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Original article

Breeding bird diversity in relation to environmental gradients in China

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ABSTRACT

Geographic variation in species richness has been explained by different theories such as energy, productivity, energy–water balance, habitat heterogeneity, and freezing tolerance. This study determines which of these theories best account for gradients of breeding bird richness in China. In addition, we develop a best-fit model to account for the relationship between breeding bird richness and environment in China. Breeding bird species richness in 207 localities (3271 km^2 per locality on average) from across China was related to thirteen environmental variables after accounting for sampling area. The Akaike's information criterion (AIC) was used to evaluate model performance. We used Moran's *I* to determine the magnitude of spatial autocorrelation in model residuals, and used simultaneous autoregressive model to determine coefficients of determination and AIC of explanatory variables after accounting for residual spatial autocorrelation. Of all environmental variables examined, normalized difference vegetation index, a measure of plant productivity, is the best variable to explain the variance in breeding bird richness. We found that species richness of breeding birds at the scale examined is best predicted by a combination of plant productivity, elevation range, seasonal variation in potential evapotranspiration, and mean annual temperature. These variables explained 47.3% of the variance in breeding bird richness after accounting for sampling area; most of the explained variance in richness is attributable to the first two of the four variables.

1. Introduction

Understanding the factors that regulate spatial variations in species richness has been one of the fundamental questions in ecology (Hutchinson, 1959; MacArthur, 1972; Currie, 1991; Gaston, 2003; Ricklefs, 2004). Numerous studies have found that broad-scale species richness is strongly correlated with current climate (Currie, 1991; Qian, 1998; Rahbek and Graves, 2001; Currie et al., 2004; Ricklefs et al., 2004; Evans et al., 2005; Rodríguez et al., 2005), suggesting the influence of current environment on species richness. Major theories proposed to explain broad-scale species richness gradients include energy, productivity, energy–water balance, habitat heterogeneity, and freezing tolerance hypotheses. The energy hypothesis postulates that energy limits diversity. The productivity hypothesis postulates that more productive areas have more individuals and therefore more species (Currie et al., 2004). The energy–water balance hypothesis states that the interaction between energy and water provides a strong explanation for species richness patterns (Hawkins et al., 2003a). The habitat heterogeneity hypothesis states that species diversity increases with increasing habitat heterogeneity (Cramer and Willig, 2002). Freezing tolerance hypothesis postulates that many organisms are limited at higher latitudes by their inability to tolerate cold winter temperatures (Hawkins et al., 2003b). Our knowledge of which of these theories can best explain species richness patterns remains incomplete.

Birds have been frequently used in studies examining richness–environment relationships (e.g., Rahbek and Graves, 2001; Hurlbert and Haskell, 2003; Ding et al., 2006; Evans et al., 2006; Zhao et al., 2006a; Davies et al., 2007). However, our knowledge of the cause of bird species richness variation remains poor, partly because richness–environment relationships vary among regions (Davies et al., 2007) and are scale-dependent (Rahbek and Graves, 2001; Whittaker et al., 2001; Rahbek, 2005). A full understanding of richness–environment relationships for a region cannot be achieved until such relationships have been examined at different scales in the region.

Compared to Europe and North America, much of which was covered by thick ice sheets during the last ice age (Pielou, 1992), East Asia in general and China in particular were much less affected by the glacial climate of the last ice age because it was not covered by an ice sheet except for areas at high elevations. Therefore, the

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degree to which species distributions are at equilibrium with current climate is potentially higher in China than in most of the remainder of northern hemisphere. Furthermore, China covers a wide range of latitudes and longitudes (Fig. 1); climate varies greatly from south to north (a striking warm-to-cold gradient) and from east to west (a striking wet-to-dry gradient). Thus, China is an ideal region for examining the species richness–environment relationship.

In this paper, we use a large dataset to examine the relationships between a number of environmental factors and the species richness of breeding birds in terrestrial areas in China. Environmental variables examined in this study include nearly all major environmental variables that are thought to determine large-scale breeding bird richness, including all factors considered in such well known theories to explain broad-scale species richness gradients as energy, productivity, energy–water balance, habitat heterogeneity, and freezing tolerance. We determine which of the above-mentioned hypotheses best account for gradients of breeding bird richness, acknowledging that these hypotheses are not mutually exclusive. We develop a best-fit model to account for the relationship between breeding bird richness and environment in China.

2. Material and methods

2.1. Species richness data

We compiled a comprehensive dataset of bird species richness in China, based on the literature. We searched all relevant literature sources, including books, theses, journal articles, survey reports of nature reserves, and other technical reports. Our searches turned up 417 localities in China. Most of these localities are protected areas (including nature reserves, national parks, and scenic sites). We excluded those localities for which information about latitude, longitude, locality area, minimum elevation, maximum elevation, or the number of species of breeding birds was not available. We also excluded aquatic and wetland localities. As a result, 207 localities were included in this study and the vast majority of them are national nature reverses. The literature for the vast majority of these localities was published in the past three decades (Supplementary Information, Appendix A). These localities are widely distributed across China (Fig. 1) and have been intensively surveyed with the aim of providing complete bird species lists for them. The average area of each locality was 3271 (±759 SE) km^2. The breeding bird richness in each site was on average 128.2, varying from 32 to 350.

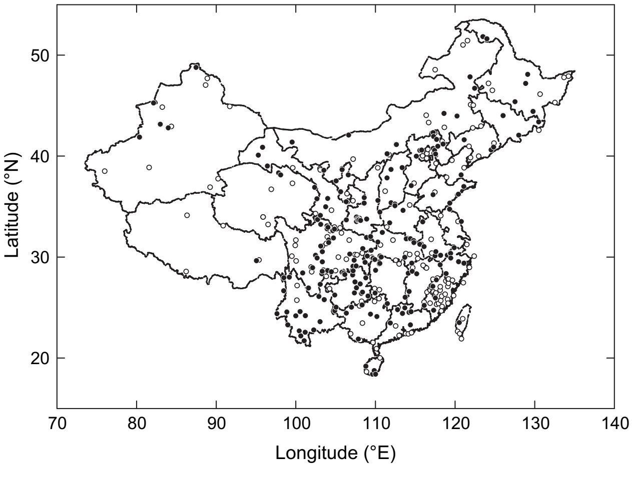

Fig. 1. Map showing the location of the avifaunas used in this study. Open symbols indicate avifaunas excluded from this study (see Materials and Methods for details).

2.2. Environmental data

We related geographic variation in breeding bird species richness to mean annul temperature (TEMP), mean temperature of the coldest month (TEMP_{min}), annual precipitation (PREC), annual actual evapotranpiration (AET), annual potential evapotranspiration (PET), normalized difference vegetation index (NDVI), elevation range (ELEV), minimum elevation (ELEV_{min}), and seasonal variation (month with the largest value minus month with the lowest value) in temperature, precipitation, actual evapotranpiration, potential evapotranspiration, and NDVI. These variables include nearly all major environmental variables that have been thought to influence large-scale breeding bird richness (Currie, 1991; Rahbek and Graves, 2001; Hurlbert and Haskell, 2003; Ding et al., 2006; Davies et al., 2007). TEMP and PET are widely used as a measure of ambient energy (Schall and Pianka, 1978; Currie, 1991; Rodríguez et al., 2005). AET combines temperature and water availability into a single variable, and is a measure of energy–water balance (Bini et al., 2004). NDVI is widely recognized as a measure of plant productivity and as a major determinant of breeding bird richness (e.g., Ding et al., 2006). It was calculated as a normalized ratio between red and near infrared bands (Tucker, 1979). Elevation range represents topographical variation and has been commonly used as a measure of habitat heterogeneity and mesoscale climatic variation in previous studies on large-scale species richness gradients (e.g., Rahbek and Graves, 2001; Rodríguez et al., 2005), although it may also influence species richness through historical processes such as speciation (Qian et al., 2007).

Data for the temperature and precipitation variables were obtained from the CRU Global Climate Dataset developed by the Climatic Research Unit (New et al., 1999). Data for the evapotranspiration variables were obtained from the Global Evapotranspiration and Water Balance Data Sets developed by Ahn and Tateishi (1994) and Tateishi and Ahn (1996). Data for NDVI were compiled by Xiao et al. (2003, 2004) for each of 10-day periods. We generated monthly NDVI values by averaging 12 values of four complete years (from January 1999 to December 2002) for each month. All the environmental datasets used in this study were compiled at the resolution of 0.5° of latitude and longitude. Data of the climate and productivity variables were assembled for the 207 localities according to their geographical midpoints.

2.3. Statistical analysis

We regressed breeding bird richness on each of TEMP, PET, NDVI, AET, ELEV, and TEMP_{min}. The models with TEMP and PET test the energy hypothesis; the model with NDVI tests the productivity hypothesis; the model with AET tests the energy–water balance hypothesis; the model with ELEV tests the habitat heterogeneity hypothesis; and the model with TEMP_{min} tests the freezing tolerance hypothesis. We determined which of these hypotheses best account for gradients of breeding bird richness in China by comparing values of the Akaike's information criterion (AIC) among regression models. The AIC is a widely used statistic approach to evaluate model performance (Burnham and Anderson, 2002; Davies et al., 2007; Kreft and Jetz, 2007). We added the quadratic term of an environmental variable to each model to allow for nonlinear relationships.

In order to find a best-fit model describing the richness–environment relationship, we then generated ordinary least squares (OLS) multiple regression models to relate breeding bird richness to different combinations of the following explanatory variables: TEMP, PREC, AET, PET, NDVI, ELEV, seasonal variation in temperature (TEMP_{var}), seasonal variation in precipitation (PREC_{var}), seasonal variation in actual evapotranpiration (AET_{var}), seasonal variation in potential evapotranspiration (PET_{var}). Because sample area was not held constant among localities, we included sample area as a covariate in all regression models to account for sample area effect. In order to improve the normality of model residual distributions (e.g., Fig. S1), bird richness, sample area (AREA), and elevation range were $\log_{10}$ transformed. The AIC was used to evaluate model performance. We used the "Model Selection and Multi-Model Inference" module implemented in SAM v3 (www.ecoevol.ufg.br/sam/) to generate models of all possible linear combinations ($n = 2047$) of the aforementioned eleven variables (i.e., TEMP, PREC, AET, PET, NDVI, ELEV, $TEMP_{var}$, AET_{var}, $PREC_{var}$, PET_{var}, and AREA). We determined the model with NDVI, ELEV, PET_{var}, TEMP, and AREA as the best-fit model because it had the lowest value of AIC (−260.4) and included the smallest number of explanatory variables. We then added the quadratic term of each environmental variable to the best-fit model to allow for nonlinear relationships. We also included interaction terms of the environmental variables but none of them improved model fit.

Spatial autocorrelation is frequently found in macroecological species richness data, which may inflate the rate of type I error in a significance test (Diniz-Filho et al., 2003) and thus cause non-significant relationships to appear significant. Spatial autocorrelation in model residuals may also affect estimates of model coefficients (Kühn, 2007; Dormann, 2007). Although previous studies for other taxa at a similar spatial scale in China (e.g., Qian et al., 2007) have shown that spatial autocorrelation is negligible, spatial autocorrelation may occur in our bird data. Accordingly, we used Moran's *I* statistic to determine if spatial autocorrelation is present in model residuals. The value of Moran's *I* ranges from −1 for negative spatial autocorrelation to +1 for positive spatial autocorrelation, where the expected values in the absence of significant spatial autocorrelation is around zero (Cliff and Ord, 1981). Moran's *I* was calculated using SAM (Rangel et al., 2006). Although Moran's *I*, ranging from 0.119 to 0.221, was low for regression models including single environmental variables in addition to sampling area, we used simultaneous autoregressive (SAR) model (Dormann et al., 2007) implemented in SAM to determine coefficients of determination and AIC of explanatory variables after accounting for residual spatial autocorrelation. Data analyses were performed with SAM software (Rangel et al., 2006) freely available at www.ecoevol.ufg.br/sam.

3. Results

Of the six SAR models each including one environmental variable, the model with NDVI was the best model because it explained the largest amount of the variance in breeding bird richness and had the lowest AIC (Table 1). The next best models included either AET or ELEV as explanatory variables. Models with a quadratic term explained, on average, 2.2% additional variance in breeding bird richness (Table 1).

The best-fit OLS model for the richness–environment relationship explained 58.5% of the variance in breeding bird richness (Table 2). This model explained 45.3% of the variance in species richness after accounting for sample area. Approximately half amount (21.2%) of the variance explained by the four environmental variables in the model was attributable to NDVI (Table 2). Elevation range explained 12.5% additional variance. PET_{var} and TEMP together explained 11.6% additional variance in breeding bird richness (Table 2). When we included the quadratic terms of the five explanatory variables to the model, the five quadratic terms together explained only 2.6% additional variance in breeding bird richness (adjusted $r^2 = 0.579$ for the model including only linear terms, adjusted $r^2 = 0.605$ for the model including both linear and quadratic terms). In other words, each quadratic term explained only 0.5% additional variance in breeding bird richness. Because including quadratic terms in the model did not significantly improve model performance, we dropped them from the final best-fit model (Table 2).

Table 1
Results of simultaneous autoregressive (SAR) models testing five richness–environment hypotheses. Model I included only the linear term of each variable, and Model II included both linear and quadratic terms. Sampling area was included in each model to account for sampling area effect.

Hypothesis	Variable	Model I		Model II	
		Model r^2	AIC	Model r^2	AIC
Energy	TEMP	0.164	−122.1	0.176	−122.7
	PET	0.251	−144.8	0.282	−151.3
Productivity	NDVI	0.440	−205.1	0.445	−204.5
Energy–water balance	AET	0.329	−167.6	0.360	−175.1
Habitat heterogeneity	ELEV	0.332	−168.3	0.356	−173.9
Freezing tolerance	$TEMP_{min}$	0.222	−136.8	0.250	−142.4

Residual spatial autocorrelation in our best-fit OLS model for the richness–environment relationship was very low—Moran's *I* was only 0.028 over the shortest distance (Fig. 2), suggesting that the spatial autocorrelation in model residuals is negligible. This was confirmed by our SAR model—the relative strength of each of the environmental variables included in the model was identical in the OLS and SAR models and fitted coefficients of the variables were comparable between the two models (Table 2).

4. Discussion

Birds have been frequently studied in addressing macroecological issues such as the relationship between species richness and environment because their breeding distributions have been well documented (Davies et al., 2007). Because large-scale field survey-based species richness data are rarely available (Hurlbert and White, 2005), most previous studies on large-scale species richness patterns of birds as well as other taxa have used species richness estimated from range maps by counting the number of species ranges that overlap each quadrat of a grid system at a given resolution of latitude and longitude. Range map-derived species richness has been used at various resolutions ranging from approximately 0.1°–10° of latitude and longitude (Rahbek and Graves, 2001; Hawkins et al., 2005; González-Taboada et al., 2007; Hurlbert and Jetz, 2007). Because species do not occur at all locations throughout their ranges, species richness estimated for a site from range maps is usually higher than actual species richness, and the degree of overestimation is greater at a finer resolution (Hurlbert and Jetz, 2007). Previous studies demonstrated that species typically occur at 40–65% of the sites over which they are expected on the basis of their distributional ranges (Hurlbert and White, 2005; Hurlbert and Jetz, 2007). Hurlbert and Jetz (2007)

Table 2
Results of ordinary least squares (OLS) model ($r^2 = 0.585$, AIC = −260.5) and simultaneous autoregressive (SAR) model ($r^2 = 0.588$, AIC = −261.8) in China.

Effect	OLS			SAR	
	Coefficient	Standardized partial regression coefficient	Partial r^2	Coefficient	Standardized partial regression coefficient
Intercept	1.545	0		1.543	0
NDVI	0.809	0.530	0.212	0.782	0.512
ELEV	0.131	0.305	0.125	0.129	0.301
PET_{var}	−0.003	−0.257	0.094	−0.003	−0.239
TEMP	−0.004	−0.143	0.022	−0.004	−0.132
AREA	0.076	0.330	0.132	0.073	0.314

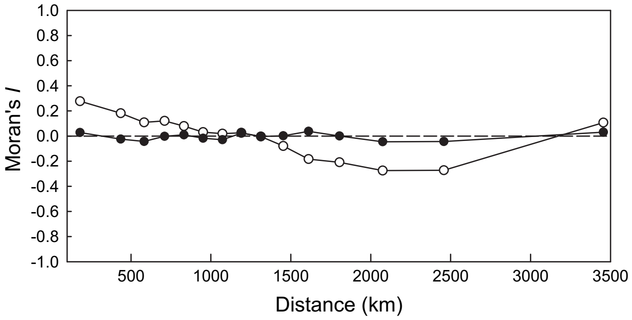

Fig. 2. Correlograms for the dependent variable (open circles) and residuals (solid circles) of the richness–environment relationship based on the OLS model reported in Table 2 for breeding birds in China.

demonstrated that the range map-based approach overestimates species richness at resolutions <2° (~48 000 km^2 near the equator), at which most previous studies examining bird richness–environment relationships were conducted, including Ding et al. (2006) who related breeding bird richness in East Asia to environmental variables (NDVI and elevation range) at the grain size of 100 × 100 km, a scale <1° of latitude and longitude near the equator. Hurlbert and White (2005) demonstrated that the relative importance of predictive variables included in a regression analysis varied not only in magnitude but also in direction because of the false species presences derived from range maps. Geographic units used in this study each have 3271 km^2 on average, which is equivalent to a spatial scale of about 0.25° in latitude and longitude. At this spatial scale, reliable richness–environment relationships cannot be developed based on range map-based richness data, as Hurlbert and Jetz (2007) demonstrated. Our data, which are based on direct local samples, differ from those used in most other macroecological analyses, which are based on overlaying distribution maps and suffer from overestimation of species richness (Hurlbert and Jetz, 2007). Field survey-based data may underestimate species richness because rare and localized species may be overlooked during field surveys, but we believe it is unlikely that underestimation has a significant effect in our study because birds are generally very vagile and thus are easy to be observed. Because our study is one of few studies using survey-based richness data at this or a similar scale, we believe our study can be an important addition to the current literature on the relationship between breeding bird richness and environment.

The best-fit regression model of our study included four environmental variables (i.e., NDVI, elevation range, intra-annual variation of PET, and mean temperature of the coldest month). Most of the variance in breeding bird richness in China is explained by NDVI and elevation range. NDVI is commonly considered as a measure of plant biomass and plant production (Hurlbert and Haskell, 2003 and references therein), and elevation range is widely used as a surrogate for topographic heterogeneity and thus a measure of habitat diversity (Rahbek and Graves, 2001; Hawkins et al., 2005; Ding et al., 2006). These two variables have been identified as important ones influencing breeding bird richness patterns at the global scale (Davies et al., 2007) and in many continental regions (e.g., Australia, Hawkins et al., 2005; North America, Hurlbert and Haskell, 2003; Seto et al., 2004; Evans et al., 2006; Africa, McPherson and Jetz, 2007), and they explained over 70% of the variance in breeding bird richness derived from range maps at the resolution of 100 × 100 km in East Asia (Ding et al., 2006). Thus, our finding is generally consistent with those of previous studies. However, the variance in bird richness explained by environmental variables is generally higher in previous studies based on range map-derived richness data than that reported in the present study. This is likely because larger spatial scales and false species occurrences, which would presumably smooth geographic gradients of species richness across a region, were used in most of previous studies on large-scale species richness.

In their studies examining the relationship between species richness of terrestrial vertebrates and several environmental variables including TEMP, AET, PET, NPP, and elevation range, Zhao et al. (2006a,b) found that bird species richness is significantly correlated with only two (AET and NPP) of the five variables that they examined, and that these two variables together explained only 12.4% of the variance in bird richness in their dataset. Elevation range alone explained 14.9% of the variance in bird richness in our study, but this variable did not enter their regression model for birds. The studies of theirs and ours are for the same area (i.e., China) and the resolutions of their and our studies are comparable. Why are the results of these studies so different? We believe that the following may be part of the reason. First, some localities included in their study are exclusively aquatic (e.g., Eastern Dongting Lake Nature Reserve and Poyang Lake Nature Reserve), while our study used only terrestrial localities. We excluded aquatic localities because bird species richness may differ substantially between terrestrial and aquatic areas under the same climate conditions and thus including localities from both terrestrial and aquatic systems in a single analysis may not be appropriate because it may obscure the results of the analysis. Second, unlike many other studies (e.g., H-Acevedo and Currie, 2003; Evans et al., 2006; Buckley and Jetz, 2007) in which species richness was transformed (usually by logarithm) to meet statistical requirements (e.g., homoscedasticty in variance), Zhao et al. used raw species richness to relate environmental variables. Their bivariate plot of bird species richness and NPP clearly shows a wider variation in species richness towards larger values of NPP, suggesting that data transformation was necessary in their study. The use of raw data in their analyses would presumably have led to a poorer model fit. Third, unlike most of the studies on bird richness in which non-breeding birds were excluded, Zhao et al. included both breeding and non-breeding birds. The following analysis indicates that including non-breeding birds would result in poorer richness–environment relationships, compared to an analysis including only breeding birds. Of the 207 avifaunas used in the present study, 204 have data for total (breeding plus non-breeding) bird species richness. When log-transformed breeding bird richness was regressed on the five variables shown in Table 2, these variables explained 59% of the variance in richness. When log-transformed total bird richness was regressed on the same five variables, these variables explained only 35% of the variance in richness. In this analysis, the effect of elevation range on total bird richness was significant ($P = 0.002$), contradictory to the findings of Zhao et al. (2006a, b).

Qian et al. (2007) examined richness–environment relationships for amphibians and reptiles in China. Their study included 245 localities, 142 (58%) of which were also included in the present study. Minimum elevation entered the best-fit models for amphibians and reptiles in Qian et al.'s (2007) study and explained over 30% of the variance in reptile species richness, but this variable did not enter the best-fit model for breeding birds in our study. Similarly, precipitation variables entered the models of both amphibians and reptiles but did not enter the best-fit model for breeding birds in China. Instead, intra-annual variation of PET entered the model for birds but did not enter the models for amphibians and reptiles. Comparing the richness–environment relationships among the three taxa, we suggest that environmental factors regulating richness–environment relationships are more similar between amphibians and reptiles than between either and breeding birds in China. This is consistent with the observation that amphibians and reptiles occupy similar habitats, which are quite different from those of birds.

In summary, this study showed that species richness of breeding birds at the scale examined is best predicted by the combination of plant productivity, elevation range, seasonal variation in potential evapotranspiration, and mean annual temperature, with the most of the explained variance in richness attributable to the first two of the four variables. These two variables have been found to be major predictors for breeding bird richness in other regions and the whole of the globe, indicating that the finding of our study at a smaller scale is to a large degree consistent with those of previous studies on breeding birds at larger scales.

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Appendix. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.actao.2009.08.009.

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