The particular species determining spatial heterogeneity in shady and terrace on the Qinghai-Tibetan Plateau, China

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ABSTRACT

Spatial patterns of plant species and patchy community are important properties in grasslands. However, research regarding spatial patterns of formed patches with various species has not fully advanced until now. Our purpose is to clarify differences in spatial pattern formed by species and community constructed under shady and terrace habitats. The three common *Kobresia-Carex* patches (Size 1, 0.6–0.9 m^2; Size 2, 3.0–3.8 m^2 and Size 3, 6.5–8.8 m^2) were selected in shady and terrace on the Qinghai-Tibetan Plateau, and corresponding quadrats of 1m×1m, 2m×2m and 3m×3m were placed for S1, S2 and S3 patches, respectively. The surveyed quadrats were divided into 20cm×20cm large cells (L-cells), and further divided into four 10cm×10cm small cells (S-cells). We used the binary occurrence system (presence/absence data) to record occurrences of all species in S-cells. The analysis shows that the power law model was well able to determine the spatial distribution pattern of species or patchy community in shady and terrace. All species and patches show aggregated distribution in shady and terrace habitats. In the shady habitat, the relative spatial heterogeneity (ε) of individual plant species was lowest at presence frequency (P) of 0.1–0.3, whereas in the terrace habitat ε was lowest at $P < 0.1$, and ε increased monotonically with increasing P. For most dominant species, P and ε values were higher in terrace than those in shady. We concluded that the dominant species largely determine spatial heterogeneity of the *Kobresia-Carex* patches, while companion and rare species have weak influence on the community-level heterogeneity in shady and terrace habitats.

1. Introduction

In grassland vegetation, species- and community-level spatial heterogeneity synthetically are the main determinants of community dynamics and stability (Mitsunaga and Fujii, 1997; Shaibur et al., 2021), and affect habitat utilization and forage selection by herbivores (Huang et al., 2012). Understanding the processes which determine the spatial pattern of plant species and community can help recognize the mechanisms of grassland degradation and species diversity (Eppinga et al., 2022). The spatial heterogeneity of grasslands is influenced by various factors: (i) species composition and mode of reproduction (Zhang, 2005; Song et al., 2008). For example, Shiyomi et al. (2001) reported that plant species on a temperate mixed-seeding pasture was distributed more

heterogeneously than a random pattern in Japan. (ii) grazing management regime (Wang et al., 2002; Wen et al., 2013) and spatial distribution of excretion by livestock (Islam et al., 2010) or root foraging by burrowing rodents (Li et al., 2009; You et al., 2014); and (iii) habitat microclimate heterogeneity (Song et al., 2008), variability of water resources (Chen et al., 2007; Pueyo et al., 2013) or micro-geomorphology (Song et al., 2010; Casalini and Bisigato, 2017). Selim et al. (2021) found that herbaceous plants reveal a strong aggregated population and accommodates four dominant clusters along with soil salinity gradients in Shyamnagar, Bangladesh.

Patchiness is an important feature in grassland ecosystems (Ludwig et al., 2005; Wintle et al., 2019; Lindenmayer, 2019). Spatial-temporal variability of environments such as fluctuation in temperature, species

composition and mode of reproduction (Zhang, 2005; Song *et al.*, 2008), selective feeding (Adler *et al.*, 2001) and soil nutrient heterogeneity (Collins, 1989) contributes to the formation of vegetation patches with different species characteristics in grasslands. Thus far, studies on vegetation patches have focused on patch connection with grassland degeneration (Zhang *et al.*, 2003), formation mechanisms and dynamics (Emmerson *et al.*, 2012; Smith *et al.*, 2014; Hao *et al.*, 2017), species composition and interspecific association (Wei *et al.*, 2016) and vegetation characteristics and soil features (Yang *et al.*, 2014; Shi *et al.*, 2015). However, few research has focused on spatial heterogeneity of species and patchy community, and how the occurrence of a given species influences the spatial pattern in two common environments in grasslands such as "shady" and "terrace" habitats. In our study, shady and terrace habitats are two typical environments of grasslands on the Qinghai-Tibetan Plateau.

The power law model was first proposed by Taylor (1961) as an empirical method for determining a population statistic with binary variable to indicate the intrinsic level of aggregation in populations. Taylor (1961) observed that when members of a population are randomly distributed in their environment, the sampling variance is equal to the mean. When they are more regularly distributed, the variance is less than the mean; and the aggregate distribution of a population indicates that variance is greater than the mean value. Hughes and Madden (1993) adopted Taylor's (1961) power law of binary variable in studying the number of infected plant individuals in phytopathology (Madden *et al.*, 2018). The power law has since been further developed and applied to study the spatial heterogeneity of individual species and community-level spatial heterogeneity in grassland vegetation (Shiyomi *et al.*, 2001, 2005; Song *et al.*, 2005; Chen and Shiyomi, 2019). Taylor's power law is an empirical formula expressed by statistical regression, and the relationship between mean and variance is affected by the size of plant species and sampling quadrat (Jiménez *et al.*, 2001; Chen *et al.*, 2007). Therefore, whether the power law can be applied to determine the spatial heterogeneity of species and small patches in shady and terrace habitats on the Qinghai-Tibetan Plateau, remains largely unknown.

Kobresia-Carex meadows are widely distributed worldwide, and patchy distribution of *Kobresia-Carex* is a common feature on the Qinghai-Tibetan Plateau (Zhao *et al.*, 2021). Patch configuration is viewed as an important factor affecting the distribution of plant species (Hemrová and Münzbergová, 2015). The diameter of larger patches is more than several tens of meters, and small patches are less than 1 m (Wen *et al.*, 2013; Mou *et al.*, 2015, 2020). Spatial distribution pattern is an important property of a plant community, and also is the fundamental parameter to describe a plant community. The actual distribution pattern of species and community reflects the current habitat and the presence of grassland degradation and species diversity. The aim of this paper is the clarification of characteristics of these two habitats based on spatial distribution of species and community. Here, we apply the power law to analyze the species- and community-level spatial heterogeneity on *Kobresia-Carex* patches with different sizes in these two different habitats in alpine meadows, and the occurrence of all species was investigated via binary occurrence counts. Our scientific questions are: (1) whether the power law can be applied to determine the spatial pattern at species- and community-levels in patches on shady and terrace habitats? (2) Do key species determine the community-level spatial heterogeneity in different habitats on the Qinghai-Tibetan Plateau? (3) How different is spatial heterogeneity between the two habitats in shady and terrace environments?

2. Methods

2.1. Study area

The study site is located at Gansu Agricultural University Experimental Station (37°12′N, 102°45′E; 2,960 m a.s.l.) in Tianzhu County, Gansu Province, China, eastern section of the Qinghai-Tibetan Plateau.

This area has been used for winter grazing by yak (*Bos grunniens*) and Tibetan sheep (*Ovis aries*) from November to the following May for more than 30 years. The climate in this region is influenced by the southeast monsoon and the Siberian high air mass, and is characterized by severe winters and short, cool summers. The mean annual temperature and precipitation are −0.1 °C and 416 mm, respectively. The temperature ranges from mean minimum of −18.3 °C in January to mean maximum 12.7 °C in July. The plant growth period is about 120 days (June to September). Soil is classified as Sub-alpine Meadow Soil according to the Chinese Soil Classification system (Wu and Tiessen, 2002).

2.2. The setting of experimental plot

Our study was conducted on contiguous habitats of shady and terrace, each area about 10 ha. Shady and terrace are two major habitat types and together form unique landscapes on the Qinghai-Tibetan Plateau. The shady habitat has a slope of about 18°, and the terrace habitat is relatively flat. Dominant plant species in the shady habitat are *Carex* spp., *Kobresia capillifolia*, *Artemisia smithii* and *Leontopodium nanum*. For the terrace habitat, dominant species are *K. capillifolia*, *Carex* spp., *Melilotoids ruthenica*, *Stipa krylovii*, and *L. nanum*. The grazing intensity was higher and 85%–90% of the aboveground biomass was consumed by animals. The grassland is composed of many mosaic patches which are dominated by different species (Wen *et al.*, 2013). The "patch" forms distinct boundaries with other vegetation units within the grassland community and named according to the dominant species (Garbin *et al.*, 2016; Mou *et al.*, 2020; Zhao *et al.*, 2021). It is possible that this mosaic distribution of vegetation on a field scale is a result of mode of reproduction (Zhang, 2005; Song *et al.*, 2008), selective grazing by livestock and changes in micro-topography (Li *et al.*, 2009; Wen *et al.*, 2013). The dominant species of "*Kobresia-Carex* patches" are *K. humilis*, *K. capillifolia* and several *Carex* spp. which together comprise more than 75% of the aboveground biomass.

Based on patch area, three sizes of *Kobresia-Carex* patches (occupying more than 65% area) were selected in shady and terrace land according to the previous survey by Mou *et al.* (2020) on the Qinghai-Tibetan Plateau: Size 1 (referred to as S1, 0.6–0.9 m^2), Size 2 (S2, 3.0–3.8 m^2) and Size 3 (S3, 6.5–8.8 m^2).

2.3. Statistics regarding plant occurrence

Eight replicates of *Kobresia-Carex* patches for three sizes were randomly selected on shady and terrace habitats (2 habitats × 3 patch sizes × 8 replicates = 48 patches). According to patch size, quadrats were placed with 1m×1m quadrats for S1 patch, 2m×2m quadrats for S2 patch, and 3m×3m quadrats for S3 patch, and more than 85% of patch area was sampled by corresponding quadrats. The quadrat was divided into 20cm×20cm large-cells (L-cells), where each L-cell was further subdivided into four 10cm×10cm small-cells (S-cells) (*i.e.*, a 1m×1m quadrat was composed of 25 L-cells, a 2m×2m quadrat composed of 100 L-cells, and a 3m×3m was composed of 225 L-cells, total 22,400 S-cells in this survey) (Fig. 1). Binary data are easier and less costly to collect in actual vegetation plots, and therefore are more commonly collected by vegetation scientists (Chen *et al.*, 2021; Yamamura *et al.*, 2021). We used a binary occurrence system to record occurrences of all species in S-cells (Shiyomi *et al.*, 2000, 2001). If a specified plant species does not occur in any of the four S-cells, we record 0; if the species occurs in any one of the four S-cells, this was record as 1; if the species occurs in any two S-cells, this was recorded as 2, *etc*. Therefore, the number of S-cells in an L-cell in which species *i* occurred was 0, 1, 2, 3, or 4 (Fig. 1b). The proportion of occurrence of species *i* in the S-cells for each patch was calculated (as values P_i). The dominant, companion and rare species were classified using frequency of occurrence, according to Mariotte's (2014) criterion: (1) "Dominant species", species with $P_i \geq 0.4$; (2) "Companion species", species with $0.1 \leq P_i < 0.4$; and (3) "Rare species", species with $P_i < 0.1$.
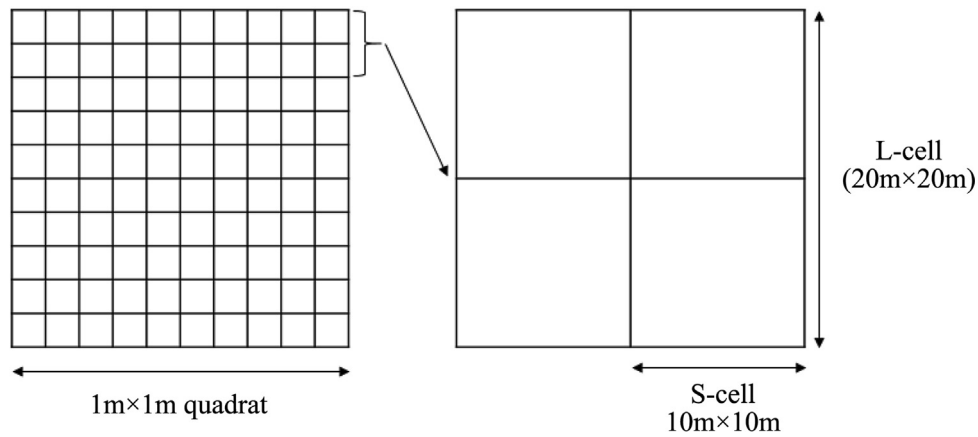
Fig. 1. The quadrats (1m×1m, 2m×2m and 3m×3m), large cells (L-cells) and small-cells (S-cells) were used in vegetation survey. The survey quadrats were divided into 20cm×20cm L-cells; and L-cell was further subdivided into four 10cm×10cm S-cells. We used binary occurrence to record occurrences of species present in the S-cell.

2.4. Model and analysis

2.4.1. The power law

We applied the power law as developed by Shiyomi et al. (2000, 2001) to determine the spatial pattern at species- and community-levels on shady and terrace, where the raw data are the sum of binary occurrences (0 or 1 for absent or present, respectively) among the L-cells of an S-cell (i.e., 0, 1, 2, 3, or 4 in this study). The raw data such as 0, 1, 2, 3, or 4 per L-cell are the sum of binary occurrences, where for an S-cell in an L-cell 0 or 1 for absence or presence for each species is allotted, respectively. In the actual survey, the relative frequency of occurrence of species i per S-cell is expressed as P_i, where $0 \leq P_i \leq 1$. If it is assumed that occurrence of species i at an S-cell is random, the probability that the species occurs in j of 4 S-cells in an L-cell is expressed by $\binom{4}{j} P_i^j (1 - P_i)^{4-j}$ (binomial distribution), and

the mean and variance are $4P_i$ and $4P_i(1-P_i)$, respectively, where 4 is the number of S-cells in an L-sell, $j = 0, 1, 2, 3, 4$. This calculation is performed for s species; $i = 1, 2, …, s$.

The principle of the power law is to compare the theoretical variance above with the variance actually observed for occurrences of species among S-cells. The logarithm of observed variance for each of the s species is regressed on the logarithm of the theoretical variance expected for a random distribution, as above, any divergence from the regression line can provide information on whether community species is aggregated or regular distribution (Shiyomi et al., 2000). Regression residuals for individual species can reveal species specific properties in the community. Here, we designate the observed variance as v_i for species i and transform both the variances divided by 16 into a logarithmic scale: $x_i = \log(P_i(1-P_i)/4)$, and $y_i = \log(v_i/16)$ (Shiyomi et al., 2000, 2001). The x_i and y_i could be empirically expressed by a linear-type equation:
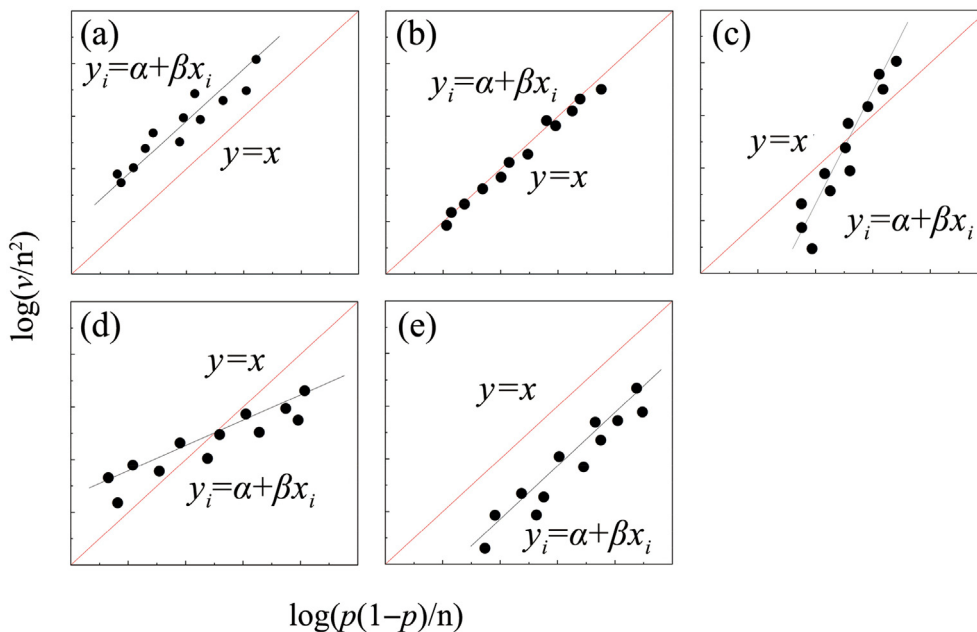
Fig. 2. Hypothetical spatial heterogeneity of vegetation estimated by the power law, where each dot indicates a species. (a) If the straight (regression) line is located above $y = x$, the overall community tendency of spatial pattern is more heterogeneous than would be expected in a random pattern; (b) If the straight line coincides with $y = x$, the overall tendency is random; (c) and (d) If the straight line intersects $y = x$, the spatial patterns of species below the straight line are less heterogeneous and the spatial patterns of species above the straight line are more heterogeneous than in a random pattern; (e) If the straight line is located below the $y = x$ line, the pattern is less heterogeneous than would be expected in a random pattern.

$y_i = \alpha + \beta x_i + \varepsilon_i$, where α and β are constants for the regression expressing community distribution properties and ε_i is a species-specific residual (referred to as "relative spatial heterogeneity" hereafter).

Since $P_i(1-P_i)/4$ for species i takes values between 0 and 1/16, log $[P_i(1-P_i)/4]$ reaches a maximum at $P_i = \frac{1}{2}$. Therefore, the value of log $[P_i(1-P_i)/4]$ increases with increase in P_i as P_i increases from 0 to $\frac{1}{2}$, and then decreases with further increase of P_i as P_i increases from $\frac{1}{2}$ to 1. The interpretation of different possible patterns in the regression given by Shiyomi *et al.* (2001) is as follows: (1) if $\alpha = 0$ and $\beta = 1$, then the community as a whole has a random spatial distribution (Fig. 2); (2) if for any α and $\beta \neq 1$, then the community as a whole exhibits more aggregated or regular than random spatial distribution (Figs. 2a–2e); (3) if $\beta < 1$, then species with larger log$[P_i(1-P_i)/4]$ (*i.e.*, P_i more near to 1/2) are displaying a more regular spatial distribution in the community than ones with smaller log$[P_i(1-P_i)/4]$, with a random distribution indicated by the point where the regression line crosses the $y = x$ line; (4) The reverse applies where $\beta > 1$ (Fig. 2).

2.4.2. The spatial heterogeneity indices at species- and community-levels

First, we define the *absolute* spatial heterogeneity for species i, δ_i. In the scatter diagram of (x_i, y_i), the vertical distance, δ_i, between y_i and the straight line $y = x$ can be calculated by $y_i - x_i$. When $\delta_i = 0$, $\delta_i > 0$ or $\delta_i < 0$, the spatial pattern of species i is referred to, respectively, as being a random pattern; as having higher heterogeneity (more aggregation) than would be found in a random pattern; or as having lower heterogeneity (more uniformity) than would be a random pattern (Shiyomi *et al.*, 2001, 2005; Chen and Shiyomi, 2019; Yamamura *et al.*, 2021).

Next, we define the *relative* spatial heterogeneity for evaluating the status of species i within a community, that is, the residual of species i, ε_i, expressed by $\varepsilon_i = y_i - \alpha - \beta x_i$, which indicates the degree of difference from the community-level heterogeneity described by the aforementioned linear equation. The following are determined for species i by $\varepsilon_i = 0$, $\varepsilon_i > 0$, or $\varepsilon_i < 0$: the relative spatial heterogeneity of species i is the same as community-level spatial heterogeneity, larger tendency than the spatial heterogeneity of whole grassland community, or smaller tendency than the whole grassland community, respectively (Guan *et al.*, 2016).

The following index, δ_C, is a community-level spatial heterogeneity value. The community-level spatial heterogeneity is represented by the following equation (Shiyomi *et al.*, 2001):

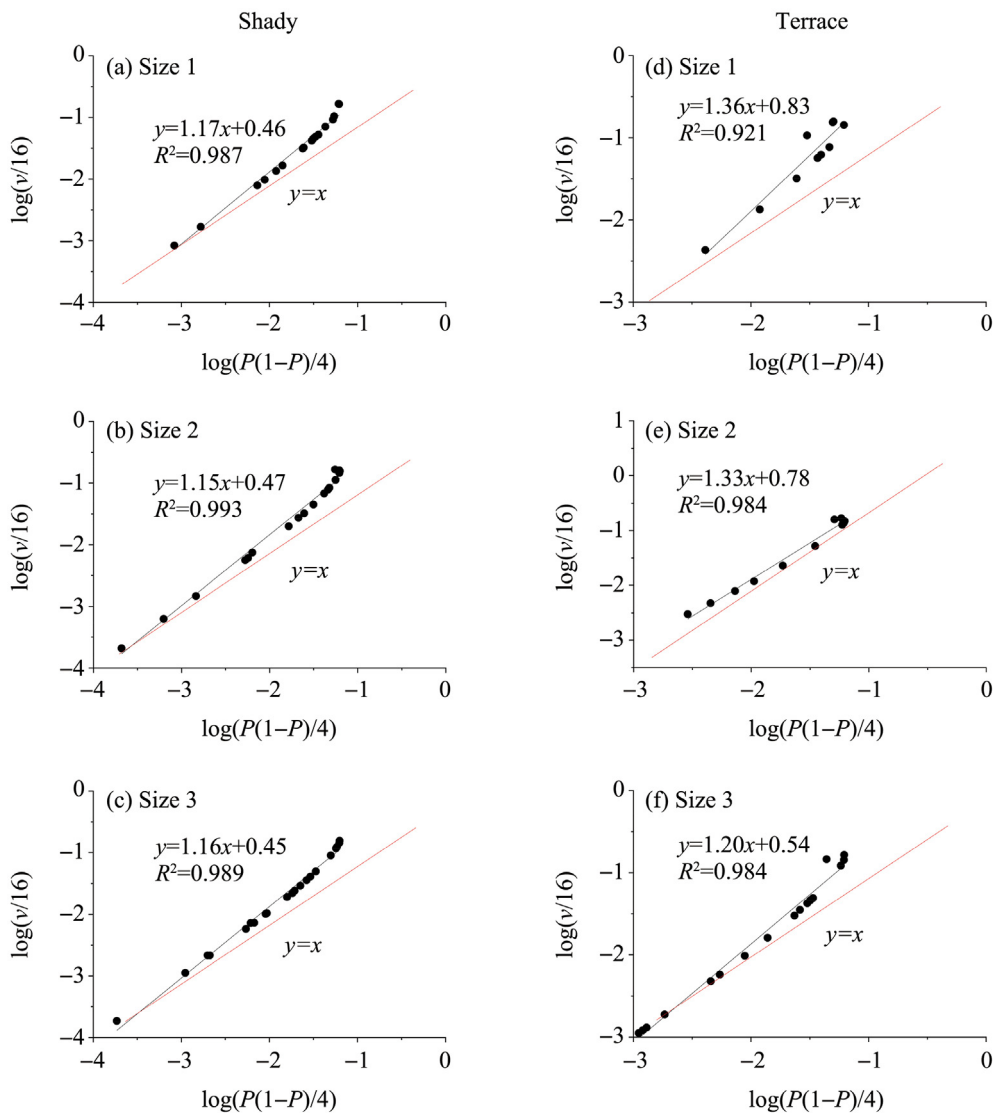$$\delta_C = \sum_{i=1}^{s} P_i \delta_i \left/ \sum_{i=1}^{s} P_i \right. \tag{1}$$

Fig. 3. Application of the power law to examine spatial heterogeneity of *Kobresia-Carex* patches of Size 1, Size 2 and Size 3 in shady (a, b and c) and terrace (d, e and f), the dot represents different plant species. Dots on red lines indicate species which are randomly distributed, and dots above red lines indicate species which distribute more heterogeneity than random pattern.

where s is the total number of species in the community, P_i and δ_i indicate the relative frequency of occurrences per S-cell and the absolute spatial heterogeneity value for species i.

2.5. Visualization of plant spatial distribution

In order to visualize the spatial distribution of plant individuals and community, we used photography combined with geographic information software to determine the location of individual plants on shady and terrace habitats. The 10m×10m community segments were randomly selected in shady and terrace habitats, then divided into 50cm×50cm quadrats, respectively. We take the photograph (Nikon D100) on each quadrat from left to right, bottom to top in 10m×10m community segments away from 1 m to ground. The photos (total 800) were imported into ArcGIS 10.8, and determined plant cluster coordinates according to the location of each plant. We established the spatial location for all plant individuals in 10m×10m community on the shady and terrace habitats, and then outputted the distribution map of total species and single species of *Kobresia-Carex*.

3. Results

3.1. Application of the power law to the Kobresia-Carex patches

Fig. 3 shows the regressions of $\log(v_i/16)$ on $\log(P_i(1-P_i)/4)$ for three patch sizes in two habitats. The coefficients of determination (R^2) for the power law regressions were high, and most of the species lie above the line of $y = x$. Consequently, the power law could determine the spatial distribution of species and patch communities with different size. These results demonstrate that species in these plant communities in both habitats show higher spatial heterogeneity (*i.e.*, spatial aggregation). In addition, for species in the shady habitat, those with high values of $\log(P_i(1-P_i)/4)$, generally also exhibited higher δ_i values (*i.e.*, $\beta > 1$) than terrace habitat. The slope $\beta \approx 1$ in terrace indicates that the spatial heterogeneity of individual plant species is not closely linked with P_i (Fig. 3e).

3.2. P and δ for each species

In the shady habitat, P and δ values for dominant species of *K. capillifolia* continuously increased with patch size, while *L. nanum* (one of the dominants) increased with patch size and then stabilized (Table 1). In the shady habitat, P and δ values for *Gentiana scabra* and *Astragalus membranaceus* were higher in S1 than S2 and S3. However, in terrace, δ values for dominants species *Melilotoids ruthenica* and *S. krylovii* monotonically decreased with patches size, while P and δ values for *K. capillifolia* and *G. scabra* were lower in patch S2 than S1 and S3.

For companion species, in the shady habitat, P and δ values for *Allium sikkimense* and *Kobresia humilis* gradually decreased from S1 to S3, but *Polygonum viviparum* increased from S1 to S2 and then decreased from S2 to S3 (Table 1); In terrace, P and δ values for *A. membranaceus* first increased with patch size and then decreased, while these two values for *K. humilis* monotonically decreased from patch S1 to S3 in terrace. For rare species, in the shady habitat, P and δ values for *Gentiana scabra* increased and then decreased with patch size, but the other rare species fluctuated among patch sizes.

In our surveys, all species show a heterogeneous pattern ($\delta_i > 0$) in two habitats with three patch sizes (Table 1).

3.3. P and ε for each species

The P and relative spatial heterogeneity (ε) varied among the three patch sizes both in shady and terrace. *K. capillifolia*, *M. ruthenica* and *Carex humilis* show high P and ε values in S3 patch in the terrace habitat; ε values for *G. scabra* and *A. membranaceus* were high at S1 patch in shady; and ε for *L. nanum* and *P. viviparum* in S3 patch in the shady

Table 1

The presence frequency (P) and absolute spatial heterogeneity (δ) for individual plant species on *Kobresia-Carex* patches of Size 1, Size 2 and Size 3 in shady and terrace.

Plant species and abbreviations under the shady and terrace	Size 1		Size 2		Size 3	
	P	δ	P	δ	P	δ
<Shady habitat>						
Carex sp.	0.577	0.435	0.243	0.232	0.354	0.314
Artemisia smithii	0.560	0.428	0.524	0.400	0.460	0.366
Leontopodium nanum	0.317	0.288	0.668	0.477	0.644	0.458
Polygonum viviparum	0.300	0.247	0.558	0.418	0.527	0.366
Kobresia capillifolia	0.220	0.219	0.498	0.397	0.500	0.398
Melilotoids ruthenica	0.173	0.167	0.687	0.482	0.135	0.147
Oxytropis kansuensis	0.157	0.165	0.148	0.157	0.120	0.131
Stipa krylovii	0.147	0.157	0.257	0.247	0.273	0.260
Kobresia pygmaea	0.140	0.146	0.006	0.007	0.009	0.011
Allium sp.	0.110	0.123	0.094	0.108	0.084	0.097
Kobresia humilis	0.107	0.120	0.338	0.302	0.373	0.326
Astragalus membranaceus	0.060	0.072	0.457	0.371	0.100	0.112
Anaphalis lactea	0.050	0.058	0.212	0.212	0.161	0.167
Veratrilla baillonii	0.037	0.045	0.022	0.027	0.038	0.046
Stellera chamaejasme	0.030	0.037	0.111	0.121	0.068	0.080
Agropyron cristatun	0.007	0.008	0.003	0.003	–	–
Stipa purpurea	0.003	0.004	–	–	–	–
Gentiana scabra	0.003	0.004	0.071	0.083	0.022	0.028
Thalictrum aquilegifolium	–	–	0.006	0.007	0.039	0.047
Youngia japonica	–	–	–	–	0.004	0.006
Elymus nutans	–	–	–	–	0.079	0.080
Leymus secalinus	–	–	0.001	0.001	–	–
Koeloria cristata	–	–	0.003	0.003	0.001	0.001
Aster ssp.	–	–	0.023	0.029	0.028	0.034
Dracocephalum heterophyllum	–	–	0.001	0.001	–	–
Poa sp.	–	–	0.001	0.001	–	–
<Terrace>						
Melilotoids ruthenica	0.860	0.551	0.628	0.459	0.551	0.423
Stipa krylovii	0.727	0.495	0.168	0.174	0.150	0.161
Kobresia capillifolia	0.720	0.495	0.714	0.497	0.772	0.520
Carex sp.	0.443	0.366	0.432	0.357	0.443	0.364
Leontopodium nanum	0.247	0.220	0.388	0.332	0.160	0.165
Astragalus membranaceus	0.197	0.198	–	–	0.119	0.132
Artemisia smithii	0.180	0.186	0.473	0.380	0.367	0.321
Kobresia humilis	0.110	0.117	0.044	0.052	0.037	0.044
Allium sp.	0.050	0.054	–	–	–	–
Oxytropis kansuensis	0.017	0.021	0.081	0.091	0.140	0.149
Potentilla bifurca	–	–	0.030	0.035	0.004	0.006
Leymus secalinus	–	–	0.018	0.022	0.105	0.108
Polygonum viviparum	–	–	0.012	0.015	0.019	0.023
Plantago lesnngi	–	–	–	–	0.059	0.069
Stellera chamaejasme	–	–	–	–	0.022	0.026
Youngia japonica	–	–	–	–	0.007	0.009
Elymus nutans	–	–	–	–	0.005	0.007
Aster ssp.	–	–	–	–	0.005	0.006

Size 1: 0.6–0.9 m², Size 2: 3.0–3.8 m², and Size 3: 6.5–8.8 m²; A dash (−) indicates that the species not found in the four S-cells.

habitat were also large and lay above $y = 0$ (Fig. 4). This indicates that their relative spatial heterogeneities were higher than the other species in the community. The ε value for *A. membranaceus* in S1 patch was shady > terrace, and this species has the maximum ε value (0.159) in S2 patch in terrace. In both habitats, ε values of most companion species lay below the line $y = 0$, indicating a tendency towards more regular distribution than the dominant species of the community. However, ε values for *S. krylovii* in S2 and S3 patches in terrace lay near $y = 0$, indicating that the spatial heterogeneity of *S. krylovii* is more coincident with the community spatial heterogeneity. For rare species, ε values were various among patch sizes.

A general pattern of ε values across species and patch size was lowest at P_i of 0.1–0.3 in shady, whereas in terrace ε was lowest at $P < 0.1$, and ε increased monotonically with P_i increasing. For most dominant species, P and ε values were higher in terrace than those in shady.

4. Discussions

4.1. Evaluation of the spatial pattern by the power law

For biological populations which may consist of a small to large number of individuals, the following indices has been developed for measuring the spatial aggregation of individuals: variance/mean ratio (David and Moore, 1954; Taylor, 1961), Morisita's I_δ-index index (1961, 1962), m-m^* method (Iwao, 1968), and k of negative binomial distribution (Pielou, 1977). However, for biological populations in which the occurrence or incidence is restricted to a binary variable such as infected or uninfected plant, and present or absent in a plant species, these indices are not applicable. Therefore, new indices for binary variables have been developed such as Morisita's (1962) I_B index, an index of spatial heterogeneity (δ) by Shiyomi et al. (1979). The δ in this study is constructed based on the same logical base as the last two measures for the binary variable by power law model. Also, the power law has been applied by many researchers (Shiyomi et al., 2001; Chen et al., 2007; Xie et al., 2009; Chen and Shiyomi, 2019; Mou et al., 2020) to analyze the spatial heterogeneity of plant communities in grasslands. High coefficients of

determination (R^2) for linear power law equations show that the spatial heterogeneity of individual species and the community could well fit the power law.

Index of spatial heterogeneity (aggregation) is sensitive to quadrat scale (Shiyomi et al., 2001; Song et al., 2005). The relationship between mean and variance in Taylor's power laws is affected by sample size (Chen et al., 2007). Crown width of species and quadrat scale could affect statistical results when using the binary occurrence system (presence/absence data) to record occurrences of all species, (Jiménez et al., 2001). In previous studies, a 50cm×50cm L-cell is used in analyzing community heterogeneity (Shiyomi et al., 2001, 2005; Song et al., 2005; Chen et al., 2007; Chen and Shiyomi, 2019; Yamamura et al., 2021). In our patch surveys, we used 20cm×20cm L-cells to evaluate the spatial heterogeneity of small patches formed by the small *Kobresia-Carex* community. The current survey not only obtained a measurement precision to the ground species survey, but also meets a high R^2 value in the power law. Thus, the quadrat size (L-cells and S-cells) should be adjusted according to characteristics of a plant community when the power law is applied to measure the spatial heterogeneity of individual species and community in the grassland.
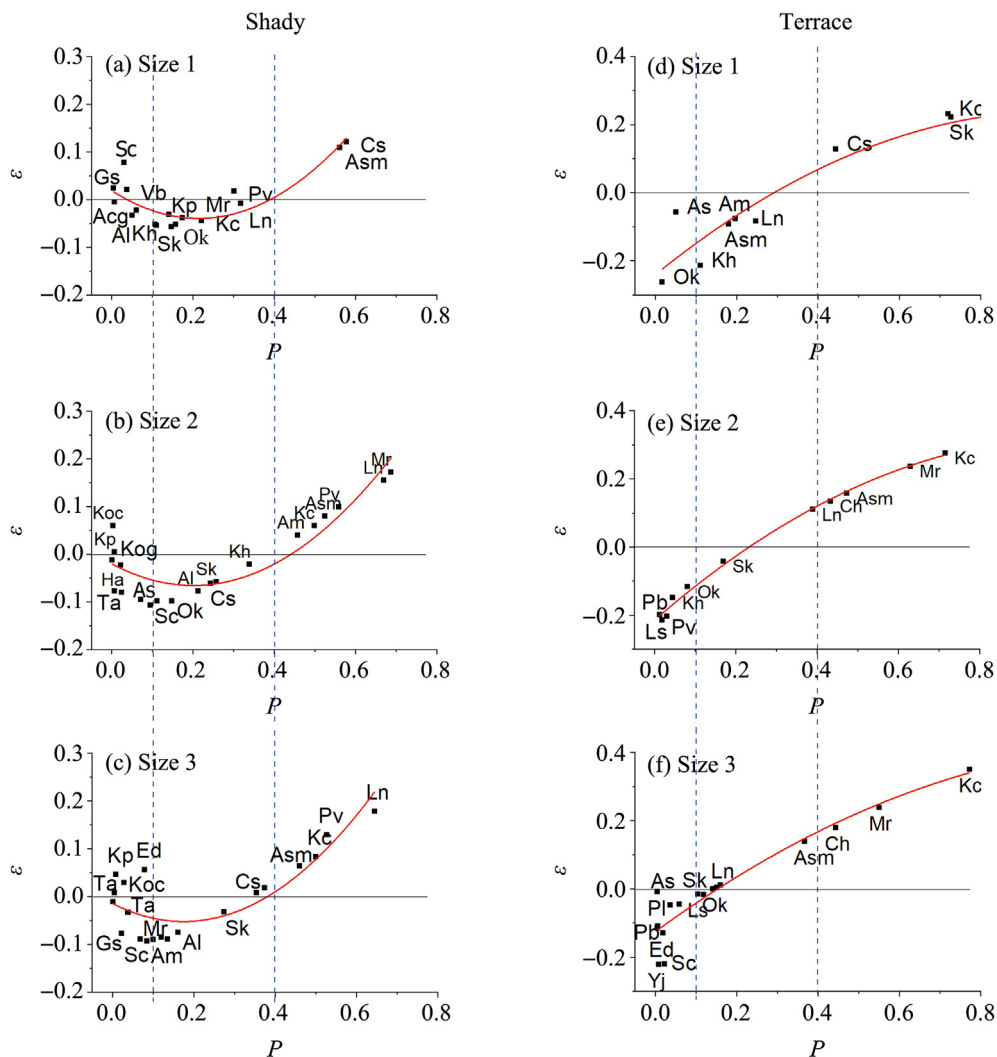
Fig. 4. The relationships between presence frequency (P) and relative spatial heterogeneity (ε) on *Kobresia-Carex* patches of Size 1, Size 2 and Size 3 in shady (a, b and c) and terrace (d, e and f). The black point represents different species. Acg, *Agropyron cristatun*; Al, *Anaphalis lactea*; Am, *Astragalus membranaceus*; As, *Allium sikkimense*; Asm, *Artemisia smithii*; Ch, *Carex humilis*; Ed, *Elymus dahuricus*; Gs, *Gentiana scabra*; Ha, *Heteropappus altaicus*; Kc, *Kobresia capillifolia*; Kh, *Kobresia humilis*; Koc, *Koeloria cristata*; Kp, *Kobresia pygmaea*; Ln, *Leontopodium nanum*; Ls, *Leymus secalinus*; Mr, *Melilotoids ruthenica*; Ok, *Oxytropis kansuensis*; Pb, *Potentilla bifurca*; Pc, *Poa crymophila*; Pl, *Plantago lesnngi*; Pv, *Polygonum viviparum*; Sc, *Stellera chamaejasme*; Stipa krylovii, *Stipa krylovii*; Sp, *Stipa purpurea*; Ta, *Thalictrum aquilegifolium*; Vb, *Veratrilla baillonii*; Yj, *Youngia japonica*. The relative spatial heterogeneity ε, is effective for analyzing within-structure of communities.

Taylor's power law is not a theoretical formula obtained by mathematical deduction, but an empirical formula obtained by statistical regression. There are problems of significance test and confidence interval estimation of its parameters, especially the estimation and test of b value (Taylor, 1961; Madden *et al.*, 2018; Chen and Shiyomi, 2019). Therefore, we plotted coordinates of $\log(v_i/16)$ to $\log(P_i(1–P_i)/4)$ for each species as scatter diagrams, and then obtained high R^2 values for the linear power law equations (higher than 0.9) in all patch sizes and habitats (Fig. 3). This high degree of fit indicates that the power law well described the spatial pattern, and that the result from our study is consistent with results reported by Chen and Shiyomi (2019). Therefore, the present study confirms that the power law can be expanded to evaluate the spatial heterogeneity of species and community on small vegetation patches in shady and terrace habitats. Our research provides a new application of the power law model to study spatial pattern of species or patchy community in grasslands as reported by Tsuiki *et al.* (2001), Song *et al.* (2005) and Xie *et al.* (2008). Also, the reasonability of the power law is discussed by Madden *et al.* (2018), and Chen and Shiyomi (2019). Thus, our first question that power law can be applied to determine the spatial pattern at species- and community-levels in patches on shady and terrace habitats is confirmed.

4.2. Effects of species on community heterogeneity (δ_C)

All species show aggregated distribution in patches on shady and terrace habitats, and that the results from our study is consistent with results reported by Shiyomi *et al.* (2001) in a temperate mixed-seeding pasture in Japan. In the present study, we found that dominant species were the key species determining community-level spatial heterogeneity (δ_C) in *Kobresia-Carex* patches, which is consistent with results of Mou *et al.* (2020). Song *et al.* (2005) also demonstrated that different species have different effects on spatial heterogeneity in grassland communities. Heterogeneity depends, in part, on the mode of propagation and reproduction (Soons *et al.*, 2004). The dominant species of *Kobresia* and *Carex* reproduce through clonal underground tillering. They can resist grazing stress, and form a dense population "mosaic patch" on overgrazed grasslands. *Leontopodium nanum* can reproduce by the production of clonal ramets or by seeding. It can replace other species with its strong adaptation and resistance when facing harsh environments or heavy grazing (Ren *et al.*, 2009). *A. membranaceus* is a species with thick-diameter roots radiating and branching from the stem base, which confers benefits for nutrient uptake and water storage. These dominants are ordinarily clonal species, and can subsequently attain a relatively
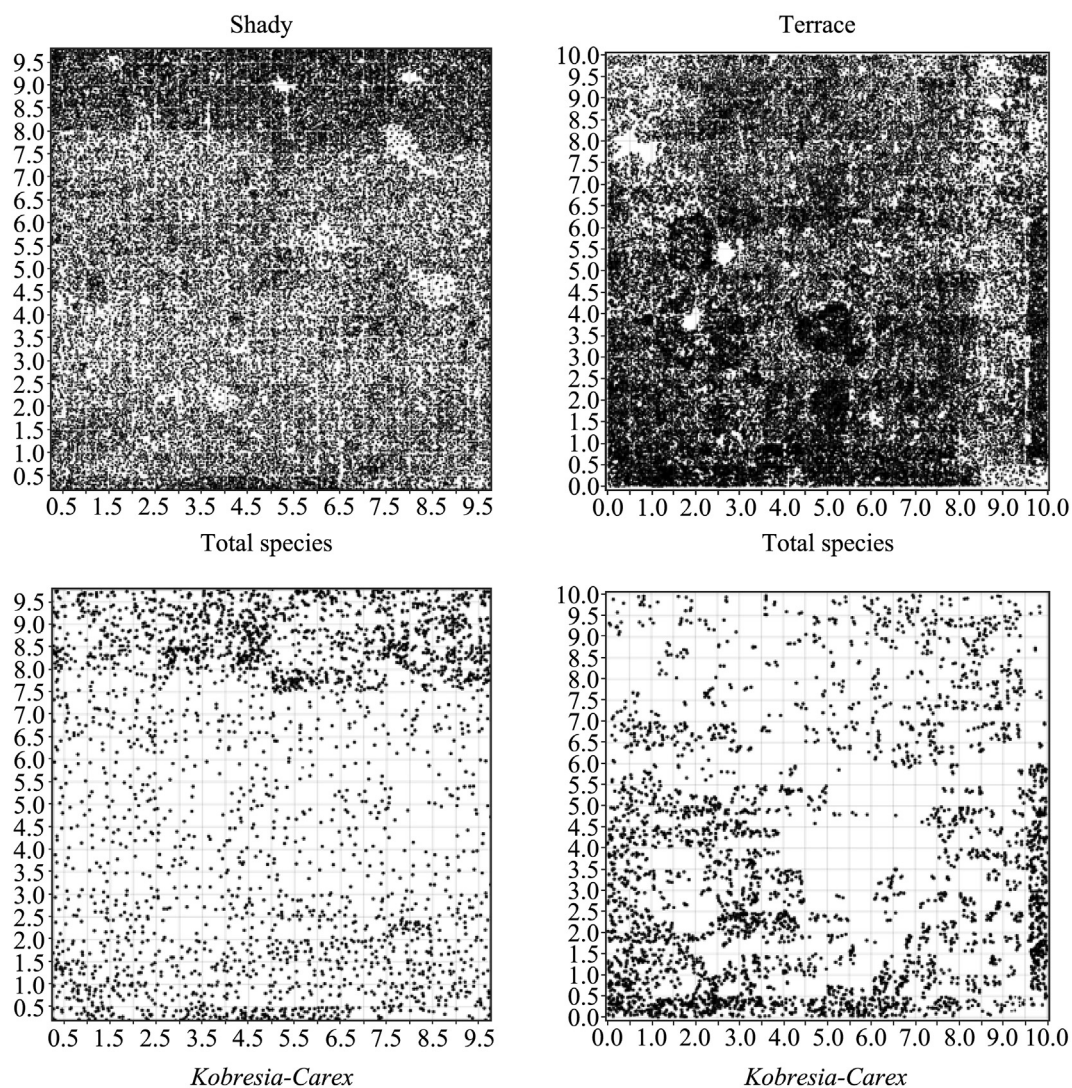

Fig. 5. The spatial distribution of individual plants (total species and *Kobresia-Carex*) in 10m×10m areas on shady and terrace habitates. The black points indicate the location of plant species in 10m×10m areas in different habitats.

high frequency, ground cover, and aboveground biomass, thus leading to a highly heterogeneous spatial distribution in these vegetation patches (Table 1). Thus, the second hypothesis that dominant species determine the community-level spatial heterogeneity in different habitats on the Qinghai-Tibetan Plateau is confirmed.

The companion species of *S. krylovii* and *P. viviparum* maintained a spatial heterogeneity (δ) close to community heterogeneity. *S. chamaejasme* is characterized by intense invasiveness, resource competitiveness and high adaptability to the environment, and then strongly suppresses growth of *S. krylovii* and *P. viviparum* (Ren *et al.*, 2009; Liu *et al.*, 2017). Additionally, *S. krylovii* populations are often overgrazed by cattle and sheep, so that they have difficulty forming a thick sward. The rare species do not have such a strong effect on the spatial aggregation of entire plant communities because these species have a small frequency presence. In addition, the heterogeneity of rare species was probably variable because their spatial pattern can be affected by accidental dispersion and concentration around mother plants or seeds. For example, *A. sikkimense* has a low frequency of occurrence and low spatial heterogeneity value (Table 1). One probable reason is that seeds are readily dispersed by wind or water (Geertsema and Sprangers, 2002; Liu *et al.*, 2013). Therefore, the contribution of rare species to community heterogeneity of patch is weak both in shady and terrace. Consequently, all species show an aggregated distribution at different patch size in shady and terrace habitats, and spatial heterogeneity of the whole community in all patches were strongly affected by the dominant species.

4.3. Relative spatial heterogeneity (ε) and habitat

The community-level spatial heterogeneity of *Kobresia-Carex* patches with three sizes differed distinctly in shady and terrace habitats (Fig. 5). Relative spatial heterogeneity (ε) of plant species in shady was lowest at *P*-values (frequency of occurrences) of 0.1–0.3 in different patch size; by contrast, the ε value increased monotonically with increases of *P* in terrace (Fig. 4). Compared to the shady habitat, the ε value in terrace was relatively high, and similar results were reported by Mou *et al.* (2015). The grazing intensity was higher and 85%–90% of the aboveground biomass was consumed by animals. The main cause of higher community-level heterogeneity in terrace than that in the shady habitat might be overgrazing (Adler *et al.*, 2001). The selective feeding of livestock greatly affects the community structure, and the high grazing intensity is an important factor affecting spatial patterns formed by species and community under different habits.

Soil dryness and compaction are caused by excessive animal trampling at heavily grazed sites, resulting in the non-uniform distribution of water and nutrients (Kubo and Isobe, 1975). These altered conditions restrict species growth with lower stress tolerance, and therefore likely enhanced community-level heterogeneity in a terrace habitat (Molla and Huq, 2002). In addition, in a terrace habitat, the remarkably high heterogeneity in dominants, may correlate with facilitating processes linked to intense interspecific competition (Gutierrez-Giron and Gavilan, 2010), further contributing to a higher spatial heterogeneity than that in the shady site (Fig. 5). The new concept of relative spatial heterogeneity is developed in this study to find differences in community structure including spatial pattern. Thus, our third question that the difference in spatial heterogeneity between the two habitats in shady and terrace environments is confirmed. The underlying mechanisms of spatial patterns of individual species and community are formed resulting from interactions between endogenous and exogenous processes. Further studies should be focused on interspecific competition (Berger *et al.*, 2008; Liu *et al.*, 2013; Garbin *et al.*, 2016), species reproduction mode (Liu *et al.*, 2017) and resource heterogeneity, to clarify and explain the spatial heterogeneity of species or patchy community in grasslands.

5. Conclusions

The power law was well able to determine the spatial distribution pattern of species or patchy community in shady and terrace environments. Relative spatial heterogeneity (ε) of plant species in shady was lowest at *P*-values (frequency of occurrences) of 0.1–0.3 in different patch size; by contrast, the ε value increased monotonically with increases of *P* in terrace. Species and patchy communities show aggregated distribution, and dominant, companion and rare species have different influences for spatial heterogeneity of a patch community. The dominant species largely determine spatial heterogeneity of the *Kobresia-Carex* patches, while companion and rare species have weak influence on community-level heterogeneity in shady and terrace habitats. Our research will promote a new application of the power law model in studying community structure including spatial pattern of species or small patchy community in grasslands.

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