



ORIGINAL
ARTICLE



Explaining the species richness of birds along a subtropical elevational gradient in the Hengduan Mountains

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ABSTRACT

Aim To document the species richness pattern of birds in the Hengduan Mountains and to understand its causes.

Location Hengduan Mountains, China.

Methods Species richness of 738 breeding bird species was calculated for each 100-m elevational band along a gradient from 100 to 6000 m a.s.l. Climate data were compiled based on monthly records from 182 meteorological stations in the Hengduan Mountains from 1959 to 2004. We calculated the planimetric area, predicted richness under geometric constraints, three-year average NDVI (normalized difference vegetation index) and EVI (enhanced vegetation index) in each elevational band. Simple and multiple regression models were used to test the explanatory power of variables associated with different factors proposed to account for elevational species richness gradients.

Results The elevational pattern in species richness, for all breeding birds, was hump-shaped, with the peak occurring at 800–1800 m elevation. Endemic and non-endemic species, as well as four elevational range size categories of birds, also showed the general hump-shaped patterns of species richness, but with peaks at different elevations. In most data sets, species richness correlated well with climatic and energy factors along the elevational gradients; seasonality and productivity had a strong statistical relationship with species richness of montane birds in this study, with geometric constraints contributing to richness patterns for larger-ranged species endemic to the gradient.

Main conclusions We found that climatic and energy factors correlate well with the richness pattern of birds, and that on the surveyed subtropical mountain, the elevational bands with highest seasonality harbour fewer species than areas with less seasonal variation in temperature. The results, however, vary somewhat among taxonomic groups. The most diverse species groups and species with the broadest ranges have a disproportionate influence on our perception of the overall diversity pattern and its underlying explanatory factors.

Keywords

Birds, China, climate, elevational gradients, geometric constraints, Hengduan Mountains, productivity, seasonality, species richness.

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INTRODUCTION

Knowledge of patterns of species richness has increased considerably over recent decades, but our understanding of the underlying mechanisms that shape such patterns is in many ways still in its infancy. Given the advantages (e.g. globally

replicated gradients and smaller spatial scale) of elevational gradients relative to latitudinal gradients (Rahbek, 2005), a growing body of research focuses on the utility of elevational gradients as tools to uncover the mechanisms and constraints that shape both patterns of biodiversity and the functioning of ecosystems (Rahbek, 1995, 2005; Colwell & Lees, 2000;

Lomolino, 2001; McCain, 2004, 2009; Fu *et al.*, 2006; Kluge *et al.*, 2006; Nogués-Bravo *et al.*, 2008; Wu *et al.*, 2013). Different elevational richness patterns have been reported from different taxa, e.g. plants (Bhattarai *et al.*, 2004; Wang *et al.*, 2007), small mammals (McCain, 2005; Wu *et al.*, 2013), birds (Kattan & Franco, 2004; McCain, 2010) and reptiles (Fu *et al.*, 2007; McCain, 2010). Rahbek (1995, 2005) documented that patterns of species richness along elevational gradients can generally be classified into four forms: monotonically decreasing richness with elevation, low-elevation richness plateaux followed by a decrease with elevation, low-elevation plateaux with mid-elevation richness peaks, and unimodal mid-elevational peaks. McCain (2009) gathered and analysed data sets from birds, and showed that they fall in each of these four categories with almost equal frequency. These generalizations on both the general pattern and the specific pattern for birds, however, are derived almost exclusively from studies of temperate-zone mountains in Europe and North America or tropical mountains in South America, Africa and islands in Southeast Asia, whereas studies, in particular on birds, from mainland subtropical continental Asia are generally lacking. Previous studies focusing on species richness patterns in mammals, reptiles, fish and plants along the elevational gradient in the Hengduan Mountains (China) demonstrated that species richness patterns differ widely among life forms, and the corresponding explanations are also diverse and controversial (Fu *et al.*, 2006, 2007; Wang *et al.*, 2007; Zhang *et al.*, 2008; Li *et al.*, 2009; Wu *et al.*, 2013). A comprehensive analysis of bird species richness patterns at the regional scale for the Hengduan Mountains is still lacking.

Area, geometric constraints, climate and productivity are the most frequently cited explanations for variations in species richness (Rahbek, 1997, 2005; Colwell *et al.*, 2004; McCain, 2004; Koh *et al.*, 2006; Nogués-Bravo *et al.*, 2008; Sanders & Rahbek, 2012). That larger areas harbour more species is well documented (Rosenzweig, 1995). Rahbek (1997) demonstrated that the area available within each elevational zone has a significant impact on the elevational species richness pattern, and subsequent studies have confirmed the role of area in shaping the species richness gradient (Bachman *et al.*, 2004; Kattan & Franco, 2004; McCain, 2005, 2009; Fu *et al.*, 2007), although none of these studies argued that the area of each elevational band was the primary driver of species richness patterns. The mid-domain effect (MDE) is the increasing overlap of species ranges towards the centre of a shared, bounded domain due to geometric boundary constraints (Colwell & Hurtt, 1994; Colwell & Lees, 2000; Colwell *et al.*, 2004, 2005). Studies have demonstrated that geometric constraints (GC) may also explain a substantial proportion of the variation in richness for some groups along elevational gradients (McCain, 2004; Colwell *et al.*, 2005; Brehm *et al.*, 2007; Rowe, 2009; Wu *et al.*, 2013).

Previous studies have shown that contemporary climate, often captured as mean annual temperature (MAT), annual precipitation (AP) and their combination (annual actual

evapotranspiration), has considerable explanatory power for both continental and elevational patterns of species richness (Rahbek, 1997; Hawkins *et al.*, 2003, 2005, 2007; Fu *et al.*, 2006; McCain, 2009; Rowe, 2009). In addition, the mean annual temperature range (MATR) has been linked to the pattern of avian richness in some data sets (Hurlbert & Haskell, 2003). Species richness, as an important basic character of an ecosystem, reflects the complexity and amounts of energy and material transfer in an ecosystem, indicating that species richness may be positively correlated with productivity. In addition, the normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI) are thought to reflect the productivity (net primary productivity or gross primary productivity) of an ecosystem, and have also been found to be good predictors of bird diversity patterns in many continental and elevational studies (Lee *et al.*, 2004; Hawkins *et al.*, 2005, 2007; Koh *et al.*, 2006).

The generality of all these findings and the role of each explanatory factor in shaping patterns of species richness needs to be assessed for different taxa and biogeographical regions, because the ecological requirements of species vary greatly even among closely related taxa – e.g. hummingbirds in South America (Graham *et al.*, 2009) and flowerpeckers in the Oriental Realm (Nyári *et al.*, 2009) – and species composition often differs substantially even in nearby regions.

Richness itself is the statistical sum of overlapping ranges and thus the overall richness pattern of all species is directly linked to the range sizes of species and the range-size frequency distribution. Biogeographical variation in regional species composition, including the proportion and distribution of endemic species versus widespread species and the comparison of species within and between taxonomic groups, may contribute to differences in richness patterns. In the current study, as in other elevational gradient studies, the choice of independent variables is limited to contemporary factors, but separate analyses on data sets of non-endemic versus endemic species, range size classes and different taxonomic orders may shed some indirect light on the degree to which evolutionary processes have a role in shaping gradients of richness (Kessler, 2000; Rahbek, 2005). Here, therefore, we explore elevational patterns in species richness for all breeding bird species in the Hengduan Mountains of China, and assess the roles of area, climate, productivity and geometric constraints in explaining the elevational patterns of species richness among different species groups.

MATERIALS AND METHODS

Study area

The Hengduan Mountains (22–32° N, 98–104° E), one of the world's 34 hotspots of plant diversity and habitat loss (Mittermeier *et al.*, 2005), lie within the Oriental and Palaearctic faunal realms. The northern and western ranges of the Hengduan Mountains encompass part of the Qinghai-Tibet Plateau at high elevations (4000 m on average), while the

southern and eastern parts lie at elevations below 300 m, including the Sichuan Basin and the Honghe (Red River) Valley. This region is characterized by a series of parallel mountain ranges and rivers running north to south, with a sharp elevational differentiation from the Honghe Valley in the southern lowlands at approximately 70 m, to the summit of Gongga Shan (7556 m), the highest peak in this region, offering an ideal gradient for elevational diversity research (Fig. 1a). The total area of the research region is about 660,000 km² (based on the STRM 90-m digital elevational data from <http://srtm.csi.cgiar.org/>) covering the eastern part of the Tibet Autonomous Region, western portions of Sichuan Province and the north-western part of Yunnan Province. Yunnan and Sichuan provinces harbour the richest and second richest bird fauna in China, respectively (Li *et al.*, 1993; Yang *et al.*, 2004). The research area is located in the subtropical monsoon climate zone, but the regional climate is also influenced by the Qinghai-Tibetan Plateau and montane climates. The Hengduan Mountains have a complicated geological topography and a classic montane climate with striking vertical climatic zonation, ranging from

the subtropical zone to the frigid zone, with diverse vegetation types and landscapes (Zhang *et al.*, 1997).

Elevational species richness

Data on the elevational distributions of species were compiled from primary-level museum records and observational records, supplemented with information from the specialized literature (see Appendix S1 in Supporting Information). Among all of these elevational records, we used the highest and lowest elevational records for each species as its final elevational range limits. All the data were quality-checked based on our personal experience within the region, and dubious outlying records that could not be verified were removed. Our synthesis summarized elevational records for 925 bird species in total, belonging to 19 orders, 88 families and 335 genera. However, only 738 bird species (belonging to 19 orders, 80 families and 295 genera) that breed in the Hengduan Mountains were analysed in our study. Because non-breeding birds migrate across this region in winter, total species richness is very sensitive to seasonality. Moreover,

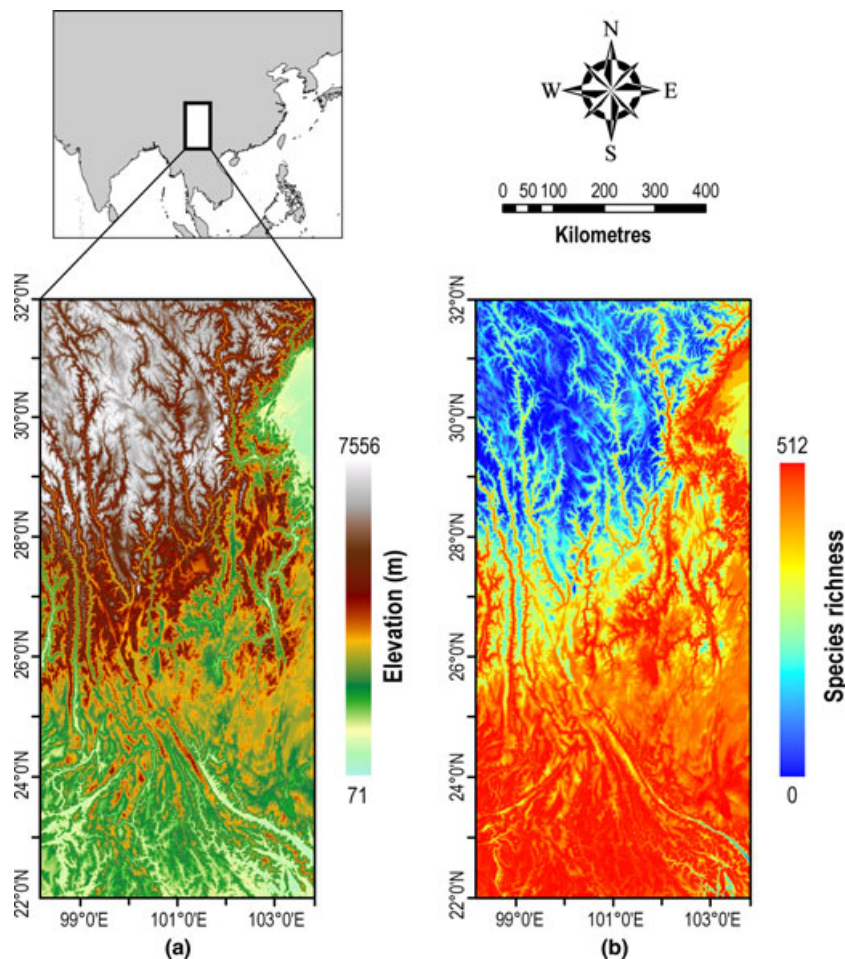


Figure 1 Map of the study area (black rectangle) in the Hengduan Mountains, under the Mollweide projection. (a) Terrain map; (b) species richness pattern of birds along the elevational gradient. Extreme topographic range and complexity make the region ideal for the study of elevational variation in species richness.

distributional data for many of these non-breeding birds are inadequate.

Each species is assumed to be present or potentially present between its highest and lowest reported elevations (range interpolation). This approach is widely regarded as valid for vagile species and allows methodological consistency because most published accounts have assumed range continuity (Rahbek, 1997; Colwell *et al.*, 2004; Fu *et al.*, 2006; Brehm *et al.*, 2007; McCain, 2009; Wu *et al.*, 2013). Species richness for these interpolated ranges was then calculated based on the number of bird ranges occurring in each 100-m elevational band (e.g. 100–199.9 m) from 100 m to 6000 m a.s.l. Endemic species ($n = 165$) are defined here as breeding birds with distributions limited to the Hengduan Mountains and the surrounding region (middle and eastern portions of the Himalayas, south-eastern portion of the Qinghai-Tibetan Plateau and northern portions of Burma, Laos and Vietnam). The remaining breeding bird species were defined as non-endemic species ($n = 573$). Endemic species that are characterized by narrow planimetric distribution patterns, however, do not always have narrow elevational distributions; thus, distributional patterns and their explanatory factors are also not necessarily similar between endemic and elevationally narrowly distributed species groups (Brehm *et al.*, 2007; Fu *et al.*, 2007; Wu *et al.*, 2013). We therefore divided all breeding bird species into four categories based on the size of each species' elevational range (200–1300 m, 1301–2600 m, 2601–3900 m, 3901–5200 m). We defined these range size categories as first ($n = 173$), second ($n = 354$), third ($n = 166$) and fourth ($n = 45$), roughly following the approach of Lees *et al.* (1999), Jetz & Rahbek (2002), and others. Geometric constraints theory predicts that wide-ranged endemic species will be the group most constrained by geometry (Colwell & Lees, 2000; Colwell *et al.*, 2004, 2005; Dunn *et al.*, 2007). To assess this prediction, we also divided endemic species by range size into four categories as above.

We adjusted elevational range for species ($n = 20$) recorded at only a single elevation (thus having a recorded elevational range value = 0) by adding 100 m to each side of the recorded elevation, following the strategy of previous studies (Stevens, 1992; Cardelús *et al.*, 2006; Brehm *et al.*, 2007), so that each of these species was assumed to have an elevational range of 200 m. This approach avoids species recorded at only a single-site from being 'lost' between sampling elevations during the randomization of range midpoints and is clearly more realistic than treating these species as having zero elevational range. Considering the vagility of birds, we assumed the smallest elevational range of birds is 200 m and also adjusted the elevational range to 200 m for other species with recorded elevational distribution range less than 200 m.

Our comprehensive data set for this rich avifauna allows us to explore the richness patterns of different species groups of birds and their relationship with environmental and geometric factors. We divided the species into several taxonomic groups (Passeriformes, Galliformes, Falconiformes, Strigiformes, Piciformes, Cuculiformes, Coraciiformes and Columbi-

formes) with different ecological habits and evolutionary histories. Taxonomic groups including fewer species ($n < 15$) were not analysed owing to inadequate elevational distribution data and small sample size. The taxonomic system used in this study followed Zheng *et al.* (2005). Species checklists of breeding birds in the Hengduan Mountains and the data sources are listed in Appendix S1.

Area

We used STRM 90-m digital elevation data from CGIAR-CSI (<http://srtm.csi.cgiar.org/>) to calculate the planimetric area of each elevational band in Hengduan Mountains (22–32° N, 98–104° E). We divided the range of elevation into 59 bands (100 m for each band) between 100 and 6000 m and examined the relationship between area and elevation (Fig. 2d). The planimetric area of each elevational band in the Hengduan Mountains was calculated in ENVI 4.7 (ITT Exelis, McLean, VA, USA) and ARCGIS 9.3 (ESRI, Redlands, CA, USA). We also calculated surface area for each band, but surface area was almost perfectly ($r = 0.999$, $P < 0.01$) correlated with planimetric area, which we chose to use for comparability with previous studies.

Geometric constraints (the mid-domain effect)

We used RANGEMODEL 5 (Colwell, 2008; <http://purl.oclc.org/rangemodel>) to calculate interpolated species richness and estimate predicted species richness under 'pure' (assuming no interaction with other factors) geometric constraints (GC). We ran 5000 randomizations of the geometrically constrained null model (random range placement) to compute the mean expected species richness and its 95% confidence interval (CI) for each elevational band (e.g. 150 m, 250 m, ...).

Climate

We calculated mean annual temperature (MAT; to facilitate reading, we write 'temperature' instead of MAT in narrative contexts in the text), annual precipitation (AP; we write 'precipitation' instead of AP) and mean annual temperature range (MATR; we write 'temperature seasonality' instead of MATR) in each elevational band (100 m for each band) based on monthly records from 182 selected local meteorological stations in the Hengduan Mountains (22–32° N, 98–104° E) covering 1959 to 2004. The mean annual temperature range is the difference between mean temperature in July and January in each year. All climatic recording data were obtained from the China Meteorological Data Sharing Service System (<http://cdc.cma.gov.cn/>). We used linear (for MAT) and LOESS (for AP and MATR) regression to estimate climatic variables for each elevational band along the elevational gradient. Those sites without climatic records were linearly or curvilinearly extrapolated or interpolated based on the data from nearby sites with records.

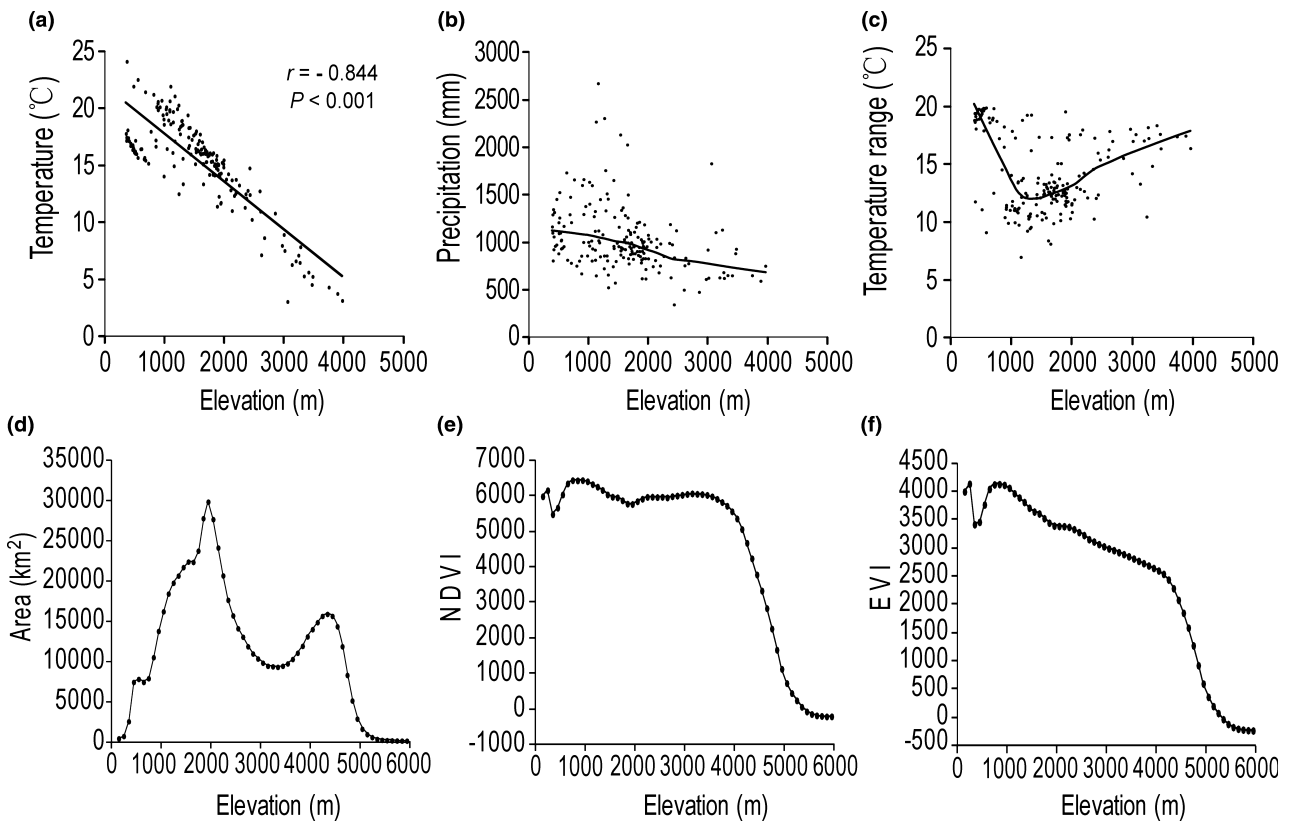


Figure 2 Elevational pattern in the Hengduan Mountains of (a) mean annual temperature (line fitted by simple linear regression), (b) annual precipitation (line fitted by LOESS regression), (c) mean annual temperature range (line fitted by LOESS regression), (d) elevational band area, (e) normalized difference vegetation index (NDVI), and (f) enhanced vegetation index (EVI).

Productivity

Longer-term averages of vegetation data help remove errors caused by heavy clouds and suspended particles. Therefore, we calculated the NDVI and EVI in each elevational band for January, April, July and October for three years (2006, 2007 and 2010) in the Hengduan Mountains. To avoid the influence of the 2008 Wenchuan earthquake (an 8.0 earthquake) on the vegetation index, we excluded the remote-sensing data for 2008 and 2009. The NDVI and EVI were calculated using MODIS Reprojection Tool 4.1 (LP DAAC, Sioux Falls, SD, USA) and ENVI 4.7. All the remote sensing data were downloaded from <http://reverb.echo.nasa.gov/reverb/>.

Statistical analysis

We performed polynomial regressions (richness as a function of elevation, elevation² and elevation³) to assess the form of the elevational distribution patterns of species richness for each species group, guided by the corrected Akaike information criterion (AIC_c) value. We used Neyman–Pearson correlation to examine the relationships among the independent variables (Area, MAT, AP, MATR, NDVI, EVI and GC). To

examine the potential of individual factors in explaining elevational patterns of species richness, we performed simple ordinary least squares (OLS) regressions of interpolated species richness for each species group (all birds, endemic and non-endemic species, larger-ranged and smaller-ranged species, Passeriformes, Galliformes, Falconiformes, Strigiformes, Piciformes, Cuculiformes, Coraciiformes and Columbiformes) against each of the potential explanatory factors (see Table S2 in Appendix S2). We also report adjusted *P*-values (*P*_{adj}) for each simple regression, based on degrees of freedom adjusted for spatial autocorrelation in regression residuals, following Dutilleul's (1993) method.

Before carrying out the multiple regressions, we checked the normality and homoscedasticity of variables (Osborne & Waters, 2002). The variables were nearly normally distributed and their variances were almost homogeneous. We selected the best model from the 63 models representing all possible combinations of simple variables, guided by the lowest AIC_c value (Anderson *et al.*, 1998). The standardized beta coefficient of the best-fit model indicates the relative importance of each factor in the models. In the case of nearly equivalent support for multiple models (i.e. AIC_c or ΔAIC_c values nearly equal, i.e. ΔAIC_c < 2), we used the model-averaging approach to compare with the selected best model and to

assess the relative importance of different explanatory variables, guided by standardized beta coefficients (Anderson & Burnham, 2002; Johnson & Omland, 2004). However, sometimes choosing the best model can be challenging (Arnold, 2010). To avoid missing other models of particular interest, all 63 models for each species groups with their ΔAIC_c , condition number (which measures multicollinearity), Moran's I and their AIC_c weights are reported in Appendix S3: Tables S7–S21.

The presence of spatial autocorrelation in regression residuals (as revealed by Moran's I) and multicollinearity among explanatory variables [as quantified by the variance inflation factor (VIF) or condition number] in the models need to be taken into account (Diniz-Filho *et al.*, 2003; Graham, 2003). We used multiple conditional autoregressive (CAR) models (with $\alpha = 2.0$) and multiple OLS models to assess the influence of spatial autocorrelation on the regression results. Because temperature and precipitation are highly correlated with productivity ($r = 0.946$, $P < 0.001$; $r = 0.88$, $P < 0.001$; Table 1), productivity may best reflect the combination of temperature and precipitation in this region, where high productivity means a warm and humid climate. Therefore, to reduce the multicollinearity in the model we conducted CAR and OLS models without temperature and precipitation variables (Graham, 2003; Koh *et al.*, 2006). Only area, temperature seasonality, productivity, and geometric constraints were tested in the multiple OLS and CAR regressions for all species groups. To evaluate the relative roles of spatial and non-spatial factors in shaping richness patterns, we used partial regression for different species groups with four variables (area, geometric constraints, temperature seasonality, productivity) partitioned into non-spatial variables (temperature seasonality and productivity) and spatial variables (area and geometric constraints) to compare the explanatory power of the seasonality, productivity and spatial factors.

Simple regression and multiple regression analyses were performed in SAM 4.0 (Rangel *et al.*, 2010; <http://www.ecoevol.ufg.br/sam>). Polynomial regression and Pearson

correlation analyses were performed in PAST 2.17 (Hammer *et al.*, 2001; <http://folk.uio.no/ohammer/past/>).

RESULTS

The elevational patterns of environmental variables and bird species richness

Mean annual temperature (MAT), based on simple linear regression ($r^2 = 0.712$, $P < 0.001$), decreases with elevation at a rate of -0.42 °C/100 m in the Hengduan Mountains (Fig. 2a). Annual precipitation (AP), based on LOESS regression, decreases almost linearly with elevation at a rate of about 116.1 mm/100 m (Fig. 2b). Mean annual temperature range (MATR), based on LOESS regression, shows a concave curve along the elevational gradient. MATR decreases at a rate of about -1.04 °C/100 m below 1200 m and increases at a rate of about 0.25 °C/100 m above 1200 m (Fig. 2c). The area in each elevational band increases with elevation up to 2000 m, then decreases with elevation up to 3400 m. From 3400 m to 4700 m, area has a second peak, as the Qinghai-Tibet plateau has a significant influence on area in the Hengduan Mountains (Fig. 2d). The patterns for the NDVI and EVI are similar along the elevational gradient. However, EVI decreases more substantially with elevation from 1200 m to 4500 m whereas NDVI shows a stable plateau at low and mid-elevations. For low and mid-elevations (the subtropical climate region), EVI is more sensitive to elevation than is NDVI (Fig. 2e,f).

The elevational species richness pattern in the Hengduan Mountains for all breeding bird species, considered together, is a hump-shaped pattern with a peak at low elevation (800–1800 m, Fig. 3a). Each of the data subsets for endemic species, non-endemic species, and first through fourth range size classes also shows a hump-shaped elevational pattern of species richness, with some differences (Fig. 3b–g). Endemic species richness peaks at mid-elevation (2200–2800 m) and shows a nearly symmetrical pattern, whereas non-endemic species richness peaks at low elevation (600–1500 m), with species richness increasing rapidly at low elevation and decreasing slowly at high elevation. Richness of species in the first (smallest) range size class peaks at low elevations (500–1000 m) and decreases slowly at middle and high elevations (Fig. 3d). Richness of species in the second range size class also peaks at relatively low elevations (1100–2000 m, Fig. 3e), while species richness for the third range size class peaks at mid-elevations (2000–3000 m, Fig. 3f). Richness of species in the fourth (largest) range size class peaks over a wide elevational plateau from low to high elevations (800–4000 m, Fig. 3g).

The species richnesses of different avian orders show a variety of patterns along the elevational gradient (Fig. 4b–i). Despite the different details of the patterns, most of these taxa show a hump-shaped pattern of richness, with the peaks occurring at low elevations (600–1500 m) except for Passeriformes and Galliformes. Passerine species richness also

Table 1 Pearson correlation coefficients for the seven selected environmental variables used in models to analyse the species richness pattern of birds in the Hengduan Mountains.

	Area	MAT	AP	MATR	NDVI	EVI
Area						
MAT	0.448*					
AP	0.419*	0.991*				
MATR	-0.860*	-0.627*	-0.596*			
NDVI	0.635*	0.819*	0.757*	-0.759*		
EVI	0.626*	0.919*	0.879*	-0.755*	0.972*	
GC	0.630*	0.062	-0.041	-0.619*	0.565*	0.395*

* $P < 0.01$.

MAT, mean annual temperature; AP, annual precipitation; MATR, mean annual temperature range; NDVI, normalized difference vegetation index; EVI, enhanced vegetation index; GC, geometric constraints.

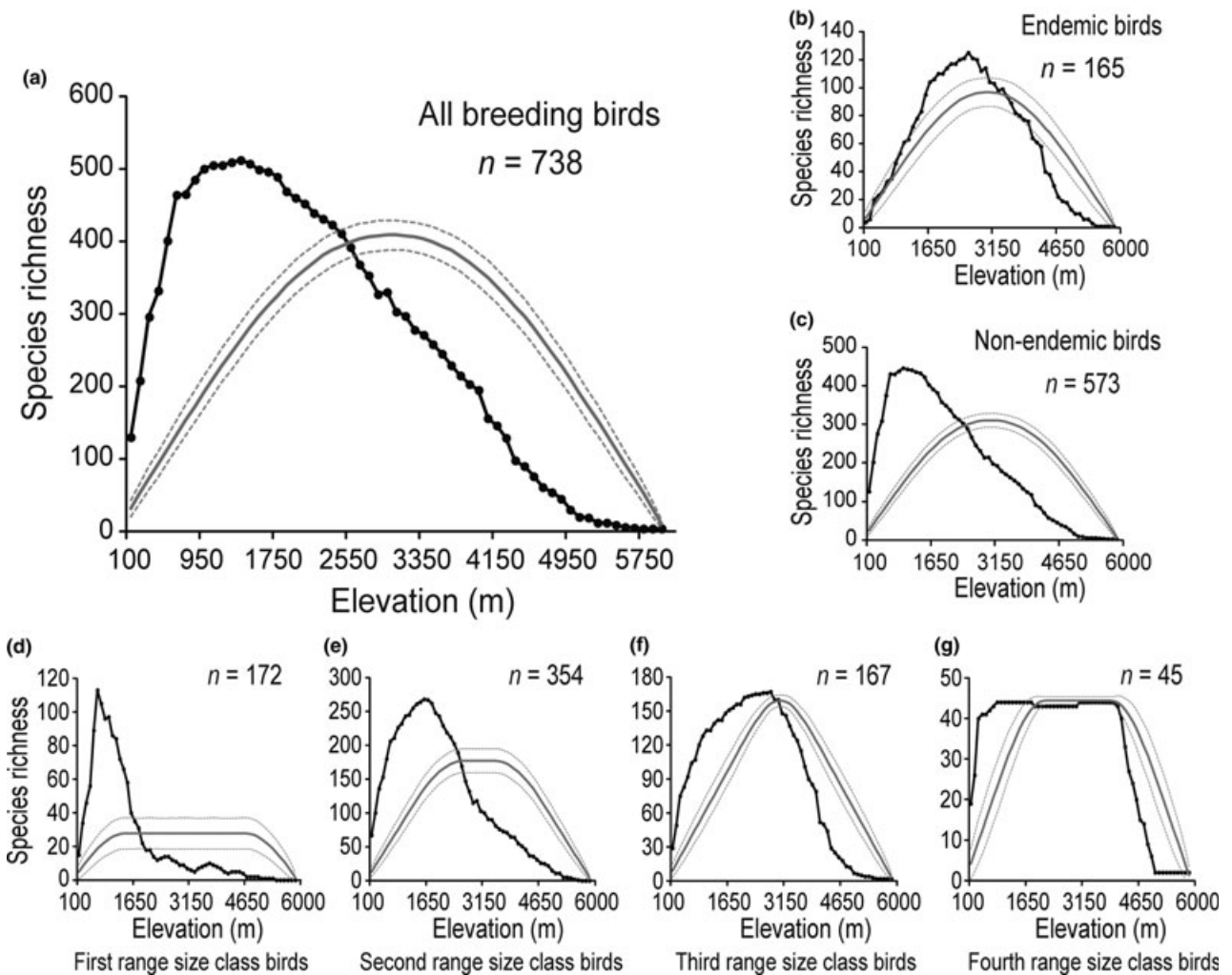


Figure 3 Elevational distribution patterns of species richness (black solid line) in the Hengduan Mountains for (a) all breeding birds, (b) endemic species, (c) non-endemic species, and (d–g) birds in the first, second, third and fourth range size classes, respectively. The predicted mean richness (grey solid line) and the upper and lower 95% confidence interval simulation limits (grey dotted lines) under the geometric constraints null model are shown.

peaked at low elevations (1000–2500 m) but at a somewhat higher elevation than other species groups (Fig. 4b). Galliform species richness peaked at mid-elevation (1200–3300 m), with two peaks, one at 1400 m and other one at 3000 m (Fig. 4c). The polynomial regressions of the species richness patterns along the elevational gradients demonstrate that all of the species groups show a hump-shaped pattern in general (Table S3 in Appendix S2), uniformly better fit by a quadratic or cubic function of elevation than a simple linear regression on elevation.

The relationship between species richness and candidate explanatory factors

Simple linear regression results for the species richness of each bird group as a function of each candidate explanatory variable appear in Table S2. Most of the variables are significantly correlated with species richness in each species group,

when spatial autocorrelation is not taken into account, except for geometric constraints and area.

Multiple regression analyses of species richness of all species groups against the six candidate explanatory factors (without taking multicollinearity and spatial autocorrelation into account) showed that different species groups had different relationships with these factors (Table 2). High standardized beta coefficients demonstrated that temperature, precipitation, temperature seasonality and productivity were the four most important factors for most of the species richness patterns. Temperature and precipitation were the two most explanatory factors for the species richness pattern of endemic birds, species in the first, second and third range size classes, Passeriformes, Falconiformes, Strigiformes, Coraciiformes and Columbiformes. In contrast, temperature seasonality best explained the richness pattern of non-endemic birds (negative) and Piciformes (negative) birds, whereas productivity best explained the richness pattern of species in

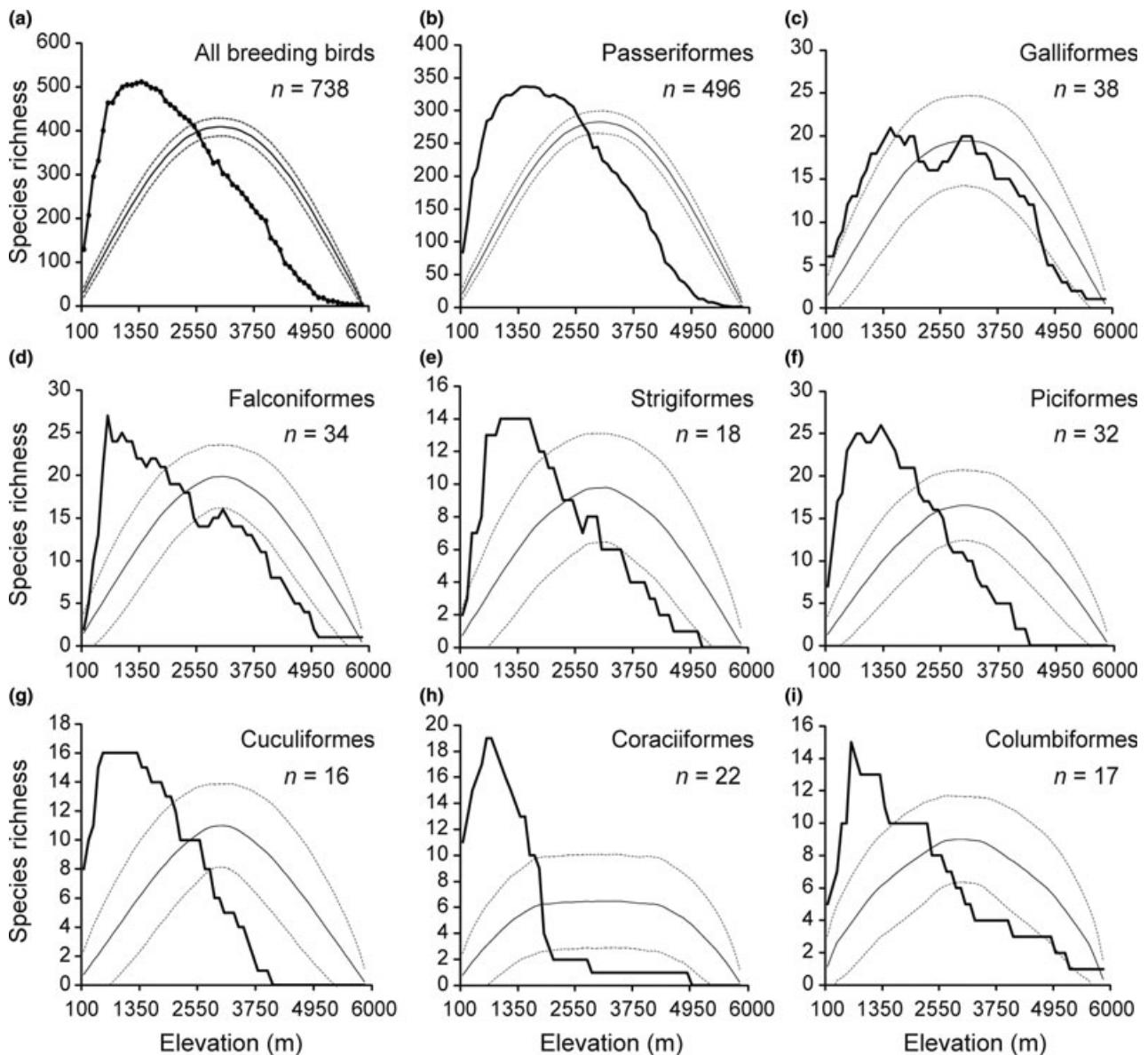


Figure 4 Elevational distribution patterns in the Hengduan Mountains of species richness (black solid line) for the best-represented avian orders. The predicted mean richness (grey solid line) and the upper and lower 95% confidence interval simulation limits (grey dotted lines) under the geometric constraints null model are shown in the figure.

the fourth range size class and Galliformes. Area and geometric constraints played important, but subordinate, roles in shaping the species richness patterns for most species groups (Table 2). The best-model-selection results were reasonably consistent with the model-averaging approach, based on the value of the standardized beta coefficient (Table S4 in Appendix S2).

The comparison of multiple OLS and CAR regressions results with only four selected variables (to minimize the multicollinearity, $VIF < 5.2$) is shown in Table 3 and Table S5 in Appendix S2. The standardized beta coefficient from the OLS multiple regressions for each species group differed from the corresponding coefficient in the model-

averaging approach. With OLS and CAR, temperature seasonality emerged as the strongest explanatory factor (negative) in the models for most of the species groups except for endemic birds, species in the fourth range size class and coraciiform birds. Productivity became the strongest explanatory factor (positive) for the richness pattern of species in the fourth range size class. Geometric constraints became the strongest explanatory factor for the richness pattern of endemics (richness under geometric constraints was negatively correlated with coraciiform richness, and thus cannot be considered explanatory, given a priori prediction of a positive relationship). Both OLS and CAR multiple regression results demonstrated that, overall,

Table 2 Parameter estimates averaged across 63 ordinary least squares (OLS) models used to analyse the species richness pattern of birds in the Hengduan Mountains.

Species groups	Standard coefficient of the model averaging							R^2_{adj}	AIC _c
	Area	MAT	AP	MATR	EVI	GC			
All birds	-0.078	0.716	-0.394	-0.78	-0.015	-0.157	0.961	604.259	
Endemic birds	0.060	3.811	-3.965	-0.792	-0.06	-0.020	0.962	431.812	
Non-endemic birds	-0.087	0.258	0.435	-0.771	0.140	-0.261	0.840	668.779	
First range size class birds	-0.534	-4.961	5.036	-0.412	0.776	0.120	0.885	460.650	
Second range size class birds	0.200	0.783	-0.475	-0.746	-0.30	-0.262	0.910	574.067	
Third range size class birds	-0.189	2.869	-2.525	-0.895	-0.329	0.197	0.927	513.696	
Fourth range size class birds	-0.121	-0.129	-0.569	-0.260	1.178	0.135	0.864	395.897	
Passeriformes	-0.032	1.910	-1.637	-0.870	-0.002	-0.256	0.972	538.221	
Galliformes	-0.110	-0.510	0.111	-0.506	0.622	0.299	0.933	244.392	
Falconiformes	-0.221	-1.667	1.668	-0.752	0.512	0.076	0.911	285.042	
Strigiformes	-0.143	-0.800	1.003	-0.954	0.176	-0.262	0.960	179.776	
Piciformes	-0.103	0.525	0.217	-0.821	-0.177	-0.345	0.946	273.846	
Cuculiformes	-0.052	1.211	-0.743	-0.684	-0.372	-0.349	0.798	304.021	
Coraciiformes	-0.339	-3.925	4.449	-0.095	0.505	0.099	0.964	203.470	
Columbiformes	-0.031	-0.625	1.048	-0.593	0.035	-0.257	0.894	214.580	

MAT, mean annual temperature; AP, annual precipitation; MATR, mean annual temperature range; EVI, enhanced vegetation index; GC, geometric constraints; AIC_c, corrected Akaike information criterion.

temperature seasonality was the most important explanatory factor for the richness pattern of most bird groups (Table 3 & Table S3). Productivity and geometric constraints play more important roles in shaping the species richness pattern when compared with area. For all species groups, species richness was positively correlated with productivity and negatively correlated with temperature seasonality. Area was relatively weakly correlated with species richness for all species groups.

Partial regression results further demonstrated that different species groups have different relationships with the grouped explanatory factors (Fig. 5). For all breeding birds and non-endemic birds, temperature seasonality and productivity explained more variation (43–48%) in species richness compared with area and geometric constraints (5–14%), whereas area and geometric constraints explained more variation (24%) in species richness for endemic birds, compared with temperature seasonality and productivity (7%). The partial regression results for other species groups are listed in Table S6 in Appendix S2.

DISCUSSION

Why does species richness of most bird groups in the Hengduan Mountains peak at low elevations?

The present study is the first to rigorously document elevational patterns of bird species richness in the Hengduan Mountains. We found that the combined species richness pattern for all breeding birds along the elevational gradient in the Hengduan Mountains is a hump-shaped pattern with a peak at about 800–1800 m (Fig. 3a), closer to the bottom of the gradient than the top, a widely-reported pattern gen-

Table 3 Multiple ordinary least squares (OLS) regression for different species groups with different variables without precipitation and temperature to analyse the species richness pattern of birds in the Hengduan Mountains. Bold numbers are the parameters for each multiple regressions model that was significant at $P < 0.05$.

Species groups	Area	MATR	EVI	GC	R^2	P
All birds	-0.126	-0.887	0.384	-0.241	0.968	< 0.001
Endemic birds	-0.075	-0.458	0.065	0.627	0.913	< 0.001
Non-endemic birds	-0.117	-0.908	0.430	-0.459	0.971	< 0.001
First range size class birds	-0.429	-0.694	0.534	-0.410	0.551	< 0.001
Second range size class birds	0.145	-0.861	0.263	-0.459	0.970	< 0.001
Third range size class birds	-0.312	-0.824	0.264	0.271	0.917	< 0.001
Fourth range size class birds	-0.156	-0.165	0.738	0.347	0.913	< 0.001
Passeriformes	-0.130	-0.845	0.364	-0.113	0.957	< 0.001
Galliformes	-0.075	-0.475	0.351	0.384	0.950	< 0.001
Falconiformes	-0.163	-0.869	0.369	-0.187	0.903	< 0.001
Strigiformes	-0.140	-1.066	0.256	-0.380	0.969	< 0.001
Piciformes	-0.164	-0.982	0.398	-0.547	0.959	< 0.001
Cuculiformes	-0.184	-0.895	0.481	-0.610	0.942	< 0.001
Coraciiformes	-0.126	-0.472	0.688	-0.787	0.825	< 0.001
Columbiformes	-0.074	-0.830	0.459	-0.520	0.907	< 0.001

MATR, mean annual temperature range (seasonality); EVI, enhanced vegetation index (productivity); GC, geometric constraints.

erally consistent with most previous elevational diversity studies of birds (Rahbek, 1995, 1997, 2005; Lee *et al.*, 2004; McCain, 2009). In contrast, the other commonly reported pattern for elevational gradients, a monotonic decrease with elevation (Graham, 1990; Rahbek, 1995, 2005; Kattan &

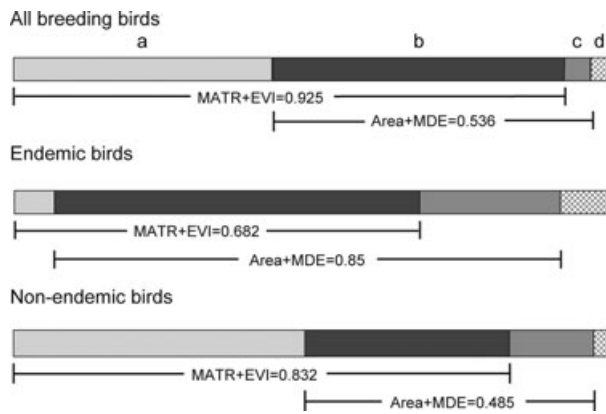


Figure 5 Partial regressions for richness of all breeding birds, endemic birds and non-endemic birds in the Hengduan Mountains, with four selected variables partitioned into non-spatial (temperature seasonality and productivity) and spatial variables (area and geometric constraints, GC). Parts 'a' and 'c' represent the independent component of non-spatial and spatial variables; 'b' is the covariance component, and 'd' is the unexplained variation. The partial regression results for other species groups are listed in Table S6 in Appendix S2. MATR, mean annual temperature range; EVI, enhanced vegetation index; MDE, mid-domain effect.

Franco, 2004; McCain, 2009), was not found in any of the many patterns reported in this study, despite the fact that the elevational patterns for key environmental variables declined monotonically (MAT, as a measure of energy, and AP, as a measure of water availability) or nearly monotonically (NDVI and EVI, as indicators of productivity) from sea level (Fig. 2). In contrast, low levels of temperature seasonality (indicated by a low MATR value) and 'pure' geometric constraints predictions (Fig. 3, grey lines) peaked at the middle of the gradient, whereas elevational band area (Fig. 2d) was bimodal. Qualitatively, these patterns suggest that richness is shaped by interactions between (or perhaps mixed responses to) climatic, energy and spatial factors, a conclusion we elaborate and support below.

At the bottom of the elevational gradient in the Hengduan Mountains, it might seem that conditions are ideal for high avian species richness because the climate is ideal (warm and moist) and the productivity (EVI) is high, but species richness of birds peaks, instead, about 1300 m higher. Our results suggest that species richness at the lowest elevations may be constrained by small elevational band area, strong geometric constraint from the sea-level domain limit and relatively strong seasonality. In turn, at the highest elevations, despite large elevational band area (band area has a second peak at about 4500 m), species richness is also low, a pattern that we attribute to the inimical climate (cold, arid and strongly seasonal) and lack of productivity (low EVI) exacerbated by strong geometric constraints near the upper domain border. Species richness of all species groups is greatest at mid-elevations, where the climate is neither too cold nor too arid and is relative stable over the year, and where high band

area and weak geometric constraints augment the effects of climate. Thus species richness is shaped by a suite of complex and interacting factors along the elevational gradient.

By examining the patterns and statistical results for data partitioned by avian orders, by endemic/non-endemic status and by range size (Figs 3 & 4), we can discover how subsets of the avifauna contribute to the overall pattern of richness for all breeding birds. Most obviously, richness for several avian orders (Falconiformes, Strigiformes, Piciformes, Cuculiformes, Coraciiformes and Columbiformes; Fig. 4d–i) peaks below 1300 m in all cases (together 18.8% of the total breeding bird richness), combining to boost low elevation richness for all species pooled. In contrast, Passeriformes (67.2% of the total species) richness peaks more broadly (at 900–1800 m elevations; Fig. 4b) and Galliformes (5.1%) richness peaks in the middle of gradient (Fig. 4c). Kessler (2000) and Rahbek (2005) suggested that conducting inter-taxon comparative studies at a high taxonomic level along the same gradient could help us to understand the underlying driving factors for diversity pattern. Our research found that patterns differed among taxonomic groups of birds, implying that differing explanatory factors shape the species richness patterns even in the same biogeographical region.

When species are partitioned by endemic versus non-endemic status, it is clearly the non-endemics (77.6% of the total species) that drive the low-elevation richness peak (for all species pooled), with endemics (22.4% of the total species) forming a mid-elevation peak (Fig. 3). Previous studies have found that species richness patterns along elevational gradients for endemic and non-endemic species were quite different (Cardelús *et al.*, 2006; Kluge *et al.*, 2006; Brehm *et al.*, 2007; Wu *et al.*, 2013). In our analyses, endemic richness peaked at mid-elevations (2200–2800 m) and was explained partly by spatial factors, whereas non-endemic richness peaked at low elevation (600–1500 m) and was best explained by climatic and energy factors (Table 3, Fig. 5). This result is consistent with previous observations and inferences that the distribution of endemic species may be more affected by geometric constraints and local history, or perhaps more constrained by evolutionary adaptations to local conditions than more widespread, non-endemic species (Jetz & Rahbek, 2002; Colwell *et al.*, 2004; Dunn *et al.*, 2007; Wu *et al.*, 2013). In our analyses, the mean elevational range size of endemic species ($n = 165$) is not significantly different ($P > 0.05$) from the mean range size of non-endemic species ($n = 573$). This result indicates that endemic birds, defined by their planimetric distributional range, do not necessarily have narrow elevational distribution ranges.

When species are partitioned by range size, the richness peak moves upslope towards mid-elevations with increasing range size (Fig. 3, and Fig. S1 in Appendix S2). This range-size shift in richness is a classic signature of geometric constraints. Geometric constraint theory predicts that the positions of larger ranges within a bounded domain are more constrained and more likely to overlap than smaller ranges, which are freer to respond to environmental or historical factors independent

of boundary constraints (Colwell & Hurtt, 1994; Colwell & Lees, 2000). By comparing richness patterns among the four species range categories of all birds (first, second, third and fourth range size classes) and their relationship with explanatory factors, we found that the correlation coefficient (r) between species richness and geometric constraints predictions increased from first range size class species (0.04) to fourth range size class species (0.64). As predicted by geometric constraint theory, a similar but even higher correlation coefficient between species richness and geometric constraints predictions is observed for endemic birds from first range size class (0.48) to fourth range size class (0.82).

Mechanistic models (Rangel & Diniz-Filho, 2005; Colwell & Rangel, 2009) and new statistical approaches (Wang & Fang, 2012) hold promise in explaining the prevalence of low-elevation richness peaks, by integrating climatic drivers of species richness with the geometric constraints posed by domain edges. Although the pooling of taxa adapted to conditions at different elevations, together with climatic factors, productivity and geometric constraints may explain the prevalence of low-elevation richness peaks, additional factors may contribute to this pattern. (1) The topography of the Hengduan Mountains allows only a relatively small area in the lower elevational bands (Fig. 1a,b), perhaps contributing to lower species richness, even though conditions may be favourable for birds. (2) The relatively greater climatic stability (lack of temperature seasonality) or suitable climate at mid-elevations may favour species or lineages sensitive to seasonal temperature fluctuations. (3) The lowland areas of the Hengduan Mountains are mostly lower reaches of rivers and valleys, which are highly suited for agriculture and are intensively cultivated, perhaps depressing contemporary bird species richness.

Comparison of species richness patterns and explanatory factors for other taxa in the Hengduan Mountains

The elevational species richness pattern for all breeding birds in the Hengduan Mountains is hump-shaped, with the peak occurring at 800–1800 m elevation (Fig. 3a). Species richness of birds on this gradient is statistically explained by climatic and energy factors, with area and geometric constraints playing secondary roles. Other recent studies in the Hengduan Mountains have documented the species richness patterns for plants, insects, reptiles and mammals (Gong *et al.*, 2005; Fu *et al.*, 2007; Zhang *et al.*, 2008; Li *et al.*, 2009; Wu *et al.*, 2013), which revealed a hump-shaped pattern with maxima occurring at different elevations along the elevational gradient. However, the hump-shaped richness patterns among these taxa were explained by quite different factors. Zhang *et al.* (2008) found that richness patterns of total, endemic and non-endemic plant species were unimodal and peaked at high elevations (3500–4500 m); plant species richness was strongly related to area and weakly correlated with precipitation. However, Wang *et al.* (2007) found that both area and

geometric constraints best explained the variation of plant species richness at a local scale (Gaoligong Mountain) in the Hengduan Mountains. Fu *et al.* (2006, 2007) found that the species richness patterns of total and non-endemic frogs, snakes and lizards along the elevational gradient are also hump-shaped, peaking at low elevations (1000–2000 m), whereas endemic species richness of frogs peaked at mid-elevations (2000–3000 m). Water and energy were the most important variables in explaining elevational patterns of non-endemic frog species richness; climatic and geometric factors best explained total and endemic species richness patterns of frogs. Land area explained a significant amount of the variation in lizard and snake species richness; water availability constrained lizard species richness but annual potential evapotranspiration was the best predictor of snake species richness. Wu *et al.* (2013) found that the overall species richness pattern of small mammals in Gongga Shan is hump-shaped, with a peak at mid-elevations (2000–3000 m), but some decreasing and other patterns also exist in this region for mammal groups. The overall richness patterns for small mammals, insectivores, endemic species and larger-ranged species showed a strong correlation with geometric constraint predictions. However, non-endemic species richness was more strongly correlated with temperature, while rodent richness was highly correlated with plant species richness (Wu *et al.*, 2013).

Clearly, elevational species richness studies in the Hengduan Mountains have demonstrated that elevational richness patterns and their explanatory factors depend on which groups of species we study, and a broader comparative approach (which is beyond the scope of this paper) would reveal that it also depends on where we study them. More work focusing on the local or regional scale, as well as a broader diversity of life forms, taxonomic groups and mountain ranges are necessary for meta-analyses and comparisons to improve our understanding of the complex species diversity patterns and their underlying mechanisms in mountainous regions of the Earth.

Conclusions and caveats

The species richness pattern of birds in the Hengduan Mountains is hump-shaped along the elevational gradient. Our study confirmed that the species richness pattern of birds along the elevational gradient in the Hengduan Mountains is influenced by multiple, interacting factors. Temperature seasonality and productivity show stronger relationships with bird species richness than area and geometric constraints predictions in most of the species groups, supporting the importance of climate and energy in driving the species richness patterns in birds, consistent with previous studies (Hawkins *et al.*, 2003, 2005; Hurlbert & Haskell, 2003; Koh *et al.*, 2006; McCain, 2009).

Despite a clear definition of our research area and the data used, results of regional studies, such as this one, must be interpreted with caution and should be considered as

tentative rather than definitive. First, environmental and historical variables for which no data are (yet) available may nonetheless be important, e.g. disturbance, the effects of the latitudinal gradient, biotic relationships (competition, food, prey...) and species' evolutionary histories. Second, simple and multiple regression results are very sensitive to the pattern of both species richness and the candidate explanatory variables along the elevational gradient. A small change in the distribution pattern of species richness or explanatory variables may bring significant change in the regression results. Third, species richness may be correlated with the explanatory variables in part because of collinearity or interaction between explanatory variables. The choice of the research area boundaries will significantly influence the data for selected explanatory variables, thus we need to define the research area and data sources very clearly to make macroecological research repeatable. Although the scale-dependence of results is common in regional macroecology studies, the sensitivity of our findings to spatial scale lies beyond the main purpose of this study. It is thus essential to work with accurate data for species richness and explanatory variables.

In closing, we wish to stress the fundamental role and irreplaceable importance of field surveys in biodiversity and biogeography studies, including the collection of primary field data, especially for local-scale diversity studies.

ACKNOWLEDGEMENTS

We thank Gexia Qiao, Chuan Xiong, Shan Guo, Danlu Cai, Zhiheng Wang, Yanhua Qu, Gang Song, Naijian Han, Shimiao Shao, Yalin Chen, Baoyan Liu and Wenjuan Wang for their kind help and suggestions in data collections and analyses. Many thanks go to Per Alström for revising an early draft, checking the elevational data and giving valuable comments. We are very grateful to the editors K. C. Burns and Rob Whitaker and three anonymous referees for their valuable comments on the manuscript. We also thank Bradford A. Hawkins for his comments regarding this study. This work was supported by the National Science Fund for Distinguished Young Scientists (no. 30925008), by the Innovation Program of the Chinese Academy of Sciences (KSCX2-EW-J-2) to L.F., by National Natural Science Foundation of China program no. J1210002 to Y.W., and by US National Science Foundation awards DEB-0639979 and DBI-0851245 to R.K.C. This work is also supported by the "Strategic Priority Research Program" of the Chinese Academy of Sciences (XDA05080703) to G.G.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Species checklists of breeding birds in the Hengduan Mountains and the data sources.

Appendix S2 Additional figure (Fig. S1) and tables (Tables S2–S6).

Appendix S3 All 63 regression models for interpolated species richness of different species groups of birds (Tables S7–S21).

DATA ACCESSIBILITY

The range data of all the birds are available by contacting the first author (Yongjie Wu, yongjie_wu@163.com) or the corresponding author (Fumin Lei, leifm@ioz.ac.cn).

BIOSKETCH

This work was completed in the Ornithological Research Group at the Institute of Zoology, Chinese Academy of Sciences (<http://english.anisys.ioz.ac.cn/Enlfm.asp>). It was part of Yongjie Wu's PhD study in the Key Laboratory of Zoological Systematics and Evolution, Chinese Academy of Sciences.

Author contributions: Y.W. and F.L. conceived the idea for this study and designed the research; Y.W., F.L., C.W., C.Z. and Q.Q. provided the data; Y.W., R.K.C., C.R. and F.L. analysed the data, developed the presentation and wrote the paper.

Editor: K. C. Burns