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BIODIVERSITY RESEARCH

Relationships between species richness of vascular plants and terrestrial vertebrates in China: analyses based on data of nature reserves

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ABSTRACT

The relationship between plant diversity and animal diversity on a broadscale and its mechanisms are uncertain. In this study, we explored this relationship and its possible mechanisms using data from 186 nature reserves across China on species richness of vascular plants and terrestrial vertebrates, and climatic and topographical variables. We found significant positive correlations between species richness in almost all taxa of vascular plants and terrestrial vertebrates. Multiple regression analyses indicated that plant richness was a significant predictor of richness patterns for terrestrial vertebrates (except birds), suggesting that a causal association may exist between plant diversity and vertebrate diversity in China. The mechanisms for the relationships between species richness of plants and animals are probably dependent on vertebrate groups. For mammals (endothermic vertebrates), this relationship probably represents the integrated effects of plants on animals through trophic links (i.e. providing foods) and non-trophic interactions (i.e. supplying habitats), whereas for amphibians and reptiles (ectothermic vertebrates), this may be a result of the non-trophic links, such as the effects of plants on the resources that amphibians and reptiles require.

Keywords

China, ectothermic vertebrates, endothermic vertebrates, nature reserves, species richness, topographical variability, vascular plants.

INTRODUCTION

A greater variety of plants should lead to a greater variety of trophic levels higher up the food chain primarily through increasing the diversity of available resources that many consumers / animals utilize or require (Hutchinson, 1959; MacArthur, 1972; Tilman, 1986; Rosenzweig, 1995). Such an association is often observed and tested at local spatial scales (e.g. Murdoch *et al.*, 1972; Southwood *et al.*, 1979; Siemann, 1998; Siemann *et al.*, 1998). Given that regional richness accounts for a large proportion of variance in local richness (Ricklefs, 1987; Gaston, 2000), knowledge of the broadscale relationship between plant and animal diversity should be the core objective of an understanding of the general correlation between different trophic levels. However, little is known about the broadscale associations between plant and animal diversity, especially for the possible mechanisms of such relationships (Hawkins & Porter, 2003; Hawkins & Pausas, 2004).

Higher taxonomic groups are more likely to show general patterns of biodiversity than lower groups (Gaston, 2000). Therefore, vertebrates can be the appropriate taxon for exploring the relationship between plant diversity and animal diversity over broad geographical extents. There have been several attempts to relate plant diversity to vertebrate species richness. For example, a strongly positive relationship was observed between amphibian richness and tree richness across North America (Currie, 1991), and between woody plant and mammal diversity in southern Africa (Andrews & O'Brien, 2000). Boone and Krohn (2000a) found that woody plant species richness was an important source of variation in mammals, birds, amphibians and reptiles in Maine, USA. Because the relationship of plant to vertebrate diversity was not the primary focus of the above-mentioned studies, the authors did not further analyse the reason for the observed relationship. Only Hawkins and Pausas (2004) made such an effort by analysing the relationship between mammals and vascular plants in Catalonia; they concluded that plant richness has no influence on mammal richness.

In this study, we explored the relationship between plant and animal diversity and its possible mechanisms using species richness data of vascular plants and terrestrial vertebrates, coupled with corresponding climatic variables and topographical variability, compiled from 186 nature reserves across China. We grouped terrestrial vertebrates into mammals, birds, amphibians

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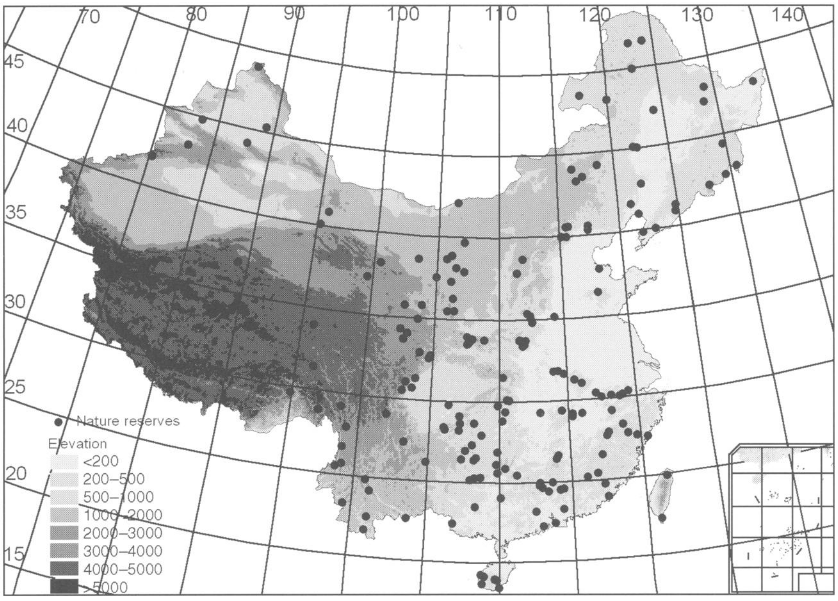

Figure 1 Location of the 186 nature reserves across China in this study. The background map shows the physiognomy of China, in Albers equal-area conic projection.

and reptiles because we found that the endothermic vertebrates (mammals and birds) were primarily determined by trophically based productivity, whereas ectothermic vertebrates (amphibians and reptiles) were strongly associated with both water and energy variables (S.Q. Zhao *et al.*, unpublished data).

METHODS

Diversity of vascular plants and vertebrates

Data on species richness of vascular plants and vertebrates were collected from 186 nature reserves covering a total area of 876,090 km^2, and occupying about 9.1% of China's territory. The reserves were located between the latitudes of 18°23′ and 51°37′ N and the longitudes of 80°17′ and 133°41′ E (Fig. 1). Species richness data were obtained from published and unpublished scientific surveys on the nature reserves (Appendix S1). Species richness was recorded for pteridophytes, gymnosperms, angiosperms, mammals, birds, amphibians and reptiles for these reserves.

Environmental variables

Climatic variables used in this study included mean annual temperature, annual precipitation, annual potential evapotranspiration (PET), annual actual evapotranspiration (AET) and annual net primary productivity (NPP). Climate data at 0.1° × 0.1° resolution were compiled from the 1961–99 temperature/precipitation database of China. These data were generated from 680 climatic stations across the country (Fang *et al.*, 2001; Piao *et al.*, 2003). PET and AET were estimated using Thornthwaite's method (Fang & Yoda, 1990). NPP was generated from a study on 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 using normalized difference vegetation index (NDVI) time series data sets at a spatial resolution of 8 × 8 km^2 and at 15-day intervals. Elevation range, as a measure of topographical variability, and the area of each reserve were also used for analysis, which were recorded in the data sources we collected.

Data analysis

We used SPSS version 10.0 for statistical analysis (Norusis, 2000). Table 1 summarizes the statistics of plant and animal species richness, reserve area, climatic variables and topographical variability. Correlation analyses between animal richness and plant richness, climatic variables and topographical variability were performed to identify the most significant variables associating with terrestrial vertebrates. Stepwise regression analyses were carried out to determine whether vascular plant richness would be a direct factor to be incorporated into the regression models to explain geographical variation in the richness of terrestrial vertebrates. Collinearity statistics (with a tolerance > 0.4 and a variance inflation factor (VIF) < 2.5) were calculated to exclude strong multicollinearity of independent variables. Specifically, only the independent variables satisfying the tolerance criterion were entered into the regression models, and an independent variable was excluded if it would cause the tolerance of another variable already in the model to drop below the tolerance criterion. To normalize the distributions of reserve area and topographical variability, we log$_{10}$-transformed them to eliminate biased data distribution (Table 1).

RESULTS

Relationship of animal richness to plant richness and other environmental variables

Bivariate correlation analyses indicated that mammals, amphibians and reptiles across China's nature reserves were strongly and

Table 1 Summary for statistics of plant and animal species richness, reserve area, climatic variables and topographical variability in the 186 nature reserves across China

Variable	Minimum	Maximum	Mean	SD	Skewness	Kurtosis
Species richness						
Pteridophytes	1	594	111.2	103.0	1.3	2.6
Gymnosperms	1	110	13.7	13.2	3.9	23.4
Angiosperms	79	3893	1142.5	762.8	0.8	0.6
Vascular plants	138	4543	1388.3	856.3	0.8	0.6
Mammals	6	117	46.3	21.9	0.8	0.6
Birds	23	427	155.5	69.4	0.7	0.9
Amphibians	1	53	13.9	10.6	1.0	0.4
Reptiles	1	74	23.8	17.7	0.8	−0.1
Location						
Mean latitude (°)	18.4	51.6	32.6	7.6	0.4	−0.6
Mean longitude (°)	80.3	133.7	110.3	9.4	−0.5	0.8
Area						
Reserve area (km^2)	4.8	318,000	4710.2	29,830.3	9.3	89.3
Climatic variables						
Annual precipitation (mm)	55.6	2295.1	984.2	546.2	0.1	−1.1
Mean annual temperature (°C)	−4.2	24.9	12.1	6.6	−0.3	−0.6
Annual PET (mm)	387.9	1396.3	777.7	207.0	0.6	0.2
Annual AET (mm)	55.7	1213.5	674.8	278.7	−0.3	−0.7
Annual NPP (Pg $C.a^{-1}$)	0	0.6	0.2	0.1	0.6	2.1
Topographical variability						
Elevation range (m)	3	7408	1517.5	1262.1	2.0	5.6

Table 2 Correlation coefficients and significance levels (*P* value) of animal richness to plant richness, reserve area, climatic variables and topographical variability in the 186 nature reserves across China

	Mammals		Birds		Amphibians		Reptiles	
Variable	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Pteridophytes	0.508	< 0.0001	0.198	0.02	0.596	< 0.0001	0.515	< 0.0001
Gymnosperms	0.356	< 0.0001	0.132	0.10	0.325	< 0.0001	0.224	0.01
Angiosperms	0.605	< 0.0001	0.322	< 0.0001	0.650	< 0.0001	0.557	< 0.0001
Vascular plants	0.540	< 0.0001	0.291	< 0.0001	0.576	< 0.0001	0.458	< 0.0001
Reserve area (log_{10} scale)	0.135	0.07	0.173	0.02	−0.196	0.01	−0.260	0.001
Annual precipitation	0.301	< 0.0001	0.159	0.03	0.716	< 0.0001	0.754	< 0.0001
Mean annual temperature	0.195	0.01	0.112	0.13	0.636	< 0.0001	0.669	< 0.0001
Annual PET	0.089	0.23	0.083	0.26	0.563	< 0.0001	0.610	< 0.0001
Annual AET	0.211	0.001	0.194	0.01	0.657	< 0.0001	0.673	< 0.0001
Annual NPP	0.423	< 0.0001	0.331	< 0.0001	0.495	< 0.0001	0.428	< 0.0001
Elevation range (log_{10} scale)	0.471	< 0.0001	0.024	0.75	0.223	0.001	0.118	0.14

positively correlated with species richness of pteridophytes, angiosperms and all vascular plants, and less strongly with gymnosperms. The richness of bird species was significantly and positively correlated with that of pteridophytes, angiosperms and all vascular plants, but was not significantly correlated with gymnosperm richness (Table 2). When tested independently, species richness of amphibians and reptiles was strongly and positively associated with all climatic variables, whereas that of mammals and birds was significantly related to only water-related climatic variables. Topographical variability was significantly correlated with diversity of mammals and amphibians, but had no significant relationship with that of birds and reptiles. The area of reserves was significantly associated with richness of birds, amphibians and reptiles. Most significantly, mammals were most strongly correlated with plant richness ($r = 0.605$, $P < 0.0001$), birds with annual NPP ($r = 0.331$, $P < 0.0001$), and amphibians and reptiles with annual precipitation ($r = 0.716$ and $r = 0.754$, $P < 0.0001$) (Table 2).

Table 3 Determinants of species richness of mammals, birds, amphibians and reptiles in China's nature reserves detected from multiple stepwise regression analyses when considering plant richness as one of the independent variables

Variable	Standard Coefficient	*P* Level	Adjusted R^2	Collinearity statistics	
				Tolerance	VIF
Mammals					
Vascular plants	0.328	< 0.0001	0.324	0.709	1.409
Mean annual NPP	0.354	< 0.0001	0.410	0.759	1.317
Area (log_{10} scale)	0.255	< 0.0001	0.485	0.942	1.062
Elevation range (log_{10} scale)	0.201	0.004	0.512	0.765	1.307
Birds					
Mean annual NPP	0.339	< 0.0001	0.080	0.797	1.255
Area (log_{10} scale)	0.463	< 0.0001	0.210	0.736	1.360
Annual AET	0.195	0.027	0.229	0.642	1.557
Amphibians					
Annual precipitation	0.400	< 0.0001	0.469	0.505	1.981
Vascular plants	0.359	< 0.0001	0.571	0.790	1.266
Mean annual temperature	0.189	0.013	0.589	0.574	1.742
Reptiles					
Annual precipitation	0.499	< 0.0001	0.542	0.455	2.196
Angiosperms	0.190	0.003	0.574	0.807	1.239
Mean annual temperature	0.221	0.009	0.595	0.479	2.089

The effect of plant richness on animal richness

To investigate the effect of plant richness on species richness of terrestrial vertebrates, we performed multiple stepwise regressions using plant richness and other environmental variables as independent variables and species richness of mammals, birds, amphibians and reptiles as dependent variables, respectively. The results showed that plant richness was a significant predictor of species richness of vertebrates (except birds) (Table 3), suggesting that richness of vascular plants influences that of vertebrates across China's nature reserves.

Vascular plant richness, NPP, reserve area and elevation range accounted for 51.2% of the variation in mammal richness, of which vascular plant richness was the most important predictor, explaining 32.4% of the variation. NPP, reserve area and annual AET explained 22.9% of the variation of bird richness, irrespective of plant richness. Annual precipitation, vascular plant richness and mean annual temperature were three determinants and explained 58.9% of the variation in amphibian richness. In reptile richness, 59.5% of the variation was predicted by three variables: annual precipitation, angiosperm plant richness and mean annual temperature (Table 3).

DISCUSSION

Our analysis indicated that plant richness drives vertebrate richness across China's nature reserves to some extent. The strength of the effect of plant richness on animal richness varied among different terrestrial vertebrate groups. Plant richness represented the primary determinant of mammal richness pattern, and was the second most important predictor of richness patterns for amphibians and reptiles (Table 3). This suggests that mammals (endothermic vertebrates) depend largely on plants more than amphibians and reptiles (ectothermic vertebrates) do.

When we included the plant richness as one of the independent variables, the environmental variables that explained the variation of vertebrate species richness changed. Table 4 shows the determinants for mammal, bird, amphibian and reptile species richness patterns without considering plant richness for the comparison. Elevation range was the most important factor affecting mammal richness. The most significant predictor of bird richness was NPP. Annual precipitation was the most important factor determining amphibian and reptile species richness. The total explanatory power (the coefficient of determination: accumulative adjusted R^2) of environmental factors for ectothermic vertebrate species richness was measurably higher than for endothermic richness. However, once the plant diversity was incorporated into the models, the most important variable determining the variation of mammal richness changed to vascular plant richness, and the total explanatory power was increased by 9.9%. On the other hand, including the plant diversity in the independent variables did not change the first predictor of amphibian and reptile species richness, and made no difference to their total explanation. More interestingly, once plant richness was entered into the regression models, elevation range had no significant effect on amphibian and reptile species richness (Tables 3 and 4), which probably implies that plant richness serves as a surrogate for topographical variability to indirectly influence amphibians and reptiles. Most amphibians and reptiles are carnivores (Pough *et al.*, 2004). Therefore, the effect of plant richness on ectothermic vertebrates, amphibians and reptiles is more likely indirect through non-trophic links, e.g. by affecting the resources that amphibians and reptiles require.

Table 4 Determinants of species richness of mammals, birds, amphibians and reptiles in China's nature reserves detected from multiple stepwise regression analyses without considering plant richness as one of the independent variables

Variable	Standard Coefficient	P Level	Adjusted R^2	Collinearity statistics	
				Tolerance	VIF
Mammals					
Elevation range ($\log_{10}$ scale)	0.342	< 0.0001	0.218	0.902	1.108
Mean annual NPP	0.333	< 0.0001	0.331	0.671	1.490
Area ($\log_{10}$ scale)	0.325	< 0.0001	0.372	0.707	1.415
Annual precipitation	0.265	< 0.0001	0.413	0.618	1.618
Birds					
Mean annual NPP	0.347	< 0.0001	0.105	0.710	1.408
Area ($\log_{10}$ scale)	0.443	< 0.0001	0.196	0.673	1.487
Annual AET	0.261	0.003	0.230	0.547	1.829
Amphibians					
Annual precipitation	0.564	< 0.0001	0.510	0.429	2.333
Elevation range ($\log_{10}$ scale)	0.170	0.001	0.547	0.944	1.060
Mean annual temperature	0.312	< 0.0001	0.571	0.410	2.439
Area ($\log_{10}$ scale)	0.188	0.002	0.593	0.692	1.444
Reptiles					
Annual precipitation	0.558	< 0.0001	0.567	0.440	2.270
Mean annual temperature	0.260	0.001	0.590	0.439	2.278
Elevation range ($\log_{10}$ scale)	0.125	0.013	0.603	0.988	1.012

Mammals feed on a great diversity of foods, including vertebrates, insects and plants. Plants are not only an important component of diets for most mammals, but also provide suitable habitats for their nesting and breeding, and serve as their shelters to avoid detection by predators (Feidhamer *et al.*, 1999). Thus, the primary dependence of mammals on plant richness may represent the integrated effects of plants on animals through trophic links (i.e. providing foods) and non-trophic interactions (i.e. supplying habitats).

Inconsistent with other vertebrates, plant richness was not a significant factor affecting the spatial variation of birds. Previous studies showed that bird diversity was related to structural characteristics of vegetation (MacArthur, 1964; Recher, 1969; Boone & Krohn, 2000b), but this was not addressed in the present study.

In conclusion, our results may suggest a causal association between plant diversity and vertebrate diversity in China's nature reserves. However, searching for the possible mechanisms of such relationships is complicated because we cannot disentangle the direct and indirect effects of plants on animals on a broadscale. In this study, we could not test the direct effects of plants on animals through the trophic interactions partly because we did not separate animals into carnivores and herbivores. Therefore, more refined studies are required to explore the mechanisms for the relationship of animal diversity to plant diversity on a broad scale.

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SUPPLEMENTARY MATERIAL

The following material is available to download from www.blackwell-synergy.com/loi/ddi.

Appendix S1 Literature list used to document data of plant and animal richness and other information of the reserves.