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RESEARCH PAPER

Patterns of fish species richness in China's lakes

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ABSTRACT

Aim To document the patterns of fish species richness and their possible causes in China's lakes at regional and national scales.

Location Lakes across China.

Methods We compiled data of fish species richness, limnological characteristics and climatic variables for 109 lakes across five regions of China: East region, Northeast region, Southwest region, North-Northwest region, and the Tibetan Plateau. Correlation analyses, regression models and a general linear model were used to explore the patterns of fish species richness.

Results At the national scale, lake altitude, energy availability (potential evapotranspiration, PET) and lake area explained 79.6% of the total variation of the lake fish species richness. The determinants of the fish richness pattern varied among physiographic regions. Lake area was the strongest predictor of fish species richness in the East and Southwest lakes, accounting for 22.2% and 82.9% of the variation, respectively. Annual PET explained 68.7% of the variation of fish richness in the Northeast lakes. Maximum depth, mineralization degree, and lake area explained 45.5% of the fish variation in the lakes of the North-Northwest region. On the Tibetan Plateau, lake altitude was the first predictor variable, interpreting 32.2% of the variation.

Main conclusions Lake altitude was the most important factor explaining the variation of fish species richness across China's lakes, and accounted for 74.5% of the variation. This may stem in part from the fact that the lakes investigated in our study span the largest altitudinal range anywhere in the world. The effects of the lake altitude on fish species richness can be separated into direct and indirect aspects due to its collinearity with PET. We also found that the fish diversity and its determinants were scale-dependent. Fish species richness was probably energy-determined in the cold region, while it was best predicted by the lake area in the relatively geologically old region. The independent variables we used only explained a small fraction of the variations in the lake fish species richness in East China and the Tibetan Plateau, which may be due to the effects of human activity and historical events, respectively.

Keywords

Altitude, aquatic ecosystems, biodiversity, China, climatic variables, energy availability, fish species richness, lakes, limnological characteristics.

INTRODUCTION

One of the oldest and most important patterns in ecology is the spatial variability in species richness over broad geographical extents (Hawkins, 2001). Much research effort in the past decades has documented the broad-scale spatial patterns of species richness and explored the mechanisms for such patterns (Gaston, 2000). Unfortunately, most efforts have been focused on terrestrial ecosystems (e.g. Currie & Paquin, 1987; Currie, 1991; O'Brien, 1993; Rahbek & Graves, 2001; Francis & Currie, 2003; Qian *et al*., 2005), and few on aquatic ecosystems (Barbour & Brown, 1974; Hugueny, 1989; Oberdorff *et al*., 1995, 1997,

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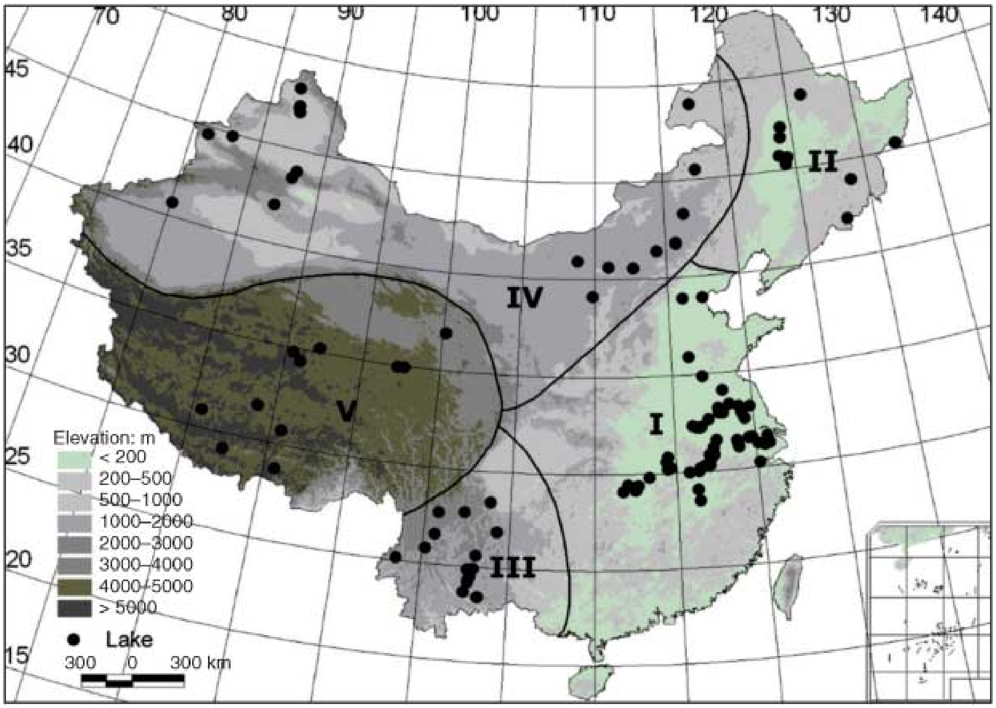

Figure 1 Location of 109 lakes across China in this study. Five physiographic regions: (I) Eastern region (II) Northeast region (III) Southwest region (IV) North-Northwest region, and (V) Tibetan Plateau, are shown, along with an altitudinal map of China in Albers equal-area conic projection.

1999; Guégan *et al.*, 1998; Rathert *et al.*, 1999; Amarasinghe & Welcomme, 2002; Irz *et al.*, 2004). Study of species diversity in aquatic ecosystems is as essential as in terrestrial ecosystems: about 12% of all animal species live in freshwater ecosystems (although they occupy < 1% of the earth's surface), and aquatic biodiversity is declining at an alarming rate due to human activities (Johnson *et al.*, 2001). Therefore, understanding the large-scale patterns of species richness in aquatic ecosystems is a major topic in the field of biogeography and macroecology. Lakes, as natural biogeographical islands, should be the ideal field for such studies.

China is rich in lakes. These lakes are widely distributed between 18° and 53° N latitude and 75° and 135° E longitude across a large climatic range from the tropical to subarctic/alpine and from rain forest to desert, and over a great altitudinal range from below sea level (–156 m high in the Turpan Desert, Northwest China) to the Qinghai–Tibet Plateau (Jin, 1995; Wang & Dou, 1998). Here, we explored the patterns of fish species richness and their possible causes in China's lakes at national and regional scales using fish species data and limnological and climatic variables compiled from 109 lakes.

MATERIALS AND METHODS

Data collection

The 109 lakes in this study cover a total area of 39,594 km^2, with a latitudinal range of 23°25′–48°55′ N and longitudinal range of 80°7.5′–132°35.5′ E (Fig. 1). Information on the fish species richness and limnological characteristics for each lake was obtained primarily from two monographs of China's lakes (Jin, 1995; Wang & Dou, 1998), which were compiled from long-term accumulation of research data on the lakes across China. There seem to be several possible sources of errors for these fish richness data. For example, fish species richness in the lakes may be underestimated due to inadequate sampling effort or recently occurring extinction. On the other hand, fish species richness may be overestimated if some species have been introduced into lakes recently. We used the largest value of fish species richness for each lake and excluded introduced species for data analyses to minimize the effects of the possible sources of errors. We also searched other published literature to broaden and adjust the data of fish species richness and limnological characteristics (see Appendix S1 in Supplementary Material). Limnological characteristics included lake area (km^2), maximum depth (m), mean depth (m), lake volume (10^8 m^3), mineralization degree (g l^{-1}) and lake altitude (m). Note that the mineralization degree (g l^{-1}) is a surrogate of lake salinity; lakes with mineralization degree ≤ 1 g l^{-1} are freshwater lakes, brackish lakes are those with 1 g l^{-1} < mineralization degree ≤ 50 g l^{-1}, and saline lakes are those with mineralization degree > 50 g l^{-1} (Wang & Dou, 1998). To explore biogeographical patterns of fish species richness, we estimated mean annual temperature, annual precipitation, potential evapotranspiration (PET), and actual evapotranspiration (AET) for each lake, based on the lakes' coordinates and a 1961–99 temperature/precipitation database of China at 0.1° × 0.1°

Table 1 Summary for statistics of fish richness, limnological characteristics, and climatic variables used in the study (n = 109). The variables marked with * were $\log_{10}$-transformed for subsequent analyses

Variables	Minimum	Maximum	Mean	SD	Skewness	Kurtosis
Species*						
Number of fish species	0	122	35.7	30.6	0.8	−0.2
Location						
Mean latitude (°)	23.4	48.9	34.3	6.9	0.6	−0.7
Mean longitude (°)	80.1	132.6	110.1	12.5	−0.8	−0.4
Limnological characteristics*						
Lake area (km^2)	0.3	4340	363.2	683.4	3.3	13.0
Maximum depth (m)	1.1	373	19.3	46.6	5.3	33.9
Mean depth (m)	0.4	204	10.5	25.8	5.3	33.5
Lake volume (10^8 m^3)	0	778	38.1	119.9	5.1	27.8
Mineralization degree (g l^{-1})	0	70	2.0	7.2	8.2	75.2
Lake altitude (m)	1.4	4854	932.8	1380.5	1.7	1.9
Climatic variables						
Annual precipitation (mm)	51.4	1642.3	813.6	441.0	−0.1	−1.3
Mean annual temperature (°C)	−6.1	19.5	10.8	6.6	−0.8	−0.7
Annual PET (mm)	328.5	1004.6	740.0	175.1	−0.8	−0.3
Annual AET (mm)	51.4	925.3	627.7	277.5	−0.6	−1.2

resolution compiled by Fang *et al.* (2001) and Piao *et al.* (2003). The calculation of PET and AET followed Thornthwaite's method (Fang & Yoda, 1990).

According to natural features (e.g. land formation and climate), and the distribution of flora and fauna of the regions in which the lakes are located (Editorial Committee for China's Physiography, 1985), we divided the 109 lakes into five regions: East region, Northeast region, Southwest region, North-Northwest region, and the Tibetan Plateau, to address possible differences in fish richness patterns by physiographic region.

Data analysis

We used SPSS version 10.0 for statistical analysis (Norusis, 2000). Table 1 summarizes the statistics of fish richness, limnological characteristics, and climatic variables in the 109 lakes. To normalize the distributions of limnological characteristics and species richness, we $\log_{10}$-transformed these variables. Correlation analyses between fish species richness, limnological characteristics, and climatic variables were performed to identify the variables related most closely to fish richness (for correlation matrix see Appendix S2 in Supplementary Material). We used second-order polynomial models to test for nonlinear relationships between environmental variables and fish species richness. We found that fish richness varied nonlinearly only with lake altitude and lake volume. All other relationships were linear. Stepwise regression analyses were conducted to generate predictive models explaining geographical variation in the fish species richness across the country and in different physiographic regions. Due to the strong collinearity among independent variables, we incorporated only environmental variables that can lead to an improvement of the explained variation by ≥ 2% into the predictive models. In addition, we used a general linear model to investigate whether the physiographic region exerts an effect on the fish species richness pattern, with region added as a categorical variable.

RESULTS

Relationship between fish species richness and limnological characteristics

Simple correlations indicated that fish species richness was related significantly to all limnological characteristics except lake area (Fig. 2). Fish species richness was correlated strongly and nonlinearly with lake altitude (Fig. 2a, $r^2 = 0.75$, $P < 0.0001$), related significantly and negatively to maximum depth (Fig. 2b, $r^2 = 0.34$, $P < 0.0001$) and mineralization degree (Fig. 2c, $r^2 = 0.26$, $P < 0.0001$), and correlated nonlinearly with lake volume (Fig. 2d, $r^2 = 0.23$, $P < 0.0001$). An unexpected finding was that lake area was not associated significantly with fish species richness of the lakes (Fig. 2e, $P = 0.13$).

Relationship between fish species richness and climatic variables

The correlation analysis showed that fish species richness was related significantly to all the climatic variables used in this study; it related strongly and positively with mean annual temperature (Fig. 3a, $r^2 = 0.43$, $P < 0.0001$), annual PET (Fig. 3b, $r^2 = 0.57$, $P < 0.0001$), annual AET (Fig. 3c, $r^2 = 0.53$, $P < 0.0001$), and annual precipitation (Fig. 3d, $r^2 = 0.40$, $P < 0.0001$). This is consistent with the findings from terrestrial ecosystems (e.g. O'Brien, 1993; Francis & Currie, 2003), where species diversity is often correlated with climatic factors.

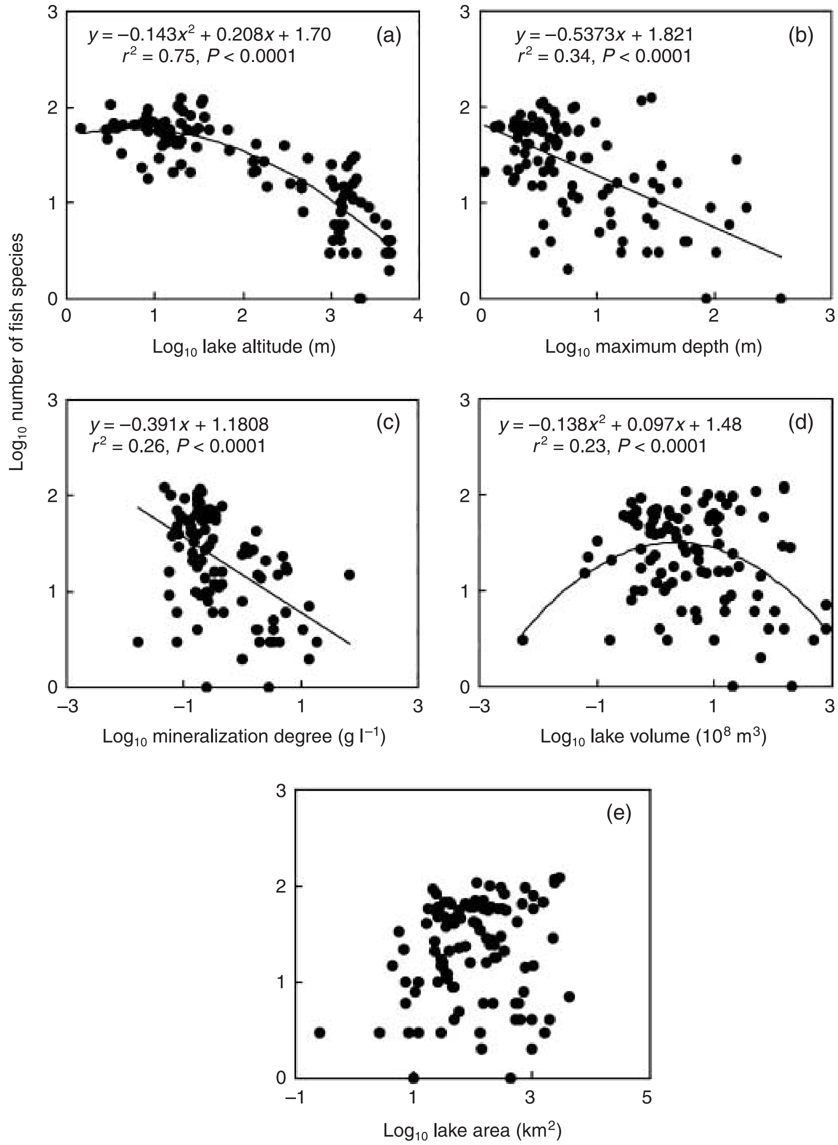

Figure 2 Relationships between fish richness and (a) lake altitude, (b) maximum depth, (c) mineralization degree, (d) lake volume, and (e) lake area across China's lakes.

Determinants affecting fish species richness at the national scale

We used five limnological attributes (lake area, water depth, lake volume, mineralization degree, and lake altitude), as well as the quadratic terms of lake altitude and lake volume, which had non-linear relationships with fish richness, and four climatic factors (mean annual temperature, annual precipitation, PET, and AET) as independent variables, and the number of fish species as a dependent variable to perform stepwise multiple regression to find the determinants affecting fish species richness in 109 lakes across China. The results showed that lake altitude was the most significant factor, and explained 74.5% of the variation of fish richness pattern. The next was energy availability (PET), which explained 2.6% of residual variation. Lake area was the third variable, explaining an additional 2.5% of the variation (Table 2).

Lake altitude is a composite variable, thus it is necessary to explore the direct and indirect effects of lake altitude on the fish species richness pattern. The indirect effect of lake altitude on fish species richness may result from the influence of other environmental variables associated with lake altitude. A correlation matrix (Appendix S2 in Supplementary Material) indicated that lake altitude was correlated strongly with maximum depth ($r = 0.646, P < 0.0001$) and PET ($r = -0.717, P < 0.0001$). Because the relationship between maximum depth and lake altitude was not causal but reflected their similar covariation with other environmental variables, such as the trophic status of the lakes (Wetzel, 2001), we considered only the indirect effect of lake altitude on fish species richness due to its collinearity with PET. We then followed the method of Legendre (1993) and Hawkins *et al.* (2003a) to perform multiple regressions using both lake altitude and PET, lake altitude only and PET only to partition the variation in fish species richness explained by lake altitude directly and indirectly (for details, see the caption of Fig. 4). The results suggested that the direct effect of lake altitude on fish species richness accounted for 20.9% of the variation, while

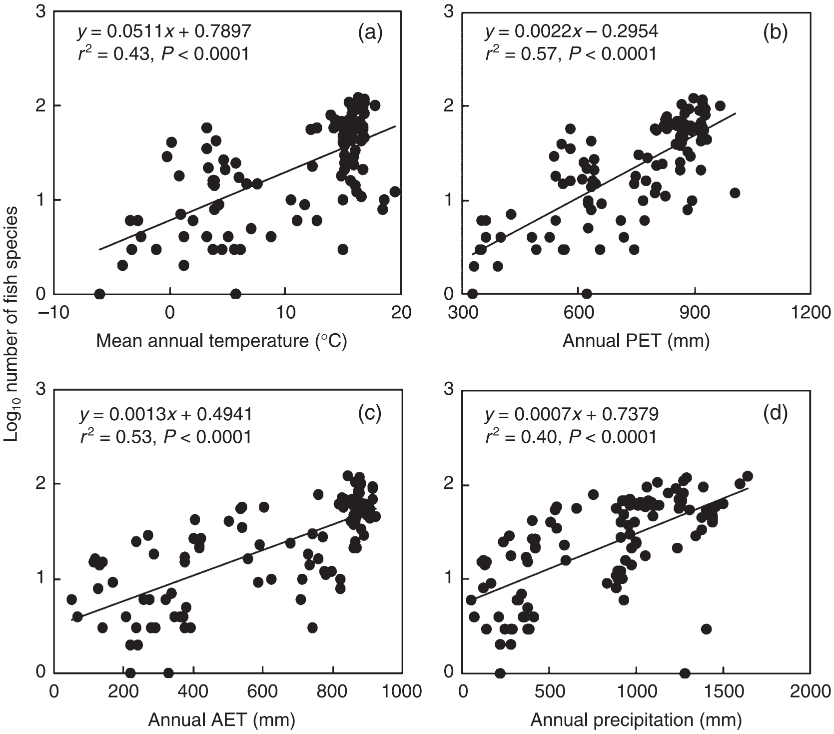

Figure 3 Relationships between fish richness and (a) mean annual temperature, (b) annual PET, (c) annual AET, and (d) annual precipitation across China's lakes.

Table 2 Determinants of lake fish richness at the national scale and in different physiographic regions and the explanatory power (R^2) detected from stepwise regressions

Variable	Coefficient	P	Adjusted R^2
National scale			
($\log_{10}$ lake altitude)^2	−0.07	< 0.0001	0.745
Annual PET	0.001	< 0.0001	0.771
Log_{10} lake area	0.116	< 0.0001	0.796
East region			
Log_{10} lake area	0.145	< 0.0001	0.222
Northeast region			
Annual PET	0.004	0.002	0.687
Southwest region			
Log_{10} lake area	0.313	< 0.0001	0.829
North-Northwest region			
Log_{10} maximum depth	−0.677	0.001	0.207
Log_{10} mineralization degree	−0.438	0.009	0.323
Log_{10} lake area	0.198	0.038	0.455
Tibetan Plateau			
($\log_{10}$ lake altitude)^2	−0.317	0.04	0.322

53.6% of the variation was explained by the indirect effect of lake altitude due to its collinearity with PET (Fig. 4).

To explore whether physiographic region has an effect on fish species richness, we performed an analysis of covariance in which physiographic region was included as a categorical variable, and lake altitude, annual PET and lake area were used as covariates. The result indicated that fish species richness varied significantly among physiographic regions after controlling for lake altitude, annual PET and lake area; region increased the explained variation by a small amount (~2%; see Table 3).

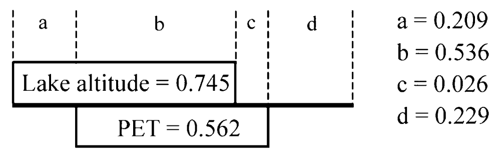

Figure 4 Partitioning the variation explained by lake altitude directly and indirectly according to the method of Legendre (1993) and Hawkins *et al.* (2003b). The unexplained variation (d) is $1 - R^2$ (coefficient of determination, 0.771) of a multiple regression model including both lake altitude and PET, which is equal to 1 – (a + b + c). The overlap between lake altitude and PET (b) represents the indirect effect of lake altitude on fish species richness due to its collinearity with PET. (a + b) is the R^2 of the regression using lake altitude, and (b + c) is the R^2 of the regression using PET. We can then obtain the variation explained directly by lake altitude (a).

Fish species richness and its determinants by physiographic region

We summarized fish species richness and environmental variables for lakes in each physiographic region (Table 4). The richest fish diversity occurred in the East region [averaged species richness, defined as number/$\log_{10}$ area, was 31 ± 11.5 (SD)], followed by the Northeast region (15.2 ± 9.2), Southwest region (7.6 ± 3.7) and North-Northwest region (5.4 ± 5.0). The lowest richness was on the Tibetan Plateau (1.2 ± 0.6).

Table 3 Analysis of differences in fish species richness among physiographic regions, when region is added as a categorical variable in a general linear model for the whole model, $F_{4,104} = 23.7$, $P < 0.0001$, Adjusted $R^2 = 0.815$

Effect	*P*	*F*	Type III sums of squares
$(\log_{10}$ lake altitude$)^2$	< 0.0001	21.139	1.037
Annual PET	0.04	3.624	0.178
Log_{10} lake area	< 0.0001	17.588	0.863
Physiographic region	0.007	3.730	0.732

In multiple regressions, the determinants of fish richness pattern varied among physiographic regions (Table 2). Lake area was the strongest predictor of fish richness in East and Southwest lakes, accounting for 22.2% and 82.9% of the variation, respectively. Annual PET explained 68.7% of variation in fish richness of the Northeast lakes. Maximum depth, mineralization degree, and lake area accounted for 45.5% of fish variation in the lakes of the North-Northwest region. On the Tibetan Plateau, lake altitude was the first predictor variable, interpreting 32.2% of the variation.

DISCUSSION

Fish richness pattern at the national scale

Our analyses indicated that lake altitude was the most important factor explaining the variation of fish species richness across lakes of China, accounting for 74.5% of the variation (Table 2). There have been several attempts to examine the fish species richness patterns in lakes over a broad scale (Table 5). Only in South American temperate lakes was lake altitude the primary predictor of fish richness pattern, explaining 45% of the variation (Amarasinghe & Welcomme, 2002). This may stem in part from the fact that the lakes investigated in most geographical areas did not span a broad altitudinal extent. The lake altitudes in our study ranged from 1.4 m to 4854 m (Table 1), which represents the largest altitudinal extent worldwide (Wang & Dou, 1998).

Among the total explanation of lake altitude for fish species richness pattern, the indirect effect due to its collinearity with PET amounted to 53.6%, and 20.9% of the effect was attributed to its direct effect (e.g. lake altitude may be a limiting factor for fish to colonize). PET *per se* was the second important predictor of fish species richness in the lakes across China. Thus, the data of China's lakes support the species richness–energy hypothesis (Wright, 1983), which claims that environments with higher available energy could support more species. This is generally consistent with previous studies documenting that energy availability accounts for most of the observed variations in terrestrial species richness patterns (Wright *et al.*, 1993; Hawkins *et al.*, 2003a) and global riverine fish diversity pattern (Guégan *et al.*, 1998).

Previous studies have demonstrated that broad scale patterns of fish species richness in lakes are predicted primarily by lake area (Table 5). In contrast, we found that lake area was not correlated

Table 4 Statistics of fish richness, limnological characteristics, and climatic variables for lakes in five physiographic regions of China

Variable	East region (n = 52)		Northeast region (n = 10)		Southwest region (n = 16)		North-Northwest region (n = 20)		Tibetan Plateau (n = 11)	
	Mean (range)	SD	Mean (range)	SD	Mean (range)	SD	Mean (range)	SD	Mean (range)	SD
Lake area (km^2)	325 (5.7–2933)	636.2	247.3 (7–1080)	342.4	69.9 (0.3–298)	93.9	385 (3–2339)	570	1039 (12.1–4340)	1258
Maximum depth (m)	4.5 (1.1–29.2)	4.8	45.9 (2–373)	115.8	37.8 (5–155)	47.3	25.5 (1.9–188.5)	47	31.9 (5.6–59)	19.7
Mineralization degree ($g\ l^{-1}$)	0.2 (0–1)	0.1	0.7 (0.1–2.6)	0.9	0.3 (0–1)	0.2	6.2 (0.1–70)	15.1	6 (0.2–18.5)	6.8
Lake altitude (m)	15 (1.4–41)	9.7	369 (69–2194)	647	1744 (1100–2691)	404	1030 (8–2072)	537	4428 (3196–4854)	458
Annual mean temperature (°C)	15.5 (12.2–17.7)	1.2	2.6 (−6.1 to 4.9)	3.3	15.4 (10.5–19.5)	2.4	4.9 (−0.2 to 11)	2.6	−0.3 (−4 to 5.6)	3.4
Annual precipitation (mm)	1153 (533–1642)	247	553 (403–1282)	265	957 (834–1403)	129	232 (51.4–386)	118	297 (213–408)	58.8
Annual PET (mm)	877 (796–967)	38.1	580 (329–643)	94	787 (624–1005)	91	618 (528–770)	68.2	390 (332–492)	55.6
Annual AET (mm)	854 (536–925)	75.1	454 (329–557)	76.1	737 (585–823)	65.2	232 (51.4–393)	119	279 (207–373)	53.5
Number of fish species (n)	61.1 (20–122)	23.8	27.9 (0–57)	15.8	12.8 (2–29)	7.7	9.8 (0–28)	7.9	3 (1–6)	1.7
Species density ($n/\log_{10}$ area)	31 (10.4–67.9)	11.5	15.2 (0–32)	9.2	7.6 (−3.3 to 12.2)	3.7	5.4 (0–21.4)	5	1.2 (0.3–1.8)	0.6

Table 5 Comparison of primary explanatory variables for fish species richness in the lakes of different geographical area. The coefficients of determination (r^2) refer to the explanatory power of the primary variable only. Abbreviation: A = lake area, Alt = lake altitude, Cond = conductivity (an estimate of mineralization degree of water), Lat = latitude, Medepth = mean depth, PET = potential evapotranspiration, SDD = secchi disc depth, and T = temperature. (–) indicates negative relationship between fish species richness and predictive variables

Geographic area	*n*	Primary variable	Other variables	r^2	Reference
Global	70	A	Lat (–)	0.31	Barbour & Brown (1974)
Africa	30	A	Alt (–)	0.65	Amarasinghe & Welcomme (2002)
US and Canada	315	A	Medepth, PH	0.44	Amarasinghe & Welcomme (2002)
Tropical Asia and America	20	A		0.71	Amarasinghe & Welcomme (2002)
Temperate Europe and Asia	25	A	Alt (–), Lat (–)	0.23	Amarasinghe & Welcomme (2002)
Temperate South America	67	Alt (–)	A, SDD (–), Cond (–), T	0.45	Amarasinghe & Welcomme (2002)
China	109	Alt (–)	PET, A	0.75	This study

significantly with fish species richness (Fig. 2e, $P = 0.13$). Although it became one of the predictors of fish species richness pattern in the multiple regression, lake area only explained an additional 2.5% of the variation (Table 2). This indicates that the range of climatic variation and altitudinal extent of the lakes across China is sufficient to overshadow the area effect.

Historical/regional influences are also the factors most often discussed as determinants of broad-scale species richness patterns (Ricklefs, 1987; McGlone, 1996; Ricklefs *et al.*, 2004). Our results showed that the physiographic region in which the lakes are located, a coarse proxy of historical/regional factor, was of only marginal importance in predicting the fish richness (the addition of the physiographic region only improved the predictive model R^2 by ~2%). Given that we did not have direct information on historical factors, such as glaciations and dispersal, more refined studies are required to explore the historical/regional influence on fish richness in Chinese lakes.

Fish richness pattern at the regional scale

The lakes in the East region are concentrated on the middle and lower reaches of the Yangtze River. Historically, most of these lakes were connected with the Yangtze River (Shi, 1989). The Yangtze River is rich in fish biodiversity (Fu *et al.*, 2003). Thus, the rich fish fauna in the Yangtze River could contribute to the diverse fish species in the lakes around the Yangtze River as shown in Table 4. On the other hand, richer fish species in these lakes may also result partly from the higher energy (the largest PET), low lake altitude, and lower mineralization degree in this region (Table 4). Lake area is the most significant predictor of fish species richness; however, it accounted for a relatively small fraction (22.2%) of the total variation in this region (Table 2). This may be due partly to lake degradation caused by human activities (Zhao *et al.*, 2005; Fang *et al.*, in press). For example, some of the small lakes in this region have been separated from larger lakes by anthropogenic reclamation, and hence have relatively more fish species than expected.

Despite its cold climate, the Northeast region has rich fauna (Zhang, 1999), and most of the lakes in this region are located at relatively low altitudes (e.g. a mean lake altitude of 369 m, Table 4). These factors may lead to the relatively higher fish richness in this region. Similar to previous studies (e.g. Kerr & Packer, 1997; Hawkins *et al.*, 2003a), the available energy (e.g. annual PET) is a major factor explaining the variation of fish richness pattern in this cold region.

The Southwest region is located mainly in the Yunnan–Guizhou Plateau, with a relatively high lake altitude (a mean lake altitude of 1744 m). Fish diversity in this region is relatively high because the lakes have relatively high energy (annual PET, 787 mm) and are less human-affected, and their mineralization degrees are low (mean, 0.3 g l^{-1}). Consistent with the theory of island biogeography (MacArthur & Wilson, 1967), lake area is the primary predictor of lake fish species richness in this region, explaining 82.9% of its variation. This is probably associated with the geological age of the lakes. It has been reported that Yunnan is one of the centres of Asian freshwater fish speciation (Gao *et al.*, 1990). The lakes in this region are relatively old and have had adequate time for occurrence of speciation to fill the larger lakes.

The North-Northwestern lakes are isolated in an inland area where water is scarce (with an annual precipitation of only 232 mm); intensive lake evaporation leads to the accumulation of total dissolved salts. Thus, most of the lakes in this region are brackish or saline (maximum mineralization degree of 70 g l^{-1}), and are very poor in fish species (Table 4). Limnological characteristics, such as maximum depth and mineralization degree, were the predictors of the fish richness pattern (Table 2). Unlike in the geologically old African lakes where species richness was positively related to water depth (Barbour & Brown, 1974), the lake fish richness in this region was negatively related to water depth. However, this is consistent with Wetzel (2001), who claimed that shallow lakes were generally more productive than deep lakes and thus could support the coexistence of more species. As indicated in Table 2, mineralization degree, a surrogate of water salinity, is another limiting factor for fish richness because osmotic pressure of body fluids increases as salinity accumulates (Wetzel, 2001). This was consistent with Barbour & Brown (1974) who reported that conductivity, an estimate of mineralization degree of water, was a primary predictor of fish richness pattern in African lakes. On the other hand, we observed that in a saline environment, increased lake area could lead to an increase in fish species.

The Tibetan Plateau is a newly developed highland with a mean altitude of > 4000 m and its uplifting events occurred primarily in the Cenozoic Era (Wu & Tan, 1991; Zhong & Ding, 1996). The low lake fish diversity (only 1.2 species per $\log_{10}$ area) on the Plateau may be related to the young geological age, the higher elevations, and the lower energy availability thereby indicating lower potential for colonization and speciation. Data to support these hypotheses are limited and further studies are needed.

In conclusion, lake altitude, available energy, and lake area together explain much of the spatial variation in the fish species richness across China's lakes. The lake altitude was the most important factor contributing to the variation of fish richness pattern at the national scale. This has not been observed in previous studies elsewhere and may be attributed to the huge altitudinal extent across China. The effect of lake altitude on fish species richness can be separated into direct and indirect aspects due to its collinearity with PET. Two main species richness hypotheses — species–energy hypothesis and species–area hypothesis — provide plausible explanations for the spatial pattern of fish species richness in the lakes across China. We also found that fish diversity and the determinants of the fish richness pattern varied among physiographic regions.

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SUPPLEMENTARY MATERIAL

The following material is available online at www.blackwell-synergy.com/loi/geb

Appendix S1 Original information on fish species richness and limnological characteristics for the 109 lakes.

Appendix S2 Correlation matrix of fish richness, limnological characteristics, and climatic variables.