

## Article

# Plant Diversity along the Eastern and Western Slopes of Baima Snow Mountain, China

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**Abstract:** Species richness and turnover rates differed between the western and eastern aspects of Baima Snow Mountain: maximum species richness (94 species in a transect of 1000 m<sup>2</sup>) was recorded at 2800 m on the western aspect and at 3400 m on the eastern aspect (126 species), which also recorded a much higher value of gamma diversity (501 species) than the western aspect (300 species). The turnover rates were the highest in the transition zones between different vegetation types, whereas species-area curves showed larger within-transect beta diversity at middle elevations. The effect of elevation on alpha diversity was due mainly to the differences in seasonal temperature and moisture, and these environmental factors mattered more than spatial distances to the turnover rates along the elevation gradient, although the impact of the environmental factors differed with the growth form (herb, shrubs or trees) of the species. The differences in the patterns of plant biodiversity between the two aspects helped to assess several hypotheses that seek to explain such patterns, to highlight the impacts of contemporary climate and historical and regional factors and to plan biological conservation and forest management in this region more scientifically.

**Keywords:** elevational gradient; mountain aspect; plant species diversity; comparative study; Baima Snow Mountain; Three Parallel River region; northwest Yunnan

## 1. Introduction

Mountains are hotspots of biodiversity at global and regional scales [1,2]. The pattern of species richness along the slopes of mountains and the factors that determine such patterns have long been a topic of interest to ecologists and biogeographers [3]. Given the growing variability of climate and changes in land use at present, together with the unprecedented rate, scale and reach of human intervention in mountain habitats, the effectiveness of biodiversity conservation strategies, particularly in the mountains, is becoming a matter for concern [4–6].

The patterns of species diversity along elevation gradients have been studied for decades, and the results of these studies are well summarized [7,8], revealing the major determinants underlying the patterns of diversity, namely environmental filters [9,10], regional processes and evolutionary history [11–13], biological interactions [14] and spatial factors, such as area, dispersal limits and boundary constraints imposed by the elevation range of the mountains [15,16]. However, the collinearity of effects among the different hypotheses has been a critical obstacle to separating the distinct contribution of each of these possible mechanisms [8], a task made even more complex by the difference in the scale of their effects.

Baima Snow Mountain (BSM) is the central section of the eastern-most of three parallel mountain ranges in the Three Parallel Rivers Region (TPRR), northwestern Yunnan Province, China.

By examining plant diversity along the elevation gradient on the eastern and western aspects of this mountain, the present study aimed to explore the effects of elevation and aspect on plant species diversity and to separate the contribution of each of the different mechanisms that determine the structure of vegetation and plant diversity. Specifically, we addressed the following questions: (1) How do vegetation zones and plant species diversity along the elevation gradient on the western aspect of the BSM differ from those on its eastern aspect? (2) What factors affect the local species richness and species turnover along the elevation gradient? (3) How do contemporary environment (current meteorological data and topographic features), historical and regional environmental factors and boundary constraints imposed by the mountain contribute to spatial patterns of plant diversity?

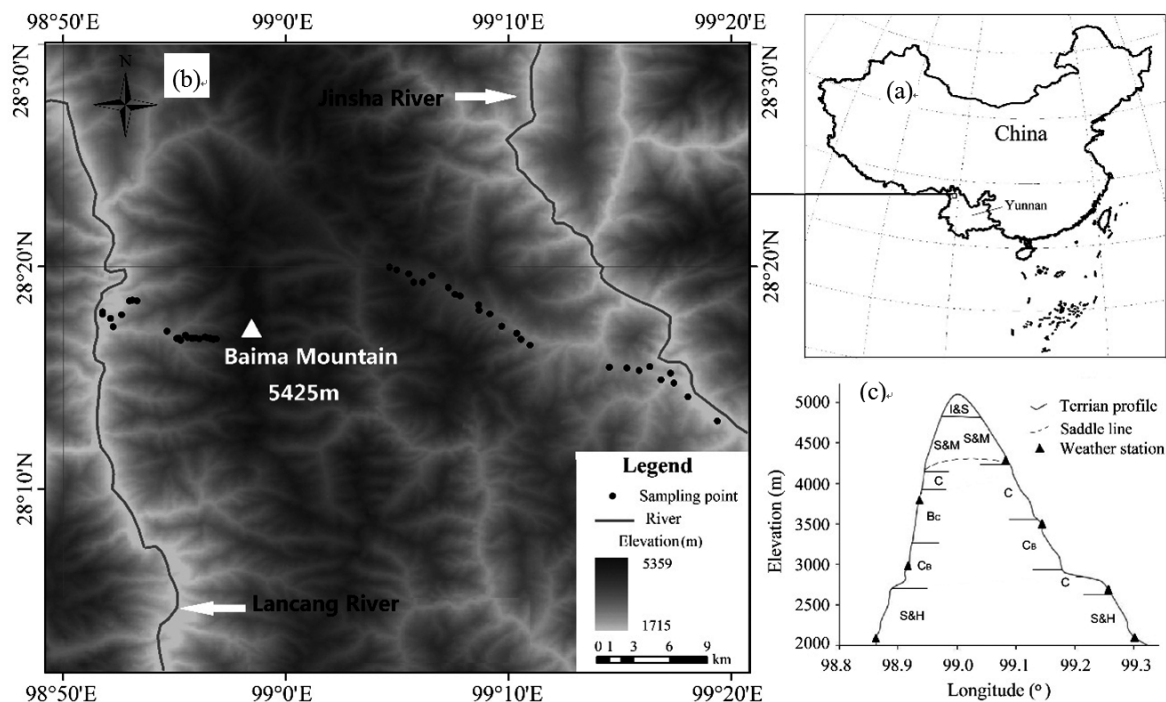
## 2. Materials and Methods

### 2.1. Study Area

Field investigations of vegetation were conducted in the northern BSM. The mountain is spread over 2816.4 km<sup>2</sup>, extending chiefly along the south–north axis; its summit rises 5429 m above the mean sea level; the base of its western aspect is at 1815 m, near the Lancang River; and the base of its eastern aspect is at 1950 m, near the Jinsha River (Figure 1). The regional climate is characterized by marked seasonal changes in both temperature and precipitation, received mostly in summer from the south–west monsoon from the Indian Ocean. The interaction between the south–west monsoon and the steep mountain slopes creates a prominent vertical zonation of climate and vegetation, from a dry–warm climate and shrub-dominated vegetation at the base (elevation less than 2600 m) through a cooler and more humid climate and tree-dominated vegetation at middle elevations (2600–4300 m), to the alpine climate dominated by shrubs and grasses at higher elevations (4300 m) [17]. The BSM is divided between two autonomous counties, Deqin and Weixi, in Yunnan province, and was designated as a national natural reserve in 1988 owing to the generally well-protected vegetation and rich biodiversity. Anthropogenic disturbance in the forms of logging and farming is mostly limited to a distance of 500 m from the main road extending into the natural reserves on both eastern and western aspects of the BSM. However, the rich wildlife of the region indicates a harmonious coexistence between the traditional communities and nature. For example, the BSM is the only remaining habitat or species range of the Yunnan snub-nosed monkey (*Rhinopithecus bieti*) [18], a flagship species for biodiversity conservation in Yunnan.

### 2.2. Meteorological Data

Meteorological data for three years (October 1981–December 1984) were obtained from seven temporary weather stations established across the east–west axis of the BSM (Figure 1, Table 1) by the Interdisciplinary Research Team for Qinghai–Tibet Plateau, the Chinese Academy of Sciences. Three stations were set up on the western aspect, one at the saddle point and the other three on the eastern aspect. Temperature and precipitation data were recorded hourly, and the monthly mean temperature and precipitation values for these sites were published [19]. These are the only data available to compare the eastern and the western aspects of the BSM along its elevation gradient.



**Figure 1.** The study area (a); distribution of field-sampling sites (b); weather stations and the vertical vegetation zones on eastern and western slopes of Baima Snow Mountain (c). S&H: shrubs and herbs zone; C: coniferous forest zone; C<sub>B</sub>: mixed coniferous and broad-leaved forest zone dominated by conifers; B<sub>C</sub>: mixed broad-leaved-coniferous forest zone dominated by broad-leaved species (mostly evergreen *Quercus*); S&M: alpine shrubs and grasses (meadows) zone; I&S: ice and snow zone.

**Table 1.** Meteorological data from seven stations on Baima Snow Mountain: 1987–1988.

| Parameter                   | Western Aspect |       |       | Saddle | Eastern Aspect |       |       |
|-----------------------------|----------------|-------|-------|--------|----------------|-------|-------|
| Station                     | No.1           | No.2  | No.3  | No.4   | No.5           | No.6  | No.7  |
| Elevation, m                | 2080           | 2747  | 3485  | 4292   | 3760           | 2988  | 2025  |
| Mean annual temperature, °C | 14.74          | 10.83 | 5.24  | −1.14  | 2.97           | 9.65  | 16.57 |
| Annual precipitation, mm    | 425.0          | 410.6 | 513.8 | 807.1  | 946.1          | 532.8 | 285.6 |

We plotted the elevation of the weather stations (black triangles in Figure 1c), the monthly mean temperature (MMT) and the monthly mean precipitation (MMP) at each station for twelve months to calculate the slopes of MMT and MMP along the elevation gradient on the eastern and western aspects and then interpolated the values of MMT and MMP for every 100-m increase in elevation from 2000 m to 4500 m along both the aspects of the BSM. Ten additional bioclimatic indexes were calculated based on the MMT and MMP (Table 2). The patterns of seasonal changes in temperature were similar for both aspects, but those of seasonal changes in precipitation were distinct. The elevation at which precipitation was maximum on the western aspect could not be determined precisely (because it kept increasing with elevation), whereas the elevation could be determined on the eastern aspect eight months of the year (except May, June, July and August). The bottoms of the slopes towards the Lancang River (western aspect) and the Jinsha River (eastern aspect) were both characterized by a hot-dry climate (especially on the eastern aspect), and precipitation increased much faster at higher elevations. Net primary productivity (NPP) was calculated using the data and the formula given in Table 2.

**Table 2.** Climatic variables used in the data analysis.

| Factors             | Index | Algorithm   | Reference |
|---------------------|-------|---|-----------|
| Energy              | Tmin  | Monthly mean temperature in the coldest month (January)   | [20]      |
|                     | Tmax  | Monthly mean temperature in the warmest month (July)  | [20]      |
|                     | MTWQ  | Mean temperature in the wettest quarter: June, July and August  | [20]      |
|                     | MTCQ  | Mean temperature of December, January and February  | [20]      |
|                     | MAT   | Mean annual temperature   |           |
|                     | PET   | Potential evapotranspiration: $58.93 \times \text{ABT}^\dagger$   | [21]      |
| Moisture            | PWQ   | Precipitation in the wettest quarter: June, July and August   | [21]      |
|                     | PDQ   | Precipitation in the driest quarter: December, January and February   | [21]      |
|                     | Pmin  | Minimum monthly precipitation (in January)  |           |
|                     | Pmax  | Maximum monthly precipitation (in August)   |           |
|                     | AP    | Annual precipitation  |           |
|                     | AET   | Actual evapotranspiration: $(P/(0.9 + (P/L)^2))^{1/2}$ , $L = 300 + 25T + 0.05T^3$  | [22]      |
|                     | MI    | Moisture index: $\text{PET}/\text{AP}$  | [21]      |
|                     | WD    | Water deficiency: $\text{PET} - \text{AET}$   | [21]      |
|                     | DI    | Drought index: $\text{AET}/P$   | [21]      |
| Productivity        | NPP   | Net primary productivity: $\min\{\text{NPP}_{\text{MAP}}, \text{NPP}_{\text{MAT}}\}$<br>$\text{NPP}_{\text{MAP}} = 0.005212(\text{MAP}^{1.12363})/e^{0.000459532(\text{MAP})}$<br>$\text{NPP}_{\text{MAT}} = 17.6243/(1 + e^{(1.3496 - 0.071514(\text{MAT}))})$ | [23]      |
| Climate seasonality | ART   | Annual range of temperature: $T7 - T1$  | [20]      |
|                     | TSN   | Temperature seasonality: $\text{SD (monthly mean temperature)} \times 100$  | [20]      |
|                     | PSN   | Precipitation seasonality: $\text{CV (monthly mean precipitation)}$   | [20]      |

$^\dagger$  ABT: annual Biotemperature ( $^\circ\text{C}$ ).  $\text{ABT} = \sum t_i/12$ .  $t_i$  is mean month temperature that larger than  $0^\circ\text{C}$ , when  $t_i > 30^\circ\text{C}$ , it is assigned to  $30^\circ\text{C}$ .

### 2.3. Field Sampling

Vegetation sampling was conducted in 2012 and 2013. Starting at 2000 m, we established a transect every 100 m along the elevation gradient, up to 4300 m on the western aspect (a total of 24 transects) and up to 4400 m on the eastern aspect (25 transects). Each transect was 10 m wide and 100 m long, with the shorter dimension along the gradient and the longer dimension across the gradient. For easy access, the sites along the road across the mountain were chosen for representation and at least 500 m away from the road to reduce the influence of human intervention. Each transect was established on a slope that was uniform in topography. Because the weather stations were also along the road, the three-year data form a spatially-representative sample of the climate of the transects.

Each transect was divided equally into 10 plots (10 m  $\times$  10 m). In each plot, the height and the girth (circumference) at breast height (1.3 m) of all of the trees were measured and the species recorded. For each species of shrub and herb, all plants within a plot were counted as abundance, and the percentage of coverage was estimated visually. The geographic coordinates and elevation of each transect were recorded using a GPS, and the gradient of the slope and its direction were measured with a compass.

### 2.4. Statistical Analysis

#### 2.4.1. Estimate of $\alpha$ and $\beta$ Diversity

Species richness of all vascular plants within a transect was counted as local species richness (or  $\alpha$  diversity), and that of trees, shrubs and herbs (including ferns) was also counted separately.  $\beta$  diversity was estimated using the Simpson dissimilarity index ( $\beta_{sim}$ ) [24] for species turnover rate between neighboring transects along the elevation gradient on the western and the eastern aspects separately.  $\beta_{sim}$  was calculated between adjacent transects, for all species within a transect, and for trees, shrubs and herbs separately, and only the presence or absence of each species in the transect was used in the calculations with the following formula:

$$\beta_{sim} = \frac{\min(b, c)}{a + \min(b, c)} \quad (1)$$

where  $a$  is the number of species shared between two transects,  $b$  is the number of species present in transect B, but not in transect C,  $c$  is the number of species present in transect C, but not in transect B, and  $\min()$  indicates the smaller of the two values between  $b$  and  $c$ .  $\beta_{sim}$  was used because it provides a fairly reliable estimate of species turnover independent of the impact of local species richness [25].

Based on the species composition of ten 10 m  $\times$  10 m plots in each transect, a species-area curve was used to describe the changes in species diversity with increasingly larger sampling areas [26]. Species-area curves for pairs of transects at the same elevation, but on different aspects (western or eastern) of the BSM were compared to find the differences in complexity of the community structures between the two aspects. Species richness of all possible combinations of a certain number  $i$  ( $i = 1, 2, 3, \dots, 10$ ) of unit plots was calculated, and the means and standard deviations of species richness were used to draw the species-area curve for each transect, with the area increasing from 100 m<sup>2</sup> to 1000 m<sup>2</sup>.

#### 2.4.2. Principal Component Analysis (PCA) of Climatic Variables

Because multiple bioclimatic variables are collinear, PCA was applied to extract principal bioclimatic information with focused indices. PCA is useful in reducing the number of dimensions of explanatory variables with acceptable information loss under most conditions [27]. All 18 climatic variables were classified into three types, namely energy, moisture and climatic seasonality. Before PCA, all indexes were normalized to have a mean of zero and a standard deviation of 1. The first principal component of three energy indexes (Energy.pc1) loaded 99.5% of the variation in energy; the first two principal components of seven moisture indexes (Moist.pc1, Moist.pc2) accounted for 97.4% of the variation in moisture, indicating the importance of rainfall during the growing season and of winter precipitation, respectively; and the first two principal components of six indices of climatic seasonality (Seasonal.pc1, Seasonal.pc2), indicating seasonal changes in temperature and precipitation, respectively, accounted for 99.9% of the variation (Table S1).

#### 2.4.3. Environmental and Spatial Interpretations of Diversity Patterns

A hierarchical variation partitioning (HVP) algorithm based on the generalized linear model (GLM) was used for examining the independent influence of environmental variables on species richness: we applied the HVP algorithm to species richness of all species and to tree, shrub or herb species separately. The algorithm creates a GLM of all possible combinations of the explanatory variables, uses Akaike's information criteria (AIC) to select the optimal model and estimates the independent contribution of each of the considered variables to the selected model [28–30]. We used the HVP algorithm for the variables included in the final model of the environmental interpretation of  $\alpha$  diversity patterns.

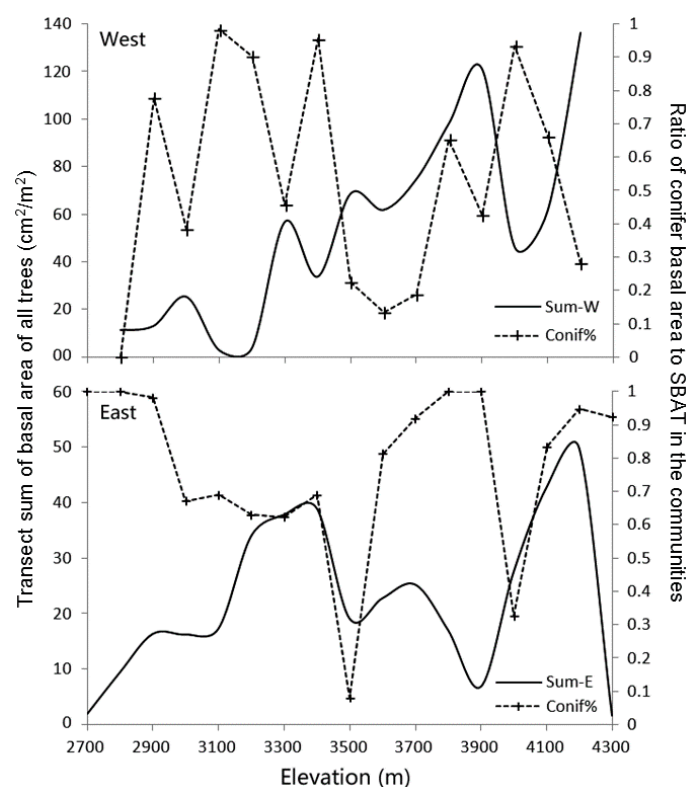
The Mantel test and the partial Mantel test are the two commonly-used methods of testing the association between two matrices, the entries of which are distances or similarities [31]. As an extension of the partial Mantel test, a multiple regression model (MRM) involves multiple regressions of a response matrix on a given number of explanatory matrices, which contain spatial distances or environmental similarities between all pairs of sampled units [32]. The model is useful in decomposing the collinear effects of space and environmental factors on the spatial patterns of  $\beta$  diversity, and we applied the MRM to the species composition of each transect considering all of the plant forms together and also the composition of tree, shrub and herb species separately. Euclidian distance was used for calculating the spatial distance and environmental dissimilarity between two transects, and latitude, longitude and elevation were used for calculating the spatial distance matrix. The dissimilarity matrix for all transects (24 on the western aspect and 25 on the eastern aspect) was calculated separately for the indexes of energy, moisture, climatic seasonality, net primary productivity (NPP) and a comprehensive environmental index. To validate the results of MRM, we also applied the Mantel test and the partial Mantel test to estimate the impact of spatial distance and of environmental differences in energy, moisture, climatic seasonality and productivity on the rate of species turnover between transects.



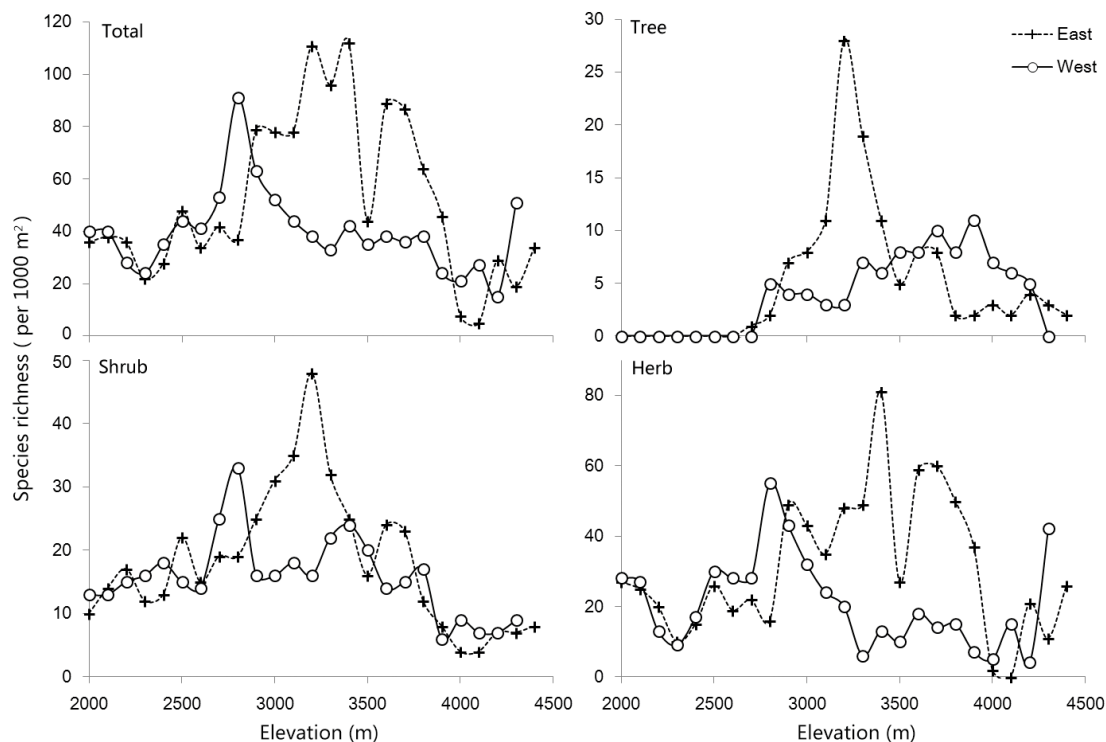
### 3. Results

#### 3.1. Vegetation Zones and Overall Species Composition along the Elevation Gradient

The vegetation zones showed distinctly different patterns between the western and the eastern aspects of the BSM (Figure 1), although the overall patterns of plant diversity on both sides were broadly similar: shrubs and herbs in the dry-warm climate at the bottom, trees at middle altitudes and shrubs and grasses in the alpine climate at higher elevations. The upper limit of the lower zone on both aspects was 2700–2900 m, above which the vegetation transitioned to the forest zone through a broad tree line ecotone. The structure of the forest zone along the elevation gradient differed between the two aspects: the western aspect showed the “C<sub>B</sub>-B<sub>C</sub>-C” pattern, which consisted of mixed coniferous and evergreen broad-leaved forests that were dominated by *Pinus* species (C<sub>B</sub>, 2800–3300 m); mixed evergreen broad-leaved and coniferous forests that were dominated by *Quercus* species (B<sub>C</sub>, 3300–3900 m); and a coniferous forest composed of *Abies* and *Larix* species (C, 3900–4200 m); the eastern aspect displayed a distinct “C-C<sub>B</sub>-C” pattern, i.e., C dominated by *Pinus* species at 2700–3000 m, C<sub>B</sub> at 3000–3600 m and C composed of *Abies* and *Larix* species at 3600–4300 m. The two aspects also showed distinct community structures across the forest zone (Figure 2). On the western aspect, the sum of the basal area of all trees (SBAT) in a transect (as a proxy for forest biomass) increased with elevation, reaching its maximum value near the upper limit of the subalpine conifer forests. On the eastern aspect, however, the SBAT showed two peaks, one at 3400 m and one at 4200 m. The contribution of coniferous trees to the SBAT showed a U-shaped pattern on the western aspect, with conifers dominating at lower elevations (2900–3400 m), as well as at higher elevations (4000–4200 m) and broad-leaved trees dominating at the middle elevations (3500–3900 m). On the eastern aspect, however, conifers dominated nearly all of the forest zones except at middle elevations (3200–3500 m), where the communities were equally rich in both conifers and broad-leaved trees (Figure 3, Figure S1).



**Figure 2.** Elevation-related patterns of the transects: sum of basal area of all trees (SBAT, solid line) and the ratio of conifer basal area to SBAT in the communities (broken line with crosses) on western and eastern aspects of Baima Snow Mountain.



**Figure 3.** Elevation-related patterns of species richness of all plants and of trees, shrubs and herbs in the transects on western and eastern aspects of Baima Snow Mountain.

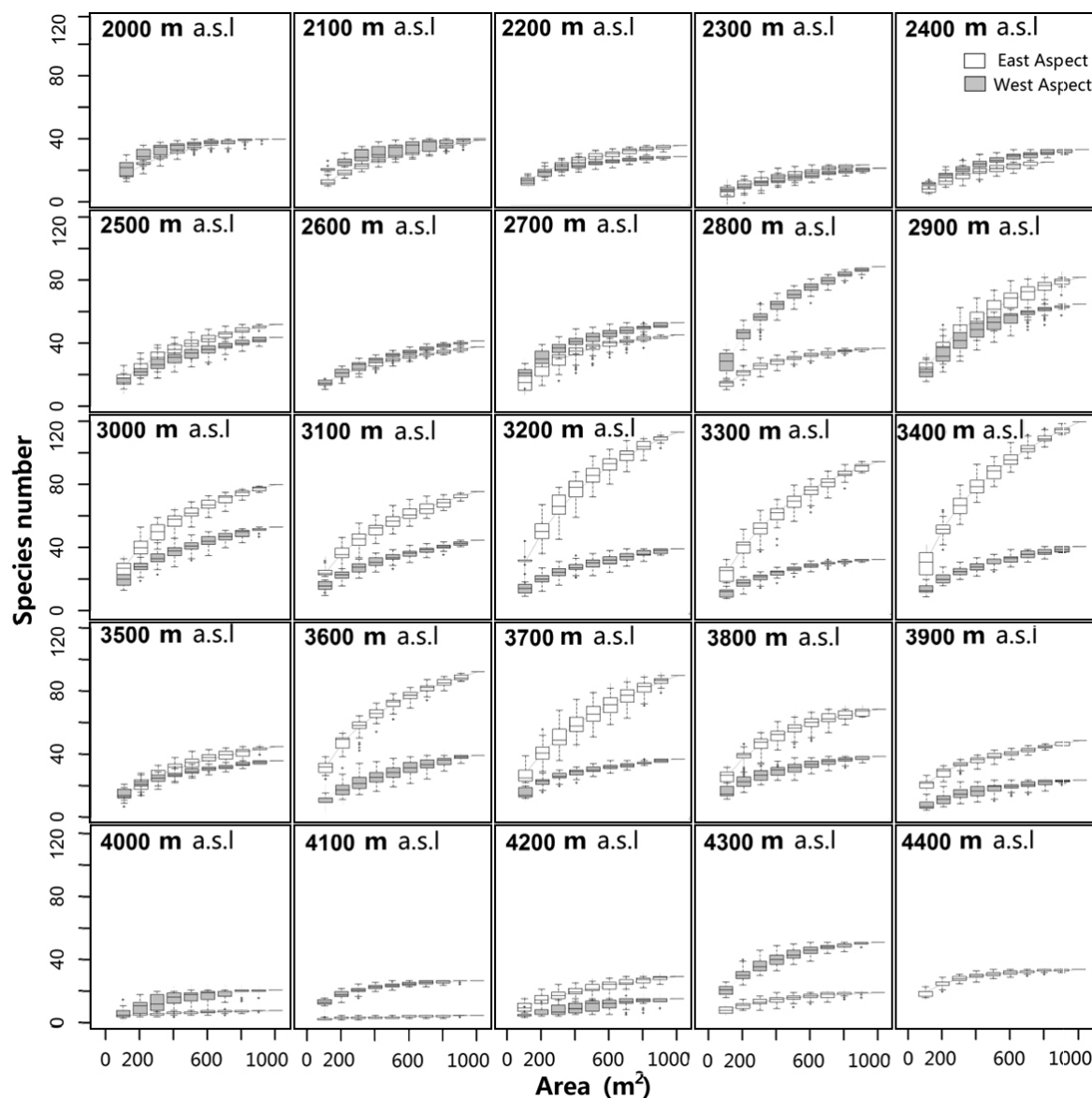
Species diversity on the eastern aspect of the BSM was higher than that on the western aspect. The eastern aspect harbored a total of 501 species of vascular plants (304 herbs, 155 shrubs and 42 tree species), representing 250 genera and 94 families; the corresponding figures for the western aspect were 300 (189, 92, and 19), comprising 194 genera and 82 families.

### 3.2. Species Richness and Species Turnover within Communities

Species richness at the transect level varied with elevation, but showed different patterns on the western and the eastern aspects (Figure 3). In general, species richness of vascular plants over sampling areas of 1000 m<sup>2</sup> each described a hump-shaped curve on both the aspects, reaching its lowest value at the upper limit of the forest zone (about 4000 m), whereas species richness of shrubs and herbs increased with elevation. Total species richness and that of shrubs and herbs peaked at 2800 m on the western aspect, in the ecotone between the lower dry shrubs-and-grasses zone and the mid-altitude forest zone. On the eastern aspect, species richness of all of the three growth forms—herbs, shrubs, and trees—peaked at 3200–3400 m. Species richness on both aspects was very similar at lower elevations (in the dry valleys below 2700 m) and also at higher elevations (the alpine shrubs-and-grasses zone above 4000 m). The greatest contrast in species richness between the two aspects occurred in the forest zone (2800–3900 m), a difference that was also evident in the structure of vegetation mentioned earlier (Figure 1).

The species-area curves of transects at the same elevation on the western and the eastern aspects were also hump shaped (Figure 4), with maximum species richness in all ten unit plots occurring at middle elevations, roughly 2800–3700 m. The two curves came close at elevations between 2000 m and 2700 m, indicating similar  $\alpha$  diversity and within-transect  $\beta$  diversity between the communities on the western and the eastern aspects. At 2800 m, the transect on the western aspect had a much larger  $\alpha$  diversity and within-transect  $\beta$  diversity (indicated by the increase of species richness along with the increasing area) than that on the eastern aspect. However, the relationship was reversed in most of the forest zone. From 2900–3900 m, transects on the eastern aspect had larger  $\alpha$  diversity and

within-transect  $\beta$  diversity than those on the western aspect. At 4000–4300 m, in the subalpine conifer forests on both aspects, the differences between the species-area curves gradually decreased, and  $\alpha$  diversity and within-transect  $\beta$  diversity tended to be greater on the western aspect more frequently.

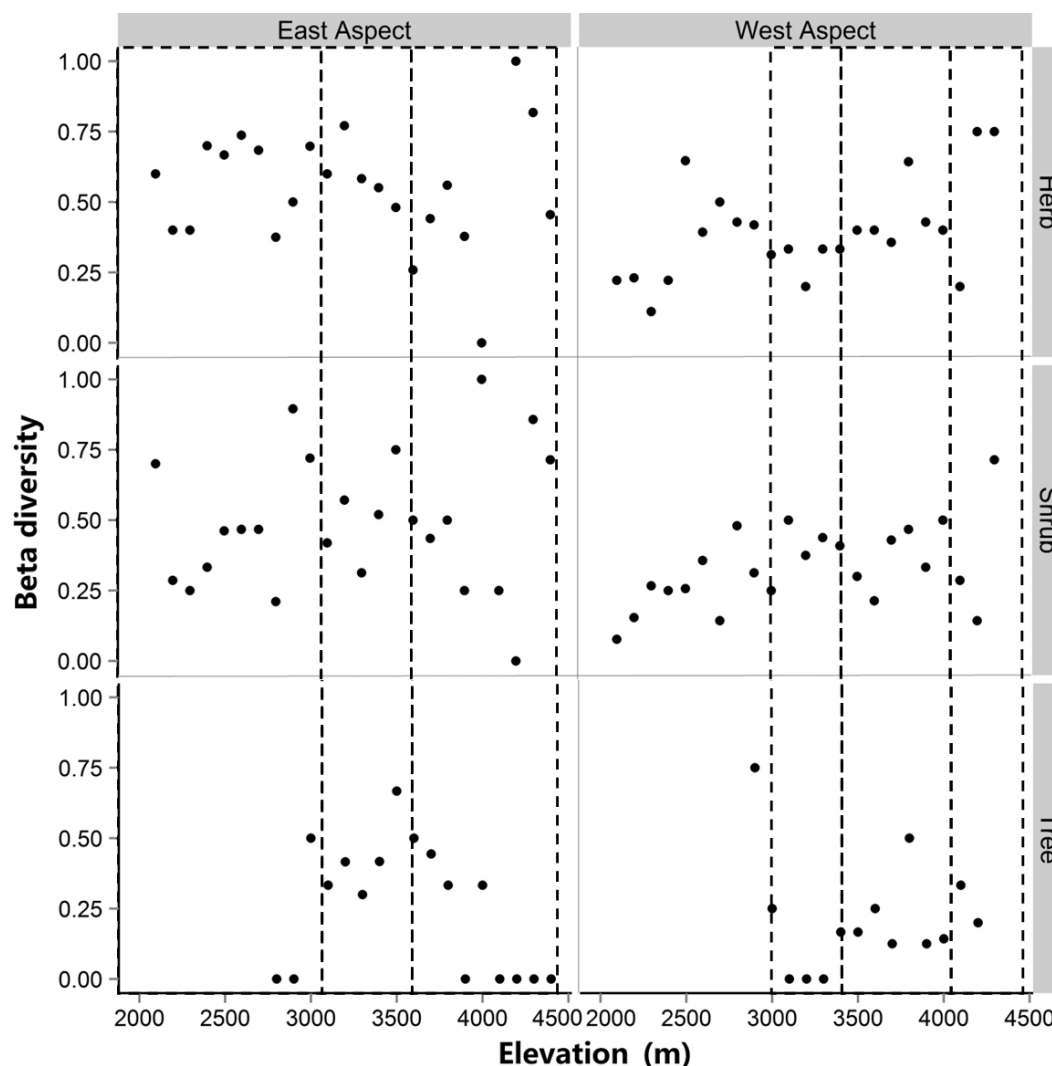


**Figure 4.** Contrast of species-area curves between pairs of transects along the elevation gradient on eastern and western aspects of Baima Snow Mountain. The horizontal line in each boxplot indicates the median species richness in a specific sampling area at different elevations and aspects and the error bar indicates 2.5 and 97.5 quantiles.

### 3.3. Vegetation Zones and Species Turnover

The average species turnover rate along the elevation gradient on the eastern aspect (mean  $\pm$  SD =  $0.53 \pm 0.37$ ) was greater ( $t = -3.51$ ,  $p < 0.001$ ) than that on the western aspect ( $0.36 \pm 0.19$ ) (Figure 5), and this difference was significant for shrubs ( $0.50 \pm 0.25$  vs.  $0.33 \pm 0.15$ ;  $t = -2.88$ ,  $p = 0.006$ ) and herbs ( $0.55 \pm 0.21$  vs.  $0.39 \pm 0.17$ ;  $t = -3.013$ ,  $p = 0.004$ ), but not for trees ( $0.25 \pm 0.23$  vs.  $0.22 \pm 0.21$ ;  $t = -0.89$ ,  $p = 0.38$ ). On both aspects, the species turnover rate was consistently the highest among herbs ( $0.47 \pm 0.21$ ) and the lowest among trees ( $0.23 \pm 0.22$ ), and the differences among all three growth forms were significant.





**Figure 5.** Species turnover rates of all plant species and of trees, shrubs and herbs along an elevation gradient on eastern and western aspects of Baima Snow Mountain.

No consistent pattern of species turnover rate (or across-transect  $\beta$  diversity) was found along the elevation gradient, either between the different growth forms or between the two aspects. As expected, a transition between two neighboring vegetation zones or sub-zones generally corresponded to an increase in the species turnover rate. On the western aspect, maximum rates of species turnover occurred at 2700–2800 m, 3800 m and 4200–4300 m, corresponding to the transitions between the dry valley shrubs-and-herbs zone and the forest zone, between the mixed-forests zone (broad-leaved and coniferous) and the conifer-forests zone and between the forest zone and the alpine shrubs-and-grasses zone. On the eastern aspect, maximum rates of species turnover occurred at 2900–3000 m, 3500 m and 4300 m, elevations that corresponded to the similar transitional zones on the western aspect.

### 3.4. Environmental Interpretation of Alpha Diversity Patterns

With the HVP algorithm, most of the variation (78.8%–95.8%) in species richness, whether for all of the growth forms together or for each of the growth forms separately, along the elevation gradient can be accounted for by the environmental factors (Table 3). In general, the proportions of species richness patterns on both of the aspects accounted for by the models were comparable, although the proportion of variation in species richness left unexplained was greater in the case of herbs than that of shrubs or trees. The environmental influence on the variation in species richness of the three growth forms was

more consistent on the eastern aspect than that on the western aspect and was primarily due to changes in seasonal temperature (annual range of temperature (ART); and temperature seasonality (TSN)), although the influences of slope and that of precipitation during the growth season (precipitation in the wettest quarter (PWQ); maximum monthly precipitation (Pmax); and actual evapotranspiration (AET)) were also important. The species richness of trees was primarily related to energy (potential evapotranspiration (PET); mean annual temperature (MAT); and minimum monthly temperature (Tmin)); of shrubs, to moisture (minimum monthly precipitation (Pmin); Pmax; and PWQ); and of herbs, to temperature (ART, TSN). The local topographic features had little impact on species richness patterns on the eastern aspect.

**Table 3.** Hierarchical variation partitioning of elevation-related species richness patterns of herb, shrub and tree species and of all species on the western and the eastern aspects of Baima Snow Mountain. Refer to Table 2 for abbreviation and definitions.

| Variable                  | Western Aspect |         |         |           | Eastern Aspect |         |         |           |
|---------------------------|----------------|---------|---------|-----------|----------------|---------|---------|-----------|
|                           | Herbs          | Shrubs  | Trees   | All Forms | Herbs          | Shrubs  | Trees   | All Forms |
| MAT                       |                | 0.080   | 0.174 * |           | 0.056          | 0.072   | 0.082   | 0.089     |
| Tmin                      |                | 0.087   | 0.174 * | 0.107     |                |         |         |           |
| PET                       |                | 0.118   | 0.281 * | 0.107     | 0.051          |         | 0.166 * | 0.078     |
| Pmin                      |                | 0.169 * |         |           | 0.100          |         |         |           |
| Pmax                      |                | 0.122 * |         | 0.211 *   |                |         | 0.075   | 0.070     |
| PDQ                       | 0.306 *        |         |         |           | 0.091          |         |         | 0.107     |
| PWQ                       |                | 0.122 * |         | 0.201 *   | 0.048          | 0.073   | 0.081   | 0.070     |
| WD                        |                | 0.073   |         | 0.114 *   |                |         |         |           |
| AET                       |                |         | 0.167 * |           | 0.050          | 0.123   | 0.064   | 0.072     |
| NPP                       | 0.068          |         |         |           | 0.159 *        |         |         |           |
| ART                       | 0.223 *        | 0.096   |         |           | 0.110          | 0.238 * | 0.178 * |           |
| TSN                       | 0.200 *        |         |         | 0.169 *   |                | 0.257 * | 0.171 * | 0.221 *   |
| PSN                       |                |         | 0.072   |           |                |         |         |           |
| Exposure                  | 0.061          |         |         |           | 0.042          | 0.028   |         | 0.027     |
| Slope                     |                |         |         |           | 0.174 *        | 0.077   |         | 0.171 *   |
| Interpreted variation (%) | 85.7           | 88.8    | 92.7    | 90.2      | 83.6           | 95.2    | 95.8    | 92.5      |

\* Significant at 95% by the Z test.

### 3.5. Climatic Interpretation of Beta Diversity Patterns

The results from MRM indicated that almost all climatic variables and the spatial distance significantly influenced the dissimilarity in species composition between the transect communities and that the impact of climatic variables was greater than that of spatial distance (Table 4). The most prominent climatic variable on both aspects was moisture in the case of changes in species composition of herbs and shrubs and energy in the case of trees: the results accounted for 62.8%–64.5% of the community dissimilarity on the western aspect, but only 46.5%–47.2% of that on the eastern aspect.

The partial Mantel test (Table S3) also indicated a generally larger impact of climatic variables than that of spatial distance on community dissimilarity. Furthermore, the impact of geographic distance on the dissimilarity was not significant for any of the growth forms in the case of the eastern aspect, whereas the impact of climatic variables was generally significant. On the western aspect, the impact of climatic variables was significant and so was that of geographic distance in the case of shrubs and herbs, although not in the case of trees. Specifically, the most prominent climatic factor accounting for the dissimilarity in shrubs and herbs was NPP (*i.e.*, the water–energy balance) on the eastern aspect and moisture on the western aspect.

**Table 4.** Regression coefficients and regression R-squared values: multiple regression on distance matrices of beta diversity on the eastern and the western aspects of Baima Snow Mountain.  $D_e$  and  $D_g$ : Euclidian distance between two transects calculated for environmental variables or geographic coordinates (including elevation), respectively.

| Distance | Variables    | Eastern Aspect |           |           | Western Aspect |           |           |
|----------|--------------|----------------|-----------|-----------|----------------|-----------|-----------|
|          |              | Herb           | Shrub     | Tree      | Herb           | Shrub     | Tree      |
| $D_e$    | Energy       | 0.156          | 0.335     | 0.995 *** | 0.180          | 0.035     | 1.269 *   |
|          | Moisture     | 0.385 **       | 0.525 **  | 0.289     | 0.513 **       | 0.618 **  | 1.133 *   |
|          | Seasonality  | 0.076          | 0.052     | 0.035     | 0.211 *        | 0.321 **  | 0.606     |
|          | Productivity | 0.172 *        | 0.217 **  | 0.035     | 0.204 **       | 0.234 **  | 0.224     |
| $D_g$    |              | 0.359 *        | 0.477 **  | 0.682 *** | 0.230          | 0.354 **  | 0.410 *   |
| Total    | $R^2$        | 47.2% ***      | 47.1% *** | 46.5% *** | 62.8% ***      | 64.6% *** | 63.8% *** |

\*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ .

## 4. Discussion

### 4.1. Interpretation of Patterns

For the BSM, the major source of precipitation is the Indian monsoon coming from the west [17], which normally arrives in May; the rainy season lasts until October [19]. Before it reaches the BSM, the monsoon crosses two mountain ranges (namely Mount Gaoligong and Mount Yunling) oriented along the north–south axis in the TPRR and deposits most of the precipitation on their windward slopes. Therefore, the precipitation on the windward slope of the BSM is much lower at the bottom of the valley and increases with elevation. Rainfall is maximum over the mountain ridge on the leeward side (the eastern aspect) at 3800–3900 m and decreases sharply as the elevation decreases [19]. Therefore, the annual mean precipitation at the lower section of the bottom of the valley (below 2500 m) on the eastern aspect of the BSM was less (285.6 mm) than that on the western aspect (425 mm). At middle and upper elevations (2600–3300 m and 3400–4200 m), however, precipitation on the eastern aspect (532.8 and 946.1 mm, respectively) was greater than that on the western aspect (440.3 and 513.8 mm, respectively) [19]. Because the transects on both the aspects were established at similar elevations, the difference in moisture levels due to the monsoon seems to be the major climatic factor influencing vegetation patterns and plant species diversity on the two aspects.

The Hengduan Mountains are a global hotspot of biodiversity [1]. In the southern part of the Hengduan Mountains, Yunnan province harbors half the plant species pool in China and two endemism centers [33], and the TPRR in northwestern Yunnan is one of them. The general pattern of biodiversity along the elevation gradient in this region is described elsewhere [34–38], but other characteristics of the distribution of species richness are not widely known, especially with regard to the impact of the Indian Ocean monsoon, a primary driver of the region's climate. In fact, plant species richness on the eastern aspect is higher than that on the western aspect of the BSM, especially within the forest zone, which also has a wider range on the eastern aspect (2700–4300 m) than on the western aspect (2800–4200 m). The evergreen oak forests in the Hengduan Mountains dominate the dry and sunny habitats [39,40], and the dominance of the *Quercus panosa* community on the western aspect of the BSM also indicates a habitat drier than the mixed coniferous-deciduous broad-leaved forests, which cover a much wider range of elevations on the eastern aspect (Figure 1).

### 4.2. Testing Competing Hypotheses

Past investigations of spatial patterns of biodiversity have narrowed the explanations to several mechanisms that govern such patterns, and these mechanisms require further study. The mechanisms include the effects of area, climate, environmental heterogeneity, historical and regional processes, as well as geometric constraints. In the species-area theory, different models predict that species richness increases with sampling area [26]. Climate-related hypotheses suggest that biodiversity is limited by

low temperatures, by cumulative warmth or by the water–energy balance indicated by the net primary productivity (summarized by Wang *et al.*, 2009 [41]). The environmental heterogeneity hypothesis predicts a positive correlation between niche diversity and species richness [8]. The historical/regional process hypothesis suggests that local species diversity is limited by the regional species pool, which is mainly regulated by the spatial patterns of climate and geomorphology on a regional scale, as well as by their historical processes, especially in the Quaternary period [8,42,43]. A geometric constraint occurs when species are randomly distributed in a domain with only a single geometric boundary constraint, and the ranges of their distribution collectively generate a hump-shaped species richness pattern along one spatial dimension, showing the middle-domain effect (MDE) [8]. The MDE hypothesis thus predicts a hump-shaped species richness pattern along an elevation gradient irrespective of the impacts of other environmental gradients [44]. Earlier studies have provided support for the influence of climatic factors, historical and regional processes and geometric constraints on elevation-related patterns of biodiversity in the TPRR [34–36], although consensus on the relative contributions of these factors is lacking.

By sampling the same area at 100-m intervals of elevation, sampling similar numbers of transects (24 and 25) and sampling similar elevation ranges (2000–4300 m and 2000–4400 m) on both aspects of the BSM, our transect data controlled for the area effect on species richness. Given the rise of the Tibet–Qinghai Plateau and the simultaneous erosion of the valleys of the Lancang River and the Jinsha River on both sides of the BSM, the glacial and interglacial cycles in the Quaternary period and the migration of plant species on the two aspects in response to these changes can also be reasonably regarded as similar. Therefore, the present study gathered a dataset useful for comparing elevation-related patterns of plant species diversity on the eastern and the western aspects of the BSM and for testing the above-mentioned hypotheses that explain the patterns of diversity (Table 5).

**Table 5.** Comparison of different hypotheses to explain the elevation-related patterns of plant species diversity in Baima Snow Mountain.  $\alpha$  diversity, species richness of transects;  $\beta$  diversity, species turnover rate between pairs of neighboring transects;  $R$  diversity, total species recorded in all transects of each (eastern or western) aspect of the BSM;  $\times$ , rejected;  $\checkmark$ , supported;  $\nabla$ , partially supported (or rejected).

| Interpretive Hypothesis         | $\alpha$ Diversity | $\beta$ Diversity | $R$ Diversity | Species–Area Curves |
|---------------------------------|--------------------|-------------------|---------------|---------------------|
| Area                            | $\times$           | $\times$          | $\times$      | $\nabla$            |
| Middle-domain effect            | $\nabla$           | $\nabla$          | $\times$      | $\times$            |
| Historical and regional process | $\checkmark$       | $\times$          | $\checkmark$  | $\nabla$            |
| Water–energy balance            | $\checkmark$       | $\checkmark$      | $\checkmark$  | $\checkmark$        |
| Habitat heterogeneity           | $\nabla$           | $\times$          | $\times$      | $\checkmark$        |

For  $\alpha$  diversity of the plant communities, the area hypothesis cannot explain the elevation-related variation in plant species richness, and the MDE hypothesis cannot be completely rejected by the generally hump-shaped pattern of elevation-related species richness. The elevation-related climatic variables (especially precipitation and seasonal changes in climatic variables), although based on a limited monitoring period of three years, correlate well with the  $\alpha$  diversity patterns (Table 3 and Table S1). Similar results have also been reported earlier [35,36]. Historical and regional processes can also predict this pattern, because the up-and-down migration of plant species during the glacial and interglacial cycles can also increase the possibility of more species ending up at middle elevations [36]. Habitat heterogeneity, although not specifically measured, cannot explain the huge difference in species richness (3–118) along the elevation gradient, unless it is linked with the variation in climate-related energy.

Neither area nor the MDE model can provide any support to the elevation-related patterns of between-transect species turnover rate ( $\beta_{sim}$ ), although changes in climatic variables had a greater impact on that rate than spatial distance did (Table 4). Since elevation-related vegetation zones reflect

climatic zones, the match between peak values of species turnover rate and transitions in the type of vegetation showed the effects of an elevation-related climate gradient on beta diversity patterns. It is reasonable to infer that an elevation-related climate gradient cannot be a more prominent cause of elevation-related patterns of beta diversity than habitat heterogeneity within each transect. The effect of spatial distance on beta diversity is linked to the limitations on species dispersal, which can be affected by regional geomorphology [45]. The characteristically steep topography of the BSM was a statistically-significant, but much weaker predictor of species richness than the environmental differences between transects.

All species recorded in all of the transects on the western and the eastern aspects were comparable in terms of their gamma ( $\gamma$ ) diversity. The differences in biodiversity between the eastern and the western slopes—501 *vs.* 300 species, 250 *vs.* 194 genera and 94 *vs.* 82 families, respectively—are among the major results of the present study. These differences could not be predicted by similar sampling areas, identical elevation boundaries of the studied domain (BSM) and within-habitat heterogeneity: none of the three factors could provide a reasonable prediction. However, the greater precipitation on the eastern aspect (at 2600–4300 m) than on the western aspect most likely contributed more to the productivity of the vegetation and, therefore, acted as a regional explanation of the difference in gamma diversity between the two aspects.

Although species richness increased with the sampling area in all transects, neither area nor geometric constraint can account for the elevation-related differences between the two aspects as seen in the species-area curves. However, the differences in the species pool as a regional factor can account for the consistently higher diversity at all scales on the eastern aspect, and the more complex canopy structure of the vegetation community on the eastern aspect might also increase the heterogeneity of the local habitat, which is critical to herb and shrub diversity.

In summary, the elevation-related patterns and the differences between the two aspects, eastern and western, of the BSM in terms of plant species diversity received prominent support from the influence of contemporary environment (primarily climate) and regional-scale environmental differentiation related to historical process, whereas the impact of area and geometric constraint was found to be somewhat weak. Although local habitat heterogeneity was not measured directly, there was no indication that it may have a major impact on plant species richness pattern on the scale of the entire elevation gradient and between the two aspects.

The large proportion of unexplained variation in the models, especially for beta diversity, indicates uncertainty in the results, and caution is warranted in interpreting them. Owing to the short-term records of climate and data on biodiversity based on only one transect at every 100-m elevational distance along each of the aspects of the mountain, further work is necessary to reveal the general differences between the two aspects of the BSM in terms of elevation-related variation in plant diversity.

#### 4.3. Implications

The TPRR, including the BSM, is listed as a United Nations World Heritage site because of its exceptional biodiversity, which comprises 20% of the total plant species richness and a quarter of the vertebrate species richness of China, and its cultural diversity, which encompasses twelve different ethnic groups [46]. Humans settled this region thousands of years ago, obviously adapted to its natural resources and environment. Since human activities are strictly prohibited in natural reserves, a conflict between the modern approach of biological conservation and the traditional strategy of natural resource management by the local communities was inevitable and sometimes intense, as has been reported from all over the world [47,48].

Therefore, it is particularly important to know more about the distribution of biodiversity within the huge expanse of TPRR and to identify priority areas for biodiversity conservation. Although one of the global centers of plant diversity, especially of gymnosperms [49], the spatial distribution of species in this region, except the patterns related to elevation, has rarely been studied. Our study provides the first community-based assessment and data on the differences between the eastern and the western

aspects of the BSM in terms of elevation-related patterns of plant species richness and changes in the species composition. The mixed coniferous and deciduous broad-leaved forests and the evergreen *Quercus* forests are two dominant forest types in this region, typically occupying the more humid or the drier aspects of the TPRR. Understanding the differences in plant diversity in these two forest types is helpful in biodiversity conservation and natural management. For example, the extraordinarily high diversity of conifer species on the eastern aspect at 3200–3300 m corresponds to the maximum plant species richness across the elevation gradient (Figure S1). Since it included ten species of conifers, representing three families and six genera, the local habitat serves as a micro-refugium for a large number of plant species and is probably a biodiversity hotspot within this region. The environmental requirements of these species deserve further study, which will inform the design of sound conservation plans and management of human–nature conflicts.

## 5. Conclusions

Although elevation-related patterns of species diversity and the underlying mechanisms have been widely discussed, few studies have compared the patterns between different aspects of the same mountain, and the present study proved to be a unique and helpful opportunity to test competing hypotheses that seek to explain such patterns. We were able to separate the distinct roles of different mechanisms that may affect the elevation-related plant diversity patterns in the BSM, to highlight the role of changes in climatic factors along the elevation gradient and to identify the difference in the effect of the monsoon between the eastern and the western aspects of the mountain. The study highlights the differences due to the aspect in patterns of plant biodiversity along the elevation gradient and provides useful insights for planning biodiversity conservation and forest management in this region.

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