ALTITUDINAL PATTERNS OF VASCULAR PLANT RICHNESS
IN HIGH MOUNTAINS: APPLYING OF GENERATIVE
ADDITIVE MODEL

ABSTRACT: To explore and describe the species richness patterns along altitudinal, high mountain gradients, two transects – northern exposure (YG) and southern exposure (TD) at Mt. Jiuding (1200–4200 m) in Western China (31°13’–31°46’N, 103°29’–104°05’E) were selected. They differ from south to north in climate conditions and vegetation zonation, and each transect was sampled according to a uniform method. Every 200 m along the altitudinal gradient we set a sampling belt of 3000 m × 5 m to record the tree species, and 30 plots of 5 m × 5 m within every vegetation belt were used to investigate shrub and herb species. We compared the composition of plant species and calculated the coefficient of similarity between the two transects. A Generalized Additive Model (GAM) was used to describe the richness patterns. For the whole Mt. Jiuding, the richness at all three levels (species, genus and family) showed a monotonically decreasing pattern. As for the different growth forms, richness of the trees, shrubs and pteridophytes showed hump-shaped patterns; and herbs showed a slow decreasing pattern along the altitudinal gradients. In TD transect, the richness of species, genus and family showed monotonically decreasing pattern. The species richness patterns for different growth forms peaked at middle altitude except for the graminoids and other herbs.

The evolutionary history of the vegetation in Mt. Jiuding was quite consistent, and different richness patterns along altitudinal gradients might be resulted from different contemporary ecological conditions. Human disturbance and different range of altitudinal gradients were also important factors for different richness patterns between the two transects. In our study, species in different growth forms showed different altitudinal patterns, but those species with similar requirements to environmental conditions showed similar richness patterns along altitudinal gradients.

KEY WORDS: altitudinal gradient, plant species richness, patterns, growth form, Mt. Jiuding

1. INTRODUCTION

Spatial patterns of taxon richness (e.g. species richness) have been fascinating biologists for a long time, and the search for their underlying mechanisms has been a central focus for ecology and biogeography since the start of this discipline (Pianka 1966, Brown and Lomolino 1998). Despite two centuries of exploration, our understanding of factors determining the distribution of life on Earth is in many ways still in its infancy (Rahbek
Quantifying spatial patterns of species richness and determining the processes that give rise to these patterns are core problems in biodiversity theory (Ren et al. 2006). Large environmental variation within a small geographical area makes altitudinal gradients ideal for investigating several ecological and biogeographical hypotheses (Körner 2000). Furthermore, understanding changes in richness of plant species along altitudinal gradients is valuable in the study of global climate change because changing climate may lead to the migration of species (Körner 2000; Klanderud and Birks 2003). Many researches have explored the altitudinal biodiversity patterns of vascular plants (Oommen and Shanker 2005), liverwort and moss species (Grau et al. 2008), birds (Rahbek 1997), mammals (Heaney 2001, McCain 2007) and insects (Sanders 2002), and different patterns have been observed for different organisms in different regions.

At least five main forms of richness patterns have been observed: a monotonically decrease with increasing elevation (e.g. Brown and Lomolino 1998, Willig et al. 2003), a hump-shaped variation with a peak at intermediate elevation (e.g. Colwell and Hurt 1994, Rahbek 2005, Zhao et al. 2005), a plateau at low elevations (Tang et al. 2006), a low value at mid-altitude (Peet 1978) and no distinct change with altitude (Wilson and Sydes 1988). The former three were more frequently found in past researches. Furthermore, ecological systems are hierarchically structured in nature (Marceau 1999), and different growth forms, such as tree, shrub, or herbaceous plant, have different altitudinal patterns of richness (Ren et al. 2006, Hofer et al. 2008). At present it is not clear if there are any common patterns of species richness along altitude (Körner 2000).

Many factors (biotic, abiotic, historical, geographical and stochastic forces) have been discussed that may be responsible for altitudinal patterns of species richness (Rahbek 1995, 2005, Willig et al. 2003). Climate, productivity and other energy-related variables are commonly proposed to explain species richness patterns along altitudinal gradients (Rahbek 1997). Area is another important factor influencing biodiversity patterns (e.g. altitudinal gradients) at different scales (He et al. 1996, Rahbek 1997). Other hypotheses include ‘Rapoport’s rule’ and the ‘mid-domain effect’. Rapoport’s rule proposes that there is a positive correlation between elevation and the elevational range of species (Brown 1998). Mid-domain effect suggests that mid-elevation peaks in species richness arise because of the increasing overlap of species ranges towards the centre of domain (Colwell et al. 2005, Hawkins and Diniz-Filho 2002, Zapata et al. 2005). These hypotheses have recently attracted much interest and caused controversy among the researchers (e.g. Hawkins and Diniz-Filho 2002, Colwell et al. 2004). Furthermore, recent studies have revealed that biodiversity patterns cannot be ascribed to one single factor but to multiple variables (e.g. location, altitudinal span, climate, habitat heterogeneity, area, human disturbance and character of natural vegetation (Jetz and Rahbek 2002, McCain 2005).

Species richness studies from different locations are also very important for tropical studies emphasize the importance of moisture and related factors (e.g. Brown 1998), whereas temperate zones stress the importance of energy as a limiting factor (e.g. Currie 1991). An increasing body of literature documents the rich biodiversity of tropical and sub-tropical mountain ecosystems, showing the highest biodiversity tends to appear in the middle altitude zone (McCain 2005). But in the temperate area, there are just few researches for the species richness pattern along altitudinal gradients (Wang et al. 2007, Zhao et al. 2005), the patterns and the underlying mechanism are still uncertain at present.

Hengduan Mountain area has been considered as one of the three centers holding the highest biodiversity in China (Ying 2001), and this area is especially rich in endemic species (Wilson 1992) and genera (Ying et al. 1993). It is also a biodiversity “hot-spot” in the world recognized by Meyers (1988) and Wilson (1992). The mountain is an ecotone between the plains region and mountainous region of Western China and the floristic transition zone from China–Himalaya forest sub-region and China–Japan forest sub-region. This area has many great mountains with a huge span of altitudinal gradients above 3000 m. The geographical extent and complex topography induce a broader range of climate, soil and other abiotic conditions,
and thus support distinct vegetation types from the lowland to alpine areas. This suggests that Hengduan Mountain area should be an ideal location to explore patterns of species richness (Zhao et al. 2005). Investigating richness patterns of the vascular species in Hengduan Mountain area is of great significance to understand altitudinal species-richness patterns in temperate area, and would give new insights for our perception of species-richness patterns on earth.

The researches for Hengduan Mountain’s biodiversity are overly insufficient so far, and most of them concentrated in the south part of Hengduan Mountain (e.g. north-west of Yunnan and south-west of Sichuan). Since there are nearly no works for altitudinal richness pattern in the north of Hengduan Mountains, it is unknown if there are different species richness patterns between north and south. In this study, the patterns of vascular plant richness along two transects on the west-facing slope of Mt. Jiuding were investigated. The aim of present study was to determine: (i) the altitudinal species richness pattern of all vascular plants, (ii) richness patterns at different taxonomic levels, (iii) richness patterns among different growth forms, and (iv) the differences in altitudinal patterns between two chosen transects.

2. STUDY AREA

The Jiuding Mountain, a region of the Chaping Mountain Range, famous as important corridor for the Giant Panda’s habitats, is located in central Sichuan, China at 31°13’–31°46’N, 103°29’–104°05’E, with an approximate area of 220 km² on the west slope. Extending from 1128 m to 4998 m a.s.l., the highest peak is the Mt. Shiziwang. A high elevation, deep valleys, and steep slopes characterize the physiognomy of Mt. Jiuding. In different parts of Mt. Jiuding, the water systems are quite different. The south part belongs to Minjiang River but the north part falls into Wenchuan County.

![Fig. 1. Location, topography and climate diagrams on the west slope of Mt. Jiuding. TD transect – in the north belongs to Fujiang River, YG transect – in the south falls into Minjiang River.](image)
Fujiang River. In this study, two transects on the west slope of Mt. Jiuding were chosen, one was YG transect belonging to Minjiang River, another was TD transect belonging to Fujiang River (Fig. 1).

The climates for these two transects are quite different. YG transect belongs to continental semiarid monsoon climate of warm-temperate zone. Consequently, the climate is dry and windy, with an annual mean temperature of 13.5 and precipitation of 516.1 mm per year under 2000 m a.s.l. (CCWC ATQnap, 1992). TD transect belongs to a part of great mountain with deep canyon in western Sichuan Province (CGSV, 1980). The climate is cool in summer, cold in winter, and the temperature changes sharply in one day. The warmest month is July with a mean temperature of 20.9°C and the coldest is January with a mean of 0.4°C (lowland). The annual mean temperature is 11.2°C and the annual precipitation is 492.7 mm; but the precipitation is unevenly distributed, 92% of the whole precipitation occurs from April to October (CCMC ATQnap, 1997).

Because of the great altitudinal gradient range, vegetation on the west slope of Mt. Jiuding varies greatly from the bottom of valley to the top of mountain. Along an altitudinal gradient on YG transect, one can find valley shrubland (1300–2000 m a.s.l.), deciduous broad-leaf forest (1800–3000 m a.s.l.), subalpine coniferous forest (2700–3500 m a.s.l.), alpine bush (3200–3800 m a.s.l.) and alpine meadow (3800–4200 m a.s.l.). The timberline was found at 3500 m above sea level. On TD transect, vegetation types along altitudinal gradients include evergreen broad-leaf forest (1100–2600 m a.s.l.), deciduous broad-leaf forest (2400–3000 m a.s.l.), subalpine coniferous forest (2900–3400 m a.s.l.), subalpine shrub (3200–3600 m a.s.l.) and subalpine meadow (3200–3600 m a.s.l.). The timberline occurred at 3400 m above sea level.

3. METHODS

3.1. Field sampling

Plant specimens were collected from 2002 to 2006. In order to compare the differences of vascular species richness between the south part and the north part, two transects were chosen, one was YG transect from Yanmengou (1400 m a.s.l.) to Guangguangshan (4200 m a.s.l.) in the south part, and another was TD transect from Tumen (1200 m a.s.l.) to Duantouya (3600 m a.s.l.) in the north.

Every 200 m along the altitudinal gradient we set a sampling belt of 3000 m × 5 m. In these belts, all the tree species were recorded and specimens were collected for identification. In addition, 30 plots of 5 m × 5 m within every vegetation belt were used to investigate shrub and herb species, and the distances between the plots were always between 80 m and 120 m. Thus, all altitudinal intervals compared on the two transects had equal numbers of plots and the same sampling size. Plots were not placed in clear-cuts or other sites with clear human impacts. In total, 38 sampling belts on the west slope of Mt. Jiuding, with a total area of about 42 000 m² were investigated. There were 15 sampling belts and 450 plots in the YG transect, and 13 sampling belts with 390 plots in the TD transect.

3.2. Data analyses

In TD and YG transects, the sum-total of the species found in every sampling belts at each altitude level was calculated. Family circumscriptions followed APG II (2003) and Wu (1994–2006) for angiosperms, Cheng (1978) for gymnosperms, and Ching (1978) for pteridophytes. Furthermore, the data of the two transects were combined together to describe the species richness for the whole Mt. Jiuding. We compared the composition of plant species and calculated the coefficient of similarity (Zhang and Zhang 1998) between the two transects using formula:

$$CS = \frac{c}{a + b - c}$$

where CS: Coefficient of similarity; a: number of species (genus or family) in TD transect; b: number of species (genus or family) in YG transect; c: number of mutual species (genus or family).

To describe the species richness patterns in relation to altitude, a generalized additive model (GAM) with a cubic smooth spline (Hastie and Tibshirani 1990) was used in S-PLUS 7.0 (Insightful Corp, 2005). The GAM approach is especially useful for data
Altitudinal patterns of plant richness in mountains

Altitudinal gradient of richness at different taxonomic level (family, genus and species) and for different growth forms (including tree, shrub and herb) was tested to reflect the impact of plant evolutionary level and plant ecology. As the altitudinal pattern of herb was quite inconspicuous, herbs were divided into three groups including pteridophyte, graminoid and other herb.

4. RESULTS

On the west slope of Mt. Jiuding, we found 1289 vascular plant species belonging to 577 genera in 146 families. In TD transect there were 681 vascular plant species belonging to 355 genera in 113 families; and in YG transect there were 733 vascular plant species belonging to 363 genera in 111 families. The coefficients of similarity for family, genus and species between the two transects were 0.8065, 0.6934 and 0.5531 respectively (Table 1).

The number of total plant species showed a monotonically decreasing pattern along the altitudinal gradient in the whole Mt. Jiuding, but it decreased very slowly at low elevation, even increasing to a degree and peaked at 1800 m above sea level. But for the two transects separately, different change tendencies could be observed. In TD transect, the species richness declined with the increase of elevation; but for YG transect, a hump-shaped pattern was found with a peak occurring at 2200 m above sea level. Genus richness and family

Table 1. Comparison of the similarity CS% (formula 1) of species composition between two transects in the west slope of Mt. Jiuding. The two transects had similar aspects and the same sampling width. TD transect – in the north from 1200 m to 3600 m a.s.l., YG transect – in the south part from 1400 m to 4200 m a.s.l.

<table>
<thead>
<tr>
<th>Item</th>
<th>Mt. Jiuding</th>
<th>TD transect</th>
<th>YG transect</th>
<th>Mutual in TD and YG transect</th>
<th>CS (%)</th>
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<td>113</td>
<td>111</td>
<td>100</td>
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<td>294</td>
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<tr>
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<td>681</td>
<td>733</td>
<td>510</td>
<td>55</td>
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Fig. 2. Altitudinal patterns of total vascular species, genus and family richness. The fitted lines represent a Generalized Additive Model (Hastie and Tashirani 1990) model with a cubic smooth spline. Both transects had similar aspects and the same sampling width in the west slope of Mt. Jiuding. TD transect – in the north from 1200 m to 3600 m a.s.l., YG transect – in the south part from 1400 m to 4200 m a.s.l.

exploration as it makes no a priori assumptions about the type of relationship being modeled. Altitudinal gradient of richness at different taxonomic level (family, genus and species) and for different growth forms (including tree, shrub and herb) was tested to reflect the impact of plant evolutionary level and plant ecology. As the altitudinal pattern of herb was quite inconspicuous, herbs were divided into three groups including pteridophyte, graminoid and other herb.
richness showed similar altitudinal patterns in Mt. Jiuding. Generally, genus richness and family richness declined with the increase of elevation both in the whole Mt. Jiuding and in TD transect, but in YG transect, the family richness and genus richness showed hump-shaped patterns with a peak at 2400 m a.s.l. for family richness and one at 2000–2200 m a.s.l. for genus richness (Fig. 2).

Tree species richness showed a different pattern from the total plant species richness. Both in the whole Mt. Jiuding and in YG transect, tree species richness showed a hump-shaped patterns. The peak of tree richness in the whole Mt. Jiuding appeared at 2200 m a.s.l. and in YG transect it was found at middle elevation about 2400–2600 m a.s.l. Tree species richness declined along the altitudinal gradient in TD transect, and the decrease was sharper at low elevation (under 2400 m a.s.l.). For shrub species richness the whole Mt. Jiuding and two transects showed similar patterns, and all of them appeared hump-shaped patterns and peaked at the elevation of 1800–2200 m a.s.l. (Fig. 3).

The altitudinal pattern of herb species was quite inconspicuous. Generally, the richness of the three kinds of herbs, i.e. pteridophytes, graminoids and others, showed quite different patterns. Pteridophyte species richness showed a hump-shaped pattern along altitudinal gradient both in the whole Mt. Jiuding and in YG transect, but in TD transect it showed a wave-like pattern and changed smoothly at middle elevation between 1800 m and 3000 m. Graminoid species richness showed a monotonically decreasing pattern in the TD transect, but exhibited a wave-like pattern both in the whole Mt. Jiuding and in the YG transect with the lowest value occurring at 3400–3600 m a.s.l. (Fig. 4).

5. DISCUSSION

Quantifying biodiversity patterns and identifying the mechanisms that create them are essential for the understanding of ecosystems as well as for conservation and management of the biodiversity. In the present study, we found three richness patterns: monotonically decreasing pattern, hump-shaped pattern and wave-like pattern. The major altitudinal richness patterns in the whole Mt. Jiuding were monotonically decreasing pattern and hump-shaped one. This is in agreement with the studies reviewed by Rahbek (1995) who found that unimodal pattern was the most common and that linear decreasing trend with altitude was also frequently observed. But our results are quite different with
Wang et al. (2007) and Zhao et al. (2005), both of them supported the rule of the "mid-altitude bulge". Previously, differences in altitudinal richness patterns had been attributed to differences in sampling methods (McCoy 1990, Rahbek 1995). In the present study, the difference in altitudinal richness patterns can not be due to differences in sampling or plot sizes.

Explanation for the differences in altitudinal richness patterns is quite complex, but it could generally be the result of two factors, evolutionary history and contemporary ecological conditions (Whittaker et al. 2001, Ricklefs 2004). We compared the similarity in plant species composition between the two transects, and got very high coefficients especially in family similarity. This indicated that the difference of plant composition between south part and north part of Mt. Jiuding was not very conspicuous. The richness patterns of family, genus and species for the whole Mt. Jiuding and for both transects individually were quite similar. For the whole Mt. Jiuding and TD transect, the richness at species, genus or family level showed a monotonically decreasing pattern. For YG transect, altitudinal gradient of richness at different taxonomic levels showed hump-shaped patterns. This indicated that the evolutionary history of vegetation in Mt. Jiuding was quite consistent, and that the different patterns of richness resulted from different contemporary ecological conditions.

In every richness patterns, it should be noticed that the tendency to change above 2800 m a.s.l. was quite similar, and that most of the differences appeared at low altitude. Comparing the ecological conditions between two transects, we tried to find underlying mechanisms of different richness patterns in Mt. Jiuding. The climates in the two transects were quite different at low elevation. In the YG transect, sparse valley shrubland was the lower vegetation zone and led to low species richness at low elevation. With the increase of air humidity vegetation became dense and the highest richness occurred at the middle elevation, i.e. the broadleaf and coniferous mixed forest zone. In TD transect, the lower vegetation zone was broad-leaf forest with abundant vascular plant species, which led to a monotonically decreasing pattern.

Anthropogenic factor also has an important impact on the vascular species richness pattern along altitudinal gradients. In Mt. Jiuding, most areas are far away from the residential and agricultural districts, so the whole vegetation is quite well preserved and maintains its primitive form. But in low altitude area, especially in those with permanent residents, the vegetation is seriously disturbed.
both in a frequent and intensive way. The human disturbance has an important destructive power; any species, community, and even a whole vegetation cover could disappear because of human activity. Thus, it is hard to assess the effect of human disturbance for the species richness. Generally, human disturbance is more concentrated on some organisms of particular interest, thus tree and shrub species are more vulnerable. With the disappearance of tree canopy, new forest gaps might provide habitats for some pioneer and invasive species, which could lead to an increase in the number of herb species in the community. At the low altitude zone of TD transect, the abundance of vascular plant species might partly be due to the frequent human disturbance.

The range of the geographical area or gradient sampled can have a pronounced impact on the derived pattern of species richness (Raillery 2005). The relatively short range of altitudinal gradients of species richness makes them particularly sensitive to effects of area, sampling regime, and/or effort (McCoy 1990, Rahbek 1995). In this study, the elevation range of TD transect was narrow for a local top. For the conical shape, mountains with peaks far exceeding the vegetation-limit would provide broader habitats for plant species than mountains with peaks under the vegetation-limit in middle and high altitude regions. In TD transect, the top of the mountain is about 3600 m a.s.l., close to the forest limit of this region. This means that the area of middle height or alpine zone could be a limiting factor for plant, and could explain a monotonically decreasing pattern in this transect.

Furthermore, trees and shrubs displayed parallel richness patterns; they exhibited hump-shaped patterns that peaked at mid-high elevations except the tree richness in the TD transect. Both trees and shrubs are woody plants, with similar requirements and responses to environmental conditions (Pausas and Austin 2001, Ren et al. 2006). In ecology, the species richness for most herb species of the understory changes more easily in a community. Indeed, the sunlight, space and other resources needed for plant growth are limited by the shrub and tree cover. So, to some degree, the herb species richness relies on the tree and shrub species. But we still noted that the number of herb species in every altitudinal gradient was far more important than the total number of shrub species and tree species, and the vascular plant species richness pattern in Mt. Juding mainly depended on the herb species richness.

As a conclusion, altitudinal variation of the species richness in the temperate zone shows different patterns. Both monotonically decreasing pattern and hump-shaped pattern can be found. Species with different growth forms show different altitudinal patterns, but the species with similar environmental requirements show similar richness patterns along altitudinal gradients. Different richness patterns can be the result of different climates, different altitudinal ranges, area factors, anthropogenic factors, etc. Different transects on the same mountain show different patterns, this suggests that using one transect to discuss plant richness pattern along altitudinal gradients is insufficient.

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6. REFERENCES

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