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Environmental determinants of amphibian and reptile species richness in China

Hong Qian, Xihua Wang, Silong Wang and Yuanliang Li

H. Qian (hqian@museum.state.il.us), Research and Collections Center, Illinois State Museum, 1011 East Ash Street, Springfield, IL 62703, USA. – X. Wang, Dept of Environmental Science, East China Normal Univ., Shanghai 200062, China. – S. Wang and Y. Li, Center for Forest Ecology and Forestry Eco-engineering, Inst. of Applied Ecology, Chinese Academy of Sciences, 72 Wenhua Road, Shenyang, Liaoning, China.

Understanding the factors that regulate geographical variation in species richness has been one of the fundamental questions in ecology for decades, but our knowledge of the cause of geographical variation in species richness remains poor. This is particularly true for herpetofaunas (including amphibians and reptiles). Here, using correlation and regression analyses, we examine the relationship of herpetofaunal species richness in 245 localities across China with 30 environmental factors, which include nearly all major environmental factors that are considered to explain broad-scale species richness gradients in such theories as ambient energy, water–energy dynamics, productivity, habitat heterogeneity, and climatic stability. We found that the species richness of amphibians and reptiles is moderately to strongly correlated with most of the environmental variables examined, and that the best fit models, which include explanatory variables of temperature, precipitation, net primary productivity, minimum elevation, and range in elevation, explain ca 70% the variance in species richness for both amphibians and reptiles after accounting for sample area. Although water and temperature are important explanatory variables to both amphibians and reptiles, water variables explain more variance in amphibian species richness than in reptile species richness whereas temperature variables explain more variance in reptile species richness than in amphibian species richness, which is consistent with different physiological requirements of the two groups of organisms.

One of the most universal features of natural systems is that species richness, the number of different species co-occurring in a given area, varies enormously from place to place (Hutchinson 1959, Currie 1991, Hawkins et al. 2003). Species richness may differ substantially between areas with comparable environments in different regions (Latham and Ricklefs 1993, Qian and Ricklefs 1999, 2000, Qian 2002, Ricklefs et al. 2004), suggesting the effect of regional and historical factors on species richness. However, it is frequently found that broad-scale species richness is strongly correlated with current climate within regions (Currie 1991, Qian 1998, Rahbek and Graves 2001, Hawkins and Porter 2003, 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. Understanding the factors that regulate spatial variations in species richness has been one of the fundamental questions in ecology for decades (Hutchinson 1959, MacArthur 1972, Currie 1991, Gaston 2003, Ricklefs 2004).

A great number of studies have been conducted to explore the relationships between species richness and environment, but our knowledge of the cause of species richness variation remains poor. This is particularly true for herpetofaunas, which include amphibians and reptiles. Because both amphibian and reptile species richness are declining globally (Gibbons et al. 2000) and because it is believed that the global warming is responsible for the decline (Pounds et al. 1999), there is urgency to understanding the relationships between herpetofaunal species richness and environmental factors.

Buckley and Jetz (2007) examined the richness and environment relationships for amphibians at the global scale. They conclude that the relationships vary between regions, suggesting that it is necessary to examine the amphibian richness–environment relationship for individual regions separately. Region effect on species richness gradients is often found in other groups of organisms (Latham and Ricklefs 1993, Qian and Ricklefs 1999, 2000, Ricklefs et al. 2004). Furthermore, the same environmental variables may influence species richness even in different directions (i.e. positive vs negative correlations) in different regions (Schall and Pianka 1978). Thus, it is necessary to examine richness–environment relationships for each region in order to better understand the cause of global biodiversity patterns.

In this paper, we use a large data set to examine the relationships between a great number of environmental factors and the species richness of amphibians and reptiles in terrestrial areas in China. China is rich in amphibian and reptile species richness – 325 species of amphibians (Fei et al. 2005) and 384 species of reptiles (Ji and Wen 2002). Amphibians and reptiles are distributed across the full ranges of latitudes and longitudes in China. Because China covers a wide range of latitudes and longitudes and hence a wide range of climate gradients, species richness of amphibians and reptiles varies greatly from south to north and from east to west (Zhang 1999). Furthermore, the modern amphibian and reptile assemblages may reflect the location of glacial refugia more than contemporary climate (Araújo and Pearson 2005, Araújo et al. 2006), suggesting that the current distributions of these taxa may not be at equilibrium with current climate at least in some regions. Compared with Europe and North America, much of which was covered by thick ice-sheets during the Last Glacial Maximum (Pielou 1992), China was much less influenced by glacial climate because it was not covered by an ice sheet except for areas at high elevations. Therefore, the 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. This is crucial to examining the species richness–climate relationship.

Our primary goal is twofold. First, we examine correlations between species richness of amphibians and reptiles and individual environmental factors. Unlike most previous studies on large-scale species richness patterns which each included only few environmental variables, we examine 30 environmental factors that are thought to influence species richness, including all factors considered in such well known theories to explain broad-scale species richness gradients as ambient energy (Turner et al. 1987, Currie 1991), water–energy dynamics (O'Brien 1993, 1998), productivity (Hutchinson 1959), habitat heterogeneity (Pianka 1966), and climatic stability (Currie 1991). Second, we determine a smaller set of environmental variables that can best account for geographical variation in species richness of amphibians and reptiles in China. In all analyses, sample area effect is accounted for.

Zhao et al. (2006) recently examined the relationship between environment and species richness of amphibians and reptiles in China; however, their study 1) used a smaller number of localities (including only nature reserves), 2) did not differentiate localities dominated by terrestrial system from those dominated by aquatic system, including both of which in a single analysis may have obscured their results, and 3) examined only few environmental variables (see Discussion for more comments on their study). Our study also examines the robustness of the conclusions drawn in their study.

Materials and Methods

Species richness data

Over 330 localities in China have been intensively surveyed with the aim of providing complete amphibian and/or reptile species lists for these localities. Most of these localities are protected areas (including nature reserves, national parks, and scenic sites). The species richness of amphibians and reptiles in these localities has been well documented in the literature including books (Zhang 1999, Wang 2003), journal articles (Ma et al. 2006, Sun et al. 2006), survey reports of nature reserves (Huang and Nong 2002), and other technical reports, from which our dataset was assembled. We excluded those localities for which information about latitude, longitude, locality area, minimum elevation, or maximum elevation was not available. We also excluded those localities which were aquatic or wetland ecosystems. As a result, 245 localities were included in this study. The literature for the vast majority of these localities was published in the past three decades. These localities are widely distributed across China (Fig. 1). The average area of each locality is 2003.4 (±454.9 SE) km^2. Of these 245 localities, 243 have species richness data for amphibians and 234 for reptiles.

Environmental data

We related the species richness of amphibians and reptiles to 30 environmental variables (Table 1, Table S1 in Appendix). These environmental variables include nearly all major environmental variables that have been used in previous studies to explain broad-scale species richness gradients. They were grouped into five major categories as follows.

1) Temperature. The temperature variables include mean annual temperature (TEM), mean temperature of

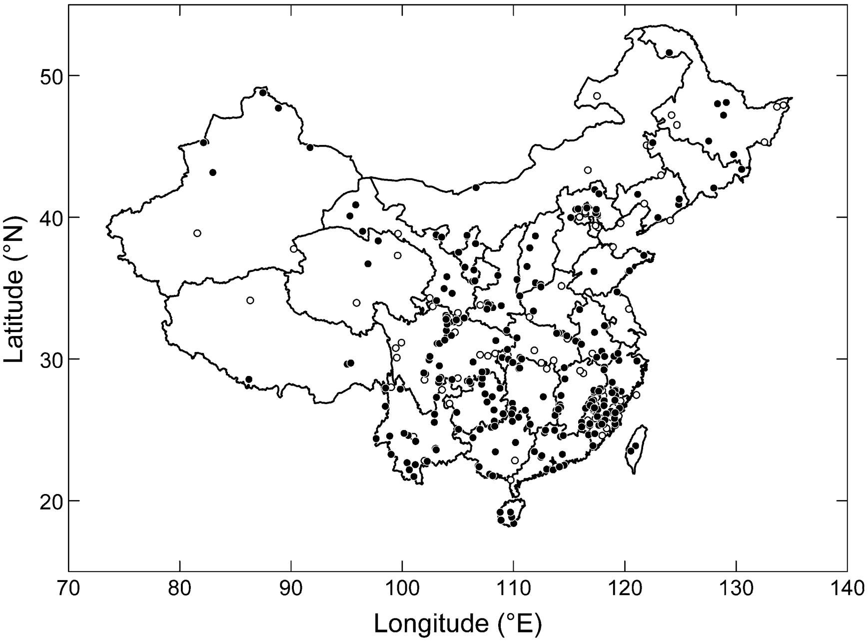

Fig. 1. Map showing the location of the herpetofaunas used in this study. Open symbols indicate herpetofaunas excluded from this study (see Materials and methods for detail).

the coldest month (TEM_{min}), mean temperature of the warmest month (TEM_{max}), and seasonal variation (seasonality) in temperature (TEM_{var}, difference between TEM_{max} and TEM_{min}). TEM is widely used as a measure of ambient energy input (Schall and Pianka 1978, Currie 1991, Rodríguez et al. 2005); TEM_{min} is related to frost and freezing tolerance.

2) Precipitation. The precipitation variables include mean annual precipitation (PREC), minimum monthly precipitation ($PREC_{min}$), maximum monthly precipitation ($PREC_{max}$), seasonal variation in precipitation ($PREC_{var}$; difference between $PREC_{max}$ and $PREC_{min}$), mean annual rainfall (RAIN), and mean summer rainfall ($RAIN_{sum}$). RAIN was estimated as the total monthly precipitation for all months with a mean temperature above 0°C (Francis and Currie 2003), and $RAIN_{sum}$ was calculated as the sum of monthly precipitation from May through August.

3) Evapotranspiration. The evapotranspiration and related variables include annual actual evapotranspiration (AET), minimum monthly actual evapotranspiration (AET_{min}), maximum monthly actual evapotranspiration (AET_{max}), seasonal variation in actual evapotranspiration (AET_{var}; calculated as AET_{max} minus AET_{min}), annual potential evapotranspiration (PET), minimum monthly potential evapotranspiration (PET_{min}), maximum monthly potential evapotranspiration (PET_{max}), seasonal variation in potential evapotranspiration (PET_{var}; calculated as PET_{max} minus PET_{min}), water deficit (WD; calculated as PET minus AET; Francis and Currie 2003), and moisture index (MI; calculated as the ratio of AET over PET; Whittaker et al. 2007). AET combines temperature and water availability into a single variable, and is a measure of energy–water balance (Bini et al. 2004). It is considered as a suitable productive energy metric (Evans et al. 2005). PET is a measure of ambient energy (Hawkins and Porter 2003).

4) Productivity. Plant productivity is widely recognized to influence species richness gradients for many plant and animal groups at a wide range of scales (Mittelbach et al. 2001). The variables used in this study to measure productivity include net primary productivity (NPP), normalized difference vegetation index (NDVI), NDVI during the course of summer ($NDVI_{sum}$), enhanced vegetation index (EVI), EVI during the course of summer (EVI_{sum}), and global vegetation index (GVI). In general, all these variables measure plant primary production that represents realized energy capture. NPP is the rate at which carbon is accumulated by autotrophs and is measured as difference between gross photosynthesis and autotrophic respiration (Jenkins et al. 1999). At a broad scale, NPP is estimated based on characterization of vegetation, climate, and soils. NDVI is a measure of greenness. It was calculated as a normalized ratio between red and near infrared bands (Tucker 1979).

5) Physiography. The physiographical variables used in this study include minimum elevation ($ELEV_{min}$), maximum elevation ($ELEV_{max}$), and topographic relief

Table 1. Correlation coefficients between $\log_{10}$-transformed species richness and environmental variables. P_{adj}-values indicate the degree of significance only for $r_{residual}$.

Variable	Code	Amphibian			Reptile		
		$r_{partial}$	$r_{residual}$	P_{adj}	$r_{partial}$	$r_{residual}$	P_{adj}
Temperature							
Mean annual temperature	TEM	0.659	0.614	<0.001	0.718	0.657	<0.001
Mean temperature of the coldest month	TEM_{min}	0.709	0.672	<0.001	0.732	0.680	<0.001
Mean temperature of the warmest month	TEM_{max}	0.436	0.372	0.009	0.526	0.461	0.003
Seasonal variation in TEM	TEM_{var}	−0.636	−0.629	<0.001	−0.584	−0.577	<0.001
Precipitation							
Annual precipitation	PREC	0.715	0.678	<0.001	0.716	0.654	<0.001
Minimum monthly precipitation	$PREC_{min}$	0.566	0.513	0.004	0.624	0.551	0.007
Maximum monthly precipitation	$PREC_{max}$	0.693	0.652	<0.001	0.683	0.618	0.001
Seasonal variation in precipitation	$PREC_{var}$	0.675	0.633	<0.001	0.647	0.584	<0.001
Annual rainfall	RAIN	0.717	0.681	<0.001	0.720	0.659	<0.001
Summer rainfall	$RAIN_{sum}$	0.716	0.678	<0.001	0.693	0.634	<0.001
Evapotranspiration							
Annual actual evapotranspiration	AET	0.783	0.759	<0.001	0.753	0.699	<0.001
Minimum monthly AET	AET_{min}	0.694	0.661	<0.001	0.725	0.678	<0.001
Maximum monthly AET	AET_{max}	0.724	0.690	<0.001	0.658	0.588	<0.001
Seasonal variation in AET	AET_{var}	0.527	0.477	<0.001	0.405	0.338	0.005
Annual potential evapotranspiration	PET	0.646	0.615	<0.001	0.661	0.620	<0.001
Minimum monthly PET	PET_{min}	0.658	0.638	<0.001	0.646	0.622	<0.001
Maximum monthly PET	PET_{max}	0.460	0.412	0.005	0.556	0.489	0.004
Seasonal variation in PET	PET_{var}	−0.333	−0.358	0.003	−0.232	−0.253	0.006
Water deficit	WD	−0.555	−0.515	<0.001	−0.464	−0.406	0.011
Moisture Index	MI	0.729	0.693	<0.001	0.604	0.537	0.002
Primary productivity							
Annual net primary production	NPP	0.789	0.773	<0.001	0.731	0.673	<0.001
Normalized difference vegetation index	NDVI	0.732	0.698	<0.001	0.651	0.585	<0.001
NDVI during the course of summer	$NDVI_{sum}$	0.478	0.427	<0.001	0.330	0.263	0.030
Enhanced vegetation index	EVI	0.749	0.718	<0.001	0.688	0.627	<0.001
EVI during the course of summer	EVI_{sum}	0.626	0.579	<0.001	0.501	0.432	0.004
Global vegetation index	GVI	0.530	0.479	<0.001	0.484	0.418	0.003
Physiography							
Lowest elevation	$ELEV_{min}$	−0.468	−0.431	0.001	−0.583	−0.531	0.003
Highest elevation	$ELEV_{max}$	−0.133	−0.075	0.433	−0.249	−0.144	0.285
Topographic relief	$ELEV_{var}$	0.135	0.137	0.039	0.086	0.077	0.376
$\log_{10}$ topographic relief	$LOGELEV_{var}$	0.198	0.214	<0.001	0.156	0.164	0.028

($ELEV_{var}$; calculated as $ELEV_{max}$ minus $ELEV_{min}$). Topographic relief has been used as a measure of habitat heterogeneity and mesoscale climatic variation in many previous studies on large-scale species richness gradients (Rahbek and Graves 2001, Rodríguez et al. 2005). We also included $\log_{10}$-transformed topographic relief ($LOGELEV_{var}$) because it is suggested to use this form of topographic relief in the study of broad-scale species richness gradients (Field et al. 2005).

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, Tateishi and Ahn 1996). Data for NPP were compiled by Cramer et al. (1999), and were averages of NPP estimated by seventeen global models of biogeochemistry. Data for NDVI and EVI were compiled by Xiao et al. (2003, 2004) for each of 10-d periods. We generated monthly NDVI and EVI values by averaging 12 values of four complete years (from January 1999 to December 2002) for each month. Data for GVI was compiled by Kineman and Hastings (1992). All the environmental datasets used in this study were compiled at the resolution of 0.5 degrees of latitude and longitude. Data of the climate and productivity variables were assembled for the 245 localities according to their geographical midpoints.

Statistical analysis

The relationships between the species richness of amphibians and reptiles and environmental variables were examined using correlation and regression analyses.

We did these analyses separately for amphibians and reptiles. Because locality area was not held constant, which may influence correlations between species richness and environmental variables, we took two approaches to statistically account for sample area effect. First, we regressed species richness on each environmental variable with sample area as a second independent variable, calculated partial coefficient of determination for each of the two independent variables (Quinn and Keough 2002), adjusted the partial coefficient of determination for each independent variable proportionally in order to achieve the equality between the sum of partial coefficients of determination of the two independent variables and the coefficient of determination for the regression, and then calculated the correlation coefficient between species richness and the environmental variable based on the adjusted partial coefficient of determination for the environmental variable (we denoted it as $r_{partial}$). Second, we followed previous authors (Howard et al. 1998, Patten 2004, Lamoreux et al. 2006, Tushabe et al. 2006) to statistically remove locality area effect before we conducted correlation analyses. Specifically, we regressed species richness on locality area, and then calculated correlation coefficient between the residuals of species richness and each environmental variable (we denoted this type of correlation coefficients as $r_{residual}$). Species richness and locality area were $\log_{10}$-transformed in all analyses of this study unless otherwise stated.

We developed the best fit species richness–environment models for amphibians and reptiles in China. Because this study includes thirty environmental variables, it was not practical to conduct regressions for every possible combination of the thirty variables. We took the following approach to select variables to be included in regression analyses. First, for each of the five categories of environmental variables, the variable that had the strongest correlation with species richness was selected. Second, if a second best variable of each category could explain $>2\%$ additional variation in species richness, it was selected. Third, if a third best variable could further explain $>2\%$ additional variation in species richness, it was selected. This approach of selecting environmental variables was taken separately for amphibians and reptiles. In total, seven environmental variables were selected for amphibians and reptiles, and they are TEM_{min}, RAIN, AET, NPP, $ELEV_{min}$, $LOGELEV_{var}$, and MI. We checked for non-linearity in the relationship between species richness and each selected variable by visual inspection of bivariate plots and by comparing the regression including only the linear term with that including both linear and quadratic terms. No apparent non-linearity was found in these variables except for RAIN (Fig. 2). Next, we regressed species richness on different combinations of the seven selected variables plus squared RAIN to determine the best fitting regression model for amphibians and reptiles. Because annual precipitation, AET and PET have been frequently used in the current literature of broad-scale species richness studies, we also included these three variables and their quadratic forms when we selected the best fit models. In each regression, locality area was included as an independent variable to account for sample area effect. The coefficients of determination (r^2) were adjusted for the number of variables in each regression in order to make comparable the coefficients of determination for regressions with different numbers of independent variables (Quinn and Keough 2002). Akaike information criterion (AIC) was used to select the best fit model – the model with the lowest AIC is considered to be the best (Burnham and Anderson 2002). We used SAM v2.0 (Rangel et al. 2006) to calculate AIC for each regression. We considered a model equivalent to the best fit model if the difference in AIC (ΔAIC) between the focal model and the model with the lowest AIC is $<2\%$ and if the difference in the coefficient of determination (Δr^2) between the focal model and the model with the highest r^2 is <0.015 (1.5%). We determined the relative importance of each explanatory variable in a regression model according to its partial coefficient of determination (Quinn and Keough 2002).

Spatial autocorrelation occurs in most large-scale ecological data; it may lead to inflated estimates of the number of degrees of freedom in significance tests (Diniz-Filho et al. 2003). To remedy this problem, for correlation analyses, we used Duttileul's method (1993) to calculate p-value for the statistical significance test of a correlation coefficient (r) based on geographically effective degrees of freedom. Similarly, for each regression model, we used Duttileul's method to correlate the observed and estimated species richness and test statistical significance of the model based on geographically effective degrees of freedom. P-value corrected for spatial autocorrelation was referred to as P_{adj}. In addition, we determined whether spatial autocorrelation structure exists in the residuals of a regression using Moran's I (Legendre and Legendre 1998). Spatial analyses were conducted using SAM (Rangel et al. 2006).

Results

Species richness varies greatly among the study localities (from 1 to 56 for amphibians, 2 to 88 for reptiles). Species richness was strongly correlated between amphibians and reptiles ($r = 0.834$ for raw species richness, $r = 0.825$ for log-transformed species richness). Environmental variables also vary strikingly among the study localities (Table S1 in Appendix). For example, mean annual temperature varies from −7.4 to 24.9°C

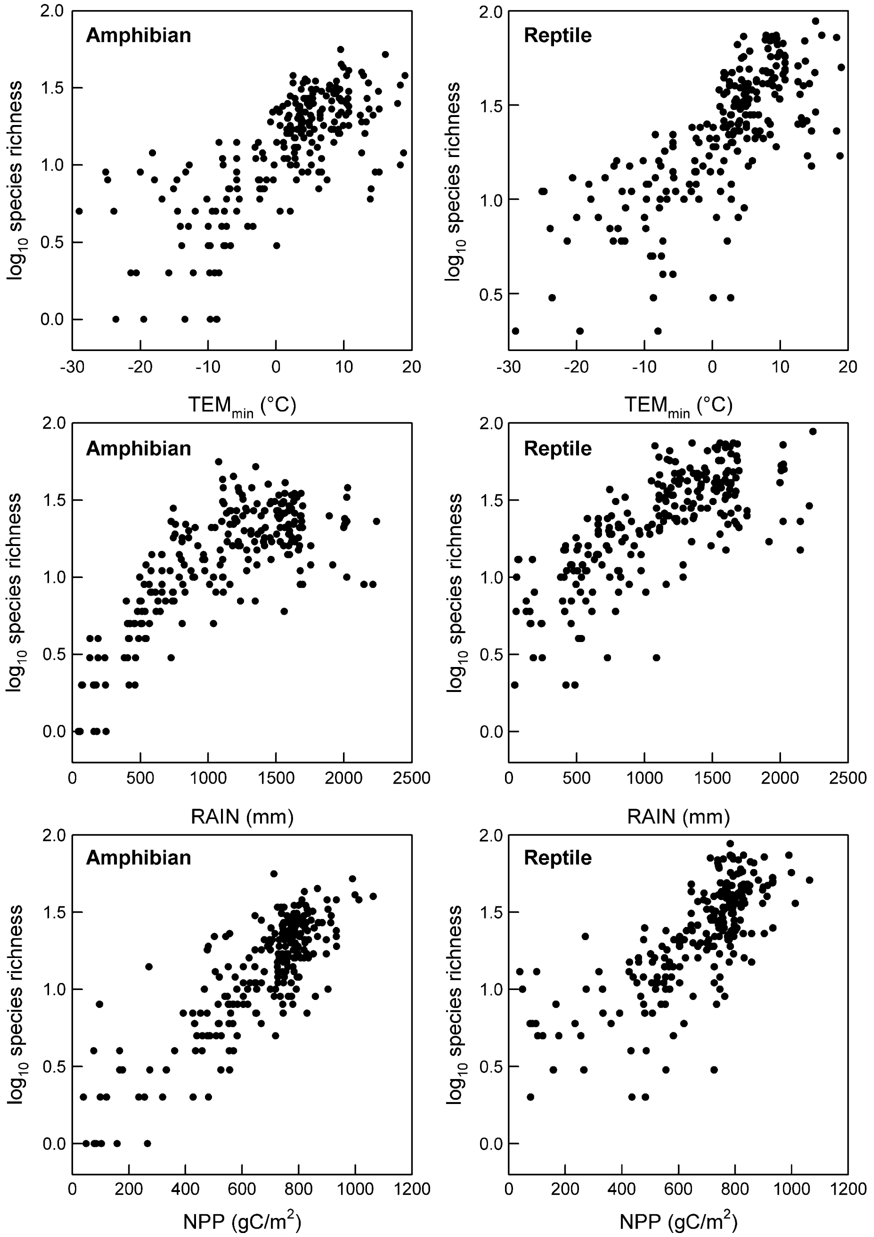

Fig. 2. Relationships between species richness of amphibians and reptiles and mean temperature of the coldest month (TEM_{min}), summer rain (RAIN), and net primary productivity (NPP).

and annual precipitation from 57 to 2240 mm. Environmental variables were correlated with each other to varying degrees (Table S2 in Appendix).

Most of the environmental variables examined were moderately to strongly correlated with herpetofaunal species richness, and the pattern of strong or weak correlations between species richness and environmental variables was generally identical for amphibians and reptiles, irrespective of the approach of calculating correlation coefficient (Table 1). For example, for both amphibians and reptiles, species richness was most closely correlated with TEM_{min} ($r_{partial} = 0.709$ for amphibians, 0.732 for reptiles) among the temperature variables, with RAIN (0.717, 0.720) among the precipitation variables, with AET (0.783, 0.753) among the evapotranspiration variables, with NPP (0.789, 0.731) among the productivity variables, and with $ELEV_{min}$ (-0.468, -0.583) among the physiographical variables.

The model with the lowest AIC included TEM_{min}, RAIN, $RAIN^2$, NPP, $LOGELEV_{var}$, $ELEV_{min}$,

$LOGELEV_{var} \times TEM_{min}$, $LOGELEV_{var} \times RAIN$, and LOGAREA for amphibians (adjusted $r^2 = 0.810$, AIC $= -871$), and TEM_{min}, RAIN, $RAIN^2$, NPP, $LOGELEV_{var}$, $ELEV_{min}$, $LOGELEV_{var} \times TEM_{min}$, and LOGAREA for reptiles (adjusted $r^2 = 0.716$, AIC $= -780$). However, because these models explained $< 1.5\%$ additional variation in species richness, compared to the model without the interaction terms (Table 2, Table S2 in Appendix) and because it is more straightforward to partition the variance explained of a model among its independent variables without interaction terms, we considered the model without interaction terms equivalent to the best fit model. The best possible models for both amphibians and reptiles explained approximately 70% of the variance in species richness after accounting for locality area effect (Table 2), indicating that the models have strong explanatory power. The Moran's I was close to zero even at the shortest distance for the residuals of both regression models (Fig. 3), indicating that the residuals do not have a distinguishable spatial structure due to spatial autocorrelation.

For amphibians, the two variables reflecting water availability (RAIN and $RAIN^2$) together explained 55.5% of the variance in amphibian species richness, and TEM_{min} explained only 1% additional variance (Table 2). In contrast, for reptiles, RAIN and $RAIN^2$ together explained only ca 2% of the variance in species richness, and TEM_{min} explained 18.3% of the variance in species richness. NPP explained 6.8% and 1.4% additional variance in species richness, respectively, for amphibians and reptiles. $ELEV_{min}$ explained much more variance (30.6%) in reptile species richness than did the other variables included in the model, and $LOGELEV_{var}$ explained another 17.2% of the variance in reptile species richness (Table 2). In contrast, these elevation variables together explained only 12.3% of the variance in amphibian species richness (Table 2).

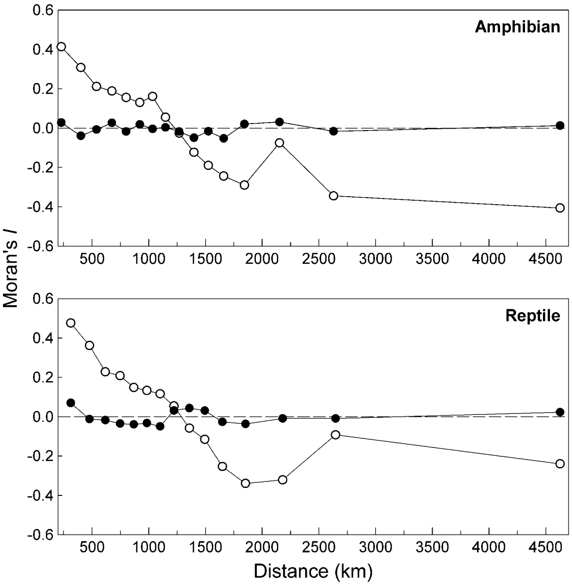

Fig. 3. Correlograms for the dependent variables (open circles) and residuals (solid circles) of the species richness-environment models reported in Table 2 for amphibians and reptiles in China.

Discussion

Few studies have examined the species richness–environment relationships for the entire groups of amphibians and reptiles. Most of the few studies each included only a small number of environmental variables, and the selection of environmental variables to include in a study has been largely based on the choice of authors. Because the choice of variables to include in analyses can influence conclusions (Montoya et al. 2007), this may explain in part why inconsistent conclusions are sometimes reported in different studies for the same taxa in the same or different regions. To our knowledge, the present study is the first attempt to examine and report the relationships of amphibian and reptile species richness with nearly all major environmental factors that are thought to influence broad-scale species richness patterns. The inclusion of a wide array of environmental variables in this study has allowed us to be able to identify a set of environmental variables best determining large-scale species richness patterns for amphibians and reptiles in China.

Table 2. Regression models for amphibians (adjusted $r^2 = 0.796$, AIC $= -855$, $P_{adj} < 0.001$) and reptiles (adjusted $r^2 = 0.712$, AIC $= -778$, $P_{adj} < 0.001$) in China. Variable abbreviations are the same as in Table 1.

Variable	Amphibian		Reptile	
	Standard coefficient	Partial r^2	Standard coefficient	Partial r^2
TEM_{min}	0.071	0.009	0.374	0.183
RAIN	1.612	0.275	0.362	0.014
$RAIN^2$	−1.128	0.230	−0.167	0.005
NPP	0.260	0.068	0.130	0.014
$LOGELEV_{var}$	0.157	0.108	0.218	0.172
$ELEV_{min}$	−0.061	0.015	−0.327	0.306
LOGAREA	0.143	0.090	0.076	0.023

The present study identifies several important environmental factors that strongly influence amphibian and reptile species richness but have rarely been considered in previous studies. For example, minimum elevation explains 30.6% of the variance in species richness in the best possible model for reptiles in China, but this variable was not included in most previous studies on reptile species richness (Rodríguez et al. 2005, Zhao et al. 2006). It is possible that minimum elevation influences species richness through its regulation of temperature in mountains: increasing elevation results in a decrease in temperature. Our study demonstrated that minimum elevation influences reptile species richness much more strongly than topographic relief. For a given range of elevations, habitat diversity can differ substantially if the elevation range starts at a different base elevation. Thus, the influences of both minimum elevation and elevation range on species richness should be taken into consideration in studies of broad-scale species richness gradients. Of the variables that have been considered as measures of primary productivity, NDVI and GVI have been most frequently used (Hawkins and Porter 2003, Ding et al. 2006, Evans et al. 2006). However, we found that NPP and EVI are better determinants of amphibian and reptile species richness than NDVI and GVI. Water deficit index (PET minus AET) has been used as a measure for water availability (Francis and Currie 2003, Montoya et al. 2007), but we found that the ratio of PET to AET, a moisture index that has been rarely used in broad-scale species richness studies (but see Whittaker et al. 2007), correlates with species richness more strongly than does the water deficit index. We suggest that future studies on species richness gradients include a wide variety of environmental variables so that more robust conclusions can be reached in each study, and species richness–environment relationships observed in different studies can be compared for the same taxa between different regions as well as for the same regions between different taxa.

Our final models included variables of temperature, water, and net primary productivity for both amphibians and reptiles. Because net primary productivity is in turn determined by temperature and water (Buckley and Jetz 2007), we conclude that geographical variation in species richness of amphibians and reptiles in China is largely driven by the balance between water and energy. This is consistent with the result of Hawkins et al.'s (2003) meta-analysis, showing that water, energy, and their interaction provide a strong explanation for global plant and animal species richness gradients. Other authors (H-Acevedo and Currie 2003, Buckley and Jetz 2007, Whittaker et al. 2007) also found that temperature, precipitation, and their interaction are important variables to explain species richness gradients. Our models demonstrate that water variables are more important to amphibian species richness whereas energy variables tend to be more important to reptile species richness. The two water terms of the model for amphibians explained ca 50% of the variance. As discussed above, minimum elevation may be considered as a temperature-determining variable. In the best possible model for reptiles, minimum elevation and average temperature of the coldest month together explained nearly 50% of the variance in species richness. Our finding that water is more important to amphibian richness and temperature is more important to reptile richness is consistent with that of Currie (2001), who demonstrates that in North America amphibian species richness is more strongly and positively related to precipitation and reptile species richness increases monotonically with temperature. Our finding is also consistent with that of Rodríguez et al. (2005), who show that in Europe AET and productivity (both closely related to water availability) are the primary predictors of amphibian species richness whereas the primary predictors of reptile species richness are PET and mean annual temperature (both as measures of ambient energy). All these results are consistent with different physiological requirements of these two groups. Amphibians usually require water for reproduction (i.e. their eggs must be laid in water in order to survive), amphibian adults require environmental humidity/moisture plus cooler temperatures, and they are sensitive to desiccation in warm/dry environments. Thus, measures of water availability describe amphibian species richness gradients best. In contrast, reptiles are extreme solar ectotherms and thus measures of energy availability describe their species richness gradients best (Rodríguez et al. 2005).

O'Brien et al. (2000) suggest using annual rainfall as a water availability variable, as opposed to annual precipitation, whereas Francis and Currie (2003) recommend using annual precipitation. Our study showed that annual rainfall explained nearly as much variation in the species richness of amphibians and reptiles as did annual precipitation (Table S3 in Appendix), suggesting that these two variables can be used interchangeably. In our study, the relationship between reptile species richness and precipitation variables is moderately strong. Soares and Brito (2006) also find that precipitation is a factor influencing the species richness of reptiles. However, these findings are contradictory to those of Rodríguez et al. (2005), who found that there is no relationship ($r^2 = 0.007$) between reptile species richness and annual precipitation in Europe, and contradictory to those of Whittaker et al. (2007), who find that reptile species richness is negatively related with water availability in Europe. Interestingly, the study area of Rodríguez et al. and Whittaker et al. is the same (i.e. Europe) but their results for reptiles are inconsistent. Given that positive correlations between precipitation and reptile species richness are found elsewhere (Currie 1991 for North America, this study for eastern Asia) and that reptile species richness is usually moderately to strongly correlated with the species richness of amphibians, birds, and mammals (Warman et al. 2004, Lamoreux et al. 2006, Qian 2007), all of which are positively correlated with precipitation (Andrews and O'Brien et al. 2000, Patten 2004), it is not clear why reptile species richness was found to be negatively correlated with water availability in Europe as shown in Whittaker et al. (2007).

Plant productivity indices (e.g. NPP, EVI, and NDVI) are correlated more strongly with amphibian species richness than with reptile species richness, a pattern consistent with that found for reptiles and amphibians in Europe (Rodríguez et al. 2005). In their global examination of the relationship between amphibian species richness and environmental variables, Buckley and Jetz (2007) found that minimum NPP is a better predictor for the Palearctic realm than the water–temperature balance. In our best fit model for amphibians, temperature and water variables together explain 7.5 times as much variance in species richness as does NPP, a finding inconsistent with that of Buckley and Jetz. Because amphibians are nearly exclusively predators as adults (Rodríguez et al. 2005), it is not clear why plant productivity is moderately to strongly correlated with amphibian species richness. Amphibian species richness may be linked to plant productivity as it controls the amount of biomass that can be supported in higher trophic levels. The productivity hypothesis is one of the two versions of species–energy hypothesis (energy measured by solar energy metrics in one version and measured by productive energy metrics in the other; Hawkins et al. 2003, Evans et al. 2005). It is also possible that the relationship between plant productivity and amphibian species richness is associated with habitat characteristics such as plant cover and resource types rather than predator–prey relationships (Rodríguez et al. 2005). The resource–speciation hypothesis suggests that the number of resource types that can support specialist species increases with increasing productivity (Abrams 1995, Srivastava and Lawton 1998, Hurlbert 2004).

Species richness is frequently related to annual temperature (Currie 1991, Francis and Currie 2003, Evans et al. 2006), and strong correlations between them are often considered as support for energy–richness hypothesis (Wright 1983, Currie 1991, Francis and Currie 2003), which proposes that species richness is determined by food availability (Wright 1983, Hawkins et al. 2003). However, our data showed that species richness of both amphibians and reptiles is correlated with mean temperature of the coldest month more strongly than with mean annual temperature. This finding may suggest that the richness–temperature gradient is driven more by the degree of physiological tolerance to cold temperature than by the degree of available energy for food production. Because the degree of species tolerance to cold temperature has resulted from historical and evolutionary processes (Latham and Ricklefs 1993), explanations for the cause of species richness–temperature gradients should involve historical processes.

Recently, Zhao et al. (2006) examined the relationship between species richness and environmental variables for terrestrial vertebrates (including amphibians and reptiles) in nature reserves in China. Although they reported that 211 nature reserves were used in their study, because some reserves did not have species richness data for amphibians or reptiles, the actual number of the reserves used for each of these two groups was fewer than what they reported – they used 187 localities for amphibians and 183 localities for reptiles (S. Zhao pers. comm.). Although the region of their study and our study is the same (i.e. China), these two studies differed in a number of ways. First, localities were restricted to only nature reserves in Zhao et al. (2006); as a result, many localities that have been well surveyed for amphibian and reptile compositions (e.g. Ermeishan in Sichuan Province, Taishan in Shandong Province) were excluded from their study. Second, in their study, some localities 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 it is well known that organisms in terrestrial and aquatic systems respond to regional climates quite differently and thus including localities from both terrestrial and aquatic ecosystems in a single analysis will obscure the results of the analysis. Second, our study included many more terrestrial localities than did their study (243 vs 187 for amphibians, 234 vs 183 for reptiles) even though their localities included aquatic systems as discussed above. Third, we related species richness of amphibians and reptiles to many more environmental variables than they did. Some richness–environment relationships found in their study are not only inconsistent with those of our study but also inconsistent with those reported in many other studies. For example, of the 56.5% of the explained variance in reptile species richness of their data, 54.3% was attributed to annual precipitation and only 2.2% was attributed to mean annual temperature. This finding contradicts those of our study as well as other studies (Currie 1991, Rodríguez et al. 2005, Whittaker et al. 2007) showing that reptile species richness is influenced more by ambient energy-related factors such as annual temperature and potential evapotranspiration than by water-related factors such as annual precipitation. Some findings of Zhao et al. (2006) for other taxa also contradict those of previous studies. For example, environmental variables usually explain over 60% of the variation in bird species richness (H-Acevedo and Currie 2003, Evans et al. 2006) and, in particular, explain over 70% of the variation in bird species richness in East Asia (Ding et al. 2006), of which China is a major part, but environmental variables only explain ca 12% of the variation in bird species richness in Zhao et al. (2006), after accounting for sample area effect. Although we don't know exactly why their findings are inconsistent with or even contradictory to those of ours and other studies, we suspect that the following may be part of the cause. First, as Qian (2007) pointed out, the inclusion of both land-dominated and water-dominated localities in a single analysis would likely have obscured their results. Second, unlike many other studies (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. (2006) used raw species richness to relate environmental variables (climate and NPP). Their bivariate plots of species richness and environmental variables clearly show a wider variation in species richness towards larger values of environmental variables, suggesting that data transformation would be necessary. The use of raw data in their analyses may have led to poorer correlations and model fit. Third, data for some localities used in their study were severely outdated. For example, in their dataset, Mabiandafengding had 7 amphibian species and 10 reptile species, and Taibaishan had 9 amphibian species and 14 reptile species (S. Zhao pers. comm.). However, according to Ma et al. (2006) and Sun et al. (2006), which were used in our study, the former had 13 and 14 species of amphibians and reptiles and the latter had 11 and 19 species of amphibians and reptiles, respectively.

In summary, we demonstrate that the species richness of amphibians and reptiles is strongly and positively associated with environmental factors representing energy (e.g. temperature, actual evapotranspiration, potential evapotranspiration), water (e.g. precipitation), and productivity. These findings are consistent with the predictions of species–energy, energy–water dynamics, and species–productivity hypotheses. In particular, the most important determinants include average temperature of the coldest month, annual rainfall, net primary productivity, range in elevation, and, for reptiles, minimum elevation. Although precipitation and temperature are important to both amphibians and reptiles, precipitation is associated with amphibian species richness more strongly whereas temperature tends to be more important to reptiles, which is consistent with different physiological requirements of the two taxa. The analyses and examinations of species richness gradients in relation to a wide range of environmental variables are the first steps to assessing negative environmental impacts on amphibians and reptiles from agricultural, industrial, and other activities that modify or degrade natural habitats.

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