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Testing functional trait-based mechanisms underpinning plant responses to grazing and linkages to ecosystem functioning in grasslands

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Abstract

Abundant evidence has shown that grazing alters plant functional traits, ecological strategies, community structure, and ecosystem functioning of grasslands. Few studies, however, have examined how plant responses to grazing are mediated by resource availability and functional group identity. We test functional trait-based mechanisms underlying the responses of different life forms to grazing and linkages to ecosystem functioning along a soil moisture gradient in the Inner Mongolia grassland. A principal component analysis (PCA) based on 9 traits × 276 species matrix showed that the plant size spectrum (i.e., individual biomass), leaf economics spectrum (leaf N content and leaf density), and light competition spectrum (height and stem-leaf biomass ratio) distinguished plant species responses to grazing. The three life forms exhibited differential strategies as indicated by trait responses to grazing. The annuals and biennials adopted grazing-tolerant strategies associated with high growth rate, reflected by high leaf N content and specific leaf area. The perennial grasses exhibited grazing-tolerant strategies associated with great regrowth capacity and high palatability scores, whereas perennial forbs showed grazing-avoidant strategies with short stature and low palatability scores. In addition, the dominant perennial bunchgrasses exhibited mixed tolerance–resistance strategies to grazing and mixed acquisitive–conservative strategies in resource utilization. Grazing increased the relative abundance of perennial forbs with low palatability in the wet and fertile meadow, but it promoted perennial grasses with high palatability in the dry and infertile typical steppe. Our findings suggest that the effects of grazing on plant functional traits are dependent on both the abiotic (e.g., soil moisture) and biotic (e.g., plant functional group identity and composition) factors. Grazing-induced shifts in functional group composition are largely dependent on resource availability, particularly water availability.

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1 Introduction

Grazing by domestic herbivores is the most dominant land use practice that affects plant growth, community structure, and ecosystem functioning and services in grasslands (Milchunas and Lauenroth, 1993; Lemaire et al., 2000; Díaz et al., 2007). Functional trait-based approaches have recently emerged as a promising way to understand plant ecological strategies, plant-herbivore interactions, and their linkages to ecosystem functioning (Westoby, 1999; Adler et al., 2004; De Bello et al., 2005; Violle et al., 2007; Laliberte et al., 2012). Plant functional traits can provide important insights into the mechanisms underpinning plant responses to grazing. For example, height, plant size, and stem-leaf biomass ratio are associated with biomass allocation and species' capacity for light competition (Poorter and Nagel, 2000; Cornelissen et al., 2003), and also linked to plant avoidance strategies to grazing (Díaz et al., 2001; Adler et al., 2004). Leaf N content and specific leaf area (SLA) are tightly linked to plant leaf economic spectrum and potential growth rate (Reich et al., 1999; Wright et al., 2004), as well as plant tolerance strategies to grazing (Díaz et al., 2001; Zheng et al., 2011). Plant palatability is a multidimensional trait, which depends on physical (e.g., toughness, hairiness) and chemical (e.g., nutritive value) attributes (Elger and Willby, 2003) and reflects the evolution of plant defense to grazing. Grazing as a selective disturbance generally favors unpalatable over palatable plants (Díaz et al., 2007). Several studies, however, have suggested that plant species and trait responses to grazing are largely dependent on site productivity or resource availability (Pakeman, 2004; Díaz et al., 2007; Laliberte et al., 2012). Thus, a better understanding of the mechanisms underpinning plant responses to grazing mediated by resource availability and linkages to ecosystem functioning is fundamental to biodiversity conservation and sustainable ecosystem management.

The resource availability hypothesis suggests that resource availability (e.g., water and nutrients) is a major determinant of both the amount and type of plant anti-herbivore defense (Coley et al., 1985). Grazing selects species with avoidance strate-

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gies in dry and infertile (less-productive) systems and species with tolerance strategies in humid and fertile (productive) systems (Coley et al., 1985; Herms and Mattson, 1992). Moreover, plant species have developed two opposite resource use strategies (conservative vs. acquisitive) to improve their competitive abilities under environmental fluctuations (Díaz et al., 2004; Wright et al., 2004; Tecco et al., 2010). Species with resource conservative strategies usually show low SLA, low leaf N content, and long leaf life-span (Reich et al., 1999; Villar and Merino, 2001; Tecco et al., 2010). In contrast, species with resource acquisitive strategies generally have high SLA, high leaf N content, and short leaf life-span (Reich et al., 1999; Díaz et al., 2004; Tecco et al., 2010; Laliberte et al., 2012). The context-dependency hypothesis proposes that plant responses to grazing are not only determined by site productivity or resource heterogeneity (Pérez-Harguindeguy et al., 2003; Daleo and Iribarne, 2009; Eldridge et al., 2013), but also by the biotic factors (e.g., plant species or functional group identity) (Wardle et al., 2008; McLaren and Turkington, 2010). Although extensive studies investigated plant responses to grazing mediated by resource availability (e.g., soil moisture and nutrients) (Adler et al., 2004; Pakeman, 2004; Díaz et al., 2007; Laliberte et al., 2012), few studies, however, have examined the context-dependent effects of the abiotic and biotic factors on plant responses to grazing.

It is increasingly clear that understanding the ecological context and complexity of trait-mediated species interactions can provide new insights into the mechanisms governing plant responses to grazing (Carmona and Fornoni, 2013; Turley et al., 2013). For example, Carmona and Fornoni (2013) found that the complexity of herbivore communities selects for mixed resistance–tolerance strategies of plants, which is contrary to a long-standing prediction that resistance and tolerance are functionally redundant (Vandermeijden et al., 1988). Selective pressures imposed by herbivores (Carmona and Fornoni, 2013), resource availability in the environment (Coley et al., 1985), and trade-offs in allocation to growth and defense (Herms and Mattson, 1992) may all constrain or promote selection on resistance or tolerance, and hence cause evolution of mixed defensive strategies. However, the adaptive evolution of mixed strategies of plant

defense against herbivory remains largely unexplored (Núñez-Farfán et al., 2007; Turley et al., 2013).

The arid and semiarid grasslands on the Mongolia plateau, which include diverse community types and distribute widely across the Eurasian Steppe region, have been historically subjected to continuous grazing by livestock with high stocking rates, leading to widespread degradation in ecosystem function and services (White et al., 2000; Bai et al., 2012). In the Inner Mongolia grassland, plant growth and primary productivity are co-limited by water and N availability (Bai et al., 2008), thus grazing impacts on functional traits and ecosystem functioning are likely mediated by resource availability. In this study, we examined the effects of grazing on plant functional traits and ecosystem functioning across three vegetation types (i.e., meadow, meadow steppe, and typical steppe) along a soil moisture gradient in the Xilin River Basin of Inner Mongolia grassland. Specifically, we address the following questions: first, how do plant functional traits across a broad range of species respond to grazing? Second, how do plant responses to grazing are affected by soil moisture and plant functional group identity across six grassland communities? Third, what are the major mechanisms controlling the responses of life forms to grazing in dry and moist communities and linkage to ecosystem functioning (i.e., shifts in functional group composition and community-weighted attributes)?

To explore the underlying mechanisms of different life-form species plant responses to grazing in the semiarid Inner Mongolia grasslands, we hypothesize that the effects of grazing on plant functional traits are dependent on both the abiotic (e.g., soil moisture) and biotic (e.g., plant functional group identity and composition) factors, and life-history strategy reflects a long evolutionary adaptation of plant species to environment. Therefore, we would expect that: (1) annuals and biennials may exhibit grazing-tolerant strategies (e.g., high leaf N content and SLA), while perennial forbs exhibit grazing-avoidant strategies (e.g., short stature, low N content and low palatability scores). Perennial grasses with high regrowth rate and high palatability would also exhibit grazing-tolerant strategies although both leaf N content and SLA are low. (2)

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Grazing may increase the relative abundance of perennial forbs with low palatability in the wet and fertile meadow, but it may promote perennial grasses with high palatability in the dry and infertile typical steppe.

2 Methods

2.1 Study area

The Xilin River Basin (43°26′–44°29′ N, 115°32′–117°12′ E) is located in the typical steppe zone of the Inner Mongolia Plateau, which covers an area of 10 786 km² and ranges in elevation from 983 to 1469 m. The Xilin River Basin is semi-arid continental temperate steppe, with mean annual temperature of 0.4 °C and mean annual precipitation of 336.9 mm yr⁻¹. Annual precipitation decreases gradually from 400 mm in the south-east to 250 mm in the north-west, and more than 80 % of precipitation occurs in the growing season (May–August). Chestnut and dark chestnut soils are the zonal soil types in this region (Bai et al., 2000). In this study, six pairs of parallel grazed and ungrazed plant communities, i.e., *Carex appendiculata* meadow, *Stipa baicalensis* meadow steppe, *Leymus chinensis* typical steppe, *S. grandis* typical steppe, *Caragana microphylla* typical steppe, and *Artemisia frigida* typical steppe were selected along a soil moisture gradient in the Xilin River Basin (Table 1). These communities are subjected to similar climatic conditions, such as temperature and precipitation, but differ in terms of floristic composition and soil properties, particularly soil moisture and nutrients (Zheng et al., 2010). The *Carex appendiculata* meadow has the highest field holding capacity and soil nutrients (i.e., soil organic matter and total nitrogen), followed by the *Stipa baicalensis* meadow steppe, and the four typical steppe communities have lower field holding capacity and soil nutrients (Table 1). The ungrazed sites of communities are the permanent field sites of the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), Chinese Academy of Sciences (Bai et al., 2004), which have been fenced from grazing for about 20–30 years (Table 1). In contrast, the grazed sites, lo-

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cated outside the fence of ungrazed sites, have been managed as free grazing pasture (mainly by sheep) since 1950s, thus they have about 60 years of grazing history (Zheng et al., 2010).

2.2 Vegetation and soil properties

5 A survey on vegetation composition of the six plant communities were conducted from 28 July to 14 August 2007, corresponding to annual peak biomass of this area by IMGERS (Bai et al., 2004). At each site, 5–10 quadrats (1 m × 1 m each) were located randomly within an area of 100 m × 100 m. Ten quadrats were used for meadow steppe and typical steppe, and 5 quadrats were for the more homogeneous meadow commu-
10 nity. For the grazed sites, these quadrats were randomly located in the areas that were not subjected to grazing during the current growing season. Within each quadrat, all living biomass and current-year dead materials were harvested, separated to species, and oven dried at 70 °C for 24 h to constant mass and weighed. Litter biomass within
15 each quadrat was collected. The number of individuals and aboveground biomass of each species were measured to estimate species abundance and community standing biomass.

Soil samples within each quadrat were collected by taking three 5 cm diameter soil cores from 0–20 cm depths, mixed in situ as one composite sample, and air-dried for soil nutrient analyses. Soil organic matter was analyzed using $K_2Cr_2O_7-H_2SO_4$ ox-
20 idation method, and total nitrogen was determined using the Kjeldahl acid-digestion method with an Alpkem autoanalyzer (Kjektec System 1026 Distilling Unit, Sweden). The field holding capacity of 0–20 cm soil layer was determined using the pressure chamber method (Sparks et al., 1996)

2.3 Plant functional traits

25 After vegetation survey, plant samples of dominant and common species were collected at each site for functional trait measurements. In this study, 149 plant species

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at ungrazed and 127 species at grazed sites (including 106 different species, 76 genera and 30 families) were collected across three vegetation types. All species were classified into plant functional groups based on their life forms, including perennial grasses (PG), perennial forbs (PF), annuals and biennials (AB), and shrubs and semi-shrubs (SS). For each ungrazed or grazed site, 10–20 fully grown individuals of each species were randomly selected. Nine plant functional traits, i.e., plant height, individual biomass, stem biomass, leaf biomass, stem-leaf biomass ratio, total leaf area and leaf density per individual, specific leaf area (SLA), and mass-based leaf N content (LNC) were determined. Plant height (PH) was measured by the distance from the basal stem to the natural crown of each individual. After the height measurement, aboveground part of each individual was collected and taken back to the laboratory for stem and leaf separation. All leaves of an individual were picked to determine the projected leaf area with a portable leaf area meter (Li-3100C, Li-Cor, Lincoln, NE, USA), and the number of leaves were recorded isochronously. Then the stem and leaf samples were oven-dried at 70 °C for 24 h to constant masses and weighted. Hence, individual leaf area, dry mass per leaf, stem biomass (SB), leaf biomass (LB), plant individual biomass (PB), total leaf area (TLA) and leaf density (LD) per individual could be calculated, and specific leaf area (SLA, $\text{cm}^2 \text{g}^{-1}$) and stem-leaf ratio (SLR) were separately calculated as the ratio of leaf area to dry mass, and ratio of stem biomass to leaf biomass. Leaf samples were ground to homogeneity with a ball mill (MM 2000, Retsch GmbH & Co, Haan, Germany) for N content analysis.

The community-weighted attributes for plant height ($\text{height}_{\text{CWM}}$), stem-leaf ratio (SLR_{CWM}), specific leaf area (SLA_{CWM}), and leaf N content (LNC_{CWM}) were computed as trait means weighted by the relative biomass of each species within the quadrat (Violle et al., 2007).

The palatability score of each plant species was calculated based on the following formula:

$$\text{Palatability score} = \text{PPI} \times \text{BSI}$$

where PPI is plant palatability index, which is calculated at the species level based on forage plants handbooks (Fu, 1990), consisting of five grades (0, 0.25, 0.5, 0.75, 1); BSI is browsing season index, which is defined based the number of seasons of sheep browsing in a year, i.e., BSI = 0.25 for one season, 0.5 for two seasons, 0.75 for three seasons, and 1 for four seasons (Fu, 1990).

2.4 Statistical analysis

Statistical analyses were performed with the software SAS version 9.2 (SAS Institute Inc., Cary, NC, USA) and Multi-variate Statistical Package (MVSP, Kovach Computing Services, Anglesey, UK). To detect general trends in 9 functional traits of 276 plant species in the Inner Mongolia grassland, we first organized the dataset into a single 9 traits (variables) \times 276 species (cases) matrix, on which we carried out a principal component analysis (PCA) based on the correlation matrix of variables (Jongman et al., 1987; Tecco et al., 2010). The effects of grazing (G), field hold capacity (F), and their interactions ($G \times F$) on five functional traits (i.e., PH, PB, SLR, SLA, and leaf N content) were tested with the general linear model (GLM). Using regression analysis, we analyzed the relationships between the responses of these functional traits to grazing and the field holding capacity for all species and each of life forms across six grassland communities. The response ratios of plant height (PH), plant individual biomass (PB), stem-leaf biomass ratio (SLR), specific leaf area (SLA), and leaf N content (LNC) were separately calculated as the ratio of mean values in the grazed to ungrazed communities (i.e., $PB_{\text{grazed}}/PB_{\text{ungrazed}}$, $SLA_{\text{grazed}}/SLA_{\text{ungrazed}}$). The effects of grazing on the relative aboveground biomass of different life forms, the community-weighted attributes (height_{CWM}, SLR_{CWM}, SLA_{CWM}, LNC_{CWM}), and SLA of four dominant perennial grasses were examined using independent-samples T test at $P < 0.05$. ANOVA and LSD tests were performed to test differences in plant functional traits among different life forms. The shrubs and semi-shrubs (SS) were excluded from analyses due to small sampling size (< 5 species).

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3 Results

3.1 Associations among species traits

Associations amongst the 9 functional traits of 276 plant species were analyzed with a PCA (Fig. 1, Table A1 in the Appendix A in Supplement), and the first three principal components together accounted for 76 % of the variance. The first principal component (PC1) explained 43 % of the total variance and represented an axis of plant size, reflecting by plant individual biomass, stem biomass, leaf biomass, and total leaf area (Fig. 1a, Table A1 in the Appendix A in Supplement). The second principal component (PC2) was strongly associated with plant height, stem-leaf biomass ratio (SLR), and specific leaf area (SLA), accounting for 19 % of the total variance (Table A1 in the Appendix A in Supplement). Species found at the positive end of this axis were tall plants with high SLA and more biomass allocation to supportive stem than leaf tissues (high SLR), corresponding to high capacity for aboveground/light competition. The third principal component (PC3), which explained an additional 14 % of the variance, was primarily driven by leaf N content and leaf density, representing an axis of nutrient acquisition and turnover consistent with the leaf economics spectrum (Fig. 1a, Table A1 in the Appendix A in Supplement). The main trend of trait variation was between fast (high leaf N content and leaf density) and slow shoot growth (low leaf N content and leaf density) (Fig. 1b).

The three principal component axes distinctly separated species from the grazed and ungrazed communities (Fig. 1c). Grazing significantly decreased the loading score of plant size along PC1 axis ($P = 0.0163$), and slightly decreased PC2 score of plant height and SLR ($P = 0.1011$), but greatly increased PC3 score of leaf N content and leaf density ($P = 0.0016$).

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3.2 Effects of grazing on plant functional traits across six communities

According to PCA analyses, five key functional traits, including plant height (PH), plant individual biomass (PB), stem-leaf biomass ratio (SLR), specific leaf area (SLA), and leaf N content (LNC) were further selected to study their responses to grazing along a soil moisture gradient across six grassland communities. The general linear model (GLM) analyses using grazing (G), field hold capacity (F , an indicator of soil moisture) and their interactions ($G \times F$) as fixed effects, showed that plant height and individual biomass were significantly affected by grazing (G), and SLR, SLA and leaf N content were greatly affected by the field hold capacity (F), while the interaction of $G \times F$ was only significant for plant height and leaf N content (Table A2 in the Appendix A in Supplement).

The response ratio of plant height ($PH_{\text{grazed}}/PH_{\text{ungrazed}}$) to grazing decreased greatly, while the response ratios of leaf N content and SLA increased with increasing field holding capacity across the six communities (Fig. 2). Grazing diminished plant height but enhanced leaf N content and SLA for most species, however, plant individual biomass and SLR showed weak responses to grazing along the soil moisture gradient. For the three life forms, plant height response ratio of annuals and biennials (AB) and perennial forbs (PF) decreased, while SLR response ratio of perennial grasses (PG) increased along the field holding capacity gradient (Fig. 3). Moreover, SLA of AB and PG, and leaf N content of three life-form species were also greatly enhanced by grazing across the six communities.

Multi-trait comparisons showed that the five plant functional traits, including plant height, SLR, SLA, leaf N content, and palatability scores differed significantly among three life forms at the ungrazed sites (Table A3 in the Appendix A in Supplement). Comparatively, annuals and biennials showed higher plant height, SLR, leaf N content and SLA, but lower palatability scores. The perennial grasses exhibited greater plant height, SLR and higher palatability scores, but lower leaf N content and SLA. The

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perennial forbs, however, showed lower plant height, SLR and leaf N content and lower palatability scores.

3.3 SLA responses of perennial grasses

The SLA of *Leymus chinensis* (a dominant perennial rhizomatous grass) was decreased by grazing in all four typical steppe communities and *Stipa baicalensis* meadow steppe (Fig. 4). For three dominant perennial bunchgrasses, i.e., *S. baicalensis*, *Agropyron cristatum* and *Cleistogenes squarrosa*, however, grazing increased their SLA values in the relatively moist *S. baicalensis* meadow steppe but decreased them in the driest *S. grandis* and *Artemisia frigida* typical steppe communities.

3.4 Shifts in plant functional group composition

The effects of grazing on plant functional group composition differed across different vegetation types. In the *Carex appendiculata* meadow, the relative biomass of perennial forbs (PF) was increased by 97%, while that of perennial grasses (PG) was decreased by 65% (Fig. 5a). In the *S. baicalensis* meadow steppe, however, grazing decreased perennial forbs by 33%, but it increased perennial grasses by 35%. In the typical steppe, grazing increased perennial grasses by 21–53% in three of the four communities, but it decreased perennial forbs by 46–48% in two communities. The relative biomass of annuals and biennials (AB) and shrubs and semi-shrubs (SS), in contrast, remained unchanged in five of the six communities. In general, grazing increased perennial grasses, but had no significant effects on three other life-forms in the Xilin River Basin.

3.5 Grazing effects on community-weighted attributes

The effects of grazing on the community-weighted attributes differed substantially across the three vegetation types. Grazing increased the community-weighted specific leaf area (SLA_{CWM}) and leaf N content (LNC_{CWM}), decreased plant height (height_{CWM}),

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and had no effect on stem-leaf ratio (SLR_{CWM}) in the *C. appendiculata* meadow (Fig. 6). In the *S. baicalensis* meadow steppe, however, grazing increased $height_{CWM}$ and SLR_{CWM} , slightly decreased SLA_{CWM} , and had no effect on leaf LNC_{CWM} . In the typical steppe, grazing greatly diminished SLA_{CWM} in all four communities, reduced LNC_{CWM} in three of the four communities, and decreased $height_{CWM}$ and SLR_{CWM} in two of the four communities.

4 Discussion

4.1 Plant strategy axes distinguish plant species responses to grazing

Our results demonstrated that three functional trait-based spectrums, i.e., individual biomass associated with plant size (PC1 axis), height, stem-leaf biomass ratio (SLR) and specific leaf area (SLA) linked to biomass allocation and light competitive capacity (PC2 axis), and leaf N content and leaf density related to leaf economics spectrum and shoot growth (PC3 axis), distinctly separated species from the grazed and ungrazed plant communities. Plant species generally showed more grazing tolerant, reflected by fast shoot regrowth (e.g., increased leaf N content and leaf density) through reducing aboveground/light competition (e.g., decreased height and SLR) and individual miniaturization (e.g., decreased plant size) (Strauss and Agrawal, 1999; Cingolani et al., 2005). These results are corroborated by previous studies (Pakeman, 2004; Díaz et al., 2007; Evju et al., 2009) and our recent studies (Zheng et al., 2011). This suggests that plant species adopt both tolerance strategies to improve regrowth capacity after defoliation and avoidance strategies to decrease herbivore selectivity. The variations in functional traits indicate the fundamental trade-offs between productivity and persistence in plant functioning (Warren and Adams, 2000; He et al., 2009), and further reflect the contrasting species-specific tolerance and defense strategies to grazing (Grime, 2001; Lind et al., 2013).

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4.2 Context-dependency of grazing effects by abiotic and biotic factors

Our results suggest that the effects of grazing on plant functional traits are mediated by soil moisture, indicated by the significant interactions of grazing and field holding capacity on plant height and leaf N content. Generally plant height was decreased, but leaf N content and SLA were increased by grazing for most species across six communities along the soil moisture gradient, indicating that plant species exhibit both avoidance and tolerance strategies to grazing (Díaz et al., 2001; Adler et al., 2004; Zheng et al., 2011). In addition, plant height and individual biomass were mainly affected by grazing, while SLR, SLA and leaf N content varied substantially across six communities due to the difference in soil moisture. Our study also demonstrated that grazing effects on plant functional traits at the community level are dependent on plant functional group identity and composition. This is supported by the evidence that the decrement in plant height was attributable to the negative responses of annuals and biennials (AB) and perennial forbs (PF) to grazing, while the increments in leaf N content and SLA were due to the positive responses of all three life forms (except PF for SLA). Compared to the annuals and biennials (20 species), perennial forbs had greater effect on the change in plant height due to their larger sampling size (90 species). Grazing had little effect on SLR across all communities was mainly arisen from the weak responses of annuals and biennials and perennial forbs. These findings support our original hypothesis that the effects of grazing on plant functional traits are dependent on both the abiotic (e.g., soil moisture) (Adler et al., 2004; Pakeman, 2004) and biotic (e.g., plant functional group identity and composition) factors (Wardle et al., 2008)

4.3 Mechanisms underpinning differential strategies of life forms

Our results suggest that the three life forms exhibited differential strategies as indicated by trait responses to grazing. Several mechanisms are likely to be responsible for the observed patterns. First, the annuals and biennials with high growth rate adopted more tolerant strategies to grazing as reflected by the increased leaf N content and SLA.

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Moreover, the annual and biennial species are mostly opportunistic or early successional species, which have short life-history, great aboveground/light competitive ability (e.g., high plant height and SLR), high growth potential (e.g., high leaf N and SLA), and high recruitment capacity (e.g., small seed and high reproductive output) (Westoby, 1998; Zheng et al., 2012). These species with low palatability scores may have the competitive advantage in rapid resource capture when other life-form species were depressed by grazing (Soriano and Sala, 1984; Westoby, 1999). Therefore, annuals and biennials show more tolerance to herbivores, especially in humid systems or wet years. Second, the perennial grasses exhibited greater grazing tolerance but due to rapid regrowth capacity, indicated by the increased SLR, SLA and leaf N content, and high palatability scores. In this study, most perennial bunchgrasses in the Inner Mongolia grassland are xerophytes, which have long life-history, low growth potential (e.g., low leaf N and SLA), and great aboveground (e.g., high plant height and SLR) and belowground competitive abilities (e.g., high root: shoot ratio and root N content) (Zheng et al., 2012). Hence, these species have developed more conservative resource-use strategies and show strong drought tolerance in the long-term process of evolutionary adaptation. In addition, most perennial grasses are reproduced by germination of dormant buds and can develop new tillers rapidly. Thus, these species show rapid regrowth capacity and more tolerance to grazing, especially in dry and infertile systems (Strauss and Agrawal, 1999; Adler et al., 2004). Third, the perennial forbs, however, adopted more avoidance strategies to grazing. Generally, these species have long life-span, short stature and low SLR, and low growth capacity (e.g., low leaf N) and low palatability scores, and some of these species have evolved chemical (e.g., secondary metabolites with odor and toxins) or physical defense (e.g., thorns, spines and hairiness) to decrease herbivore selectivity (Milchunas and Noy-Meir, 2002). In addition, these species are dicotyledon with axial roots and seed reproduction and thereby exhibit relatively slow recruitment rate, leading to a moderate response to grazing. These findings support our original hypothesis that life-history strategy reflects a long evo-

lutionary adaptation of plant species to environment, and are consistent with our first prediction.

Our study demonstrated that the dominant perennial bunchgrasses, such as *Stipa baicalensis*, *S. grandis*, *Agropyron cristatum*, and *Cleistogenes squarrosa* in the Inner Mongolia grassland exhibited mixed tolerance–resistance strategies to grazing and mixed resource acquisitive–conservative strategies to precipitation fluctuations. This is supported by the evidence that grazing increased SLA of these species in the relatively moist meadow steppe, but it decreased their SLA values in the driest typical steppe communities. It is known that SLA is a relatively stable functional trait, and has been widely recognized to be positively linked to potential growth rate (Reich et al., 1999; Wright et al., 2004), resource acquisitive strategies (Díaz et al., 2004; Tecco et al., 2010), and plant tolerance to grazing (Díaz et al., 2001; Zheng et al., 2011); while high leaf mass per area (LMA, inverse of SLA) is tightly related to physical toughness (Villar and Merino, 2001; Wright et al., 2004), resource conservative strategies (Díaz et al., 2004; Tecco et al., 2010), and plant resistance to grazing (Hanley et al., 2007). Our results suggest that the dominant perennial bunchgrasses select resource acquisitive and grazing-tolerance strategies in the wet and fertile habitats, but resource conservative and grazing-resistance strategies in the dry and infertile habitats. In contrast, the dominant perennial rhizomatous grass, *Leymus chinensis*, did not show mixed strategies of resource-use and herbivore-defense as indicated by decreased SLA values in all five grassland communities. These findings were partly in line with a recent study that natural selection by herbivores favors the evolution of mixed defensive strategies in plants (Carmona and Fornoni, 2013). Our results showed that grazing widely increased perennial bunchgrasses in the Inner Mongolia, implying that the selective pressure imposed by long-term grazing and fluctuations in water availability may together promote the mixed strategies of plant anti-herbivore defense (tolerance–resistance) and resource utilization (acquisitive–conservative) in the arid and semiarid grasslands.

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4.4 Water-mediated grazing effects on ecosystem functioning

Our findings indicate that the grazing-induced shifts in functional group composition are largely dependent on site productivity, particularly water availability. In the wet and fertile meadow, grazing caused a shift in dominance from perennial grasses to perennial forbs, however, grazing promoted perennial grasses but diminished perennial forbs in the dry and infertile typical steppe. This is because, in the meadow, perennial forbs with low palatability showed more avoidance strategies to grazing, which allow them to achieve rapid growth and become more dominant in moist and fertile habitats (Díaz et al., 2004; Tecco et al., 2010; Laliberte et al., 2012). In the typical steppe, however, perennial grasses with high palatability exhibited more grazing-tolerance strategies and conservative resource-use strategies associated with low growth rate, which allow them to be more dominant in dry and infertile habitats (Villar and Merino, 2001; Tecco et al., 2010). Therefore, grazing enhanced the community-weighted specific leaf area (SLA_{CWM}) and leaf N content (LNC_{CWM}) in the meadow, but it diminished SLA_{CWM} , LNC_{CWM} , $height_{CWM}$, and SLR_{CWM} in most communities of the typical steppe. In the meadow steppe with moderate soil water and nutrient availability, perennial forbs were replaced by perennial grasses, and the effects of grazing on community-weighted attributes were intermediate between the meadow and typical steppe. These findings are consistent with our second prediction. Given that plant growth is extremely limited by water availability in the Inner Mongolia grassland (Bai et al., 2008), and the six plant communities had hundreds and thousands years of grazing history, the dominance of perennial grasses with high palatability may be attributable to their long-term evolutionary adaptation to dry environment and co-evolution with herbivores, particularly in the dry typical steppe.

4.5 Implications for ecosystem functioning under global change

Our findings have important implications for understanding ecosystem structure and functioning and managing arid and semiarid grasslands. First, future climate change

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is likely to produce more frequent extreme precipitation and drought events (Easterling et al., 2000; Maestre et al., 2012), which may have profound impacts on shifts in species dominance in the Inner Mongolia grassland. The dominance of perennial forbs with low palatability is likely to increase in wet years because their grazing-avoidance strategies. In dry years, however, perennial grasses with high palatability may become predominant because of their conservative resource-use and grazing-tolerant strategies. Second, the increase in prolonged droughts together with heavy grazing may accelerate the shifts in dominance from perennial rhizomatous grasses to perennial bunchgrasses in the typical steppe, and consequently decrease biodiversity and ecosystem functioning and services. In the long run, the dominance of perennial bunchgrasses in the Inner Mongolia grassland may be greatly promoted under climatic change due to their mixed strategies of defense and resource utilization, and evolutionary adaptation to dry environments and co-evolution with herbivores (de Mazancourt and Loreau, 2000; Turley et al., 2013). Third, it seems clear that destocking rate is an important management tool for restoring the vast degraded grasslands and mitigating the impacts of shifts in plant functional group composition and alterations in ecosystem functioning in the Inner Mongolia grassland and beyond.

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Author contribution. Y. F. Bai and S. X. Zheng conceived and designed the experiments. S. X. Zheng, H. Y. Ren, W. H. Li, Z. C. Lan and K. B. Wang performed the experiments. S. X. Zheng prepared the manuscript with contributions from all co-authors.

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Table 1. Geographical and soil properties of six grassland communities in the Xilin River Basin of Inner Mongolia, China.

No.	Community type	Vegetation type	Location	Altitude (m)	Field holding capacity (%)	Soil organic matter (g kg ⁻¹)	Soil total nitrogen (g kg ⁻¹)	Land use type
1	<i>Carex appendiculata</i>	Meadow	43°38' N, 116°41' E	1150	51.75	121.20	5.25	Ungrazed site (fenced since 1989)
2	<i>Stipa baicalensis</i>	Meadow steppe	43°27' N, 116°47' E	1380	34.63	32.41	1.87	Ungrazed site (fenced since 1979)
3	<i>Leymus chinensis</i>	Typical steppe	43°33' N, 116°41' E	1250	31.80	28.45	1.58	Ungrazed site (fenced since 1979)
4	<i>S. grandis</i>	Typical steppe	43°33' N, 116°33' E	1180	29.75	28.45	1.71	Ungrazed site (fenced since 1979)
5	<i>Caragana microphylla</i>	Typical steppe	43°36' N, 116°44' E	1190	22.95	21.21	1.19	Ungrazed site (fenced since 1983)
6	<i>Artemisia frigida</i>	Typical steppe	43°38' N, 116°41' E	1200	22.60	13.10	0.71	Ungrazed site (fenced since 1989)

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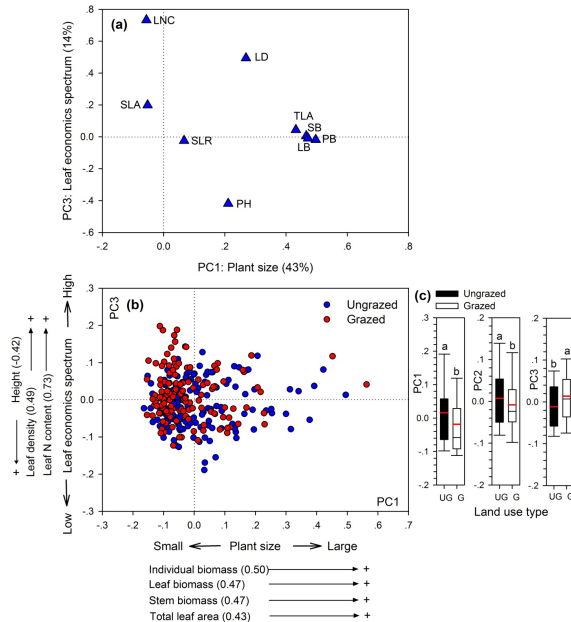


Figure 1. PCA biplot of 276 plant species based on the variance in 9 functional traits explained by the first (PC1) and third (PC3) principal axes. **(a)** Loading plot of traits. **(b)** PCA ordination of 149 plant species (blue circles) from the ungrazed and 127 species (red circles) from the grazed communities. Labels display traits with the highest eigenvector scores on PC1 and PC3 axes, with the brackets showing the corresponding scores. **(c)** Box plots illustrate the score distribution of plant species from ungrazed (UG, in black, $n = 149$) and grazed (G, in white, $n = 127$) communities along the three principal axes. Abbreviations: PH, plant height; PB, plant individual biomass; SLR, stem-leaf biomass ratio; SB, stem biomass; LB, leaf biomass; TLA, total leaf area; LD, leaf density; SLA, specific leaf area; LNC, mass-based leaf N content. Significant differences between the grazed and ungrazed communities along PC1 ($P = 0.0163$), PC2 ($P = 0.1011$) and PC3 ($P = 0.0016$) axes are indicated by different letters. Box plots show the interquartile range, median (black thin line), and mean (red thick line).

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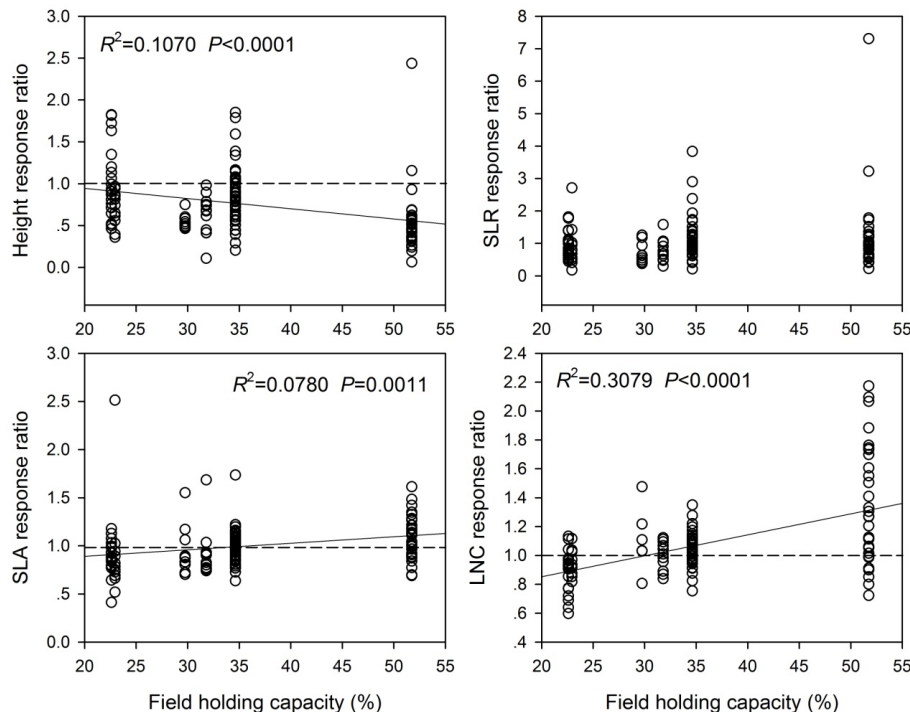


Figure 2. Relationships between the responses of plant functional traits to grazing and field holding capacity across six grassland communities. The response ratio of each trait was calculated as the ratio of mean values in the grazed to ungrazed communities (i.e., $SLA_{\text{grazed}}/SLA_{\text{ungrazed}}$). The reference line (dashed line) in each panel indicates no change in response ratio of trait. Abbreviations: SLR, stem-leaf biomass ratio; SLA, specific leaf area; LNC, leaf N content.

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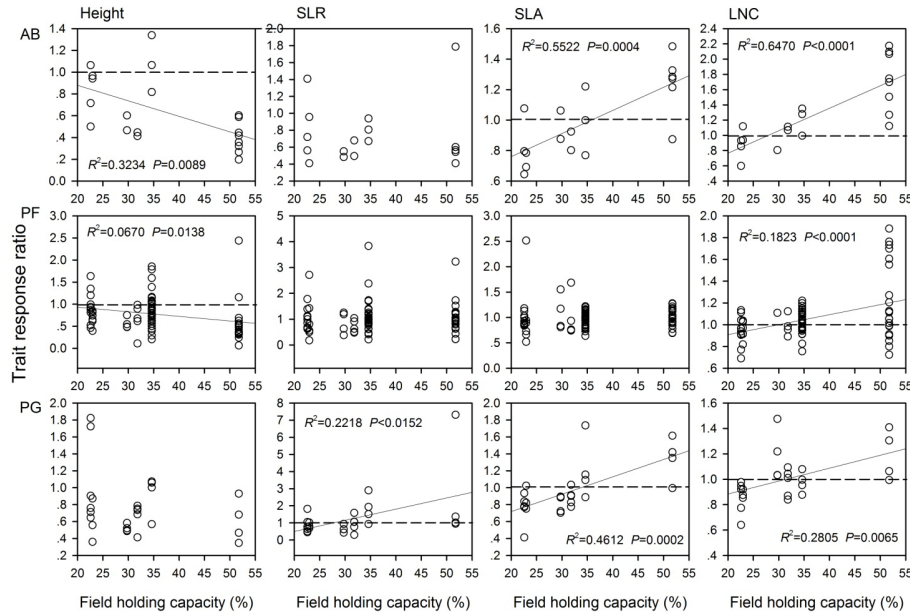


Figure 3. Relationships between the responses of plant functional traits to grazing and field holding capacity for three life forms. The reference line (dashed line) in each panel indicates no change in response ratio of trait. Abbreviations: AB, annuals and biennials; PF, perennial forbs; PG, perennial grasses; SLR, stem-leaf biomass ratio; SLA, specific leaf area; LNC, leaf N content.

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Functional mechanisms of plant responses to grazing

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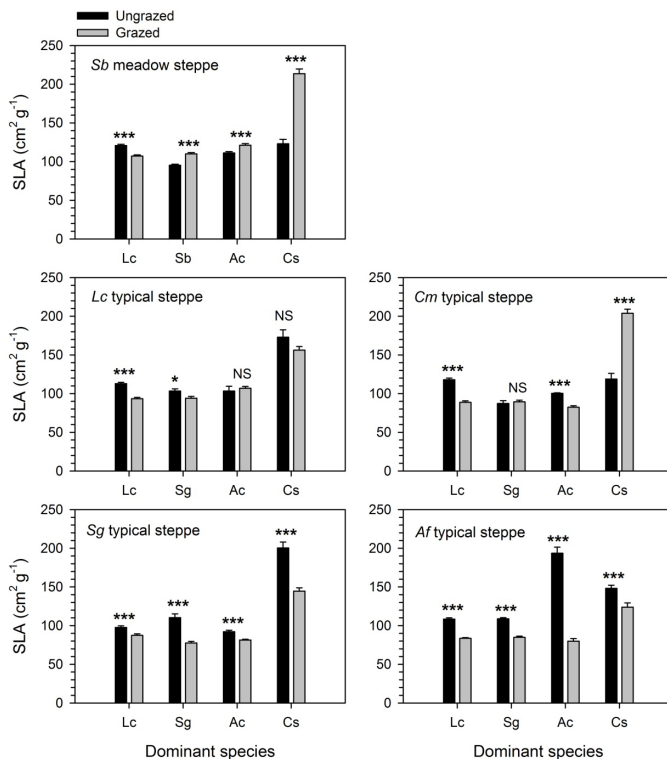


Figure 4. Effects of grazing on specific leaf area (SLA) of four dominant species in *Stipa baicalensis* meadow steppe and four typical steppe communities. Abbreviations: Lc, *Leymus chinensis*; Sb, *Stipa baicalensis*; Sg, *S. grandis*; Ac, *Agropyron cristatum*; Cs, *Cleistogenes squarrosa*; Cm, *Caragana microphylla*; Af, *Artemisia frigida*. Significant differences between the grazed and ungrazed communities are reported from ANOVA as NS, $P > 0.1$; *, $P < 0.05$; ***, $P < 0.001$. The error bars denote SE ($n = 30$).

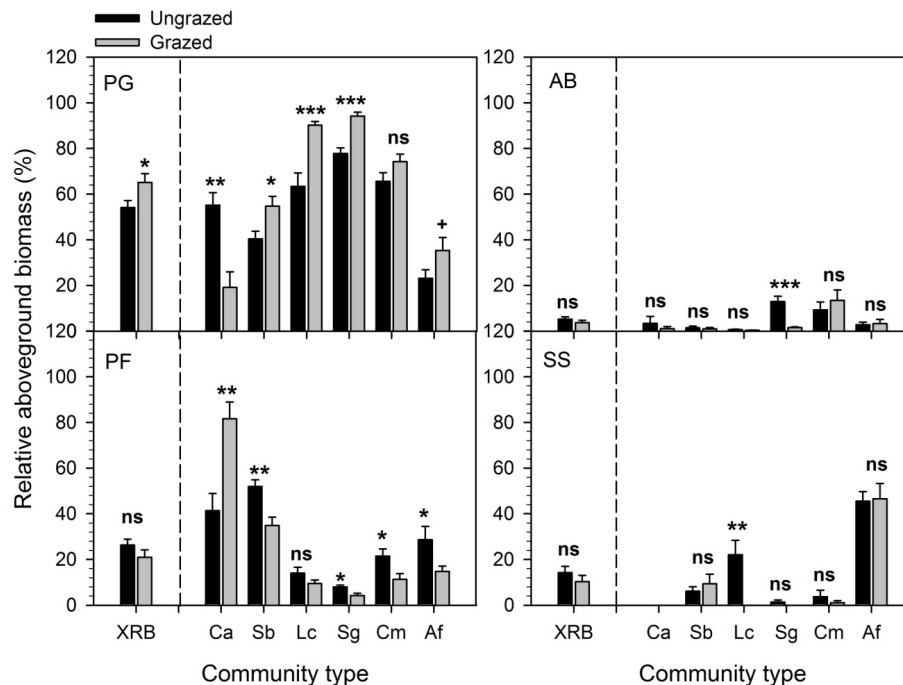


Figure 5. Effects of grazing on plant functional group composition in six grassland communities (error bars denote SE). Abbreviations: PG, perennial grasses; PF, perennial forbs; AB, annuals and biennials; SS, shrubs and semi-shrubs; Ca, *Carex appendiculata* meadow; Sb, *Stipa baicalensis* meadow steppe; Lc, *Leymus chinensis* typical steppe; Sg, *S. grandis* typical steppe; Cm, *Caragana microphylla* typical steppe; Af, *Artemisia frigida* typical steppe; and XRB, Xilin River Basin. Significant differences between the grazed and ungrazed communities are reported from ANOVA as ns, $P > 0.1$; +, $0.05 < P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

