

# Multiscale spatial patterns of species diversity and biomass in subalpine meadows on the east of the Loess Plateau, China

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**Background.** Researchers frequently discuss spatial distribution patterns of species diversity and biomass together with their correlations along geographical gradients. Typical subalpine meadows occur widely on the east of the Loess Plateau, China. In recent years, with a rapid development of tourism and pasture husbandry, subalpine meadows have experienced extensive and severe degradation caused by humans in the mountain systems of the Plateau, where their environments are sensitive and fragile, meadows degradation had been increasing, and biodiversity has been threatened seriously.

**Methods.** In our study, we selected nine mountains belonging to four mountain systems from north to south on the east of the plateau. We analyzed five latitudinal and longitudinal gradients together with six elevational gradients to study the spatial distribution patterns of species diversity (including  $\alpha$ ,  $\beta$ , and  $\gamma$  diversity) and biomass plus with their relationships at various scales. **Results.** For diversity,  $\alpha$ -Diversity manifested unimodal variation patterns in horizontal spaces, peaking at high latitude and low longitude. However,  $\alpha$ -diversity was not sensitive to elevation in vertical spaces and tended to decrease with increasing elevation. With increased latitude, longitude, and elevation,  $\beta$ -Diversity diminished; meanwhile, the rate of species turnover decreased and the similarity of community composition enlarged.  $\gamma$ -Diversity demonstrated quadratic function changes that were initially incremental and then decreased with increasing longitude, elevation, and latitude from 37.5° to 40°. For biomass, changes of aboveground biomass (AB) were more obvious along latitudinal gradients, whereas variations of belowground biomass (BB) had smaller differences along longitudinal and latitudinal gradients. More biomass was allocated to BB toward the north and east, whereas total biomass (TB) allocation was more evident at greater latitude than greater longitude. With increased elevation, more TB was also allocated to BB, and the relationship of biomass to elevation was closer in AB. In addition, species diversity had the strongest positive influence on AB. The Patrick and Shannon indices had correlations of power functions with AB and root-to-shoot ratio, respectively, indicating that an allometric model could be used

to model relationships between species diversity and biomass. **Discussion.** The unique geomorphological structures with a series of basins between mountain systems on the east of the Loess Plateau, meant that subalpine meadows were mostly distributed along latitudinal directions, so the spatial distribution of species diversity and biomass was more evident along latitudinal gradients, and thus the response of aboveground biomass was more sensitive to variations of spatial gradients and species diversity.

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# ABSTRACT

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**Methods.** In our study, we selected nine mountains belonging to four mountain systems from north to south on the east of the plateau. We analyzed five latitudinal and longitudinal gradients together with six elevational gradients to study the spatial distribution patterns of species diversity (including  $\alpha$ ,  $\beta$ , and  $\gamma$  diversity) and biomass plus with their relationships at various scales.

**Results.** For diversity,  $\alpha$ -Diversity manifested unimodal variation patterns in horizontal spaces, peaking at high latitude and low longitude. However,  $\alpha$ -diversity was not sensitive to elevation in vertical spaces and tended to decrease with increasing elevation. With increased latitude, longitude, and elevation,  $\beta$ -Diversity diminished; meanwhile, the rate of species turnover decreased and the similarity of community composition enlarged.  $\gamma$ -Diversity demonstrated quadratic function changes that were initially incremental and then decreased with increasing longitude, elevation, and latitude from 37.5° to 40°.

For biomass, changes of aboveground biomass (AB) were more obvious along latitudinal gradients, whereas variations of belowground biomass (BB) had smaller differences along longitudinal and latitudinal gradients. More biomass was allocated to BB toward the north and east, whereas total biomass (TB) allocation was more evident at greater latitude than greater longitude. With increased elevation, more TB was also allocated to BB, and the relationship of biomass to elevation was closer in AB. In addition, species diversity had the strongest positive influence on AB. The Patrick and Shannon indices had correlations of power functions with AB and root-to-shoot ratio, respectively, indicating that an allometric model could be used to model relationships between species diversity and biomass.

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40 **Subjects** Ecology, Plant Science

41 **Keywords** Species diversity, Biomass, Geographical gradient, Spatial distribution, Subalpine meadow,

42 Loess Plateau

# INTRODUCTION

Plants serve vital roles in terrestrial ecosystems and provide humans with many ecological services in regulating climate, improving soil fertility, protecting biodiversity, and promoting productivity (*Fraser et al., 2015; Yuan et al., 2015; Chen et al., 2016; Grace et al., 2016*). Studies of species diversity and plant biomass have become important research topics related to ecology and geography, focusing on their spatial distribution and correlations along geographical gradients.

Biodiversity contributes significantly to sustaining a global ecological balance and to promoting sustainable development for humans (*Tilman et al., 1996; Tilman, 2000; Ge, 2017*). As a measurable index of a community, biodiversity reflects essential features of ecosystems, represents variations that occur in ecosystem, and helps to maintain ecosystem productivity. Biodiversity is produced by competition among species in a community or in the processes involved in coordinating resources so that various species can coexist (*Loreau et al., 2001; Cardinale et al., 2006; Jin et al., 2017*); as a result, biodiversity provides provenance bases and supporting conditions for the operation and turnover of ecosystem functions (*Hector & Bagchi, 2007; Nguyen et al., 2012; Carnicer et al., 2015; Shanafelt et al., 2015*). Species diversity is a manifestation of biodiversity at the species level and is an important indicator that can be used to quantify and document community structure and composition. Species diversity reveals the organizational levels of a community and induces changes in the functional characteristics of a biotic community; it can even alter a shortage of critical species in a community or the utilization patterns of environmental resources by species, and thus lead to modifications in ecosystem structure and function (*Tilman, 2000; Hector et al., 2002; Li et al., 2017; Yao et al., 2017; Zhao et al., 2017*). Variations in species diversity mirror changes of species richness and evenness in a community or habitat, as well as the relationships between a community and different natural geographical conditions (*Zhu et al., 2017*). Thereby, studying and measuring species diversity is important and helps researchers to probe its patterns of variation along geographical gradients in modern studies of biodiversity.

Measurements of species diversity are primarily conducted at three spatial scales known as  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity (*Godfray & Lawton, 2001; Whittaker et al., 2001; Rey Benayas & Scheiner, 2002*). The first scale is within-habitat diversity, that is,  $\alpha$ -diversity, which mainly focuses on species number in local homogeneous habitat. At this scale, the principle factors that affect diversity are ecological niche diversity and interspecific interaction, so  $\alpha$ -diversity is closely related to environmental energy. The second scale is between-habitat diversity, that is,  $\beta$ -diversity, which indicates differences of species composition among

different habitats and communities or differences in turnover rates of species along environmental gradients. The dominant ecological factors that control  $\beta$ -diversity are soil, landform, and disturbance. The last scale is regional diversity, that is,  $\gamma$ -diversity, which describes species number at regional or continental scales. The ecological processes that drive  $\gamma$ -diversity chiefly include hydrothermal dynamics, climate, as well as species development and evolution. Among these three types of diversity,  $\alpha$ - and  $\beta$ -diversity constitute the overall diversity of communities or ecosystems, or habitat heterogeneity of a certain district.

Similar to species diversity, biomass is also a primary quantitative characteristic of ecosystems and reflects plants productivity; thus species diversity is a basic part of the study ecosystem function (Li *et al.*, 2017). Biomass allocation among various organs mirrors the growth strategy a plant uses to adapt to an environment and plays a crucial role in the growth of plant individuals, species coexistence, and vegetation recovery (Weiner, 2004; Poorter *et al.*, 2012). Strategies of biomass allocation among leaves, stems, and roots, together with allometric relationships between plant organs provide a foundation in the study of species evolution, maintenance of diversity, and carbon cycling in ecosystems, and also are important to our understanding of the distribution of carbon in ecosystems and the function of carbon sinks (McCarthy & Enquist, 2007; Duncanson *et al.*, 2015; Wang *et al.*, 2017). Therefore, biomass allocation, especially the allocated models under the effects of different geographical gradients, is important in studies of biomass.

The mountainous regions of the Loess Plateau in China have typical terrain, and many subalpine belts have developed at the higher elevation, where mountainous terrain determines the distribution of hydrothermal resources and thus influences species diversity and biomass in subalpine belts (Chen *et al.*, 2016; Grace *et al.*, 2016). Subalpine meadows are one grassland type of the Loess Plateau and mainly are distributed in high-elevation mountains where their species diversity and biomass is obviously affected by the mountainous terrain (Niu *et al.*, 2017). Latitude, longitude, and elevation are dominant terrain indicators of mountainous subalpine meadows; they directly affect the spatial distribution of solar radiation and rainfall, and thus they result in an uneven distribution of soil moisture and temperature (Tan *et al.*, 2017; Zhu *et al.*, 2017). Large areas of subalpine meadows on the east of the Loess Plateau have an abundance of species. These meadows not only provide excellent natural pastures but also serve as famous eco-attractions—for example, Heyeping has been honored as the “plateau jade,” Shunwangping as the “Jiuzhaigou of north China,” and Wutai Mountain as “the roof of north China.” In recent years, with a rapid development of tourism and pasture husbandry, subalpine meadows have experienced extensive and severe degradation caused by humans in the mountain systems of Liuleng, Wutai, Lvliang, and Zhongtiao, where

their environments are sensitive and fragile, meadows degradation had been increasing, and biodiversity has been threatened seriously (Qin et al., 2015; Tong et al., 2016; Xu et al., 2017).

Hence, we chose typical subalpine meadows to install experimental plots on the east of the Loess Plateau and analyzed variations of species diversity and biomass for a single vegetation type in natural conditions at the community level. The purpose of this study was to answer the following scientific questions: (1) What are the distribution patterns of species diversity with latitude, longitude, and elevation at different spatial scales ( $\alpha$ ,  $\beta$ , and  $\gamma$  diversity) in subalpine meadows? (2) What are the patterns of variation in biomass and its allocation at horizontal and vertical spaces in subalpine meadows? (3) What are the correlations between species diversity and biomass in subalpine meadows?

## MATERIALS AND METHODS

### Description of study area

Shanxi Province (34°34'–40°43' N, 110°14'–114°33' E) lies on the east of the Loess Plateau, which serves as a dividing line between the second and third steps of topography in China in a region where subalpine meadows are distributed most intensively in the Plateau. The complex and changeable topography of Shanxi has the Taihang and Lvliang mountains in the east and the west, respectively, and a series of basins from north to south in the central region. These basins are successively the Datong, Xinding, Taiyuan, Changzhi, Linfen, and Yuncheng basins. Mountainous areas occupy more than 80% of the province. The temperate continental monsoon climate features an annual mean temperature of 4–14°C, summer mean temperature of 22–27°C, winter mean temperature of –12 to –2°C, annual precipitation of 400–600 mm, and a frost-free season of 4–7 months (Qin et al., 2015). In this region with complicated geomorphic features and combinations of water and heat, vegetation of temperate regions dominates as the vegetation type in this province. Among larger mountain systems, meadows that approach a subalpine form cover an area of about 353,000 hm<sup>2</sup>; these are mainly distributed in high-elevation belts above the timberline in the Liuleng, Lvliang, Wutai, and Zhongtiao mountain systems. Plants in the subalpine meadows principally include perennial herbs that are suitable for low temperature and moderate moisture conditions; for example, *Carex*, *Kobresia*, Asteraceae, Leguminosae, and other cyperaceous species were common (Tong et al., 2016). The subalpine meadow soil is high organic content and has thick litter layer.

### Arrangement of experimental plots

When compared with a vegetation-type map of the Loess Plateau and a topographic map of Shanxi Province, the locations of the distributions of subalpine meadows were identified along the east of the



Loess Plateau. Then, experimental plots were selected in typical subalpine meadows. These were investigated from July to August in 2016 in areas with little human disturbance, flat terrain, and a uniform distribution of vegetation. On the entire east, nine subalpine meadows were successively surveyed in different mountain ranges moving from north to south. In total, nine mountains belonged to four mountain systems were surveyed using plots. The names of these mountains were Dianding (DD) Mountain in the Liuleng mountain system, Beitai (BT) and Dongtai (DT) mountains in Wutai mountain system, Malun (ML), Heyeping (HY), Yunzhong (YZ) and Yunding (YD) mountains in the Lvliang mountain system, and Shunwangping (SU) and Shengwangping (SE) mountains in the Zhongtiao mountain system (Fig. 1).

### Measurement of plant diversity

On each of these nine mountains, we chose a single plot with an appropriate habitat. Six 1 m<sup>2</sup> quadrats were installed randomly within each plot to survey plant diversity at a community scale or a total of 54 quadrats on all mountains. We used 1 m × 1 m quadrat frames as measurement tools, which we divided into 100 uniform grids (0.1 m × 0.1 m). In each grid, we measured plant height, abundance, coverage, and frequency of each species; the data were used to calculate species diversity indices in the plots (see 1.5 Data analysis). Meanwhile, we recorded the latitude, longitude, and elevation of each plot by a portable GPS (Table 1).

### Measurement of plant biomass

At each of nine mountain sites, we randomly located five quadrats for use in measuring diversity, with 45 quadrats in total. A 0.2 m × 0.2 m subquadrat was placed in the center of each quadrat with its plants being evenly distributed, so that 45 subquadrats were also acquired in total. We used subquadrats to survey plant biomass at the community scale using the following method. In each subquadrat, aboveground plant parts were clipped near the ground surface and belowground plant parts were then excavated in the entire 0.2 m × 0.2 m subquadrat to a depth of 0.2 m. Samples of aboveground plant parts and soil blocks with volumes of 0.2 m × 0.2 m × 0.2 m were sealed and brought to laboratory for post-processing. In this process, soil blocks and withered grass were removed from samples of aboveground plant parts and only live plants were retained. Samples of belowground plant parts were first sieved by a standard soil sieve with a bore diameter of 0.42 mm to eliminate stones and coarse debris from the soil. Then, the soil samples were sieved using a standard soil sieve with a bore diameter of 0.18 mm to eliminate fine roots with diameters no smaller than 0.18 mm. Next, live roots were separated from root systems according to color, suppleness, and whether or not hair roots were present. Live roots and treated stems and leaves were placed into an oven and dried to constant weight at a high temperature of 80°C. Last, dry samples were weighed as below-

and aboveground plant biomass by an electronic balance with an accuracy of 0.001 g.

## Data analysis

### (1) $\alpha$ -Diversity

We calculated the important species values based on the relative height, abundance, coverage, and frequency of each species; then  $\alpha$ -diversity indices were obtained, including the Simpson, Shannon, and Pielou indices.  $\alpha$ -Diversity indices plus the richness index of Patrick were used to explore the characteristics of spatial distribution of subalpine meadows at the scale of  $\alpha$ -diversity along with changes in latitude, longitude, and elevation. Corresponding computational formulas of these  $\alpha$ -diversity indices were as follows (Xu *et al.*, 2017):

$$IV = \frac{rh + ra + rc + rf}{4}, \quad (\text{Eq. 1})$$

$$R = S, \quad (\text{Eq. 2})$$

$$H' = 1 - \sum_{i=1}^S p_i^2, \quad (\text{Eq. 3})$$

$$H = -\sum_{i=1}^S p_i \ln(p_i), \quad (\text{Eq. 4})$$

$$E = \frac{H}{\ln(S)}, \text{ and} \quad (\text{Eq. 5})$$

$$p_i = \frac{IV_i}{IV_{total}}, \quad (\text{Eq. 6})$$

where  $IV$  is the importance value,  $rh$  is relative height,  $ra$  is relative abundance,  $rc$  is relative coverage, and  $rf$  is relative frequency; in addition,  $R$ ,  $H'$ ,  $H$ , and  $E$  are the Patrick, Simpson, Shannon, and Pielou indices, respectively;  $i$  is a plant species  $i$  and  $S$  are the sum of all plant species in the plots.

### (2) $\beta$ -Diversity

Using the horizontal directions of latitude and longitude, the nine study plots were divided into five and five latitudinal and longitudinal gradient belts with  $0.5^\circ$  and  $0.45^\circ$  intervals arranged from south to north and from west to east, respectively. The nine plots were divided into six elevational gradient belts from low to high elevation with an interval of 100 m (Table 2). Species in different plots were merged in each geographical gradient belt and variations of  $\beta$ -diversity indices were analyzed between two adjacent gradient belts to probe the differentiation in the characteristics of subalpine meadows at the scale of

$\beta$ -diversity with latitude, longitude, and elevation. Measurements of  $\beta$ -diversity chiefly included two aspects: (1) community dissimilarity based on species composition and (2) species replacement based on the distribution boundary (He & Chen, 1997). Unlike  $\alpha$ -diversity, measurements of  $\beta$ -diversity could be separated into two methods: binary attribute data and quantitative data, respectively. Hence, we used two indices, the Cody and Sørensen indices, in the analysis of  $\beta$ -diversity based on binary attribute data; in addition, we used the Bray-Curtis index based on quantitative data. Corresponding computational formulas of these  $\beta$ -diversity indices are as follows:

$$\beta_C = \frac{a + b - 2c}{2}, \quad (\text{Eq. 7})$$

$$\beta_S = 1 - \frac{2c}{a + b}, \text{ and} \quad (\text{Eq. 8})$$

$$\beta_{B-C} = \frac{2cIV}{a + b}, \quad (\text{Eq. 9})$$

where  $\beta_C$ ,  $\beta_S$ , and  $\beta_{B-C}$  are the Cody, Sørensen, and Bray-Curtis indices, respectively;  $a$  and  $b$  are the number of species in plots A and B, respectively, and  $c$  is the number of common species between plots A and B; and  $cIV$  is the sum of the relatively small important values of species common to both A and B, that is,  $cIV = \sum \min(cIV_a, cIV_b)$ .

### (3) $\gamma$ -Diversity

$\gamma$ -Diversity indicates species richness of all habitats within a certain geographical range and is usually used to demonstrate species number in a region or on a continent (He & Chen, 1997). Here, regional scales were employed using five latitudinal and longitudinal gradients together with six elevational gradients; these regions were divided into nine groups of subalpine meadows. Total species number (i.e., total species richness of  $S$ ) in each geographic gradient belt was defined as an indicator to investigate spatial distribution patterns of subalpine meadows at the scale of  $\gamma$ -diversity.

### (4) Biomass

Below- and aboveground biomass was added to calculate total biomass and the root-to-shoot ratio was also found for each unit. Therefore, aboveground biomass, belowground biomass, total biomass, and the root-to-shoot ratio were adopted as biomass indicators and were used to analyze variations of plant community biomass at different latitude, longitude, and elevation in subalpine meadows.

## RESULTS

# Spatial distribution characteristics of species diversity in subalpine meadows

## $\alpha$ -Diversity

We observed large differences in different mountain ranges for the Simpson ( $H'$ ), Shannon ( $H$ ), Pielou ( $E$ ), and Patrick ( $R$ ) indices in subalpine meadows, with their means of 0.88, 2.50, 0.86, and 19.11, respectively. However, these  $\alpha$ -diversity indices had relatively consistent trends that all presented variations in wave curves ranging from the northernmost DD to the southernmost SE (Fig. 2). Maximums of  $\alpha$ -diversity indices appeared in YZ (average, 7.75), and their minimum appeared in ML (average, 3.56). The maximums and minimums for the  $\alpha$ -diversity indices all appeared in central mountains and their differences were significant ( $P < 0.05$ ), showing a greater fluctuation of  $\alpha$ -diversity in the central mountains than elsewhere. From ML to YD in the central mountains, their  $\alpha$ -diversity indices initially increased and then decreased ( $P < 0.05$ ; average, 5.35). From DD to DT in the northern mountains, their  $\alpha$ -diversity indices initially decreased and then increased ( $P < 0.05$ ; average, 6.33). From SU to SE in the southern mountains, their  $\alpha$ -diversity indices had no significant trends ( $P > 0.05$ ; average, 6.08). Thus the variations in  $\alpha$ -diversity of subalpine meadows were less obvious in the southern mountains based on trends; in quantitative terms,  $\alpha$ -diversity of the subalpine meadows was smallest in the central mountains, whereas it was greater in the northern and southern mountains with no larger differences between them. Except for  $E$ , changes were very consistent for  $H'$ ,  $H$ , and  $R$ , and reached significant levels ( $P < 0.05$ ) between adjacent mountains from DD to YD; meanwhile, changes of  $E$  were significant ( $P < 0.05$ ) only between adjacent mountains from DT to HY. However, from YD to SE, the  $\alpha$ -diversity indices had insignificant differences ( $P > 0.05$ ) (Table 3).

In horizontal spaces,  $\alpha$ -diversity indices of subalpine meadows showed similar patterns of change with latitude and longitude (Fig. 3). With increasing latitude and longitude,  $R$ ,  $H'$ ,  $H$ , and  $E$  tended to initially increase and then decrease and had larger values at high latitudes and low longitudes, presenting unimodal curves with peak values being at high latitudes and low longitudes along latitudinal and longitudinal gradients, respectively. Maximums of  $R$ ,  $H'$ ,  $H$ , and  $E$ , which were 26.3, 0.92, 2.86, and 0.88, respectively, all existed near  $38.7^\circ$  N and  $112.4^\circ$  E. Trends of  $\alpha$ -diversity indices had larger discrepancies with latitude and longitude at a latitudinal boundary of  $38^\circ$ . When latitude was below  $38^\circ$ ,  $\alpha$ -diversity indices changed more gently with latitude and the differences between maximums and minimums of  $R$ ,  $H'$ ,  $H$ , and  $E$  were 8.5, 0.04, 0.39, and 0.05, respectively; with longitude,  $\alpha$ -diversity indices experienced symmetrical changes with an axis of symmetry at  $112.3^\circ$ . When latitude was greater than  $38^\circ$ ,  $\alpha$ -diversity indices

changed more dramatically with latitude, and the corresponding differences among  $R$ ,  $H'$ ,  $H$ , and  $E$  were 15.6, 0.11, 0.93, and 0.07 between the maximums and minimums. With longitude,  $\alpha$ -diversity indices showed asymmetrical changes that was more dramatic initially and then less so. With changes in elevation,  $R$ ,  $H'$ ,  $H$ , and  $E$  had negative correlations with elevation (mean coefficients,  $-0.363$ ), but correlations were all insignificant ( $P > 0.05$ ), demonstrating that  $\alpha$ -diversity was affected insignificantly by elevation and tended to decrease with increasing elevation (Table 3).

### $\beta$ -Diversity

Various trends existed in  $\beta$ -diversity with changes in latitude, longitude, and elevation in subalpine meadows, but in the same type of gradient belts, more consistent trends were shown for Cody ( $\beta_C$ ), Sørensen ( $\beta_S$ ), and Bray-Curtis ( $\beta_{B-C}$ ) indices (Fig. 4).

Along latitudinal gradients, relative to an initial belt (belt number 1),  $\beta_C$ ,  $\beta_S$ , and  $\beta_{B-C}$  all decreased between different latitudinal belts with amplitudes of 26.9%, 29.8%, and 32.7%, respectively. Between adjacent latitudinal belts,  $\beta_C$ ,  $\beta_S$ , and  $\beta_{B-C}$  exhibited decreased trends with amplitudes being obviously greater at 46.2%, 42.5%, and 62.8%, respectively. Overall,  $\beta_C$ ,  $\beta_S$ , and  $\beta_{B-C}$  all declined along latitudinal gradients with mean amplitudes of 36.55%, 36.15%, and 47.75%, respectively.

Along longitudinal gradients, relative to an initial belt (belt number 1),  $\beta_C$  and  $\beta_{B-C}$  initially increased and then decreased with reduced amplitudes of  $-11.1\%$  and  $-8.1\%$ , respectively. Meanwhile,  $\beta_S$  initially decreased and then increased by 0.7% between different longitudinal belts. Between adjacent longitudinal belts,  $\beta_C$  and  $\beta_{B-C}$  also exhibited trends of initially increasing and then decreasing with a reduced amplitude of  $-27.8\%$  for  $\beta_C$  and an increased amplitude of 6.6% for  $\beta_{B-C}$ . Meanwhile,  $\beta_S$  manifested a complex trend of initially decreasing, then increasing, and decreasing with an overall reduced amplitude of  $-31.24\%$ . Overall,  $\beta_C$ ,  $\beta_S$ , and  $\beta_{B-C}$  all decreased with increasing longitude and their reduced amplitudes were  $-19.45\%$ ,  $-15.27\%$ , and  $-0.75\%$ , respectively.

Along elevational gradients, relative to an initial belt at the lowest elevation (belt number 1),  $\beta_C$  had a wave pattern of change and tended to decline with increasing elevation (an amplitude of 3.9%). Meanwhile,  $\beta_{B-C}$  initially showed a trend and then decreased (an increase in amplitude of 15.7%), whereas  $\beta_S$  tended to increase (an increase in amplitude of 54.7%) between different elevational belts. Between adjacent elevational belts,  $\beta_C$  tended to decrease (an amplitude of  $-62.75\%$ ),  $\beta_S$  initially demonstrated a decreasing trend and then increased (a reduced amplitude of  $-22\%$ ), and  $\beta_{B-C}$  tended to decrease (an amplitude of  $-75.4\%$ ). Overall, with an increasing trend,  $\beta_C$  and  $\beta_{B-C}$  declined with corresponding mean amplitudes of

–33.33% and –29.85%, whereas  $\beta_s$  increased with its amplitude being 16.35%.

# $\gamma$ -Diversity

The spatial distribution of subalpine meadows was highly consistent at the scale of  $\gamma$ -diversity (Fig. 5). Along latitudinal gradients, total species richness ( $S$ ) generally exhibited a decreasing trend of a logarithmic function ( $R^2=0.185$ ,  $P>0.05$ ), but it presented a significant variation of a quadratic function with a trend of initially increasing and then decreasing at latitudinal belts from 37.5° to 40° ( $R^2=0.885$ ,  $P<0.01$ ). Along longitudinal gradients,  $S$  significantly demonstrated the variation of a quadratic function with a tendency of initially increasing and then decreasing ( $R^2=0.784$ ,  $P<0.01$ ); its peak value appeared at longitudinal belts between 112.05° and 112.5°. Along elevational gradients,  $S$  also showed a quadratic function variation with a trend of initially increasing and then decreasing ( $R^2=0.598$ ,  $P<0.05$ ), while peaking at elevational belts between 2200 m and 2300 m. Averages of  $S$  along latitudinal, longitudinal, and elevational gradients were 47.6, 48.6, and 40.3, respectively, illustrating that species distribution was slightly greater in horizontal spaces than that with changes in elevation at regional scales.

## Spatial distribution characteristics of biomass in subalpine meadows

Biomass indices of subalpine meadows fluctuated in various mountains (Table 4). Ranges of variation ranges in aboveground biomass (AB), belowground biomass (BB), total biomass (TB), and the root-to-shoot ratio (R/S) were 54.85–344.95 g/m<sup>2</sup>, 258.05–901.4 g/m<sup>2</sup>, 364.9–1023.1 g/m<sup>2</sup>, and 1.34–10.88, respectively. Corresponding coefficients of variation were 0.614, 0.437, 0.373, and 0.668, demonstrating that the fluctuation in AB was larger than BB in subalpine meadows but was smaller for TB. From the northernmost site, DD, to the southernmost, SE, AB was varied with a wave form and tended to increase ( $R^2=0.402$ ,  $P>0.05$ ) with larger values existing in the southern sites of SE and SU as well as the central site of HY. The AB was significantly larger in southern mountains (319.05 g/m<sup>2</sup>) than that in northern (112.35 g/m<sup>2</sup>) and central (126.4 g/m<sup>2</sup>) mountains ( $P<0.05$ ). BB changed with a wave form and tended to decrease ( $R^2=0.206$ ,  $P>0.05$ ) with larger values appearing in the northern sites of BT and DD as well as the central HY site. Meanwhile, BB in northern mountains (622.62 g/m<sup>2</sup>) was significantly greater than that in the central (431.39 g/m<sup>2</sup>) and southern (437.18 g/m<sup>2</sup>) mountains ( $P<0.05$ ). TB had no obvious trends ( $R^2=0.018$ ,  $P>0.05$ ) with larger values presenting in the central HY site, the northern BT, and the southern SE site. The TB in central mountains (557.79 g/m<sup>2</sup>) was significantly smaller than that in the northern (734.97 g/m<sup>2</sup>) and southern (756.23 g/m<sup>2</sup>) mountains ( $P<0.05$ ). The R/S also changed in a wave pattern and tended to decrease ( $R^2=0.315$ ,  $P>0.05$ ) with larger values being in the northern BT and central YD and ML sites. The R/S in

the southern mountains (1.49) was obviously smaller than that in the northern (6.19) and central (4.34) mountains ( $P<0.05$ ). In addition, from DD to DT in the northern mountains, AB tended to initially decrease and then increase, whereas BB, TB, and R/S all had tendencies of initially increasing and then decreasing, indicating that more biomass was allocated to belowground plant parts in northern mountains.

The horizontal spatial distribution of biomass had obvious characteristics in subalpine meadows (Fig. 6). With increasing latitude and longitude, AB generally tended to decline, whereas BB, TB, and R/S all tended to increase. That is, more biomass was allocated to belowground plant parts with developmental directions to the north and east in subalpine meadows. Tendencies of AB were apparently stronger with changes in latitude ( $R^2=0.6075$ ) than longitude ( $R^2=0.0677$ ). The BB had slightly smaller tendencies with latitude ( $R^2=0.0691$ ) than longitude ( $R^2=0.1384$ ). Tendencies of TB were also slightly smaller with latitude ( $R^2=0.0187$ ) than longitude ( $R^2=0.0673$ ). The R/S obviously became larger with latitude (0.4896) than with longitude (0.0868). That is, changes in AB were more evident along latitudinal gradients, whereas changes in BB were smaller along latitudinal and longitudinal gradients. Along elevational gradients, trends of biomass existed with some differences as well (Fig. 7). AB decreased significantly with elevation ( $P<0.05$ ), but the increases in BB and TB were all not significant with increasing elevation ( $P>0.05$ ), illustrating that correlations were stronger between AB and elevation. Moreover, the R/S had significant increasing correlations with increasing elevation ( $P<0.01$ ), indicating that more biomass was also allocated to belowground plant parts with increasing elevation.

### Relationships between species diversity and biomass in subalpine meadows

We conducted regression analysis between pairs of  $\alpha$ -diversity and biomass indices to discuss relationships between species diversity and biomass in subalpine meadows (Fig. 8). The regression analysis showed that only  $R$  and  $H$  had significant correlations with AB and R/S, respectively, indicating that species diversity had greater effects on AB than on the R/S. AB had significantly positive correlations with  $R$  and  $H$  ( $P<0.05$ ), whereas R/S had most significantly negative correlations with  $R$  and  $H$  ( $P<0.01$ ); this means that with increasing species diversity, AB increased and more biomass tended to be allocated to aboveground plant parts. In addition, regressive relationships of  $R$  and  $H$  all conformed to power functions with AB and R/S, respectively, and their power exponents had gaps larger than 1, demonstrating that species diversity had an allometric relationship with biomass in subalpine meadows.

## DISCUSSION

### Spatial distribution of species diversity



Species distribution patterns are outcomes of many ecological processes, which are controlled by species evolution (establishment, migration, and extirpation), variations in geography, and environmental factors (geology, geomorphology, climate, and soil); these then create relatively large discrepancies for patterns of species diversity along geographical gradients for researchers (Noss, 1990; Whittaker et al., 2001; Willis & Whittaker, 2002). This primarily occurred in two ways: horizontally and based on elevation. First, in horizontal patterns of distribution, some studies found that species richness had tendencies to decrease with increasing latitude and longitude (Green, 1994; Kaufman, 1995; Zhu et al., 2017). Other studies, however, showed that species richness had no significant trends or presented quadratic function variations along latitudinal and longitudinal gradients (Coates, 1998; La et al., 2014). Second, in vertical distribution patterns along elevational gradients, some studies indicated that  $\alpha$ -diversity peaked at central elevations (Ma et al., 2010; Duan et al., 2011; Luo et al., 2014), whereas other studies showed that  $\alpha$ -diversity tended to decline gradually with increasing elevation (Lu et al., 2010) or had no relationships with elevation (He & Chen, 1997). Our study found that  $\alpha$ -diversity had unimodal change patterns with peak values being at high latitude and low longitude in horizontal spaces in subalpine meadows of the Loess Plateau; trends were more distinct along latitudinal gradients, but  $\alpha$ -diversity was not sensitive to elevation in vertical spaces and tended to decline with increasing elevation.

From research studies on patterns of variation in  $\beta$ -diversity along elevational gradients, many scholars also obtained different results. These could be roughly divided into three types. First,  $\beta$ -diversity had no regular changes with elevation, and greater values usually appeared in community ecotones (Dolezal & Srutek, 2002). In the second type,  $\beta$ -diversity had monotonic decrements with increasing elevation (Sklenar & Ramsay, 2001; Wang et al., 2002). Last,  $\beta$ -diversity rarely changed at low elevation, but sharply increased at high elevations and with increasing elevation (Odland & Birks, 1999). In our research on subalpine meadows, with increasing latitude, longitude, and elevation, the species turnover rate declined and community composition similarity was magnified; therefore,  $\beta$ -diversity was diminished, and amplitudes of variation were the greatest along latitudinal gradients, taking second place along elevational gradients, and were smallest along longitudinal gradients.

$\gamma$ -Diversity presented two universal distribution patterns along elevational gradients. One was partial peak in distribution patterns with peak values of different studies appearing in different regions (Grytnes & Vetaas, 2002; Wang et al., 2002) and the other featured negative correlation patterns with linearly decreasing trends (Tang & Fang, 2004). Our study found that total species richness had significant changes



with a quadratic function that initially increased and then decreased with longitude and elevation as well as at latitudes of 37.5–40° in subalpine meadows of the Loess Plateau. We found that spatial distributions of  $\gamma$ -diversity were in accordance with unimodal change patterns and species distribution was slightly greater in horizontal spaces than with changes in elevation.

Patterns of the distribution of species diversity were closely correlated to scale and environmental factors; in addition, these factors controlled patterns of species diversity that varied tremendously at different scales (Ge, 2017). Therefore, various scales ought to be sufficiently considered in studies of patterns of species diversity. These scales not only should include scales of environmental gradient, but also should incorporate scales of classification hierarchy (Ge, 2017). Distribution patterns of species diversity along environmental gradients varied widely among species with various biotypes. For herbaceous communities, these were familiar distribution patterns for  $\alpha$ -diversity showing unimodal patterns with latitude and reduced trends with increasing elevation. For species with different life-forms,  $\beta$ -diversity possessed similar distribution patterns along environmental gradients that decreased with increasing gradients. For  $\gamma$ -diversity, it mostly exhibited partial peak distribution patterns with environmental gradients. Hence, distribution patterns of species diversity were different for various vegetation forms and spatial scales. Therefore, many researchers have proposed different theories and hypotheses that can be used to decipher these differences, such as Rapoport's law, the energy hypothesis, and the mid-domain effect (Wright, 1983; Colwell & Lees, 2000).

The horizontal spatial distribution of species diversity approximated unimodal change patterns in subalpine meadows of the Loess Plateau; these distributions were more obvious along latitudinal gradients, which were intimately related to the local natural environment and human activities. The Loess Plateau has climatically severe environments caused by the dry climate, concentrated precipitation, sparse vegetation, and serious soil erosion, as well as the influence of human disturbance such as grazing and tourism. From north to south on the east of the Loess Plateau, the elevation of mountains gradually becomes lower, but human disturbance tends to be enhanced, so that serious human disturbance has negative effects on species diversity at low latitudinal regions. However, in high latitudinal regions, the cold climate slows soil formation and plant growth, where other adverse environments exceed the limitations of tolerance of the majority of species such as intense solar radiation and large differences between day and nighttime temperatures. Therefore, the central latitudinal regions serve as transitional areas with plant species differentiation falling between the above extremes, and these area have relatively greater species diversity

([Xu et al., 2017](#)). This conclusion verified the advantages of the mid-domain effect. Regarding the elevation in our study area, the mean elevation was 2472 m in subalpine meadows, but they were mostly between elevations of 2250 m and 2745 m with differences being less than 500 m. This indicates that the elevational differences of the mountains on the east of the Loess Plateau were too small to have apparent effects on local species diversity. However,  $\alpha$ -diversity of subalpine meadows slightly decreased with increasing elevation, whereas  $\beta$ -diversity tended to decrease along spatial gradients, demonstrating that species diversity was high in areas with relatively high temperature ([Supplementary Figure](#)). This conclusion agreed perfectly with the environmental energy hypothesis and also provided further proof of the validity of Rapoport's law. This finding inferred that climates were relatively frigid in high elevational and latitudinal regions and changed more dramatically than climates at low elevational and latitudinal regions, which resulted in broader distribution ranges of plants at high elevational and latitudinal regions. Thus, their species turnover rates between adjoining gradient belts were smaller than in low elevational and latitudinal regions.

### **Spatial distribution of biomass**

Since the 20th century, additional research on biomass has been conducted on forest plants growing in mountainous areas ([Oleksyn et al., 1992, 1998](#); [Hölscher et al., 2002](#)). However, few research studies have addressed biomass allocation for alpine herbaceous plants along spatial gradients; the vast majority of studies have merely been limited to a certain spatial scale such as slope position and elevation with study areas being mostly concentrated on the Qinghai-Tibetan Plateau and the Swiss Alps ([Körner & Renhardt, 1987](#); [Li et al., 2008](#); [Yang et al., 2009, 2010](#); [Ma et al., 2010](#)). As a result, research on the distribution and allocation of herbaceous biomass is extremely rare at different spatial scales in other high-elevation and mountainous regions.

Studies on alpine meadows have illustrated that plants allocate more biomass to belowground parts with increasing elevation, and individual plants tended to become dwarfed as one moves from subalpine areas to snow belts; this change leads to decrements in ratios of aboveground plant biomass to belowground biomass and total biomass, respectively ([Ma et al., 2010](#)). This finding demonstrates that the allocation of plants to sexual reproduction declined and asexual reproduction was augmented with increasing elevation; in addition, R/S increased with decreasing stem biomass and increasing root biomass (especially fine roots with diameters less than 2 mm). This promoted belowground plant parts to acquire sufficient nutrients and to adapt temperatures in order to adapt to extreme environments, such as strong wind, low temperature, and

depleted soil in high-elevation mountains (*Mack & D'Antonio, 2003; Luo et al., 2005; Mokany et al., 2006*).

As is well-known, subalpine meadows develop in mountains at relatively high elevations, with relatively low micro-habitat temperatures. As trade-offs for meadow plants on resource investments for growth and development, cold environments induced plants to allocate more assimilation substances to belowground organs, especially to underground storage organs, allowing the plants to facilitate the establishment of plants through germination and a resistance of alpine environmental stress; this caused individual plants to produce larger R/S (*Ma et al., 2010*).

We concluded that the spatial distribution of aboveground biomass tended to be more obvious at high environmental gradients in subalpine meadows of the Loess Plateau with variations of aboveground biomass being greater along latitudinal gradients and belowground biomass having smaller differences along latitudinal and longitudinal gradients. Toward the north and east in the study area, more biomass was allocated to belowground plant parts and biomass allocation was more evident along latitudinal gradients than longitudinal gradients. From low to high elevation, biomass allocation also tended to emphasize belowground plant parts while the amount of aboveground biomass was significantly reduced, demonstrating that a close correlation existed between aboveground biomass and elevation. In previous studies, plant biomass in mountainous areas exhibited horizontal variation patterns of increasing from west to east and from north to south (*Gao et al., 2009; Zhang & Chen, 2015; Zhu et al., 2017*). However, the vertical distribution of plant biomass was more complex and assumed either negative correlations (*Fabbro & Körner, 2004*), unimodal patterns (*Li et al., 2017*), or nonlinear response relationships (*Oleksyn et al., 1998*) with variations in elevation. The causes of various patterns of change in biomass are still uncertain along spatial gradients, and a majority of studies show that ratios of water to heat were a primary reason that gave rise to differential distributions of biomass (*Adler et al., 2011; Dorji et al., 2014; Fraser et al., 2015*); however, other mechanisms remain unclear. Moreover, plants of different function groups possessed differential responses to changes in environmental factors (*Lin et al., 2017*). Therefore, plants of subalpine meadows allocated more biomass to belowground parts with spatial gradients increasing with elevation in the Loess Plateau. Thus, it is important to explore the influence of environmental factors on a plant community by studying the effects of environmental gradients on species diversity and biomass from the level of plant population.

### **Relationship between species diversity and biomass**

Relationships between species diversity and biomass can reveal how ecosystems function and can help

researchers understand the processes involved in biodiversity as it relates to ecosystem functioning (*Condit et al., 2002; Tilman et al., 2006; Worm et al., 2006; Ives & Carpenter, 2007*). In our research, relationships between species diversity and biomass were in accordance with allometric models in subalpine meadows of the Loess Plateau; biomass allocation tended toward producing aboveground plant parts with increments of species diversity, and thus produced enlargements on aboveground biomass. Researchers have generally acknowledged that biomass was enhanced with increasing species diversity and showed that a power function relationship between them (*Jie et al., 2016*). Results from human-made ecosystems have indicated that systems with the most abundant species produced the greatest biomass, that is, poly-species systems had larger biomass than rare-species systems (*Naeem et al., 1994; Loreau et al., 2001*); experiments in natural grasslands and abandoned lands also illustrated that species diversity had distinct effects on maintaining biomass levels (*Tilman & Downing, 1994; Tilman et al., 1996*). Nevertheless, this might be caused by sampling effects as well, that is, when more species were selected from a species pool, greater probabilities existed for finding high-biomass species, and then ecosystem productivity increased, which was not induced by increments of species diversity (*Huston et al., 2000; Wardle et al., 2000*). Under field conditions, because species diversity is influenced by environmental and human disturbance, correlations had complex relationships between species diversity and biomass (*Lin et al., 2017*), which was usually manifested in four types: linear relationships (*Zhao et al., 2017*), nonlinearly unimodal relationships (*Declerck et al., 2005*), S-type curves (*Loreau et al., 2001; Thiele-Bruhn & Beck, 2005*), and non-correlated relationships (*Tilman & Downing, 1994; Hooper et al., 2000*). Studies in recent years have principally emphasized the effects of human factors on species diversity, while correlations between species diversity and biomass have not been given enough attention under natural conditions (*Liu et al., 2016; Sun et al., 2017; Yao et al., 2017; Zhao et al., 2017*).

Furthermore, owing to discrepancies in study scales, projects, and areas, conclusions from studies on correlations also had great differences between species diversity and biomass (*Kessler et al., 2014*). For example, in several studies (*Ali et al., 2016; Chen et al., 2016; Bai et al., 2007; Bracken et al., 2017; Pedro et al., 2017*), (1) topographical disturbances were eliminated by using studies at larger geographical scales, but concrete differences in community diversity were neglected when geographical units had small scales; (2) simulation studies were carried out in homogeneous habitats and artificial communities at small scales, but the influence of stronger spatial heterogeneity caused by enlargements of scale were omitted in studies of diversity and productivity; and (3) in mountainous research studies, scales were focused only on a single

space level and lacked systematic research in mountains at overall space hierarchies.

The positive correlation of species diversity with biomass in our study was probably a result that agreed with the biogeographic affinity hypothesis; that is, the ability of species to tolerate climate probably developed under dual effects of Earth's climates and species evolution in ecological niches (Harrison & Grace, 2007; Zhu et al., 2017). Meanwhile, this result supports our common understanding that high levels of species diversity provide an important way for ecosystems to maintain biomass, that is, greater species diversity realizes accommodation to an environment by providing for species redundancy and functional complementation, and thus sustained the relative stability of productivity in alpine grasslands (Zhu et al., 2017). Thereby, from a level of plant population in natural conditions, species diversity has important significance to the discussion of spatial distributions and correlations of species diversity and biomass at various levels; this illuminates the internal mechanisms of functional relationships between biodiversity and ecosystems. Given this, typical subalpine meadows were used as research objects on the east of the Loess Plateau. These ecosystems were divided into different latitudinal, longitudinal, and elevational belts, and then the following three scientific problems were addressed: (1) spatial distribution patterns of species diversity at the three scales of  $\alpha$ ,  $\beta$ , and  $\gamma$  diversities in subalpine meadows; (2) patterns of variation in biomass and biomass allocation at horizontal and elevational scales in subalpine meadows; and (3) correlations between species diversity and biomass in subalpine meadows.

## CONCLUSION

We reported the distribution patterns and correlations of species diversity and biomass at various spatial scales in subalpine meadows on the east of the Loess Plateau in China. We concluded that species diversity and biomass of subalpine meadows effectively verified the mid-domain effect, the environmental energy hypothesis, and the biogeographic affinity hypothesis on the Loess Plateau.

(1)  $\alpha$ -Diversity of subalpine meadows presented unimodal change patterns with smaller values in the central mountains. This was more obvious along latitudinal gradients, but it was not sensitive to the effects of elevation.  $\beta$ -Diversity had tendencies to decrease with increasing spatial gradients and amplitudes of variation that were greatest along latitudinal gradients.  $\gamma$ -Diversity generally conformed to unimodal change patterns in spatial distribution, which was slightly larger in horizontal spaces than with elevation.

(2) The spatial distribution of biomass in subalpine meadows tended to exhibit high geographical gradients and more biomass was allocated to belowground plant parts with increased spatial gradients. However, responses of aboveground AB to variations in spatial gradient were more sensitive than that of

BB. Correlations of species diversity with biomass were in accordance with an allometric model in subalpine meadows; biomass allocation tended to favor belowground plant parts with increasing species diversity, and thus enlarged aboveground biomass.

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### Competing interests

The authors declare that they have no competing interests.

### Author Contributions

- MHX and ML conceived and designed the experiments.
- MHX, SXZ, XYY, and JW performed the experiments.
- MHX and SXZ analysed the data.
- ML contributed reagents, materials, and analysis tools.
- MHX wrote the paper.

545 ● MHX, SXZ, XYY, JW, and ML revised the manuscript.

# 546 Data Availability

547 The following information was supplied regarding data availability:

548 The raw data is provided as [Data S1](#).

# 549 Supplemental Information

550 Supplemental information for this article can be found online at

# FIGURE LEGENDS

**Figure 1 Study area and experimental plots.** Light and dark colors show low and high elevation, respectively.

**Figure 2 Spatial distribution of  $\alpha$ -diversity in subalpine meadows.**  $\alpha$ -Diversity indices included Simpson, Shannon, Pielou, and Patrick indices. The data were collected from six quadrats on each of nine mountain sites (54 quadrats in total); means for each mountain site were used in the analysis. Therefore, each  $\alpha$ -diversity index had nine values, one for each site.

**Figure 3 Variations of  $\alpha$ -diversity with latitude and longitude in subalpine meadows.**  $\alpha$ -Diversity indices included the Patrick, Simpson, Shannon, and Pielou indices. The data were collected from six quadrats on each of nine mountain sites (54 quadrats in total) with different latitude and longitude; means for each mountain site were used in the analysis. Therefore, each index had nine values, one for each site.

**Figure 4 Changes on spatial distribution of  $\beta$ -diversity in subalpine meadows.**  $\beta$ -Diversity indices included the Cody, Sørensen, and Bray-Curtis indices. Numbers from 1 to 6 in x-coordinates represented corresponding numbers of latitudinal, longitudinal, and elevational belts in Table 2. Intervals of 1–2, 2–3, 3–4, 4–5, and 5–6 indicated comparisons between adjacent belts, whereas 1–2, 1–3, 1–4, 1–5, and 1–6 indicated comparisons of the initial belt (belt 1) with other belts. The study employed five latitudinal, five longitudinal, and six elevational belts. Each index had values for four latitudinal, four longitudinal, and five elevational belts.

**Figure 5 Spatial distribution of  $\gamma$ -diversity in subalpine meadows.** The study employed corresponding belts along five latitudinal, five longitudinal, and six elevational gradients, with five, five, and six values respectively. Each belt had one value.

**Figure 6 Variations of biomass with latitude and longitude in subalpine meadows.** Biomass indices included aboveground, belowground, and total biomass as well as the root:shoot ratio. The data were collected from six quadrats on each of nine mountain sites (54 quadrats in total); means for each mountain site were used in the analysis. Therefore, each index had nine values.

**Figure 7 Changes of biomass with elevation in subalpine meadows.** The data were collected from six quadrats on each of nine mountain sites (54 quadrats in total); means for each mountain site were used in the analysis. Therefore, each biomass index had nine values.

**Figure 8 Regression analysis between  $\alpha$ -diversity and biomass in subalpine meadows.** The data were



collected from six quadrats on each of nine mountain sites (54 quadrats in total); means for each mountain site were used in the analysis. Therefore, each  $\alpha$ -diversity and biomass index had 54 values. Significant relationships were selected between  $\alpha$ -diversity and biomass indices.

**Supplementary Figure Temperature data for nine mountain sites analyzed in this study in 2016.** In this figure, the upper and lower parts provide the deciphered trends of mean monthly temperature with various months on nine mountains and a significant trend of annual mean temperature on nine mountains ( $P < 0.05$ ). Table 1 provides the full names for each mountain with acronyms only used in this figure.

# TABLE LEGENDS

**Table 1 Geographical data and abbreviations for nine mountains** surveyed on the east of the Loess Plateau with two, four, and two mountains in its northern, central, and southern parts, respectively.

**Table 2 Demarcations on geographical gradient belts of various mountains.** Latitudinal, longitudinal, and elevational gradients were divided into five, five, and six belts with intervals of  $0.5^\circ$ ,  $0.45^\circ$ , and 100 m, respectively. The initial belts were all numbered 1 with different gradient ranges. Mountain names indicated by abbreviated letters are shown in Table 1.

**Table 3 Correlation and significance analyses of  $\alpha$ -diversity with elevation and among various mountains, respectively.**  $\alpha$ -Diversity indices included the Patrick, Simpson, Shannon, and Pielou indices. Mountains were DD, BT, DT, ML, HY, YZ, YD, SU, and SE; mountain names indicated by abbreviated letters are shown in Table 1. Different or the same small letters present significant or insignificant differences ( $P < 0.05$  and  $P > 0.05$ ), respectively. The data for correlation coefficients in the analyses of  $\alpha$ -diversity with elevation are listed with the corresponding  $P$  values in brackets. In significance analyses of  $\alpha$ -diversity among various mountains, significance levels were expressed with different small letters. The data were collected from six quadrats on each of nine mountain sites (54 quadrats in total); means for each mountain site were used in the analysis. Therefore, each mountain site had one elevation, so nine  $\alpha$ -diversity values were used in each correlation analysis. However, the six plots in each mountain were not averaged, so six value were used in each significance analysis for each site.

**Table 4 Spatial distribution of biomass in subalpine meadows.** Mountain names indicated by abbreviated letters are shown in Table 1. AB, BB, TB, and R/S represent aboveground, belowground, and total biomass, as well as the root:shoot ratio, respectively. Different or the same small letters indicate significant and insignificant differences ( $P < 0.05$  and  $P > 0.05$ ), respectively. The data are shown with mean  $\pm$  S.E. with six values given for each mountain.

**Supplementary Table Abbreviations of indices in this study:**  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity, along with biomass had four, three, one, and four abbreviated indices, respectively.

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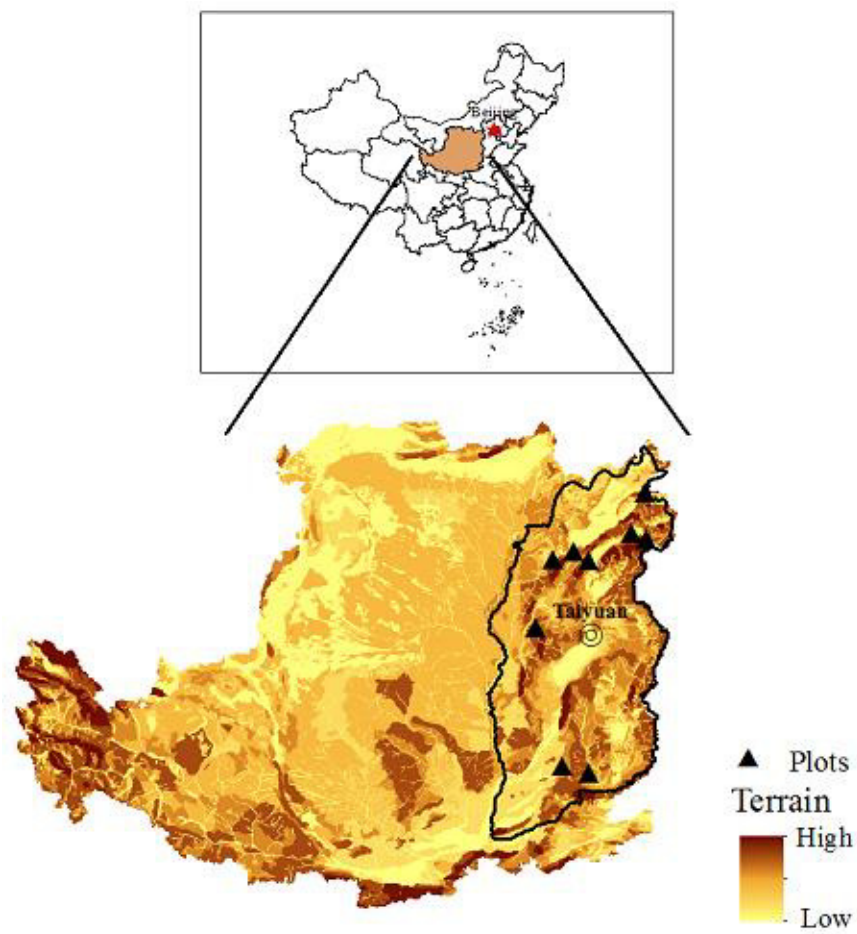
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# **Figure 1**(on next page)

Figure 1 Study area and experimental plots.

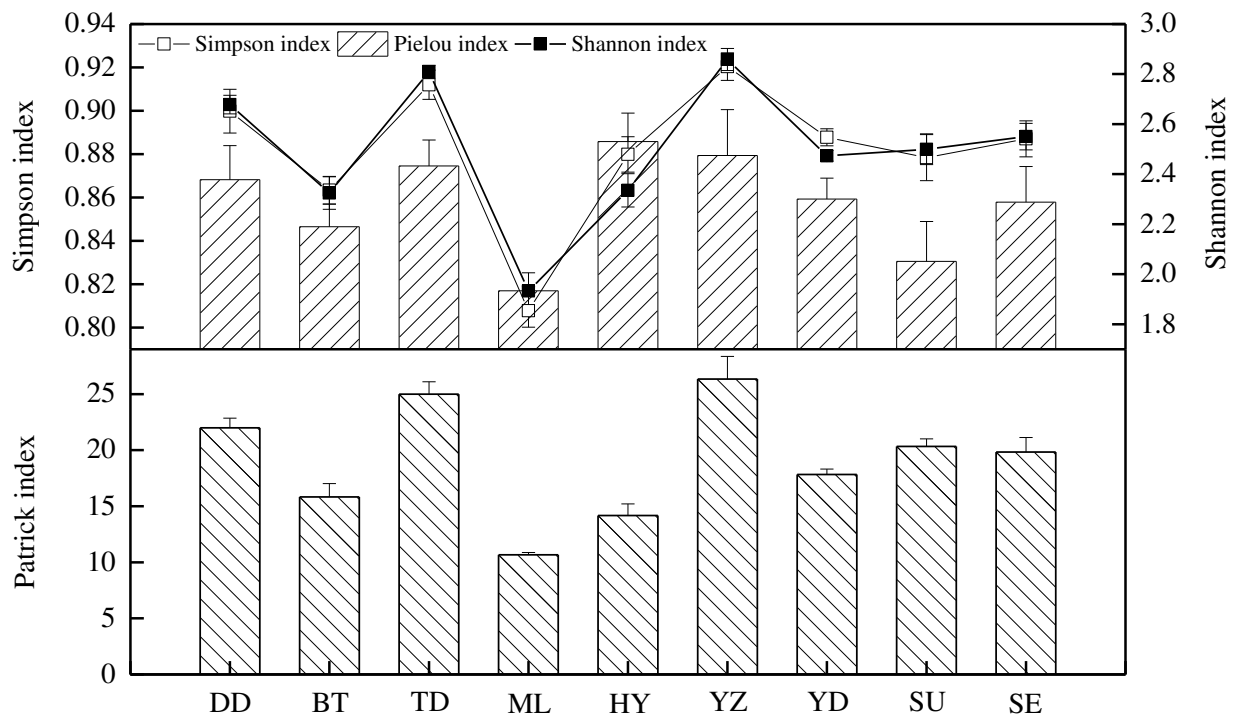
Figure 1



## Figure 2 (on next page)

Figure 2 Spatial distribution of  $\alpha$ -diversity in subalpine meadows.

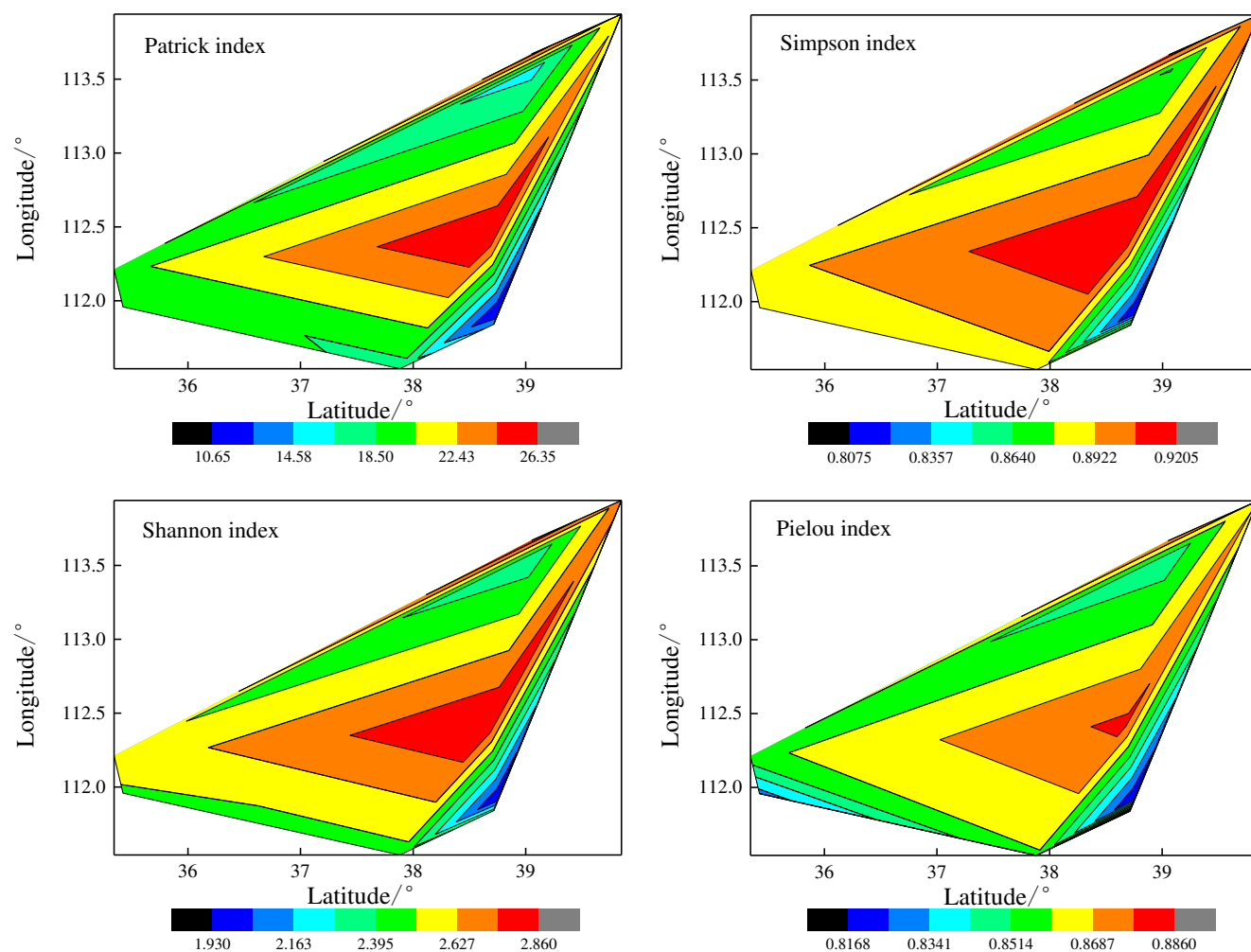
Figure 2



# **Figure 3**(on next page)

Figure 3 Variations of  $\alpha$ -diversity with latitude and longitude in subalpine meadows.

Figure 3

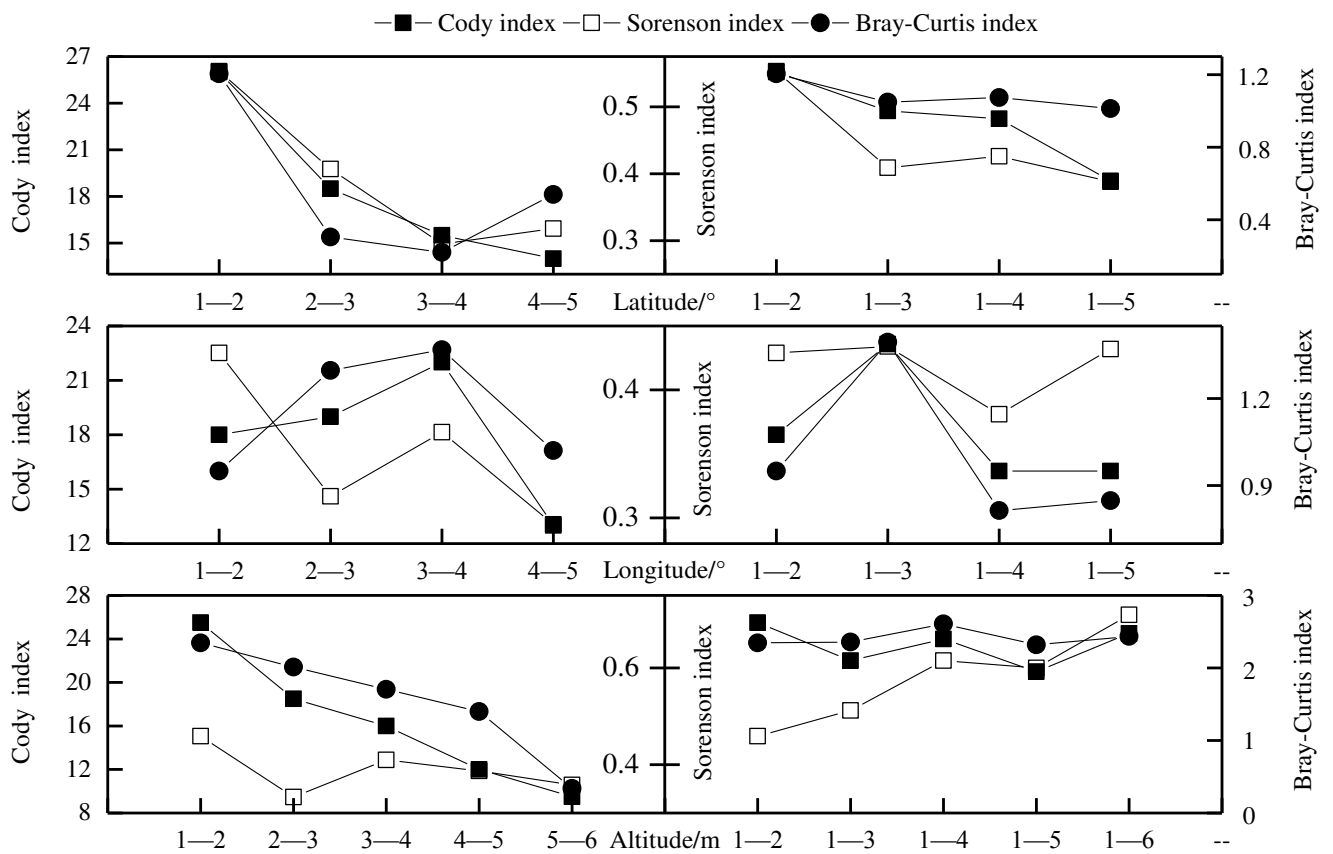




# Figure 4(on next page)

Figure 4 Changes on spatial distribution of  $\beta$ -diversity in subalpine meadows.

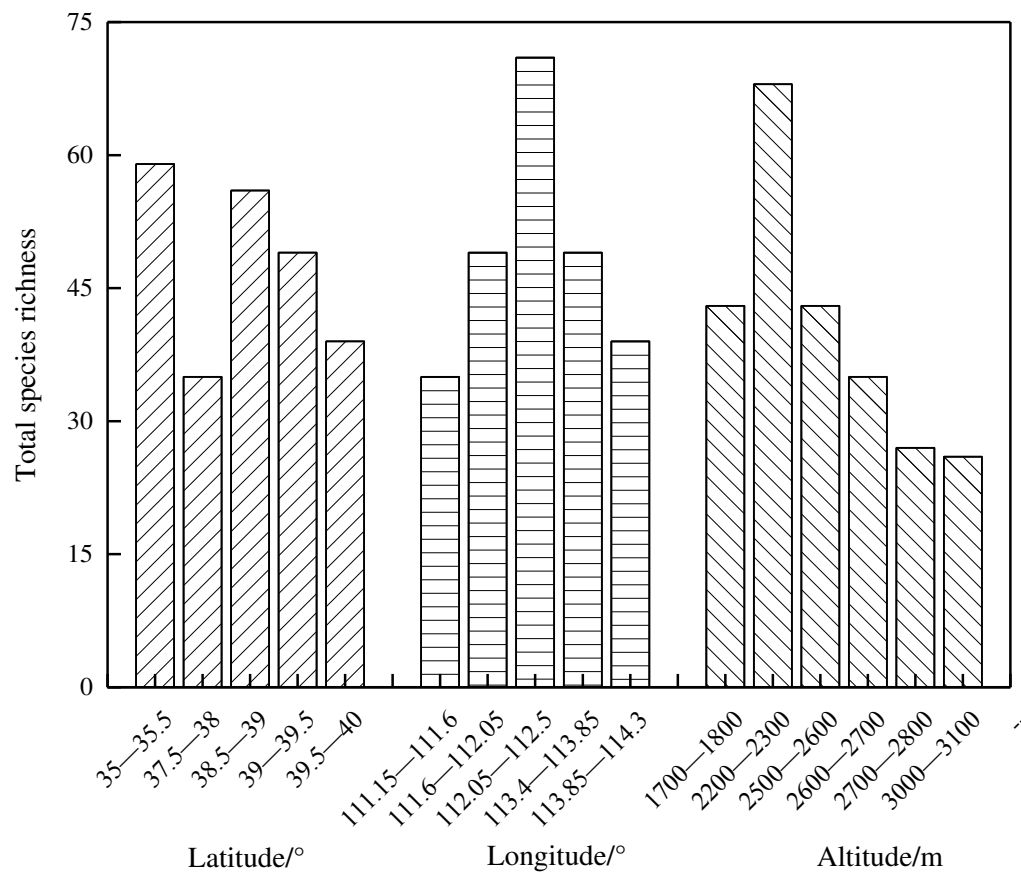
Figure 4



## Figure 5 (on next page)

Figure 5 Spatial distribution of  $\gamma$ -diversity in subalpine meadows.

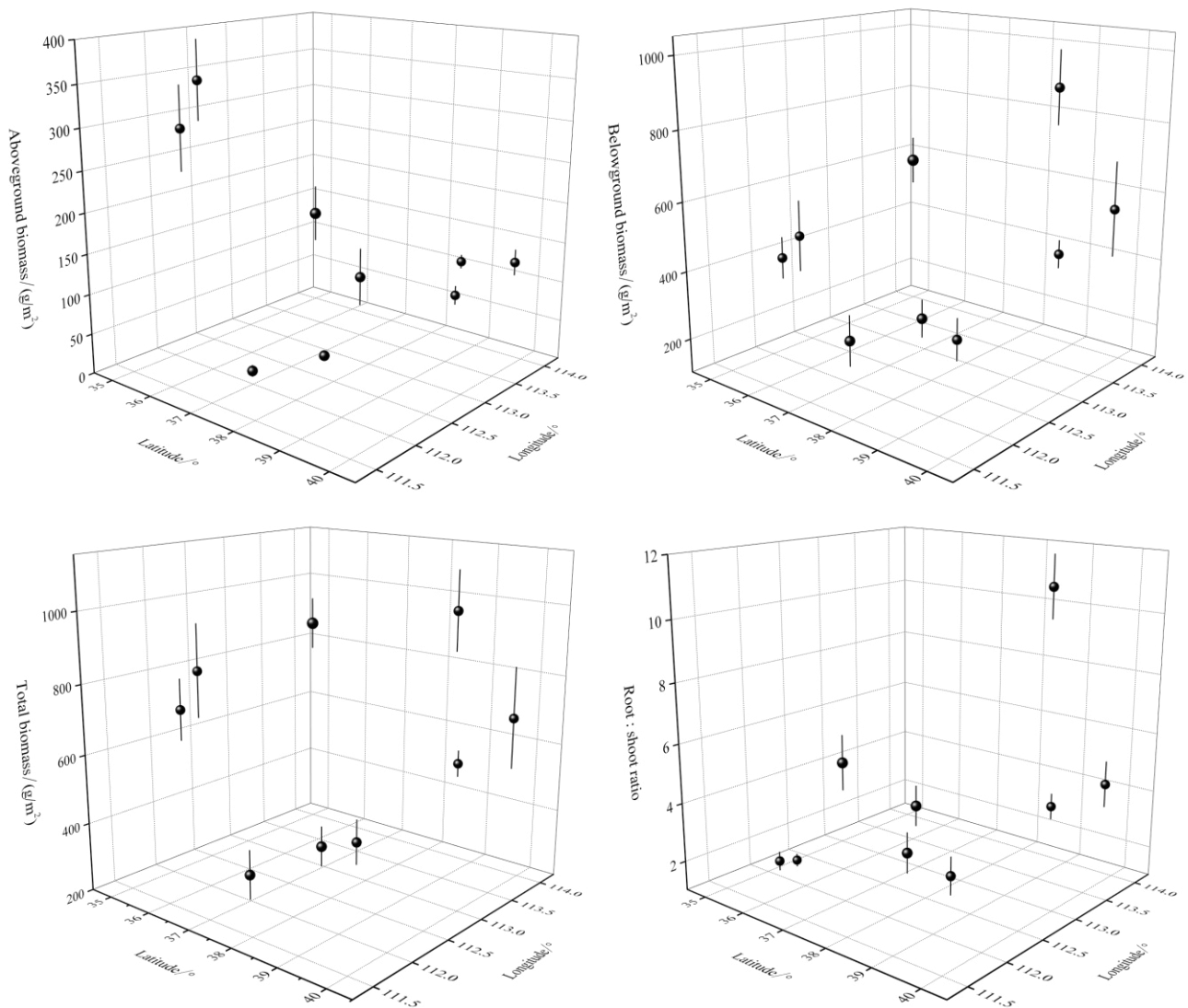
Figure 5



## Figure 6 (on next page)

Figure 6 Variations of biomass with latitude and longitude in subalpine meadows.

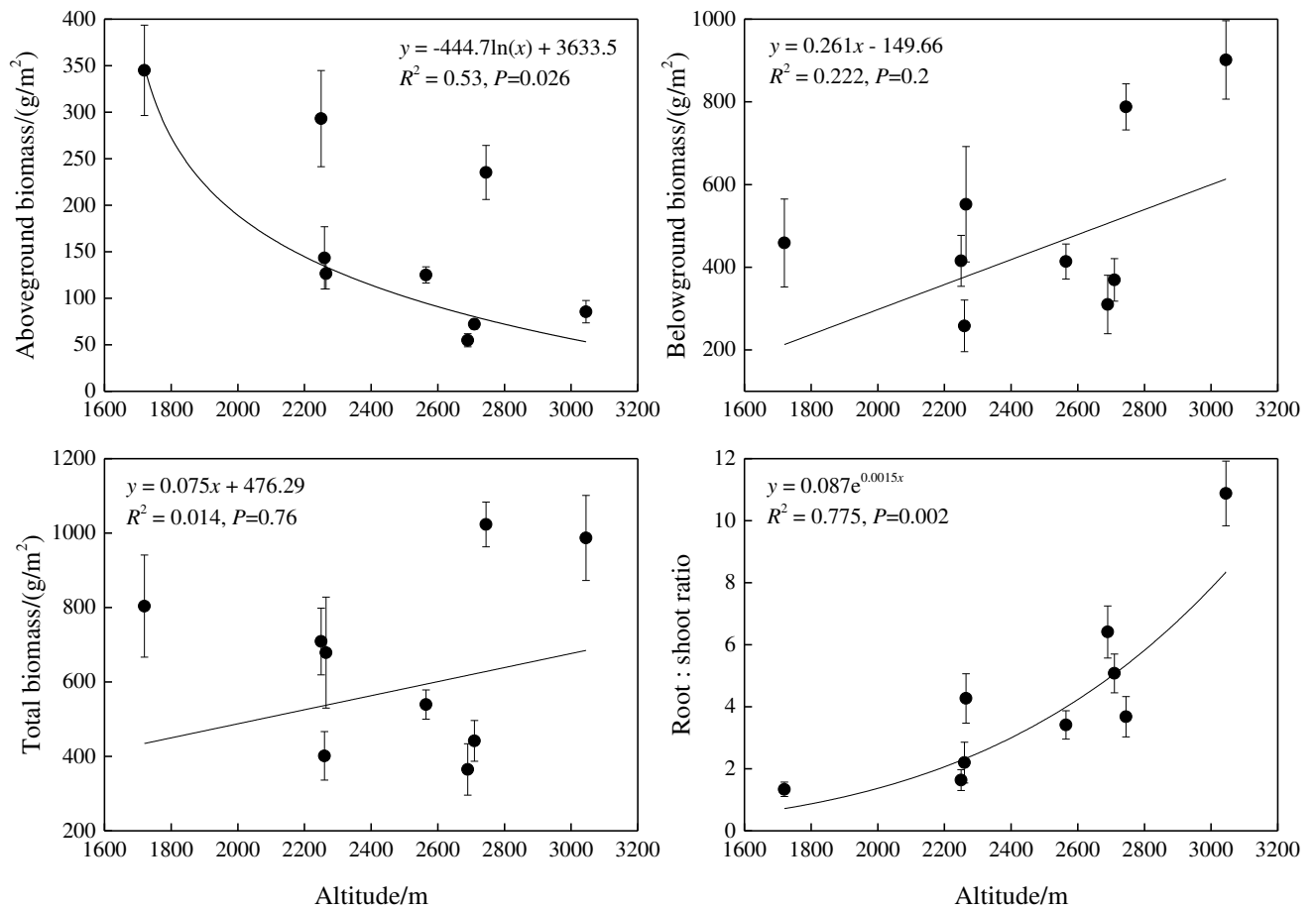
Figure 6



## Figure 7 (on next page)

Figure 7 Changes of biomass with elevation in subalpine meadows.

Figure 7

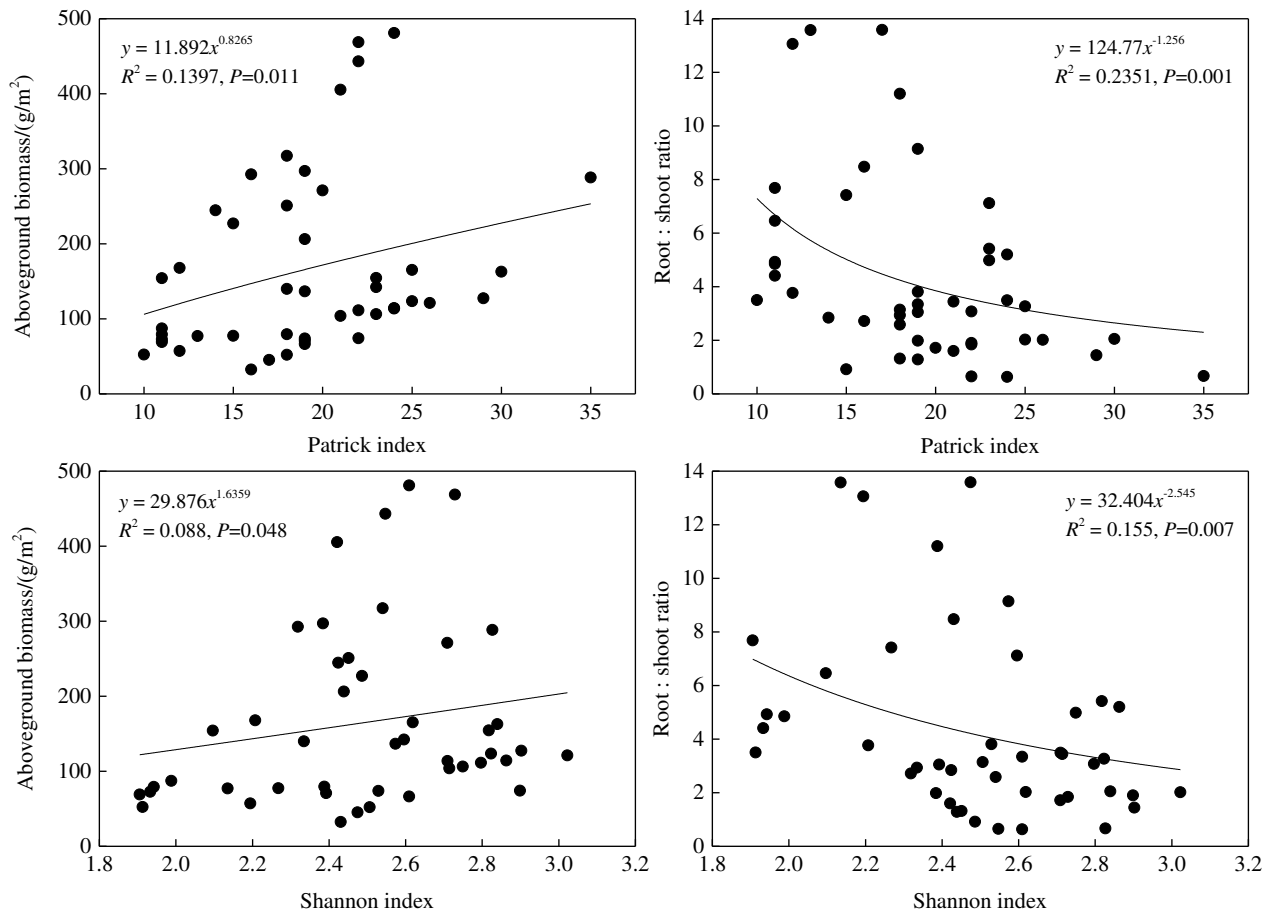




## Figure 8 (on next page)

Figure 8 Regression analysis between  $\alpha$ -diversity and biomass in subalpine meadows.

Figure 8



# **Table 1**(on next page)

Table 1 Geographical data and abbreviations for nine mountains.

**Table 1**

Location	Mountain name/abbreviation	Latitude/°N	Longitude/°E	Elevation/m
Northern part	Dianding (DD)	39.85	113.94	2265
	Beitai (BT)	39.08	113.57	3045
	Dongtai (DT)	39.05	113.67	2565
Central part	Malun (ML)	38.75	111.93	2710
	Heyeping (HY)	38.71	111.84	2745
	Yunzhong (YZ)	38.68	112.43	2260
	Yunding (YD)	37.88	111.54	2690
Southern part	Shunwangping (SU)	35.42	111.96	2250
	Shengwangping (SE)	35.34	112.21	1720

## Table 2 (on next page)

Table 2 Demarcations on geographical gradient belts of various mountains.

**Table 2**

Geographical gradient belt	Belt number	Geographical gradient range	Geographical gradient	Mountain name
Latitudinal belt (0.5° intervals)/°N	1	35–35.5	35.34	SE
			35.42	SU
	2	37.5–38	37.88	YD
	3	38.5–39	38.68	YZ
			38.71	HY
			38.75	ML
	4	39–39.5	39.05	DT
			39.08	BT
	5	39.5–40	39.85	DD
Longitudinal belt (0.45° intervals)/°E	1	111.15–111.6	111.54	YD
	2	111.6–112.05	111.84	HY
			111.93	ML
			111.96	SU
	3	112.05–112.5	112.21	SE
			112.43	YZ
	4	113.4–113.85	113.57	BT
			113.67	DT
	5	113.85–114.3	113.94	DD
Elevational belt (100 m intervals)/m	1	1700–1800	1720	SE
	2	2200–2300	2250	SU
			2260	YZ
			2265	DD
	3	2500–2600	2565	DT
	4	2600–2700	2690	YD
	5	2700–2800	2710	ML
			2745	HY
	6	3000–3100	3045	BT

Table 1 lists the full mountain names and abbreviations.

# **Table 3**(on next page)

Table 3 Correlation and significance analyses of  $\alpha$ -diversity with elevation and among various mountains, respectively.

**Table 3**

Analysis type	Items	Patrick Index	Simpson Index	Shannon Index	Pielou Index
Correlation	Elevation/m	$-0.5$ ( $P = 0.17$ )	$-0.387$ ( $P = 0.303$ )	$-0.463$ ( $P = 0.21$ )	$-0.103$ ( $P = 0.792$ )
Significance	DD	<i>bc</i>	<i>ab</i>	<i>bc</i>	<i>ab</i>
	BT	<i>ef</i>	<i>c</i>	<i>e</i>	<i>abc</i>
	DT	<i>ab</i>	<i>a</i>	<i>ab</i>	<i>ab</i>
	ML	<i>g</i>	<i>d</i>	<i>f</i>	<i>c</i>
	HY	<i>f</i>	<i>bc</i>	<i>e</i>	<i>a</i>
	YZ	<i>a</i>	<i>a</i>	<i>a</i>	<i>a</i>
	YD	<i>de</i>	<i>bc</i>	<i>d</i>	<i>abc</i>
	SU	<i>cd</i>	<i>bc</i>	<i>d</i>	<i>bc</i>
	SE	<i>cd</i>	<i>bc</i>	<i>cd</i>	<i>abc</i>

Table 1 lists the full mountain names and abbreviations.



# **Table 4**(on next page)

Table 4 Spatial distribution of biomass in subalpine meadows.

**Table 4**

Mountain name	AB/(g/m <sup>2</sup> )	BB/(g/m <sup>2</sup> )	TB/(g/m <sup>2</sup> )	R/S
DD	126.400 ± 16.348 <i>d</i>	552.350 ± 139.573 <i>bc</i>	678.750 ± 149.120 <i>bcde</i>	4.268 ± 0.800 <i>bcd</i>
BT	85.550 ± 12.002 <i>d</i>	901.400 ± 104.680 <i>a</i>	986.950 ± 114.034 <i>ab</i>	10.880 ± 1.041 <i>a</i>
DT	125.100 ± 8.622 <i>d</i>	414.100 ± 42.257 <i>c</i>	539.200 ± 39.461 <i>cde</i>	3.417 ± 0.456 <i>bcd</i>
ML	72.100 ± 5.233 <i>d</i>	369.600 ± 51.519 <i>c</i>	441.700 ± 54.890 <i>de</i>	5.075 ± 0.626 <i>bc</i>
HY	235.250 ± 29.123 <i>bc</i>	787.850 ± 55.681 <i>ab</i>	1023.100 ± 60.086 <i>a</i>	3.675 ± 0.650 <i>bcd</i>
YZ	143.400 ± 33.474 <i>cd</i>	258.050 ± 62.421 <i>c</i>	401.450 ± 65.011 <i>de</i>	2.202 ± 0.657 <i>cd</i>
YD	54.850 ± 6.957 <i>d</i>	310.050 ± 70.802 <i>c</i>	364.900 ± 68.983 <i>e</i>	6.412 ± 0.839 <i>b</i>
SU	293.150 ± 51.611 <i>ab</i>	415.600 ± 61.728 <i>c</i>	708.750 ± 89.694 <i>abcd</i>	1.638 ± 0.334 <i>d</i>
SE	344.950 ± 48.528 <i>a</i>	458.750 ± 106.270 <i>c</i>	803.700 ± 137.171 <i>abc</i>	1.337 ± 0.232 <i>d</i>

Note: AB, aboveground biomass; BB, belowground biomass; TB, total biomass; R/S, root:shoot ratio. Table 1 lists the full mountain names and abbreviations.