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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

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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-
5 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
10 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-
15 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, $cm^2 g^{-1}$) 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
20 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 ($height_{CWM}$), 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
25 (Violle et al., 2007).

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

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

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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 ($height_{\text{CWM}}$),

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

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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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References

- Adler, P. B., Milchunas, D. G., Lauenroth, W. K., Sala, O. E., and Burke, I. C.: Functional traits of graminoids in semi-arid steppes: a test of grazing histories, *J. Appl. Ecol.*, 41, 653–663, 2004.
- 5 Bai, Y. F., Li, L. H., Wang, Q. B., Zhang, L. X., Zhang, Y., and Chen, Z. Z.: Changes in plant species diversity and productivity along gradients of precipitation and elevation in the Xilin River Basin, Inner Mongolia, *Acta Phytoecol. Sin.*, 24, 667–673, 2000.
- Bai, Y. F., Han, X. G., Wu, J. G., Chen, Z. Z., and Li, L. H.: Ecosystem stability and compensatory effects in the Inner Mongolia grassland, *Nature*, 431, 181–184, doi:10.1038/nature02850, 2004.
- 10 Bai, Y. F., Wu, J. G., Xing, Q., Pan, Q. M., Huang, J. H., Yang, D. L., and Han, X. G.: Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau, *Ecology*, 89, 2140–2153, 2008.
- Bai, Y. F., Wu, J. G., Clark, C. M., Pan, Q. M., Zhang, L. X., Chen, S. P., Wang, Q. B., and Han, X. G.: Grazing alters ecosystem functioning and C:N:P stoichiometry of grasslands along a regional precipitation gradient, *J. Appl. Ecol.*, 49, 1204–1215, doi:10.1111/j.1365-2664.2012.02205.x, 2012.
- 15 Carmona, D. and Fornoni, J.: Herbivores can select for mixed defensive strategies in plants, *New Phytol.*, 197, 576–585, doi:10.1111/nph.12023, 2013.
- Cingolani, A. M., Posse, G., and Collantes, M. B.: Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands, *J. Appl. Ecol.*, 42, 50–59, doi:10.1111/j.1365-2664.2004.00978.x, 2005.
- 20 Coley, P. D., Bryant, J. P., and Chapin, F. S.: Resource availability and plant anti-herbivore defense, *Science*, 230, 895–899, doi:10.1126/science.230.4728.895, 1985.
- Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., ter Steege, H., Morgan, H. D., van der Heijden, M. G. A., Pausas, J. G., and Poorter, H.: A handbook of protocols for standardised and easy measurement of plant functional traits worldwide, *Aust. J. Bot.*, 51, 335–380, doi:10.1071/bt02124, 2003.
- 25 Díaz, S., Noy-Meir, I., and Cabido, M.: Can grazing response of herbaceous plants be predicted from simple vegetative traits?, *J. Appl. Ecol.*, 38, 497–508, 2001.
- Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Marti, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Diez, P.,
- 30 Funes, G., Hamzehee, B., Khoshnevi, M., Perez-Harguindeguy, N., Perez-Rontome, M. C., Shirvany, F. A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martinez, M., Romo-Diez, A., Shaw, S., Siavash, B., Villar-Salvador, P., and Zak, M. R.: The plant traits that drive ecosystems: evidence from three continents, *J. Veg. Sci.*, 15, 295–304, 2004.
- Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D. G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H., and Campbell, B. D.: Plant trait responses to grazing – a global synthesis, *Glob. Change Biol.*, 13, 313–341, doi:10.1111/j.1365-2486.2006.01288.x, 2007.
- 10 Daleo, P. and Iribarne, O.: Beyond competition: the stress-gradient hypothesis tested in plant-herbivore interactions, *Ecology*, 90, 2368–2374, doi:10.1890/08-2330.1, 2009.
- De Bello, F., Leps, J., and Sebastia, M. T.: Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean, *J. Appl. Ecol.*, 42, 824–833, doi:10.1111/j.1365-2664.2005.01079.x, 2005.
- 15 de Mazancourt, C. and Loreau, M.: Grazing optimization, nutrient cycling, and spatial heterogeneity of plant-herbivore interactions: should a palatable plant evolve?, *Evolution*, 54, 81–92, 2000.
- Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., and Mearns, L. O.: Climate extremes: observations, modeling, and impacts, *Science*, 289, 2068–2074, 2000.
- 20 Eldridge, D. J., Soliveres, S., Bowker, M. A., and Val, J.: Grazing dampens the positive effects of shrub encroachment on ecosystem functions in a semi-arid woodland, *J. Appl. Ecol.*, 50, 1028–1038, doi:10.1111/1365-2664.12105, 2013.
- Elger, A. and Willby, N. J.: Leaf dry matter content as an integrative expression of plant palatability: the case of freshwater macrophytes, *Funct. Ecol.*, 17, 58–65, 2003.
- 25 Evju, M., Austrheim, G., Halvorsen, R., and Mysterud, A.: Grazing responses in herbs in relation to herbivore selectivity and plant traits in an alpine ecosystem, *Oecologia*, 161, 77–85, doi:10.1007/s00442-009-1358-1, 2009.
- Fu, X. Q.: Forage Plants of Inner Mongolia, Inner Mongolia People's Press, Hohhot, 1990.
- 30 Grime, J. P.: Plant Strategies, Vegetation Processes, and Ecosystem Properties, 2nd edn., John Wiley and Sons, Chichester, 2001.

- Hanley, M. E., Lamont, B. B., Fairbanks, M. M., and Rafferty, C. M.: Plant structural traits and their role in anti-herbivore defence, *Perspect. Plant Ecol.*, 8, 157–178, doi:10.1016/j.ppees.2007.01.001, 2007.
- He, J. S., Wang, X. P., Flynn, D. F. B., Wang, L., Schmid, B., and Fang, J. Y.: Taxonomic, phylogenetic, and environmental trade-offs between leaf productivity and persistence, *Ecology*, 90, 2779–2791, 2009.
- Herms, D. A. and Mattson, W. J.: The dilemma of plants: to grow or defend, *Q. Rev. Biol.*, 67, 283–335, 1992.
- Jongman, R. H. G., ter Braak, C. J. F., and van Tongeren, O. F. R.: *Data Analysis in Community and Landscape Ecology*, Pudoc, Wageningen, the Netherlands, 1987.
- Laliberte, E., Shipley, B., Norton, D. A., and Scott, D.: Which plant traits determine abundance under long-term shifts in soil resource availability and grazing intensity?, *J. Ecol.*, 100, 662–677, doi:10.1111/j.1365-2745.2011.01947.x, 2012.
- Lemaire, G., Hodgson, J., de Moraes, A., de Carvalho, P. C. F., and Nabringer, C. (Eds.): *Grassland Ecophysiology and Grazing Ecology*, CABI Publishing, New York, 2000.
- Lind, E. M., Borer, E., Seabloom, E., Adler, P., Bakker, J. D., Blumenthal, D. M., Crawley, M., Davies, K., Firn, J., Gruner, D. S., Harpole, W. S., Hautier, Y., Hillebrand, H., Knops, J., Melbourne, B., Mortensen, B., Risch, A. C., Schuetz, M., Stevens, C., and Wragg, P. D.: Life-history constraints in grassland plant species: a growth-defence trade-off is the norm, *Ecol. Lett.*, 16, 513–521, doi:10.1111/ele.12078, 2013.
- Maestre, F. T., Salguero-Gomez, R., and Quero, J. L.: It is getting hotter in here: determining and projecting the impacts of global environmental change on drylands Introduction, *Philos. T. R. Soc. B*, 367, 3062–3075, doi:10.1098/rstb.2011.0323, 2012.
- McLaren, J. R. and Turkington, R.: Ecosystem properties determined by plant functional group identity, *J. Ecol.*, 98, 459–469, doi:10.1111/j.1365-2745.2009.01630.x, 2010.
- Milchunas, D. G. and Lauenroth, W. K.: Quantitative effects of grazing on vegetation and soils over a global range of environments, *Ecol. Monogr.*, 63, 327–366, 1993.
- Milchunas, D. G. and Noy-Meir, I.: Grazing refuges, external avoidance of herbivory and plant diversity, *Oikos*, 99, 113–130, 2002.
- Núñez-Farfán, J., Fornoni, J., and Valverde, P. L.: The evolution of resistance and tolerance to herbivores, *Annu. Rev. Ecol. Evol. S.*, 38, 541–566, doi:10.1146/annurev.ecolsys.38.091206.095822, 2007.

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- Pérez-Harguindeguy, N., Díaz, S., Vendramini, F., Cornelissen, J. H. C., Gurvich, D. E., and Cabido, M.: Leaf traits and herbivore selection in the field and in cafeteria experiments, *Austral Ecol.*, 28, 642–650, 2003.
- Pakeman, R. J.: Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis, *J. Ecol.*, 92, 893–905, 2004.
- Poorter, H. and Nagel, O.: The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients and water: a quantitative review, *Aust. J. Plant Physiol.*, 27, 595–607, doi:10.1071/pp99173, 2000.
- Reich, P. B., Ellsworth, D. S., Walters, M. B., Vose, J. M., Gresham, C., Volin, J. C., and Bowman, W. D.: Generality of leaf trait relationships: a test across six biomes, *Ecology*, 80, 1955–1969, 1999.
- Soriano, A. and Sala, O.: Ecological strategies in a Patagonian arid steppe, *Vegetatio*, 56, 9–15, 1984.
- Sparks, D. L., Page, A. L., Helmke, P. A., Loeppert, R. H., Soltanpour, P. N., Tabatabai, M. A., Johnston, C. T., and Sumner, M. E.: *Methods of Soil Analysis Part 3: Chemical Methods*, Soil Science Society of America Inc., and American Society of Agronomy Inc., Madison, WI, USA, 1996.
- Strauss, S. Y. and Agrawal, A. A.: The ecology and evolution of plant tolerance to herbivory, *Trends Ecol. Evol.*, 14, 179–185, 1999.
- Tecco, P. A., Díaz, S., Cabido, M., and Urcelay, C.: Functional traits of alien plants across contrasting climatic and land-use regimes: do aliens join the locals or try harder than them?, *J. Ecol.*, 98, 17–27, doi:10.1111/j.1365-2745.2009.01592.x, 2010.
- Turley, N. E., Godfrey, R. M., and Johnson, M. T. J.: Evolution of mixed strategies of plant defense against herbivores, *New Phytol.*, 197, 359–361, doi:10.1111/nph.12103, 2013.
- Vandermeijden, E., Wijn, M., and Verkaar, H. J.: Defense and regrowth, alternative plant strategies in the struggle against herbivores, *Oikos*, 51, 355–363, doi:10.2307/3565318, 1988.
- Villar, R. and Merino, J.: Comparison of leaf construction costs in woody species with differing leaf life-spans in contrasting ecosystems, *New Phytol.*, 151, 213–226, 2001.
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., and Garnier, E.: Let the concept of trait be functional!, *Oikos*, 116, 882–892, doi:10.1111/j.2007.0030-1299.15559.x, 2007.

13178

- Wardle, D. A., Lagerstrom, A., and Nilsson, M. C.: Context dependent effects of plant species and functional group loss on vegetation invasibility across an island area gradient, *J. Ecol.*, 96, 1174–1186, doi:10.1111/j.1365-2745.2008.01437.x, 2008.
- Warren, C. R. and Adams, M. A.: Trade-offs between the persistence of foliage and productivity in two *Pinus* species, *Oecologia*, 124, 487–494, 2000.
- Westoby, M.: A leaf-height-seed (LHS) plant ecology strategy scheme, *Plant Soil*, 199, 213–227, 1998.
- Westoby, M.: The LHS strategy scheme in relation to grazing and fire, in: VIth International Rangeland Congress, edited by: Eldridge, D. and Freudenberger, D., International Rangeland Congress, Townsville, Australia, 893–896, 1999.
- White, R., Murray, S., and Rohweder, M.: Pilot analysis of global ecosystems: grassland ecosystems, World Resources Institute, Washington DC, 2000.
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M. L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J., and Villar, R.: The worldwide leaf economics spectrum, *Nature*, 428, 821–827, doi:10.1038/nature02403, 2004.
- Zheng, S. X., Ren, H. Y., Lan, Z. C., Li, W. H., Wang, K. B., and Bai, Y. F.: Effects of grazing on leaf traits and ecosystem functioning in Inner Mongolia grasslands: scaling from species to community, *Biogeosciences*, 7, 1117–1132, doi:10.5194/bg-7-1117-2010, 2010.
- Zheng, S. X., Lan, Z. C., Li, W. H., Shao, R. X., Shan, Y. M., Wan, H. W., Taube, F., and Bai, Y. F.: Differential responses of plant functional trait to grazing between two contrasting dominant C₃ and C₄ species in a typical steppe of Inner Mongolia, China, *Plant Soil*, 340, 141–155, doi:10.1007/s11104-010-0369-3, 2011.
- Zheng, S. X., Ren, H. Y., Li, W. H., and Lan, Z. C.: Scale-dependent effects of grazing on plant C:N:P stoichiometry and linkages to ecosystem functioning in the Inner Mongolia grassland, *PLoS One*, 7, e51750, doi:10.1371/journal.pone.0051750, 2012.

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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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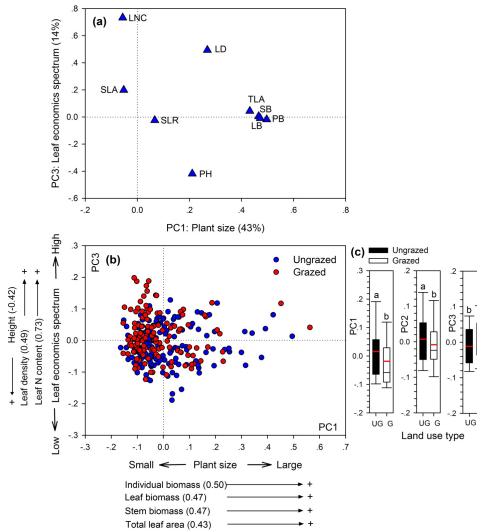


Figure 1. PCA biplot of 276 plant species based on the variance in 9 functional traits explained by the first (PC1) and third (PC3) principal axes. **(a)** Loading plot of traits. **(b)** PCA ordination of 149 plant species (blue circles) from the ungrazed and 127 species (red circles) from the grazed 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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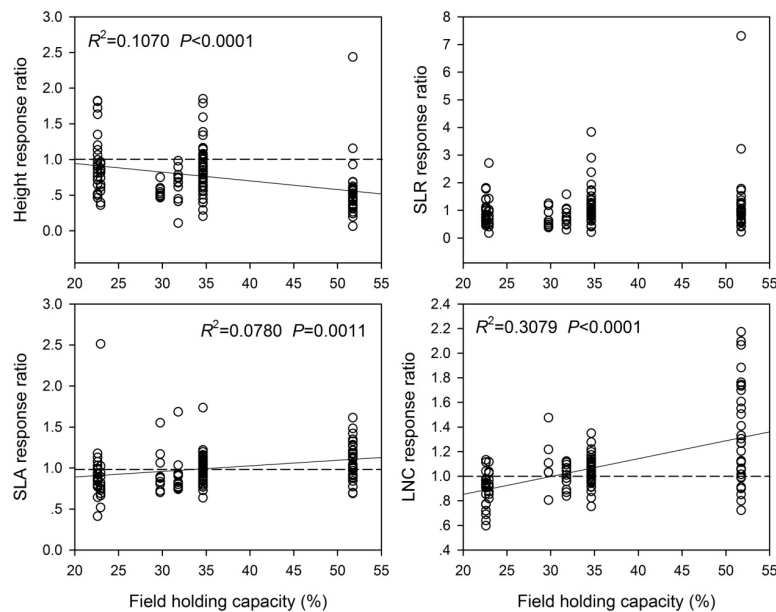


Figure 2. Relationships between the responses of plant functional traits to grazing and field holding capacity across six grassland communities. The response ratio of each trait was calculated as the ratio of mean values in the grazed to ungrazed communities (i.e., $SLA_{\text{grazed}}/SLA_{\text{ungrazed}}$). 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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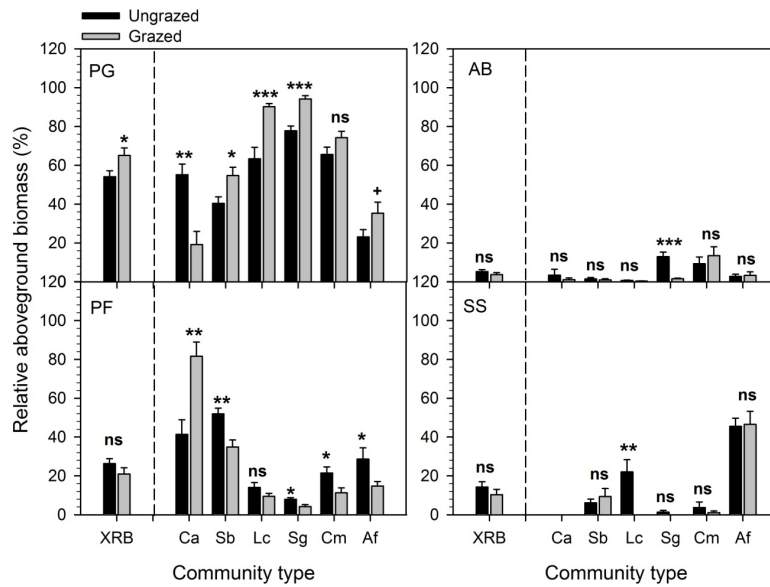


Figure 5. Effects of grazing on plant functional group composition in six grassland communities (error bars denote SE). Abbreviations: PG, perennial grasses; PF, perennial forbs; AB, annuals and biennials; SS, shrubs and semi-shrubs; Ca, *Carex appendiculata* meadow; Sb, *Stipa baicalensis* meadow steppe; 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, $P > 0.1$; +, $0.05 < P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

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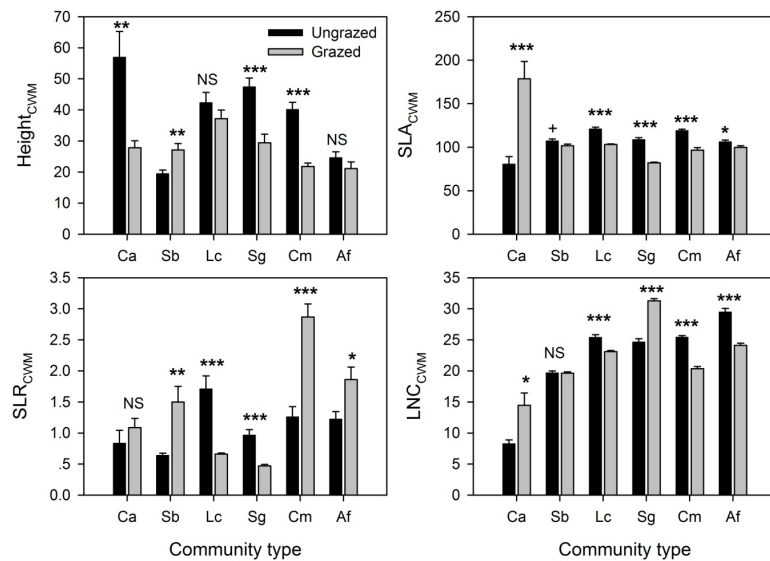


Figure 6. Effects of grazing on the community-weighted attributes for plant height ($height_{CWM}$), stem-leaf ratio (SLR_{CWM}), specific leaf area (SLA_{CWM}), and leaf N content (LNC_{CWM}) in the six communities. Abbreviations and significant levels are derived as in Fig. 5.

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