RESEARCH PAPER

High plant species richness and stable climate lead to richer but phylogenetically and functionally clustered avifaunas

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Abstract

Aims: Glacial–interglacial climate stability and contemporary climate could affect bird diversity through their direct effects on diversification and physiological tolerance, and indirect effects on plant species richness, which could provide more food and ecological niches. This study aims to quantitatively assess the direct and indirect effects of these drivers on species richness, phylogenetic and functional structure of bird assemblages.

Location: Mainland China.

Taxon: Birds.

Methods: Ordinary least squares models and simultaneous autoregressive models were used to test the associations between glacial–interglacial climate anomaly, contemporary climate, plant species richness, elevation range and species richness, phylogenetic structure, functional structure of bird assemblages in mainland China. Structural equation models were used to distinguish between direct and indirect effects of these variables on bird diversity.

Results: High bird species richness with phylogenetically and functionally clustered structure occurred in regions with more plant species and stable glacial–interglacial climate. Notably, the phylogenetically clustered bird assemblages were composed of young lineages. Contemporary precipitation and elevation range affected bird diversity through their indirect effects on plant species richness.

Main Conclusions: These findings suggest that more plant species and stable glacial–interglacial climate may promote bird diversity through their effects on in situ diversification and species dispersal rate in southwestern China. Therefore, the well-preserved plant and bird diversity through the long-term climate fluctuations should be of great importance of biodiversity conservation in China.

KEYWORDS
Birds, China, functional structure, glacial–interglacial climate stability, phylogenetic structure, plant species richness, species diversification

1 | INTRODUCTION

What drives the uneven distribution of biodiversity at macro-ecological scales is a central question in ecology and biogeography

(Fine, 2015; Flesch, 2019; Ricklefs, 2004). It is widely acknowledged that biodiversity gradually decreases from low latitudes to high latitudes, and varies with elevation (Hillebrand, 2004; Jansson, Rodriguez-Castaneda, & Harding, 2013; McCain, 2009). These

biodiversity gradients are assumed to be mainly controlled by local biotic interactions, contemporary climate, palaeoclimate and regional geological history (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Pavoine & Bonsall, 2011; Svenning, Eiserhardt, Normand, Ordonez, & Sandel, 2015).

Contemporary climate, e.g., temperature and precipitation, could both directly and indirectly affect the current distribution of biodiversity (Currie et al., 2004; Hawkins, Field, et al., 2003). For example, the physiological tolerance hypothesis suggests that the tolerance of individual species for different climate could affect species richness, predicting that there would be more species in warm and wet regions than in cold and dry conditions (Currie et al., 2004; Remeš & Harmáčková, 2018). In addition, warm and wet regions could also harbour high productivity, allowing high plant species richness, which would then indirectly affect species richness of other organism groups through their effects on resource availability and the food chain (Hawkins, Porter, & Diniz, 2003; Roll, Geffen, & Yom-Tov, 2015).

In addition to contemporary climate, impacts of palaeoclimate, e.g., glacial–interglacial climate change and global patterns of historical climate, are also widely reported to be important (Duchêne & Cardillo, 2015; Fjeldså & Lovett, 1997; Hawkins, Diniz-Filho, Jaramillo, & Soeller, 2007; Svenning et al., 2015). Specifically, the refuge hypothesis assumes that the long-term climatic stability during the glacial–interglacial periods could promote high species richness and over-dispersed phylogenetic structure by both facilitating speciation and preventing the extinction of ancient species (Fjeldså & Lovett, 1997; Qu et al., 2015; Svenning et al., 2015). Moreover, the tropical niche conservatism hypothesis suggests that most major groups of organisms originated in the historically widely distributed tropics, and these groups have difficulties in dispersing to the more recent temperate regions because of niche conservatism (Duchêne & Cardillo, 2015; Hawkins et al., 2007).

Besides these climate related hypotheses, the role of biotic interactions in shaping the geographical distribution of biodiversity has also been widely tested (Speed et al., 2019; Svenning et al., 2014; Wisz et al., 2013). For example, interspecific competition could affect the geographic range of birds, improve prediction of bird distributions and structure bird communities (Heikkinen, Luoto, Virkkala, Pearson, & Körber, 2007; Laube, Graham, Böhning-Gaese, & McGill, 2013; Srinivasan, Elsen, Tingley, & Wilcove, 2018). In addition, predation or food availability could directly affect patterns of bird species richness on macro-ecological scales (Ferger, Schleuning, Hemp, Howell, & Böhning-Gaese, 2014; Liang et al., 2018; Zhang, Kissling, & He, 2013). Notably, strong biotic interactions could also increase the opportunity for evolutionary diversification (Condamine, Antonelli, Lagomarsino, Hoorn, & Liow, 2018; Currie et al., 2004).

Being one of the most biodiverse countries in the world, especially in the Northern Hemisphere, China harbours 1,445 bird species and about 33,000 vascular plant species (López-Pujol, Zhang, & Ge, 2006; Zheng, 2017). The relatively stable glacial–interglacial climate, diverse vegetation types, large gradients of contemporary climate and topography are suggested to be the main drivers of China's

high biodiversity (López-Pujol et al., 2006; Zhang et al., 2017). Previous studies have linked bird species richness in China with these multiple-scale variables (Cai et al., 2018; Lei, Qu, Song, Alstrom, & Fjeldså, 2015; Wu, DuBay, Colwell, Ran, & Lei, 2017), while few studies have tested their associations with phylogenetic and functional structure of bird assemblages in China, which could reflect the evolutionary history and ecological differences of bird assemblages (Mönkkönen, Devictor, Forsman, Lehikoinen, & Elo, 2017; Monnet et al., 2014; Sobral & Cianciaruso, 2016), and provide new insight for the assembly processes of bird assemblages.

In this study, for the first time, we simultaneously linked species richness, phylogenetic structure, and functional structure of bird assemblages with glacial–interglacial climate stability, contemporary climate, plant species richness and elevation range to assess their direct and indirect effects in shaping the geographic distribution of bird diversity in China. We hypothesized that (a) stable glacial–interglacial climate would lead to more bird species with over-dispersed phylogenetic structure by both promoting speciation and preventing extinction; (b) more plant species could promote high bird species richness with over-dispersed functional structure by providing diverse ecological niches; (c) glacial–interglacial climate stability, contemporary climate and elevation range could indirectly affect bird diversity through their direct effects on plant species richness.

2 | MATERIALS AND METHODS

2.1 | Bird and plant distribution data

Distribution data of 1,290 species, including 1,130 breeding birds, in 214 prefectures (including downtown, suburb, farmland and other nature vegetation covered by the polygon) in mainland China was compiled from national, regional and provincial avifaunas and faunas, e.g., *A Checklist on the Classification and Distribution of the Birds of China* (Zheng, 2017), S*tudies on Birds and Their Ecology in Northeast China* (Gao, 2006), *A Checklist on the Distribution of the Birds in Xinjiang* (Ma, 2011), *The Avifauna of Yunnan China* (Yang, 1995; Yang & Yang, 2004). Detailed descriptions about bird occurrence in prefectures could be found in these faunas, based on massive fieldwork and professional knowledge of many experienced local ornithologists. Because there were no provincial avifaunas in Henan, Hebei, Hunan, Hubei, Jiangsu, Anhui, Jiangxi and Fujian, we did not include these provinces in our analyses. In addition, because the administrative division in Hainan (with poor distribution data) and Taiwan was not clear, e.g., changed a lot recently and some prefectures were surrounded by other prefectures, we also excluded these two islands from our analyses. Still, this dataset represents 90% of China's native avifauna. Angiosperm plant species richness in these prefectures was obtained from the Chinese Vascular Plant Distribution Database, which was also compiled from national, regional and provincial floras, as well as information from herbarium specimens (Lu et al., 2018). Plant species richness could be interpreted as food

resources for some herbivores and habitat diversity for most groups (Lee & Rotenberry, 2005; Zhang et al., 2013). Because migrant species are not closely associated with local features, this study only focused on breeding birds.

2.2 | Environmental data

Mean annual temperature (MAT), mean annual precipitation (MAP), MAT in last glacial maximum (MAT in LGM), and MAP in LGM (MAP in LGM) were downloaded from WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). MAT in LGM and MAP in LGM were the mean values of two models, i.e., the Model for Interdisciplinary Research on Climate version 3.2 (MIROC3.2; Hasumi & Emori, 2004) and the Community Climate System Model version 3 (CCSM3; Hijmans et al., 2005; Otto-Bliesner et al., 2006). Anomaly in MAT and anomaly in MAP (contemporary MAT/MAP minus LGM MAT/MAP) were used to represent climate change (Sandel et al., 2011). Elevation data were obtained from EarthEnv-DEM90 digital elevation model (http://www.earthenv.org/DEM. html; Robinson, Regetz, & Guralnick, 2014), and elevation range was measured as the difference between the maximum and minimum values in each prefecture. The resolution of climate variables and elevation was 2.5 arc-min and the mean values of all cells in a prefecture were used for the following analyses. Because the area of prefectures was not a strong predictor of bird diversity, it was not included in this study.

2.3 | Phylogeny and functional dendrogram

A phylogeny including all 1,290 bird species covered by our study was extracted from a global bird phylogeny under the option of 'Hackett All Species: a set of 10,000 trees with 9,993 OUTs each' (Jetz et al., 2014). We sampled 5,000 trees from the pseudo-posterior distribution and calculated a maximum clade credibility tree using mean node heights in the software TreeAnnotator (version 1.8.2) of the BEAST 2 package (Bouckaert et al., 2014).

Four key ecological traits of 1,287 bird species (no trait information for three species), i.e., body size, trophic level (omnivores, granivores, frugivore, nectarivores, insectivores, piscivores and carnivores), migrant status (resident, partial migrant, and full migrant) and habitat specificity (the number of habitats a species is recorded in; Wang et al., 2018), were used to build a functional dendrogram, which was then used for the functional structure analyses. Gower's distance and 'complete' cluster in "vegan" R package (Oksanen et al., 2015) were used to build the functional dendrogam.

2.4 | Statistical analyses

Species richness is the number of bird species that occurred in each prefecture. Phylogenetic and functional structure of bird assemblages in each prefecture were calculated using the Net Relatedness Index (NRI), which is computed as:

$$NRI = -1 \times \frac{MPD_{obs} - meanMPD_{rnd}}{sdMPD_{rnd}}$$

where MPD_{obs} is the observed mean pairwise distance (MPD) of birds in each prefecture, calculated from the phylogenetic tree or functional dendrogram; $meanMPD_{rnd}$ is the mean MPD of the null models (the choice of null model was 'taxa.lables' and run 999 times), and $sdMPD_{rnd}$ is the standard deviation of MPD of the null models. Positive NRI means birds in a prefecture are more closely related (or functionally similar) than expected, while negative NRI means birds in a prefecture are more distantly related (or functionally different) than expected from random communities (Webb, Ackerly, McPeek, & Donoghue, 2002). NRI was calculated using R function 'ses.mpd' in package 'picante' (Kembel et al., 2010).

To better understand the patterns of phylogenetic structure of bird assemblages in each prefecture, we also calculated the standardized effect size of sum of terminal branch length, i.e., sum of species age (SES.age). SES.age is computed as:

$$SES.age = \frac{age_{obs} - mean\left(age_{rnd}\right)}{sd(age_{rnd})}$$

where age_{obs} is the observed sum of terminal branch length (age) of birds in each prefecture, $mean\left(age_{rnd}\right)$ is the mean age of the null models (shuffle distance matrix labels 999 times), and $sd(age_{rnd})$ is the standard deviation of age of the null models. Positive SES.age means sum of terminal branch length of birds in a prefecture are larger than expected, i.e., species are relatively older; while negative SES.age means sum of terminal branch length of birds in a prefecture are smaller than expected, i.e., species are relatively younger (Webb et al., 2002). The code for SES.age is in the Appendix S1.

To test the associations between species richness, phylogenetic structure, functional structure and each explanatory variable, single-variable ordinary least squares (OLS) models were used. All dependent and independent variables (Appendix S2) were standardized (standard deviation = 1 and mean = 0) to allow for comparison of regression coefficients. Furthermore, to control the spatial autocorrelation of regression residuals, simultaneous autoregressive (SAR) models were also performed using R function 'errorsarlm' in 'spdep' package (Bivand et al., 2015).

Multiple regressions using SAR models were also used to find the combination of variables most associated with species richness diversity, phylogenetic structure and functional structure of bird assemblages. For each dependent variable, the combination of variables with highest Akaike weight was selected as the best fitting model. Because climate variables and elevation range could also indirectly affect bird diversity through their effects on plant species richness, structural equation models (SEM) were also performed to examine the direct and indirect effects of these variables on these diversity indices of bird assemblages.

In addition, since MAT was highly correlated with MAP (0.84) and anomaly in MAT (−0.72), we did not include MAT in the multiple regression and structural equation models (Table S1). Also because MAP and anomaly in MAT were correlated (−0.61), we divided them into two groups for multiple SAR models and SEM models (Table S1). Lastly, as our species richness data were biased by incomplete sampling, we performed the SEM models using different species richness thresholds, i.e., using prefectures with species richness more than 50, 100, 150 and 200. SEM models were performed using R function 'sem' in lavaan package (Rosseel, 2012). All analyses were conducted in R version 3.6.0 (R Core Team, 2016).

3 | RESULTS

Generally, prefectures in southwestern China (lower latitude and middle longitude) had more species, clustered phylogenetic and functional structure, as well as relatively young lineages (Figure 1; Figure S1). The single-variable ordinary linear squares models and SAR models showed similar patterns about the associations between bird species richness, phylogenetic structure, functional structure and each explanatory variable (Table 1). Phylogenetic and functional structure were more associated with explanatory variables than species richness (Figure 2; Table 1). Plant species richness was a consistently important variable for explaining bird

species richness, phylogenetic and functional structure, and especially so for species richness (Figure 2; Table 1). Elevation range was the other important predictor for species richness, anomaly in MAT was the other important predictor for phylogenetic and functional structure, and MAP was consistently associated with bird species richness, phylogenetic and functional structure (Figure 2; Table 1). Notably, the relations between functional structure and MAP, anomaly in MAT, as well as between phylogenetic structure and MAP tended to be nonlinear (Figure 2). Therefore, we reanalysed these relations by adding a nonlinear term and found higher r^2 (Figure 2).

Multiple regressions using SAR models showed that the combination of variables most associated with bird species richness, phylogenetic and functional structure always included plant species richness and anomaly in MAT (Table 2; Table S2). Furthermore, the Akaike weight of the two variables based on all combinations of variables were also very high (Table 2).

Structural equation models showed that plant species richness and anomaly in MAT consistently had direct effects on bird species richness, phylogenetic and functional structure (Figure 3). MAP and elevation range indirectly affect bird diversity through their effects on plant species richness (Figure 3; Figure S2). The analyses with different species richness thresholds showed that the positive effects of anomaly in MAT decreased and became negative with the increasing of species richness thresholds (Figure 4).
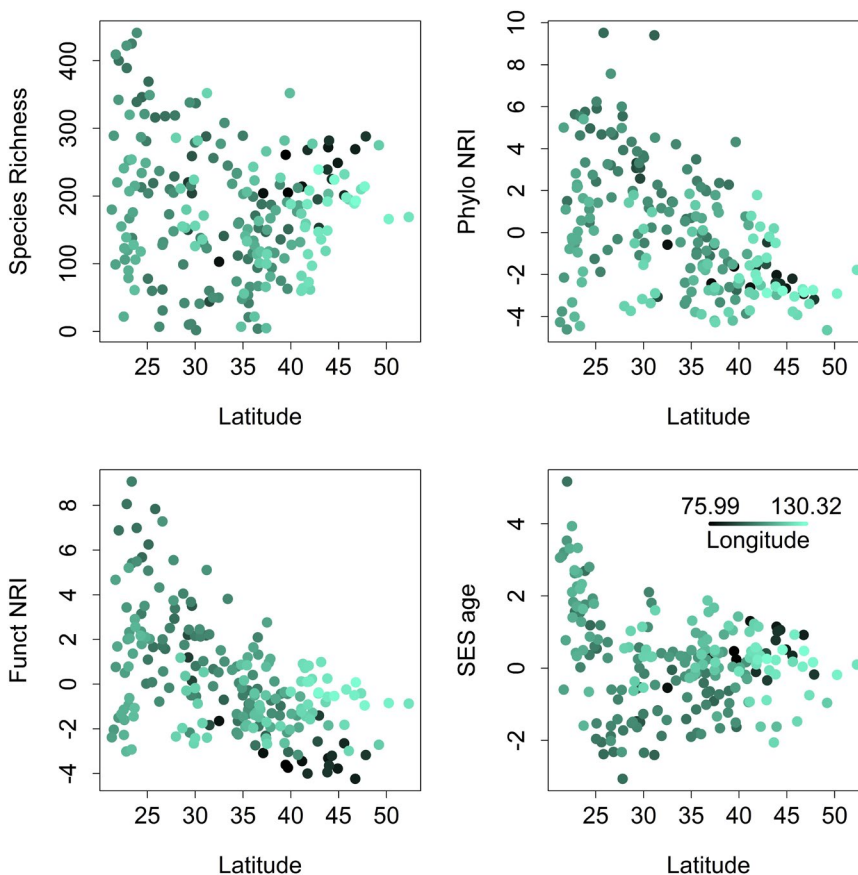

FIGURE 1 Scatter plots of bird species richness, phylogenetic structure (Phylo NRI), functional structure (Funct NRI), SES age against latitude and longitude. More species (relatively young) are phylogenetically and functionally clustered in regions with lower latitude and middle longitude (southwestern China) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Results of the single variable ordinary linear squares models (OLS) and simultaneous autoregressive (SAR) models of the associations between bird species richness, phylogenetic structure (Phylo NRI), functional structure (Funct NRI) and each predictor

	Species richness				Phylo NRI				Funct NRI			
	$Coef_{OLS}$	r^2_{OLS}	$Coef_{SAR}$	AIC_{SAR}	$Coef_{OLS}$	r^2_{OLS}	$Coef_{SAR}$	AIC_{SAR}	$Coef_{OLS}$	r^2_{OLS}	$Coef_{SAR}$	AIC_{SAR}
MAT	0.06	0	−0.01	576	0.19	0.04**	0.11	515	0.38	0.14**	0.35	471
MAP	0.17	0.03*	0.25	571	0.28	0.08**	0.30	510	0.46	**0.21****	0.55	**459**
Anomaly$_{MAT}$	−0.02	0	0.03	576	−0.48	**0.23****	−0.48	**501**	−0.44	0.20**	−0.50	467
Anomaly$_{MAP}$	−0.04	0	0.02	576	0.14	0.02*	0.22	512	0.10	0.01	0.13	478
ELE$_{Range}$	0.26	**0.07****	0.37	**560**	0.27	0.07**	0.21	510	0.04	0	0.13	477
Plant$_{SR}$	0.57	**0.33****	0.69	**481**	0.56	**0.31****	0.31	**500**	0.59	**0.35****	0.32	**458**

Note: Standardized regression coefficients (coef) and r^2 of OLS models, coef and AIC of SAR models were given. The two highest r^2 and two lowest AIC in each column were in bold. *$p < 0.05$, **$p < 0.01$.

Abbreviations: Anomaly$_{MAP}$, contemporary-Last Glacial Maximum anomaly in MAP; Anomaly$_{MAT}$, contemporary-Last Glacial Maximum anomaly in MAT; ELE$_{Range}$, elevation range; MAP, mean annual precipitation; MAT, mean annual temperature; Plant$_{SR}$, plant species richness; SAR, simultaneous autoregressive.

FIGURE 2 Scatter plots of bird species richness, phylogenetic structure (Phylo NRI), functional structure (Funct NRI) and their three most associated variables. Plant SR is plant species richness. MAP is mean annual precipitation. Anomaly MAT is the contemporary-Last Glacial Maximum anomaly in MAT. ELE Range is elevation range. Linear regression fits and r^2 are given (in black). Three nonlinear regression fits and r^2 are also presented (in blue). MAT, Mean annual temperature. *$p < 0.05$, **$p < 0.01$
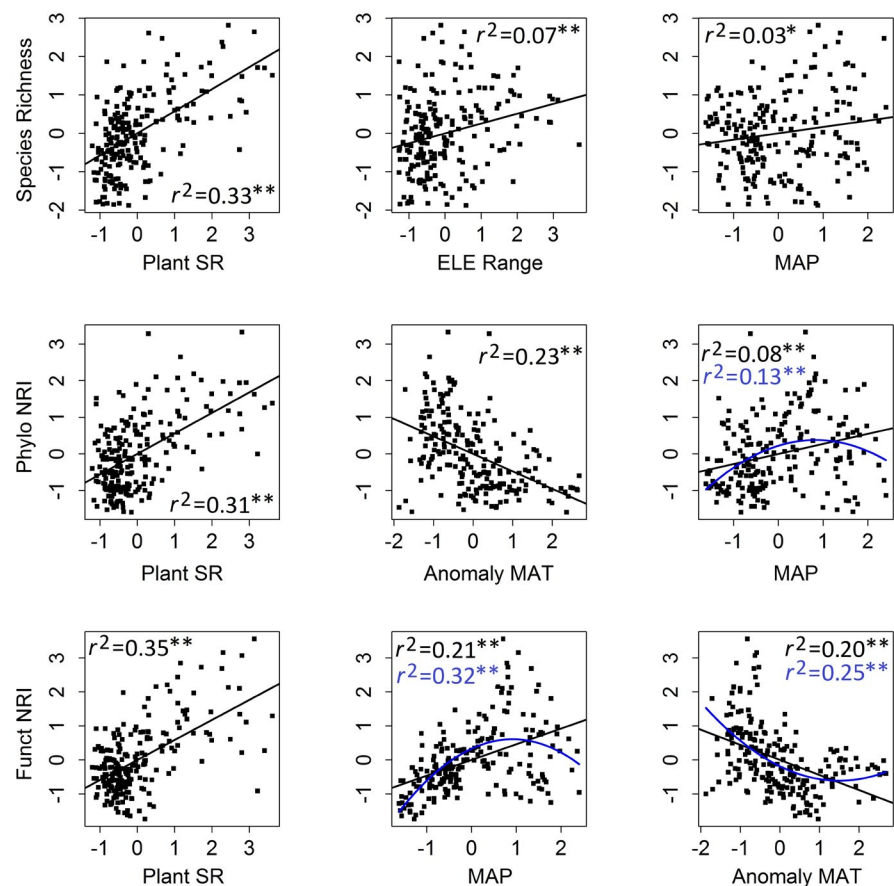
4 | DISCUSSION

Being the first study simultaneously linking bird species richness, phylogenetic structure, and functional structure with plant species richness, glacial–interglacial climate change, contemporary climate and elevation range in China, our results showed that high bird species richness with a clustered phylogenetic and functional structure occurred in regions with high plant species richness and stable glacial–interglacial climate. Notably, the phylogenetically clustered bird assemblages were composed of relatively young lineages.

4.1 | Distinct patterns of bird species richness due to data limitation

The relatively weak associations between explanatory variables and species richness compared with phylogenetic and functional structure may result from the sampling bias of bird species in these prefectures, e.g., Beijing and Shanghai had exceptionally high bird species richness. Bejing and Shanghai had more universities and institutes for biodiversity research as well as high levels of socio-economic development than other prefectures. Collections of biodiversity data could be affected by many

	Species Richness		Phylo NRI		Funct NRI	
	Coef	w	Coef	w	Coef	w
ELE$_{Range}$		0.30		0.44		0.46
Anomaly$_{MAT}$	0.30**	0.98	−0.38**	1	−0.38**	0.99
Anomaly$_{MAP}$		0.39	0.15*	0.71		0.32
Plant$_{SR}$	0.73**	1	0.28**	0.99	0.30**	1
Pseudo r^2	**0.49**		**0.46**		**0.55**	
W	**0.41**		**0.40**		**0.36**	

TABLE 2 Results of multiple regressions using simultaneous autoregressive models of bird species richness, phylogenetic structure (Phylo NRI) and functional structure (Funct NRI) against combinations of explanatory variables
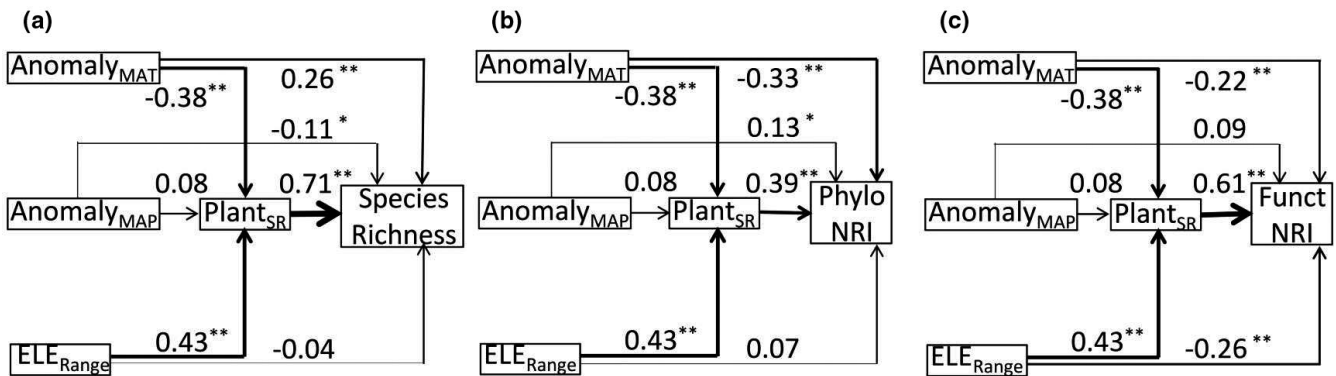
Note: Standardized coefficients (Coef) of the variables in the model with the highest Akaike weight (w), and the Akaike weight (w) for each variable based on the full model sets were listed. w and pseudo r^2 of the best model were in bold. *$p < 0.05$, **$p < 0.01$.

Abbreviations: MAP, mean annual precipitation; MAT, Mean annual temperature.

FIGURE 3 Results of structural equation models examining the direct and indirect effects of the contemporary-Last Glacial Maximum anomaly in MAT/MAP (Anomaly$_{MAT}$/Anomaly$_{MAP}$), elevation range (ELE$_{Range}$) and plant species richness (Plant$_{SR}$) on bird species richness (a), phylogenetic structure (b) and functional structure (c). Standardized regression coefficients were given. MAP, mean annual precipitation; MAT, Mean annual temperature. *$p < 0.05$, **$p < 0.01$

socio-economic and environmental factors (Reddy & Dávalos, 2003; Yang, Ma, & Kreft, 2014). Notably, these biased species richness data in this study may have greatly affected its relations with the explanatory variables, especially for the anomaly in MAT. With the increase of species richness thresholds (from 50 to 100, 150 and 200), the positive associations between species richness and anomaly in MAT became negative.

4.2 | Plant species richness and bird diversity

Plant species richness was the variable most associated with bird species richness in this study ($r^2 = 0.33$, and r^2 of the second important variable was 0.07). This finding was consistent with many previous studies at different scales and regions, e.g., counties in northern China, boreal forest sites in western Canada, 0.5° grid cells in Kenya, and nature reserves and provinces in China (Kissling, Field, & Bohning-Gaese, 2008; Liang et al., 2018; Qian & Kissling, 2010; Zhang et al., 2013). It has been suggested that more plant species could promote high bird diversity directly by providing more food for herbivores, and indirectly by supplying complex vegetation structure, which means larger ecological niche space for most avian groups (Kissling et al., 2008; Liang et al., 2018; Zhang et al., 2013). In addition, the complex vegetation structure provided by high plant species richness may also indicate

greater persistence of other organisms during periods of climatic instability (Oliveira & Scheffers, 2019).

Notably, our results showed that phylogenetic and functional structure of Chinese bird assemblages were also most strongly associated with plant species richness. And more importantly, phylogenetic and functional structure was increasingly clustered with more plant species, contrasting with our prediction. Besides increased diversification with more plant species, another explanation could be that bird species in these regions with high plant species richness, which are mainly mountain forest, have low dispersal rate, while bird species in other regions are mainly widespread species (Sobral & Cianciaruso, 2016). In addition, these closely related species are mainly composed of young lineages, which should occur in habitats near their ancestors and then produce the phylogenetically and functionally clustered bird assemblages (Sobral & Cianciaruso, 2016).

4.3 | Glacial–interglacial climate change and bird diversity

With the increase in sampling completeness, the association between bird species richness and glacial–interglacial climate change became negative, indicating that more bird species
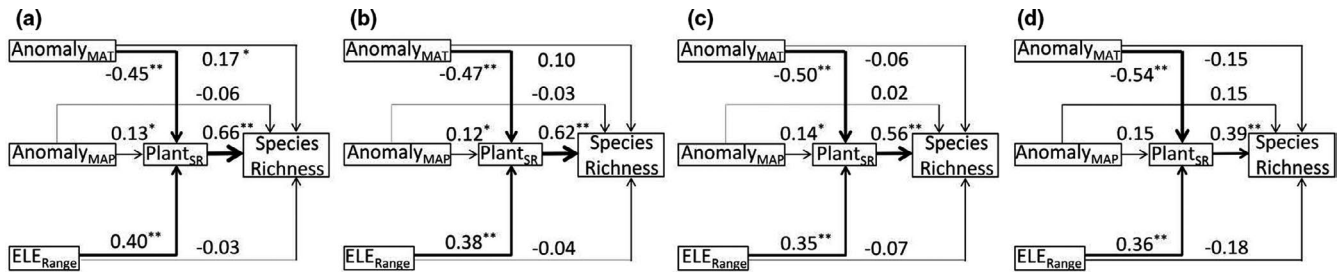
FIGURE 4 Results of structural equation models examining the direct and indirect effects of the contemporary-Last Glacial Maximum anomaly in MAT/MAP (Anomaly$_{MAT}$/Anomaly$_{MAP}$), elevation range (ELE$_{Range}$), and plant species richness (Plant$_{SR}$) on bird species richness. The thresholds for bird species richness are (a) bird species richness >50; (b) bird species richness >100; (c) bird species richness >150; (d) bird species richness >200. Standardized regression coefficients were given. MAP, mean annual precipitation; MAT, Mean annual temperature. $*p < 0.05$, $**p < 0.01$

occurred in regions with stable palaeoclimate. This finding was also in line with previous studies. For example, small-ranged birds, mammals and amphibians are concentrated in areas with stable late Quaternary climate at global scale (Sandel et al., 2011). Climate stability could also promote the aggregate of restricted distributed birds and plants in African forest (Fjeldså & Lovett, 1997).

In addition to bird species richness, our results also showed consistent associations between glacial–interglacial climate change and phylogenetic and functional structure of Chinese bird assemblages. Notably, the clustered phylogenetic and functional structure in regions with stable glacial–interglacial climate contradicted our hypothesis. The clustering of relatively young lineages indicates the prevalence of in situ diversification in these regions (Cai et al., 2018; Kissling et al., 2012; Lei et al., 2015). Previous studies about birds in China have suggested that the mountains in southwestern China with many glacial refuges may promote the evolution of extremely species-rich and specialized montane avian fauna, and also prevent the species dispersal after glacial periods (Cai et al., 2018; Lei et al., 2015; Wu et al., 2017). The nonlinear relation between functional structure and anomaly in MAT is mainly resulted from the large anomaly in MAT and the relative random functional structure in northeastern China, which may due to the complex interactions among diverse vegetation types, high precipitation and large anomaly in MAT in this region. Our study provides direct and strong evidence for the role of glacial–interglacial climate stability in shaping the geographic distribution of phylogenetic and functional structure of bird assemblages in China.

4.4 | Other explanatory variables and bird diversity

In addition to plant species richness and anomaly in MAT, MAP and elevation range were also associated with Chinese bird diversity, mainly through their indirect effect on plant species richness. Numerous studies have shown that precipitation could affect the geographic distribution of birds through both direct and indirect effects, supporting the influence of physiological tolerance and vegetation complexity (Hawkins, Field, et al., 2003; Remeš & Harmáčková, 2018). For example,

bird species richness in Australia increases with wetter climate, and in wetter and more productive northern and eastern Australia there is also high accumulation of bird lineages (Remeš & Harmáčková, 2018). Notably, both phylogenetic and functional structure were most clustered in regions with median precipitation, i.e., southwestern China, and then become less clustered and even over-dispersed in regions with more precipitation, i.e., southeastern China. This finding is consistent with the Australian avian study, which suggests that the wet northern and eastern Australia harbours divergent lineages (Remeš & Harmáčková, 2018). Larger elevation range would also have more plant species by providing higher environmental heterogeneity and more ecological niches, and then promote high bird species richness (López-Pujol et al., 2006; Zhang et al., 2017).

5 | CONCLUSIONS

In summary, this study finds that high bird species richness is phylogenetically and functionally clustered in southwestern China, a region of high plant species richness and stable glacial–interglacial climate. In addition, these clustered bird assemblages are composed of young lineages. These findings suggest that in situ diversification and perhaps limited dispersal resulting from the diverse plant species and stable climate are the dominant processes affecting the geographic distribution of Chinese birds. Therefore, these diverse bird communities that survived the glacial–interglacial climate fluctuations of the Quaternary should be of great importance to biodiversity conservation in China.

DATA AVAILABILITY STATEMENT

The data are available in supplementary files.

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BIOSKETCH

Gang Feng is interested in combining community ecology with macroecology and biogeography to assess the relative roles of local, regional and historical factors in shaping diversity patterns.

Author contributions: G.F. conceived the ideas; L.M., N.W. and X.Y. collected the data; N.W. and G.F. analysed the data; X.S. wrote the code for SES.age; N.W., G.F., X.S., Y.W. and W.E. led the writing.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.