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Effects of Grazing Exclusion on Plant Functional Group Diversity of Alpine Grasslands along a Precipitation Gradient on the Northern Tibetan Plateau

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Abstract

Tibetan alpine grasslands are viewed to be sensitive to climate change and grazing disturbance. But it is not well understood how and to what extent grazing exclusion affects species assembly on the Northern Tibetan Plateau. We conducted a multisite transect along a precipitation gradient to detect species compositional changes at 25 grazed versus nongrazed paired pastures in summers of 2009 and 2010 in the Changtang Natural Reserve. Species richness and relative frequency were estimated for plant functional groups (PFGs: grasses, sedges, forbs, and legumes). Species richness at community level responds positively to precipitation and differs among vegetation types: meadow (22.63 ± 1.73) > steppe (11.23 ± 1.00) > desert-steppe (6.75 ± 0.63). Variations in species richness and relative frequency of PFGs are partly dependent on vegetation type. Three to four years of grazing exclusion has not significantly changed species richness or relative frequency at PFG level. Grazing exclusion has slightly changed PFGs' correlations in species richness but significantly altered their correlations in relative frequency within and across vegetations. Stepwise linear regressions indicate that PFGs respond to climate gradients in discrete ways. This study implies that specific adaptation mechanisms of different taxonomic groups to climatic change and grazing disturbance should be seriously considered in further studies.

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Introduction

Grazing is a universal disturbance exerted on both alpine and temperate grasslands all over the world. It affects species composition not only because of animals' selective grazing behavior, but also because of plants' differential responses to being grazed (Tilman et al., 1997; Olff and Ritchie, 1998), and thus decreases foliar biomass with livestock rate increasing (Christiansen and Svejcar, 1988). Alpine grasslands on the Qinghai-Tibetan Plateau are very sensitive to natural climate changes (White et al., 2000; Chou et al., 2008; Xu et al., 2010) and grazing disturbance (Zhou et al., 2006; Wei et al., 2008; Cao et al., 2011). There most alpine grasslands are still traditionally grazed by yaks and/or sheep of single or multi-families (Zhou et al., 2006; Cao et al., 2011). Due to climate changes and overgrazing over past decades, some alpine pastures on the Northern Tibetan Plateau have been severely degraded with invasions of locoweed species of *Astragalus* and *Oxytropis*, such as *Astragalus strictus* and *Oxytropis glacialis* (Gao et al., 2006; Li et al., 2008; Gao et al., 2009; Cao et al., 2011). To improve the degraded pastures' recovery, metal enclosures have been built since 2006 on the Northern Tibetan Plateau. However, there is lack of knowledge on how grazing exclusion affects species composition and individual's performance.

There is no universal effect of grazing exclusion from livestock on compositional changes in species, functional group, or growth form (Cingolani et al., 2005; Diaz et al., 2007). It has been hotly debated whether ceasing of grazing would alter species richness and interactions among species. Milchunas and Lauenroth (1993) found that changes in species composition were primarily a function of site productivity and evolutionary history of grazing, with level of animals' consumption third in importance. Diaz et al. (2007) suggested that plant functional type classifications and

response rules need to be specified to vegetations with different climate and species assembly in studies related to grazing management. However, a long-term grazing exclusion may result in a decline or little change in species richness (Lenzi-Grillini et al., 1996; Courtois et al., 2004; Shi et al., 2010) due to the differentiation and complementarity of ecological niches among species (Bluthgen and Klein, 2011; Papanikolaou et al., 2011). Moreover, compositional changes in functional diversity might not be concurrent across grassland types subjected to different grazing management. Changes in dominant species are more sensitive to varying ecosystem-environmental variables than to varying grazing variables (Milchunas and Lauenroth, 1993). Therefore, grazing may not necessarily alter species richness but significantly affects community functional trait assembly due to its selective effects on the species individuals' performance (Rusch and Oesterheld, 1997; Tilman et al., 1997; Zhou et al., 2006; Mayer et al., 2009). These inconsistent findings make it more complex but necessary to clarify how different species and functional groups respond to shifts in grazing management (Villouta et al., 2001; Papanikolaou et al., 2011).

Moreover, complementarity and competitiveness among different functional groups determine the stability and resilience of alpine grassland communities to climate change and human disturbance. Climate determines availabilities of nutrients and moisture at top soils, and thereby affects plants' growth and community biomass production (Paruelo et al., 1999; Dinga and Walker, 2011). Precipitation during the growing season (mostly from May to September) decreases westward, and moisture availability controls the spatial distribution and primary production of zonal alpine grasslands on the Northern Tibetan Plateau (Hu et al., 2010; Yang et al., 2010; Shen et al., 2011). Seasonal grazing exclusion by metal enclosures could improve species richness and

forage production at a single site in the degraded alpine *Kobresia* meadow zone on the Eastern Qinghai-Tibetan Plateau (Zhou et al., 2006; Wei et al., 2008; Gao et al., 2009; Li et al., 2009; Li et al., 2011b), with narrow variations in growing season precipitation or temperature there. However, it is still not clear whether species richness and relative frequency of different plant functional groups (PFGs) have also changed under short-term grazing exclusion from livestock along climate-related gradients in this region.

Therefore, in this study we focus on the two aspects of plant functional diversity: species richness and relative frequency. We aim to (1) test whether the short-term grazing exclusion (started since 2006) has compositionally changed the functional groups of the three zonal grassland types: alpine meadows (AM), steppes (AS), and desert-steppes (ADS); (2) clarify whether grazing exclusion has altered intergroup relationships among PFGs (forbs, sedges, legumes, and grasses) compared to those in grazed pastures; and (3) identify whether grazing exclusion has significantly changed the response of community functional diversity to regional precipitation variation compared to that in traditional grazed pastures.

Materials and Methods

STUDY AREA

The Northern Tibetan Plateau (29°53'–36°32'N; 78°41'–92°16'E), locally known as Changtang, locates in the northwestern hinterlands of the Qinghai-Tibet Plateau and is surrounded by huge mountain ranges such as Kunlun, Gangdise, Tanglha, and Nyainqntanglha (Fig. 1, part a). Changtang has an area of approximately 5.95 million km², where natural grassland resource covers 48 million hm² and provides the most fundamental life insurance for local Tibetan herdsman (Wu et al., 2013). It is an ideal place to examine how alpine grasslands respond to climate changes and human disturbance (mainly referring to pasture management and livestock grazing control), not only because of the evident climatic gradients, but also because of the grazing intensity ranges across the Northern Tibetan Plateau (Wu et al., 2013).

Growing season in Changtang usually starts in May and ends in September, with 65% to 85% of annual precipitation falling during this period, as well as mean daily temperature being over 5.0 °C. Therefore, the aridity gradient is evident westward across the Northern Tibetan Plateau, with mean annual growing season precipitation (GSP) declining from more than 400 mm at the easternmost site to less than 100 mm at the westernmost site (Fig. 1, part c) and mean annual growing season temperature (GST) from lower than 5.0 °C in the northeast increasing to higher than 10.0 °C in the southwest (Fig. 1, part b). The spatial distribution of natural zonal grasslands, as well as aboveground net primary production (ANPP), is consistent with the general climate pattern (Zhong et al., 2010). The zonal vegetation varies westward from alpine meadow (AM, dominated by *Kobresia pygmaea*, *K. humilis*, and *Carex moorcroftii*) to alpine steppe (AS, dominated by *Stipa purpurea*, *S. capillacea*, *S. subsessiliflora* var. *basiplumosa*) and to alpine desert steppe (ADS, dominated by *S. purpurea*, *Ceratoides latens*, and *S. glareosa*) (Li et al., 2011a; Wu et al., 2012, 2013), with climate shifting from semi-humid to semi-arid to arid, respectively.

To protect the natural alpine grasslands, metal grazing enclosures (mostly larger than 30 hm² in size) have been established since 2006 on the Northern Tibetan Plateau, most of which are supported by the Ecological Security Barrier

Construction Program (Shi et al., 2010). It means that in the Changtang Region, most metal enclosures are built for vegetation recovery, with livestock being excluded all year-round. These metal enclosures are also effective to exclude large wildlife herbivores, such as *Pantholops hodgsoni*, *Procapra picticaudata*, and *Equus kiang*, but ineffective to small ones such as pika and marmot. Open pastures adjacently outside these enclosures are still traditionally grazed by livestock of single or multiple families throughout the year or only during the cold months from October to the following May (Wu et al., 2013). There is no accurate information (timing, intensity, and frequency) on grazing activities and pasture management in these open pastures sampled in our study, but the actual averaged stocking rate ranges from 0.16 sheep units · hm⁻² of the westernmost county to 2.05 sheep units · hm⁻² in the easternmost county for the study region.

Limited by budgets, time, and severe environments, we could not perform enough field work once to reveal effects of grazing exclusion on species richness and relative frequency of different plant functional groups. Instead, we sampled 10 pairs of grazed vs. nongrazed sites in 2009 and the remaining 15 pairs in 2010 along the actual annual climate gradients (Fig. 1). Grazing-excluded sites chosen in this study were well matched with the adjacent open pastures. And we defined the grazed site within 1000 m outside from the enclosure edges to make sure that each pair sites were as similar as possible in slope, aspect, and soils. At each sample location, we measured species richness and relative frequency of different plant functional groups (PFGs) within a plot area of 200 × 200 m. In addition, it is noteworthy that we did not choose the heavily degraded pastures damaged by pika because it may have confounded effect on species compositional changes with precipitation gradients.

SPECIES-AREA CURVES FOR THE THREE ZONAL ALPINE GRASSLANDS

In 2009, we developed specific species-area relationships at three sites subjected to alpine meadow, steppe, and desert-steppe, respectively (Fig. 2). Within a 200 × 200 m sample area at each site, we established five multiscale Modified-Whittaker plots at 20-m intervals along a 100-m-long sample line (Stohlgren et al., 1998). The Modified-Whittaker plot was 1 × 1 m in size, in which a set of subplots in size of 0.25 × 0.25 m (0.0625 m²), 0.25 × 0.50 m (0.125 m²), 0.25 × 0.75 m (0.1875 m²), 0.50 × 0.5 m (0.25 m²), 50 cm × 75 cm (0.375 m²), 50 cm × 100 cm (0.50 m²), 75 cm × 75 cm (0.5625 m²), 75 cm × 100 cm (0.75 m²) were nested. Species richness recorded using five 1 × 1 m plots only accounted for 59.7%, 71.4%, and 51.0% of species records from the thirty 0.1 m² circles within the same sample area at alpine meadow, steppe, and desert-steppe sites, respectively (Wu et al., 2014). Therefore, we argued that thirty 0.1-m² circles along one 100-m sample transect captured most of the species at each sampling location. Nevertheless, the area of sampling units (0.1-m² circle) might be too small to capture variation of each plant functional group. In addition, local species pool is so poor at the alpine desert-steppe that it might be meaningless to enlarge sample size or to add sampling circles (Fig. 2).

SPECIES RICHNESS AND RELATIVE FREQUENCY OF DIFFERENT PFGS

Field data collection was performed during late July to early August in 2009 and 2010, with 25 grazed vs. nongrazed paired

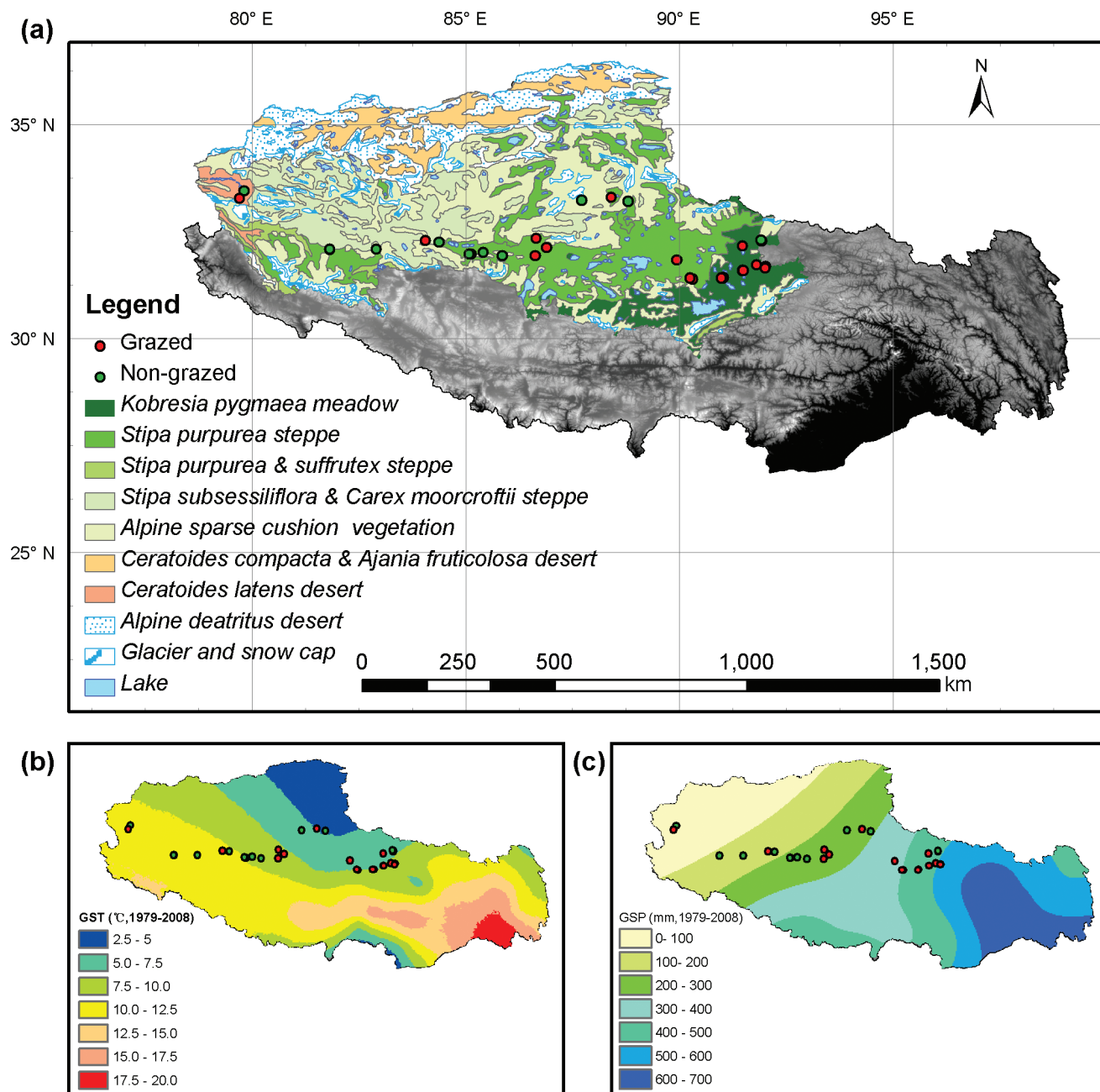


FIGURE 1. Locations of the 25 pairs of grazed vs. nongrazed sites on the Northern Tibetan Plateau and spatial patterns of mean growing season temperature (GST) and precipitation (GSP) from 1979 to 2008 over the Tibet Autonomous Region. Here growing season is defined from May to September.

sites in total, subjected to the three zonal grassland types, chosen on the Northern Tibetan Plateau (Fig. 1). At each sample location, we noted all vascular plant species captured in thirty 0.1-m² sample circles along one 100-m sample transect within the 200 × 200 m plot. Species were classified into four plant functional groups (PFGs): grasses, legumes, sedges, and forbs (Ma et al., 2010). From the sampling records, we estimated species richness at both community and plant functional group levels. To explore the potential impacts of grazing exclusion on compositional changes, we also estimated variation in relative frequency of each functional group, defined as the ratio of the occurrences

of species belonging to a certain group to the occurrences of species captured in the thirty 0.1-m² circles. In addition, we also calculated the Simpson index (D) and Shannon index (H) as the plant functional group diversity following Equations 1 and 2, grouping “as a species” taxa categorized in the same functional group (Papanikolaou et al., 2011):

$$D = \frac{1}{\sum_{i=1}^n RF_i^2} \quad (1)$$

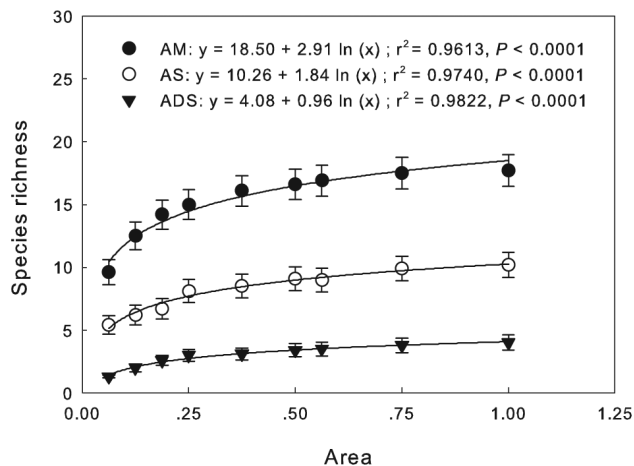


FIGURE 2. The specific species richness–area relationship at the three zonal grassland types: AM, alpine meadows; AS, alpine steppes; ADS, alpine desert-steppes. Regressions model: $y = a + \ln(x)$.

$$H = \sum_{i=1}^n RF_i \ln RF_i \quad (2)$$

where RF_i is the relative frequency of PGF_i , with i ranging from 1 to 4 (four prior defined $PGFs$).

GROWING SEASON CLIMATIC INFORMATION FOR EACH SAMPLED SITE

Daily climatic data were downloaded from the National Meteorological Information Centre (NMIC) of the China Meteorological Administration (CMA) from the daily air temperature and precipitation records for the 39 meteorological stations in the Tibet Autonomous Region from May to September in 2009 and 2010. First, we interpolated climatic data into specific raster surfaces in ANUSPLIN 4.3 (Hutchinson, 2004) in ArcView 3.2 (ERSI, Redlands, California, U.S.A.). Then we calculated growing season precipitation (GSP), growing season temperature (GST), accumulated temperature sum above 5 °C (AccT), and the substitute for climatic moisture index (GSP/AccT) in 2009 and 2010. Finally, we extracted specific meteorological information from these climatic surfaces for each sample site according to its location in ArcGIS 9.2 (ESRI, Redlands, California, U.S.A.). Using one-way analysis of variance (ANOVA) with Least-Significant-Difference (LSD) test, we tested for differences in climatic variables between 2009 and 2010. Significant differences in GST ($F = 10.025$, $P < 0.01$) and AccT ($F = 10.025$, $P < 0.01$). Nevertheless, there was no significant difference in GSP ($F = 0.016$, $P > 0.1$) or GSP/AccT ($F = 1.756$, $P > 0.1$) between the two study years. Therefore, there was an evident moisture gradient with GSP linearly (Fig. 3, part a) and GSP/AccT exponentially (Fig. 3, part c) increasing eastward when the two-year data were pooled together for further analysis.

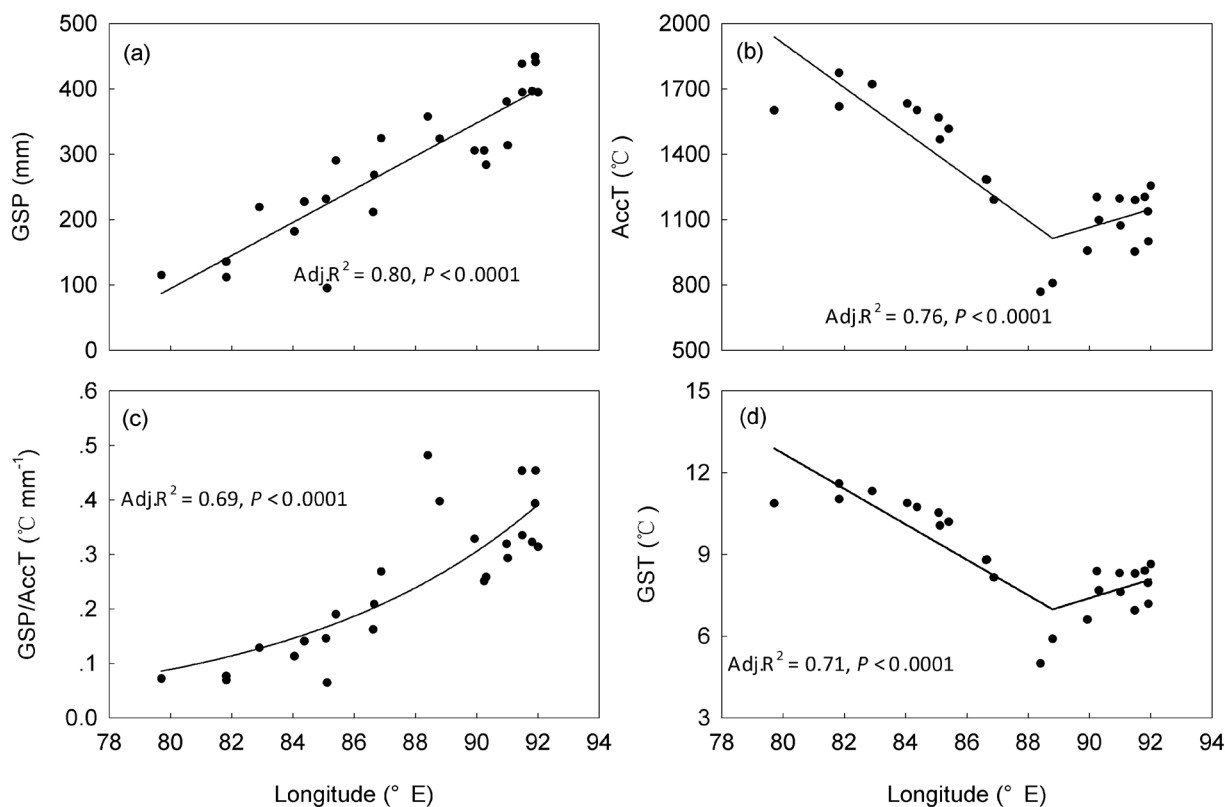


FIGURE 3. The longitudinal patterns of growing season precipitation (GSP), accumulated temperature above 5 °C (AccT), the ratio of GSP/AccT, and mean growing season temperature (GST) on the Northern Tibetan Plateau.

First, we performed regression analyses of species richness and functional diversity along the precipitation gradient on the Northern Tibetan Plateau and examined whether grazing exclusion has changed the response manner compared to in grazed pastures. Second, using one-way ANOVA with Student-Newman-Keuls (SNK) test, we examined differences in species richness and functional diversity across alpine grassland types using the three subsets of data: total, grazed, and nongrazing sites, respectively. Third, paired samples *t*-test was used to examine differences in both species richness and relative frequency of each PFG between grazed and nongrazed paired pastures within and across alpine grassland types. Following, we compared the Spearman correlation coefficients of both species richness and relative frequency among the different PFGs between grazed and nongrazed pastures (Papanikolaou et al., 2011). Finally, stepwise linear regressions were used to explore how species richness and relative frequency of different PFGs respond to climatic variables.

Data analyses were performed in SPSS 17.0 (SPSS, Chicago, Illinois, U.S.A.); figures were plotted in SigmaPlot 10.0 (Systat Software, Chicago, Illinois, U.S.A.); and all significant differences were at $P < 0.05$.

Results

SPATIAL PATTERNS OF FUNCTIONAL DIVERSITY ALONG PRECIPITATION GRADIENT

Species richness exponentially increases with increasing precipitation during the plant growing months (May to September) at the community level (overall sites, adj. $R^2 = 0.59$, $P < 0.0001$; grazed sites, adj. $R^2 = 0.63$, $P < 0.0001$; nongrazed sites, adj. $R^2 = 0.55$, $P < 0.0001$). There was no significant difference in the response patterns between grazed and nongrazed pastures within the 95% confidence band (Fig. 4, part a). Simpson's D and Shannon's H linearly increase with increasing growing season precipitation (GSP) across the Northern Tibetan Plateau (overall sites: adj. $R^2 = 0.07$, $P < 0.05$ for Simpson's D ; adj. $R^2 = 0.14$, $P < 0.01$ for Shannon's H). There was no significant relationship between Simpson's D and precipitation for the grazed (adj. $R^2 = 0.10$, $P > 0.05$) or nongrazed sites (adj. $R^2 = 0.01$, $P > 0.1$) (Fig. 4, part b). Shannon's H showed significant (adj. $R^2 = 0.15$, $P < 0.05$) linear response across grazed sites, but marginal linear response (adj. $R^2 = 0.10$, $P = 0.07$) across nongrazed sites to the regional variation of the growing season precipitation (Fig. 4, part c).

FUNCTIONAL DIVERSITY BETWEEN GRAZED AND NON-GRAZED PASTURES

Species richness at the community level differs among the three zonal alpine grassland types: alpine meadow (22.6 ± 1.7) > alpine steppe (11.2 ± 1.0) > alpine desert-steppe (6.8 ± 0.6) for overall sites ($P < 0.05$, Fig. 5, part a). Simpson's D was similar between alpine meadows (2.84 ± 0.10) and alpine steppes (3.02 ± 0.82) for overall sites ($P > 0.05$, Fig. 5, part b), and significantly higher than alpine desert-steppes (2.29 ± 0.16) ($P < 0.05$, Fig. 5, part b). Shannon's H showed similar patterns to Simpson's D among the three zonal grassland types (Fig. 5, part c). Meanwhile, decreases in species richness of grazed sites were found significant for sedges across alpine grasslands ($p < 0.05$) and marginally significant for legumes at alpine meadows ($p = 0.08$) compared

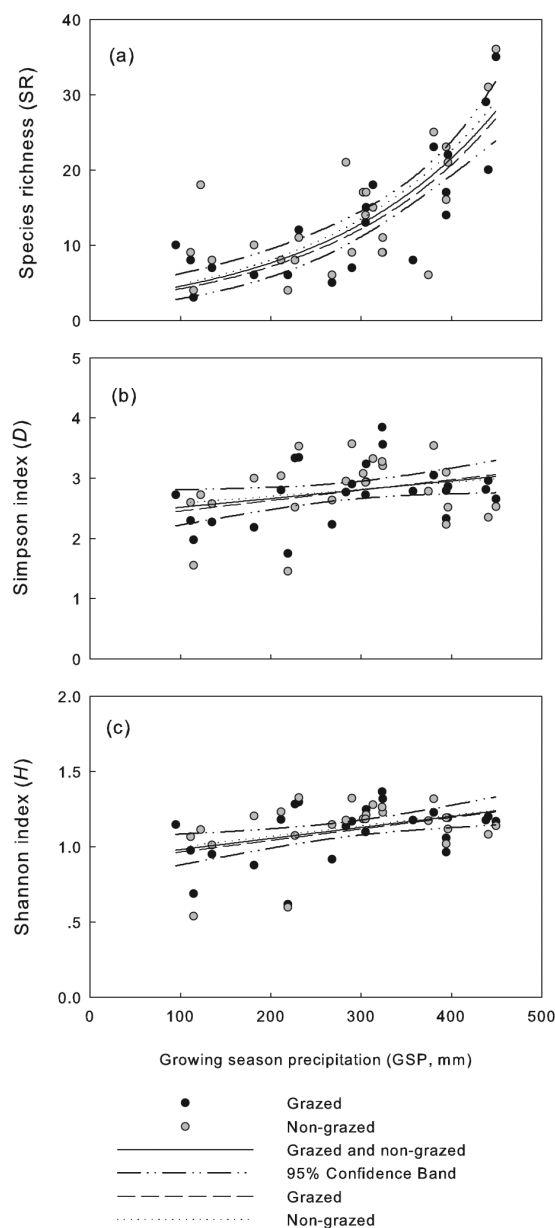


FIGURE 4. Responses of (a) species richness (SR), (b) Simpson's D , and (c) Shannon's H to growing season precipitation (GSP, mm) across the grazed, nongrazed, and overall sites on the Northern Tibetan Plateau.

to nongrazed ones (Table 1, paired samples *t*-test). No evident variation in relative frequency of each PFG was between grazed and nongrazed paired sites within or across alpine grassland types (Table 1).

Species richness (SR) and relative frequency (RF) of each PFG also were partly dependent on grassland types. For overall sites, species richness of forbs at meadows (13.9 ± 1.5) was higher than steppes (5.9 ± 0.8) and desert-steppes (2.9 ± 0.4) (Fig. 6, part a), while relative frequency of forbs declined from $48.1\% \pm 2.5\%$ at meadows to $35.7\% \pm 2.2\%$ at steppes and to $34.6\% \pm 4.6\%$ at desert-steppes (Fig. 6, part e). No significant difference was in species richness or relative frequency of

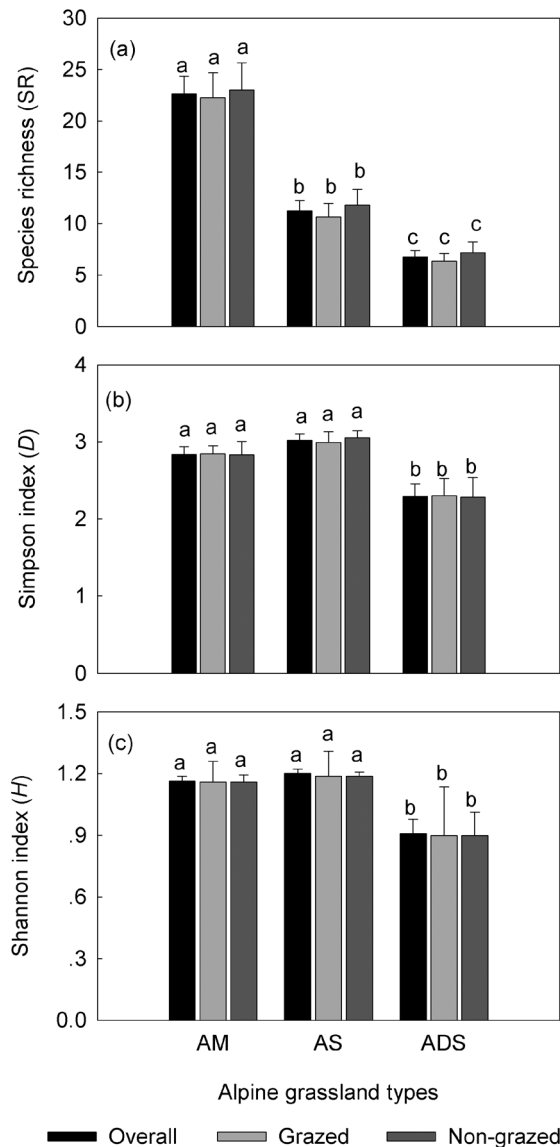


FIGURE 5. Comparisons of (a) species richness (SR), (b) Simpson index (D), and (c) Shannon index (H) between alpine grassland types (AM, alpine meadows; AS, alpine steppes; ADS, alpine desert-steppes) for overall, grazed and nongrazed sites, respectively. One-way ANOVA (S-N-K test), different letters over the bars indicated significantly different at $P < 0.05$.

forbs between steppe and desert-steppe (Fig. 6, parts a and e). Species richness of grasses at meadows (3.8 ± 0.2) was higher than steppes (2.0 ± 0.2) and desert-steppes (2.3 ± 0.3), with no significant difference between steppes and desert-steppes (Fig. 6, part a). Relative frequency of grasses increased from $25.7\% \pm 2.2\%$ at meadows, to $36.5\% \pm 2.5\%$ at steppes and to $52.9\% \pm 4.8\%$ at desert-steppes (Fig. 6, part e). Legumes have the lowest values in species richness (0.6 ± 0.3) and relative frequency ($4.1\% \pm 2.3\%$) at desert-steppes. Species richness of legumes at meadows (2.1 ± 0.4) was higher than at steppes (1.7 ± 0.1), while its relative frequency at meadows ($7.9\% \pm 1.3\%$) was lower than at steppes ($15.0\% \pm 1.8\%$). Species richness of sedges declines from 2.8 ± 0.2 at meadows to 1.6 ± 0.2 at steppes and to $0.9 \pm$

0.2 at desert-steppes, while its relative frequency declines from $18.3\% \pm 1.2\%$ at meadows to $12.8\% \pm 1.7\%$ at steppes and to $8.4\% \pm 2.0\%$ at desert-steppes.

GRAZING EXCLUSION AFFECTS CORRELATIONS BETWEEN FUNCTIONAL GROUPS

Species richness correlation of grasses-sedges was 0.340 at the overall grazed sites ($p > 0.05$) compared to 0.470 at nongrazed pastures ($p < 0.05$). Species richness correlation of grasses-forbs changed from positive at grazed sites (0.707 , $p > 0.05$) to negative at nongrazed ones (-0.098 , $p > 0.05$) in desert-steppe zone. Relative frequency correlations of grasses-forbs were insignificant at grazed sites (alpine steppes, -0.491 ; alpine desert-steppes, -0.290 ; $p > 0.05$) but significant at nongrazed sites (alpine steppes, -0.629 ; alpine desert-steppes, -0.493 ; $p < 0.01$). Evident changes in relative frequency correlations were also found for sedges-grasses across overall sites, as well as for sedges-legumes at alpine meadows and alpine steppes. In sum, the short-term grazing exclusion slightly changed species richness correlations but significantly altered relative frequency correlations between functional groups within and across alpine grassland types (Table 2).

CLIMATIC FACTORS ON SPECIES RICHNESS AND RELATIVE FREQUENCY

Stepwise multiple regression analyses indicated that species richness of communities and functional groups are mainly controlled by growing season precipitation, with significant positive partial correlations ranging from 0.474 to 0.713 . In contrast, community functional diversity (Simpson's D and Shannon's H) is negative correlated to AccT. There was not any climatic variable entered in the regression model for forbs' relative frequency. Relative frequency for legumes and grasses was negatively correlated to temperature (partial $R = -0.400$, $P = 0.004$) and precipitation (partial $R = -0.523$, $P < 0.001$), respectively. Sedges' relative frequency positively responded to the ratio of GSP/AccT (partial $R = 0.401$, $P = 0.004$) (Table 3).

Discussion

The effects of grazers on plant assemblages are partly dependent on the ecosystem productivity and the size of plant individuals (Symstad and Jonas, 2011). The response of individual species to fencing from grazing is also productivity dependent, with plant size playing a central role (Osem et al., 2004). Aboveground productivity of alpine grasslands on the Northern Tibetan Plateau is very low, ranging from 7.4 to 68.2 g m⁻² (Wu et al., 2013). Lower temperature and precipitation primarily control the patterns of species richness, diversity, and productivity of alpine grasslands in this region (Wu et al., 2012; Yang et al., 2010). Most constructive species in alpine meadows, steppes, and desert-steppes are very short, such as *K. pygmaea*, *K. humilis*, *C. moorcroftii*, *S. purpurea*, *S. capillacea*, *S. purpurea*, and *S. glareosa*. Previous studies reveal that shorter species are generally more tolerant to grazing than taller species (Hickman et al., 2004; Milchunas and Noy-Meir, 2004; Osem et al., 2004) and that low-productivity communities often show less response to grazing than high-productivity ones (Milchunas et al., 1998). Deleglise et al. (2011) found that evenness and richness showed

TABLE 1

Paired samples T-test for the grazed vs. non-grazed differences of species richness (SR) and relative frequency (RF, %) of forbs, grasses, legumes, and sedges within and across alpine grassland types (AGTs): AM, alpine meadows; AS, alpine steppes; ADS, alpine desert-steppes.

AGTs	Difference for SR						Difference for RF					
	Mean	SEM	Lower*	Upper*	<i>t</i>	<i>p</i>	Mean	SEM	Lower*	Upper*	<i>t</i>	<i>p</i>
Overall												
Forbs	-0.28	0.88	-2.10	1.54	-0.32	0.75	-0.02	0.02	-0.06	0.03	-0.81	0.43
Grasses	0.04	0.12	-0.21	0.29	0.33	0.75	0.03	0.02	-0.01	0.08	1.50	0.15
Legumes	-0.32	0.21	-0.76	0.12	-1.50	0.15	0.00	0.01	-0.03	0.02	-0.38	0.71
Sedges	-0.40	0.15	-0.72	-0.08	-2.62	0.02	-0.01	0.01	-0.04	0.02	-0.79	0.44
AM, n = 8												
Forbs	0.63	2.36	-4.96	6.21	0.27	0.80	0.00	0.03	-0.07	0.07	-0.02	0.99
Grasses	0.00	0.27	-0.63	0.63	0.00	1.00	0.01	0.02	-0.04	0.05	0.32	0.76
Legumes	-0.75	0.37	-1.62	0.12	-2.05	0.08	-0.02	0.01	-0.04	0.01	-1.34	0.22
Sedges	-0.63	0.32	-1.39	0.14	-1.93	0.10	0.01	0.03	-0.05	0.07	0.36	0.73
AS, n = 11												
Forbs	-1.00	1.11	-3.48	1.48	-0.90	0.39	-0.01	0.02	-0.06	0.03	-0.55	0.60
Grasses	0.09	0.16	-0.27	0.45	0.56	0.59	0.03	0.02	-0.03	0.08	1.11	0.29
Legumes	0.09	0.29	-0.54	0.73	0.32	0.76	0.01	0.02	-0.04	0.06	0.41	0.69
Sedges	-0.36	0.24	-0.91	0.18	-1.49	0.17	-0.03	0.02	-0.07	0.02	-1.37	0.20
ADS, n = 6												
Forbs	-0.17	0.48	-1.39	1.06	-0.35	0.74	-0.05	0.08	-0.25	0.14	-0.69	0.52
Grasses	0.00	0.26	-0.66	0.66	0.00	1.00	0.07	0.07	-0.12	0.26	1.00	0.36
Legumes	-0.50	0.50	-1.79	0.79	-1.00	0.36	-0.02	0.01	-0.05	0.02	-1.08	0.33
Sedges	-0.17	0.17	-0.60	0.26	-1.00	0.36	-0.01	0.03	-0.07	0.06	-0.31	0.77

*The lower and upper of the 95% confidence interval of the grazed versus non-grazed difference.

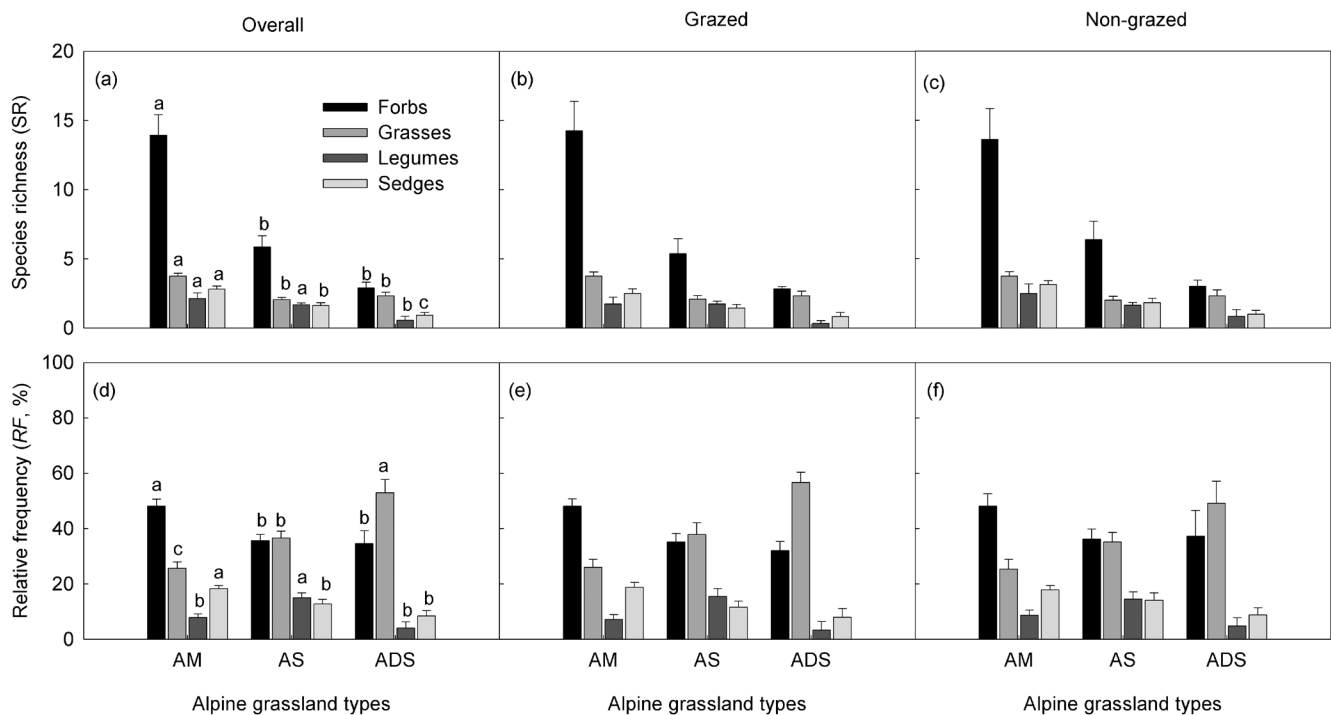


FIGURE 6. Means (\pm SE) of both species richness (SR) and relative frequency (RF) of the four plant functional groups (PGFs, forbs, grasses, legumes and sedges) across overall, grazed, and nongrazed sites subjected to the three zonal alpine grassland types: AM, alpine meadows; AS, alpine steppes; ADS, alpine desert-steppes. One-way ANOVA (S-N-K test), different letters over the bars indicated significantly different at $P < 0.05$.

TABLE 2

Spearman correlation analyses for the species richness (SR) and relative frequency (RF, %) of forbs, grasses, legumes, and sedges at the grazed and non-grazed sites within and across alpine grassland types (AGTs): AM, alpine meadows; AS, alpine steppes; ADS, alpine desert-steppes.

	AGTs	Correlations for SR			Correlations for RF		
		Grasses	Legumes	Sedges	Grasses	Legumes	Sedges
Grazed	Overall $n = 25$						
	Forbs	0.604**	0.380	0.608**	-0.677**	-0.256	-0.293
	Grasses		0.058	0.304		-0.356	-0.581**
	Legumes			0.327			-0.114
	AM, $n = 8$						
	Forbs	-0.299	0.379	0.266	-0.738*	-0.263	0.095
	Grasses		-0.066	-0.811*		0.132	-0.500
	Legumes			0.116			-0.659
	AS, $n = 11$						
	Forbs	0.206	0.196	0.332	-0.491	-0.427	0.145
	Grasses		0.030	0.000		-0.327	-0.527
	Legumes			0.033			-0.236
	ADS, $n = 6$						
	Forbs	0.707	0.316	0.566	-0.290	-0.270	-0.754
	Grasses		0.112	0.033		-0.600	-0.118
	Legumes			0.671			0.446
Non-grazed	Overall $n = 25$						
	Forbs	0.490*	0.378	0.649**	-0.807**	-0.222	0.132
	Grasses		0.115	0.470*		-0.134	-0.320
	Legumes			0.223			-0.296
	AM, $n = 8$						
	Forbs	-0.382	0.325	0.668	-0.810*	-0.333	-0.024
	Grasses		0.029	-0.765*		-0.028	0.071
	Legumes			-0.225			-0.786*
	AS, $n = 11$						
	Forbs	0.437	-0.036	0.156	-0.629*	-0.318	0.109
	Grasses		0.127	0.299		-0.273	0.137
	Legumes			-0.205			-0.673*
	ADS, $n = 6$						
	Forbs	-0.098	0.783	0.456	-0.943**	-0.091	-0.143
	Grasses		0.033	0.359		0.030	0.086
	Legumes			0.456			-0.030

* and **Correlation is significant at the 0.05 and 0.01 level, respectively.

a strongly productivity-dependent response, but they increased following grazing exclusion in less productive community and decreased in more productive ones. In our study, species richness or relative frequency appears to not be significantly changed by three to four years grazing exclusion compared to sites under grazing. The low productivity and the small size of plant individuals might contribute to the resistance of alpine grasslands in species assembly to the short-term grazing exclusion.

At a regional scale, both species richness and productivity of grasslands are primarily driven by environmental forces, such as temperature, precipitation, available nutrients, and moisture in soils. Wu et al. (2012) reported that species richness and diversity index aboveground productivity of Tibetan alpine grasslands were mainly controlled by growing season precipitation, while both Yang et al. (2010) and Hu et al. (2010) also found that aboveground productivity increased with increasing precipitation. In our results,

TABLE 3

Stepwise regression analyses of plant functional diversity (PFGs) with growing season temperature (GST), growing season precipitation (GSP), the active accumulated temperature over 5 °C (AccT), and their combination index (GSP/AccT). Partial correlation coefficient (partial R) and significance levels (P) of factors in the final regression models are shown.

PFGs	Species richness			Relative frequency		
	Factors	Partial R	P	Factors	Partial R	P
TSR	GSP	0.713	<0.001	AccT ^a	−0.437	0.002
				AccT ^b	−0.518	<0.001
Forbs	GSP	0.638	<0.001	Model ^{nv}		
Grasses	GSP	0.497	<0.001	GSP	−0.523	<0.001
Legumes	GSP	0.474	0.001	GST	−0.400	0.004
				GST; Acct	−0.408; 0.377	0.004; 0.008
Sedges	GSP	0.546	<0.001	GSP/Acct	0.401	0.004

Model^{nv}, no variable entered the final model. Superscripted a and b, the final models for the functional diversity: Simpson's D and Shannon's H, respectively.

species richness of different functional groups is well explained by growing season precipitation, while relative frequency responds to climate variables in discrete ways. Grasses can be well predicted by precipitation, while legumes only respond well to temperature. Forbs appear to not be related with climatic conditions, while sedges may be controlled by the combination of precipitation and temperature. Furthermore, species richness and relative frequency of legumes appear to be not related with other functional groups in both grazed and nongrazed pastures. In other words, short-term grazing exclusion couldn't change the associations of legumes with other different functional groups in this study. One reasonable explanation might be the legumes' functional traits, longer roots in more arid habitat. Moreover, no significant change in associations between different functional groups may also result from niche complementarity, species renew rate, and species pool size (Mokany et al., 2008; Bluthgen and Klein, 2011). The species pool of alpine grasslands on the Northern Tibetan Plateau is very poor, with species richness ranging from 3 to 36 (Wu et al., 2012). The poor species pool may limit species renew rate for short-term grazing exclusion. Therefore, in this study three to four years grazing exclusion appears to not result in significant compositional changes in plant functional group assembly compared with grazed pastures within and across alpine grassland types.

Climatic conditions play dominant roles in shaping species assembly of Tibetan alpine grasslands (Xu et al., 2010; Yu et al., 2010). Grazing exclusion indeed can impose certain assembly rules on alpine grassland communities; however, the underlying mechanism is still unclear. Probably due to the co-evolution mechanisms between local species pool, climate regimes, interspecies/group relationship, and historical grazing disturbance, plant assemblage composition may be difficult to reverse or significantly changed by short-term grazing exclusion in this region. Spatial variability of species composition is useful for detecting within-community changes in response to grazing management and such spatial variability in species composition can induce spatial organization of plant traits that may be important for community functioning (Diaz et al., 2007; Deleglise et al., 2011). Therefore, an effective management and conservation of these sensitive landscapes requires strategies based on better understanding of responses across species individuals, functional

groups, and alpine communities to environmental changes and social economic activities.

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