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The relationships between terrestrial vertebrate species richness in China's nature reserves and environmental variables

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Abstract: Explaining species richness patterns over broad geographic scales is a central issue of biogeography and macroecology. In this study, we took spatial autocorrelation into account and used terrestrial vertebrate species richness data from 211 nature reserves, together with climatic and topographical variables and reserve area, to explain terrestrial vertebrate species richness patterns in China and to test two climatically based hypotheses for animals. Our results demonstrated that species richness patterns of different terrestrial vertebrate taxa were predicted by the environmental variables used, in a decreasing order, as reptiles (56.5%), followed by amphibians (51.8%), mammals (42%), and birds (19%). The endothermic vertebrates (mammals and birds) were closely correlated with net primary productivity (NPP), which supports the productivity hypothesis, whereas the ectothermic vertebrates (amphibians and reptiles) were strongly associated with both water and energy variables but weakly with NPP, which supports the physiologically based ambient climate hypothesis. The differences in the dependence of endothermic and ectothermic vertebrates on productivity or ambient climate may be due in part to their different thermoregulatory mechanisms. Consistent with earlier studies, mammals were strongly and positively related to geomorphologic heterogeneity, measured by elevation range, implying that the protection of mountains may be especially important in conserving mammalian diversity.

Résumé : L'explication des patrons de richesse spécifique sur de grandes échelles géographiques est l'un des objectifs principaux de la biogéographie et de la macroécologie. Dans notre étude, nous avons utilisé l'autocorrélation spatiale et étudié les données de richesse spécifique des vertébrés terrestres de 211 réserves fauniques réparties dans toute la Chine, ainsi que les variables topographiques et climatiques et les surfaces des réserves, pour expliquer les patrons de richesse spécifique des vertébrés terrestres et pour tester deux hypothèses basée sur le climat applicable aux animaux. Nos résultats démontrent que les patrons de richesse spécifique pour les différents taxons de vertébrés terrestres peuvent être prédits à partir des variables environnementales utilisées, avec le plus de succès chez les reptiles (56,5 %), puis chez les amphibiens (51,8 %), les mammifères (42 %) et les oiseaux (19 %). Il existe une forte corrélation entre les vertébrés endothermes (mammifères et oiseaux) et la productivité primaire nette (NPP), ce qui est compatible avec l'hypothèse de la productivité; au contraire, les vertébrés ectothermes (amphibiens et reptiles) sont fortement associés au variables reliées à l'eau et à l'énergie, mais peu avec la NPP, ce qui appuie l'hypothèse du climat ambiant avec base physiologique. Les différences de dépendance des vertébrés endothermes et ectothermes vis-à-vis de la productivité ou du climat ambiant peuvent être dues en partie à leurs mécanismes de thermorégulation différents. En accord avec les études antérieures, nous observons une forte relation positive des mammifères avec l'hétérogénéité géomorphologique, mesurée par l'étendue de l'altitude; cela laisse croire que la protection des montagnes est d'importance particulière pour la conservation de la diversité des mammifères.

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Introduction

Many hypotheses have been proposed to explain the mechanisms driving broad-scale species richness patterns (Pianka 1966; Huston 1979; Wright 1983; Rosenzweig 1995; Colwell and Lees 2000; Gaston 2000). However, most of the explanations are not mutually exclusive, and the climatically based energy hypothesis has received a great deal of support (e.g., Wright et al. 1993; Hawkins et al. 2003). It is widely accepted that both water and energy availability constrain plant diversity (Stephenson 1990; O'Brien 1993; Francis and Currie 2003), but the situation appears to be more complicated for animals. There are two major climatically based hypotheses that are related to patterns of animal diversity. The trophically based productivity hypothesis posits that solar energy is captured and converted into organic matter by plant photosynthesis and becomes available to other organisms via food webs (Connell and Orias 1964; Wright 1983; Huston 1994; Mittelbach et al. 2001), thus the effect of climate on animal diversity is indirect through plant productivity. The physiologically based ambient climate hypothesis proposes crude atmospheric climate, such as ambient energy, rather than assimilated energy directly influences animal diversity (Schall and Pianka 1978; Turner et al. 1987, 1988; Currie 1991). Additionally, many studies have demonstrated that geomorphologic heterogeneity, such as elevation range, accounts for some of the spatial variation in animal diversity (Fraser 1998; Rahbek and Graves 2001).

In this study, we took spatial autocorrelation into account and used terrestrial vertebrate species richness data from 211 nature reserves, together with climatic and topographical variables, to evaluate the contributions of two climatically based hypotheses and of geomorphologic heterogeneity in explaining species richness patterns of Chinese mammals, birds, amphibians, and reptiles. The objectives of this study were to answer the following two questions: (1) is the species richness pattern of terrestrial vertebrate taxa in China best explained by the climatic factors addressed by the productivity hypothesis or by the ambient climate hypothesis and (2) does the pattern vary among different terrestrial vertebrate taxa.

Materials and methods

Data collection

The 211 nature reserves in this study covered a total area of 905 000 km², thus occupying about 9.4% of the country's area, with a latitudinal range of 18°29′–51°37′N and a longitudinal range of 80°17′E–133°41′E (Fig. 1). Terrestrial vertebrate richness data were obtained for each of the 211 nature reserves in this study from two books (Liu 1996; Wang 2003) and from published and unpublished scientific surveys on the nature reserves that were carried out by professional zoologists who were asked to collect data with a special focus on obtaining complete species lists (for details see the list of citations provided as supplementary data).[3] These data included the number of mammal, bird, amphibian, and reptile species. There seems to be several possible sources of errors in these richness data. For example, species richness in the reserves may be underestimated owing to inadequate sampling effort or recently occurring extinction. On the other hand, species richness may be overestimated if some species have been recently introduced into the reserves. We used the largest value of species richness for each reserve and excluded introduced species from the data analyses to minimize the effects of the possible sources of errors. Note that the bird species richness is the total list of observed species, including the breeding, wintering, and resident taxa, which may bias the results explaining bird richness pattern. We kept the bird information based on the total observed list to ensure the integrality of the terrestrial vertebrate taxa. Reserve area, geographical range, minimum elevation, and maximum elevation were also recorded in these data sources. Elevation range (maximum elevation minus minimum elevation) was used as a measure of geomorphologic heterogeneity.

Climate data, assigned to each reserve based on its location, were used to analyze the relationship between climate and species richness. These data at a 0.1° × 0.1° resolution were compiled from a 1961 to a 1999 temperature/precipitation database of China, generated from 680 climatic stations across the country (Fig. 1; see also Fang et al. 2001; Piao et al. 2003). Climatic factors used in this study included ambient climate hypothesis associated variables (mean annual temperature, annual precipitation, and annual potential evapotranspiration (PET)) and productivity hypothesis related variables (annual actual evapotranspiration (AET) and annual net primary productivity (NPP)). PET and AET were estimated using Thornthwaite's method (Fang and Yoda 1990). NPP was generated from a study of China's primary vegetation production (Fang et al. 2003, Piao et al. 2005), which estimated NPP for all of China based on a satellite-based carbon cycle model called CASA (Carnegie–Ames–Stanford approach; Potter et al. 1993) and used normalized difference vegetation index (NDVI) time series data sets at a spatial resolution of 8 km × 8 km and at 15-day intervals.

Data analysis

We used SAM version 1.0 for statistical analysis (Rangel et al. 2005). Before analyses, we log-transformed reserve area and square-root-transformed elevation range to obtain an appropriate distribution for the data. Simple correlations of species richness to each independent environmental variable were carried out to understand the relationships between them (correlation matrix, see Table S1).[4] All environmental variables were tested for nonlinear relationships with species richness of all terrestrial vertebrate taxa using second-order polynomial models and no significant nonlinearities were

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[3] Supplementary data are available on the journal Web site (http://cjz.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5092. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

[4] Table S1 is available on the journal Web site (http://cjz.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5092. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

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Fig. 1. Locations of the 211 nature reserves and the climate stations used in the study. The background map shows the physiognomy of China in an Albers equal-area conic projection.
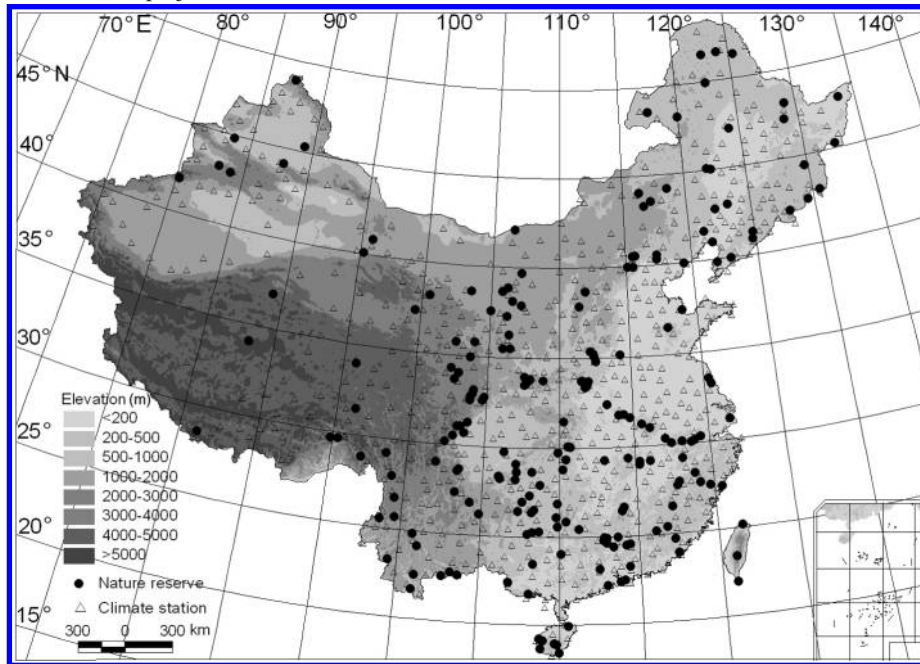
found. Therefore, the relationships of animal richness and environmental variables tended to be linear. Multiple regression analyses were conducted to generate predictive models that explain the variation in species richness of different terrestrial vertebrate taxa. Because of the strong collinearity among independent variables, we only incorporated environmental variables that improved the explanation of the variation by ≥2% into the predictive models.

Because of spatial autocorrelation in the data, the significance levels of the environmental variables with species richness in simple correlations and multiple regressions can be much higher than they should be (Lennon 2000). Hence, we used the modified t test developed by Dutilleul (1993) to compute the adjusted significance level (adjusted p value) to remove the effect of spatial autocorrelation on the significance of the correlations (see Table 1). We followed the method of Diniz-Filho et al. (2003) using Moran's I values to test the effect of spatial autocorrelation on the significance of the multiple regression models. We calculated Moran's I values of the raw species richness data and the residuals of the multiple regression models at 15 distance classes. If there is no detectable spatial autocorrelation in the residuals (Moran's I value is close to zero), then the species richness pattern can be safely explained by the predictive variables in the models. In contrast, significant remaining spatial autocorrelation among the residuals indicates that there is statistical bias in the overall regression analyses.

Results

Relationships of animal species richness to environmental variables used in the study

Most environmental variables appeared much more significant in the simple correlations than they should be because of spatial autocorrelation in the data (Table 1), so we de-

scribed the results of simple correlations based on unbiased estimates of the significance of correlations (adjusted p values). Among the climatic variables, species richness of mammals and birds was significantly related to only NPP (Table 1). Amphibians and reptiles were strongly and positively associated with all climatic variables: they were most strongly associated with annual precipitation and mean annual temperature and most weakly associated with NPP (Table 1). Mammalian species richness was strongly and positively correlated with geomorphologic heterogeneity, measured by elevation range ($r = 0.499$, adjusted $p < 0.0001$). Species richness of birds, amphibians, and reptiles was not significantly correlated with elevation range. Bird species richness was significantly and positively associated with reserve area ($r = 0.177$, adjusted $p = 0.027$), whereas mammals, amphibians, and reptiles had no significant relationship with reserve area (Table 1).

Predictors of Chinese terrestrial vertebrate richness patterns

The regression analyses showed that elevation range, NPP, annual precipitation, and reserve area accounted for 42% of the variation in mammal richness, of which elevation range was the most important predictor that explained 25.3% of the variation. NPP, reserve area, and annual AET explained 19% of the variation of bird richness, irrespective of elevation range. Annual precipitation was the primary determinant of species richness of amphibians and reptiles, accounting for 45.8% and 54.3% of the variation, respectively. In addition, elevation range and mean annual temperature were also the predictors of amphibian richness, explaining 6% of residual variation. As for reptiles, mean annual temperature accounted for an additional 2.2% of the variation (Table 2). The relationship between the species richness for different terrestrial vertebrate taxa and the primary explanatory variables in the regression models is shown in Fig. 2.

Table 1. Simple correlation coefficients (*r*) and significance levels (*p* and adjusted *p*) between species richness for different terrestrial vertebrate taxa and climatic variables, geomorphologic heterogeneity, and reserve area.

Variable	Mammal			Bird			Amphibian			Reptile		
	r	p	Adjusted p	r	p	Adjusted p	r	p	Adjusted p	r	p	Adjusted p
Annual precipitation	0.27	<0.0001	0.076	0.139	0.044	0.186	**0.634**	<0.0001	0.004	**0.689**	<0.0001	0.004
Mean annual temperature	0.17	0.013	0.244	0.098	0.157	0.291	**0.562**	<0.0001	0.008	**0.613**	<0.0001	0.006
Annual PET	0.068	0.322	0.637	0.068	0.326	0.49	**0.482**	<0.0001	0.025	**0.551**	<0.0001	0.017
Annual AET	0.164	0.017	0.276	0.185	0.007	0.06	**0.569**	<0.0001	0.009	**0.605**	<0.0001	0.01
Annual NPP	**0.426**	<0.0001	<0.0001	**0.275**	<0.0001	0.002	**0.413**	<0.0001	<0.0001	**0.348**	<0.0001	0.009
Elevation range (square root)	**0.499**	<0.0001	<0.0001	0.065	0.346	0.423	0.168	0.014	0.268	0.078	0.255	0.628
Reserve area (log scale)	0.099	0.152	0.37	**0.177**	0.001	0.027	-0.2	0.006	0.116	-0.289	<0.0001	0.057

Note: Adjusted *p* values were computed using the modified *t* test developed by Dutilleul (1993) to remove the effect of spatial autocorrelation in the data on the significance of the correlations. Values in boldfaced type are statistical significant. AET, actual evapotranspiration; NPP, net primary productivity; PET, potential evapotranspiration.

Species richness data for different terrestrial vertebrate taxa were spatially autocorrelated at 15 distance classes, and the spatial autocorrelations among mammals and birds were weaker than those among amphibians and reptiles (Fig. 3, solid symbols). Spatial autocorrelation in the residuals was almost removed from the species richness data of the four terrestrial vertebrate taxa after the addition of predictive variables in the models (Fig. 3, open symbols), suggesting that there was no statistical bias in the regression model for each terrestrial vertebrate taxa and that the species richness patterns could be safely explained by the predictive variables.

Discussion

Productivity or ambient climate hypothesis for Chinese terrestrial vertebrates
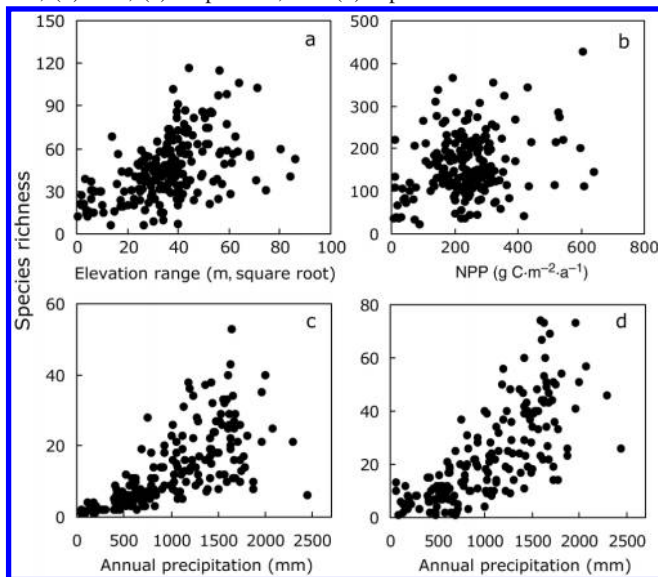
Earlier published studies have shown support for either the productivity hypothesis or the ambient climate hypothesis. For example, Turner et al. (1987, 1988) found that British butterfly and bird richness can best be predicted by temperature and hours of sunshine, but they did not include productivity-related variables in their analysis. Guegan et al. (1998) noted that NPP was a strong predictor of global riverine fish diversity, but they did not consider ambient climate effects. There have been several attempts to determine the impacts of these two hypotheses on species richness. Currie (1991) and Kerr et al. (1998) found all terrestrial vertebrate and lepidopteran species richness in North America to be more closely related to potential evapotranspiration (ambient energy) than to actual evapotranspiration (a surrogate of productivity). A large-scale study of reptile and amphibian species richness in Europe showed that amphibians were strongly associated with actual evapotranspiration, whereas reptiles were strongly associated with potential evapotranspiration; it concluded that ambient energy accounted for the reptile richness and that productivity-related water–energy balance best explained the amphibian richness (Rodriguez et al. 2005). It is apparent that animal richness patterns are dependent on geographic scale and on the taxonomic species being studied. When both productivity (NPP and its surrogate AET) and ambient climate related variables (PET, mean annual temperature, and annual precipitation) were included in the same model, the endothermic vertebrates (mammals and birds) were only correlated with NPP, while the ectothermic vertebrates (amphibians and reptiles) were strongly associated with both water and energy variables, but weakly with NPP. Our results also indicated that the relationships of both amphibians and reptiles to ambient energy variables (e.g., temperature and PET) were stronger than the relationship of both to NPP, but weaker than to commonly used NPP surrogates such as precipitation or AET. This result suggests that the relationships of vertebrates to surrogate measures of NPP must be interpreted cautiously when investigating animal-associated energy theory.

The differences in the dependence of endothermic and ectothermic vertebrates on productivity or ambient climate may be related to their different thermoregulatory metabolic requirements. The crude atmospheric climate is allocated to two pathways: "maintenance" and "productivity" (Brody 1945; Connell and Orias 1964). As ambient temperature de-

Table 2. Multiple regression models of environmental variables predicting species richness for different terrestrial vertebrate taxa.

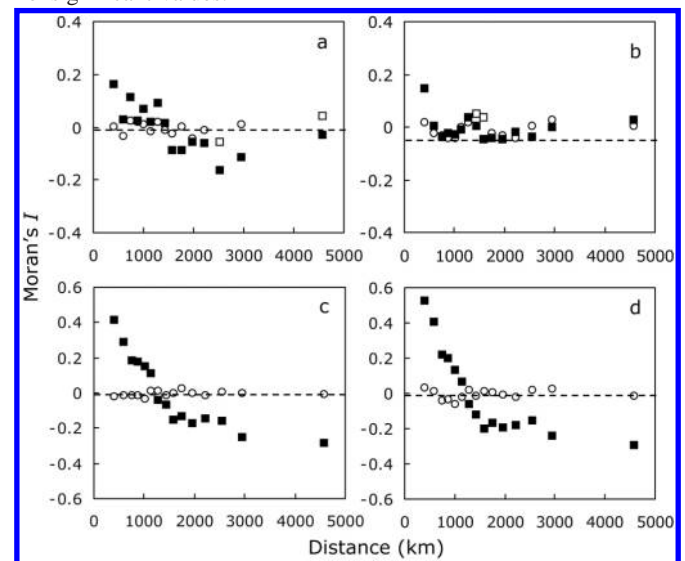| Variable	Standard coefficient	p	R^2	Adjusted R^2
Mammal	Overall $F = 37.9$, $P < 0.0001$, adjusted $R^2 = 42\%$			
Elevation range (square root)	0.413	<0.0001	0.257	0.253
Annual NPP	0.300	<0.0001	0.126	0.124
Annual precipitation	0.248	<0.0001	0.022	0.019
Reserve area (log scale)	0.196	0.003	0.026	0.024
Bird	Overall $F = 17.4$, $P < 0.0001$, adjusted $R^2 = 19\%$			
Annual NPP	0.263	<0.0001	0.076	0.071
Reserve area (log scale)	0.424	<0.0001	0.077	0.074
Annual AET	0.292	<0.0001	0.048	0.045
Amphibian	Overall $F = 67.6$, $P < 0.0001$, adjusted $R^2 = 51.8\%$			
Annual precipitation	0.518	<0.0001	0.461	0.458
Elevation range (square root)	0.208	<0.0001	0.042	0.039
Mean annual temperature	0.231	0.003	0.023	0.021
Reptile	Overall $F = 119.3$, $P < 0.0001$, adjusted $R^2 = 56.5\%$			
Annual precipitation	0.557	<0.0001	0.545	0.543
Mean annual temperature	0.241	0.001	0.025	0.022

Note: Because of the number of independent variables, the critical α value was adjusted to 0.007 by a Bonferroni correction; however, this adjusment had no influence on the selection of the final model. AET, actual evapotranspiration; NPP, net primary productivity.

Fig. 2. Relationships between species richness and primary explanatory variables in the regression models (see Table 2): (*a*) mammal, (*b*) bird, (*c*) amphibian, and (*d*) reptile.

Fig. 3. Correlograms for original species richness (solid) and residuals (open) of the regression models for different terrestrial vertebrate taxa (see Table 2): (*a*) mammal, (*b*) bird, (*c*) amphibian, and (*d*) reptile. Moran's *I* values were computed using 15 irregular distance class intervals with the similar number of connection pairs within each class. Squares indicate significant Moran's *I* values (after a Bonferroni correction for multiple tests) and circles indicate nonsignificant values.

creases, the endothermic vertebrates will consume 80%–90% of its productivity to maintain a constant body temperature (Bartholomew 1968), whereas the body temperature of ectothermic vertebrates will decrease independent of productivity (Bennett and Ruben 1979). Therefore, endothermic vertebrates will depend more on productivity, while ectothermic vertebrates will strongly relate to ambient climate.

Predictors of Chinese terrestrial vertebrate richness patterns

Our results suggested that the environmental variables we used predicted, in decreasing order, reptile richness, amphibian richness, mammal richness, and bird richness. Similar to the findings of Boone and Krohn (2000), the ectothermic vertebrate richness was more strongly correlated with climatic variables than endothermic vertebrate richness.

Climatic variables, especially water availability, accounted for most of the explained variation in the ectothermic ver-

tebrate richness. Geomorphologic heterogeneity, measured by elevation range, was only marginal important in explaining amphibian richness and was not a significant predictor of reptile richness. Birds did not covary with geomorphologic heterogeneity. However, we did find that broad-scale geomorphologic heterogeneity is the first important factor that explained the variance in mammal richness. The strong association between mammals and topographical variability was also observed in earlier studies (Simpson 1964; Kiester 1971; Owen 1990; Boone and Krohn 2000), suggesting that the protection offered by mountains may be especially important in conserving mammalian diversity. Reserve area was a significant predictor of bird richness, was only marginal important in predicting mammal richness, and had no effect on amiphibian and reptile richness. This finding indicates that the range of climatic variation and topography across China are likely sufficient to mask the area effect since the effects of area size are greater in homogenous environments.

We explained only a small proportion of the variation in birds (19%), indicating that some unknown variable not included in our study, such as plant diversity, may contribute to bird richness. Indeed, endothermic vertebrates likely depend on productivity-related variables (Zhao et al. 2006). The fact that the environmental variables we examined cannot sufficiently explain the bird richness pattern may also be related to our inability to differentiate migratory and resident bird species according to the size of their geographic ranges. Data to support this assumption are limited and further studies are needed.

In summary, species richness of different terrestrial vertebrate taxa in China's nature reserves were predicted by the environmental variables used in our study, in a decreasing order, as reptiles (56.5%), amphibians (51.8%), mammals (42%), and birds (19%). The effect of climate on ectothermic vertebrates (amphibians and reptiles) was more likely to be direct through ambient water and energy variables, whereas the effect of climate on endothermic vertebrates (mammals and birds) may be indirect through assimilated plant productivity.

Acknowledgments

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