local scale was fully covered.

2.2 Species data

Species sampling followed the taxonomy of the IOC world bird list 5.4 (Gill & Donsker, 2015). For all species, we collected occurrence data from online databases of the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/), eBird (http://ebird.org/), xeno-





canto (http://www.xeno-canto.org) and China Bird Report (http:// www.birdreport.cn), museum and personal collections (see Acknowledgements). Data were updated to July 2017. After removing duplicates, we had a total of 56,286 occurrence points (average 531 points/species). Then, we predicted species distribution maps for each species by integrating occurrence records and expert distribution maps (Merow, Wilson, & Jetz, 2017) using nine selected environmental layers in MAXENT 3.3.3k (Phillips & Dudík, 2008) (for methods, see Appendix S1 in Supporting Information).

Using a Behrman equal-area projection, we divided our study area into grid cells 55×55 km in size (Figure 1b). By overlaying the distribution maps of all species on cells, we could determine the presence/absence of each species and evaluate the corresponding species richness in each grid cell (Table S3.1 see Appendix S3 in Supporting Information). If a species range overlapped <50% of the area of a grid cell, we defined this species as absent from that grid. We removed grid cells with small assemblages (<3 species) to avoid the spurious effects of low sample size, resulting in a total of 1,822 grids used in the following analyses.

2.3 | Phylogeny and divergence times

We estimated a phylogeny of 161 pheasant species and four outgroups from four mitochondrial and six nuclear genes (Table S3.2; for methods see Appendix S1). To calibrate the divergence time, we used three documented fossil calibrations. The final phylogeny was generally well supported and consistent with findings of previous studies (Crowe et al., 2006; Stein, Brown, & Mooers, 2015; Wang, Kimball, Braun, Liang, & Zhang, 2013) (Figure S2.1, 2.2 see Appendix S2 in Supporting Information).

Eight of the 71 species in the Sino-Himalayas were excluded from the time-calibrated phylogeny because no sequences are available. We placed them into our tree by identifying the closest relative of each species based on data from previous publications and morphological similarity (del Hoyo, Elliot, & Sargatal, 1994; Randi et al., 2000). The node for each missing species was arbitrarily placed at the middle of the branch of its closest relative in our phylogeny. This method to integrate missing species into phylogeny has been widely used in large-scale analyses and has been found to have little qualitatively affect on results (Algar, Kerr, & Currie, 2009; Qian, Wiens, Zhang, & Zhang, 2015).

2.4 Niche diversity

We calculated niche diversity (NicheDiv) in assemblages using species traits because they characterize divergence in behaviour and morphology of sympatric species and their ability to make use of different resources (Price et al., 2014). We computed functional diversity using the functional dispersion (FDisp), which measures the average distance of species traits in a principal co-ordinates analysis (PCoA) space to the centroid (Laliberté & Legendre, 2010). FDisp is very suitable for testing the ecological constraints hypothesis because it is not sensitive to species richness in the community. We Journal of Biogeography -WILEY-

selected body mass, body length, wing length, tail length, tarsus length, bill length, diet and habitat as functional traits (Table S3.3). When estimated FDisp, we used the Gower's (1966) distance to measure functional distance for our mixed original trait matrix (binary and continuous variables). Then, we performed a PCoA analysis and used the first four PCoA axes (95.4% of total inertia) to quantify FDisp using package 'FD' (Laliberté, Legendre, Shipley, & Laliberté, 2014) in R 3.3.1 (R Core Team, 2016).

2.5 | Energetic predictors

We utilized the mean annual temperature (MAT), the annual temperature range (ATR), the range of the mean annual temperature in grids (RMAT), the mean annual precipitation (MAP) and the annual net primary productivity (NPP) values to measure the energy and water balance in each grid cell. MAT and MAP were estimated based on climate data from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), with a 1-km resolution. For estimates of NPP, we used the data from Imhoff et al. (2004), which has a spatial resolution of one-quarter degree. The ATR was the difference of the mean temperature in July and January. The RMAT was calculated using the maximum and minimum MAT values in each cell to estimate the temperature gradient and determine the effectiveness of topographic barriers (Ruggiero & Hawkins, 2008).

2.6 | Diversification rate

We used the equal splits measure of evolutionary isolation to estimate the species-level DivRate following Jetz, Thomas, Joy, Hartmann, and Mooers (2012). DivRates for each species i were calculated as follows:

$$DivRate_i = (\sum_{j=1}^{N_i} l_i \frac{1}{2^{j-1}})^{-1}$$

where N_i is the number of edges on the path from species *i* to the root, and l_i is the length of edge *j*. To infer the community-level Div-Rates in each grid cell, we calculated the geometric mean of the weighted species-level DivRates of all species found in the grid cell. Following Jetz et al. (2012), the species-level DivRates were weighted by the inverse of the area over which species' ranges extended across the world. This method avoids pseudo-replication resulting from the presence of wide-ranging species in many grid cells and narrow-ranging species in only a few grid cells (Jetz & Rahbek, 2002).

2.7 Basal and derived species

We defined basal and derived species based on the root-path distance, which was the number of nodes on the path from the tips to the root in the phylogeny (Fjeldså & Rahbek, 2006; Fjeldså et al., 2012). The observed root-path distances in our phylogeny ranged from 3 to 17 nodes. Thus, we defined the quartile (25%) of species Journal of Biogeography

with the shortest root-paths (3–7 nodes) as basal species and the rest (75%) of the species (8–17 notes) as derived species (Figure S2.2). Then, we projected all basal and derived species distribution maps into grid cells to examine large-scale differences in accumulation of species with few near relatives and species representing terminal radiation.

2.8 | Evolutionary time in the grid cells

The phylogenetic relatedness among species captures the evolutionary history of species assemblages, where an assemblage with a long EvolTime is characterized by phylogenetic evenness, while a relatively recent assemblage shows a phylogenetic clustering structure (Algar et al., 2009; Qian et al., 2015). Thus, a common approach to test the time-for-speciation effect is to compare phylogenetic structures in different species assemblages and then to relate this pattern to species richness. We estimated phylogenetic relatedness using the phylogenetic species variability (PSV) (Helmus, Bland, Williams, & Ives, 2007), which has been successfully used in previous studies to test the time-for-speciation effect (Algar et al., 2009; Qian et al., 2015). The PSV is standardized from zero (phylogenetic clustering and young assemblages) to one (phylogenetic evenness and a long evolutionary history) (Helmus et al., 2007).

2.9 | First colonization time and colonization frequency in subregions

We conducted an ancestral range analysis to identify the most likely range at each node in a time-calibrated phylogeny and then estimated the first colonization time and colonization frequency in each geographic range. In this analysis, we included all pheasants considering that species are typically not produced locally in a small area, and many descendants of the early nodes may diversify further outside the mountain region. Moreover, four outgroups were added into this analysis, considering our preliminary analyses showing that geographic ranges of outgroups had a strong influence on the results of ancestral region estimates for ingroups. We coded the distribution of each species in nine geographic ranges identified from fauna and montane forests (Collar et al., 2001; Holt et al., 2013). Ancestral ranges were reconstructed in the 'BioGeoBEARS' package (Matzke, 2014) in R using six likelihood models. The best model was selected using the Akaike information criteria (AIC) after computing the loglikelihood score. Then, we calculated the probabilities of the ancestral states at all nodes in the phylogeny under the best model (for methods, see Appendix S1).

The first colonization time in a given geographic range was estimated using the crown age of the clade that first occupied that region. For some colonizations in a region represented by only a single species, we arbitrarily used the half age when the species split from its sister species. Colonizations were defined as founder-event speciation, by which descendant species are isolated in a new region compared to its ancestral region (Matzke, 2014). For example, if the ancestral range of a clade is A and one of its descendants is distributed in B, we can identify a colonization event from A to B. In these two analyses, ancestral ranges were the highest probabilities of the ancestral states at each node, which were inferred under the best model from the BioGeoBEARS results.

2.10 Statistical analyses

We conducted log-transformations of species richness, DivRate and EvolTime, square-transformations of NicheDiv, and square root-transformations of MAP, NPP and RMAT to improve normality and linearity (Rangel, Diniz-Filho, & Bini, 2010). Pearson's correlation analyses were conducted to examine the relationships between the richness and predictors. In large-scale data analyses, spatial autocorrelation can increase the chances of a type I error and bias. Thus, we recalculated *p*-values to account for the spatial autocorrelation using SAM 4.0 (Rangel et al., 2010).

To estimate the direct and indirect effects of ecological (NicheDiv and NPP) and evolutionary (DivRate and EvolTime) variables on the species richness, we used structural equation modelling (SEM), which uses statistical methods to define causal relationships and mutually interconnected equations among the variables of interest. Here, we did not add the multiple colonizations hypothesis into SEMs because we were unable to compute colonization frequency in each grid cell. Before modelling, we first standardized each variable to a mean of zero and a variance of one to allow for the direct comparison of the path coefficients in the SEMs (Algar et al., 2009). To account for spatial correlation, we used the generalized least squares (GLS), which allows full spatial error to be fitted in SEMs. All SEMs were performed in R using the 'piecewiseSEM' package (Lefcheck, 2016).

In addition to carrying out analyses using all grids in the study area, we also conducted analyses for three subregions: Indochina, the Himalayas and Hengduan Mountains (Figure S2.3). We expected that the influence of different underlying mechanisms would vary because the geological history, glacial activities and fauna differed substantially among these subregions.

3 | RESULTS

The species richness of pheasants displayed substantial geographic variations with 3–21 species per sampled cell, showing two diversity hotspots: south-eastern margin of the QTP and Qinling Mountains. Cells with higher species richness were associated with mountain ranges in the Himalayas, Hengduan Mountains, Qinling Mountains, Qilian Mountains and highlands in Indochina (Figure 1b), but species richness was sparse in the topographically subdued parts of the central QTP and lowlands in Indochina, Indian Subcontinent and southern China.

Pearson's correlations (Table 2) showed that species richness was significantly correlated with DivRate, NicheDiv, NPP and RMAT after accounting for spatial autocorrelation across the entire area and three subregions and was related to DivRate and NicheDiv relatively more strongly than other predictors. However, the

TABLE 2 Pearson's correlation coefficients of pheasant richness in the Sino-Himalayas related to the diversification rate (DivRate), niche diversity (NicheDiv), the mean annual temperature (MAT), the annual temperature range (ATR), the mean annual precipitation (MAP), range of mean annual temperature (RMAT) and the annual net primary productivity (NPP) in the entire area and three subregions. The *p*-value in parentheses was recalculated according to geographically effective degrees of freedom to account for spatial autocorrelation

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Region	DivRate	EvolTime	NicheDiv	MAT (°C)	MAP (mm)	NPP (g·m ^{-2} ·a ^{-1})	RMAT (°C)	ATR (°C)
Entire area	0.54 (<.001)	0.19 (.07)	0.51 (<.001)	0.06 (.645)	0.27 (.014)	0.31 (.021)	0.32 (<.001)	-0.19 (.233)
Himalayas	0.57 (<.001)	0.47 (<.001)	0.55 (<.001)	0.20 (.208)	0.61 (<.001)	0.59 (<.001)	0.37 (.007)	-0.51 (.007)
Indochina	0.72 (<.001)	0.01 (.963)	0.45 (<.001)	-0.41 (.003)	0.20 (.12)	0.25 (.018)	0.44 (<.001)	0.22 (.155)
Hengduan Mountains	0.26 (.004)	0.25 (.064)	0.51 (<.001)	0.18 (.07)	0.34 (.021)	0.41 (.001)	0.43 (<.001)	-0.43 (.014)



FIGURE 2 Pheasant richness is composed in terms of lineages with basal and derived species in the Sino-Himalayas and Southeast Asia. (a) Richness patterns of basal species which represent species with the shorter root-path distance (25%). (b) Richness patterns of derived species which represent species with the longer root-path distance (75%) [Color figure can be viewed at wileyonlinelibrary.com]

correlation of species richness with EvolTime was weak and became significant after accounting for spatial autocorrelation (except in the Himalayas).

The root-path quartile analyses (Figure 2) showed the greatest accumulation of species with no near relatives (basal species) in Sundaland (highlands of northern Sumatra and Borneo) and the Sino-Himalayan mountains, corresponding to areas where evergreen vegetation was maintained throughout the Late Tertiary. Derived species showed less diversification in Sundaland and lowland Indochina, but more radiations in regions with a monsoon climate in India, southern China and some parts of Sino-Himalayan mountains.

In reconstructions of the biogeographic history of pheasants, the dispersal-extinction-cladogenesis with founder-event speciation model (DEC+J) received the lowest AIC score (Table S3.4) and was selected as the best model to calculate the highest probabilities of the ancestral states at all nodes (Figure 3a). The origin of pheasants was most probably in Africa in the early Oligocene (95% highest posterior distribution [HPD]: 28.7–38.2 Ma) followed by

colonizations into the Sino-Himalayas, Sundaland, Australia and the Palearctic. We observed the highest colonization frequencies into Sino-Himalayan mountains from adjacent regions, especially a dispersal event from Africa that occurred in the mid-Oligocene (95% HPD: 24.5–32.2 Ma) leading to a rapid diversification in the Phasianinae clade. Regional richness was strongly related to the colonization frequencies into each geographic range (the least square regression, $R^2 = .74$, p < .001; Figure 3b).

At the continental scale, species richness correlated strongly with DiveRate (β = 0.40, p < .001) and NicheDiv (β = 0.42, p < .001), but weakly related to NPP (β = 0.18, p < .001) and EvolTime (β = 0.08, p = 0.018) (Figure 4a). NPP had a stronger effect on EvolTime (β = 0.41, p < .001) and DivRate (β = 0.36, p < .001), while its effect on NicheDiv was weak (β = -0.06, p = .56). NicheDiv was weakly related to EvolTime (β = 0.12, p < .001) and DivRate (β = 0.18, p < .001). The same results were supported in the subregions of Indochina and Hengduan Mountains (Figure 4b,c). However, in the Himalayas (Figure 4d), species richness was related to NPP



(a)

-0.06

FIGURE 3 (a) Results of the reconstructed ancestral ranges of pheasants at each node computed using the DEC+J model in BioGeoBEARS. Pie charts at the nodes show the probability of regional occurrence, and letters indicate the highest probability of ancestral regional states. Arrows show the dispersal events. (b) Relationship between colonization frequency and species richness in each geographic range (Africa was excluded here because it was an origin centre) [Color figure can be viewed at wileyonlinelibrary.com]

(β = 0.47, *p* < .001) and EvolTime (β = 0.30, *p* < .001) relatively more strongly than DiveRate (β = 0.24, *p* < .001) and NicheDiv (β = 0.23, *p* < .001).

4 | DISCUSSION

NPP

In this study, we explored the causes of species richness patterns in the Sino-Himalayas, integrating both ecological and evolutionary processes. Our results indicate that ecological constraints, energetic constraints, the DivRate and multiple colonizations all played roles in species richness patterns and that ecological and evolutionary mechanisms therefore may act in concert. We therefore discuss each in turn and then combine them to get a better understanding of the various processes underlying species richness gradients.

0.18

0.08

EvolTime

4.1 | Ecological and energetic constraints

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Our study lends support to the ecological constraints hypothesis, which predicts that the increased richness in the Sino-Himalayas is a direct consequence of a greater diversity of available niches. This hypothesis is also supported by previous studies on passerine birds that have demonstrated that competition for niche space affects species diversification and accumulation in the Himalayas (Kennedy et al., 2012; Price et al., 2014). Our support for the ecological constraints hypothesis is unsurprising given that the Sino-Himalayas show the most prominent topological features and the strongest ecological gradients in temperature and precipitation, providing a variety of terrestrial habitats and great ecological diversity for various species (Favre et al., 2015).

Several recent studies have examined the relationship between species richness and ecological space in the Sino-Himalayas (Ding

0.10

0.15

0.6]

SR

EvolTime



(b)

0.07

NPP

10

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et al., 2006; Zhang et al., 2016). However, these studies have used the topographic heterogeneity (e.g. elevation range) as a measure of NicheDiv. In fact, topographic heterogeneity may not be a good proxy to estimate the diversity of available niches (Kennedy et al., 2012). A recent study has attempted to measure available niches using functional traits; the results, however, do not support the richness–niches relationship (Belmaker & Jetz, 2015). However, our results have found a significant relationship between species richness and NicheDiv measured from functional traits, which was also supported by the Andes frugivorous birds (Dehling et al., 2014).

Some previous studies have suggested that energetic factors may not be sufficient to explain spatial richness patterns of species with small ranges in a mountain region (Fieldså & Rahbek, 2006; Jetz & Rahbek, 2002; Rahbek et al., 2007), but some montane pheasants have such small ranges (mostly in the genera Tetraophasis, Arborophila and Tragopan) and our results show that NPP plays a prominent role for predicting the variation in species richness in the Sino-Himalayas (Table 2). A productivity-richness relationship has been detected in previous studies that investigated richness patterns of all birds in mountains (Ding et al., 2006; Ruggiero & Hawkins, 2008). Our findings also support the conclusions of a previous study on babblers richness gradients in the Hengduan Mountains, where the species richness was highly related to NPP and RMAT (Wu et al., 2014). Both pheasants and babblers are primarily ground-dwelling species with limited volant abilities, and most species occupy specific niches in mountains. This evolutionary conservatism in the thermal niches may result in increased opportunities for allopatric isolation, speciation and the accumulation of species in tropical or subtropical mountains (Cadena et al., 2011).

4.2 | Evolutionary hypotheses

Our results reveal that high Sino-Himalayan species richness is explained by an accelerated DivRate (Table 2; Figure 4), confirming the DivRate hypothesis (Smith et al., 2007; Wiens et al., 2007). Rapid diversification in the Sino-Himalayan mountains has been hypothesized in some previous studies (Li et al., 2009; Wu et al., 2014), but rarely supported (Leneveu et al., 2009; Xing & Ree, 2017). However, some studies from other montane regions do support the DivRate hypothesis, see for instance Schnitzler et al. (2011) for South Africa's Cape region and Fjeldså and Rahbek (2006) for the Andes. This suggests that the DivRate hypothesis is a common mechanism underpinning high diversity in mountains.

Our support for the DivRate hypothesis is expected because rapid orogeny in the Sino-Himalayas creates conditions for accelerating diversification of resident lineages (Che et al., 2010; Xing & Ree, 2017). In the Sino-Himalayan mountains, particularly in the Hengduan Mountains and eastern Himalayas, the climate remained relatively warm and stable during the Quaternary glacial period (Owen, Finkel, & Caffee, 2002), providing an ideal refuge area with good opportunities for in situ speciation and low extinction risks during Pleistocene glacial periods (Qu et al., 2014; Xing & Ree, 2017). It is supported by our path-root analyses, which demonstrate high accumulation of both basal and derived species in the Sino-Himalayas (Figure 2).

The QTP is regarded as a relative old mountain system that started to uplift shortly after the beginning of the collision at 55-50 Ma, and reached a height of 4,000 m at 40 Ma (Favre et al., 2015; Renner, 2016), leaving a long time for species accumulation relative to adjacent regions. Despite this, we are surprised to find little evidence of the time-for-speciation effect, given that some studies have suggested a greater role of EvolTime in the Sino-Himalayas (Li et al., 2009; Wu et al., 2014). This is probably because the different EvolTime-spatial scale and species groups were selected in different studies. From the ancestral range analysis, we conclude that pheasants in the Sino-Himalayan mountains arrived from Africa during the mid-Oligocene (~28 Ma), followed by dispersal into tropical lowlands in Sundaland and Indochina almost at the same time (Figure 3a). Thus, the Sino-Himalayan mountains and their adjacent tropical lowlands have the same EvolTime to accumulate considerable richness of basal species (Figure 2a). But the slower diversification, possibly due to an increased extinction rate, occurred in the tropical lowlands probably because of the disappearance of evergreen forests caused by the development of monsoon climate since mid-Oligocene, resulting in relative lower diversity in the lowlands (Sheldon. Lim, & Moyle, 2015).

Our results also suggest an alternative evolutionary process in building up diversity hotspots in the Sino-Himalayas by frequent colonizations from adjacent regions, as predicted by the multiple colonizations hypothesis (Johansson et al., 2007; Päckert et al., 2012). In contrast to the Oriental origin of pheasants (Wang, Kimball, Braun, Liang, & Zhang, 2017), we suggest that ancestral pheasants may have originated in tropical Africa (Figure 3a) (Crowe et al., 2006). from where subsequent dispersal events to Eurasia and Australia occurred. The earliest colonization of pheasants from Africa occurred in the Sino-Himalayan mountains in the mid-Oligocene, and they then diversified through in situ speciation and colonized Sundaland, southern China, the Indian Subcontinent, the Palearctic and North America. Backward colonizations into the Sino-Himalayan mountains occurred frequently, and mostly from Sundaland, southern China, the Palearctic and Africa at around 10 Ma. These multiple colonizations led to considerable species richness accumulation in the Sino-Himalayan mountains.

4.3 Combination of ecological and evolutionary hypotheses

The species richness of pheasants in the Sino-Himalayas is directly related to DivRate and NicheDiv, and indirectly correlated with NPP via DivRate (Figure 4a). This result indicates that DivRate and available niches constrain species accumulation in the Sino-Himalayan mountains, while the effect of EvolTime is relatively weak. The productivity–richness relationship is well documented in previous studies (Currie et al., 2004; Evans et al., 2005; Wright, 1983). The most common explanation for this relationship is that productivity reflects

available resources or NicheDiv, but our results find no evidence to support the hypothesis that higher diversity in the highly productive regions results from more niches (Evans et al., 2005). Instead, the productivity–richness relationship seems to be related to more available resources to sustain larger populations, resulting in an increased speciation rate and a lower extinction rate, which promote the rapid accumulation of species (Evans et al., 2005; Rosenzweig, 1995).

The relative roles of ecological and evolutionary mechanisms in driving species richness patterns vary among different mountains (Figure 4b–d). Compared with Indochina and the Hengduan Mountains, NPP has a stronger direct effect on species richness in the western Himalayas. This probably resulted from the harsh local climate; the weather is cold and arid, resulting in a relative low level of productivity (Owen et al., 2002). Thus, productivity is more important than others because it determines the availability of food resources in the western Himalayas. In contrast, productivity is less constrained in the eastern Himalayas, Hengduan Mountains and Indochina, and the species richness is therefore directly controlled here by other factors (e.g. NicheDiv and DivRate).

4.4 | Limitations

We recognize two methodological limitations for addressing the causes of species richness patterns in this study. First, the measure of DivRate may be imprecise. Our estimation of DivRate only relies on the phylogeny of extant species and does not consider extinct lineages. Thus, we cannot disentangle the roles of speciation and extinction rate independently, or explore to what extent the montane diversity hotspots resulting from accelerated speciation or absence of extinction. Moreover, the DivRate estimated in our study is a constant net rate that does not account for possible variation over time (Belmaker & Jetz, 2015). Likewise, it is also impossible to consider species dispersals among regions through time when we estimate the DivRate within assemblages. All these issues with estimating DivRate may have potential influences on testing the DivRate hypothesis, which needs to be examined in further studies.

Secondly, contemporary data of productivity and NicheDiv were used to predict historical processes that were contributed to species richness patterns in our SEMs, which could cause problems such as unmatched timescales of predictors regarding species richness. Obviously, contemporary productivity and NicheDiv cannot influence on past evolutionary processes. However, we lack historical data or alternative statistical tools to examine the relative roles of past and present ecological and evolutionary factors. Therefore, many previous studies have used contemporary variables in SEMs to examine their effects on evolutionary processes (Algar et al., 2009; Belmaker & Jetz, 2015; Qian et al., 2015). We justify this approach because (1) most of our study area is located in tropical and subtropical regions; thus, past climate and productivity may be highly related to today's (Owen et al., 2002). (2) Although our estimate of DivRate and EvolTime describe historical processes, they only represent the status or results of extant species. Therefore, we can consider the DivRate, EvolTime, productivity and NicheDiv being matched at timescales.

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In conclusion, our study shows that high diversity in the Sino-Himalayan mountains was generated by the combined contributions of more available niches, rapid diversification and multiple colonizations. Compared with previous studies testing or supporting only one or two hypotheses, our study offers new insights on species accumulated in the Sino-Himalayan mountains, which is controlled by both ecological and evolutionary processes. However, limitations of statistical methods and historical climate data cause difficulties with disentangling these processes, which need to be improved in future studies. Notwithstanding, this study provides a useful model for understanding species richness patterns in other taxa and geographic regions.

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REFERENCES

- Algar, A. C., Kerr, J. T., & Currie, D. J. (2009). Evolutionary constraints on regional faunas: Whom, but not how many. *Ecology Letters*, 12, 57– 65. https://doi.org/10.1111/j.1461-0248.2008.01260.x
- Belmaker, J., & Jetz, W. (2015). Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients. *Ecology Letters*, 18, 563–571. https://doi.org/10. 1111/ele.12438
- Cadena, C. D., Kozak, K. H., Gómez, J. P., Parra, J. L., McCain, C. M., Bowie, R. C., ... Roberts, T. E. (2011). Latitude, elevational climatic zonation and speciation in New World vertebrates. *Proceedings of the Royal Society of London B: Biological Sciences*, 272, 194–201.
- Che, J., Zhou, W., Hu, J., Yan, F., Papenfuss, T. J., Wake, D. B., & Zhang, Y. (2010). Spiny frogs (Paini) illuminate the history of the Himalayan

region and Southeast Asia. Proceedings of the National Academy of Sciences, 107, 13765–13770. https://doi.org/10.1073/pnas.1008415107

- Chesson, P. (2000). Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics, 31, 343–366. https://doi. org/10.1146/annurev.ecolsys.31.1.343
- Collar, N. J., Andreev, A., Chan, S., Crosby, M., Subramanya, S., & Tobias, J. (2001). Threatened birds of Asia: The BirdLife International red data book. Cambridge: Birdlife International.
- Crowe, T. M., Bowie, R. C. K., Bloomer, P., Mandiwana, T. G., Hedderson, T. A. J., Randi, E., ... Wakeling, J. (2006). Phylogenetics, biogeography and classification of, and character evolution in, gamebirds (Aves: Galliformes): Effects of character exclusion, data partitioning and missing data. *Cladistics*, *22*, 495–532. https://doi.org/10.1111/j.1096-0031.2006.00120.x
- Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guégan, J. F., Hawkins, B. A., ... O'Brien, E. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121–1134. https://doi.org/10.1111/j.1461-0248.2004.00671.x
- Dehling, D. M., Fritz, S. A., Töpfer, T., Päckert, M., Estler, P., Böhning-Gaese, K., & Schleuning, M. (2014). Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. *Ecography*, 37, 1047–1055.
- del Hoyo, J., Elliot, A., & Sargatal, J. (1994). Handbook of the birds of the world. Barcelona: Lynx Editions.
- Ding, T., Yuan, H., Geng, S., Koh, C., & Lee, P. (2006). Macro-scale bird species richness patterns of the East Asian mainland and islands: Energy, area and isolation. *Journal of Biogeography*, *33*, 683–693. https://doi.org/10.1111/j.1365-2699.2006.01419.x
- Evans, K. L., Warren, P. H., & Gaston, K. J. (2005). Species-energy relationships at the macroecological scale: A review of the mechanisms. *Biological Reviews*, 80, 1–25. https://doi.org/10.1017/S1464793 104006517
- Favre, A., Packert, M., Pauls, S. U., Jahnig, S. C., Uhl, D., Michalak, I., & Muellner-Riehl, A. N. (2015). The role of the uplift of the Qinghai-Tibetan Plateau for the evolution of Tibetan biotas. *Biological Reviews*, 90, 236–253. https://doi.org/10.1111/brv.12107
- Fjeldså, J., Bowie, R. C. K., & Rahbek, C. (2012). The role of mountain ranges in the diversification of birds. Annual Review of Ecology, Evolution, and Systematics, 43, 249–265. https://doi.org/10.1146/annurevecolsys-102710-145113
- Fjeldså, J., & Rahbek, C. (2006). Diversification of tanagers, a species rich bird group, from lowlands to montane regions of South America. *Integrative and Comparative Biology*, 46, 72–81. https://doi.org/10.1093/ icb/icj009
- Gill, F., & Donsker, D. (2015). IOC world bird list (v 5.4). https://doi.org/ 10.14344/ioc.ml.5.4
- Gower, J. C. (1966). Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika*, 53, 325–338. https://doi.org/10.1093/biomet/53.3-4.325
- Helmus, M. R., Bland, T. J., Williams, C. K., & Ives, A. R. (2007). Phylogenetic measures of biodiversity. *The American Naturalist*, 169, E68– E83. https://doi.org/10.1086/511334
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978. https://doi.org/10.1002/(ISSN)1097-0088
- Holt, B. G., Lessard, J.-P., Borregaard, M. K., Fritz, S. A., Araújo, M. B., Dimitrov, D., . . . Jønsson, K. A. (2013). An update of Wallace's zoogeographic regions of the world. *Science*, 339, 74–78. https://doi.org/ 10.1126/science.1228282
- Imhoff, M., Bounoua, L., Ricketts, T., Loucks, C., Harriss, R., & Lawrence, W. T. (2004). Global patterns in net primary productivity. HANPP collection: Global patterns in net primary productivity (NPP). Palisades, NY:

NASA Socioeconomic Data and Applications Center (SEDAC). https://doi.org/10.7927/h40z715x Accessed 25 Sep 2014.

- Jetz, W., & Rahbek, C. (2002). Geographic range size and determinants of avian species richness. *Science*, 297, 1548–1551. https://doi.org/ 10.1126/science.1072779
- Jetz, W., Rahbek, C., & Colwell, R. K. (2004). The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecology Letters*, 7, 1180–1191. https://doi.org/10.1111/j. 1461-0248.2004.00678.x
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, 491, 444– 448. https://doi.org/10.1038/nature11631
- Johansson, U. S., Alström, P., Olsson, U., Ericson, P. G., Sundberg, P., & Price, T. D. (2007). Build-up of the Himalayan avifauna through immigration: A biogeographical analysis of the *Phylloscopus* and *Seicercus* Warblers. *Evolution*, 61, 324–333. https://doi.org/10.1111/j.1558-5646.2007.00024.x
- Kennedy, J. D., Weir, J. T., Hooper, D. M., Tietze, D. T., Martens, J., & Price, T. D. (2012). Ecological limits on diversification of the Himalayan core Corvoidea. *Evolution*, 66, 2599–2613. https://doi.org/10. 1111/j.1558-5646.2012.01618.x
- Körner, C., Paulsen, J., & Spehn, E. M. (2011). A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. *Alpine Botany*, 121, 73–78. https://doi.org/10.1007/s00035-011-0094-4
- Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305. https://doi.org/10.1890/08-2244.1
- Laliberté, E., Legendre, P., Shipley, B., & Laliberté, M. E. (2014). Package 'FD'. Version, 1, 12.
- Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology* and Evolution, 7, 573–579. https://doi.org/10.1111/2041-210X.12512
- Leneveu, J., Chichvarkhin, A., & Wahlberg, N. (2009). Varying rates of diversification in the genus *Melitaea* (Lepidoptera: Nymphalidae) during the past 20 million years. *Biological Journal of the Linnean Society*, 97, 346–361. https://doi.org/10.1111/j.1095-8312.2009.01208.x
- Li, J., He, Q., Hua, X., Zhou, J., Xu, H., Chen, J., & Fu, C. (2009). Climate and history explain the species richness peak at mid-elevation for *Schizothorax* fishes (Cypriniformes: Cyprinidae) distributed in the Tibetan Plateau and its adjacent regions. *Global Ecology and Biogeography*, 18, 264–272. https://doi.org/10.1111/j.1466-8238.2008.00430.x
- Marchese, C. (2015). Biodiversity hotspots: A shortcut for a more complicated concept. Global Ecology and Conservation, 3, 297–309. https://d oi.org/10.1016/j.gecco.2014.12.008
- Matzke, N. J. (2014). Model selection in historical biogeography reveals that founder-event speciation is a crucial process in Island Clades. *Systematic Biology*, 63, 951–970. https://doi.org/10.1093/sysbio/ syu056
- Merow, C., Wilson, A. M., & Jetz, W. (2017). Integrating occurrence data and expert maps for improved species range predictions. *Global Ecol*ogy and Biogeography, 26, 243–258. https://doi.org/10.1111/geb. 12539
- Moen, D., & Morlon, H. (2014). Why does diversification slow down? Trends in Ecology & Evolution, 29, 190–197. https://doi.org/10.1016/j. tree.2014.01.010
- Owen, L. A., Finkel, R. C., & Caffee, M. W. (2002). A note on the extent of glaciation throughout the Himalaya during the global Last Glacial Maximum. Quaternary Science Reviews, 21, 147–157. https://doi.org/ 10.1016/S0277-3791(01)00104-4
- Päckert, M., Martens, J., Sun, Y. H., Severinghaus, L. L., Nazarenko, A. A., Ting, J., ... Tietze, D. T. (2012). Horizontal and elevational phylogeographic patterns of Himalayan and Southeast Asian forest passerines (Aves: Passeriformes). *Journal of Biogeography*, *39*, 556–573. https://d oi.org/10.1111/j.1365-2699.2011.02606.x

- Price, T. D., Hooper, D. M., Buchanan, C. D., Johansson, U. S., Tietze, D. T., Alstrom, P., ... Mohan, D. (2014). Niche filling slows the diversification of Himalayan songbirds. *Nature*, 509, 222–225. https://doi. org/10.1038/nature13272
- Qian, H., Wiens, J. J., Zhang, J., & Zhang, Y. (2015). Evolutionary and ecological causes of species richness patterns in North American angiosperm trees. *Ecography*, 38, 241–250. https://doi.org/10.1111/ ecog.00952
- Qu, Y., Ericson, P. G. P., Quan, Q., Song, G., Zhang, R., Gao, B., & Lei, F. (2014). Long-term isolation and stability explain high genetic diversity in the Eastern Himalaya. *Molecular Ecology*, 23, 705–720. https://doi. org/10.1111/mec.12619
- R Core Team. (2016). R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/.
- Rabosky, D. L. (2009). Ecological limits on clade diversification in higher taxa. The American Naturalist, 173, 662–674. https://doi.org/10. 1086/597378
- Rahbek, C., Gotelli, N. J., Colwell, R. K., Entsminger, G. L., Rangel, T. F. L. V. B., & Graves, G. R. (2007). Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proceedings of the Royal Society of London B: Biological Sciences*, 274, 165–174. https://d oi.org/10.1098/rspb.2006.3700
- Randi, E., Lucchini, V., Armijo-Prewitt, T., Kimball, R. T., Braun, E. L., & Ligon, J. D. (2000). Mitochondrial DNA phylogeny and speciation in the Tragopans. Auk, 117, 1003–1015. https://doi.org/10.1642/0004-8038(2000)117[1003:MDPASI]2.0.CO;2
- Rangel, T. F., Diniz-Filho, J. A. F., & Bini, L. M. (2010). SAM: A comprehensive application for spatial analysis in macroecology. *Ecography*, 33, 46–50. https://doi.org/10.1111/j.1600-0587.2009.06299.x
- Renner, S. S. (2016). Available data point to a 4-km-high Tibetan Plateau by 40 Ma, but 100 molecular-clock papers have linked supposed recent uplift to young node ages. *Journal of Biogeography*, 43, 1479– 1487. https://doi.org/10.1111/jbi.12755
- Rosenzweig, M. L. (1995). Species diversity in space and time. Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9780511 623387
- Ruggiero, A., & Hawkins, B. A. (2008). Why do mountains support so many species of birds? *Ecography*, 31, 306–315. https://doi.org/10. 1111/j.0906-7590.2008.05333.x
- Schnitzler, J., Barraclough, T. G., Boatwright, J. S., Goldblatt, P., Manning, J. C., Powell, M. P., ... Savolainen, V. (2011). Causes of plant diversification in the Cape biodiversity hotspot of South Africa. Systematic Biology, 60, 343–357. https://doi.org/10.1093/sysbio/syr006
- Sheldon, F. H., Lim, H. C., & Moyle, R. G. (2015). Return to the Malay Archipelago: The biogeography of Sundaic rainforest birds. *Journal of Ornithol*ogy, 156, 91–113. https://doi.org/10.1007/s10336-015-1188-3
- Smith, S. A., de Oca, A. N., Reeder, T. W., & Wiens, J. J. (2007). A phylogenetic perspective on elevational species richness patterns in Middle American treefrogs: Why so few species in lowland tropical rainforests? *Evolution*, *61*, 1188–1207. https://doi.org/10.1111/j.1558-5646.2007.00085.x
- Stein, R. W., Brown, J. W., & Mooers, A. Ø. (2015). A molecular genetic time scale demonstrates Cretaceous origins and multiple diversification rate shifts within the order Galliformes (Aves). *Molecular Phylogenetics and Evolution*, 92, 155–164. https://doi.org/10.1016/j.ympev. 2015.06.005
- Stephens, P. R., & Wiens, J. J. (2003). Explaining species richness from continents to communities: The time-for-speciation effect in emydid turtles. *The American Naturalist*, 161, 112–128.
- Wang, N., Kimball, R. T., Braun, E. L., Liang, B., & Zhang, Z. (2013). Assessing phylogenetic relationships among galliformes: A multigene

phylogeny with expanded taxon sampling in Phasianidae. *PLoS ONE*, 8, e64312. https://doi.org/10.1371/journal.pone.0064312

- Wang, N., Kimball, R. T., Braun, E. L., Liang, B., & Zhang, Z. (2017). Ancestral range reconstruction of Galliformes: The effects of topology and taxon sampling. *Journal of Biogeography*, 44, 122–135. https://doi.org/10.1111/jbi.12782
- Wiens, J. J., & Donoghue, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, 19, 639–644. https://doi.org/10.1016/j.tree.2004.09.011
- Wiens, J. J., Parra-Olea, G., García-París, M., & Wake, D. B. (2007). Phylogenetic history underlies elevational biodiversity patterns in tropical salamanders. *Proceedings of the Royal Society B: Biological Sciences*, 274, 919–928. https://doi.org/10.1098/rspb.2006.0301
- Wright, D. H. (1983). Species-energy theory: An extension of speciesarea theory. Oikos, 41, 496–506. https://doi.org/10.2307/3544109
- Wu, Y., Colwell, R. K., Han, N., Zhang, R., Wang, W., Quan, Q., ... Lei, F. (2014). Understanding historical and current patterns of species richness of babblers along a 5000-m subtropical elevational gradient. *Global Ecology* and Biogeography, 23, 1167–1176. https://doi.org/10.1111/geb.12197
- Wu, Y., Colwell, R. K., Rahbek, C., Zhang, C., Quan, Q., Wang, C., & Lei, F. (2013). Explaining the species richness of birds along a subtropical elevational gradient in the Hengduan Mountains. *Journal of Biogeography*, 40, 2310–2323. https://doi.org/10.1111/jbi.12177
- Xing, Y., & Ree, R. H. (2017). Uplift-driven diversification in the Hengduan Mountains, a temperate biodiversity hotspot. *Proceedings of the National Academy of Sciences*, 114, E3444–E3451. https://doi.org/10. 1073/pnas.1616063114
- Zhang, C., Quan, Q., Wu, Y., Chen, Y., He, P., Qu, Y., & Lei, F. (2016). Topographic heterogeneity and temperature amplitude explain species richness patterns of birds in the Qinghai-Tibetan Plateau. *Current Zoology*, 63, 131–137.

BIOSKETCH

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Author contributions: F.L. designed the study program; T.C., Y.W. and F.L. conceived the ideas; T.C., Q.Q. and S.S. collected the data; T.C., J.F., S.S, Y.C. and X.L. carried out the statistical analyses; and all authors drafted the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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