



Patterns of diversity, altitudinal range and body size among freshwater fishes in the Yangtze River basin, China

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ABSTRACT

Aim To document patterns in diversity, altitudinal range and body size of freshwater fishes along an elevational gradient in the Yangtze River basin.

Location The Yangtze River basin, China.

Methods We used published data to compile the distribution, altitudinal range and body size of freshwater fishes. Correlation, regression, clustering and graphical analyses were used to explore patterns in diversity, altitudinal range and body size of freshwater fishes in 100-m elevation zones from 0 to 5200 m.

Results Species richness patterns across the elevational gradient for total, non-endemic and endemic fishes were different. The ratio of endemics to total richness peaked at mid elevation. Land area on a 500-m interval scale explained a significant amount of the variation in species richness. Species density displayed two peaks at mid-elevation zones. The cluster analysis revealed five distinct assemblages across the elevation gradient. The relationship between elevational range size and the midpoint of the elevational range revealed a triangular distribution. The frequency distribution of log maximum standard length data displayed an atypical right-skewed pattern. Intermediate body sizes occurred across the greatest range of elevation while small and large body sizes possessed only small elevational amplitudes. The size-elevation relationship between the two major families revealed a very strong pattern of body size constraint among the Cobitidae with no corresponding elevational constraint and a lot of body size and elevational diversification among the Cyprinidae.

Main conclusion The data failed to support either Rapoport's rule or Bergmann's rule.

Keywords

Bergmann's rule, body size, China, diversity, elevational gradient, freshwater fish, geographical range, macroecology, Rapoport's rule, Yangtze River.

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INTRODUCTION

The field of macroecology is the study of emergent patterns of assemblages of species distributed over geographical spatial scales and evolutionary time scales (Brown & Maurer, 1989; Brown, 1995). Macroecological patterns on gradients of species diversity, range size and body size have been documented to describe variation within and among species (Brown, 1995; Gaston & Blackburn, 2000). The study of these emergent properties has centred largely on terrestrial systems (Smith & Brown, 2002). Information on freshwater systems is still limited. This paper contributes to understanding the distribution of freshwater

organisms. We document patterns in diversity, altitudinal range and body size that characterize freshwater fish assemblages along an elevational gradient in the Yangtze River basin, China. Information on faunal composition of freshwater fish species in the Yangtze River basin is derived from Fu *et al.* (2003).

Diversity

Understanding variation in species richness has been a central aim of community ecology for decades (MacArthur, 1972; Ricklefs & Schluter, 1993; Rosenzweig, 1995). As predictions of the loss of global biodiversity grow increasingly pessimistic,

identifying the factors that determine species richness has become a hot topic (Willis & Whittaker, 2002). The latitudinal decrease in species richness from low at the poles to high at the equator has been known for over a century (Wallace, 1878; Pianka, 1966; Rohde, 1992; Brown & Lomolino, 1998; Rohde, 1999; Willig *et al.*, 2003). Altitudinal trends in species richness were generally thought to mimic latitudinal trends in species richness (e.g. Brown, 1988; Stevens, 1992; Brown & Lomolino, 1998). However, growing evidence suggested that mid-elevational peaks in species richness for a wide variety of taxa are perhaps more general (Rahbek, 1995; Brown, 2001; Lomolino, 2001; Sanders, 2002).

Climatic, biological, geographical and historical factors have been suggested as causes of variation in species richness along elevational gradients (Rahbek, 1995; Rosenzweig, 1995; Lomolino, 2001; Whittaker *et al.*, 2001). In this paper, we examine the effect of land area on freshwater fish diversity. Area is a principal factor to affect species richness (Rosenzweig, 1995; Whittaker *et al.*, 2001), and the effect of area on species richness has been described as one of ecology's few laws (Lawton, 1999). In general, land area should decrease with increasing elevation (Körner, 2000; Lomolino, 2001). If land area influences fish species richness, we should expect that species richness declines with increasing elevation.

Range size

Rapoport's rule (Stevens, 1989) states that a general positive relationship is found between the latitudinal extent of an organism's geographical range size and latitude. An elevational equivalent of Rapoport's rule was suggested following the idea that organisms at low elevation tend to have more restricted elevational ranges than organisms at high elevation (Stevens, 1992). The 'altitudinal Rapoport's rule' was explained in terms of differential abilities of species to attain large range sizes. Species at low elevations are approaching their upper elevation range limits, while taxa that inhabit higher elevations have comparatively large climatic tolerances and thus can be found across a greater elevational range (Stevens, 1992). Unfortunately, conclusions on the generality of Rapoport's rule are precluded by the uneven taxonomic and latitudinal representation of organisms examined thus far (Gaston & Chown, 1999; Rohde, 1999; Ashton, 2001; Willig *et al.*, 2003). The general conclusion is that the rule is a local effect, limited to the northern hemisphere (Rohde, 1996; Gaston *et al.*, 1998).

Analyses of the latitudinal range of marine teleosts in the Indo-Pacific and Atlantic Oceans did not support Rapoport's rule (Rohde *et al.*, 1993; Macpherson & Duarte, 1994; Rohde & Heap, 1996). However, a bathymetric equivalent of Rapoport's rule has been reported to apply to marine teleosts (Stevens, 1996; Smith & Brown, 2002). For freshwater fishes, Rapoport's rule was reported only to apply to North American and North European fishes above a latitude of approximately 40° N (Rohde *et al.*, 1993). To our knowledge, the relationship between the elevational ranges of species and elevation for freshwater fishes remains relatively unstudied. This paper tests for the 'altitudinal Rapoport's rule' in freshwater fishes.

Body size

Body size plays an important role in the organization of ecological communities (Lawton, 1990; Holling, 1992; Blackburn *et al.*, 1993; Brown, 1995; Maurer, 1999). Body size distributions are an important component of community structure (Preston, 1962a,b; May, 1986; Brown, 1995). Since Bergmann (1847) first reported a positive relationship between body size and latitude (i.e. Bergmann's rule), there has been a growing interest in understanding the processes that generate spatial patterns in body size, especially across major environmental gradients such as those associated with latitude and bathymetry (Cushman *et al.*, 1993; Brown, 1995; Hawkins & Lawton, 1995; Blackburn & Gaston, 1996; Blackburn *et al.*, 1999; Rex *et al.*, 1999; Roy & Martien, 2001; Smith & Brown, 2002). However, there are few studies of altitudinal variation in body size among species (but see Hawkins & DeVries, 1996; Blackburn & Ruggiero, 2001; Hausdorf, 2003). Some examples refer to the intraspecific geographical variation in body size patterns not conforming to Bergmann's rule for freshwater fishes (Mills, 1988; Power & McKinley, 1997; Belk & Houston, 2002). Given these results, it remains unclear if there are general trends in the altitudinal variation of body size among freshwater fish species. In this study, we use maximum standard length to analyse the relationships between body size and elevation for freshwater fishes in the Yangtze River basin.

MATERIALS AND METHODS

Location

The Qinghai-Tibet Plateau (26°00'–39°46' N, 73°19'–104°47' E) had three successive phases of uplifting after India collided with Asia *c.* 55 Ma (Zhang *et al.*, 2000; Tapponnier *et al.*, 2001). In the late Eocene, the Himalayan Movement of the first phase compelled the Tethys Sea to evacuate entirely the whole Qinghai-Tibet region. The Himalayan Movement of the second phase caused the Himalayan Mountains to uplift in the middle Miocene epoch. The primal plateau surface was characterized by gentle undulations at *c.* 1000 m altitude, with a warm and humid climate, and numerous rivers and lakes. From the end of the Pliocene to the early Quaternary, the Himalayan Movement of the third phase started a new epoch of 'World Ridge' development. Just in the last 10,000 years, the plateau has uplifted 300–700 m, and it is still rapidly uplifting (Bingyuan & Baofu, 1983). As a result of the intense uplift of the Qinghai-Tibet Plateau and the large-scale settlement of the eastern plains, the Chinese stepped land features were formed (Zhang *et al.*, 2000). According to geological discontinuities, Chinese land can be divided into five elevation zones: (1) < 1000 m; (2) 1000–2000 m; (3) 2000–4000 m; (4) 4000–6000 m; (5) > 6000 m (Zhang *et al.*, 2002).

The Himalayan orogeny in the late Tertiary and early Quaternary, along with the occurrence of the monsoon-driven precipitation system, shaped the Yangtze River (Chen *et al.*, 2001). The river reached the coast not earlier than 100 Ma (Wang, 1997). The geographical range of the Yangtze River basin is

24°17'–35°54' N, 90°33'–122°15' E, and the drainage area is almost $180 \times 10^4 \text{ km}^2$ (Changjiang Hydrological Committee of Hydrology Ministry, 1999). The basin covers a very large elevational range, divided into four zones: (1) < 1000 m; (2) 1000–2000 m; (3) 2000–4000 m; (4) > 4000 m according to geological discontinuities (Zeng, 1990). The higher than 4000 m elevational zone is located in the Qinghai-Tibetan Plateau. The 2000–4000 m belt represents a transition from the Qinghai-Tibetan Plateau to the Yunnan-Guizhou Plateau and the Sichuan basin. The 1000–2000 m elevational zone includes the Yunnan-Guizhou Plateau and part of the Qinling mountain range. The < 1000 m belt includes the Sichuan basin and almost all the middle and low reaches of the Yangtze River basin. Detailed descriptions of the Yangtze River basin can be found in Chen *et al.* (2001) and Fu *et al.* (2003).

Data sources

The data for this study were obtained from our previous study (Fu *et al.*, 2003) on freshwater fish biodiversity in the Yangtze River basin. We documented 361 species and subspecies that had been recorded and described from the basin. Among these, 177 species are endemic. In this study, one non-native species, *Gambusia affinis* was excluded from the analyses. The body size (maximum standard length) and elevational distribution data (minimal and maximal elevation of occurrence) of each fish species in this database were compiled through an exhaustive search of the primary literature and from major museum collections.

Statistical analysis

To examine the relationship between species richness and elevation, we divided the range of elevation into 100-m bands and calculated the total number of species in each band. We assumed that a species occurred at all elevation bands between its minimum and maximum elevation records.

An exact estimate of the area for each 100-m interval is not available, but an estimate of the area for each 500-m interval was obtained by using a 1 : 1,000,000 Digital Elevation Model (DEM) of the People's Republic of China from the official agency (Chinese National Fundamental Geographic Information System, <http://nfgis.nsd.gov.cn/nfgis/chinese>). The data were used to examine the influence of area on species richness pattern along an elevational gradient. The area of each 500-m interval was also used to calculate the species density (species number per 10^4 km^2) to examine the relationship between species density and elevation.

To explore community composition pattern along the elevational gradient, we compared community composition among 200-m interval elevation bands. An analysis of similarity measure was conducted using the Jaccard (1901) index. Pairwise similarities among all bands were computed to compose a similarity coefficient matrix. The unweighted pair-group average agglomerative method was used in the cluster analysis based on this matrix.

To examine a relationship between fish species' elevational ranges and the breadth of elevation of those ranges, the differ-

ence between minimal and maximal elevation of occurrence of each species was used as the elevation range. To overcome statistical non-independence of spatial data, we used the 'mid-point method' (Rohde *et al.*, 1993) as a measure of central tendency. The mean between the minimum and maximum elevation reported for each species was used to represent that species' characteristic elevation.

To determine if there is a relationship between body size and elevation, maximum standard length was used as an estimate of body size. Because fish display indeterminate growth and no typical adult body size within a species, body size is often estimated as maximum adult body size (Matthews, 1998; Rosenfield, 2002). In this study, we quantify the body size-elevation relationships for total species, endemic species and non-endemic species. Rex & Etter (1998) reported that interspecific size-bathymetry trends were best studied using closely related and ecologically similar species. Thus, the two major families (Cypriniformes: Cyprinidae and Cobitidae) were also selected to explore the body size-elevation relationships. For all the analyses, body size data were \log_{10} transformed, and a length-frequency distribution was computed from these data.

The graphical analysis was used to explore patterns in diversity, altitudinal range and body size of freshwater fishes. The linear regression analysis was used to test associations between species richness and area. The Pearson product-moment correlation coefficient was used to express the sign and strength of the relationship between elevational range size and body size. The *Shapiro-Wilk W*-test was used to test normality. All analyses were done using STATISTICA version 6.

RESULTS

Diversity

The maximum elevational distribution of *Herzensteinia microcephalus* and *Triplophysa stewarti* (Cypriniformes: Cyprinidae) was 5200 m above sea level (a.s.l.). These two species may have the highest elevational maxima among freshwater fishes on earth. Species richness patterns along the basin elevational gradient of total, non-endemic and endemic fishes were different (Fig. 1a). Non-endemic richness showed a significant decrease with increasing elevation ($P < 0.001$). Endemic richness had two peaks, a major peak in the 500-m band and a minor peak in the 1800-m band. Total richness decreased slightly from 100 m to 200 m, increased from 200 m to 500 m, and then tended to decrease rapidly with increasing elevation. The ratio of endemics to total richness peaked at mid elevations (Fig. 1b).

Area decreased with increasing elevation on a 500-m interval scale (Fig. 2). Area explained a significant amount of the variation in species richness for total ($y = 1.565x - 6.416$, $r^2 = 0.911$, $P < 0.001$), endemic ($y = 1.535x - 6.540$, $r^2 = 0.848$, $P < 0.001$), and non-endemic ($y = 1.625x - 7.098$, $r^2 = 0.926$, $P < 0.001$) freshwater fishes.

Species density had two peaks at mid elevation zones for total, endemic and non-endemic freshwater fishes (Fig. 2). Comparing endemics and non-endemics, neither showed a unimodal

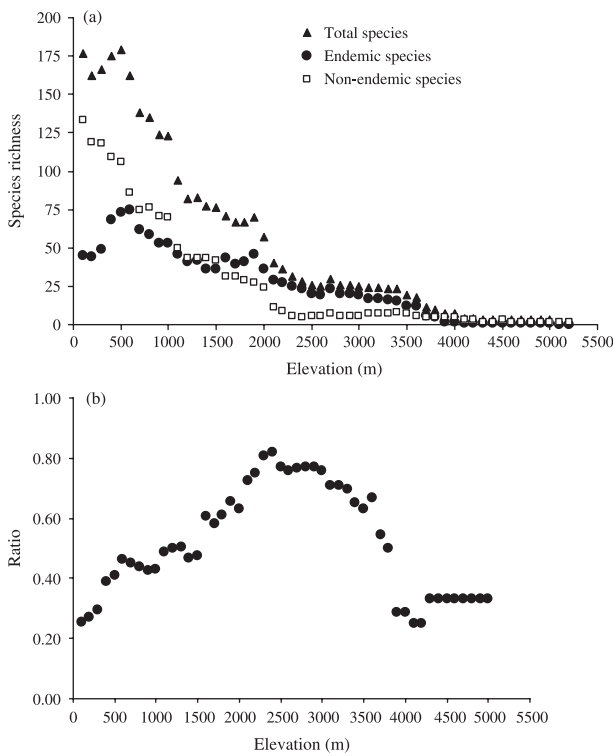


Figure 1 (a) The relationship between species richness and elevation for total ($n = 360$), endemic ($n = 177$) and non-endemic ($n = 183$) species of freshwater fishes in the Yangtze River basin; (b) The relationship between the ratio of endemics to total richness and elevation.

distribution. Major peaks did not coincide, minor peaks did coincide.

The cluster analysis revealed five distinct assemblages along the basin elevational gradient (Fig. 3). The elevational boundaries

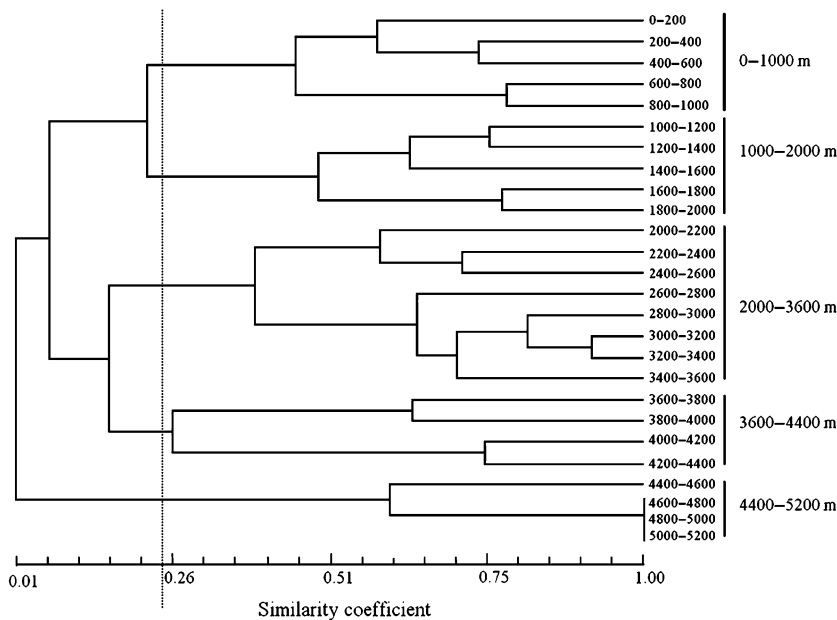


Figure 3 The classification of 200-m elevational intervals between 0 and 5200 m using Jaccard similarity measure. The unweighted pair-group average agglomerative method was used for the cluster analysis based on the similarity coefficient matrix ($n = 360$ species).

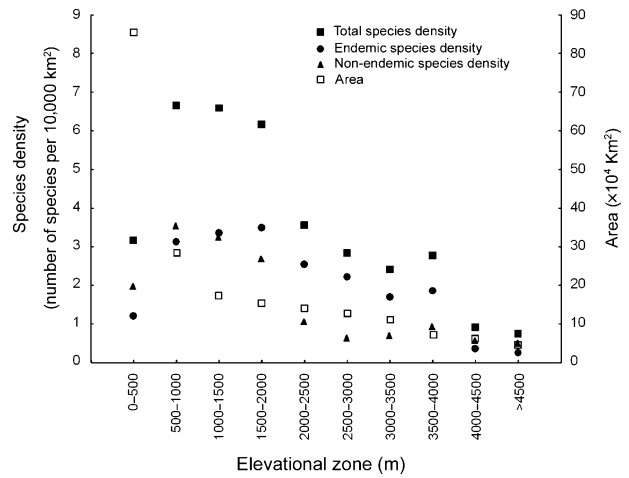


Figure 2 The relationship between species density or area and elevational zone of 500-m intervals.

of the five assemblages were: (1) 0–1000 m; (2) 1000–2000 m; (3) 2000–3600 m; (4) 3600–4000 m; (5) > 4000 m.

Range size

The relationship between elevational range size and midpoint of the elevational range revealed a triangular distribution for endemic and non-endemic species (Fig. 4). Species at mid elevations displayed the complete range of range sizes while species at lower elevations or higher elevations possessed only small range sizes.

Body size

The frequency distribution of log maximum standard length data was not a normal distribution (Shapiro-Wilk $W = 0.845$,

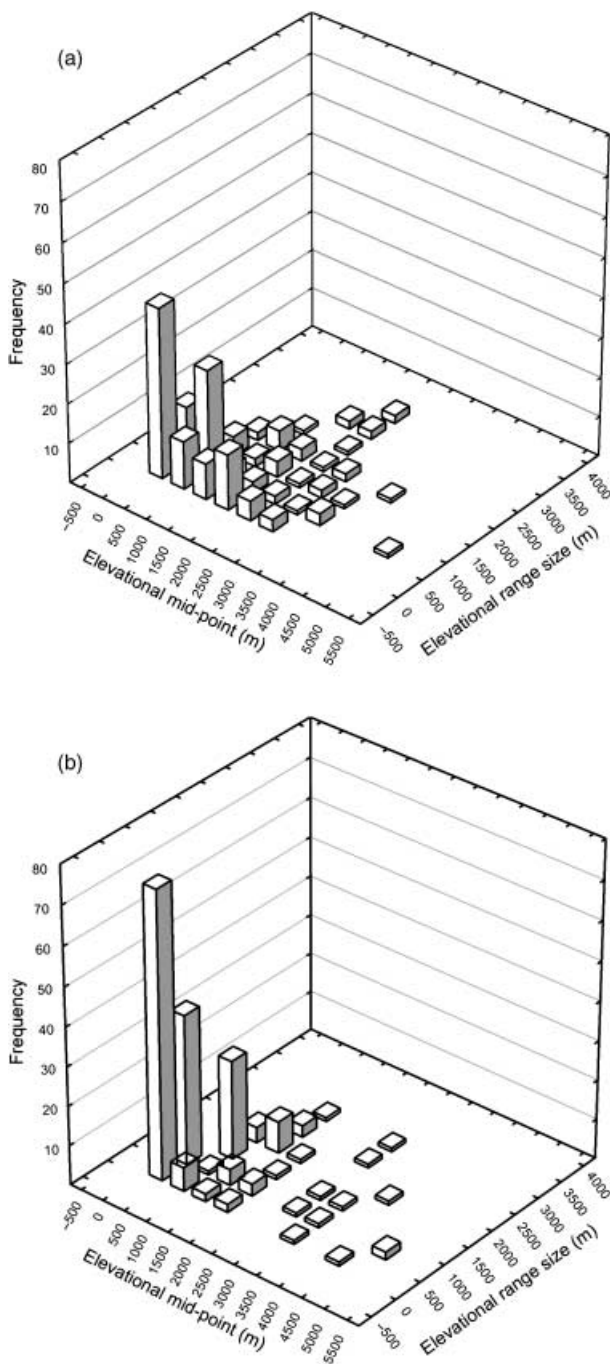


Figure 4 The relationship between elevational range size and midpoint of the elevational range for (a) endemic ($n = 177$) and (b) non-endemic ($n = 183$) species of freshwater fishes in the Yangtze River basin.

$P < 0.001$), and displayed an atypical right-skewed pattern (Fig. 5). The curve was not very 'smooth', and there were body sizes with fewer organisms than adjacent body size categories. Holling (1992) referred to these as gaps.

For endemics, non-endemics and the Cyprinidae, body size-elevation relationships revealed a triangular distribution (Figs 6 and 7). The greatest range of body sizes occurred at the lower

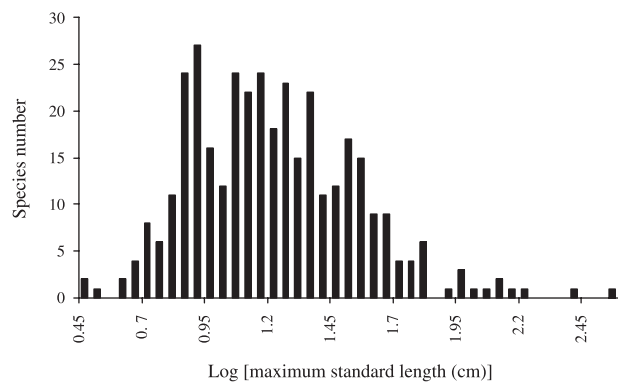


Figure 5 The length-frequency distribution of freshwater fishes ($n = 360$) in the Yangtze River basin.

elevations, and intermediate body sizes of log equal to about 1.5 occurred across the greatest range of elevations while small and large body sizes possessed only small elevational amplitudes. For the Cobitidae, the body size-elevation relationship also revealed a very strong pattern of body size constraint with no corresponding elevational constraint (Fig. 7).

DISCUSSION

Diversity

Both hump-shaped and monotonically decreasing patterns of richness in relation to altitude have been commonly reported (see review in Rahbek, 1995). Since Rahbek's review, some studies have further confirmed a hump-shaped altitudinal richness pattern (Rahbek, 1997; Fleishman *et al.*, 1998; Heaney, 2001; Pyrz & Wojtusiak, 2002; Grytnes, 2003; Li *et al.*, 2003), while others have supported monotonically decreasing richness with altitude (Patterson *et al.*, 1998; Odland & Birks, 1999; Austrheim, 2002; Sanders *et al.*, 2003). The latter pattern was also observed for non-endemic fish species along an elevational gradient in the Yangtze River basin. Endemic and total richness exhibited some peaks below the median of complete elevational gradients, and declined monotonically from mid to high elevation (Fig. 1a). This was not in accordance with a unimodal pattern and a linear decreasing trend with altitude. However, our data still support the generalizations that species richness generally declines monotonically from mid to high elevation on local and regional scales, and that patterns of species richness below the median of complete elevation gradients vary considerably among taxa and geographical regions (Rahbek, 1995, 1997). We caution that in the present study, we assumed that species occurred at all elevations between their minimum and maximum elevation records and so the range of rare species could be underestimated if the minimum and maximum elevations were not detected accurately. Nonetheless, the pattern of species diversity described in this study may be a real feature of freshwater fish diversity along the basin elevation gradients, reflecting effects of current environmental conditions or historical effects on the elevational distributions of fishes.

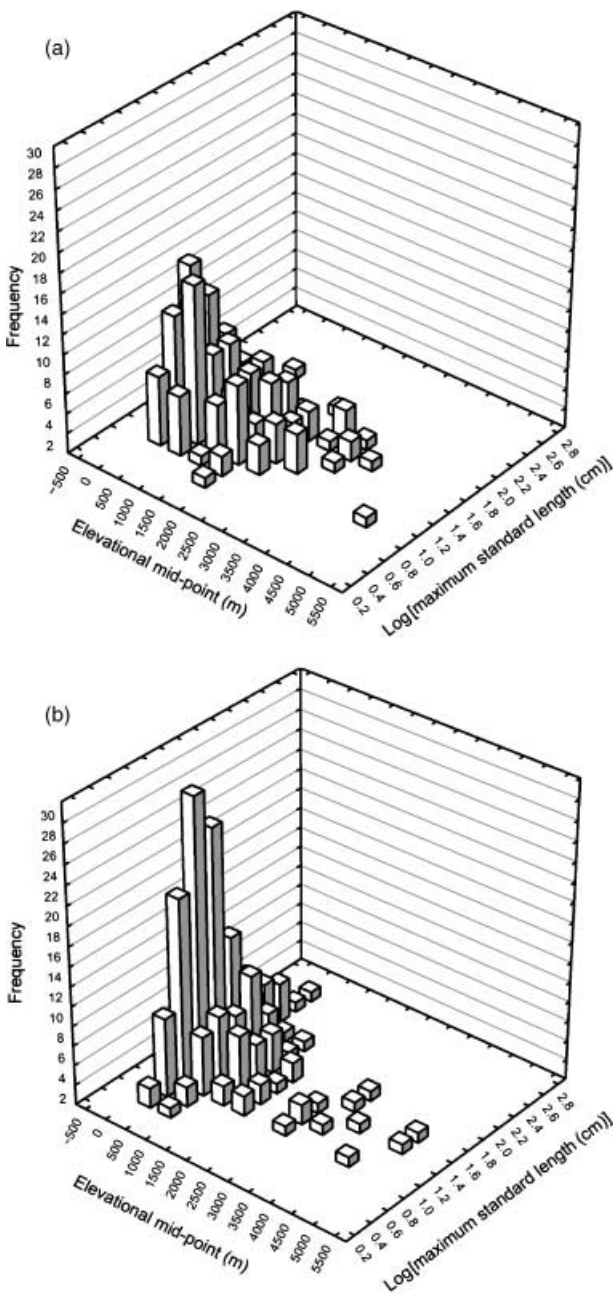


Figure 6 The relationship between \log_{10} (maximum standard length) and midpoint of the elevational range for (a) endemic ($n = 177$) and (b) non-endemic ($n = 183$) species of freshwater fishes in the Yangtze River basin.

Space and time are two important factors controlling the ability of speciation to increase species richness in a region (Rosenzweig, 1995). Because each new species of organism evolved in one particular, restricted area, its distribution would be limited by the barriers that surrounded its area of origin (Cox & Moore, 2000). In North America, freshwater fish species geographical ranges were smaller than those for terrestrial vertebrates, and isolation might be responsible for the tremendous richness and endemism of the freshwater fish fauna (Rosenfield,

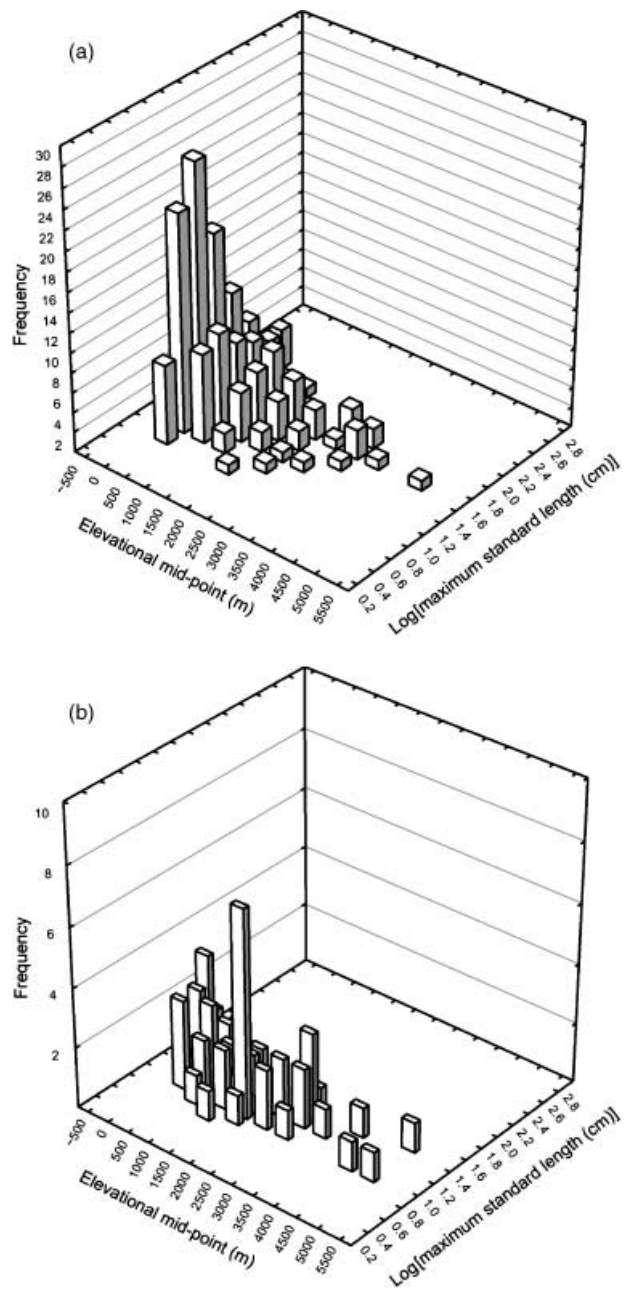


Figure 7 The relationship between \log_{10} (maximum standard length) and midpoint of the elevational range for (a) the Cyprinidae ($n = 195$) and (b) the Cobitidae ($n = 61$).

2002). Increased isolation and reduced dispersal might have resulted in increased differentiation and higher endemism with increasing elevation (Brown, 2001). In the present study, the ratio of endemics to total richness peaked at mid elevations (Fig. 1b). This pattern of species diversity may reflect the length of time and the spatial heterogeneity of the areas encompassed in each 100-m interval elevation zone.

In this study, area explained species richness variation, i.e. richness (corrected for area) declined with increasing elevation. Area decreases and isolation increases with increasing elevation

(Körner, 2000; Brown, 2001; Lomolino, 2001). The reduced area might result in high extinction rates, and the increased isolation might result in reduced dispersal and low rates of colonization (Brown, 2001).

Species density had two peaks at mid elevations in the basin (Fig. 2). This pattern was largely in accordance with the prediction of Lomolino (2001). He predicted that species density should peak at an intermediate elevation and the peak should occur at a transition zone between the two species-rich, juxtaposed communities. In addition to this major peak, species density should exhibit repeated minor peaks at transitions between other zonal communities.

Species diversity in the Yangtze River basin was divisible into five distinct assemblages along the basin elevation gradient. This indicated that the fish community composition pattern was strongly influenced by the basin stepped geomorphology. The cluster analysis based on community similarity also revealed a high elevation species assemblage largely distinct from those of lower elevations (Fig. 3). Similar patterns have been observed in other studies (Patterson *et al.*, 1998; Pyrcz & Wojtusiak, 2002; Sanders *et al.*, 2003).

Range size

In this study, a triangular pattern was found for the relationship between range size and elevation, and species at intermediate elevations had the broadest amplitudes (Fig. 4). Similar patterns have been documented for birds and mice in the Andes of south-eastern Peru (Patterson *et al.*, 1998). The results complement other evidence indicating a lack of an altitudinal Rapoport pattern (Stotz *et al.*, 1996; Rahbek, 1997; Ruggiero & Lawton, 1998; Nathan & Werner, 1999).

Body size

The right-skewed pattern of the frequency distribution of body size has been documented in most taxonomic groups (Hutchinson & MacArthur, 1959; Blackburn & Gaston, 1994; Brown, 1995). Freshwater fishes in the Yangtze River basin also displayed the right-skewed size-frequency distribution (Fig. 5). However, the log (body size) frequency distribution in this study was less right skewed than similar plots for North American freshwater fishes (Knouft & Page, 2003). The Yangtze possessed more mid-bodied fishes than North America. The difference could be induced by different fauna in the two regions. The Cypriniformes is the main component of fish fauna in the Yangtze basin, accounting for 75.6% of the total species (Fu *et al.*, 2003), a greater degree of dominance than in North America. Taxonomic constraints on body size have also been revealed by analysing the body size distribution pattern in the world's birds, for which the species body size distributions of different orders exhibit wide variance in skew (Maurer, 1998). In this study, there were many gaps in the frequency distribution of body size. This pattern could be explained by the prediction of the Textural-Discontinuity Hypothesis (Holling, 1992), which proposed that the clumps and gaps in body size distributions of mammals and birds in biomes

reflects structural characteristics of the vegetation and landscape. The landscape discontinuities in the Yangtze River basin may cause gaps in the distribution of body size among freshwater fish species.

Bergmann's rule, which predicts a positive correlation between body size of species in a monophyletic group and the latitude inhabited by those species (Blackburn *et al.*, 1999), could not be confirmed by the altitudinal body-size pattern of freshwater fishes in the Yangtze River basin. Inter-specific altitudinal variation in body size patterns not conforming to Bergmann's rule have also been reported in other studies (Hawkins & DeVries, 1996; Blackburn & Ruggiero, 2001; Hausdorf, 2003; Brehm & Fiedler, 2004). These results suggest that more studies on body size-altitude relationships are needed before we can make generalizations on the altitudinal variation in body size among species.

The greatest range of body sizes among freshwater fishes in the basin occurred at the lower elevations. This pattern may result from the presence of fewer small-bodied species at high elevations, whereas large-bodied species occupy both high and low elevations. This would be expected from the positive relationship between elevational range size and body size for endemics ($r = 0.207$, $P < 0.006$), non-endemics ($r = 0.149$, $P < 0.044$) and the Cyprinidae ($r = 0.246$, $P < 0.001$). Intermediate body sizes occurred across the greatest range of elevations while small and large body sizes possessed only small elevational amplitudes. One plausible explanation for this pattern was that the environmental conditions in the Yangtze River basin appeared to restrict the body sizes to a certain optimum range. Empirical evidence for an optimal body size in other ectothermic taxa have been reported elsewhere (Boback & Guyer, 2003). Another plausible explanation relates to taxonomic idiosyncrasies. The history of the Qinghai-Tibet Plateau formation (Materials and methods) must have played an important role for speciation and extinction of freshwater fishes in the basin. The tectonic activity promoted the species adaptive radiation of the *Triplophysa* (Cobitidae) and the Schizothoracinae (Cyprinidae), and extinction of other taxa in the basin's higher elevations (Cao *et al.*, 1981; Wu & Wu, 1992; Chen *et al.*, 1996). Thus, most of the species in the *Triplophysa* and the Schizothoracinae were mid-bodied species, which should result in mid-body sizes possessing the greatest altitudinal amplitude. The data in this study further revealed that only 27 species possess an elevational midpoint above 2350 m. Among these fishes, 12 species (log(body size) range: 0.81–1.32; mean \pm standard deviation (SD): 1.07 ± 0.16) belong to the *Triplophysa*, and 15 species (log(body size) range: 1.11–1.64; mean \pm SD 1.48 ± 0.17) belong to the Schizothoracinae. In addition, the *Triplophysa* and the Schizothoracinae are the main component of fish fauna in the basin, accounting for 14.7% of the total species, and 23.2% of the total endemics (Fu *et al.*, 2003).

In this study, the size-elevation relationship for the Cobitidae revealed a very strong pattern of body size constraint with no corresponding elevational constraint, and there was also no significant relationship between elevational range size and body size ($r = 0.218$, $P > 0.092$). This may indicate an upper limit to body size achievable by the species in this family, acting as a reflecting boundary, precluding body size to evolve away from

this limit. Further study is necessary to test if an optimum body size exists for species in the Cobitidae (cf. Maurer *et al.*, 1992; Brown *et al.*, 1993).

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REFERENCES

- Ashton, K.G. (2001) Are ecological and evolutionary rules being dismissed prematurely? *Diversity and Distributions*, **7**, 289–296.
- Austrheim, G. (2002) Plant diversity patterns in semi-natural grasslands along an elevational gradient in southern Norway. *Plant Ecology*, **161**, 193–205.
- Belk, M.C. & Houston, D.D. (2002) Bergmann's rule in ectotherms: a test using freshwater fishes. *American Naturalist*, **160**, 803–808.
- Bergmann, C. (1847) Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*, **3**, 595–708.
- Bingyuan, L. & Baofu, L. (1983) *Tibet Quaternary geology*. Science Publication House, Beijing, China.
- Blackburn, T.M., Brown, V.K., Doube, B.M., Greenwood, J.J.D., Lawton, J.H. & Stork, N.E. (1993) The relationship between abundance and body size in natural animal assemblages. *Journal of Animal Ecology*, **62**, 519–528.
- Blackburn, T.M. & Gaston, K.J. (1994) The distribution of body sizes of bird species in the New World. *Oikos*, **70**, 127–130.
- Blackburn, T.M. & Gaston, K.J. (1996) Spatial patterns in the body sizes of bird species in the New World. *Oikos*, **77**, 436–446.
- Blackburn, T.M., Gaston, K.J. & Loder, N. (1999) Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions*, **5**, 165–174.
- Blackburn, T.M. & Ruggiero, A. (2001) Latitude, elevation and body mass variation in Andean passerine birds. *Global Ecology and Biogeography*, **10**, 245–259.
- Boback, S.M. & Guyer, C. (2003) Empirical evidence for an optimal body size in snakes. *Evolution*, **57**, 345–351.
- Brehm, G. & Fiedler, K. (2004) Bergmann's rule does not apply to geometrid moths along an elevational gradient in an Andean montane rain forest. *Global Ecology and Biogeography*, **13**, 7–14.
- Brown, J.H. (1988) Species diversity. *Analytical biogeography: an integrated approach to the study of animal and plant distribution* (ed. by A.A. Myers and P.S. Giller), pp. 57–89. Chapman & Hill, New York.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.
- Brown, J.H. (2001) Mammals on mountainsides: elevational patterns of diversity. *Global Ecology and Biogeography*, **10**, 101–109.
- Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*, 2nd edn. Sinauer, Sunderland.
- Brown, J.H., Marquet, P.A. & Taper, M.L. (1993) Evolution of body size: consequences of an energetic definition of fitness. *American Naturalist*, **142**, 573–584.
- Brown, J.H. & Maurer, B.A. (1989) Macroecology: the division of food and space among species on continents. *Science*, **243**, 1145–1150.
- Cao, W., Chen, Y., Wu, Y. & Zhu, S. (1981) Origin and evolution of the Schizothoracinae and its relationship with uplift of the Tibetan Plateau. *The era, range and shape of the Tibetan plateau's uplift* (ed. by Anonymous), pp. 118–130. Science Press, Beijing, China.
- Changjiang Hydrological Committee of Hydrology Ministry (1999) *Atlas of the Yangtze River basin*. Chinese Map Press, Beijing, China.
- Chen, Z., Yu, L. & Gupta, A. (2001) The Yangtze River: an introduction. *Geomorphology*, **41**, 73–75.
- Chen, Y., Chen, Y.F. & Liu, H. (1996) Studies on the position of the Qinghai-Xizang Plateau region in zoogeographic divisions and its eastern demarcation line. *Acta Hydrobiologia Sinica*, **20**, 97–103.
- Cox, C.B. & Moore, P.D. (2000) *Biogeography: an ecological and evolutionary approach*, 6th edn. Blackwell Science, Oxford.
- Cushman, J.H., Lawton, J.H. & Manly, B.F.J. (1993) Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia*, **95**, 30–37.
- Fleishman, E., Austin, G.T. & Weiss, A.D. (1998) An empirical test of Rapoport's rule: elevational gradients in montane butterfly communities. *Ecology*, **79**, 2482–2493.
- Fu, C., Wu, J., Chen, J., Wu, Q. & Lei, G. (2003) Freshwater fish biodiversity in the Yangtze River basin of China: patterns, threats and conservation. *Biodiversity and Conservation*, **12**, 1649–1685.
- Gaston, K.J. & Blackburn, T.M. (2000) *Pattern and process in macroecology*. Blackwell Science, Berlin, Germany.
- Gaston, K.J., Blackburn, T.M. & Spicer, J.I. (1998) Rapoport's rule: time for an epitaph? *Trends in Ecology and Evolution*, **13**, 70–74.
- Gaston, K.J. & Chown, S.L. (1999) Why Rapoport's rule does not generalize. *Oikos*, **84**, 309–312.
- Grytnes, J.A. (2003) Species richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography*, **26**, 291–300.
- Hausdorf, B. (2003) Latitudinal and altitudinal body size variation among north-west European land snail species. *Global Ecology and Biogeography*, **12**, 389–394.
- Hawkins, B.A. & DeVries, P.J. (1996) Altitudinal gradients in the body sizes of Costa Rican butterflies. *Acta Oecologica*, **17**, 185–194.
- Hawkins, B.A. & Lawton, J.H. (1995) Latitudinal gradients in butterfly body sizes: is there a general pattern. *Oecologia*, **102**, 31–36.
- Heaney, R.H. (2001) Small mammal diversity along elevational

- gradients in the Philippines: an assessment of patterns and hypotheses. *Global Ecology and Biogeography*, **10**, 15–39.
- Holling, C.S. (1992) Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs*, **62**, 447–502.
- Hutchinson, G.E. & MacArthur, R.H. (1959) A theoretical ecological model of size distributions among species of animals. *American Naturalist*, **93**, 117–125.
- Jaccard, P. (1901) Distribution de la flore alpine dans le Bassin des Dranes et dans quelques regions voisines. *Bulletin Societe Vaudoise Des Science Naturelles*, **37**, 241–272.
- Knouft, J.H. & Page, L.M. (2003) The evolution of body size in extant groups of North American freshwater fishes: speciation, size distribution, and Cope's rule. *American Naturalist*, **161**, 413–421.
- Körner, C. (2000) Why are there global gradients in species richness? Mountains may hold the answer. *Trends in Ecology and Evolution*, **15**, 513–514.
- Lawton, J.H. (1990) Species richness and population dynamics of animal assemblages: patterns in body size–abundance space. *Philosophical Transactions of the Royal Society B*, **330**, 283–291.
- Lawton, J.H. (1999) Are there general laws in ecology? *Oikos*, **84**, 177–192.
- Li, J., Song, Y. & Zeng, Z. (2003) Elevational gradients of small mammal diversity on the northern slopes of Mt. Qilian, China. *Global Ecology and Biogeography*, **12**, 449–460.
- Lomolino, M.V. (2001) Elevational gradients of species diversity: historical and prospective views. *Global Ecology and Biogeography*, **10**, 3–13.
- MacArthur, R.H. (1972) *Geographical ecology*. Princeton University Press, Princeton, New Jersey.
- Macpherson, E. & Duarte, C.M. (1994) Patterns in species richness, size, and latitudinal range of east Atlantic fishes. *Ecography*, **17**, 242–248.
- Matthews, W.J. (1998) *Patterns in freshwater fish ecology*. Kluwer Academic Publishers, Norwell.
- Maurer, B.A. (1998) The evolution of body size in birds. I. Evidence for non-random diversification. *Evolutionary Ecology*, **12**, 925–934.
- Maurer, B.A. (1999) *Untangling ecological complexity*. University of Chicago Press, Chicago.
- Maurer, B.A., Brown, J.A. & Rusler, R.D. (1992) The micro and macro in body size evolution. *Evolution*, **46**, 939–953.
- May, R.M. (1986) The search for patterns in the balance of nature: advances and retreats. *Ecology*, **67**, 1115–1126.
- Mills, C.A. (1988) The effect of extreme northerly climatic conditions on the life history of the minnow, *Phoxinus phoxinus* (L.). *Journal of Fish Biology*, **33**, 545–561.
- Nathan, R. & Werner, Y.L. (1999) Reptiles and breeding birds on Mt. Hermon: patterns of altitudinal distribution and species richness. *Israel Journal of Zoology*, **45**, 1–33.
- Odland, A. & Birks, H.J.B. (1999) The altitudinal gradient of vascular plant species richness in Aurland, western Norway. *Ecography*, **22**, 548–566.
- Patterson, B.D., Stotz, D.F., Solari, S., Fitzpatrick, J.W. & Pacheco, V. (1998) Contrasting patterns of elevational zonation for birds and mammals in the Andes of south-eastern Peru. *Journal of Biogeography*, **25**, 593–607.
- Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *American Naturalist*, **100**, 33–46.
- Power, M. & McKinley, R.S. (1997) Latitudinal variation in lake sturgeon size as related to thermal opportunity for growth. *Transactions of the American Fisheries Society*, **126**, 549–558.
- Preston, F.W. (1962a) The canonical distribution of commonness and rarity: Part I. *Ecology*, **43**, 185–215.
- Preston, F.W. (1962b) The canonical distribution of commonness and rarity: Part II. *Ecology*, **43**, 410–432.
- Pyrz, T.W. & Wojtusiak, J. (2002) The vertical distribution of pronophiline butterflies (Nymphalidae, Satyrinae) along an elevational transect in Monte Zepa (Cordillera de Mérida, Venezuela) with remarks on their diversity and parapatric distribution. *Global Ecology and Biogeography*, **11**, 211–221.
- Rahbek, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, **18**, 200–205.
- Rahbek, C. (1997) The relationship between area, elevation, and regional species richness in Neotropical birds. *American Naturalist*, **149**, 875–902.
- Rex, M.A. & Etter, R.J. (1998) Bathymetric patterns of body size: implications for deep-sea biodiversity. *Deep-Sea Research*, **II** (45), 103–127.
- Rex, M.A., Etter, R.J., Clain, A.J. & Hill, M.S. (1999) Bathymetric patterns of body size in deep-sea gastropods. *Evolution*, **53**, 1298–1301.
- Ricklefs, R.E. & Schluter, D. (1993) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago, Chicago.
- Rohde, K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, **65**, 514–527.
- Rohde, K. (1996) Rapoport's rule is a local phenomenon and cannot explain latitudinal gradients in species diversity. *Biodiversity Letters*, **3**, 10–13.
- Rohde, K. (1999) Latitudinal gradients in species diversity and Rapoport's rule revisited: a review of recent work and what can parasites teach us about the causes of the gradients? *Ecography*, **22**, 593–613.
- Rohde, K. & Heap, M. (1996) Latitudinal ranges of teleost fish in the Atlantic and Indo-Pacific Oceans. *American Naturalist*, **147**, 659–665.
- Rohde, K., Heap, M. & Heap, D. (1993) Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. *American Naturalist*, **142**, 1–16.
- Rosenfield, J.A. (2002) Pattern and process in the geographical ranges of freshwater fishes. *Global Ecology and Biogeography*, **11**, 323–332.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Roy, K. & Martien, K.K. (2001) Latitudinal distribution of body size in north-eastern Pacific marine bivalves. *Journal of Biogeography*, **28**, 485–493.
- Ruggiero, A. & Lawton, J.H. (1998) Are there latitudinal and altitudinal Rapoport effects in the geographic ranges of Andean

- passerine birds? *Biological Journal of the Linnean Society*, **63**, 283–304.
- Sanders, N.J. (2002) Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. *Ecography*, **25**, 25–32.
- Sanders, N.J., Moss, J. & Wagner, D. (2003) Patterns of ant species richness along elevational gradients in an arid ecosystem. *Global Ecology and Biogeography*, **12**, 93–102.
- Smith, K.F. & Brown, J.H. (2002) Patterns of diversity, depth range and body size among pelagic fishes along a gradient of depth. *Global Ecology and Biogeography*, **11**, 313–322.
- Stevens, G.C. (1989) The latitudinal gradient in geographical ranges: how so many species coexist in the tropics. *American Naturalist*, **133**, 241–256.
- Stevens, G.C. (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *American Naturalist*, **140**, 893–911.
- Stevens, G.C. (1996) Extending Rapoport's rule to Pacific marine fishes. *Journal of Biogeography*, **23**, 149–154.
- Stotz, D.F., Fitzpatrick, J.W., Parker, T.A.I.I.I. & Moskovits, D.K. (1996) *Neotropical birds: ecology and conservation*. University of Chicago Press, Chicago.
- Tapponnier, P., Xu, Z., Roger, F., Meyer, B., Arnaud, N., Wittlinger, G. & Yang, J. (2001) Oblique stepwise rise and growth of the Tibet Plateau. *Science*, **294**, 1671–1677.
- Wallace, A.R. (1878) *Tropical nature and other essays*. Macmillan, New York.
- Wang, P.X. (1997) The last fifty million years — on origin of the modern natural macro-environmental pattern. *Sinica Science*, **49**, 18–22.
- Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453–470.
- Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution and Systematics*, **34**, 273–309.
- Willis, K.J. & Whittaker, R.J. (2002) Species diversity: scale matters. *Science*, **295**, 1245–1248.
- Wu, Y. & Wu, C. (1992) *The fishes of the Qinghai-Xizang Plateau*. Sichuan Publishing House of Science and Technology, Chengdu, Sichuan, China.
- Zeng, X. (1990) *Fishery resources of the Yangtze River basin*. Marine Press, Beijing, China.
- Zhang, D., Fengquan, L. & Jianmin, B. (2000) Eco-environmental effects of the Qinghai-Tibet Plateau uplift during the Quaternary in China. *Environmental Geology*, **39**, 1352–1358.
- Zhang, Y., Li, B. & Zheng, D. (2002) A discussion on the boundary and area of the Tibetan Plateau in China. *Geography Study*, **21**, 1–8.

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