

Rapid loss of leguminous species in the semi-arid grasslands of northern China under climate change and mowing from 1982 to 2011 postprint

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Date: 2020-11-25T00:00:00+00:00

Abstract

Effects of mowing on the composition and diversity of grasslands varied with climate change (e.g., precipitation and temperature). However, the interactive effects of long-term mowing and climate change on the diversity and stability of leguminous and non-leguminous species in the semi-arid grasslands are largely unknown. Here, we used in situ monitoring data from 1982 to 2011 to examine the effects of continuous mowing and climate change on the plant biomass and diversity of leguminous and non-leguminous species, and soil total nitrogen in the typical semi-arid grasslands of northern China. Results showed that the biomass and diversity of leguminous species significantly decreased with the increasing in the biomass and diversity of non-leguminous species during the 30-a period. Variations in biomass were mainly affected by the long-term mowing, while variations in diversity were mainly explained by the climate change. Moreover, the normalized change rates of diversity in leguminous species were significantly higher than those in non-leguminous species. Mowing and temperature together contributed to the diversity changes of leguminous species, with mowing accounting for 50.0% and temperature 28.0%. Temporal stability of leguminous species was substantially lower than that of non-leguminous species. Consequently, soil total nitrogen decreased in the 2000s compared with the 1980s. These findings demonstrated that leguminous species were more sensitive to the long-term mowing and climate change than non-leguminous species in the semi-arid grasslands. Thus, reseeding appropriate leguminous plants when mowing in the semi-arid grasslands may be a better strategy to improve nitrogen levels of grassland ecosystems and maintain ecosystem biodiversity.

Full Text

Preamble

Rapid Loss of Leguminous Species in the Semi-Arid Grasslands of Northern China Under Climate Change and Mowing from 1982 to 2011

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Abstract: Effects of mowing on grassland composition and diversity vary with climate change (e.g., precipitation and temperature). However, the interactive effects of long-term mowing and climate change on the diversity and stability of leguminous and non-leguminous species in semi-arid grasslands remain largely unknown. Here, we used in situ monitoring data from 1982 to 2011 to examine the effects of continuous mowing and climate change on plant biomass and diversity of leguminous and non-leguminous species, as well as soil total nitrogen, in typical semi-arid grasslands of northern China.

Results showed that the biomass and diversity of leguminous species significantly decreased while those of non-leguminous species increased during the 30-year period. Variations in biomass were mainly affected by long-term mowing, while variations in diversity were mainly explained by climate change. Moreover, the normalized change rates of diversity in leguminous species were significantly higher than those in non-leguminous species. Mowing and temperature together contributed to the diversity changes of leguminous species, with mowing accounting for 50.0% and temperature 28.0%. Temporal stability of leguminous species was substantially lower than that of non-leguminous species. Consequently, soil total nitrogen decreased in the 2000s compared with the 1980s. These findings demonstrate that leguminous species were more sensitive to long-term mowing and climate change than non-leguminous species in semi-arid grasslands. Thus, reseeded appropriate leguminous plants when mowing in semi-arid grasslands may be a better strategy to improve nitrogen levels of grassland ecosystems and maintain ecosystem biodiversity.

Keywords: climate change; diversity; legume; mowing; productivity; succession; temporal stability

1 Introduction

Rapid loss of global biodiversity in grasslands, the largest terrestrial ecosystem worldwide, has greatly affected community composition and ecosystem functioning at a broad scale [?, ?, ?]. Previous experimental studies conducted in

extensive natural grassland systems have demonstrated that ongoing decreases in biomass production are associated with declines in plant species diversity [?, ?, ?]. Explanations for this trend focus on hypotheses that less diverse communities occupy smaller niche spaces, preventing full utilization of distributed resources and thus reducing plant-plant interactions [?]. Consistent with these hypotheses, biodiversity loss also indicates that important plant species or functional groups have been lost [?, ?].

A large body of research has examined climatic and anthropogenic factors as causal mechanisms underlying diversity loss and productivity declines in grasslands [?, ?]. For example, simulated precipitation experiments have shown that precipitation importantly affects grass and forb species diversity and ecosystem production [?, ?]. Nevertheless, one study concluded that temperature was a better indicator than precipitation for predicting plant community assembly across dryland regions [?]. Lin et al. [?] found that warming significantly increased biomass by 12.3% across all terrestrial plants. This terrestrial plant biomass response to warming would potentially lead to changes in community composition and structure, biodiversity, and ecosystem functioning in a warmer environment. In addition to climatic factors, anthropogenic activities may play more important roles in altering grassland diversity-productivity relationships [?, ?]. As one of the major management techniques for natural grasslands, mowing has markedly altered vegetation community composition and diversity [?, ?, ?]. Elucidating the effects of mowing, climate change, and their possible interactions on productivity and diversity will help conserve biodiversity and stability of grassland ecosystems under global change scenarios.

Vegetation communities consist of various functional groups, including legumes and non-N₂-fixing grasses and forbs [?, ?]. Leguminous species, a crucial plant functional group in grassland ecosystems, are critical for maintaining grassland sustainability and performing ecosystem functions (e.g., biomass production and nutrient cycling) [?, ?, ?]. Meanwhile, nitrogen symbiotically fixed by legumes is one of the key drivers of the positive relationship between productivity and biodiversity [?]. Yang et al. [?] found that climate change, e.g., increased precipitation, could differentially affect the abundance of legumes and non-legumes in a 6-year study period. However, to date, there has been a lack of studies examining the response of leguminous plant functional groups to human disturbances (e.g., long-term mowing and climate change), posing serious challenges for predicting vegetation community dynamics under projected global climate change scenarios.

The temperate steppe of northern China, a typical biome consisting of semi-arid regions, has important and long-term provision capacity for people living there and has experienced a great deal of anthropogenic disturbances and climate change [?, ?]. However, the effects of these changes on plant species sensitivity differ between long-term and short-term studies. For example, long-term mowing increased plant diversity [?], but short-term mowing did not affect vegetation community structure in a semi-arid steppe [?]. Here, our study was conducted

to evaluate the effects of long-term mowing and climate change on functional group sensitivity of leguminous and non-leguminous species using detailed monitoring data from 1982 to 2011. Specifically, we focused on two questions: (i) why do leguminous and non-leguminous species respond differently to climate change and mowing? and (ii) which functional group responds more strongly to environmental change?

2.1 Study Area

This study was conducted at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS; 43°38' N, 116°42' E; 1200 m a.s.l.) of the Chinese Academy of Sciences, located in the Xilin Gol League of Inner Mongolia Autonomous Region, China. This region is characterized by a temperate semi-arid continental climate, with an annual mean temperature of approximately 0.5°C and a mean annual (1982–2011) precipitation of approximately 350 mm, 60%–80% of which falls during the growing season (June–August) [?] and coincides with the highest annual temperatures [?]. The site has sandy-loam dark chestnut soil (Calcic Chernozem according to the US soil taxonomy classification system), including a humus layer of 20–30 cm and a calcic layer at approximately 50 cm depth [?]. Before the experiment began, the grasslands had experienced mowing for haymaking and grazing by sheep and cattle at a low stocking rate. The dominant plant was *Leymus chinensis*, comprising 55% ($\pm 15 \pm 12 \pm 4\%$), respectively [?].

2.2 Mowing Experiment

The mowing experiment conducted from 1982 to 2011 was previously described in detail by Baoyin et al. [?]. The mowing experiment consisted of four treatments: mowing once every other year; mowing once per year for two successive years, with no mowing for the third year; mowing once every year; and mowing twice every year, which have been continually maintained since 1982. No mowing was considered the control treatment. The long-term monitoring data of two treatments were used in this study: mowing once every year and no mowing treatment. Each treatment had six replicates that were randomly assigned to six plots. Each plot was 2 m × 2 m, and there were 12 plots in total. Plots were separated by 1-m walkways.

2.3 Variables for Community Structure

All plants were cut and kept to 6 cm height aboveground over each plot at each mowing, but only the plants at the center of each plot were sampled to determine aboveground plant biomass and species diversity. Plants were sorted into leguminous and non-leguminous species, oven-dried at 65°C for 48 h and weighed. Plants were approximately mowed on 16 August from 1982 to 2011 (the specific mowing date was determined by the meteorological conditions of the current year) [?].

2.4 Soil Sampling and Analysis

In the 1980s and 2000s, three topsoil cores (3 cm in diameter and 30 cm in depth) were randomly collected from each plot and then mixed to form one uniform soil sample per plot. After the soil was gently mixed and roots were removed, the moist soil was passed through a 2-mm mesh sieve, air-dried and used to determine total nitrogen (TN) with a Kjeltec analyzer (Kjeltec 2300 Analyzer Unit, Foss, Sweden). All results are expressed on a dry matter basis.

2.5 Meteorological Data Collection

From 1982 to 2011, meteorological factors including monthly mean temperature and mean monthly precipitation at the experimental site were recorded by IMGERS. The dynamic characteristics of temperature and precipitation during the growing season from 1982 to 2011 are shown in Figure S1.

2.6 Statistical Analysis

Aboveground biomass (AGB), relative aboveground biomass (RAGB), Shannon-Wiener diversity index (H), and relative Shannon-Wiener diversity index (RH) of leguminous and non-leguminous species were calculated. We calculated H as follows: $H = -\sum p_i \times \ln(p_i)$, where p_i is the relative abundance of species i . Specifically, RAGB and RH are the proportions of AGB and H of leguminous or non-leguminous species in the total biomass or diversity of the whole community, respectively. The diversity effect is the ratio of AGB to H in leguminous and non-leguminous species. Change rate (CR) of the diversity effect was calculated by the slope between the diversity effect and year.

A one-way ANOVA (analysis of variance) with Duncan's multiple-range tests was performed to test the effect of mowing on diversity from 1982 to 2011. We also used linear regression to determine the dynamics of AGB, RAGB, H and RH of leguminous and non-leguminous species.

In addition, the AGB, RAGB, H and RH values of leguminous and non-leguminous species were further normalized, and normalized change rate (NCR) was used to assess the sensitivity of leguminous and non-leguminous species to mowing. The normalized values were calculated using the following equation [?]:

$$D_N = \frac{D_{\text{origin}} - D_{\text{mean}}}{D_{\text{mean}}}$$

where D_N , D_{origin} , and D_{mean} are the normalized, original and mean values of AGB, RAGB, H and RH of leguminous and non-leguminous species, respectively. Further, we calculated NCR values of AGB, RAGB, H and RH of leguminous and non-leguminous species from 1982 to 2011 using the least squares method given by the following equation [?]:

$$\text{NCR} = \frac{\Delta D_N}{\Delta \text{year}} \quad (1)$$

where ΔD_N and Δyear are the changed normalized values and changed year values of AGB, RAGB, H and RH of leguminous and non-leguminous species, respectively.

We analyzed the degrees of temporal stability (TS) of leguminous and non-leguminous species in the sampled communities using a stability index represented by the reciprocal of the coefficient of variation (CV) [?]:

$$\text{TS} = \frac{D_{\text{mean}}}{\text{SD}} \quad (2)$$

where SD and D_{mean} are the standard deviation and mean values of AGB in the main species as well as the functional groups of leguminous and non-leguminous species, respectively.

Structural equation modeling (SEM) was performed to analyze different hypothetical pathways that may explain the linkages between mowing and climatic factors (including temperature and precipitation) to leguminous and non-leguminous species. In the SEM approach, we developed preliminary models based on hypothesized relationships between AGB and diversity of leguminous and non-leguminous species with mowing and climatic factors [?]. Then, according to the significant regression weights, it was also necessary to change the relationship among variables. The utility of AGB and diversity of leguminous and non-leguminous species within the SEM was compared through a number of measures. The maximum likelihood ² goodness-of-fit tests and Akaike information criterion (AIC) were used to examine the goodness-of-fit of the preliminary modeling.

We conducted all standard statistical analyses using SPSS software version 19.0 (IBM Corp., Armonk, NY, USA) at $P < 0.05$ and $P < 0.01$ levels. The SEM analysis was performed by the AMOS 18.0 software package (SPSS Inc., Chicago, IL, USA). All graphs were prepared using SigmaPlot version 12.0 (Systat Software Inc., San Jose, CA, USA).

3.1 AGB and Species Diversity

The AGB and RAGB of leguminous species gradually declined from the 1980s to the 2010s (Fig. 1a [Figure 1: see original paper] and b). Mowing significantly decreased AGB by 54.43% ($P < 0.01$) and RAGB by 25.26% ($P < 0.05$) of leguminous species compared with control (Fig. 1a and b). In addition, mowing decreased AGB but significantly increased RAGB of non-leguminous species (Fig. S2).

According to normalized analyses, the absolute biomass and relative biomass of NCR of leguminous species were significantly higher than those of non-leguminous species (Fig. 1c and d). The significant decreases in H and RH of leguminous species were also observed from 1982 to 2011 (Fig. 2a [Figure 2: see original paper] and b), while an increase in RH of non-leguminous species was found (Fig. S2). The absolute biomass and relative biomass of NCR of leguminous species were significantly higher than those of non-leguminous species under mowing, but there were no significant differences between them under control (Fig. 2c and d).

SEM analysis was further used to determine the factors driving the sensitivity of leguminous species. Variations in AGB could be explained by mowing, with 39.0% of the total variation for leguminous species and 52.0% for non-leguminous species (Fig. 3a [Figure 3: see original paper] and b). However, variations in species diversity could be explained by climatic factors, with 56.0% of the total variation for leguminous species and 67.0% for non-leguminous species (Fig. 3a and b). For the relative biomass, about 70.0% of variation could be indirectly explained for leguminous species (Fig. 3c), with climatic factors accounting for 63.4% and mowing 7.5% (Fig. 3d).

3.2 Relationship Between AGB and H

There was a significantly positive correlation between AGB and H of leguminous and non-leguminous species under mowing (Fig. 4 [Figure 4: see original paper]). The H of leguminous species significantly decreased over time, but there was no change for non-leguminous species (Fig. 5a [Figure 5: see original paper] and b). Mowing significantly decreased H by 68.28% compared with control (Fig. 5a). The CR of biomass/diversity ratio under mowing for leguminous species was much higher than that for non-leguminous species under control (Fig. 5c). The NCR of biomass/diversity ratio for leguminous species was significantly higher than that for non-leguminous species under both mowing and control (Fig. 5d). Furthermore, the divergent effects of H of leguminous and non-leguminous species could be explained by differences in their responses to mowing and climatic factors (Fig. 6 [Figure 6: see original paper]; Table 1). The H of leguminous species was mainly explained by both mowing and temperature, with mowing accounting for 50.0% and temperature 28.0% (Fig. 6a). However, the H of non-leguminous species was mainly explained by mowing, with 54.0% of the total variation (Fig. 6b).

3.3 Temporal Stability

Mowing slightly decreased the temporal stability of AGB of leguminous and non-leguminous species (Fig. 7a [Figure 7: see original paper]). But the temporal stability of AGB in leguminous species was substantially lower than that of non-leguminous species (Fig. 7a). There was a significantly positive correlation between temporal stability and relative biomass (Fig. 7b; Table 2).

During the initial stage (1980s) of this study, there was no significant difference in TN content between mowing and control. However, TN content under mowing significantly decreased compared with control in the 2000s (Fig. 8a [Figure 8: see original paper]). Accordingly, the response ratio (the Napierian logarithm of the ratio of N under mowing to N under control) in the 2000s was higher than that in the 1980s (Fig. 8b).

4.1 Sensitivity of Structure and Composition of Plant Functional Group to Climate Change

Previous studies have demonstrated that climate change (e.g., temperature and precipitation) alters the composition of plant functional groups in some ecosystems located in cold regions, such as Arctic tundra [?], alpine meadows and wetlands [?]. In temperate grasslands, however, plant functional groups are rather resistant to increased temperature alone [?]. Most of these experiments were conducted within 5 years [?]. Shi et al. [?] found that the response of community composition to experimental warming in the first 7 years of their study was also resistant in temperate grasslands, while altered environments under long-term climate change could induce changes in community composition [?]. Our results showed that increased temperature resulted in rapid decrease in the relative diversity of leguminous species from 1982 to 2011, with a corresponding increase in the relative diversity of non-leguminous species. This is consistent with findings obtained by Butterfield [?] and Butterfield and Munson [?], who found that ecological communities tracked variation in temperature much more closely, intimating strong responses to temperature increases.

Three possible reasons may partly be responsible for the rapid loss in relative diversity of leguminous species under long-term climate change. First, in arid or semi-arid grasslands, leguminous species have relatively small proportional abundance in the community, resulting in lower competitive ability for water and nutrient resources compared with non-leguminous species. Second, warming-induced reduction of interspecific interactions between leguminous and non-leguminous species may reduce the growth responses of leguminous species to elevated temperature [?]. Finally, in water-limited grasslands, leguminous species are more sensitive to changes in water availability [?]. Therefore, reduced water availability in the surface soil under long-term warming [?] may result in fewer leguminous species.

Furthermore, 63.4% of variation in the relative biomass decline of leguminous species could be indirectly explained by climatic factors (e.g., temperature). Miller et al. [?] have predicted that the advantage of leguminous over non-leguminous species will be lost as a result of accelerated soil nitrogen mineralization and availability under climate warming. Our findings of a tendency for leguminous relative biomass to reduce and non-leguminous relative biomass to increase under warming partially support this prediction. This may be attributable to spatial variations in plant functional traits, such as plant growth rates and variable drivers of plant nitrogen use efficiency between leguminous

and non-leguminous species.

In addition, when leguminous species persist in communities, diversity effects are manifest through their influence on vegetation dynamics and abiotic factors [?, ?]. In this study, the diversity effects of leguminous species significantly decreased from 1982 to 2011, which was partly explained by the negative effect of elevated temperature. The temporal stability of leguminous species was significantly lower than that of non-leguminous species. This finding is consistent with previous studies showing that greater plant diversity in grasslands may improve AGB stability in the face of human or abiotic disturbances [?, ?]. This reveals that large species pools likely possess one or more stress-tolerant species to resist disturbance (e.g., mowing) [?]. Stress-tolerant species can compensate for the loss of other species during a disturbance, and thus help stabilize biomass across time [?]. For example, increasing diversity can also stabilize communities by increasing component species stability [?]. In our experiment, the sensitivity of leguminous species appeared to weaken species interactions between leguminous and non-leguminous species, which can diminish the temporal stability of leguminous species. This is likely caused by weakened species interactions failing to promote niche partitioning or facilitation [?].

4.2 Sensitivity of Structure and Composition of Plant Functional Group to Mowing

Long-term mowing has significant effects on community structure and composition in grasslands [?]. In our study, an obvious decrease in AGB and species diversity for leguminous and non-leguminous species was observed under mowing from 1982 to 2011. However, the magnitude of mowing effects on biomass and diversity was modified by plant functional group, with a higher change rate in leguminous species than in non-leguminous species. This may result from the same underlying mechanism that mowing leads to significant differences in energy partitioning between leguminous and non-leguminous species [?]. This is consistent with results obtained by Liu et al. [?], who performed a survey on changes in plant diversity, composition and productivity in semi-arid grasslands, finding that mowing significantly reduced above-ground net primary productivity by 21.7%. However, they also found that community structure was not altered by short-term mowing, which was not in line with our results. This indicates that plant community composition changes little under short-term mowing, but long-term mowing has great effects on vegetation community composition, such as the rapid loss of leguminous species. This discrepancy may be associated with differences in experimental periods. The positive feedback between aboveground vegetation communities and soil microorganisms might be weakened or offset over the course of our long-term mowing treatment. This strongly suggests the decline in potential for overcompensation of different plant functional groups in response to continuous mowing [?].

Our results suggest that soil TN content decreases under long-term mowing. However, this finding does not agree with a previous study conducted by Rob-

son et al. [?], who proposed that positive feedback between grassland management regimes and dominant plant functional strategies maintained high nitrogen availability in subalpine grasslands. In their study, no mowing could actually reduce nitrogen availability and nitrogen transformation processes, which was correlated with a shift in the vegetation community towards more conservative functional strategies and greater dominance by grasses [?]. This difference with our findings may be explained by the following phenomena: (1) vegetation community composition in subalpine grassland is shaped by a colder climate, which is different from the climate of temperate grasslands, therefore this feedback mechanism may be weakened or even disappear; and (2) a short-term experiment may be unable to detect the effect of long-term climate variation on biogeochemical cycles. More importantly, long-term mowing may decrease organic matter decomposition and plant nutrient availability, causing a decline in total soil nitrogen in semi-arid grasslands [?, ?].

4.3 Implications of Mowing- and Climate-Induced Vegetation Community Changes for the Semi-Arid Grasslands

Overall, our results concerning the responses of leguminous and non-leguminous species to long-term mowing and climatic factors have several implications for sustainable management and utilization strategies in semi-arid grasslands. First, mowing across entire grasslands may decrease spatial heterogeneity and therefore not be the most appropriate option for maximizing plant biomass and species diversity in grasslands [?]. Köhler et al. [?] suggested that applying regular mowing in the central portion of a meadow but with unmown or less frequently mown strips can be a better management alternative. In the long run, this may also be a better mowing strategy for typical semi-arid grasslands, where a variable mowing regime is favorable for vegetation community succession and preserving soil nutrient levels (especially by leaving unmown strips). Second, our results show that soil TN decreased along with leguminous AGB and species diversity. Leguminous species are characterized by their ability to biologically fix N₂, which has the benefits of being ecologically benign and reducing the use of fossil fuels in agriculture. Accordingly, planting leguminous species is usually a more effective agronomic practice for supplying nitrogen for agricultural production relative to artificial nitrogen application [?, ?]. We therefore suggest that reseeded appropriate leguminous plants into semi-arid grasslands when mowing may be a better strategy to improve nitrogen levels of grassland ecosystems and thus maintain ecosystem biodiversity.

Acknowledgements

This study was supported by the National Key Research and Development Program of China (2016YFC0500604), the National Natural Science Foundation of China (31860681), the China Agriculture Research System (CARS-34), and the Natural Science Foundation of Inner Mongolia Autonomous Region, China (2017MS0317).

References

- Baez S, Collins S L, Pockman W T, et al. 2013. Effects of experimental rainfall manipulations on Chihuahuan Desert grassland and shrubland plant communities. *Oecologia*, 172(4): 1117–1127.
- Bai Y F, Han X G, Wu J G, et al. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, 431(7005): 181–184.
- Baoyin T G T, Li F Y H, Bao Q H, et al. 2014. Effects of mowing regimes and climate variability on hay production of *Leymus chinensis* (Trin.) Tzvelev grassland in northern China. *Rangeland Journal*, 36(6): 593–600.
- Blessing C H, Mariette A, Kaloki P, et al. 2018. Profligate and conservative: water use strategies in grain legumes. *Journal of Experimental Botany*, 69(3): 349–369.
- Bulleri F, Bruno J F, Silliman B R, et al. 2016. Facilitation and the niche: implications for coexistence, range shifts and ecosystem functioning. *Functional Ecology*, 30(1): 70–78.
- Butterfield B J. 2015. Environmental filtering increases in intensity at both ends of climatic gradients, though driven by different factors, across woody vegetation types of the southwest USA. *Oikos*, 124(10): 1374–1382.
- Butterfield B J, Munson S M. 2016. Temperature is better than precipitation as a predictor of plant community assembly across a dryland region. *Journal of Vegetation Science*, 27(5): 938–947.
- Cardinale B J, Wright J P, Cadotte M W, et al. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences of the United States of America*, 104(46): 18123–18128.
- Cardinale B J, Duffy J E, Gonzalez A, et al. 2012. Biodiversity loss and its impact on humanity. *Nature*, 486(7401): 59–67.
- Chen D M, Pan Q M, Bai Y F, et al. 2016. Effects of plant functional group loss on soil biota and net ecosystem exchange: a plant removal experiment in the Mongolian grassland. *Journal of Ecology*, 104(3): 734–743.
- Cowles J M, Wragg P D, Wright A J, et al. 2016. Shifting grassland plant community structure drives positive interactive effects of warming and diversity on aboveground net primary productivity. *Global Change Biology*, 22(2): 741–749.
- Downing A L, Brown B L, Leibold M A. 2014. Multiple diversity-stability mechanisms enhance population and community stability in aquatic food webs. *Ecology*, 95(1): 173–184.
- Finn J A, Kirwan L, Connolly J, et al. 2013. Ecosystem function enhanced by combining four functional types of plant species in intensively managed grass-

- land mixtures: a 3-year continental-scale field experiment. *Journal of Applied Ecology*, 50(2): 365–375.
- Gao D D, Wang X L, Fu S L, et al. 2017. Legume plants enhance the resistance of soil to ecosystem disturbance. *Frontiers in Plant Science*, 8: 1295.
- Gherardi L A, Sala O E. 2015. Enhanced interannual precipitation variability increases plant functional diversity that in turn ameliorates negative impact on productivity. *Ecology Letters*, 18(12): 1293–1300.
- Grime J P, Fridley J D, Askew A P, et al. 2008. Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences of the United States of America*, 105(29): 10028–10032.
- Hautier Y, Tilman D, Isbell F, et al. 2015. Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science*, 348(6232): 336–340.
- He L, Cheng L L, Hu L L, et al. 2016. Deviation from niche optima affects the nature of plant-plant interactions along a soil acidity gradient. *Biology Letters*, 12(1): 20150925, doi: 10.1098/rsbl.2015.0925.
- Hobbie S E. 2015. Plant species effects on nutrient cycling: revisiting litter feedbacks. *Trends in Ecology & Evolution*, 30(6): 367–374.
- Hoover D L, Knapp A K, Smith M D. 2014. Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology*, 95(9): 2646–2656.
- Isbell F I, Polley H W, Wilsey B J. 2009. Biodiversity, productivity and the temporal stability of productivity: patterns and processes. *Ecology Letters*, 12(5): 443–451.
- Jensen E S, Hauggaard-Nielsen H. 2003. How can increased use of biological N₂ fixation in agriculture benefit the environment? *Plant and Soil*, 252(1): 177–186.
- Karhu K, Auffret M D, Dungait J A J, et al. 2014. Temperature sensitivity of soil respiration rates enhanced by microbial community response. *Nature*, 513(7516): 81–84.
- Köhler B, Gigon A, Edwards P J, et al. 2005. Changes in the species composition and conservation value of limestone grasslands in Northern Switzerland after 22 years of contrasting managements. *Perspectives in Plant Ecology Evolution and Systematics*, 7(1): 51–67.
- Korell L, Schmidt R, Bruelheide H, et al. 2016. Mechanisms driving diversity-productivity relationships differ between exotic and native communities and are affected by gastropod herbivory. *Oecologia*, 180(4): 1025–1036.
- Lavorel S, McIntyre S, Landsberg J, et al. 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution*, 12(12): 474–478.

- Li B, Li Y Y, Wu H M, et al. 2016. Root exudates drive interspecific facilitation by enhancing nodulation and N₂ fixation. *Proceedings of the National Academy of Sciences of the United States of America*, 113(23): 6496–6501.
- Li X L, Liu Z Y, Wang Z, et al. 2015. Pathways of *Leymus chinensis* individual aboveground biomass decline in natural semiarid grassland induced by overgrazing: a study at the plant functional trait scale. *PloS ONE*, 10(5): e0124443.
- Lin D, Xia J Y, Wan S Q. 2010. Climate warming and biomass accumulation of terrestrial plants: a meta-analysis. *New Phytologist*, 188(1): 187–198.
- Liu Y Z, Miao R H, Chen A Q, et al. 2017. Effects of nitrogen addition and mowing on reproductive phenology of three early-flowering forb species in a Tibetan alpine meadow. *Ecological Engineering*, 99: 119–125.
- Liu Y Z, Ma G G, Zan Z M, et al. 2018. Effects of nitrogen addition and mowing on rodent damage in an Inner Mongolian steppe. *Ecology and Evolution*, 8(8): 3919–3926.
- Miko L, Storch D. 2015. Biodiversity conservation under energy limitation: possible consequences of human productivity appropriation for species richness, ecosystem functioning, and food production. *Ecosystem Services*, 16: 146–149.
- Miller A E, Schimel J P, Sickman J O, et al. 2007. Mineralization responses at near-zero temperatures in three alpine soils. *Biogeochemistry*, 84(3): 233–245.
- Moritz C, Agudo R. 2013. The future of species under climate change: resilience or decline? *Science*, 341(6145): 504–508.
- Niu S L, Wan S Q. 2008. Warming changes plant competitive hierarchy in a temperate steppe in northern China. *Journal of Plant Ecology*, 1(2): 103–110.
- Peng H Y, Li X Y, Li G Y, et al. 2013. Shrub encroachment with increasing anthropogenic disturbance in the semiarid Inner Mongolian grasslands of China. *CATENA*, 109: 39–48.
- Polley H W, Isbell F I, Wilsey B J. 2013. Plant functional traits improve diversity-based predictions of temporal stability of grassland productivity. *Oikos*, 122(9): 1275–1282.
- Robson T M, Lavorel S, Clement J C, et al. 2007. Neglect of mowing and manuring leads to slower nitrogen cycling in subalpine grasslands. *Soil Biology and Biochemistry*, 39(4): 930–941.
- Roscher C, Temperton V M, Scherer-Lorenzen M, et al. 2005. Overyielding in experimental grassland communities—irrespective of species pool or spatial scale. *Ecology Letters*, 8(4): 576–577.
- Rumpel C, Crème A, Ngo P T, et al. 2015. The impact of grassland management on biogeochemical cycles involving carbon, nitrogen and phosphorus. *Journal of Soil Science and Plant Nutrition*, 15(2): 353–371.

- Shao C, Chen J, Li L, et al. 2012. Ecosystem responses to mowing manipulations in an arid Inner Mongolia steppe: an energy perspective. *Journal of Arid Environments*, 82: 1-10.
- Shi Z, Sherry R, Xu X, et al. 2015. Evidence for long-term shift in plant community composition under decadal experimental warming. *Journal of Ecology*, 103(5): 1131-1140.
- Smith M D, Knapp A K, Collins S L. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology*, 90(12): 3279-3289.
- Suter M, Connolly J, Finn J A, et al. 2015. Nitrogen yield advantage from grass-legume mixtures is robust over a wide range of legume proportions and environmental conditions. *Global Change Biology*, 21(6): 2424-2438.
- Talle M, Deak B, Poschlod P, et al. 2016. Grazing vs. mowing: a meta-analysis of biodiversity benefits for grassland management. *Agriculture, Ecosystems & Environment*, 222: 200-212.
- Tilman D. 1999. Diversity by default. *Science*, 283(5401): 495-496.
- Tilman D, Reich P B, Knops J M H. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441(7093): 629-632.
- Tracy B F, Sanderson M A. 2004. Forage productivity, species evenness and weed invasion in pasture communities. *Agriculture, Ecosystems & Environment*, 102(2): 175-183.
- Walker M D, Wahren C H, Hollister R D, et al. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America*, 103(5): 1342-1346.
- Wan S Q, Hui D F, Wallace L, et al. 2005. Direct and indirect effects of experimental warming on ecosystem carbon processes in a tallgrass prairie. *Global Biogeochemical Cycles*, 19(2): GB2014.
- Wu G L, Liu Y, Tian F P, et al. 2016. Legumes functional group promotes soil organic carbon and nitrogen storage by increasing plant diversity. *Land Degradation and Development*, 28(4): 1336-1344.
- Yang H J, Li Y, Wu M Y, et al. 2011. Plant community responses to nitrogen addition and increased precipitation: the importance of water availability and species traits. *Global Change Biology*, 17(9): 2936-2944.
- Yang H J, Jiang L, Li L H, et al. 2012. Diversity-dependent stability under mowing and nutrient addition: evidence from a 7-year grassland experiment. *Ecology Letters*, 15(6): 619-626.
- Yang Z L, Jiang L, Su F L, et al. 2016. Nighttime warming enhances drought resistance of plant communities in a temperate steppe. *Scientific Reports*, 6(1): 23267.

Yang Z L, Zhang Q, Su F L, et al. 2017. Daytime warming lowers community temporal stability by reducing the abundance of dominant, stable species. *Global Change Biology*, 23(1): 154–163.

Zahran H H. 1999. Rhizobium-legume symbiosis and nitrogen fixation under severe conditions and in an arid climate. *Microbiology and Molecular Biology Reviews*, 63(4): 968–989.

Zhou Z, Sun O J, Huang J, et al. 2006. Land use affects the relationship between species diversity and productivity at the local scale in a semi-arid steppe ecosystem. *Functional Ecology*, 20(5): 753–762.

Appendix

Fig. S1 Characteristics of precipitation (a) and temperature (b) during the growing season from 1982 to 2011

Fig. S2 AGB (a and b) and H (c and d) in non-leguminous species from 1982 to 2011. Inset bar graphs in the four panels compare variable changes between control (black) and mowing (white) from 1982 to 2011. **, $P < 0.01$ level; *, $P < 0.05$ level; ns, $P > 0.05$ level. Bars are standard errors.

Fig. S3 Biomass/diversity ratios of both leguminous (a) and non-leguminous (b) species under mowing and control. **, $P < 0.01$ level. Bars are standard errors.

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