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Small-scale species richness and its spatial variation in an alpine meadow on the Qinghai-Tibet Plateau

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Abstract We investigated how the high small-scale species richness of an alpine meadow on the Qinghai-Tibet Plateau, China, is maintained. This area is characterized by strong wind and severe cold during long winters. In winter, most livestock is grazed on dead leaves in small pastures near farmers' residences, whereas in the short summer, livestock is grazed in mountainous areas far from farmers' residences. The number of plant species and the aboveground biomass were surveyed for three adjacent pastures differing in grazing management: a late-winter grazing pasture grazed moderately from 1 February to 30 April, an early-winter grazing pasture grazed lightly from 20 September to late October, and a whole-year grazing pasture grazed intensively throughout the entire year. In each pasture, we harvested the aboveground biomass from 80 or 100 quadrats of 0.01 m^2 along a transect and classified the contents by species. We observed 15.5–19.7 species per 0.01 m^2, which is high richness per 0.01 m^2 on a worldwide scale. The species richness in the two winter grazing pastures was higher than that in the whole-year grazing pasture. The spatial variation in species richness and species composition in the two winter grazing pastures in which species richness was high was greater than that in the whole-year grazing pasture in which species richness was lower. Most of the leaves that are preserved on the winter grazing pastures during summer are blown away by strong winds during winter, and the remaining leaves are completely exhausted in winter by livestock grazing. A pasture with a high richess is accompanied by a high spatial variation in species richness and species composition. There is a high possibility that the characteristic of spatial variation is also caused by traditional grazing practices in this area.

Keywords Grazing · *Kobresia* meadow · Qinghai alpine meadow · Winter grazing

Introduction

The Qinghai-Tibet Plateau, which ranges in altitude from 3,000 to 6,000 m, is an important source of water for central and northern China, as the headwaters of the Yangtze and Yellow rivers are located here. It is also important in determining global atmospheric circulation and global climate (Schaller 1998; Zhou et al. 2005). Despite the high altitude of this region, grasslands develop due to the relatively mild climate, and people have used these grasslands to raise livestock such as yaks and sheep in a traditional manner for centuries (Zhou et al. 1987; Zhou 2001).

The traditional use of grassland in this area differs from grassland use in other areas. In summer, farmers graze the livestock in alpine meadows located on hills and mountainous areas located several kilometers from their residences (Cincotta et al. 1992; Zhao and Zhou 1999). In September, when the severe winter begins, farmers take their livestock from the mountainous areas to small pastures near their residences and graze it in these areas until the following May. Most of the standing crop, standing dead matter, and litter that are

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preserved on this resident grassland area during summer is blown away and lost because of strong winter winds, or is exhausted during the long winter grazing season (James and Calvin 1986; Vickery 1992; Pierre 1998; Liu et al. 1999; Thomas et al. 1999).

Grasslands in the Qinghai-Tibet Plateau, particularly the Qinghai alpine meadows with their characteristic species *Kobresia* spp. and *Potentilla fruticosa* (shrub), are among the most beautiful in the world (Wang et al. 1999). The grasslands have been grazed by animals at appropriate densities for centuries (Zhou et al. 2005). Even when the growth and reproduction of plants in alpine or arid areas are suppressed by severe low temperatures or drought, the plants can recover after several years if there is no heavy anthropogenic disturbance (Jiang 1997). Thus, these grasslands are maintained semipermanently under the traditional grazing regime. The maintenance of species diversity and stable biomass in grasslands is presumably associated with the sustainable management of grazing pastures (McNaughton 1979; Noy-Meir et al. 1989; Belsky 1992; Yiruhan et al. 2001; Tsutsumi et al. 2003).

In natural grasslands, invasion, establishment, intra/interspecific competition, and natural perturbations cause and amplify the heterogeneity of vegetation (Rusch and Fernandez-Palacios 1995; Adler et al. 2001). In addition, small-scale disturbances such as feeding, trampling, and excreting on grazed grasslands accelerate the formation of spatial heterogeneity (Hakamata and Hirashima 1978; Hirata et al. 1987; Haynes and Williams 1993; Shiyomi et al. 2000). Species diversity and composition, along with spatial variability, are dependent on small-scale geographical and biological spatial variation and are contingent on invasions or establishment from the environment (Collins 1992; Adler et al. 2001; Wang et al. 2002). The overall large-scale diversity is dependent on the sum of such local, small-scale diversity (Currie 1991; Chen et al. 2005).

We examined how high species richness is maintained in small areas (e.g., 0.01 m^2) in a Qinghai alpine meadow, where the overall richness of the area is thought to be high (Wang et al. 1999). We also examined whether grazing styles such as winter grazing and year-round grazing alter species richness, spatial variation in richness, and species composition.

Study area and methods

The study was conducted at the Haibei Alpine Meadow Ecosystem Research Station (37°29′–37°45′ N, 101°12′–101°23′ E; 3200 m a.s.l.) of the Chinese Academy of Sciences. The Haibei Station is located on the east side of Lenglongling, the northern branch of Qilian Mountain, on the northeastern edge of the Qinghai-Tibet Plateau. The climate in the Haibei Research Station area is dominated by the southeast monsoon and high pressure from Siberia. The annual mean air temperature and precipitation at the research station are −1.7°C and 600 mm, respectively (Wang et al. 1994; Zhao and Zhou 1999; Zhou 2001). The soil type of the study area is alpine meadow soil (Cryo-sod soil), rich in nitrogen, phosphorus, and potassium (Zhao and Zhou 1999). The study area is located in a basin 3,200 m in altitude surrounded by mountains that are 4,000–5,000 m in altitude.

One sheep-day is defined as a grazing intensity that an adult sheep is grazed a day per hectare. Therefore, sheep days were calculated as (total body weight of grazing sheep in kilograms) × (number of grazing days)/(50 kg × total grazing pasture area in hectares), where 50 kg is the standard body weight of a Tibetan sheep (a local breed of *Ovis aries*). One adult yak is equivalent to five sheep in body weight.

We surveyed the vegetation in a farmer's pasture at the research station. In summer (beginning of May to end of September), the farmer of this pasture grazes his livestock in mountainous areas located several kilometers from his residence; he grazes his livestock in pastures near his residence only in winter (from October to end of April). We surveyed three pastures that differ in grazing management, i.e., two winter grazing pastures and one whole-year grazing pasture: (1) a flat late-winter grazing (LWG) pasture, grazed by five Tibetan sheep per hectare from 1 February to 30 April every year since 1997 (yearly grazing intensity, approximately 450 sheep days); (2) an early-winter grazing (EWG) pasture that has a gentle slope to the south, grazed with lower grazing intensity than the LWG from 20 September to late October every year since 1997 (yearly grazing intensity, approximately 200 sheep days); and (3) a flat whole-year grazing (WYG) pasture, grazed with higher grazing intensity than the LWG from October to April and with a few hundred sheep days from May to 20 September every year since 1998, for the rehabilitation of animals after medical treatment or illness (yearly grazing intensity, approximately 1,000 sheep days). The WYG is a public pasture that is open to all village farmers. These three adjoining pastures were separated by fences, and livestock is strictly excluded from the LWG and EWG by fences in summer. Most of the dead herbage biomass that remains in pastures until winter is blown away and lost from the pastures by the strong winter wind, and sheep can graze only a small part of the remaining herbage mass (Li and Zhou 1998, Zhou et al. 2005). The per-capita body weight of an adult Tibetan sheep is approximately 65 kg in the warm season and approximately 40 kg in the cold season because of the shortage of feed and the cold weather (Zhao and Zhou 1999). The daily per-capita intake of herbage biomass measured in dry weight for one adult sheep is 3–4% of live body weight (Li and Zhou 1998).

The soil water content values, from ground level to 25 cm in depth, measured at the survey sites on 1 August 2002 were 27.5–29.2% (cm^3/cm^3). The soil water content did not differ among the sites.

We conducted surveys in August of 2002 and 2003. In 2002, we established a survey plot with 80 consecutive 10 × 10 cm quadrats along an 8 m transect in each of the pastures (EWG, LWG, and WYG) and harvested the aboveground parts in every quadrat. The plants were classified to species, dried at 70°C for 48 h, and weighed. In 2003, we established a survey plot with 100 quadrats of 10 × 10 cm every 50 cm along a 50 m transect in the LWG and WYG pastures. The aboveground parts were harvested, identified to species, and weighed as in 2002. Different sites were sampled in each year. There were no replications of survey.

The following similarity index (*S*) was used to quantify the compositional relationship between quadrats expressed by species presence/absence (Zhang 2004):

$$S = 1 - \frac{\sum_{i=1}^{r} \left| x_{ij} - x_{ik} \right|}{\sum_{i=1}^{r} \left(x_{ij} + x_{ik} \right)}, 0 \leq S \leq 1, \quad (1)$$

where r indicates the number of species occurring in a survey, and x_{ij} and x_{ik} express presence/absence data for species i in the j-th and k-th quadrats, respectively (1 for present, 0 for absent). A large S indicates high similarity (i.e., low spatial variation) in species composition among quadrats.

Results

Dominant species

We identified 51 genera and 81 species belonging to 22 families in the entire set of the study area. We frequently observed species of Leguminosae (10 species), Compositae (10), Ranunculaceae (8), and Gentianaceae (8), followed by species of Poaceae, Scrophulariaceae, and Cyperaceae.

The 10 dominant species measured by biomass are shown in Table 1. Species of Poaceae such as *Festuca ovina*, *Stipa aliena*, and *Elymus nutans*; *Kobresia humilis* (Cyperaceae), which is the characteristic species of this area; and *Gueldenstaedtia diversifolia* (Leguminosae) were decidedly abundant, followed by *Saussurea katochaete* (Compositae) and *Carex moorcroftii* (Cyperaceae). Many species were common in both the winter grazing pastures (EWG and LWG) and the WYG pasture. Species of Rosaceae, including *Potentilla anserina* and *Potentilla nivea*, and *Poa alpigena* (Poaceae), which are trample-resistant plants, frequently occurred in the WYG pasture. Fifteen species, represented by *Morina chinensis* (Dipsacaceae) and *Thermopsis lanceolata* (Leguminosae; Table 1), were found only in the winter grazing pastures. At each plot, more than three of the ten dominant species were endemic in the connecting plateaus of Qinghai-Tibet, Gansu, and Sichuan [species underlined in Table 1; Northwest Plateau Institute of Biology (NPIB) 1997].

Table 1 Ten most dominant species based on aboveground biomass. Numbers indicate the percentage of aboveground biomass contributed by each species to total aboveground biomass. *Festuca ovina* and *Stipa aliena* were grouped, because separate identification of these species was not possible in August. *EWG* early winter grazing pasture, *LWG* late winter grazing pasture, *WYG* whole-year grazing pasture

Order	EWG		LWG				WYG			
	2002		2002		2003		2002		2003	
1	*Festuca ovina* + *Stipa aliena* [a]	21.8	*Festuca ovina* + *Stipa aliena*	33.3	*Festuca ovina* + *Stipa aliena*	22.1	*Elymus nutans*	23.3	*Elymus nutans*	14.4
2	*Elymus nutans*	8.37	*Saussurea katochaete*	5.82	*Saussurea katochaete*	8.65	*Festuca ovina* + *Stipa aliena*	11.39	*Kobresia humilis*	10.2
3	*Anemone obtusiloba*	6.02	*Morina chinensis*	5.66	*Morina chinensis*	6.02	*Potentilla anserina*	9.03	*Festuca ovina* + *Stipa aliena*	8.8
4	*Morina chinensis*	5.25	*Trigonella ruthenica*	5.51	*Gueldenstaedtia diversifolia*	5.91	*Carex moorcroftii*	7.00	*Gentiana straminea*	7.9
5	*Carex moorcroftii*	5.13	*Aster flaccidus*	5.17	*Gentiana farreri*	5.37	*Poa alpigena*	6.12	*Potentilla anserina*	6.6
6	*Kobresia humilis*	5.06	*Gentiana farreri*	4.94	*Elymus nutans*	4.93	*Halerpestes tricuspis*	5.80	*Scirpus distigmaticus*	6.6
7	*Gueldenstaedtia diversifolia*	4.98	*Elymus nutans*	3.46	*Aster flaccidus*	4.59	*Gueldenstaedtia diversifolia*	4.39	*Poa alpigena*	5.3
8	*Saussurea katochaete*	3.65	*Kobresia humilis*	3.03	*Kobresia humilis*	4.48	*Kobresia humilis*	3.82	*Gueldenstaedtia diversifolia*	5.2
9	*Thermopsis lanceolata*	3.17	*Gueldenstaedtia diversifolia*	2.61	*Carex moorcroftii*	3.02	*Geranium pylzowianum*	3.40	*Carex moorcroftii*	4.5
10	*Saussurea superba*	3.13	*Thalictrum alpinum*	2.60	*Gentiana straminea*	2.91	*Saussurea katochaete*	3.31	*Potentilla nivea*	3.5

[a] Underlined names indicate species endemic to the connecting plateaus of Qinghai-Tibet, Gansu, and Sichuan

Table 2 Mean species richness observed in 80 quadrats of 0.01 m^2 in 2002 and 100 quadrats of 0.01 m^2 in 2003, variance in richness among quadrats and coefficient of variation (CV) of richness, and total aboveground biomass per 0.01 m^2 quadrat

Item	EWG	LWG		WYG	
	2002	2002	2003	2002	2003
Mean species richness (number of species 0.01 m^{-2}) ± SE	19.36 ± 0.30	19.09 ± 0.33	19.69 ± 0.38	16.11 ± 0.24	15.51 ± 0.30
Evenness for species biomass[a]	0.770	0.688	0.775	0.727	0.780
Variance for richness (0.01 m^{-2})	7.22	8.79	14.64	4.51	9.08
Observed CV of richness	0.139	0.155	0.194	0.132	0.194
Theoretical CV of richness[b]	0.137	0.144	0.146	0.145	0.156
Observed CV/theoretical CV	1.01	1.08	1.33	0.91	1.24
Biomass (g/0.01 m^2) ± SE	3.32 ± 0.115	3.10 ± 0.097	3.02 ± 0.081	3.26 ± 0.109	3.14 ± 0.099

[a] Calculated as the natural logarithm
[b] Calculated by the formula of $\{\Sigma p_i(1-p_i)/(\Sigma p_i)^2\}^{1/2}$, where p_i denotes the occurrence rate per quadrat for species i, and Σ means sum for all species appeared. The theoretical CV-value was calculated under the assumption that each species was distributed at random quadrats

Species richness and biomass

The mean number of species per 0.01 m^2 was between 19 and 20 in the winter grazing pastures (EWG and LWG) and approximately 16 in the WYG (Table 2). The mean number of species was considerably higher in EWG and LWG than in the WYG pasture (Table 2), indicating that whole-year grazing reduced the species richness. The maximum number of species in a 0.01 m^2 quadrat was 30 in the LWG in 2003.

The aboveground biomass ranged from 3.0 to 3.3 g per 0.01 m^2 among the five surveys, each of which were composed of 80 or 100 quadrats, and no large differences were observed among surveys (Table 2). No standing dead matter or litter was present at the time of the August survey in any quadrats. Pielou's (1975) evenness values for the five suveys were relatively high, with no large differences among them (Table 2).

Spatial variation in species richness

The spatial variation in species richness, i.e., the degree of heterogeneity in species richness among quadrats, was expressed using the variance and the coefficient of variation (CV) among quadrats, which indicates variation standardized by the mean value. The variance was larger in 2003 than in 2002 (F-test, $P < 0.05$; Table 2). Owing to differences in the survey method between the two years, the degree of heterogeneity was compared within each year. The heterogeneity measured by the variance in the winter grazing pastures (EWG and LWG), in which the species richness was high, was higher than the heterogeneity in the WYG pasture, in which the species richness was lower (F-test, $P < 0.01$; Table 2). The observed CV, calculated based on data, in EWG and LWG was equal to or larger than that in the WYG pasture for within-year comparisons (Table 2). Furthermore, we calculated a theoretical CV under the assumption that each species was randomly distributed among quadrats, and compared the observed and theoretical CVs (CV ratio; Table 2). The CV ratios were greater for the EWG and LWG pastures than for the WYG pasture for within-year comparisons.

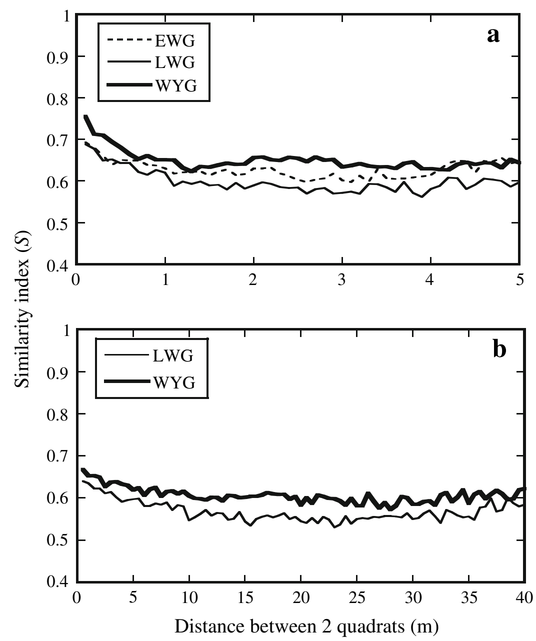

Fig. 1 Similarity index (S) quantifying the relationship of species composition expressed by the presence/absence between two quadrats along a transect. **a** 2002, **b** 2003

Figure 1 indicates similarities, calculated using Eq. 1, in the species composition between quadrat pairs separated by different distances along on each transect. The similarity in the species composition between two nearby quadrats was somewhat higher than that between two distant quadrats. Similarities in the WYG pasture were higher than those in the EWG and LWG pastures for both 2002 and 2003. The similarity between several nearby quadrats was higher based on data from 2002 than data from 2003, possibly because the survey method differed between the two years. All similarities measured appeared to reach a stationary value between quadrats at approximately 1–2 m in 2002 and 5–10 m in 2003.

Discussion

At the study sites, the mean number of species per 0.01 m^2 quadrat ranged from 15.5 to 19.7 (maximum 30; Table 2). This area has one of the highest species richness in the world for very small areas i.e., 0.01 m^2.

Examples from other studies that used small-scale quadrats are shown in Table 3 to allow comparison to the richness in this Qinghai alpine meadow. Kull and Zobel (1991) surveyed a wooded meadow at Laelatu, on the coast of eastern Estonia, using 0.01 m^2 quadrats. Although the species richness differed greatly among the sites surveyed, the mean number of species per 0.01 m^2 quadrat at a site that contained the maximum recorded richness was 17.7 (maximum per quadrat 25). The richness at Öland, Sweden, was also very high, with a maximum of 16.3 species per 0.01 m^2 (van der Maarel and Sykes 1993). Most of such high richness occurred in alvar habitat, which occurs on limestone bedrock with little or no soil on islands or coasts of the Baltic Sea. Researchers have conducted surveys in these grasslands to examine the niche partitioning among so many plant species, and they were confident that their experimental sites represented the richest areas in the world in terms of small-scale species diversity. The small-scale species richness of the Qinghai alpine meadow was equivalent to that of these sites near the Baltic Sea (Tables 2, 3).

The characteristics of grassland vegetation are usually expressed using species richness or diversity and, secondly, using spatial variation in species richness and composition (Collins 1992; van der Maarel et al. 1995; Wang et al. 2000). Here, we describe characteristics of the spatial variation in species richness and composition among Qinghai alpine meadow pastures differing in grazing management (Table 2, Fig. 1). The winter grazing pastures (EWG and LWG) exhibited higher richness and higher spatial variation in species richness than did the WYG pasture (Table 2), indicating that species richness and spatial variation might be positively related. The similarity index (S) for species composition was lower in the EWG and LWG pastures than in the WYG pasture (Fig. 1). That is, the spatial variation in species composition was larger in the EWG and LWG than in the WYG pastures. This low similarity (i.e., high spatial variation) in the EWG and LWG pasture suggests that high spatial variation might also be positively related to high species richness because higher species richness theoretically causes a more variable species combination, i.e., high spatial variation in species composition.

We infer two reasons for the high species richness in the Qinghai alpine meadow. The first is dependent on grazing types, and the second is related to the vertical structure of the plant community. The research site was

Table 3 Species richness per small quadrat (0.01–0.04 m^2) in grassland

Study area	Vegetation type	Altitude (m)	Quadrat size (m^2)	Mean species richness	Remarks
Laelatu, Estonia	Wooded meadow of *Sesleria coerulea-Filipendula hexapetala*	Coast	0.01	4.0–17.7 (30)[a]	Mean ± SE: 4.0 ± 0.22, 17.7 ± 0.49; Maximum richness: 25; Kull and Zobel 1991
Limburg, The Netherlands	Chalk grassland of *Mesobrometum erecti*	130–170	0.01	5.85–12.87 (50)	Willems et al. (1993)
Öland, Sweden	Alvar habitat of *Veronica spicata-Avenula pratensis*	Coast	0.01	12.1–16.3 (40)	Maximum richness, 29; van der Maarel and Sykes (1993)
Öland, Sweden	Alvar habitat of *Veronica spicata-Avenula pratensis*	Coast	0.01	9.5–13.1 (10 to 35)	Mean ± SE:9.5 ± 0.34, 13.1 ± 0.42; van der Maarel et al. (1995)
Öland, Sweden	Alvar habitat of *Veronica spicata-Avenula pratensis*	Coast	0.01	11.2, 12.5, 13.3 (10)	Data at 3 different sites; Wilson et al. (1995)
Saaremaa and Muhu, Estonia	Alvar type grassland of *Filipendula hexapetala-Trifolium montanum*	Coast	0.04	10–25 (10)	Pärtel and Zobel (1999)
Hanila, Estonia	Alvar grassland of *Filipendula-Trifolium montani*	Coast	0.01	13.2–17.1 (60)	Mean ± SE: 13.2 ± 0.22, 17.1 ± 0.23; Zobel et al. (2000)
Czech Republic	*Bromus electus* and *Carex montana* dominated grassland	440	0.015625	29 (1)	Observed by 5 persons; Klimeš et al. (2001)

[a] The number of quadrats measured for estimating mean species richness

located in a typical winter grazing pasture. In the LWG and EWG pastures, grazing occurs only in winter, and the plants are not damaged during the summer growing season. Thus, the complete loss of live aboveground biomass of herbaceous plants, standing dead matter, and litter due to consumption by animals occurs only in winter, and no aboveground standing dead matter or litter was observed in the following summer (Table 2). The elimination of litter and standing dead matter generally facilitates light penetration in summer, which causes increased photosynthesis, and reduces the mechanical obstruction of plant growth (Klein et al. 2004). Under such pasture conditions, both inferior and superior species, with respect to interspecific competition in summer and grazing and trampling, are able to survive and invade gaps that were formed by trampling and feeding in winter, especially in the two winter grazing pastures. This would allow them to germinate and become established, as explained by Grubb's (1977) regeneration niche. High species richness resulting from a mixture of superior and inferior plant species could have been maintained in this way in the meadows of the two winter grazing pastures. In contrast, in the WYG pasture, which has lower richness compared with that in the two winter grazing pastures, inferior species that are intolerant to summer grazing (e.g., *Morina chinensis* and *Thermopsis lanceolata*) might have been eliminated by interspecific competition in summer. Although the grazing intensity was higher in the WYG pasture than in the two winter grazing pastures, it was not great enough to cause overgrazing; the biomass in the WYG pasture (>3 g/0.01 m^2; Table 2) was common for this area (e.g., Li and Zhou 1998) and not smaller than in the other two pastures.

The vegetation of the Qinghai alpine meadow is dense and relatively short (5–20 cm high; Zhou et al. 2005), and the canopy is open because *Elymus nutans* and *Saussurea katochaete*, which are the most common species in these plots, are tall, erect types (Zhou et al. 1987; NPIB 1997). Therefore, sunlight can penetrate to the bottom layer of the community, allowing shorter species to use the light resources effectively and to survive. This is the second reason for the high species richness. Thus, the high species richness and spatial heterogeneity in the EWG and LWG pastures are also maintained by grazing only during winter and light penetration to the bottom layer of the vegetation. We need another experiment to definitely evaluate why the high species richness is maintained in such a small area.

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References

Adler P, Raff D, Lauenroth W (2001) The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465–479

Belsky AJ (1992) Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. J Veg Sci 3:187–200

Chen J, Hori Y, Shiyomi M, Yamamura Y, Yasuda T, Takahashi H, Iki M (2005) Community structure of a semi-natural grassland and an abandoned, forested grassland (in Japanese). Grassl Sci 51:143–151

Cincotta RP, Zhang YQ, Zhou XM (1992) Transhumant alpine pastoralism in northern Qinghai Province: an evaluation of livestock population response during China's agrarian economic reform. Nomad People 30:3–25

Collins SL (1992) Fire frequency and community heterogeneity in tallgrass prairie vegetation. Ecology 73:2001–2006

Currie DJ (1991) Energy and large-scale patterns of animal- and plant-species richness. Am Nat 137:27–49

Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol Rev 52:107–145

Hakamata T, Hirashima T (1978) Evaluation of cattle excreta on pasture fertility. 1. The excreta dispersion models and their applicable conditions (in Japanese). J Jpn Soc Grassl Sci 24:162–171

Haynes RJ, Williams PH (1993) Nutrient cycling and soil fertility in the grazed pasture ecosystems. Adv Agron 49:119–199

Hirata M, Sugimoto Y, Ueno M (1987) Distributions of dung pats and ungrazed areas in Bahiagrass (*Paspalm notatum* Flügge) pasture. J Japn Soc Grassl Sci 33:128–139

James EB, Calvin FB (1986) Vegetation response to long term sheep grazing on mountain rangesss. J Range Manage 39:431–434

Jiang S (1997) Sustainable utilization of grassland resources in China (in Chinese). Grassl China 2:73–79

Klimeš L, Dančák M, Hájek M, Jongepierová I, Kučera T (2001) Scale-dependent biases in species counts in a grassland. J Veg Sci 12:699–704

Klein JA, Harte J, Zhao XQ (2004) Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. Ecol Let 7:1170–1179

Kull K, Zobel M (1991) High species richness in an Estonian wooded meadow. J Veg Sci 2:711–714

Li W, Zhou X (1998) Ecosystems of Qinhai-Xizang (Tibetan) Plateau and approach for their sustainable management (in Chinese). Guangdong Science & Technology Press, Guanzhou, pp 8–18, 163–164

Liu W, Wang QJ, Wang X, Zhou L (1999) Ecological process of forming "black soil type" deteriorate grassland (in Chinese). Acta Agres Sin 7:300–307

McNaughton SJ (1979) Grazing as an optimization process: grass-ungulate relationships in the Serengeti. Am Nat 113:691–703

Northwest Plateau Institute of Biology, The Chinese Academy of Sciences (NPIB) Liu SW (ed) (1997) *Flora Qinhaiica*, vol. I–IV (in Chinese). Qinhai People's Publishing House, Xining

Noy-Meir I, Gutman M, Kaplan Y (1989) Responses of Mediteranean grassland plants to grazing and protection. J Ecol 77:290–310

Pärtel M, Zobel M (1999) Small-scale plant richness in calcareous grasslands determined by the species pool, community age and shoot density. Ecography 22:153–159

Pielou EC (1975) Ecological diversity. Wiley, New York, pp 14–17

Pierre H (1998) Effects of grazing on plant species composition and spatial distribution in grasslands of the Sahel. Plant Ecol 138:191–202

Rusch G, Fernandez-Palacios JM (1995) The influence of spatial heterogeneity on regeneration by seed in a limestone grassland. J Veg Sci 6:417–426

Shiyomi M, Takahashi S, Kirita H (2000) Roles of plant biomass and vegetational heterogeneity, and energy-matter cycling in grassland sustainability. Ecol Model 132:135–149

Schaller GB (1998) Wildlife of the Tibetan steppe. University of Chicago Press, Chicago

Thomas JS, Lisa DS, Brain VH (1999) How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecol Appl 9:45–64

Tsutsumi M, Shiyomi M, Wang YS, Tsuiki M, Yu XR (2003) Species diversity of grassland vegetation under three different grazing intensities in the Heilongjiang steppe of China. Grassl Sci 48:510–516

Van der Maarel E, Sykes MT (1993) Small-scale species turnover in a limestone grassland: the carousel model and some comments on the niche concept. J Veg Sci 4:179–188

Van der Maarel E, Noest V, Palmer MW (1995) Variation in species richness on small grassland quadrats: niche structure or small-scale plant mobility? J Veg Sci 6:741–752

Vickery PJ (1992) Grazing and net primary production of a temperate grassland. J Appl Ecol 9:307–314

Wang Q, Zhou X, Shen Z, Zhang Y (1994) The structure of Tibetan *Kobresia* community and its utilization of the alpine swampy meadow in Qinghai Province. In: Li B (ed) Proceedings of the international symposium on grassland resources, Agricultural Scientech Press, Beijing, pp 359–365

Wang Q, Zhou X, Wang W (1999) A preliminary study of species diversity of main plant communities in alpine meadow (in Chinese). Acta Biol Plate Sin 14:77–87

Wang W, Zhou L, Wang Q, Jiang W (2000) The effect of different grazing intensity to plant spatial patterns in alpine meadow. In: Zheng D, Zhu L (eds) Formation and environment changes and sustainable development on the Tibetan Plateau, Academy Press, Beijing, pp 413–421

Wang YS, Shiyomi M, Tsuiki M, Tsutsumi M, Yu XR, Yi R (2002) Spatial heterogeneity of vegetation under different grazing intensities in the Northwest Heilongjiang steppe of China. Agric Ecosys Env 90:217–230

Willems JH, Peet RK, Bik L (1993) Changes in chalk-grassland structure and species richness resulting selective nutrient additions. J Veg Sci 4:203–212

Wilson JB, Sykes MT, Peet RK (1995) Time and space in the community structure of a species-rich limestone grassland. J Veg Sci 6:729–740

Yiruhan, Shiyomi M, Takahashi S, Okubo T, Akiyama T, Koyama N, Tsuiki M (2001) Analysis of long-term grazing experiment at central Japan. 1. Seasonal and yearly changes in herbage biomass. Grassl Sci 47:344–361

Zhang J (2004) Quantitative ecology (in Chinese). Science Press, Beijing, pp 125–132

Zhao XQ, Zhou XM (1999) Ecological basis of alpine meadow ecosystem management in Tibet: Haibei Alpine Meadow Ecosystem Research Station. Ambio 28:642–647

Zhou HK, Zhao XQ, Tang YH, Zhou L (2005) Alpine grassland degradation and its control in the source region of the Yangtze and Yellow Rivers, China. Grassl Sci 51:191–203

Zhou XM (2001) *Kobresia* meadow in China (in Chinese). Science Publishers, Beijing

Zhou XM, Wang ZB, Du Q (1987) The vegetation of Qinghai (in Chinese). Qinghai People's Publishers, Xining

Zobel M, Otsus M, Liira J, Moora M, Möls T (2000) Is small-scale species richness limited by seed availablility or microsite availability? Ecology 81:3274–3282