

Climatic control of plant species richness along elevation gradients in the Longitudinal Range-Gorge Region

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To explore the elevation gradients in species richness in the Longitudinal Range-Gorge Region (LRGR) and evaluate how climatic variables and area may explain the patterns of species richness, 5 mountains are selected. According to the elevation dimensional gradients of the mountains, species richness, the values of area and climatic variables are calculated in each 100 m zone. The relationships between seed plant species richness and climatic variables and area along elevation gradients are analyzed. The results have shown that: (1) Elevational patterns of species richness are not uniform and can be divided in to two types. The values of species richness are higher in the lowlands and then decrease monotonically with increasing elevation in the tropical mountains. Species richness has unimodal patterns with a bias towards high values in the lower half of the elevation gradients in the subtropical mountains. (2) The patterns of species density are the same as that in species richness along elevation gradients. (3) Among the climate variables, actual evapotranspiration (AET) as a measurement of water-energy balance has strong relationships with species richness. The decline in species richness is due to the higher temperature and less precipitation in the lowlands of the subtropical mountains.

species richness, species density, elevation gradient, climate, Longitudinal Range-Gorge Region (LRGR)

One of the most significant intellectual challenges to ecologists and biogeographers is to understand spatial patterns in biodiversity^[1,2]. Latitudinal gradients in diversity and the species-area relationship are viewed to be the most general ecological patterns and have been reported much^[3–6]. Elevation gradients in species richness have received more and more attention in recent years. The decline in species richness with increasing elevation is subjected to empirical challenge^[7–11]. After a quantitative review of the literature, Rahbek^[2] concluded that hump-shaped relationships between species richness and elevation are most common rather than monotonic decrease in species richness. A reevaluation of the patterns of species richness along elevational gradients has become the focus of research on mountain

ecosystem^[7]. Many hypotheses have been proposed to explain spatial patterns in species richness. However, it is possible to narrow the list of most plausible explanations^[13]. Some of the most common diversity theories put forward for the grand clines in species richness can be collapsed to dynamic hypotheses based on climate or historical explanations. The explanation for biogeographic patterns of distinctiveness requires theories focusing on evolution and historical contingencies, whilst species richness patterns can often be related to

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contemporary ecological processes and controls^[14]. The species-energy hypothesis claims that available energy determines richness gradients^[15]. O'Brien found that geographical gradients in plant species richness were determined by water-energy dynamics and developed a theoretical model to explain plant species richness patterns^[16–18]. Therefore, potential evapotranspiration (PET, a measure of ambient energy) and actual evapotranspiration (AET, a measure of water-energy balance)^[19] have been widely used to predict spatial patterns in species richness^[13,20,21].

Numerous studies have suggested that biodiversity enhances ecosystem reliability and affects ecosystem services and functioning^[22–24]. Species diversity as the simplest measurement of biodiversity in community or regional scale is the focal point of studies in biodiversity^[25]. Most analyses of spatial patterns of species diversity concern biodiversity as measured by species richness^[1]. The Longitudinal Range-Gorge Region (LRGR) lying in the southwest of China is composed of a great many mountains and valleys running south to north. As one of the biodiversity hotspots in the world, it comprises numerous community and ecosystem types^[26,27]. It provides an excellent system for study on elevation gradients in species richness and their relationships with climatic variables. The effect of area on the relationship between species richness and elevation has rarely been considered^[12]. Further, many studies did not include data spanning the entire gradient, potentially hiding a hump-shape at lowlands of the mountains^[2,12,28]. Most of studies were conducted in a single mountain^[7–9,29,30]. Comparisons of elevation trends in diversity and environmental variables among mountain ranges are helpful to further understanding the patterns of biodiversity^[2].

With this finding, 5 mountains in the LRGR are selected. Xishuangbanna belongs to the tropical mountains. Ailao Mountains, Wuliang Mountains, Gaoligong Mountains and Baima Snow Mountains are subtropical mountains (Figure 1). The elevation patterns of species richness, area and climatic variables are analyzed. This study attempts to answer the following questions: (1) how do the patterns of species richness vary along the elevation gradients in the 5 mountains? (2) how does area affect species richness patterns? (3) how do climatic variables explain the variation in species richness patterns along the elevation gradients?

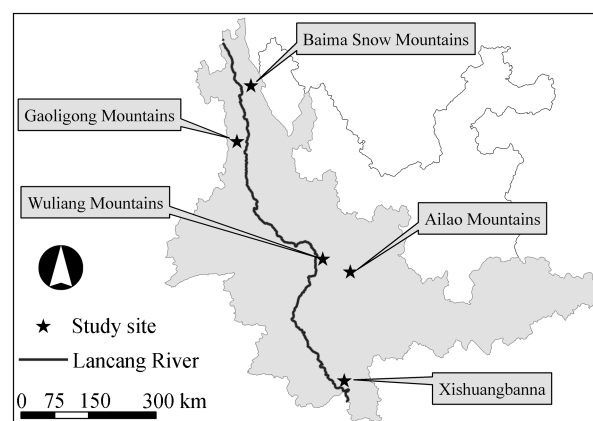


Figure 1 Location of the study site.

1 Data and methods

1.1 Botanic data

Data sources of this research are from: *Database of the Flora in Xishuangbanna* (provided by the Herbarium of Xishuangbanna Tropical Botanical Garden), *Checklist of the Flora in the Ailao Mountains*^[31], *A Systematic Checklist of the Seed Plants in the Wuliang Mountains*^[32], *A Systematic Checklist of the Seed Plants in the Gaoligong Mountains*^[33] and *Checklist of the Vascular Plants in the Baima Snow Mountains*^[34]. According to the records of species in the data, elevation ranges of species are extracted and a database of the flora in the study region is compiled. A comparative study on the elevation patterns of vascular plant species richness and fern species richness is made in the Xishuangbanna, Ailao Mt. and Baima Snow Mt. There are no remarkable differences between the two patterns. As there are not comprehensive records of fern species in the Wuliang Mt. and Gaoligong Mt., seed plant species richness in the 5 mountains is analyzed in this study. The exotic and planted species are excluded. To explore the relationships between species richness and elevation, the whole elevation gradients are divided into several 100 m elevation intervals. Species is assumed to be present in every 100 m elevation interval between its upper and lower elevation limits. Species richness is defined as the total number of species found in each 100 m elevation band. The distributive ranges of families and genera are determined by the elevation ranges of all the species that they consist of. The statistic methods of family richness and genus richness in each elevation zone are the same as that of species richness.

1.2 Climatic data

Mean annual temperature (MAT) and mean annual precipitation (MAP) are regressed against elevation based on the vertical observation data of climatic variables in these mountains. The regressions are performed by generalized linear models. The regression of mean annual precipitation against elevation can be performed by parabola or linear equations. Linear equations are more suitable for the mountains in Yunnan Province^[35], as the same result has been got in this research. The parameters of the regress equations are shown in Tables 1 and 2. The values of temperature and precipitation in each 100 m band are interpolated. The lapse rates of climatic variables are different on western and eastern slopes of the mountains. Because that the elevation range records of species are the synthesis on different slope, mean values of temperature and precipitation in each 100 m elevation band on different slope are correlated with species richness. As there is no climatic observation data in the Wuliang Mt., the corresponding regression is not made.

Expressions of climatic variables:

Vertical regress equations of MAT and MAP.

$$T=a + b E, \quad (1)$$

$$P=a + b E, \quad (2)$$

where T is mean annual temperature, P is mean annual precipitation, E is elevation (hm), and a , b are parameters to be estimated.

Actual evapotranspiration (AET)^[29,36]:

$$AET=P/(0.9+(P/L)^2)^{1/2}, \quad (3)$$

$$L=300+25T+0.05T^3, \quad (4)$$

where AET is actual evapotranspiration, P is mean annual precipitation, T is mean annual temperature.

Potential evapotranspiration (PET) and moisture index (MI)^[30,37]:

$$PET=58.93 \times ABT \quad (ABT > 0^\circ\text{C}), \quad (5)$$

$$MI= PET/P, \quad (6)$$

where PET is potential evapotranspiration, ABT is mean annual bio-temperature, MI is moisture index, P is mean annual precipitation.

1.3 Area and species density

Topographic data is the LRGR's 1:250000 Digital Elevation Model (DEM) obtained from the State Bureau of Surveying and Mapping, and its resolution cell is 100 m \times 100 m. Area in each 100 m band is extracted based on the DEM. Species richness tends to increase with increasing area. Taking area into account, species density is calculated as follows^[38]:

$$D=S/\log A, \quad (7)$$

where D is species density, S is species richness, and A is area.

2 Results and analysis

2.1 Elevation gradients in seed plant richness

Plant richness is measured by species richness, genus richness and family richness. The values of species, ge-

Table 1 Parameters of vertical regress equations of MAT

Study site	a	b	r	Ref.
Western slope of Baima Snow Mountains		0.71 ^{a)}		[35]
Eastern slope of Baima Snow Mountains		0.78 ^{a)}		[35]
Western slope of Gaoligong Mountains	25.29	-0.59	0.99 ^{b)}	this study
Eastern slope of Gaoligong Mountains	26.86	-0.63	0.99 ^{b)}	this study
Western slope of Ailao Mountains	25.84	-0.60	0.99 ^{b)}	this study
Eastern slope of Ailao Mountains	28.38	-0.70	0.99 ^{b)}	this study
Xishuangbanna	24.98	-0.57	0.98 ^{b)}	this study

a) Lapse rate; b) $P < 0.01$.

Table 2 Parameters of vertical regress equations of MAP

Study site	a	b	r	Ref.
Western slope of Baima Snow Mountains	35.70	16.40	0.91 ^{b)}	[35]
Eastern slope of Baima Snow Mountains	-244.20	27.20	0.91 ^{b)}	[35]
Western slope of Gaoligong Mountains	561.41	75.13	0.97 ^{c)}	this study
Eastern slope of Gaoligong Mountains	-160.49	99.22	0.99 ^{c)}	this study
Western slope of Ailao Mountains	884.40	36.16	0.98 ^{b)}	this study
Eastern slope of Ailao Mountains	657.40	34.16	0.99 ^{c)}	this study
Xishuangbanna	987.50	42.50	0.96 ^{a)}	[35]

a) $P < 0.1$; b) $P < 0.05$; c) $P < 0.01$.

nus and family richness vary less and are shown in the higher level in the elevation range of 500–900 m in Xishuangbanna (tropical mountains in the lower latitude in the LRGR). The natural vegetation types in this zone are tropical seasonal rain forests and monsoon forests^[39]. Seed plant richness decreases sharply from 900 m to the summit (Figure 2(a)). The patterns of seed plant richness along elevation gradients are hump-shaped in the subtropical mountains (Ailao Mt., Wuliang Mt., Gaoligong Mt. and Baima Snow Mt., subtropical mountains in the higher latitude in the LRGR). Seed plant richness increases remarkably to the maximum and gradually decreases afterwards with a bias towards high values in the lower half of the elevation gradients. Maximum seed plant richness is observed between 1500 and 2500 m and species richness peaks at 2000 and 2100 m in the Ailao Mt., Wuliang Mt. and Gaoligong Mt. (Figure 2(b)–(d)).

The regional vegetation types consist of mid-mountain humid evergreen broad-leaved forests, monsoon evergreen broad-leaved forests and semi-humid evergreen broad-leaved forests^[31, 33, 40]. Maximum plant richness is observed between 2500 and 3500 m and species richness peaks at 3000 m in the Baima Snow Mt. (Figure 2(e)). The corresponding vegetation types in this zone are cold-temperate needle-leaved forests and cool-temperate needle-leaved forests^[34].

Summarily, the patterns of species richness along elevation gradients can be divided to two types: a smooth to monotonic decrease in the tropical mountains and hump-shaped patterns in the subtropical mountains. The elevation peaks in family richness, genus richness and species richness of seed plants emerge at higher elevation in the mountains with the increasing latitude (Figure 3).

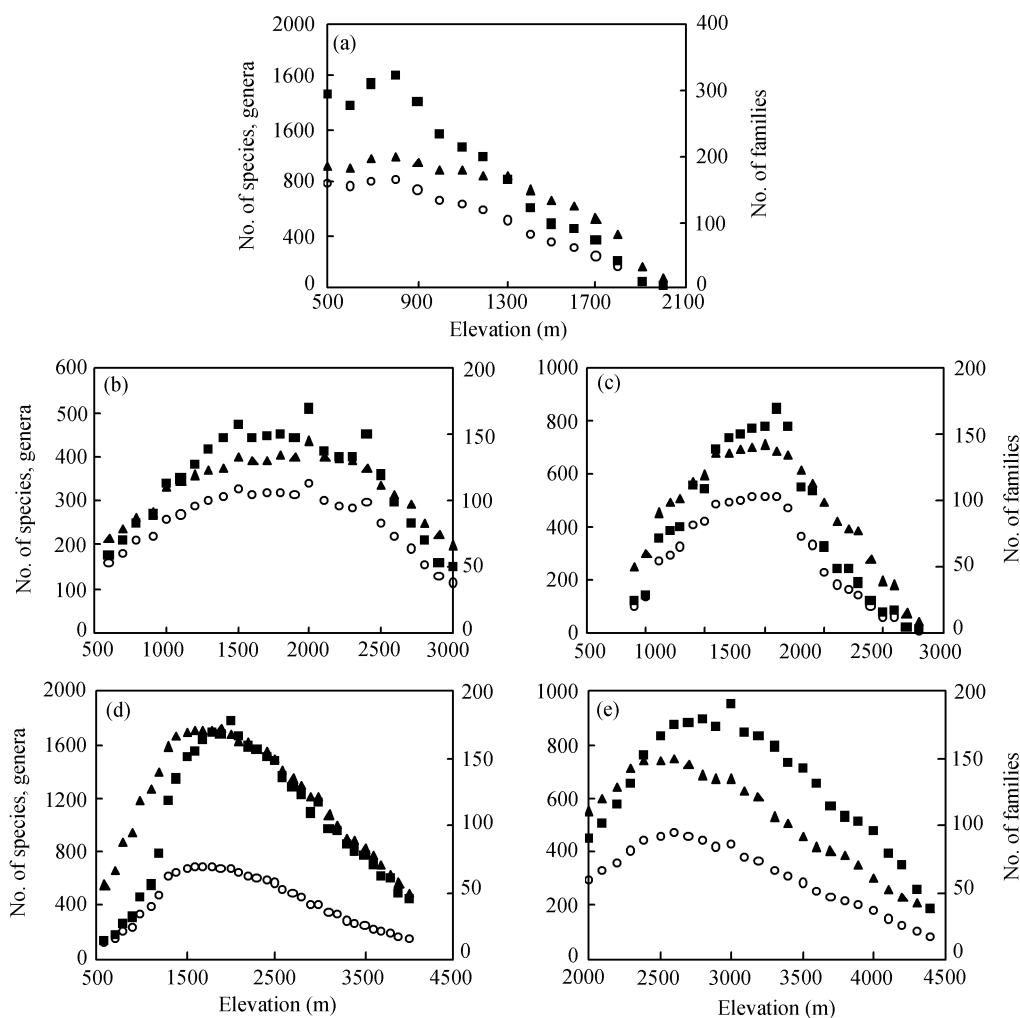


Figure 2 Patterns of family richness, generic richness and species richness of seed plants versus elevation. (a) Xishuangbanna; (b) Ailao Mt.; (c) Wuliang Mt.; (d) Gaoligong Mt.; (e) Baima Snow Mt. ■, Species; ○, genera; ▲, family.

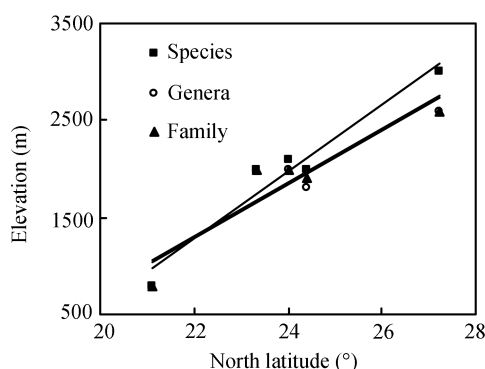


Figure 3 Elevation peaks in family richness, generic richness and species richness of seed plants versus latitude in five mountains.

2.2 Species density along the elevation gradients

Species richness tends to increase with increasing area under homogeneous environmental conditions^[6,13,41]. The topography of mountains has a great impact on area along elevation gradients^[42]. Taking area into account, estimates of the area in each 100 m band are extracted from the DEM in the study region and species density is calculated.

The relationships between area and elevation are unimodal as the steeper terrain in the lowlands adjunct to the valleys (Figure 4(a)). As species richness is adjusted for area, the patterns of species density remain the same as that of species richness along elevation gradients (Figure 2 and Figure 4(b)). Because the elevation patterns in family density and genus density are the same as that in species richness, they are not shown with figures. Maximum species density peaks at 500 m in Xishuangbanna and the point has not been shown because of the limit of the scale in the figure. As the patterns of area and species richness along elevation gradients are not the same in Xishuangbanna and species richness does

not peak at the elevation where the area is the largest for all the 5 mountains (Figure 2 and Figure 4(a)), the effect of area on the patterns of species richness along elevation gradients is not remarkable.

2.3 Patterns of climatic variables

Many components of climate including temperature and precipitation vary along elevation gradients and species richness should vary with local climatic conditions. Analyses of clines in climatic variables both within and among mountain ranges in particular those directly associated with causal explanations for the observed patterns are helpful to understanding the spatial patterns of diversity^[2]. The patterns of climatic variables along elevation gradients are shown in Figure 5. MAT and PET decrease monotonically with increasing elevation. The values of PET vary less in the same elevation band among mountains (Figure 5(a) and (c)). MAP has a positive increase with elevation. The lapse rates of MAP vary much among mountains (Figure 5(b)). As actual evapotranspiration takes both temperature and precipitation as its parameters, the elevation patterns of AET are totally different among mountains (Figure 5(d)).

2.4 Relationships between climatic variables and species richness

(i) Potential evapotranspiration. Species richness has a positive increase with PET in Xishuangbanna and fluctuates in the lowlands when the values of PET are the highest. There is not a marked decrease in species richness in the lower elevation (Figure 6). Species richness has unimodal relationships with PET in the subtropical mountains. Species richness peaks at intermediate elevations and decreases towards higher (lowland)

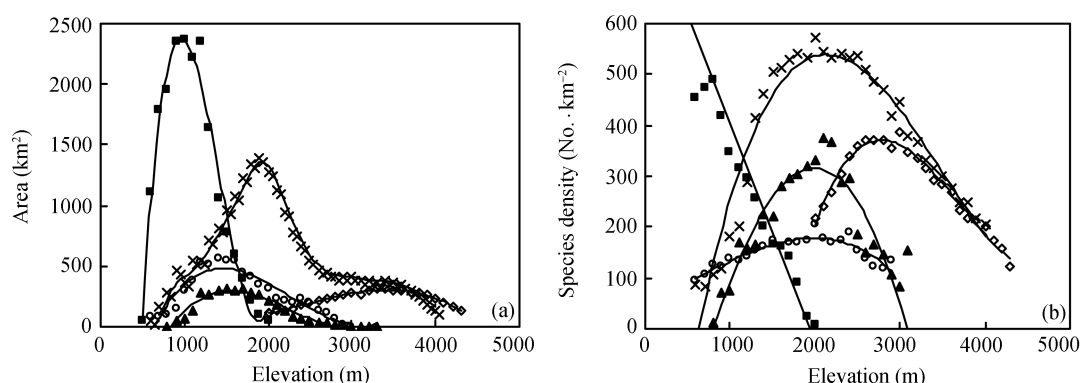


Figure 4 Relationships between elevation and (a) area, (b) species density. ■, Xishuangbanna; ○, Ailao Mt.; ▲, Wsuliang Mt.; ×, Gaoligong Mt.; ◇, Baima Snow Mt.

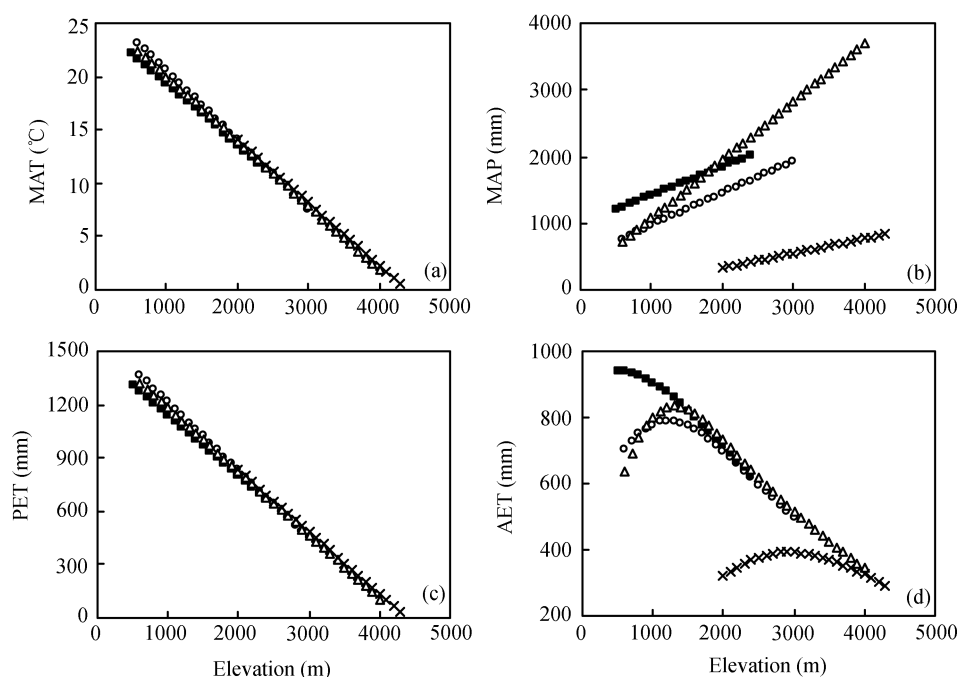


Figure 5 Relationships between elevation and (a) mean annual temperature (MAT), (b) mean annual precipitation (MAP), potential evapotranspiration (PET), (d) actual evapotranspiration (AET). ■, Xishuangbanna; ○, Ailao Mt.; △, Gaoligong Mt.; ×, Baima Snow Mt.

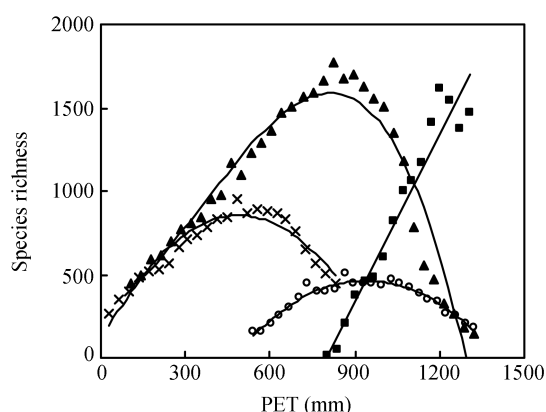


Figure 6 Relationships between species richness and potential evapotranspiration (PET). ■, Xishuangbanna; ○, Ailao Mt.; ▲, Gaoligong Mt.; ×, Baima Snow Mt.

and lower (highland) values of PET (Figure 6). The lapse rates of species richness are higher in the lower half of the subtropical mountains than that in the higher half along PET gradients. In general, there are not uniform linear patterns in species richness along PET gradients.

(ii) Actual evapotranspiration. The patterns of species richness and AET along the elevation gradients are the same in four mountains (Figure 7). There is a strong relationship between species richness and AET. The patterns of species richness and AET are not synchronous and species richness peaks at higher elevation than

AET along elevation gradients in the Ailao Mt. and Gaoligong Mt.. Factors causing variation in species richness may differ between life forms of plants and species richness of different life forms (herbs, shrubs, trees and climbers) may vary along elevation gradients^[8,43]. The synthesis of variation in species richness of different life forms along elevation gradients should be one of the possible causes. Further studies are required.

Through the comparisons of the elevation patterns of temperature and precipitation among mountain ranges, it can be concluded that the unimodal relationships between AET and elevation are caused by the climatic conditions of higher temperature and less precipitation in the lowlands of the subtropical mountains (Figure 5). A deduction has been made that the hump-shaped patterns of species richness along the subtropical elevation gradients are caused by the “inferior” climatic conditions (higher temperature and less precipitation). To prove the deduction, the values of MI in each 100 m elevation intervals are calculated by the formula of Holdridge^[30,37]. The values of MI in the elevation range of 500–900 m are less than 1 in Xishuangbanna. It belongs to the humid climate conditions and humidity is not the limitation for species richness in this zone. The values of MI are much higher than 1 in the lowlands of

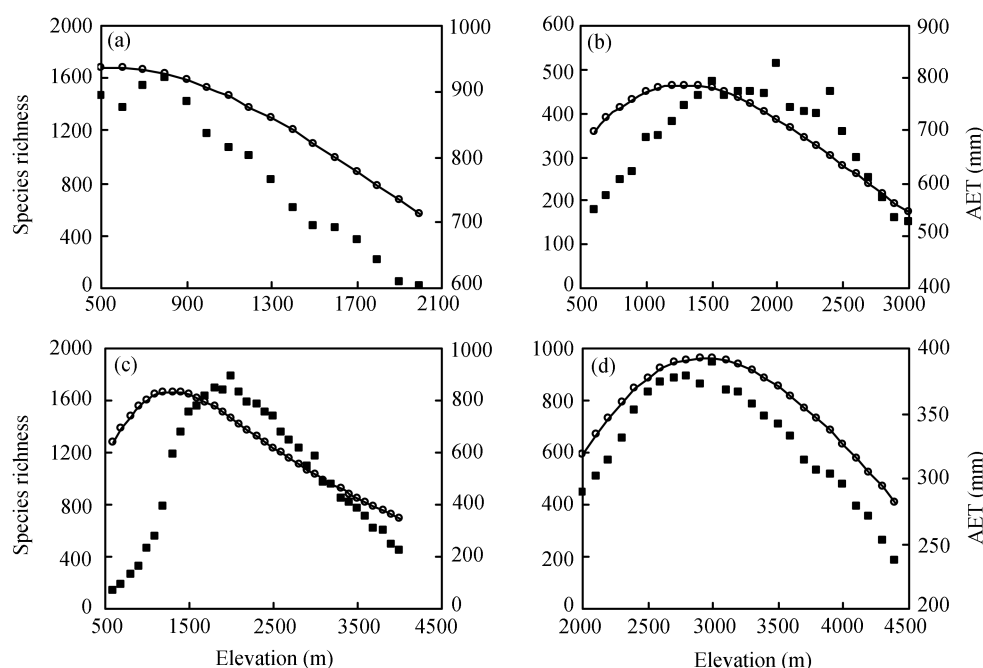


Figure 7 Relationships between species richness and actual evapotranspiration (AET). (a) Xishuangbanna; (b) Ailao Mt.; (c) Gaoligong Mt.; and (d) Baima Snow Mt. ■, Species richness; ○, AET.

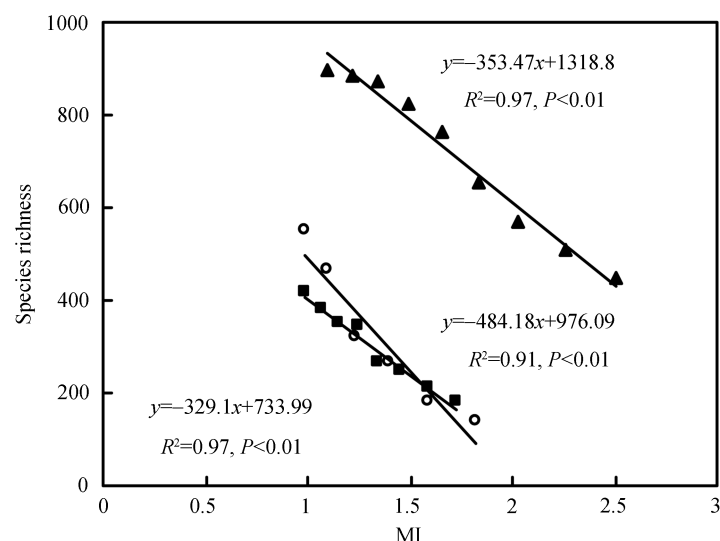


Figure 8 Relationships between species richness and moisture index (MI) when $MI \geq 1$. ■, Ailao Mt.; ○, Gaoligong Mt.; ▲, Baima Snow Mt.

the subtropical mountains. It is classed to semiarid climate conditions. Species richness is limited by the negative water-balance. The patterns of species richness along MI gradients when the values of MI exceed 1 are shown in Figure 8. Species richness decreases significantly with increasing MI as the reinforcements of the arid climate conditions.

3 Discussion and conclusion

There are strong relationships between species richness

and AET along the elevation gradients in this study. The ecological meaning is that the patterns of species richness are determined by both temperature and humidity. Higher temperature that causes the reduction of humidity is the limitation for species richness in the lowlands of the mountains and lower temperature is the limitation in the higher part of the mountains. The optimal climatic conditions lead to higher species richness. For the lowlands of the tropical mountains (Xishuangbanna), humidity is not the limitation and there is not a marked

decrease in species richness. Higher temperature and less precipitation lead to negative water-balance climate conditions and lower humidity in the lowlands of the subtropical mountains. As temperature and humidity limit species richness at both extremes of the subtropical mountains, species richness has a unimodal relationship with elevation.

The evolutionary history of different regions can influence large-scale diversity gradients and biotic factors may affect diversity gradients at large extents^[13]. The intensity of anthropogenic disturbance also cannot be excluded^[2]. Many ecological and biological mechanisms will affect diversity patterns on local scales, whilst at the macro-scale they are dependent largely upon climatic controls for their operations^[14]. The elevation patterns of species richness among mountain ranges have been explained by water-energy variables in this study.

In summary, the results have shown that: (1) The pat-

terns of species richness along elevation gradients can be divided into two types in the LRGR. Species richness is higher in the lowlands and then decreases monotonically with increasing elevation in the tropical mountains and has unimodal relationships with elevation in the subtropical mountains. (2) The patterns of species density are the same as that in species richness along elevation gradients. (3) There are strong relationships between species richness and actual evapotranspiration (AET, a measure of water-energy balance). Species richness decreases significantly with increasing MI in the lowlands of the subtropical mountains.

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