

Article

Topographic heterogeneity and temperature amplitude explain species richness patterns of birds in the Qinghai–Tibetan Plateau

Chunlan ZHANG^{a,b,c,**}, Qing QUAN^{a,b,**}, Yongjie WU^d, Youhua CHEN^e,
Peng HE^f, Yanhua QU^{a,*}, and Fumin LEI^{a,*}

^aKey Laboratory of the Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China, ^bCollege of Life Science, University of Chinese Academy of Sciences, Beijing 100049, China, ^cGuangdong Entomological Institute (South China Institute of Endangered Animals), Guangzhou 510260, China, ^dKey Laboratory of Bioresources and Ecoenvironment (Ministry of Education), College of Life Sciences, Sichuan University, Chengdu 610064, China, and ^eDepartment of Zoology, University of British Columbia, Vancouver, V6T 1Z4, Canada, and ^fNational Zoological Museum, Chinese Academy of Sciences, Beijing 100101, China

*Address correspondence to Yanhua Qu, E-mail: quyh@ioz.ac.cn; and Fumin Lei, E-mail: leifm@ioz.ac.cn.

**These authors contributed equally to this work.

Received on 18 December 2015; accepted on 12 January 2016

Abstract

Large-scale patterns of species richness have gained much attention in recent years; however, the factors that drive high species richness are still controversial in local regions, especially in highly diversified montane regions. The Qinghai–Tibetan Plateau (QTP) and the surrounding mountains are biodiversity hot spots due to a high number of endemic montane species. Here, we explored the factors underlying this high level of diversity by studying the relationship between species richness and environmental variables. The richness patterns of 758 resident bird species were summarized at the scale of $1^\circ \times 1^\circ$ grid cell at different taxonomic levels (order, family, genus, and species) and in different taxonomic groups (Passeriformes, Galliformes, Falconiformes, and Columbiformes). These richness patterns were subsequently analyzed against habitat heterogeneity (topographical heterogeneity and land cover), temperature amplitude (annual temperature, annual precipitation, precipitation seasonality, and temperature seasonality) and a vegetation index (net primary productivity). Our results showed that the highest richness was found in the southeastern part of the QTP, the eastern Himalayas. The lowest richness was observed in the central plateau of the QTP. Topographical heterogeneity and temperature amplitude are the primary factors that explain overall patterns of species richness in the QTP, although the specific effect of each environmental variable varies between the different taxonomic groups depending on their own evolutionary histories and ecological requirements. High species richness in the southeastern QTP is mostly due to highly diversified habitat types and temperature zones along elevation gradients, whereas the low species richness in the central plateau of the QTP may be due to environmental and energetic constraints, as the central plateau is harsh environment.

Key words: birds, habitat heterogeneity, Qinghai–Tibetan plateau, species richness, temperature amplitude, topography.

Understanding species richness patterns is fundamental to biodiversity conservation (Olson et al. 2001). In the passing decades, most studies have focused on large-scale patterns of species richness at global scales (Brown 1984; Myers 2000). Plenty of hypotheses, including water and energy availability, productivity, habitat heterogeneity, climatic variability, and geometric constraints, have been proposed to explain the mechanisms underlying these patterns (Nores 1999; Colwell and Lees 2000; Gaston 2000; Rahbek and Graves 2001a, 2001b; Hawkins et al. 2003b; Hurlbert, 2004; Diniz et al. 2007; Hawkins et al. 2007;). Some of these factors, (e.g., water and energy availability and climatic variability) may well explain overall patterns of richness, but the predominant factors are still unclear and controversial in local regions (Evans et al. 2005; Rahbek 2005; Wu et al. 2013a). Thus, most studies have been focused on organisms with wide distributions at continental scales. In contrast, patterns of species richness and their underlying driving factors in local regions may be largely dependent on the location of the study areas and the groups of species selected for study (Wu et al. 2013a).

Montane regions contain half of the currently recognized biodiversity hot spots, mostly as a consequence of the large number of endemic and endangered species (Stattersfield et al. 1998; Fjeldsø et al. 2012). Because montane areas are composed of rugged landscapes and heterogeneous habitats, habitat heterogeneity must be considered to fully explain the high diversity in the mountain regions (Rahbek and Graves 2000, 2001a, 2001b). In addition, temperature amplitude (including seasonal and elevational temperature amplitude) may also contribute to species richness in montane regions (Janzen 1967). Montane species can evolve narrow thermal tolerance and thereby be able to permanently reside within distinct elevational zones. This pattern, in turn, leads to high species turnover on elevational gradients and thus contributes to high species richness (Ghalambor et al. 2006; McCain 2009).

Habitat heterogeneity and temperature amplitude are mostly studied in tropical montane regions (Ghalambor et al. 2006; Fjeldsø & Bowie 2008; McCain 2009; Fjeldsø 2012) but have rarely been studied in temperate regions (e.g., in the Qinghai-Tibetan Plateau [QTP]). The QTP is the highest plateau in the world, with an average elevation of 4,500 meter above sea level (m.a.s.l.) and an area of more than 2.3 million km² (Lei et al. 2014). The QTP represents one of the most prominent topographic structures, with a flat interior surrounded by high montane ranges. The southeastern part of the QTP, the eastern Himalayas, contains the highest number of species and endemic species in China (Lei et al. 2003a, 2003b). In contrast to the rather flat central platform of the QTP, the eastern Himalayas are characterized by a series of parallel alpine ranges climbing to altitudes more than 5,000 m.a.s.l., with the differences in altitude from valley to mountaintops often exceeding 2,000 m.a.s.l. This broad altitudinal range has created dramatic habitat heterogeneity. In addition to geomorphological differentiation, the climate is also drastically varied in the QTP. The central platform is characterized by a constant low temperature and arid climate, while topographical heterogeneity in the eastern Himalayas has created a temperature gradient and diversified vegetation types. Species richness and its underlying factors in the QTP have been explored for only few organisms, including aphids (Huang 2006) and mammals (Wu et al. 2005; Tang et al. 2006). These studies have revealed that habitat heterogeneity and temperature amplitude have strongly contributed to overall patterns of species richness. Nevertheless, species richness patterns and potential contributed factors have not well been systematically evaluated in birds, although the QTP represents one of the highest avian biodiversity centers (Jetz et al. 2007, 2012, 2014; Rull 2011; La Sorte et al. 2014; Lei

et al. 2014). Therefore, in this study, we began by summarizing patterns of species richness in the QTP using 758 resident bird species. We then analyzed how different environmental variables (e.g., habitat heterogeneity, temperature amplitude, and the vegetation index [net primary productivity]) have contributed to current species richness patterns.

Materials and Methods

Study area

Our study area is situated between 26°00'12"N and 39°46'50"N, 73°18'52"E and 104°46'59"E with an elevation range between 891 and 8,233 m.a.s.l. This area covers an area of approximately 2.3 million km² (Thompson et al. 2000). The QTP is a central high plateau with an average elevation of 4,500 m.a.s.l. and is bounded to the north by the Tarim Basin and to the south by the eastern Himalayas (Turner et al. 1996). The QTP includes the entire Tibet autonomous region, Qinghai Province, and part of Yunnan, Sichuan and Gansu provinces, and Xinjiang Uygur Autonomous Region (Figure 1). The climate and environment of the QTP are complex. The central plateau of QTP is dominated by cold and dry conditions year-round, and the vegetation type is characterized by alpine meadows and grasslands (Cheng 1982; Cheng et al. 1987; Tang 1996; Zhang et al. 1997; Zhou et al. 2006). The eastern Himalayan region, however, is warmer and wetter at low elevations but cooler and drier at high elevations (Liu et al. 2002; Kou et al. 2006). Along the elevational gradient, the vegetation is tropical and subtropical at low elevations; broadleaved forests, temperate evergreen coniferous, and broadleaved mixed forests at mid elevations; and alpine meadow and grassland at high elevations (Wang et al. 2001; Yu et al. 2007).

Species distribution data

A total of 758 resident birds distributed on the QTP were used to generate species richness patterns. These birds covered 21 orders, 77 families, and 324 genera. We collected distribution records of each species from specimen collections of the National Zoological Museum of the Institute of Zoology, Chinese Academy of Sciences. We also used distribution records from the literature and geographical distribution data from BirdLife International (<http://www.birdlife.org>). Distribution records of these species were used to generate their ranges, which were subsequently transformed into 1°×1° grid maps in ArcGIS 9.3.

Patterns of species richness were summarized at the species, genus, family, and order level. Among 21 orders, we selected 4 orders that contained a high number of species, Passeriformes (504), Galliformes (35), Falconiformes (48), and Columbiformes (24), to compare species richness patterns of taxonomic groups with different evolutionary histories and ecological requirements.

Environmental factors

For habitat heterogeneity, we selected topographic heterogeneity and vegetation diversity, which are robust proxies of habitat heterogeneity. Topographic heterogeneity was estimated using altitude range (ALT), and vegetation diversity was estimated using land cover, as has been described in previous studies (LANDCOVER) (Rahbek and Graves 2000; Jetz and Rahbek 2002; Hawkins et al. 2005; Davies et al. 2007; Rahbek et al. 2007). To estimate climatic factors, we used 4 variables that represented the temperature amplitude, annual temperature (AMT), annual precipitation (AP), precipitation seasonality (PS), and temperature seasonality (TS). The QTP has an alpine climate; thus, extreme values of temperature may

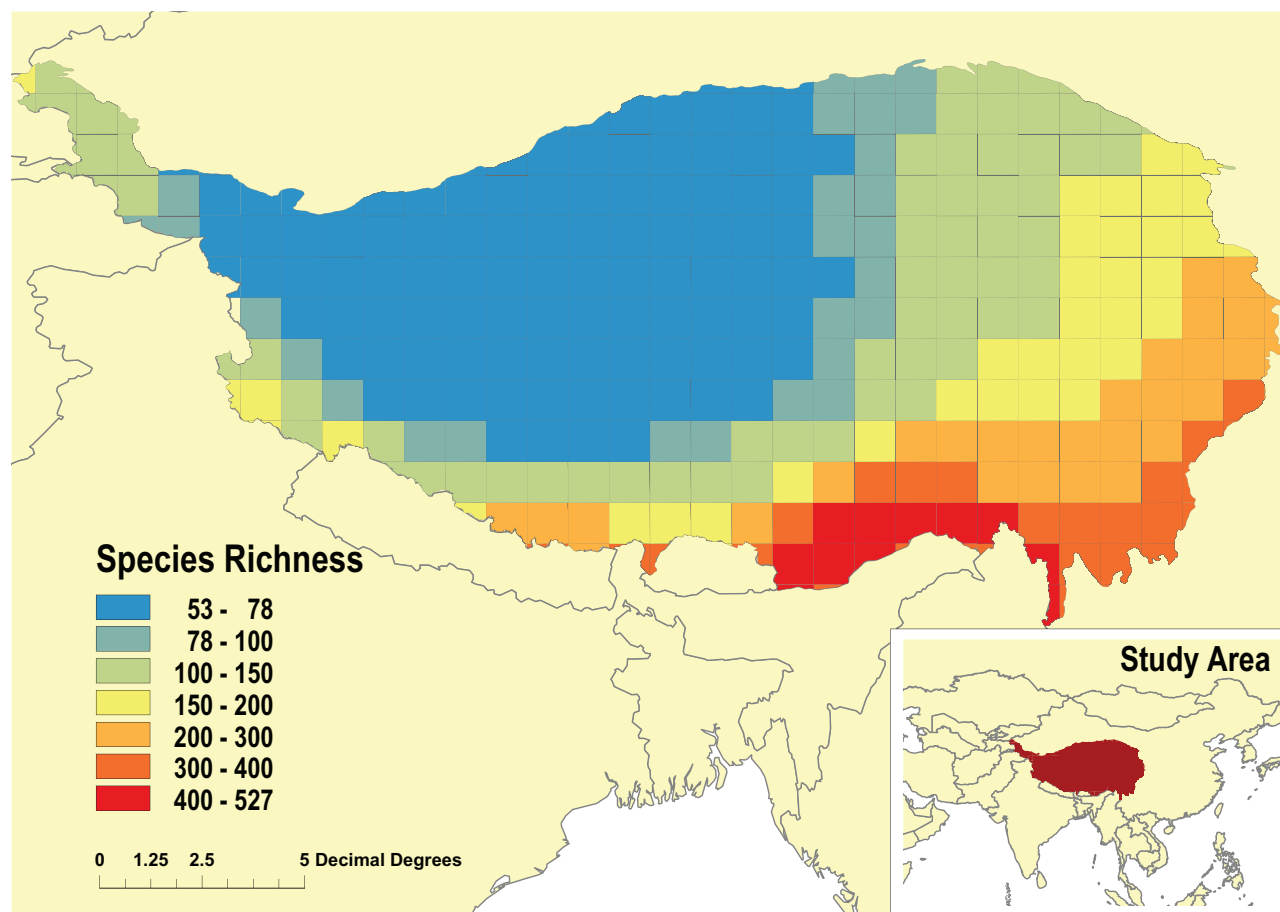


Figure 1. The study area and overall pattern of species richness in the Qinghai-Tibetan Plateau.

constitute the physiological limits for species living there. Additionally, we also estimated other factors that may potentially influence species richness, such as Normalized Difference Vegetation Index (NDVI) to measure net primary productivity (Currie 1991; Andrews and O'Brien 2000).

Climatic data were collected at a resolution of 30 arc second (ca. 1 km at the equator) from the WorldClim website between 1950 and 2000 (<http://www.worldclim.org/current.htm>). Digital elevation model data from 30 arc seconds grids were downloaded from <http://lpdaac.usgs.gov/gtopo30/gtopo30.asp>. LANDCOVER data were obtained at a 1-km resolution from http://edcdaac.usgs.gov/glcc/globe_int.html. We used the number of distinct land cover types to determine LANDCOVER values. NDVI data were downloaded from <http://edcsns17.cr.usgs.gov/1KM/> between 2000 and 2011.

Statistical analysis

We investigated the relationships between species richness and environmental variables using standard ordinary least squares (OLS) regression. All of the possible combinations of variables were examined, and the model with the lowest Akaike information criterion (AIC) was selected (Wu et al. 2013a, 2013b). An adjusted R^2 was provided for the selected models. Considering that multicollinearity affect analysis of these variables, we also used a simultaneous autoregressive regression (SAR) approach to analyze relationships while accounting for the effects of multicollinearity.

Next, we used 2 approaches to specifically examine the effect of topographical heterogeneity (ALT) and altitudinal temperature

amplitude on patterns of species richness. For this analysis, all AMT values in a grid were averaged to obtain average annual temperature along elevation gradients in this grid (RAMT). First, we used partial regression to estimate independent effects, shared effects, and unexplained variation in ALT and RAMT on patterns of species richness. Second, we used a path model to distinguish the direct effect and indirect effects of ALT and RAMT on species richness, respectively, based on maximum likelihood methods (Hatcher 1994). All variables were standardized before analyses. All statistical analyses were conducted with the “spdep” and “agricolae” packages in R libraries (<http://www.r-project.org/>).

Results

Species richness pattern of birds in the QTP

For all 758 bird species, species richness was the highest in the southeast of the QTP, with a range between 300 and 527 species. The lowest species richness was in the central and northwestern platform, with a range between 53 and 100 species (Figure 1). Consistently, richness patterns at the genus (Supplementary Figure 1A), family (Supplementary Figure 1B), and order level (Supplementary Figure 1C) were similar: species richness was highest in the eastern Himalayas (genus, 150–271; family, 49–74; order, 17–21) and lowest in the central platform of the QTP (genus, 41–70; family, 20–38; order, 9–14).

A close correlation was found between overall patterns revealed by all species and patterns revealed by the 4 representative orders,

Passeriformes ($r=0.99$), Galliformes ($r=0.72$), Falconiformes ($r=0.81$), and Columbiformes ($r=0.82$, Table 1). The eastern Himalayas contains the highest number of species for each order (Passeriformes, range between 150 and 352, Figure 2a; Galliformes, range between 9 and 14, Figure 2b; Falconiformes, range between 16 and 35, Figure 2c; and Columbiformes, range between 9 and 17, Figure 2d), whereas the central platform had the lowest number of species for each order (Passeriformes, range between 34 and 100, Figure 2a; Galliformes, range 0 and 6, Figure 2b; Falconiformes, range between 0 and 12, Figure 2c; and Columbiformes, range between 0 and 5, Figure 2d).

Latitudinal and longitudinal distributions of 758 resident birds were fitted to a binomial model (Figure 3). Bird richness decreased 3 times with latitude from N27° to N35°, followed by an increase twice until N40° (Figure 3). A pattern with much fewer fluctuations

was observed with longitude, where richness slightly changed by approximately 100 species (Figure 3).

Multiple regression between species richness and environmental variables

OLS revealed that ALT was strongly and AMT, PS, and TS were significantly, but less strongly than ALT, correlated with overall patterns of species richness at the species (ALT, 0.46***; AMT, 0.24***; PS, -0.22***; TS, -0.23***), genus (ALT, 0.41***; AMT, 0.23***; PS, -0.21***; TS, -0.19***), family (ALT, 0.42***; AMT, 0.22***; PS, -0.23***; TS, -0.27***) and order level (ALT, 0.54***; AMT, 0.09; PS, -0.22***; TS, -0.19***, Table 2). SAR results revealed a similar pattern: ALT was the strongest predictor of species richness patterns in all comparisons (species, 8.09***; genus, 7.19***; family, 6.31***; order, 6.97***). AMT was a significant factor at genus level (2.45*). PS was a significant factor at the genus (-2.7*) and family level (-2.41*). TS was a significant factor at the species (-2.03*) and order level (-1.78*).

Although the 4 orders, Passeriformes, Galliformes, Falconiformes, and Columbiformes, were analyzed separately, the dominant correlated factors were found to differ between orders (Table 3). ALT was found to be the strongest predictor of species richness for Passeriformes (OLS, 0.45***; SAR, 6.94***), but ALT was not a significant predictor of species richness for Falconiformes. LANDCOVER was the best predictor of species richness for Galliformes (OLS, 0.33***; SAR, 3.14**), but LANDCOVER was not a significant predictor

Table 1. Correlation coefficients between species richness patterns of all birds and different orders

	All birds	Passeriformes	Columbiformes	Galliformes
All birds	0.99*			
Passeriformes				
Columbiformes	0.82*	0.81*		
Galliformes	0.72*	0.74*	0.73*	
Falconiformes	0.81*	0.81*	0.86*	0.85*

Note: * $P < 0.01$.

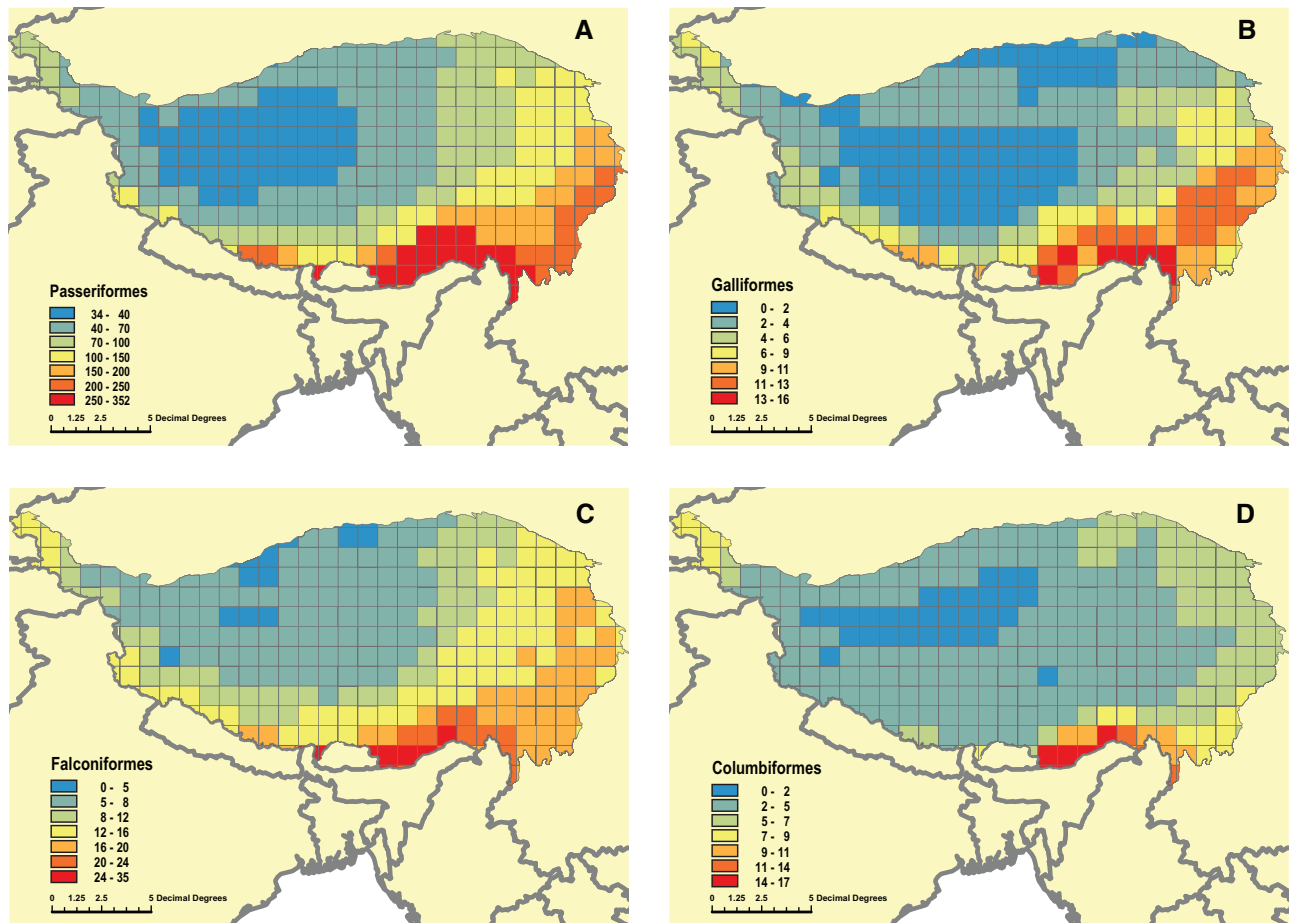


Figure 2. Species richness patterns of 4 orders: (a) Passeriformes, (b) Galliformes, (c) Falconiformes, (d) Columbiformes.

of richness for Passeriformes or Columbiformes. TS was the strongest predictor of the species richness for Falconiformes (OLS, -0.26^{***} ; SAR, -4.87^{***}), and AMT was the most important factor for Columbiformes (OLS, -0.2^{***} ; SAR, -2.22^*).

Partial regression of ALT, RAMT, and overall patterns of species richness revealed that only 3% and 1% of the variation in species richness was explained by ALT and RAMT, respectively. However, there was an interaction between ALT and RAMT that explained half of the total variation (50%). The path model revealed that both

ALT and RAMT have contributed to high species richness, although the effect of ALT was more than twice (0.54) than that of RAMT (0.2). Both variables were strongly correlated (0.94).

Discussion

Species richness patterns of birds in the QTP

For all of the 758 species, the highest levels of species richness were in the eastern Himalayas and the southeastern part of the QTP, and

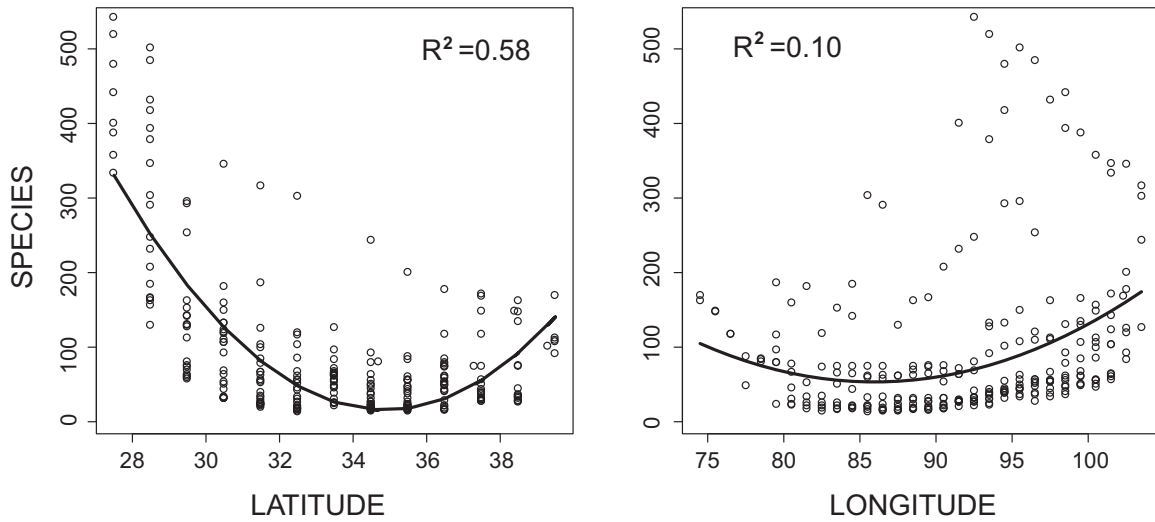


Figure 3. Species richness distribution along the latitude and longitude gradients.

Table 2. Results of regressions of bird richness and environment variables

		ALT	NDVI	AMT	LANDCOVER	AP	PS	TS	Adjusted R ²	AIC
Species	OLS	0.46 ^{***}	—	0.24 ^{***}	—	—	-0.22 ^{***}	-0.23 ^{***}	0.71	467.86
	SAR	8.09 ^{***}	—	2.53	—	—	-2.95	-2.03 [*]	—	391.87
Order	OLS	0.54 ^{***}	—	0.09	—	—	-0.22 ^{***}	-0.19 ^{***}	0.6	118.01
	SAR	6.97 ^{***}	—	0.54	—	—	-2.48	-1.78 [*]	—	70.39
Family	OLS	0.42 ^{***}	0.17 ^{**}	0.22 ^{**}	—	-0.14	-0.23 ^{***}	-0.27 ^{***}	0.68	217.02
	SAR	6.31 ^{***}	0.87	1.53	—	-0.27	-2.41 [*]	-1.68	—	125.2
Genus	OLS	0.41 ^{***}	—	0.23 ^{***}	0.09	—	-0.21 ^{***}	-0.19 ^{***}	0.7	399.57
	SAR	7.19 ^{***}	—	2.45 [*]	0.45	—	-2.70 [*]	-1.71	—	312.18

Note: NDVI, Normalized Difference Vegetation Index; LANDCOVER, Landcover diversity; ALT, elevation range; PS, precipitation seasonality; TS, temperature seasonality; AMT, annual mean temperature; AP, annual precipitation.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 3. Results of regressions of bird richness and environment variables in different taxonomic groups

		ALT	NDVI	AMT	LANDCOVER	AP	PS	TS	Adjusted R ²	AIC
All birds	OLS	0.46 ^{***}	—	0.24 ^{**}	—	—	-0.22 [*]	-0.23 [*]	0.71	467.86
	SAR	8.09 ^{***}	—	2.53	—	—	-2.95	-2.03 [*]	—	391.87
Passeriformes	OLS	0.45 ^{***}	0.14	0.27 ^{***}	0.13	—	-0.19 ^{**}	-0.21 ^{**}	0.6	542
	SAR	6.94 ^{***}	0.36	2.01 [*]	0.32	—	-2.34 [*]	-1.38	—	471.54
Galliformes	OLS	0.30 ^{***}	0.22 ^{**}	-0.13 [*]	0.33 ^{***}	—	-0.23 ^{***}	-0.17 ^{**}	0.68	373.21
	SAR	2.79 ^{**}	-0.32	-2.02 [*]	3.14 ^{**}	—	-1.74	-1.70	—	136.64
Falconiformes	OLS	—	—	0.24 ^{***}	0.31 ^{***}	—	-0.26 ^{***}	-0.26 ^{***}	0.7	81.88
	SAR	—	—	0.59	2.74 ^{**}	—	-3.25 ^{***}	-4.87 ^{***}	—	35.01
Columbiformes	OLS	0.22 ^{***}	0.16 [*]	0.39 ^{***}	0.12	0.17 [*]	-0.20 ^{***}	-0.21 ^{***}	0.5	23.14
	SAR	2.21 ^{***}	-0.42	2.69 ^{**}	0.49	2.48 [*]	-2.22 [*]	2.13 [*]	—	-94.05

Note: NDVI, Normalized Difference Vegetation Index; LANDCOVER, Landcover diversity; ALT, elevation range; PS, precipitation seasonality; TS, temperature seasonality; AMT, annual mean temperature; AP, annual precipitation.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

the lowest levels of species richness were in the central platform, no matter what taxonomic levels were analyzed (species, genus, family, and order). These patterns are also consistent with the results from the 4 avian orders that we examined, although each order differs in their evolutionary history and ecological habitat requirements. These patterns have been previously observed in aphids (Huang et al. 2006), amphibians (Chen and Bi 2007), mammals (Wu et al. 2005; Tang et al. 2006), grasshoppers (Xu 2005), spiders (Ment et al. 2008), and endemic birds in China (Lei et al. 2003a, 2003b).

Using multiple regression models, we investigated the most important environmental factors that explain high species richness. All patterns of species richness examined from the species, genus, family, and order level, consistently revealed that altitude range, which is a proxy for topographic heterogeneity, is the strongest predictor of high species richness. However, when we examined different avian orders, the strongest predictors were different. For Passeriformes, altitude range and annual temperature were the strongest predictors. This pattern in Passeriformes was the same as the pattern that characterized all 758 species. This is not surprising given that Passeriformes consists of ~70% of the current recognized species in the QTP. Thus, Passeriformes receives the highest weight during model building. For Galliformes, vegetation diversity and altitude range are the dominant predictors, which may be because most pheasants are ground-living birds with poor mobility, unlike passerines that are more mobile. Therefore, different vegetation types would greatly affect the movement and distribution of pheasants. Unlike most other avian orders, temperature seasonality and precipitation seasonality, rather than altitude range, are the best predictors for Falconiformes. This finding may be because most Falconiformes are highly mobile species. Thus, in this case, seasonal temperature and precipitation variables better explain regional variation in the most wide-ranging species (Jetz and Rahbek 2002; Rahbek et al. 2007). Overall, although topographic heterogeneity and temperature amplitude are factors that explain overall patterns of species richness in the QTP, the specific effect of each environmental variable may vary in different bird orders, depending on their evolutionary histories and ecological requirements.

Topographical heterogeneity and altitudinal temperature amplitude contribute to the high species richness in the eastern Himalayas

Mountain areas cover nearly half of the currently defined global biodiversity hot spots (Kohler and Maselli 2009), such as the Andes, Afromontane regions, and eastern Himalayas in the southeastern part of the QTP. Previously, studies from the Andes and Afromontane regions have revealed that topographical heterogeneity and altitudinal temperature amplitude have contributed to high species richness (Ghalambor et al. 2006; Fjelds  and Bowie 2008; McCain 2009; Fjelds  2012). Our study in the QTP confirms this result, although the QTP has a different geological history, topography, and climatic zones. The eastern Himalayas consist of clusters of mountain systems with altitudinal differences often exceeding 2,000 m.a.s.l. between valleys and mountain tops. Such topographical complexity within a rather small geographical area leads to dramatic ecological stratification and heterogeneous environments (Fjelds  et al. 2012). Along altitudinal gradients, species may evolve narrow thermal tolerances, enabling them to reside within a distinct altitudinal zone (Wu et al. 2013a, 2013b, 2014). Overall, topographic heterogeneity and temperature amplitude along altitudinal gradients in the eastern Himalayas together have contributed to an accumulation of narrowly ranged species.

Harsh climate is attributed to the lowest richness of birds in the central platform of the QTP

Unlike the unusually high species richness found in the eastern Himalayas, the platform of the QTP contains the lowest number of species. The QTP has a rather flat platform in the central region with an average elevation of 4,500 m, which is accompanied by a constant low temperature and arid climate. The annual mean temperature is normally approximately -2.8° , but sometimes the winter temperature can drop to -40° . Annual precipitation is usually less than 300 mm per year. The prominent vegetation types in the platform region are alpine meadow and steep (Zhao et al. 2004). Cold, arid climate, and bare vegetation types create an extremely hostile environment for most species (Wiens and Donoghue 2004). Only a few alpine species, *Parus humilis*, *Onychostruthus taczanowskii*, *Montifringilla* spp., *Pyrgilaud* spp., manage to survive (Lei et al. 2003a). Taken together, physical and energetic constraints due to harsh environments in the platform region of the QTP facilitate local extinction and prevent the expansion of lowland colonists.

Funding

This study was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDA05080703 and XDB13020300), the State Key Program of National Science Foundation of China (31330073; 31471990), the Knowledge Innovation Program of the Chinese Academy of Sciences (KSCX2-EW-Z-5), the Chinese Science Database (XXH12504-1-12) and Science and Technology Foundation Project (2014FY210200).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.cz.oxfordjournals.org/>.

Acknowledgments

We thank Gexia Qiao, Zhiheng Wang, Gang Song, Wenjuan Wang, and Yanmei Xiong for their kind help and suggestions. We especially thank Bradford A. Hawkins and Carsten Rahbek for many good suggestions for designing the study. We also thank Yili Zhang for providing the map of QTP.

References

- Andrews P, O'Brien EM, 2000. Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *J Zool* 251:205–231.
- Brown JH, 1984. On the relationship between abundance and distribution of species. *Am Nat* 124: 255–279.
- Chen Y, Bi J, 2007. Biogeography and hotspots of amphibian species of China: implications to reserve selection and conservation. *Curr Sci* 92: 480–489.
- Cheng TH, 1982. On the evolution of *Garrulax* Timaliinae, with comparative studies of the species found at the center and those in the periphery of the distributional range of the genus. *Acta Zool Sinica* 28:205–209.
- Cheng TH, Long ZY, Zheng BL, 1987. *Fauna Sinica (Aves, Vol. 11 Passeriformes, Muscicapidae II Timaliinae)*. Beijing: Science Press.
- Colwell RK, Lees DC, 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends Ecol Evol* 15:70–76.
- Currie DJ, 1991. Energy and large-scale patterns of animal-species and plant-species richness. *Am Nat* 137:27–49.
- Davies RG, Orme CD, Storch D, Olson VA, Thomas GH et al., 2007. Topography, energy and the global distribution of bird species richness. *Proc R Soc Lond Biol* 274:1189–1197.
- Diniz JaF, Rangel TFLVB, Bini LM, Hawkins BA, 2007. Macroevolutionary dynamics in environmental space and the latitudinal diversity gradient in New World birds. *Proc R Soc Lond Biol* 274:43–52.

- Evans KL, Warren PH, Gaston KJ, 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biol Rev* 80:1–25.
- Fjelds  J, Bowie RCK, 2008. New perspectives on Africa’s ancient forest avifauna. *Afr J Ecol* 46:235–47.
- Fjelds  J, Bowie RCK, Rahbek C, 2012. The role of mountain ranges in the diversification of birds. *Annu Rev Ecol Evol Syst* 43:249–265.
- Gaston KJ, 2000. Global patterns in biodiversity. *Nature* 405:220–227.
- Ghalambor CK, Huey RB, Martin PR, Tewksbury JJ, Wang G, 2006. Are mountain passes higher in the tropics? Janzen’s hypothesis revisited. *Integr Comp Biol* 46:5–17.
- Hatcher L, 1994. *A Step-by-Step Approach to Using the SAS System for Factor Analysis and Structural Equation Modeling*. Cary (NC): The SAS Institute, Inc.
- Hawkins BA, Diniz-Filho JAF, Jaramillo CA, Soeller SA, 2007. Climate, niche conservatism, and the global bird diversity gradient. *Am Nat* 170:S16–S27.
- Hawkins BA, Diniz JAF, Soeller SA, 2005. Water links the historical and contemporary components of the Australian bird diversity gradient. *J Biogeogr* 32:1035–1042.
- Hawkins BA, Porter EE, Diniz JAF, 2003. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology* 84:1608–1623.
- Huang XL, Qiao GX, Lei F, 2006. Diversity and distribution of aphids in the Qinghai–Tibetan Plateau–Himalayas. *Ecol Entomol* 31:608–615.
- Hurlbert AH, Haskell JP, 2003. The effect of energy and seasonality on avian species richness and community composition. *Am Nat* 161:83–97.
- Janzen DH, 1967. Why mountain passes are higher in tropics. *Am Nat* 101:233.
- Jetz W, Rahbek C, 2002. Geographic range size and determinants of avian species richness. *Science* 297:1548–1551.
- Jetz W, Thomas G, Joy J, Redding D, Hartmann K et al., 2014. Global distribution and conservation of evolutionary distinctness in birds. *Curr Biol* 24:919–930.
- Jetz W, Thomas H, Joy J, Hartmann K, Mooers A, 2012. The global diversity of birds in space and time. *Nature* 491:444–448.
- Jetz W, Wilcove D, Dobson A, 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol* 5:e157.
- La Sorte F, Butchart S, Jetz W, Bohning-Gaese K, 2014. Range-wide latitudinal and elevational temperature gradients for the world’s terrestrial birds: implications under global climate change. *PLoS ONE* 9:e98361.
- Lei F, Qu Y, Lu J, Liu Y, Yin Z et al., 2003a. Conservation on diversity and distribution patterns of endemic birds in China. *Biodivers Conserv* 12:239–254.
- Lei F, Qu Y, Tang Q, An S, 2003b. Priorities for the conservation of avian biodiversity in China based on the distribution patterns of endemic bird genera. *Biodivers Conserv* 12:2487–2501.
- Lei F, Qu Y, Song G, 2014. Species diversification and phylogeographical patterns of birds in response to the uplift of the Qinghai–Tibet Plateau and Quaternary glaciations. *Curr Zool* 60:149–161.
- Liu J, Yu G, Chen X, 2002. Paleoclimatic simulation of 21 ka for the Qinghai–Tibetan plateau and eastern Asia. *Clim Dynam* 19:575–583.
- Kohler T, Maselli D, 2009. *Mountains and Climate Change: from Understanding to Action*. Bern: Centre for Development and Environment (CDE), Institute of Geography, University of Bern.
- Kou XY, Ferguson DK, Xu JX, Wang YF, Li CS, 2006. The reconstruction of paleovegetation and paleoclimate in the Late Pliocene of West Yunnan, China. *Climatic Change* 77:431–448.
- McCain CM, 2009. Global analysis of bird elevational diversity. *Glob Ecol Biogeogr* 19:346–60.
- Meng K, Li SQ, Murphy RW, 2008. Biogeographical patterns of Chinese spiders (Arachnida: Araneae) based on a parsimony analysis of endemism. *J Biogeogr* 35:1241–1249.
- Moritz C, Patton JL, Schneider CJ, Smith TB, 2000. Diversification of rainforest faunas: an integrated molecular approach. *Annu Rev Ecol Syst* 31:533–563.
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J, 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- Nores M, 1999. An alternative hypothesis for the origin of Amazonian bird diversity. *J Biogeogr* 26:475–485.
- Olson DM, Dinerstein ED, Wikramanayake ED, Burgess ND, Powell GVN et al., 2003. Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* 51:933–938.
- Rahbek C, 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol Lett* 8:224–239.
- Rahbek C, Gotelli NJ, Colwell RK, Entsminger GL, Rangel TFLVB et al., 2007. Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proc R Soc Lond Biol* 274:165–174.
- Rahbek C, Graves GR, 2000. Detection of macro-ecological patterns in South American hummingbirds is affected by spatial scale. *Proc R Soc Lond B Biol* 267:2259–2265.
- Rahbek C, Graves GR, 2001a. Multiscale assessment of patterns of avian species richness. *Proc Natl Acad Sci USA* 98:4534–4539.
- Rahbek C, Graves GR, 2001b. Multiscale assessment of patterns of avian species richness. *Proc Natl Acad Sci USA* 98:4534–4539.
- Rull V, 2011. Neotropical biodiversity: timing and potential drivers. *Trends Ecol Evol* 26:508–513.
- Stattersfield AJ, Crosby MJ, Long AJ, Wege DC, 1998. *Endemic Bird Areas of the World*. Cambridge: BirdLife Int.
- Tang Z, 1996. *Birds of the Hengduan Mountains Region*. Beijing: Sciences Press.
- Tang Z, Wang Z, Zheng C, Fang J, 2006. Biodiversity in China’s mountains. *Frontiers Ecol Environ* 4:347–52.
- Thompson LG, Yao T, Thompson EM, Davis ME, Henderson KA et al., 2000. A high-resolution millennial record of the South Asian monsoon from Himalayan ice cores. *Science* 289:1916–1919.
- Turner S, Arnaud N, Liu J, Rogers N, Hawkesworth C et al., 1996. Post-collision, shoshonitic volcanism on the Tibetan plateau: implications for convective thinning of the lithosphere and the source of ocean island basalts. *J Petrol* 37:45–71.
- Vuilleumier F, Monasterio M, 1986. *High Altitude Tropical Biogeography*. Oxford: Oxford University Press.
- Wang YJ, Cheng H, Edwards RL, 2001. A high-resolution absolute-dated Late Pleistocene monsoon record from hulu cave, China. *Science* 294:2345–2348.
- Wiens JJ, Donoghue MJ, 2004. Historical biogeography, ecology and species richness. *Trends Ecol Evol* 19:639–644.
- Wu YJ, Colwell RK, Rahbek C, Zhang CL, Quan Q et al., 2013a. Explaining the species richness of birds along a subtropical elevational gradient in the Hengduan Mountains. *J Biogeogr* 40:2310–2323.
- Wu YJ, Yang QS, Wen ZX, Xia L, Zhang Q et al., 2013b. What drives the species richness patterns of nonvolant small mammals along a subtropical elevational gradient? *Ecography* 36:185–196.
- Wu Z, Sun H, Zhou Z, Peng H, Li DZ, 2005. Origin and differentiation of endemism in the flora of China. *Acta Bot Yunnan* 27:577.
- Xu S, 2005. Distribution and area of endemism of Catantopidae grasshopper species endemic to China. *Acta Zool Sinica* 51:624.
- Yu G, Gui F, Shi Y, Zheng Y, 2007. Late marine isotope stage 3 palaeoclimate for East Asia: a data-model comparison. *Palaeogeogr Palaeoclimatol Palaeoecol* 250:167–183.
- Zhang RZ, Zheng D, Yang QY, Liu YH, 1997. *Physical Geography of Hengduan Mountains*. Beijing: Science Press.
- Zhao L, Ping CL, Yang D, Cheng G, Ding Y et al., 2004. Changes of climate and seasonally frozen ground over the past 30 years in Qinghai–Xizang (Tibetan) Plateau, China. *Global Planet Change* 43:19–31.
- Zhou S, Wang X, Wang J, Xu L, 2006. A preliminary study on timing of the oldest Pleistocene glaciation in Qinghai–Tibetan plateau. *Quatern Int* 154–155:44–51.