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Elevational patterns of bird species richness on the eastern slope of Mt. Gongga, Sichuan Province, China

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Abstract

Background: In biological systems, biological diversity often displays a rapid turn-over across elevations. This defining feature has made mountains classic systems for studying the spatial variation in diversity. Because patterns of elevational diversity can vary among lineages and mountain systems it remains difficult to extrapolate findings from one montane region to another, or among lineages. In this study, we assessed patterns and drivers of avian diversity along an elevational gradient on the eastern slope of Mt. Gongga, the highest peak in the Hengduan Mountain Range in central China, and a mountain where comprehensive studies of avian diversity are still lacking.

Methods: We surveyed bird species in eight 400-m elevational bands from 1200 to 4400 m a.s.l. between 2012 and 2017. To test the relationship between bird species richness and environmental factors, we examined the relative importance of seven ecological variables on breeding season distribution patterns: land area (LA), mean daily temperature (MDT), seasonal temperature range (STR), the mid-domain effect (MDE), seasonal precipitation (SP), invertebrate biomass (IB) and enhanced vegetation index (EVI). Climate data were obtained from five local meteorological stations and three temperature/relative humidity smart sensors in 2016.

Results: A total of 219 bird species were recorded in the field, of which 204 were recorded during the breeding season (April–August). Species richness curves (calculated separately for total species, large-ranged species, and small-ranged species) were all hump-shaped. Large-ranged species contributed more to the total species richness pattern than small-ranged species. EVI and IB were positively correlated with total species richness and small-ranged species richness. LA and MDT were positively correlated with small-ranged species richness, while STR and SP were negatively correlated with small-ranged species richness. MDE was positively correlated with large-ranged species richness. When we considered the combination of candidate factors using multiple regression models and model-averaging, total species richness and large-ranged species richness were correlated with STR (negative) and MDE (positive), while small-ranged species richness was correlated with STR (negative) and IB (positive).

Conclusions: Although no single key factor or suite of factors could explain patterns of diversity, we found that MDE, IB and STR play important but varying roles in shaping the elevational richness patterns of different bird species categories. Model-averaging indicates that small-ranged species appear to be mostly influenced by IB, as opposed to large-ranged species, which exhibit patterns more consistent with the MDE model. Our data also indicate that the species richness varied between seasons, offering a promising direction for future work.

Keywords: Mt. Gongga, Elevational gradient, Environmental factors, Species richness, Stable microclimate

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Background

In recent decades, studies of altitudinal gradients have become increasingly popular for uncovering the spatial variation in organismal diversity (Colwell and Lees 2000; Rahbek 2005; Nogués-Bravo et al. 2008; McCain 2009; Wu et al. 2013a; Price et al. 2014; Quintero and Jetz 2018). Different patterns of elevational diversity may occur in different systems, for example, because of variation in the scale of the gradient, or regional differences in climate, climatic history and evolutionary history (Kozak and Wiens 2010; Sanders and Rahbek 2012; Price et al. 2014; Pontarp and Wiens 2017; O'Connor et al. 2018).

Numerous factors have been implicated as underlying causes of elevational diversity patterns, such as land area, geometric constraints, climate, food availability and productivity (Colwell et al. 2004; McCain 2004; Koh et al. 2006; Nogués-Bravo et al. 2008; Sanders and Rahbek 2012; Price et al. 2014; Hu et al. 2017). For example, the area of a regional elevational band can influence the species richness of that band (Rahbek 1997; McCain 2005; Romdal and Grytnes 2007; Williams et al. 2010). The mid-domain effect, on the other hand, describes the increasing overlap of species' ranges towards the center of a shared bounded domain due to geometric constraints (Colwell and Hurr 1994; Colwell and Lees 2000; Colwell et al. 2004; McCain 2004), which can also play a role in shaping diversity patterns along elevational gradients. However, the fit of this model to different taxonomic groups and gradients is still uncertain and needs further testing in additional biogeographic regions (Hu et al. 2017). Additionally, the influence of climate on diversity can be both direct and indirect. Climate can directly set limits on species distributions given a species' physiological tolerances, while species distributions can be indirectly influenced by temperature and precipitation, which affect photosynthetic activity and rates of biological processes in the environment. Climatic variables such as mean daily temperature and precipitation are widely supported environmental predictors of biodiversity patterns (Hurlbert and Haskell 2003; Wu et al. 2013b; Peters et al. 2016). Seasonal temperature range, i.e. the difference between the mean temperature of the coldest and warmest month in a given period, has also been linked to patterns of bird species richness (Wu et al. 2013b, 2014). Furthermore, since species richness patterns can reflect the complexity of energy and material transfer (i.e. productivity), the enhanced vegetation index, which is quantified as the concentration of green leaf vegetation, could also be a predictor of bird diversity patterns (Hawkins and Soeller 2005; Koh et al. 2006; Hawkins 2007). Finally, as many birds are insectivorous,

invertebrate biomass, which can also be linked to climate and/or vegetation indices, may have explanatory power in predicting patterns of bird diversity across elevations (Price et al. 2014).

Most studies that look at geographic patterns of diversity have traditionally focused on total species richness patterns. However, species with large ranges disproportionately influence richness patterns because they contribute larger number of distribution records compared to small-ranged species. Thus, discrimination between large- and small-ranged species might be important for understanding the determinants of species richness patterns (Jetz and Rahbek 2002). Previous studies have demonstrated that different patterns and processes can determine the elevational diversity of large-ranged and small-ranged species (Cardelús et al. 2006; Wu et al. 2013b; Pan et al. 2016; Hu et al. 2017). Because richness itself is the statistical sum of overlapping ranges, the overall richness pattern of total species is directly linked to the range sizes of species and the range-size frequency distribution (Wu et al. 2013a, b). Variation in regional community composition, including the proportion and distribution of endemic species versus widespread species, may affect richness patterns; patterns may also vary from one taxonomic category to another (Kessler 2000; Rahbek 2005).

Mt. Gongga (Gongga Shan), is the highest mountain in the Hengduan Range. It is located at the southeastern margin of the Qinghai-Tibetan Plateau in Sichuan Province, China, in the center of one of the world's 34 biodiversity hotspots (Mittermeier et al. 2005). The Hengduan Range supports high species diversity and a high level of regional endemism (Wu et al. 2013a, 2017a). The stark elevational relief (6400 m) and remarkable vertical bioclimatic zonation of Mt. Gongga make it an ideal location to study elevational diversity patterns. Several previous studies on climate (Thomas 1997; Zhong 1999), plant diversity (Shen and Wu 2001; Shen et al. 2004) and small mammal diversity (Wu et al. 2013a) have been conducted along this elevational gradient. However, comprehensive studies of species diversity patterns in birds are still lacking for Mt. Gongga. To date, one study has described bird diversity on Mt. Gongga (Wu et al. 2017b), but this study does not explore the factors underlying these patterns. Here, we further document the elevational species richness patterns of birds on the eastern slope of Mt. Gongga, and assess the role of seven contemporary explanatory factors, both spatial (land area, mid-domain effect) and environmental (mean daily temperature, seasonal temperature range, seasonal precipitation, enhanced vegetation index, invertebrate biomass) in explaining patterns of bird species richness on this mountain.

Methods

Study area

Mt. Gongga (peak elevation 7556 m) is located in a sharp transition zone between the Sichuan Basin and the Qinghai-Tibetan Plateau (29°20'–30°39'N, 101°30'–102°12'E, Fig. 1). Mt. Gongga is the highest peak in the Hengduan Mountains, with an elevational span of approximately 6400 m from the bank of Dadu River (1100 m) to the summit. The planimetric distance from the foot of Mt. Gongga to the summit is 29 km (Zhong 1999). The mountain has a complex geological structure, varied vegetation types, high species richness and regional endemism (Zhong 1999; Wu et al. 2017b). There is striking vertical climatic zonation along the steep elevational gradient, with microclimates ranging from subtropical to alpine. Below 1400 m along the Dadu River valley, a dry, hot climate is produced by the foehn effect (Zhong 1999).

Mt. Gongga has eight major vegetation zones (Cheng and Luo 2002). Below 2000 m, these include a sparsely wooded shrub and grass sub-belt (1100–1400 m), an agroforestry belt (1000–1800 m), and an evergreen

broadleaf forest sub-belt (1400–1800 m). The vegetation below 1800 m is degraded due to agricultural activity (Cheng and Luo 2002). Above 2000 m, vegetation types turn over rapidly with increasing altitude: evergreen broadleaf forest and deciduous broadleaf mixed forest belt (2000–2400 m); coniferous and deciduous broadleaf mixed forest belt (2400–2800 m); montane dense coniferous forest belt (2800–3600 m); shrub and grass belt (3600–4200 m); and remnant meadow and rock-scrub belt (4200–4900 m). Above 4900 m is permafrost. We conducted all surveys in the valley of Hailuoguo, which drains the eastern slope of Mt. Gongga. Hailuoguo has five meteorological stations spanning elevations from 1600 to 3350 m, which provide precise climate data across elevations (Fig. 1). Permits for this study were obtained from the National Nature Reserve of Mt. Gongga prior to data collection.

Bird and invertebrate surveys

We conducted five field surveys of birds from 1200 to 4400 m a.s.l. between 2012 and 2017. The lower

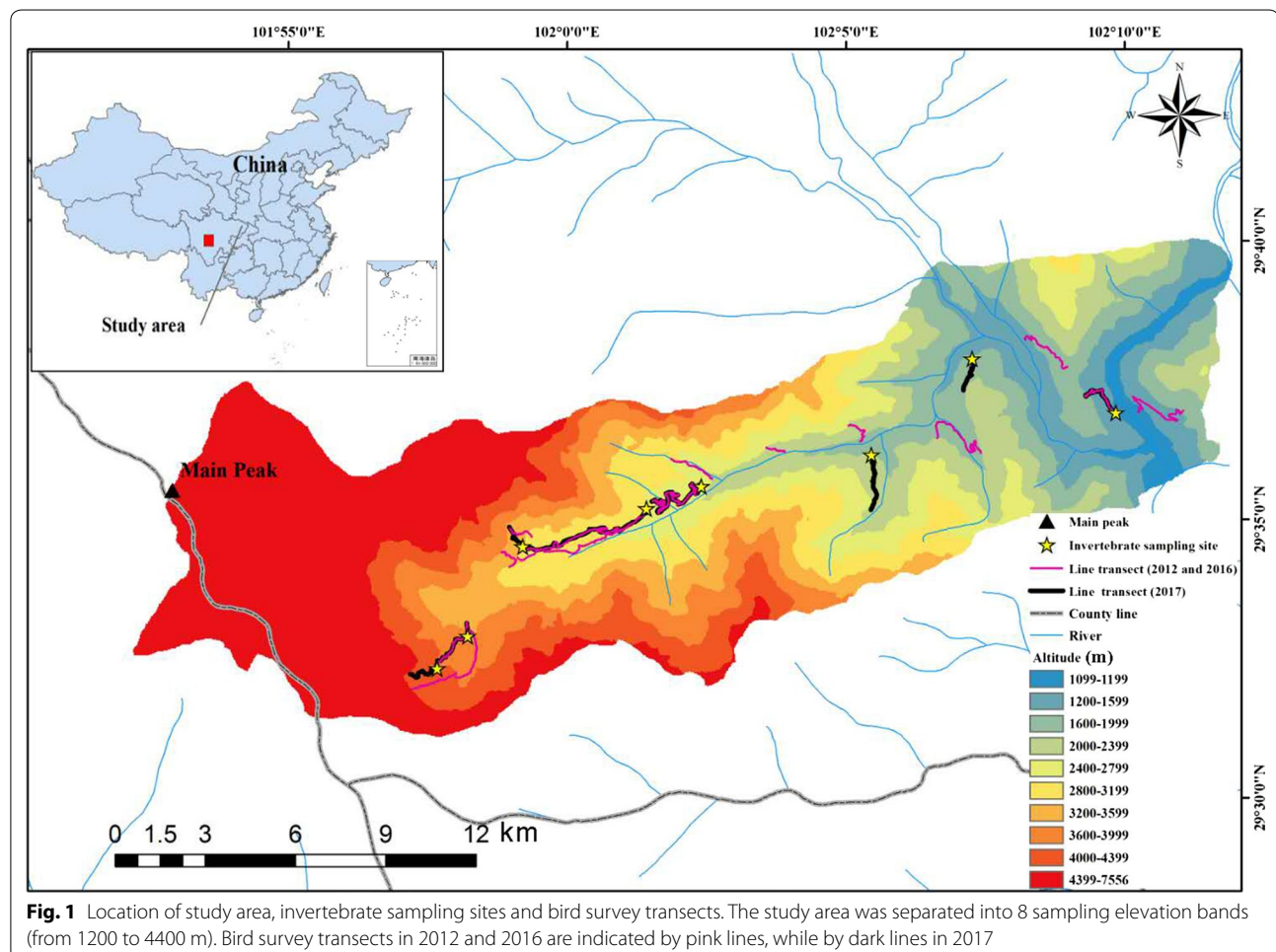


Fig. 1 Location of study area, invertebrate sampling sites and bird survey transects. The study area was separated into 8 sampling elevation bands (from 1200 to 4400 m). Bird survey transects in 2012 and 2016 are indicated by pink lines, while by dark lines in 2017

elevational limit of our survey was set by the Dadu River, and the upper elevational limit was set by the presence of permanent snow. Three complete bird surveys were conducted in the breeding season, from April to August (two surveys were conducted in 2012, and one survey was conducted in 2017), which we used for subsequent breeding-season analyses. In addition, we conducted one survey during the transition between winter and spring (March–April) in 2016. This survey, however, was only conducted from 1200–3200 m because of heavy snow above 3000 m. A final survey was conducted in late autumn/early winter, from November to December 2017. We divided the elevational gradient into eight bands of 400 m, and the bird surveys span the entire elevational band.

Within each sampling band, transects were set up to cover the main vegetation types, although the transects were limited by the availability of trails and roads. Our survey methods were slightly modified in the different survey years due to weather and research conditions. The aspects of the surveys that were modified were: survey season, time, survey intensity and surveyors. Some transects (1600–2000 m, 2000–2400 m, 4000–4400 m) were changed to the areas near to the original transect locations because of increasing human disturbance and/or landslides. These changes, however, should not impact our overall conclusions because the survey methods in each year were largely kept the same and because we are looking at species richness pattern rather than abundance patterns. For each survey, we recorded the presence and abundance of bird species using a line transect method with information regarding the birds' positions using a handheld GPS. To detect elusive or rare species and cover a variety of habitats, we surveyed two transects in each elevational band in 2012 and 2016, except at the highest elevational band (we only surveyed one transect in this band) from dawn to dusk by walking slowly to record all individual birds seen or heard. In 2017, to detect as many species as possible at each transect, we surveyed each transect twice each morning and twice each evening (one survey walking upslope and one survey walking downslope, separated by 20 min), for a total of four surveys per transect in each survey band (Elsen et al. 2017). As a result, in 2017 we only surveyed one transect and the survey distance was shorter than in 2012 and 2016 for each elevational band, but the elevational spans of the surveys were kept the same. In addition, more replicates were recorded in the 2017 survey but these pooled replicates did not influence the richness pattern. Surveys in 2017 were conducted between 30 min after dawn and 11:30 a.m. and between 3:00 p.m. and 30 min before sunset. Surveys were not conducted at mid-day or during inclement weather owing to low bird

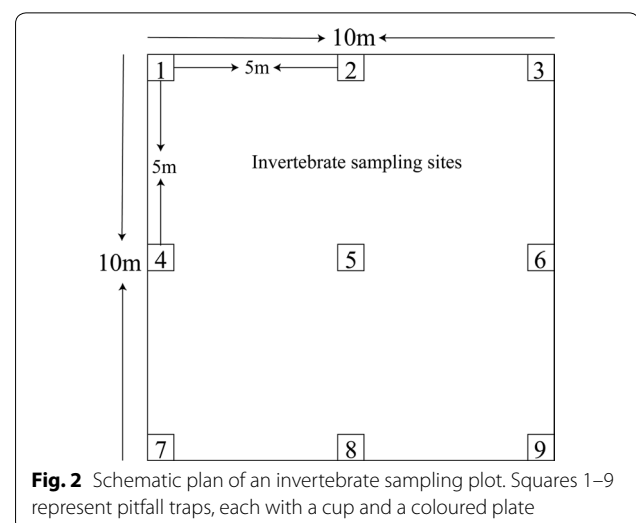
activity. The locations of the eight 400 m elevational transects can be seen in Fig. 1.

Invertebrate surveys

In May 2017, we sampled ground-dwelling and airborne invertebrates from 10 m × 10 m plots in each of the eight elevational bands in representative vegetation types. In each plot, nine pitfall traps with a cup and a color plate (three yellow plates, three red plates and three blue plates) were evenly spaced in three rows, with a distance of 5 m between each trap (Fig. 2). The color plates were used because they are thought to attract airborne insects (Harborne 1994). Each cup and color plate was filled with 100–200 mL of ethylene glycol and water (1:1 mixture), with a drop of liquid soap to break surface tension (Röder et al. 2016). Traps were left open for three days while bird surveys were conducted within a given elevational band. We stored invertebrates in ethanol and subsequently calculated the invertebrate biomass per trap for each sampling site. Total biomass for each site was calculated by summing up the values from each of the nine traps at a given site. We did not sample arboreal invertebrates due to the logistical constraints. We used ground and airborne invertebrate sampling methods as a proxy to test the relationship between invertebrate biomass (IB; the total invertebrate biomass captured by traps at each site) and bird species richness.

Environmental and spatial factors

To test the hypothesis that land area influences species richness, we calculated the land area for each 400 m band within the valley using ArcGIS 10.2 (ESRI, Redlands, CA, USA) and based on STRM 90 m digital elevation data from CGIAR-CSI (Robert 2018) (Fig. 1).



We used RangeModel 5 (Colwell 2006) to calculate interpolated species richness and estimate predicted species richness under ‘pure’ geometric constraints (assuming no interaction with other factors) (Colwell 2008). We ran 5000 randomizations of the mid-domain effect (MDE) null model (random range placement) to get mean expected species richness with 95% confidence interval for each elevational band.

As proxies for above-ground net primary productivity, we averaged the enhanced vegetation index (EVI) data in the breeding season during April to August in 2014 and 2015 for each elevational band. EVI was calculated using ArcGIS 10.2 (ESRI, Redlands, CA, USA). All remote sensing data were downloaded from Geospatial Data Cloud (Geospatial Data Cloud Development Core Team 2018).

We calculated mean daily temperature (MDT), seasonal precipitation (SP; the total precipitation from the breeding season [April to August] and seasonal temperature range (STR; the difference between the mean temperature of the coldest and warmest months from April to August) in each 400 m elevational band based on daily records from the five local meteorological stations and three temperature/relative humidity smart sensors (SSN-22E, Yowexa, Shenzhen, China) in Hailuoguo in 2016. The five meteorological stations were established by the Institute of Mountain Hazards and Environment and located at 1600 m, 2300 m, 2800 m, 3000 m and 3350 m, while the three smart sensors were placed at 1200 m, 2000 m and 4000 m. We used linear (for MDT) and LOESS (for SP and STR) regression to estimate climatic variables for each elevational band along the elevational gradient. Sites without climate records were linearly or curvilinearly extrapolated or interpolated based on the data from nearby sites.

Statistical analysis

We plotted richness patterns for each of the five field surveys for comparisons among different methods and months. We used the combined observed species richness from the three surveys made from April to August (2012. 4–5, 2012. 7–8, and 2017. 5), roughly corresponding with the breeding period of local birds, to analyze the relationship between richness and environmental factors. The breeding season environmental factors (mean daily temperature, seasonal precipitation, seasonal temperature range, invertebrate biomass, enhanced vegetation index) were collected from April to August. To assess the effect of elevational range size on species richness patterns, we divided birds into two additional categories: “large-ranged species”, with elevational ranges equal to or above the median size (1600 m); and “small-ranged species”, with elevational ranges below the median size (Wu et al. 2013b).

Because it is impossible to detect all species in natural communities through short-term surveys (Colwell and Coddington 1994; Chao et al. 2005; Walther and Moore 2005), we used non-parametric estimators (Chao2 and Jackknife2) to estimate species richness (Colwell and Coddington 1994) using the statistical software program EstimateS 9.0 (Colwell 2013). To assess whether species diversity was adequately sampled across the elevational gradient, we regressed the observed species richness against the estimated species richness.

We performed polynomial regressions (richness as a function of elevation, elevation² and elevation³) to assess the elevational distribution patterns of species richness for each of the three species categories (total species, ‘large-ranged’ species, and ‘small-ranged’ species) guided by the corrected Akaike information criterion (AICc) value, with smaller AICc values indicating a better fit. Neyman-Pearson correlation was used to examine the relationships among the independent variables (LA, MDT, SP, STR, EVI, MDE and IB). To examine the potential of individual factors to explain elevational patterns of species richness, the seven candidate variables (LA, MDT, SP, STR, EVI, MDE and IB) were tested by simple ordinary least squares (OLS) regression of interpolated species richness for each of the three species categories. We tested for normality and homoscedasticity for each variable before the multiple regression (Osborne and Waters 2002). Then the selected factors were tested with multiple regressions to compare their influence on species richness patterns. The best model was selected from the 15 tested models (all possible combinations of simple variables), guided by the lowest AICc. 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 ($\Delta AICc < 2$), we used the model-averaged approach to assess the relative importance of different explanatory variables, guided by standardized beta coefficients (Anderson and Burnham 2002; Johnson and Omland 2004).

The spatial autocorrelation in regression residuals and multicollinearity among explanatory variables could affect the credibility of the results and needs to be taken into account (Diniz et al. 2003; Graham 2003). However, multiple conditional autoregressive (CAR) analyses are not robust to small sample sizes (Wu et al. 2013b). Instead, multiple OLS models were used to assess the influence of spatial autocorrelation on the regression results. However, no *p* value was reported for the multiple regressions (Graham 2003; Brehm et al. 2007). Because MDT, EVI and SP were highly correlated with STR (Table 1), we conducted multiple regression models without MDT, SP and EVI to reduce the multicollinearity

Table 1 Spearman correlation coefficients for the seven selected factors

	LA	EVI	STR	MDT	IB	SP
LA						
EVI	0.524					
STR	−0.31	−0.833*				
MDT	0.238	0.905*	−0.929*			
IB	0.19	0.69	−0.738*	0.81*		
SP	−0.31	−0.81*	0.857*	−0.762*	−0.524	
MDE	0.286	−0.024	0.214	−0.024	0.31	0.024

LA land area, EVI enhanced vegetation index, STR seasonal temperature range, MDT mean daily temperature, IB invertebrate biomass, SP seasonal precipitation

* $p < 0.01$

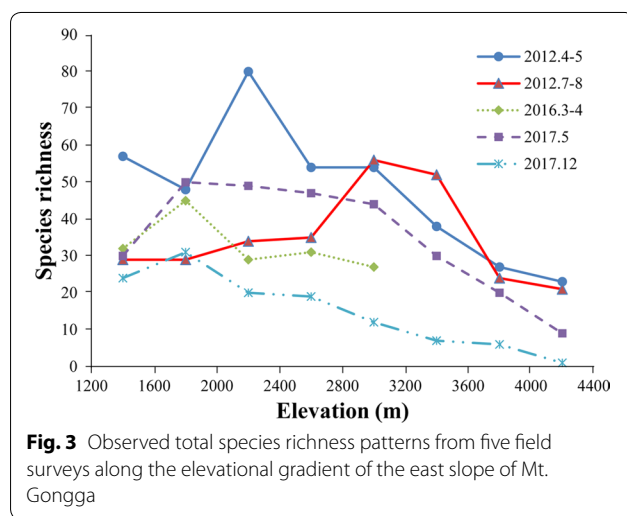


Fig. 3 Observed total species richness patterns from five field surveys along the elevational gradient of the east slope of Mt. Gongga

in the model. Only LA, IB, MDE and STR were tested in the multiple regressions for all species categories. All analyses were performed in the R packages “MuMIn” (Kamil 2018) and “vegan” (Oksanen et al. 2013).

Results

A total of 219 bird species were recorded from the eastern slope of Mt. Gongga during the five surveys. Species richness varied between seasons, with lower elevational peaks and lower diversity in March–April and December than in breeding season months (April–August) (Fig. 3). A total of 204 bird species were recorded from the three breeding season surveys (Additional file 1: Table S1). In the breeding season, the observed and interpolated species richness patterns along the elevational gradient were hump-shaped (Figs. 4, 5). The richness curves for total species and small-ranged species both peaked at 2200 m, whereas the richness of large-ranged species peaked at 2600 m asl. (Fig. 4). The polynomial regressions of species richness patterns along the elevational gradients demonstrated that the total and large-ranged species better fit a quadratic or cubic

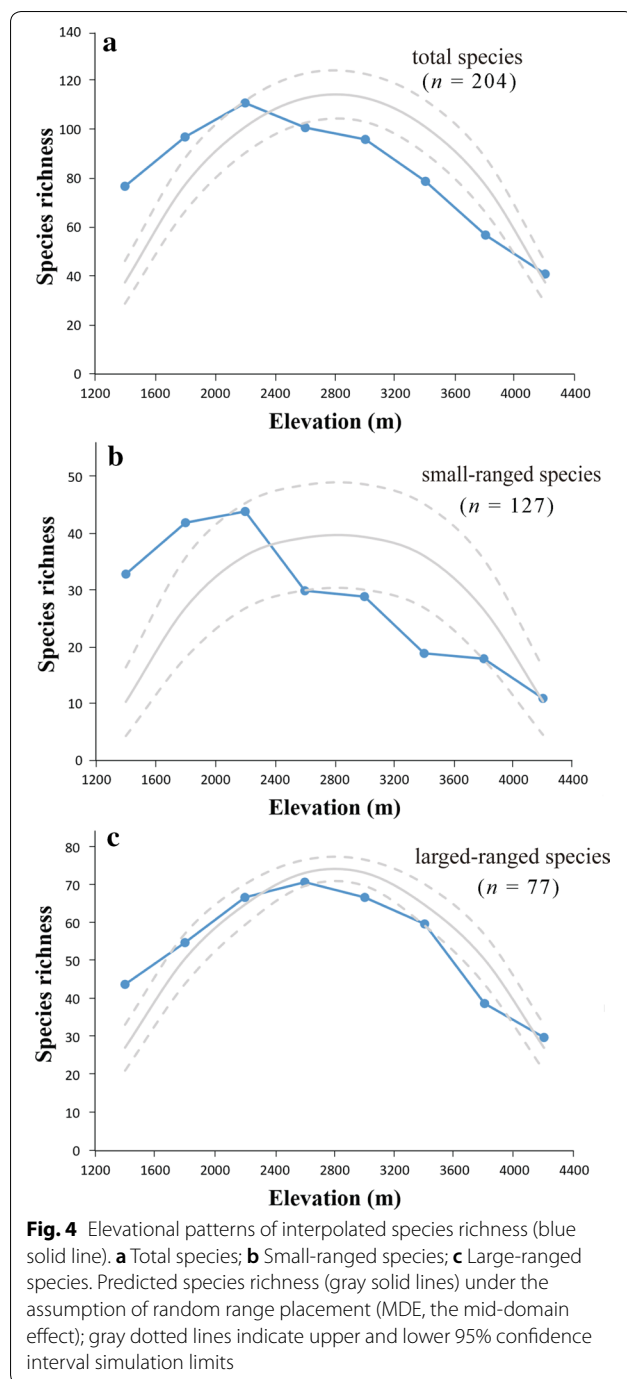
function across elevations than a simple linear regression. Small-ranged species richness is heavily skewed toward lower elevations, so the relationship is more linear (Table 2).

LA and IB each had two distinct peaks along the elevation gradient: LA peaked at 1800 m and 3000 m, whereas IB peaked at 1400 m and 2600 m. SP and STR peaked at 3400 m and 3800 m, respectively, and EVI peaked at 1800 m. MDT generally decreased with increasing elevation (Fig. 6). The regressions of the observed species richness against the estimated species richness (Fig. 5, Chao 2, $r^2 = 0.879$, $p < 0.001$; Jackknife 2, $r^2 = 0.955$, $p < 0.001$) indicate that sampling adequately captured the species richness patterns along the elevational gradient.

Simple linear regression results for the species richness patterns as a function of each candidate explanatory variable appear in Table 3. EVI and IB were positively correlated with total species richness. LA, EVI, MDT and IB were positively correlated with small-ranged species richness, while STR and SP were negatively correlated with small-ranged species richness. MDE was only positively correlated with large-ranged species richness when spatial autocorrelation was not taken into account (Table 3).

Multiple regression analyses of species richness for all species categories against the four candidate explanatory factors (taking multicollinearity and spatial autocorrelation into account) showed that the different species categories have different relationships with these factors. STR was negatively correlated with total species richness and small-ranged species richness, while MDE was positively correlated with total species richness and large-ranged species richness (Table 4).

The beta coefficient for the models of best-fit (with the lowest AICc values) demonstrated that total species richness and large-ranged species richness were correlated with STR (negative) and MDE (positive), while small-ranged species richness was only positively



correlated with IB (Table 5). The best-model-selection result for total species was more reliable than the model averaging, for which only one model's $\Delta AIC_c < 2$. The results of model-averaging show that total and large-ranged species richness were correlated with STR (negative) and MDE (positive), while small-ranged species richness was correlated with STR (negative) and IB (positive; Table 6).

Table 2 Polynomial regressions of species richness patterns along the elevational gradient

Regressions	Total species	Large-ranged species	Small-ranged species
First-order r^2	0.46	0.157	0.767*
AIC	75.799	75.548	61.308
Second-order r^2	<i>0.956*</i>	<i>0.958*</i>	0.858*
AIC	<i>68.654</i>	<i>60.861</i>	66.666
Third-order r^2	0.99*	0.963*	0.944*
AIC	79.421	78.623	77.91

Numbers in italics indicate the best regression model selected by lowest AIC value

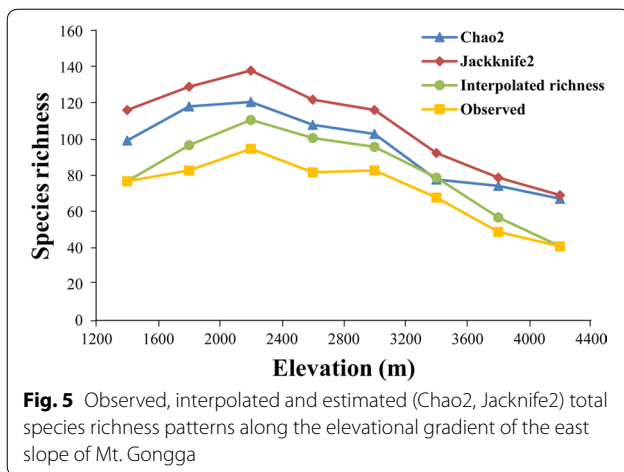
*Significant at $p < 0.01$

Discussion

Species richness patterns of birds along the elevational gradient

Our study reveals that bird species richness along the eastern slope of Mt. Gongga is hump-shaped, which is consistent with previous elevational diversity patterns of birds (Rahbek 2005; McCain 2009; Price et al. 2014; Pan et al. 2016). The hump-shaped pattern we observed on the eastern slope of Mt. Gongga has also been found in the broader Hengduan Mountain Range for plants (Zhang et al. 2009), invertebrates (Gong et al. 2005), fishes (Li et al. 2009), reptiles (Fu et al. 2007), mammals (Wu et al. 2013a) and birds (Wu et al. 2013b, 2017b).

We found that bird richness peaks at higher elevations on Mt. Gongga (2200 m a.s.l.) than in studies of all birds in the Hengduan Mountains (c. 800–1800 m a.s.l.; Wu et al. 2013b) and passerines in the eastern Himalayas (c. 1800 m a.s.l.; Price et al. 2014). We suggest two explanations for this. First, the bottom of the gradient is at 1100 m, not sea-level. Hailuoguo Valley is separated from the continuous lowlands of the Sichuan Basin to the east by some 50–100 km of mountainous terrain. In addition to having poor connectivity to the lowlands, the total land area below 2000 m in the vicinity of Mt. Gongga is very small. These factors could reduce species richness at the lower end of the gradient. Second, the foehn effect contributes to a relatively arid climate in the lowest parts of our gradient, which may reduce species diversity relative to that found at similar altitudes in the eastern Himalayas. Third, Mt. Gongga has the highest elevation in the Hengduan Mountain and the eastern slope of Gongga faces warm and moist air current from the Sichuan Basin which cause high precipitation at high elevations making the treeline on Mt. Gongga higher than other mountain in the Hengduan Mountain (Zhong 1999; Ran et al. 2014).



Total species richness varied between seasons, with lower elevational peaks and diversity in March–April and December than in April–August. This reflects the fact that many birds on Mt. Gongga move downslope or away from the mountain when the weather cools and invertebrate food becomes seasonally scarce at higher elevations. Furthermore, overall richness patterns in breeding season data varied between 2012 and 2017. Differently shaped curves between April–May and Aug surveys are probably due to reduced birdsong (i.e., reduced detectability) in the late summer, and inter-annual variation in breeding season species richness is likely attributable to varying observer experience. These factors, however, should not meaningfully bias the species range estimates.

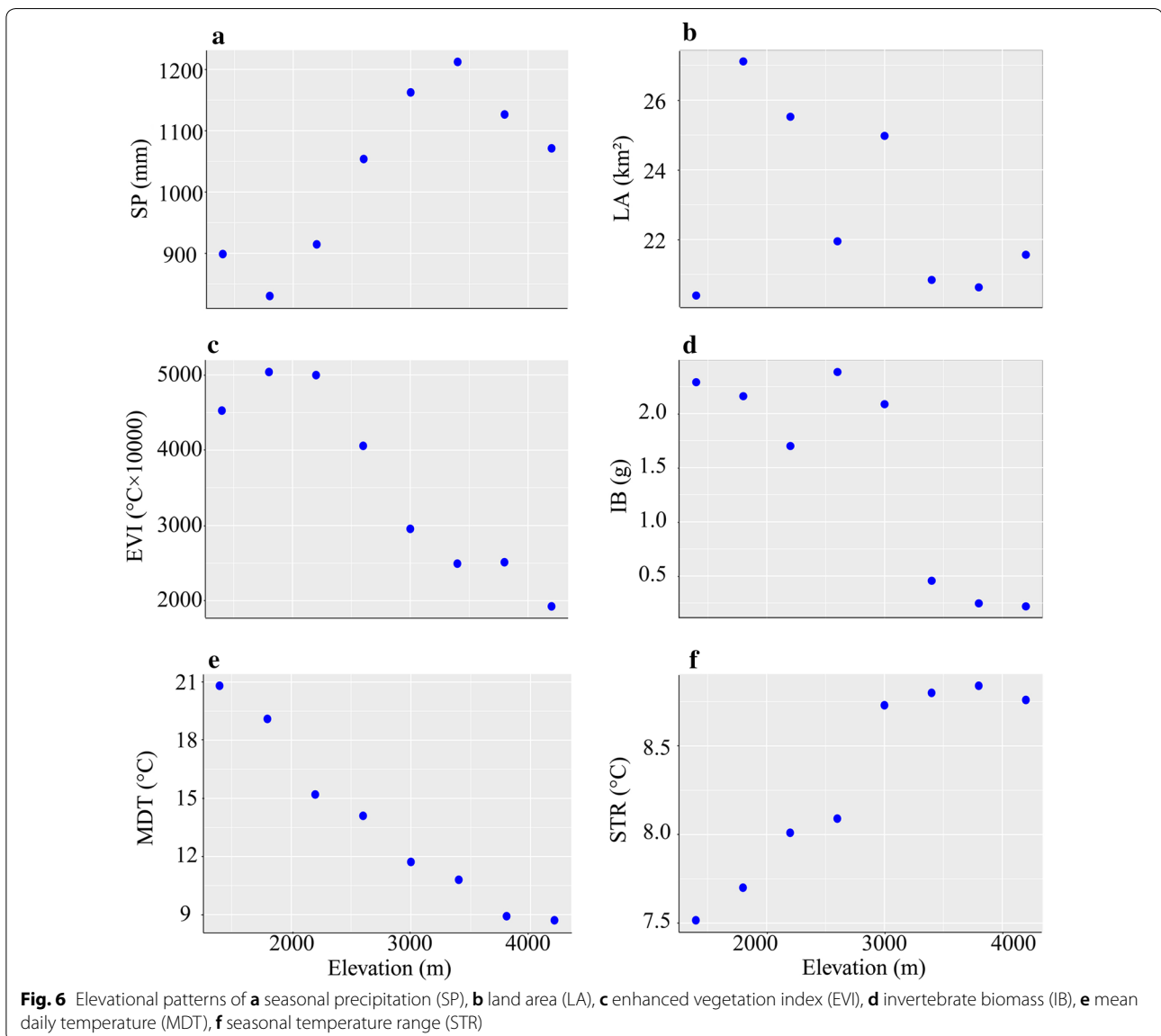


Table 3 Simple ordinary least squares (OLS) regression analyses of interpolated species richness against seven factors for different species categories

Species categories	Factors						
	LA	EVI	STR	MDT	IB	SP	MDE
<i>Total species</i>							
r^2	0.42	0.577	0.254	0.286	0.596	0.123	0.494
r^2_{adj}	0.324	0.507	0.13	0.168	0.529	− 0.023	0.41
p	0.082	0.029	− 0.203	0.172	0.025	0.394	0.052
<i>Large-ranged species</i>							
r^2	0.222	0.213	0.036	0.053	0.37	< 0.001	0.797
r^2_{adj}	0.092	0.08	− 0.125	− 0.104	0.265	− 0.167	0.763
p	0.239	0.25	− 0.655	0.582	0.11	0.949	0.003
<i>Small-ranged species</i>							
r^2	0.51	0.925	0.624	0.632	0.65	0.558	0.1
r^2_{adj}	0.427	0.912	0.562	0.571	0.59	0.484	− 0.05
p	0.047	< 0.001	− 0.02	0.018	0.016	− 0.033	0.448

r^2_{adj} is the adjusted r^2 value for multiple regressions

Negative relationships are indicated by "−"

LA land area, EVI enhanced vegetation index, STR seasonal temperature range, MDT mean daily temperature, IB invertebrate biomass, SP seasonal precipitation, MDE the mid-domain effect

Numbers in italics indicate significant r^2 values ($p < 0.05$)

Table 4 Multiple regression of interpolated species richness against four selected factors (LA, STR, IB, and MDE) for the three species categories

Species categories	LA	STR	IB	MDE	r^2	r^2_{adj}	p
Total species	1.457	− 25.25	1.507	0.583	0.969	0.928	0.013
Large-ranged species	− 0.173	− 7.704	2.449	0.737	0.957	0.899	0.022
Small-ranged species	1.554	− 18.24	− 1.205	0.379	0.955	0.896	0.023

r^2_{adj} is the adjusted r^2 value for multiple regressions

Negative relationships are indicated by "−"

LA land area, STR seasonal temperature range, IB invertebrate biomass, MDE the mid-domain effect

Numbers in italics indicate significant r^2 values ($p < 0.05$)

Table 5 Parameter estimates for the best-fit multiple regression models

Species categories	Standard coefficient of the best model						
	LA	STR	IB	MDE	r^2	r^2_{adj}	p
Total species		− 30.51		0.661	0.95	0.93	< 0.001
Large-ranged species		− 11.15		0.784	0.951	0.932	< 0.001
Small-ranged species			9.763		0.649	0.591	0.015

r^2_{adj} is the adjusted r^2 value for multiple regressions

LA land area, STR seasonal temperature range, IB invertebrate biomass, MDE the mid-domain effect

Table 6 Model-averaging coefficients of $\Delta AIC_c \leq 2$ model set and relative importance calculated for species richness

Species category	Factors	Estimate	SE	<i>p</i>	W_i
Large-ranged species	MDE	0.736	0.111	< 0.001	1
	STR	− 11.152	2.8	0.002	0.69
	IB	6.109	1.758	0.008	0.31
Small-ranged species	IB	9.763	2.931	0.008	0.63
	STR	− 17.059	5.009	0.005	0.37
	MDE	0.497	0.158	0.016	0.21
	LA	2.316	0.783	0.024	0.15

W_i is the importance value for model-averaging

LA land area, STR seasonal temperature range, IB invertebrate biomass, MDE the mid-domain effect

Integrative factors shape the richness pattern

Increasing numbers of studies from around the world are revealing that hump-shaped richness patterns are common for birds along elevational gradients. However, there are no consistent explanations for this pattern. MDE, STR, LA, SP, MDT, EVI and IB have been shown to contribute in different ways among studies (Lee et al. 2004; McCain 2009; Wu et al. 2013b; Price et al. 2014; Pan et al. 2016). Our results show that EVI and IB have significant influence on total species richness patterns based on simple regression analyses (Table 3). Peak elevational bird diversity coincides with relatively high EVI and IB values. These results are consistent with previous studies which have supported the energy (resource)-diversity hypothesis (Hurlbert and Haskell 2003; Wu et al. 2013b; Price et al. 2014; Pan et al. 2016), which states that sites with greater available energy are able to support more individual organisms and, hence, more species.

We found different richness patterns for small-ranged and large-ranged species. Interpretation of these results must take into account that the gradient defined in this study begins at 1200 m rather than at sea level. As a consequence of this cutoff, the “small-ranged species” category contains both montane species with truly narrow elevational distributions, and lowland species with marginal occurrence near the bottom of the gradient (often altitudinally and geographically widespread generalists). Thus, our “small-ranged species” can be considered to have small niches strictly within the context of our defined gradient, but not necessarily in a pure ecological sense. The main practical implication is that the small-ranged species curve is skewed toward lower altitudes. Similar skew is seen in other studies looking at truncated mountain gradients and discriminating between small- and large-ranged species (e.g., Wu et al. 2013a; Pan et al. 2016).

The distribution of small-ranged species on the gradient appears to be closely tied to environmental factors. This is best understood in light of the lowland species that heavily influence the shape of the curve, causing a more linear decline in richness with decreasing altitude. This mirrors the more-or-less linear incline or decline of the environmental factors SP, EVI, IB, MDT and STR, and thus they are statistically linked. Ecological interpretation is complicated by the fact that “small-ranged species” is an ecologically incoherent group; nevertheless, it is useful to separate out this group to gauge how the influence of MDE on richness curves varies with range size.

All regression models suggested that MDE was the main explanatory variable for large-ranged species. This could be due to large-ranged species having wider environmental and/or physiological tolerances than small-ranged species, and thus being less sensitive to STR and SP. Our study provides support for the geometric constraint hypothesis: that the positions of larger ranges within a bounded domain are more constrained and more likely to overlap than smaller ranges, while smaller ranges are more likely to be tied to environmental factors independent of boundary constraints (Colwell and Hurlt 1994; Colwell and Lees 2000). However, in the present case, the richness of all species categories peaked at elevation lower than that predicted by the MDE null model, indicating that MDE alone does not determine the richness pattern.

Future perspectives

Our knowledge of the mechanisms governing elevational diversity is still limited, yet this knowledge is necessary to understand how montane diversity is responding to global change. To better understand how diversity patterns are shaped will require long-term standardized surveys that cover different spatial and temporal scales (across years and seasons), as well as sampling a broader diversity of taxonomic categories. Resource and habitat associations among organisms at different elevations need to be better characterized. For example, invertebrate surveys should be strengthened to better assess the associations between invertebrate richness and bird richness, as invertebrates are an important food resource for many birds. Additionally, most bird surveys are limited to the breeding season, despite accounting for a portion an organism's life history. Improved knowledge of elevational distributions during the non-breeding seasons is thus needed. Lastly, additional studies of species abundance on Mt. Gongga would help us gain a more accurate understanding of the mechanisms shaping montane communities across elevational gradients.

Conclusions

No single factor or suite of factors explain the species richness patterns across all species categories. Model-averaging indicates that small-ranged species appear to be mostly influenced by IB, as opposed to large-ranged species, which exhibit patterns more consistent with the MDE model. We also find that species richness varied between seasons, offering a promising direction for future research that may help us better understand diversity patterns and their underlying causes in seasonal montane environments, like Mt. Gongga.

Additional file

Additional file 1. The checklist and elevational distribution of birds in the eastern Mt. Gongga.

Authors' contributions

YW, XH and JR conceived and designed the experiment, XH, SD, PA and YW conducted the experiments and collected field data. QL provided the climate data and helped analyze the data. XH, and XW performed data analyses. XH, XW, SD, AHR, PA, JR and YW led the writing. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets used in the present study are available from the corresponding author on reasonable request.

Consent for publication

Not applicable.

Ethics approval and consent to participate

The experiments comply with the current laws of China in which they were performed.

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