

Article

Ecological and evolutionary constraints on regional avifauna of passerines in China

Tianlong CAI^{a,#}, Qing QUAN^{a,b,#}, Gang SONG^{a,*}, Yongjie WU^{a,c}, Zhixin WEN^a, Chunlan ZHANG^b, Yanhua QU^a, Gexia QIAO^{a,d}, and Fumin LEI^{a,d,e,*}

^aKey Laboratory of the Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China, ^bGuangdong Key Laboratory of Animal Conservation and Resource Utilization, Guangdong Public Laboratory of Wild Animal Conservation and Utilization, Institute of Zoology, Guangdong Academy of Sciences, Guangzhou 510260, China, ^cKey Laboratory of Bio-resources and Eco-environment of Ministry of Education, College of Life Sciences, Sichuan University, Chengdu 610065, China, ^dCollege of Life Sciences, University of Chinese Academy of Sciences, Beijing 100049, China and ^eCenter for Excellence in Animal Evolution and Genetics, Chinese Academy of Sciences, Kunming 650223, China

*Address correspondence to Fumin Lei, E-mail: leifm@ioz.ac.cn and Gang Song, E-mail: songgang@ioz.ac.cn.

#These authors have contributed equally to this work.

Handling editor: Zhi-Yun Jia

Received on 21 August 2020; accepted on 1 December 2020

Abstract

Strong correlations between species diversity and climate have been widely observed, but the mechanism underlying this relationship is unclear. Here, we explored the causes of the richness–climate relationships among passerine birds in China by integrating tropical conservatism and diversification rate hypotheses using path models. We found that assemblages with higher species richness southwest of the Salween–Mekong–Pearl River Divide are phylogenetically overdispersed and have shorter mean root distances (MRDs), while species-rich regions northeast of this divide (e.g., north Hengduan Mountains–south Qinling Mountains) are phylogenetically clustered and have longer MRDs. The results of the path analyses showed that the direct effect of climatic factors on species richness was stronger than their indirect effects on species richness via phylogenetic relatedness, indicating that neither tropical conservatism nor diversification rate hypotheses can well explain the richness–climate relationship among passerines in China. However, when path analyses were conducted within subregions separately, we found that the tropical conservatism hypothesis was well supported in the southwestern Salween–Mekong–Pearl River Divide, while the diversification rate hypothesis could explain the richness–climate relationship well in the northeastern divide. We conclude that the diversity patterns of passerines in different subregions of the Eastern Himalayas–Mountains of Southwest China may be shaped by different evolutionary processes related to geological and climatic histories, which explains why the tropical conservatism or diversification rate hypothesis alone cannot fully explain the richness–climate relationships.

Key words: avifauna, diversification rate hypothesis, diversity hotspots, Eastern Himalayas–Mountains of Southwest China, phylogenetic relatedness, tropical conservatism hypothesis

Species richness is distributed heterogeneously across the Earth's surface, and the tropics have higher diversity than temperate and

pole regions (Rosenzweig 1995; Gaston 2000). Research on the mechanism underlying this well-known diversity gradient has

challenged many biogeographers and ecologists in recent centuries (Rosenzweig 1995). A strong correlation between species richness and climatic factors (e.g., water and energy) has been found in many taxa, indicating an important role of climate in driving global biodiversity distributions (Rosenzweig 1995; Hawkins et al. 2003; Currie et al. 2004; Evans et al. 2005). However, climatic factors cannot change the number of species and their compositions in a region without the direct roles of evolutionary processes (e.g., speciation, extinction, and dispersal) (Wiens and Donoghue 2004). Therefore, it is necessary to integrate these evolutionary processes to fully understand the species richness–climate relationship (Wiens and Donoghue 2004; Mittelbach et al. 2007; Algar et al. 2009; Qian et al. 2016).

One hypothesis that integrates evolutionary and climatic factors to explain the spatial variation in global diversity is the niche conservatism hypothesis, which is defined as the maintenance of ancestral climatic niches over evolutionary time among closely related species (Wiens and Graham 2005; Losos 2008). The tropical conservatism hypothesis postulates that most clades of current species originate in tropical environments, and subsequent evolutionary events rarely produce a clade that has the ability to tolerate freezing temperatures and cross ecophysiological barriers to colder environments (Wiens and Graham 2005; Ricklefs 2006; Losos 2008; Qian et al. 2013). Under this hypothesis, warm and humid environments have higher species richness because these regions are characterized by their ancestral niches and have a long time to accumulate more distantly related species (sometimes called “time-for-speciation effects”; Stephens and Wiens 2003), while colder and dryer regions have lower diversity; moreover, most clades tend to be younger and phylogenetically more related to each other (phylogenetic clustering) (Wiens and Donoghue 2004; Losos 2008; Qian et al. 2013). The climatic niche conservatism of regional taxa creates variation in species diversity along environmental gradients (e.g., temperature and precipitation), resulting in stronger correlations between species richness and climatic factors.

Alternatively, species richness–climate relationships might be explained by the diversification rate hypothesis, which predicts that certain climatic regimes may have more species because of the higher net diversification rate (speciation minus extinction rates) (Stenseth 1984; Rohde 1992). Climatic factors might affect the diversification rate through various mechanisms. For example, productive areas (e.g., characterized by warm and moist climates) may provide more resources and support more individuals, enabling species to maintain larger and more viable populations, which reduces their extinction risk (Currie et al. 2004; Evans et al. 2005; Mittelbach et al. 2007). Moreover, the evolutionary rate could be faster in warmer environments (e.g., tropics) than in colder regions because higher temperatures could increase the metabolic rate, which influences the consumption of oxygen and production of oxygen-free radicals and in turn may increase genetic mutation rates (Mittelbach et al. 2007; Dowle et al. 2013). Other mechanisms, such as narrower physiological tolerances reducing dispersal abilities across unfavorable environments (Janzen 1967) and stronger biotic interactions causing greater specialization in tropical organisms (Currie et al. 2004; Mittelbach et al. 2007), might also contribute to rapid speciation in warm and humid climate regimes. The processes could cause differences in the net diversification rates among regions, leading to variations in species richness along climate gradients.

Both hypotheses could be tested by comparing phylogenetic relatedness among species in different climatic regimes and correlating

these patterns to climatic characters and species richness (Algar et al. 2009; Qian et al. 2015, 2016). Specifically, if climate constrains species richness patterns, as indicated by the tropical conservatism hypothesis, species richness should be strongly related to climatic factors. Furthermore, species in the regions with lower richness should be closely related to each other (phylogenetic clustering), while regions with higher richness should have more distantly related species (phylogenetic overdispersion) due to longer times for diversification in these habitats. Alternatively, if the diversification rate underlies the richness–climate relationships, the mean root distance (MRD) (Kerr and Currie 1999) among species in assemblages, which indicates a higher diversification rate, should directly correlate to species richness, while climate should indirectly correlate to richness via MRD. For example, Qian et al. (2015) used path analysis to examine relationships among species richness, climatic factors including minimum temperature of coldest month (MTCM) and annual precipitation (AP), and phylogenetic relatedness of MRD (Kerr and Currie 1999), net relatedness index (NRI) (Webb et al. 2002) and phylogenetic species variation (PSV) (Helmus et al. 2007) (measuring phylogenetic structure) using angiosperm trees as a group. They found that species richness was directly correlated with NRI and PSV and indirectly correlated with MTCM, which strongly supported the tropical conservatism hypothesis underlying the richness–climate relationships in North America (Qian et al. 2015).

China includes a large land area (~ 9.6 million km^2) ranging from tropical to boreal zones and from a very low altitude of -156 m in Turpan, Xinjiang, to the world’s highest mountain of Mount Qomolangma (8848 m) in Tibet (Tregear 2017). This geographic and climatic diversity results in almost all types of habitats on Earth ranging from rainforests to deserts (Tang et al. 2006), which are home to more than 35,000 species of vascular plants and 6,300 species of vertebrates (Ministry of Environmental Protection 2008). Species richness varies clearly along climatic gradients (e.g., temperature and precipitation) in China, which is suggested to be driven by contemporary and historical climates (Ding et al. 2006; Lei et al. 2015; Wang et al. 2020) or different evolutionary histories (e.g., speciation, extinction, and dispersal) (López-Pujol et al. 2011; Lei et al. 2015). However, few studies (but see Cai et al. 2018; Lu et al. 2018) have tested how climate affected evolutionary processes and indirectly shaped contemporary species richness patterns.

In this study, we examined whether tropical conservatism and/or diversification rate hypotheses are linked to diversity variations along climate gradients using passerine birds in China as a model system. Specifically, we combined species distribution maps, time-calibrated phylogeny, and climatic factors to estimate phylogenetic structure, diversification rate and climate in grids and subsequently tested the causes of richness–climatic relationships using path models. Here, we estimated the MRD (Kerr and Currie 1999), NRI, and nearest taxon index (NTI) (Webb et al. 2002) as measurements of phylogenetic relatedness in regional assemblages. We postulated the following explicit relationships. If climate constrains species richness through tropical conservatism, we would expect that geographic variations in the NRI and NTI should be related to climatic variables, and species richness should correlate negatively with the NRI and NTI (Supplementary Figure S1A and B). On the other hand, if the diversification rate regulates richness–climate relationships, species richness should be positively related to MRD and indirectly related to climate variables via MRD (Supplementary Figure S1C and D).

Materials and Methods

Study area

Our study area spans a large region of mainland China. Taiwan, Hainan, and other oceanic islands were excluded because of their different geological histories and evolutionary processes of regional assemblages from the mainland (MacArthur and Wilson 2001; Ding et al. 2006). Following the Albers projection, we divided mainland China into grid cells of 100×100 km in size. Grid cells covering the margins of mainland surfaces ($<7,000$ km²; 70%) were deleted to avoid area effects. Finally, a total of 937 grid cells were used in our analyses.

Species distribution data

The species distribution maps used in the analyses were downloaded from BirdLife International and NatureServe (2014). The distributions of introduced and invasive species were excluded from the species range maps. Only resident and breeding ranges were used in the following analyses. To obtain accurate distribution maps, we manually checked and adjusted the distributions by referring to the occurrence records from museum collections, the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org/>), eBird (<http://ebird.org/>), the Chinese Bird Report (<http://www.birdreport.cn/>), and primary literature. All records were georeferenced and plotted into grids. If a species had more than two records at least 10 km apart in one grid, it was labeled present. By overlaying all the range maps and observation records to grids, we obtained bird assemblages and summed the number of species as species richness in each grid cell (Supplementary Table S1). In total, our study included 611 nonmigratory passerine birds.

Climatic variables

Climatic variables were sampled for the same 937 grid cells (Supplementary Table S2). For each grid cell, we estimated the mean annual temperature (MAT), maximum temperature of warmest month (MTWM), MTCM, temperature annual range (TAR), AP, precipitation seasonality (PS), precipitation of wettest month (PWM), precipitation of driest month (PDM), net primary productivity (NPP), and velocity of climatic change (VCC) to characterize the energy and water balance. MAT, MTWM, MTCM, TAR, AP, PS, PWM, and PDM were obtained from WorldClim 1.4 (Hijmans et al. 2005). NPP in grids was measured using the layer with a spatial resolution of one-quarter degree from Imhoff et al. (2004). The VCC (km yr⁻¹) was computed by dividing the rate of projected temperature change (°C yr⁻¹) by the spatial gradients of climate (°C km⁻¹), which represents the initial rate at which species must migrate across the Earth's surface to maintain constant climatic conditions (Loarie et al. 2009; Hamann et al. 2015). We estimated the velocity of MAT change from the Last Glacial Maximum (LGM) (approximately 22,000 years ago) to present in grids using a distance-based approach (Loarie et al. 2009). MAT in the LGM was also sampled from WorldClim 1.4 (Hijmans et al. 2005), with a resolution of one-quarter degree.

Phylogeny and measurements of phylogenetic relatedness

Our analyses were based on phylogenetic trees from VertLife (<http://vertlife.org/phylosubsets>). Using phylogeny by Hackett et al. (2008) as backbones, we sampled 5,000 “stage 2” trees (9,993 species) (Jetz et al. 2012), which were summarized to produce a maximum clade credibility (MCC) time-calibrated phylogeny. Then, an MCC

tree was pruned to include 611 species in our dataset. The pruned tree (Supplementary Figure S2) was used to measure phylogenetic relatedness in the following analyses.

We applied two commonly used indices, the NRI and NTI (Webb et al. 2002), to measure the phylogenetic structures of passerine birds in assemblages. NRI measures the mean phylogenetic distance (MPD) between all pairs of taxa within a grid cell, while NTI measures the MPD between a species and its nearest relative (being called mean nearest taxon distance, MNTD) in a grid cell. Therefore, the NRI mainly reflects structure at deeper parts (distant taxa) of the phylogeny, while the NTI primarily reflects shallower parts (tips) of the phylogeny (Webb et al. 2002). NRI and NTI were calculated as follows:

$$\text{NRI} = -1 \times \frac{\text{MPD}_{\text{obs}} - \text{MPD}_{\text{rand}}}{\text{sd}(\text{MPD}_{\text{rand}})} \quad (1)$$

$$\text{NTI} = -1 \times \frac{\text{MNTD}_{\text{obs}} - \text{MNTD}_{\text{rand}}}{\text{sd}(\text{MNTD}_{\text{rand}})} \quad (2)$$

where MPD_{obs} and MNTD_{obs} are the observed MPD and MNTD in grids; MPD_{rand} and $\text{MNTD}_{\text{rand}}$ are the average values of the expected MPD and MNTD of a null model that was created by randomly shuffling the phylogenetic distance matrix labels for a grid across all taxa included in the phylogenetic distance matrix ($n = 999$); and $\text{sd}(\text{MPD}_{\text{rand}})$ and $\text{sd}(\text{MNTD}_{\text{rand}})$ are the standard deviations of MPD_{rand} and $\text{MNTD}_{\text{rand}}$ for the null model. The negative values of NRI and NTI indicate phylogenetic overdispersion, whereas positive values indicate phylogenetic clustering in a grid.

MRD measures how distant species in a grid are separated from the root of the phylogeny (Kerr and Currie 1999), which was calculated by the average number of nodes that separate each species in a grid from the root of the passerine tree. Thus, a strong correlation between MRD and a given climatic factor and between that climatic factor and species richness may suggest that the climatic factor promotes higher net diversification rates and that these higher net diversification rates may explain the richness–climate relationship among grids (Algar et al. 2009; Qian et al. 2015). To examine whether the MRD was significantly higher or lower than the expected value in a grid, we calculated the standardized effect size of MRD (SES.MRD) based on a null model by shuffling taxa labels across the tips of the phylogeny 999 times. SES.MRD was calculated by dividing the difference between the observed value (MRD_{obs}) and expected values (MRD_{rand}) by the standard deviation of the null distribution ($\text{sd}(\text{MRD}_{\text{rand}})$):

$$\text{SES.MRD} = \frac{\text{MRD}_{\text{obs}} - \text{MRD}_{\text{rand}}}{\text{sd}(\text{MRD}_{\text{rand}})} \quad (3)$$

Statistical analyses

Before analyses, we conducted log transforms of species richness, AP, PDM, PWM, and NPP to improve normality and linearity. First, we used univariate simultaneous autoregressive (SAR) models to identify the predictors that had a stronger influence on species richness and phylogenetic relatedness. Second, we built multivariate SAR models of species richness against phylogenetic relatedness and climatic factors and of phylogenetic relatedness against climatic factors. Some of the climatic variables were excluded from the multivariate SAR models because they had lower explanatory power (Supplementary Tables S3–S6) for the geographic patterns of species richness or phylogenetic relatedness. As Pearson's correlation analyses found correlations among some

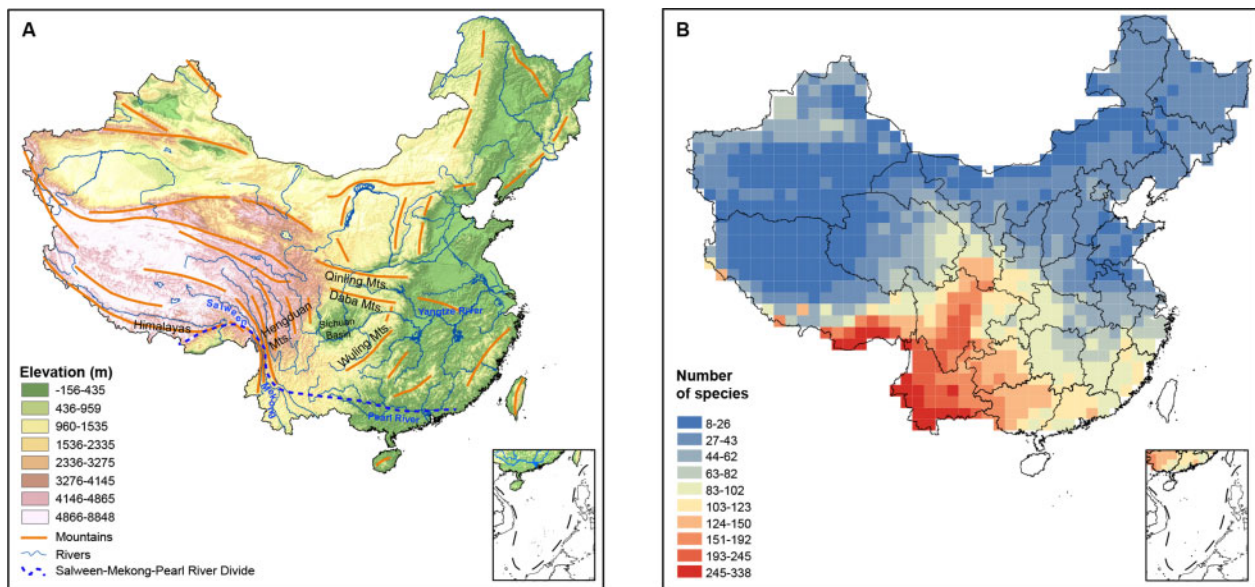


Figure 1. (A) Mountains and topographic characteristics of China. (B) Species richness of passerine birds across mainland China. Source of the administrative map from the National Geomatics Center of China (<http://www.webmap.cn>).

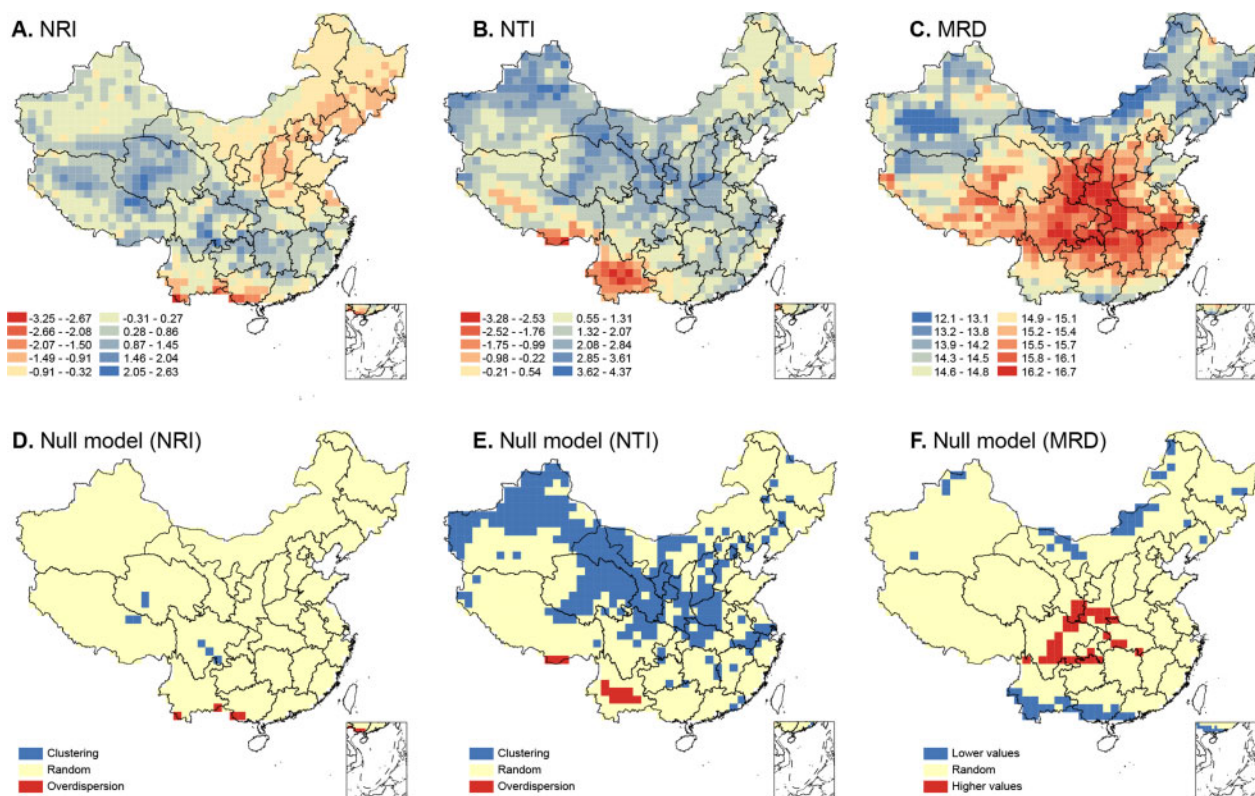


Figure 2. Geographic patterns of (A) NRI, (B) the NTI, and (C) MRD of passerine birds and corresponding null models (D-F) in mainland China. Source of the administrative map from the National Geomatics Center of China (<http://www.webmap.cn>).

of the predictors (Supplementary Table S7), we used the variance inflation factor ($VIF < 4$) to check for multicollinearity of predictors in the multiple model in R 3.6.0 (R Core Team 2019). SAR models were analyzed in the SAM 4.0 (Rangel et al. 2010). The alpha parameter was set to three to obtain a good description of the fine-scale spatial structure of SAR models (Rangel et al.

2010). For the large-scale data analyses, spatial autocorrelation may inflate the probability of type I error in significance tests. To remove the influence of spatial autocorrelation on significance tests, we recalculated P -values of the coefficient of determination R^2 based on geographically effective degrees of freedom using the approach of Dutilleul et al. (1993).

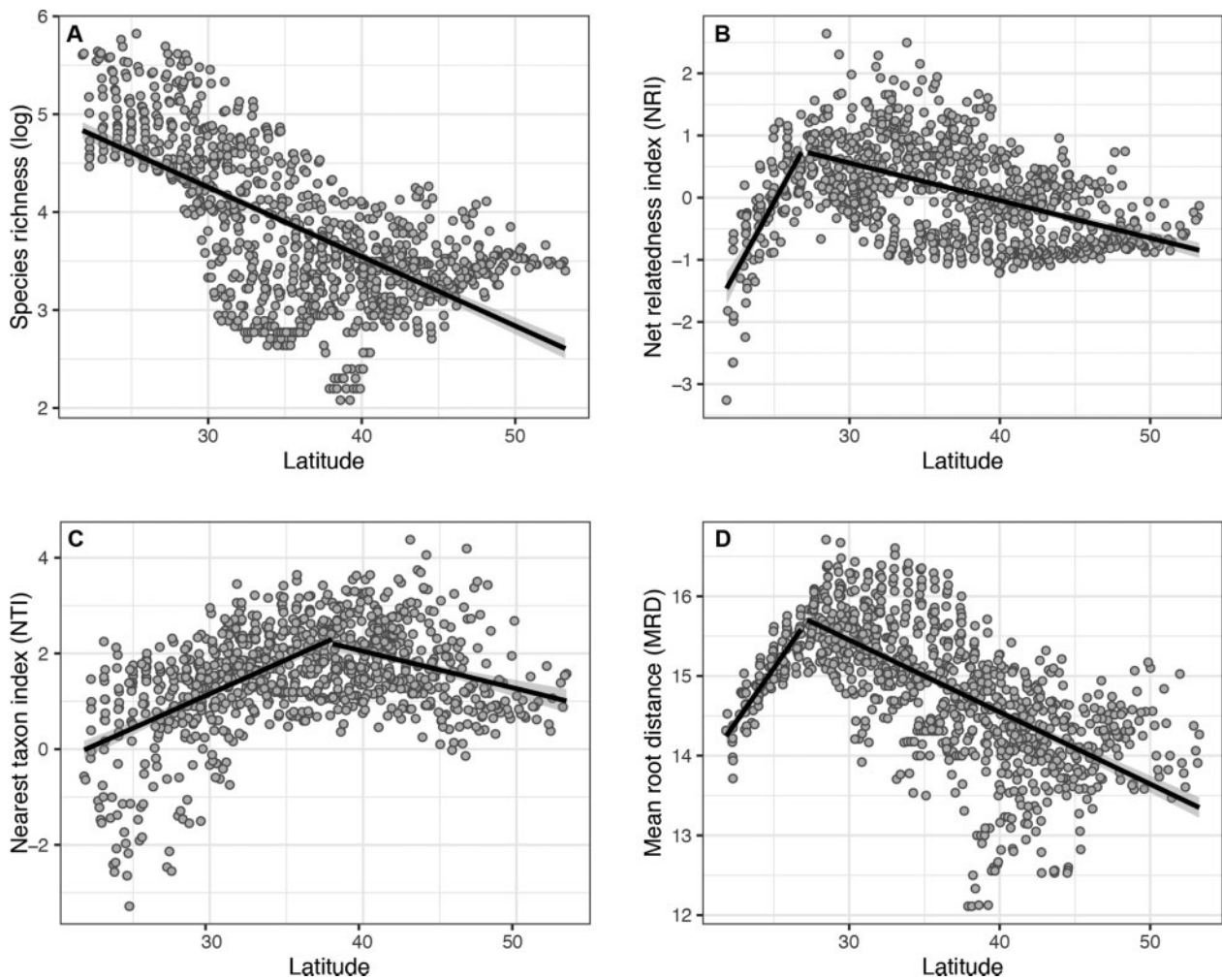


Figure 3. Scatter points showing variation in (A) species richness, (B) NRI, and (C) the NTI and (D) MRD of passerine birds along latitude gradients in mainland China.

The univariate SAR models identified AP, PWM, NPP, TAR, and MTCM as the strongest predictors of both species richness and phylogenetic relatedness (Supplementary Tables S3–S6). Therefore, path models were built assuming that phylogenetic relatedness (NTI and MRD) could influence species richness directly, while climatic factors (TAR, MTCM, and AP) could influence species richness directly and indirectly via their effects on phylogenetic relatedness (Algar et al. 2009; Qian et al. 2015, 2016) to further compare the relative effects of phylogenetic and climatic variables on the geographic pattern of species richness. NPP and PWM were not included in path models because they were highly related to AP (Supplementary Table S7). NTI was included instead of NRI as a proxy of phylogenetic overdispersion in the path models because NRI had a weaker impact on species richness and was less affected by climate than NTI (Supplementary Tables S3–S5). We independently examined the tropical conservatism hypothesis and diversification rate hypothesis in different path models. To directly compare the path coefficients in the model, we standardized each variable to a mean of zero and a variance of one before modeling (Algar et al. 2009). The path models were built in R using the “lavaan” package (Rosseel 2012). We used the root mean square error of approximation (RMSEA) and Tucker–Lewis index (TLI) (Rosseel 2012) to assess the overall fit of path models. To account for spatial autocorrelation, we used *lavSpatialCorrect.R* (available at

https://github.com/jebyrnes/spatial_correction_lavaan/blob/master/lavSpatialCorrect.R) to recalculate *P*-values based on geographic distance in all models.

The preliminary findings showed that the geographic patterns of the NRI, NTI, and MRD were different on two sides of the Salween–Mekong–Pearl River Divide (see the “Results” section). Therefore, in addition to across the entire study area, multivariate SAR regressions and path model analyses were also conducted within each of two subregions: southwest and northeast of the Salween–Mekong–Pearl River Divide. We expected that tropical conservatism and diversification rate hypotheses would play different roles in explaining geographic patterns of species richness in the two subregions because the geological and glacial histories and evolution of avifauna differed substantially between these subregions.

Sensitivity analysis

Analyses were conducted to estimate the robustness of our results to known sources of sampling biases. First, to examine the effects of phylogenetic trees on the estimation of phylogenetic relatedness, we randomly sampled 100 trees from 5,000 trees and estimated values of NRI, NTI, and MRD in grids using each tree. Subsequently, Pearson’s correlation analyses were used to check whether the NRI, NTI, and MRD based on the consensus tree (Supplementary Figure

S2) were related to those estimated from 100 trees. Second, we estimated species richness and phylogenetically related and climatic variables in grids 200 × 200 km in size and then used these variables to conduct SAR regressions. This method tests whether the size of grid cell affects the results.

Results

The species richness and phylogenetic relatedness of passerine birds varied substantially across mainland China (Figures 1 and 2). Sensitivity analyses using 100 trees suggested that the phylogenetic relatedness estimated by a consensus tree was robust (Supplementary Figure S3). The results showed that species diversity generally decreased with increasing latitude, as suggested by the latitudinal diversity gradient theory, while the relationships between phylogenetic relatedness measurements and latitude were nonlinear (Figure 3). Species richness was higher in the southwestern areas of China, such as the eastern Himalayas, Hengduan Mountains, southwestern Yunnan and southern Qinling Mountains, while northern, northeastern and northwestern China had fewer species (Figure 1). For the deeper parts of the phylogeny (NRI; Figure 2A and D), only a few cells in southern Yunnan–Guangxi displayed phylogenetic overdispersion, and a few cells in the Qinghai–Tibet Plateau (QTP) and southern margin of the Sichuan Basin showed phylogenetic clustering, while most grid cells were randomly assembled. For the shallow parts of the phylogeny (NTI; Figure 2B and E), grids with phylogenetic overdispersion were mainly distributed in middle Yunnan and eastern Himalayas, while phylogenetic clustering was widely distributed in Northwest China, the Mongolian Plateau, and the Middle-Lower Yangtze Plains. MRD values were significantly higher in the mountains around the Sichuan Basin but significantly lower in the tropical–subtropical and boreal regions (Figure 2C and F). In general, geographic patterns of phylogenetic relatedness were contrasted on different sides of the Salween–Mekong–Pearl River Divide (Figures 1 and 2): assemblages southwest of the divide showed phylogenetic overdispersion with lower MRD values, while assemblages in northeastern regions (e.g., northern Hengduan Mountains–Qinling Mountains) of this divide were clustered in shallow parts of the phylogeny with higher MRD values.

The results of univariate SAR models (Supplementary Tables S3–S6) indicated that climatic variables had stronger effects on species richness than phylogenetic relatedness variables. The results were robust when the analyses were conducted in grids 200 × 200 km in size (Supplementary Tables S8–S11). For the phylogenetic metrics, MRD explained geographic patterns of species richness very well ($R^2 = 0.40$, $P = 0$), while NRI ($R^2 = 0.01$, $P < 0.05$) and NTI ($R^2 = 0.08$, $P < 0.0001$) had weak explanatory power on species richness. Generally, climatic variables could predict MRD well ($R^2 = 0.22$ – 0.37) but had lower effects on NRI and NTI ($R^2 = 0$ – 0.11). Multivariate SAR models (Table 1) yielded similar results, which suggested that species richness was better explained by the climatic variables ($R^2 = 0.73$) than by the phylogenetic variables ($R^2 = 0.54$). Both climatic and phylogenetic variables could explain 74% of the geographic variations in species richness. Climatic variables (TAR, MTWM, VCC, AP, and PS) had stronger explanatory power on MRD ($R^2 = 0.52$) than on NRI ($R^2 = 0.42$) and NTI ($R^2 = 0.29$) (Table 1).

All path models fit the data well (all RSMEAs < 0.05 and TLIs > 0.95). For the models related to the tropical conservatism hypothesis in the entire region (Figure 4A), species richness was largely determined directly by climatic variables (AP: $\beta = 0.46$, $P < 0.001$;

Table 1. Results of multivariate SAR models to explain geographic patterns of species richness (SR), NRI, the NTI, and MRD

Response	Predictor	Coefficient	<i>P</i>	R^2
SR	TAR	−0.021	<0.001	0.73
	VCC	−0.005	<0.001	
	AP	0.269	<0.001	
	PS	−0.005	<0.001	
SR	NRI	−0.061	<0.001	0.53
	NTI	−0.040	0.002	
	MRD	0.363	<0.001	
SR	TAR	−0.020	<0.001	0.74
	VCC	−0.004	<0.001	
	AP	0.209	<0.001	
	PS	−0.003	0.002	
	NRI	−0.083	<0.001	
	NTI	0.001	0.993	
	MRD	0.235	<0.001	
	NRI	TAR	0.042	
MTWM	−0.029	<0.001		
VCC	−0.005	<0.001		
AP	0.153	0.044		
NTI	PS	−0.004	0.083	0.29
	TAR	0.054	<0.001	
	MTWM	−0.029	0.001	
	VCC	−0.003	0.005	
	AP	−0.121	0.273	
MRD	PS	−0.006	0.058	0.52
	TAR	0.013	0.105	
	MTWM	−0.002	0.650	
	VCC	−0.004	<0.001	
	AP	0.343	<0.001	
	PS	−0.009	<0.001	

Predictors are TAR, VCC, AP, PS, and MTWM.

TAR: $\beta = -0.45$, $P < 0.001$), while the indirect effect of climate on species richness via phylogenetic structure was very weak ($\beta = 0.02$, $P = 0.32$). In contrast, models related to the diversification rate hypothesis suggested that MRD explained some of the variance in species richness ($\beta = 0.18$, $P < 0.05$), but its effect was smaller than the direct effects of climatic variables (AP: $\beta = 0.40$, $P < 0.001$; TAR: $\beta = -0.38$, $P < 0.001$). When the data were analyzed separately for the two subregions (Figure 4B and C), species richness was better explained by the tropical conservatism hypothesis model ($R^2 = 0.56$) than by the diversification rate hypothesis model ($R^2 = 0.37$) in the southwestern divide, while the pattern was reversed in the northeastern divide. In the southwest of the divide, species richness was negatively and directly related to NTI ($\beta = -0.72$, $P < 0.001$), which was positively related to AP ($\beta = 0.27$, $P < 0.001$) (Figure 4B). In contrast, climatic factors had stronger indirect effects via MRD than their direct effects on species in the northeastern divide (Figure 4C). These results were robust when MTCM was used as a proxy of temperature in the path models (Figure 5).

Discussion

Our results identified the warm and humid regions in the Eastern Himalayas—Mountains of Southwest China as the major diversity hotspots for passerine birds in China, which is consistent with previous findings (Ding et al. 2006; Fjelds a 2013; Wang et al. 2020). Generally, species diversity varied strongly along latitudinal and climatic gradients (e.g., TAR, MTCM, and AP). We explored the

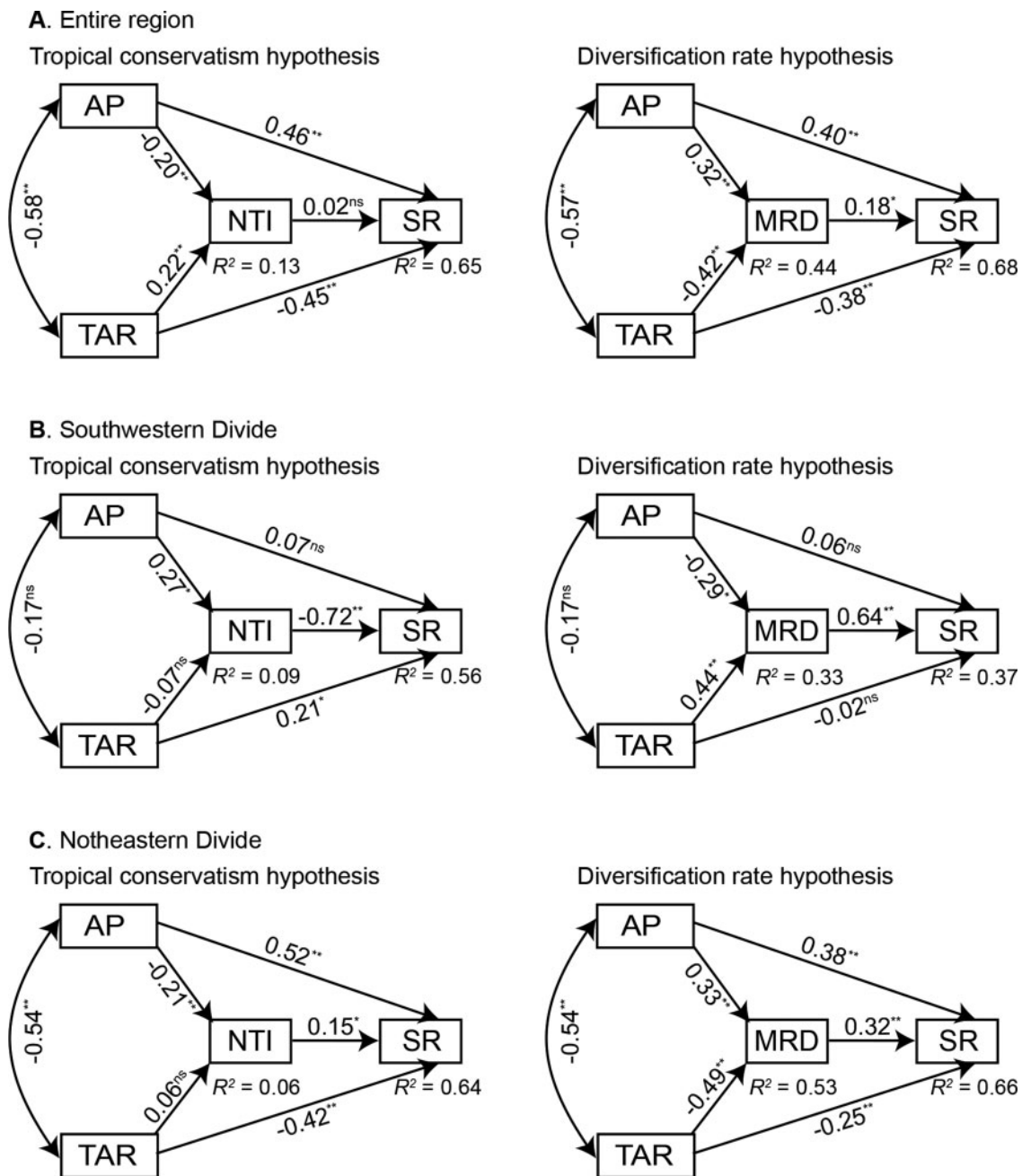


Figure 4. Diagrams of path analyses to test the tropical conservatism hypothesis and diversification rate hypothesis in the entire region (A), southwestern Divide (B), and northeastern Divide (C). The tested variables were species richness (SR), AP, TAR, NTI, and MRD. The numbers are path coefficients. ns = not significant; * $P < 0.05$; ** $P < 0.001$.

causes of the richness–climate relationships of passerine birds in China, integrating tropical conservatism and diversification rate hypotheses using path models. The results showed that AP, MTCM, and TAR had a strong direct influence on species richness, while their indirect effects on species richness via NTI and MRD were relatively weak. Thus, our results do not support the idea of tropical conservatism and diversification rate hypotheses underlying the richness–climate relationships of passerine birds in China.

The lack of support for the tropical conservatism and diversification rate hypothesis in this study is particularly unexpected given that many previous studies have found geographic patterns of regional flora regulated by climatic factors. For example, Wang et al.

(2020) found that the clustering phylogenetic structures of birds occurred in warm and humid mountains in Southwest China, and Lu et al. (2018) discovered that the turnover of the phylogenetic structure of angiosperm assemblies coincided with the 500-mm isoline of precipitation. In addition, some other studies have suggested that higher diversity in the Eastern Himalayas—Mountains of Southwest China could be well explained by the long evolutionary time for diversification due to long-term stability of the regional climate or rapid speciation driven by mountain build-up (Fjelds a 2013; Qu et al. 2014; Lei et al. 2015; Xing and Ree 2017; Cai et al. 2020; Ding et al. 2020). Using path models, Qian et al. (2016) found that minimum temperature primarily constrained the species richness of

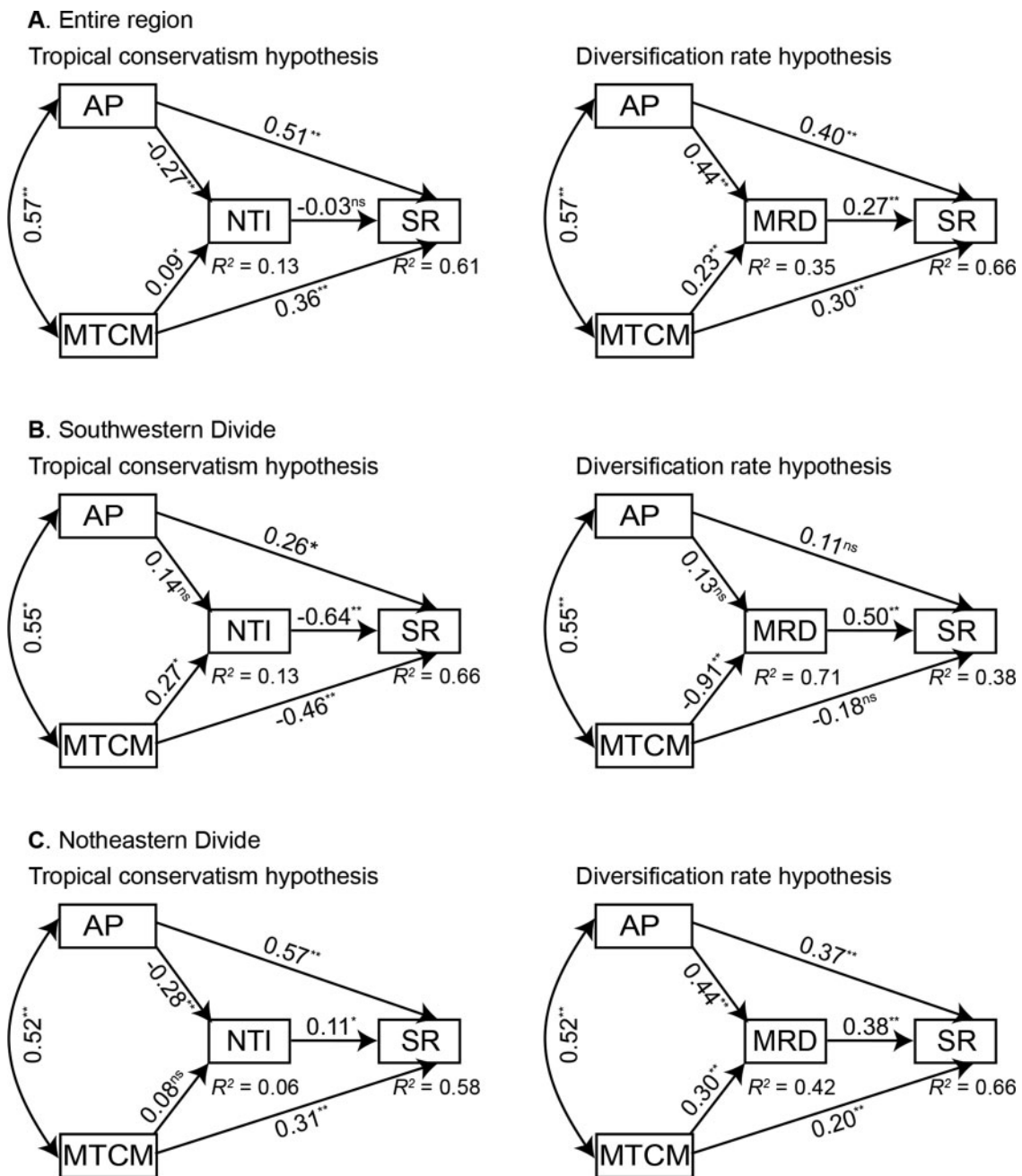


Figure 5. Diagrams of path analyses to test the tropical conservatism hypothesis and diversification rate hypothesis in the entire region (A), southwestern Divide (B), and northeastern Divide (C). The tested variables were species richness (SR), AP, MTCM, NTI, and MRD. The numbers are path coefficients. ns = not significant; * $P < 0.05$; ** $P < 0.001$.

angiosperm trees in China via its effects on phylogenetic structure. However, Cai et al. (2018) found that the species diversity of pheasants in the Sino-Himalayan Mountains was directly regulated by the net diversification rate and indirectly regulated by productivity via the diversification rate. These findings indicate that the tropical conservatism hypothesis and diversification rate hypothesis could be major explanations for species richness along temperature gradients in China.

The discrepancy between our results and previous studies may be mainly dependent on the study area used in analyses considering that our results reveal the contrasting geographic patterns of phylogenetic relatedness on different sides of the Salween–Mekong–Pearl

River Divide (Figures 1 and 2). The Divide is consistent with the north boundary of zoogeographical subregion of South China put forward by Zhang (1999). Further analyses using path models (Figures 4B and C and 5B and C) have suggested that areas with warm, humid, and stable climates characterized by the highest diversity in the southwest of the divide tend to have more distant relatives (lower NTI and NRI values), indicating longer evolutionary times to gradually accumulate more phylogenetically distant species (Stephens and Wiens 2003; Qian et al. 2013). However, in the northeastern divide, warm areas with more species tend to have longer evolutionary distances from the root to tip in the phylogeny (higher MRD) than species-poor environments, indicating rapid

diversification in these areas to accumulate more species (Algar et al. 2009; Qian et al. 2015). Thus, our path models support that richness–climate relationships in the southwest of the Salween–Mekong–Pearl River Divide can be well explained by the tropical conservatism hypothesis, while variation in species diversity along climatic gradients in the northeast of the divide can be explained by the diversification rate hypothesis. These findings are consistent with the results of Cai et al. (2018), which revealed the varied roles of tropical conservatism and diversification rate hypotheses in explaining diversity patterns of pheasants in different subregions of the Sino-Himalayan Mountains.

Our support for the tropical conservatism hypothesis in the southwest of the Salween–Mekong–Pearl River Divide is unsurprising given that the region is considered a relatively old montane region and can provide suitable habitats for ancestor passerines. The region was formed by the uplift of the QTP and reached a height of 4,000 m by 40 Ma (Favre et al. 2015). The subsequent formation of the Asian monsoon created a warm and wet climate on the southern margins of the QTP (e.g., eastern Himalayas and northern Indo-China) (Favre et al. 2015), resulting in stable habitats covered by broadleaf forests since the Miocene (Deng et al. 2014). Previous studies (Päckert et al. 2012; Fjeldså 2013) based on phylogenetic analyses have suggested that the foothills of the Himalayas and northern Indo-China were occupied first by an initial invasion of ancestral passerine birds from Australia and New Guinea in the upper Tertiary (Barker et al. 2004; Oliveros et al. 2019). This early invasion in the region left more time for accumulating old species and generating new species, leading to phylogenetic overdispersion in regional assemblages (e.g., eastern Himalayas and western–southern Yunnan see Figure 2). In addition, evidence from paleoclimatology suggests that the Pleistocene glaciations have strongly affected the QTP, Central and North China, but did not affect the lower slopes or valleys below 2,000 m of the Eastern Himalayas–Mountains of Southwest China (Shi et al. 1987). Thus, southwestern regions of the Salween–Mekong–Pearl River Divide could be a refuge for accumulating more distantly related relict species (Zhang 2004; Lei et al. 2015).

In the northeastern Salween–Mekong–Pearl River Divide, the Hengduan Mountains and south Qinling Mountains harbor more passerines and have higher MRDs than the other regions (Figures 1 and 2), indicating rapid diversification to accumulate more species. Although the southern marginal regions of the QTP reached their current elevations by the mid-Miocene, it is generally believed that its southeastern margins (e.g., Hengduan Mountains and southern Qinling Mountains) formed relatively late, mainly between the late Miocene and late Pliocene (Favre et al. 2015). Dramatic uplift of the southeastern margins of the QTP creates physical barriers and climatic gradients along elevation, which are likely to promote allopatric or parapatric speciation by facilitating local adaptation, geographical isolation, and restricting gene flow among populations (Qu et al. 2014), resulting in rapid diversification of regional fauna (Lei et al. 2015; Xing and Ree 2017; Wang et al. 2020). Furthermore, the climate in the Hengduan Mountains and southern Qinling Mountains has been relatively warm and humid since the late Miocene because higher mountains (e.g., Qinling Mountains) blocked warm and moist air from the ocean and kept cold air outside of the northern mountains (Shi et al. 1987; Favre et al. 2015), providing stable habitats for the continuous diversification of regional fauna during the Pleistocene glaciations. This is supported by the results of path models, suggesting that regional species richness is directly related to MRD, which is positively regulated by

precipitation and minimum temperature and negatively driven by TAR (Figures 4C and 5C).

In conclusion, our results suggest that the richness–climate relationships of passerines in the entire region of China cannot be well explained by tropical conservatism or diversification rate hypotheses. However, the analyses based on subregions on different sides of the Salween–Mekong–Pearl River divide reveal that species diversity could be well explained by the tropical conservatism hypothesis in the southwest and by the diversification rate hypothesis in the northeast of the divide. Therefore, the mechanisms underlying the build-up of diversity hotspots vary in different montane regions of the Eastern Himalayas–Mountains of Southwest China, which could be driven by the complex geological and evolutionary histories. Our study also offers new insights for future research on Chinese fauna—more attention should be devoted to subregions with different geological histories rather than only focusing on whole regions.

Acknowledgments

The authors thank Marcel Holyoak, Bradford A. Hawkins, Per Alström, Zhiheng Wang, Youhua Chen, Shan Guo, and Shimiao Shao for their kind help and suggestions in data analyses and for giving valuable comments regarding the manuscript. They also thank the National Animal Collection Resource Center (Institute of Zoology, Chinese Academy of Science), GBIF, eBird and Chinese Bird Report for providing the occurrence points used in this project.

Funding

This research was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences [XDA19050202], the National Natural Science Foundation of China [31630069], the Second Tibetan Plateau Scientific Expedition and Research (STEP) programme [2019QZKK05010112 and 2019QZKK0304], and other programs [KGFZD-135-19-05].

Author contributions

F.L. and G.S. designed the study program. T.C., Q.Q., G.S., and F.L. conceived the ideas. Q.Q., Y.W., and C.Z. collected the data. T.C., Q.Q., and Z.W. carried out the statistical analyses. T.C. and Q.Q. drafted the manuscript. All authors modified the manuscript.

Conflict of interest statement

The authors declare that there is no conflict of interest.

Supplementary material

Supplementary material can be found at <https://academic.oup.com/cz>.

References

- Algar AC, Kerr JT, Currie DJ, 2009. Evolutionary constraints on regional faunas: whom, but not how many? *Ecol Lett* 12: 57–65.
- Barker FK, Cibois A, Schikler P, Feinstein J, Cracraft J, 2004. Phylogeny and diversification of the largest avian radiation. *Proc Natl Acad Sci U S A* 101: 11040–11045.
- BirdLife International and NatureServe, 2014. *Bird Species Distribution Maps of the World*. Cambridge and Arlington: BirdLife International and NatureServe. Available from: <http://datazone.birdlife.org/>.
- Cai T, Fjeldså J, Wu Y, Shao S, Chen Y et al., 2018. What makes the Sino-Himalayan Mountains the major diversity hotspots for pheasants? *J Biogeogr* 45: 640–651.

- Cai T, Shao S, Kennedy JD, Alström P, Moyle RG et al., 2020. The role of evolutionary time, diversification rates and dispersal in determining the global diversity of a large radiation of passerine birds. *J Biogeogr* 47: 1612–1625.
- Currie DJ, Mittelbach GG, Cornell HV, Field R, Guégan JF et al., 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol Lett* 7: 1121–1134.
- Deng X-D, Li J-W, Vasconcelos PM, Cohen BE, Kusky TM, 2014. Geochronology of the Baye Mn oxide deposit, Southern Yunnan Plateau: implications for the Late Miocene to Pleistocene Paleoclimatic conditions and topographic evolution. *Geochim Cosmochim Acta* 139: 227–247.
- Ding T, Yuan H, Geng S, Koh C, Lee P, 2006. Macro-scale bird species richness patterns of the East Asian Mainland and Islands: energy, area and isolation. *J Biogeogr* 33: 683–693.
- Ding W-N, Ree RH, Spicer RA, Xing Y-W, 2020. Ancient orogenic and monsoon-driven assembly of the world's richest temperate alpine flora. *Science* 369: 578–581.
- Dowle E, Morgan-Richards M, Trewick S, 2013. Molecular evolution and the latitudinal biodiversity gradient. *Heredity* 110: 501–510.
- Dutilleul P, Clifford P, Richardson S, Hemon D, 1993. Modifying the T test for assessing the correlation between two spatial processes. *Biometrics* 49: 305–314.
- Evans KL, Warren PH, Gaston KJ, 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biol Rev* 80: 1–25.
- Favre A, Päckert M, Pauls SU, Jähnig SC, Uhl D et al., 2015. The role of the uplift of the Qinghai-Tibetan plateau for the evolution of Tibetan biotas. *Biol Rev* 90: 236–253.
- Fjeldså J, 2013. The global diversification of songbirds (Oscines) and the build-up of the Sino-Himalayan diversity hotspot. *Chinese Birds* 4: 132–143.
- Gaston KJ, 2000. Global patterns in biodiversity. *Nature* 405: 220–227.
- Hackett SJ, Kimball RT, Reddy S, Bowie RC, Braun EL et al., 2008. A phylogenomic study of birds reveals their evolutionary history. *Science* 320: 1763–1768.
- Hamann A, Roberts DR, Barber QE, Carroll C, Nielsen SE, 2015. Velocity of climate change algorithms for guiding conservation and management. *Glob Change Biol* 21: 997–1004.
- Hawkins BA, Field R, Cornell HV, Currie DJ, Guegan JF et al., 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84: 3105–3117.
- Helmus MR, Bland TJ, Williams CK, Ives AR, 2007. Phylogenetic measures of biodiversity. *Am Nat* 169: E68–E83.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A, 2005. Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25: 1965–1978.
- Imhoff M, Bounoua L, Ricketts T, Loucks C, Harriss R, Lawrence WT, 2004. Global patterns in net primary productivity. In: *HANPP Collection: Global Patterns in Net Primary Productivity (NPP)* Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). Available from: <http://dxdoiorg/107927/H40Z715X> (accessed 25 September 2014).
- Janzen DH, 1967. Why mountain passes are higher in the tropics. *Am Nat* 101: 233–249.
- Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO, 2012. The global diversity of birds in space and time. *Nature* 491: 444–448.
- Kerr JT, Currie DJ, 1999. The relative importance of evolutionary and environmental controls on broad-scale patterns of species richness in North America. *Ecoscience* 6: 329–337.
- Lei F, Qu Y, Song G, Alström P, Fjeldså J, 2015. The potential drivers in forming avian biodiversity hotspots in the east Himalaya Mountains of Southwest China. *Integr Zool* 10: 171–181.
- Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB et al., 2009. The velocity of climate change. *Nature* 462: 1052–1055.
- López-Pujol J, Zhang F-M, Sun H-Q, Ying T-S, Ge S, 2011. Centres of plant endemism in China: places for survival or for speciation? *J Biogeogr* 38: 1267–1280.
- Losos JB, 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol Lett* 11: 995–1007.
- Lu L-M, Mao L-F, Yang T, Ye J-F, Liu B et al., 2018. Evolutionary history of the angiosperm flora of China. *Nature* 554: 234–238.
- MacArthur RH, Wilson EO, 2001. *The Theory of Island Biogeography*. USA: Princeton University Press.
- Ministry of Environmental Protection, 2008. *China's Fourth National Report on Implementation of the Convention on Biological Diversity*. Beijing: People's Republic of China.
- Mittelbach GG, Schemske DW, Cornell HV, Allen AP, Brown JM et al., 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol Lett* 10: 315–331.
- Oliveros CH, Field DJ, Ksepka DT, Barker FK, Aleixo A et al., 2019. Earth history and the passerine superradiation. *Proc Natl Acad Sci U S A* 116: 7916–7925.
- Päckert M, Martens J, Sun YH, Severinghaus LL, Nazarenko AA et al., 2012. Horizontal and elevational phylogeographic patterns of Himalayan and Southeast Asian forest passerines (Aves: passeriformes). *J Biogeogr* 39: 556–573.
- Qian H, Field R, Zhang JL, Zhang J, Chen S, 2016. Phylogenetic structure and ecological and evolutionary determinants of species richness for angiosperm trees in forest communities in China. *J Biogeogr* 43: 603–615.
- Qian H, Wiens JJ, Zhang J, Zhang Y, 2015. Evolutionary and ecological causes of species richness patterns in North American angiosperm trees. *Ecography* 38: 241–250.
- Qian H, Zhang Y, Zhang J, Wang X, 2013. Latitudinal gradients in phylogenetic relatedness of angiosperm trees in North America. *Glob Ecol Biogeogr* 22: 1183–1191.
- Qu Y, Ericson PGP, Quan Q, Song G, Zhang R et al., 2014. Long-term isolation and stability explain high genetic diversity in the eastern Himalaya. *Mol Ecol* 23: 705–720.
- R Core Team, 2019. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available from: <https://www.r-project.org/>.
- Rangel TF, Diniz-Filho JAF, Bini LM, 2010. Sam: a comprehensive application for spatial analysis in macroecology. *Ecography* 33: 46–50.
- Ricklefs RE, 2006. Evolutionary diversification and the origin of the diversity-environment relationship. *Ecology* 87: S3–S13.
- Rohde K, 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65: 514–527.
- Rosenzweig ML, 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.
- Rosseel Y, 2012. Lavaan: an R package for structural equation modeling. *J Stat Softw* 48: 1–36.
- Shi Y, Cui Z, Li J, 1987. Reassessment of quaternary glaciation problems in East China. *Earth Sci* 2: 45–54.
- Stenseth NC, 1984. The tropics: cradle or museum? *Oikos* 43: 417–420.
- Stephens PR, Wiens JJ, 2003. Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *Am Nat* 161: 112–128.
- Tang Z, Wang Z, Zheng C, Fang J, 2006. Biodiversity in China's mountains. *Front Ecol Environ* 4: 347–352.
- Tregear TR, 2017. *A Geography of China*. New Brunswick and London: Transaction Publishers.
- Wang N, Mao L, Yang X, Si X, Wang Y et al., 2020. High plant species richness and stable climate lead to richer but phylogenetically and functionally clustered avifaunas. *J Biogeogr* 47: 1945–1954.
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ, 2002. Phylogenies and community ecology. *Annu Rev Ecol Syst* 33: 475–505.
- Wiens JJ, Donoghue MJ, 2004. Historical biogeography, ecology and species richness. *Trends Ecol Evol* 19: 639–644.
- Wiens JJ, Graham CH, 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu Rev Ecol Syst* 36: 519–539.
- Xing Y, Ree RH, 2017. Uplift-driven diversification in the Hengduan Mountains, a temperate biodiversity hotspot. *Proc Natl Acad Sci U S A* 114: E3444–E3451.
- Zhang R, 1999. *China Animal Geography*. Beijing: Science Press.
- Zhang R, 2004. Relict distribution of land vertebrates and quaternary glaciation in China. *Acta Zool Sin* 50: 841–851.