Plant Soil
https://doi.org/10.1007/s11104-021-04970-5

REGULAR ARTICLE

Grazing impacts on ecosystem functions exceed those from mowing

Yuanjun Zhu · Manuel Delgado-Baquerizo · Dan Shan · Xiaohui Yang · David J. Eldridge

Received: 18 January 2021 / Accepted: 19 April 2021

Abstract
Aims Land use change due to the increasing anthropogenic activities is the most important driver leading to alteration of multiple ecosystem functions. Overgrazing is thought to be one of most pervasive and significant degrading processes in grasslands, but direct comparisons with other comparable drivers of land use intensification are lacking. Our results aimed to test how single land use practices (grazing, mowing), and combined land use practices (both grazing and mowing), influence biodiversity, soils and plant function, and the coupling of aboveground and belowground functions and properties in a Eurasian steppe grassland.
Methods We examined changes in individual functions associated with aboveground and belowground plant and soil compartments, and multiple combined functions (hereafter 'multifunctionality') at 317 sites along an extensive climatic gradient in Northern China. Further, we investigated the correlations (coupling) between aboveground and belowground processes under the three land use scenarios.
Results We found a mixture of effects of grazing, mowing and mowing plus grazing. However, values of many aboveground and belowground attributes were lower when sites were grazed. Although grazed sites had lower values of soil carbon and nutrients, there were no grazing-induced changes in root carbon, nitrogen and phosphorus. More importantly, the most intense land use scenario (grazing combined with mowing) decoupled the correlations between belowground and aboveground functions compared with that of single land uses.
Conclusions Our study demonstrates that mowing is a better long-term management method than grazing for semi-natural grasslands in the Eurasian steppe are heavily grazed. Our results demonstrate that additional land use pressures imposed when mowing and grazing are applied together can decouple the positive associations between plant richness and functions. This knowledge is

Responsible Editor: Wen-Hao Zhang.

Y. Zhu · D. Shan · X. Yang (✉)
Institute of Desertification Studies, Chinese Academy of Forestry, No.1 Dong Xiaofu, Xiangshan Road, Haidian District, Beijing 100091, China
e-mail: yangxh@caf.ac.cn

Y. Zhu
e-mail: neidazhuyuanjun@163.com
D. Shan
e-mail: shandhlbe@163.com

M. Delgado-Baquerizo
Departamento de Ecología and Instituto Multidisciplinar para el Estudio del Medio "Ramón Margalef ", Universidad de Alicante, Carretera de San Vicente del Raspeig s/n, San Vicente del Raspeig, 03690 Alicante, Spain
e-mail: m.delgadobaquerizo@gmail.com

D. Shan
School of Agriculture and Forestry, Hulunbuir University, Hulunbuir 021008, China

D. J. Eldridge
Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia
e-mail: d.eldridge@unsw.edu.au

Published online: 30 April 2021

critical if we are to adopt strategies to maintain diverse grassland ecosystems and the important services and functions that they provide.

Keywords Eurasian grassland · Ecosystem functions · Multifunctionality · Grazing · Mowing · Plant diversity · Ecosystem services

Introduction

Land use intensification has increased over the past century to meet the food needs of an increasing global population (Tilman et al. 2011). Land use intensification includes overgrazing by domestic livestock, vegetation removal and land clearing for agriculture, and fertilization, and has been shown to reduce diversity and productivity, and therefore ecosystem functioning and stability (Allan et al. 2015; Blüthgen et al. 2016; Chillo et al. 2016; Habel et al. 2013; Travers et al. 2019). Most studies to date have examined the effects of single land use drivers, or the effects of different drivers on multiple functions simultaneously, and the majority has focussed on aboveground processes (hereafter aboveground multifunctionality; Garland et al. 2020). However, the impacts of grazing on plant and plant processes (particularly root traits) and soil functions compared with those of similar land use drivers (e.g., mowing) are less well understood. Similarly, very little is known about the effects of mowing and grazing on soil ecosystem functions across different soil depths. This knowledge is important because land use intensification often involves multiple landuse drivers (e.g., grazing and fertilization), which have different effects on both aboveground and belowground functions.

Land use intensification practices such as mowing for hay production and livestock grazing would be expected to negatively affect aboveground ecosystem functions, by reducing, for example, the amount of plant biomass, altering species composition, and potentially removing keystone species such as perennial grasses that are critically important for sustaining productive and stable ecosystems (Bai et al. 2012). However, we know very little about how these processes might affect the biomass of belowground components (e.g., root biomass). Similarly, the effects of mowing or grazing on soil carbon (C), nitrogen (N) and phosphorus (P) concentrations are expected to be more pronounced in the upper surface layers where most C and nutrients are found. Leaching and erosion processes associated with mowing and grazing might impact the concentration of soil C, N and P with depth, but the extent of these practices is little known because any effects of grazing or mowing on these important elements have been little studied at different soil depths. We know, for example, that soil C and nutrients in drylands (semi-arid to dry subhumid) soils are concentrated in the uppermost layers (< 10 cm), so many studies of grazing effects on soils have tended to focus at these depths (e.g., Eldridge et al. 2016). Similarly, the effects of mowing could influence soils by reducing photosynthesis and therefore C substrates, increasing surface temperatures, or increasing soil respiration, but these effects have generally been tested at only relatively shallow depths (< 10 cm, Han et al. 2012).

Herbivory by livestock could induce similar effects to those of mowing because they remove aboveground biomass. Thus, it could be hypothesized that mowing and grazing impacts on ecosystem functions are similar. Notwithstanding the positive effects of livestock on ecosystems and their biota (e.g. Lu et al. 2017), livestock not only remove plants, but also compact the soil and affect soil processes such as the decomposition of organic matter and the turnover of nutrients. This is important because land use changes that alter aboveground attributes such as litter and plant production are likely to affect decomposition and mineralization processes, and therefore soil microbial functions, with feedbacks to pastoral production and resistance to, and resilience from, disturbance, particularly as Earth's climate becomes more variable. We posit, therefore, that the effects of grazing can be far more important than those of mowing in terrestrial ecosystems. The functional impacts of grazing compared with mowing could be particularly pronounced in nutrient-poor ecosystems wherein herbivore dung has affects nutrient availability for plants and microbes (Cai et al. 2014). Understanding the relative importance of different land use drivers in altering ecosystem functions is essential to predict how future changes in land use intensification under global change scenarios will alter ecosystem productivity and sustainability.

Climate change and land use intensification can alter the relationships among belowground and aboveground processes i.e. the extent to which they are coupled, leading to changes in critical ecosystem functions. The strength of these direct and indirect linkages (Risch et al. 2018) reflects a greater ecosystem stability and therefore greater resistance and resilience (Ochoa-Hueso et al. 2019). For example, increasing aridity has been shown to decouple soil C and N in steppe grasslands (Ye et al. 2013), and C, N and P stoichiometry in drylands globally (Delgado-Baquerizo et al. 2013). However, we know relatively less about how aboveground and belowground functions are linked and how the connections are likely to change under various land use scenarios.

Here we describe a study where we aimed to test how single land use practices (grazing, mowing), and combined land use practices (both grazing and mowing), influence biodiversity, soils and plant function, and the coupling between aboveground and belowground functions and properties in a Eurasian steppe grassland. We examined changes in individual functions associated with aboveground and belowground plant and soil compartments, and multiple combined functions (hereafter 'multifunctionality') at 317 sites along an extensive climatic gradient in Northern China. Further, we investigated the coupling (i.e., the lack or reduction in environmental correlation among ecosystem attributes in response to disturbance) among aboveground and belowground processes under the three land use scenarios. We predicted that there would be greater coupling under single land uses, and that the more intense land use practice (grazing combined with mowing) would lead to a decoupling of aboveground and belowground functions. Our study provides a scientific basis for determining policy in relation to appropriate levels of land use intensity needed to sustain healthy productive grasslands, on which human livelihoods depend.

Methods

Site description

This study was conducted in the Hulun Buir steppe, located across an area of about 113,000 km^2 in the Hulun Buir region of Inner Mongolia, China (47°05′-53°20'N and 115°31′-123°00′E, 650–1050 m asl). The study area lies among China, Mongolia and Russia (Zhu et al. 2019). The region experiences a temperate semi-arid continental climate. Mean annual temperature ranges from 0 to 3 °C, with the lowest monthly mean temperature (−22 °C) in January and the highest monthly mean temperature in August (18.5 °C). Mean annual precipitation is 250–350 mm and approximately 80% is concentrated between June and September; the frost-free period ranges from 85 to 155 days and with an annual sunshine period of 2650–3000 h (climatic data from the Hulun Buir Meteorological Station). The natural vegetation is steppe dominated by the grasses *Stipa grandis* P. Smirn., *Stipa krylovii* Roshev, *Leymus chinensis* (Trin.) Tzvel. and *Stipa baicalensis* Roshev (Zhu et al. 2019). The major soil types of this region are chernozems and chestnuts (CENMN 1985). There are two dominant land uses; hay production for sale as fodder (hereafter 'mowing'), and in situ sheep, goat and cattle grazing for meat and wool (hereafter 'grazing'), with some land owners practicing both land uses (hereafter 'mowing plus grazing'). All the studied grasslands were unfertilized, and the land use of each site was verified by interviewing local pastoralists.

Sampling procedures

Over the period of two growing seasons in 2017 and 2018, we surveyed 317 sites within the Hulun Buir steppe using four west-east trending transects of about 300 km running from the eastern end of the western foothills of the Great Khingan Mountains to the western end of the China-Mongolia border. Our field sites were spaced at distances of 2 to 3 km along these transects in areas of homogeneous steppe. Urban or disturbed areas, riparian and lakeside sites were avoided. At each site we located three 1m^2 plots to investigate the plant community and soils ($n = 951$ quadrats). Within each quadrat we measured the total cover of all vascular plants by species, and recorded the land use (grazed, mown, grazed + mown) using interviews with local pastoralists.

In the Hulun Buir grasslands, each herder (pastoral) family generally subdivides their rangeland plot into two parts, one that is grazed for meat and wool production, and the other mown, to produce fodder for sale off-farm. Rangelands are grazed year-round, except during May, which is the period when perennial grasses begin to germinate. Government bans on grazing on all rangelands during May aim to encourage grassland regeneration. The rangelands are grazed by sheep, goats and cattle, at average stocking rates of about 110–170 sheep units per square kilometre, equivalent to 22–34 livestock (cattle) units per square kilometre. Overgrazing is a substantial issue, and herders typically respond to grazing-reduced grassland productivity by increasing livestock densities in order to maintain living standards (Gao et al. 2016). Mowing, using tractorbased mowers and hay balers, is carried out in areas that have not been grazed, in late August to early September, at the end of the grassland growing season. Herders that practice both grazing and mowing graze their previously mown grasslands until the following March (Zhu et al. 2019; NSBC 2019). Although the mixed (grazing + mowing) grassland management system is believed to be environmentally and financially better than continuous grazing (Schönbach et al. 2011), free-range continuous grazing, without mowing, is the most widely practiced system, while mowing practiced mainly by those who have access to hay-making machinery.

All aboveground plants were harvested in each plot, oven-dried at 45 °C and weighed to calculate aboveground biomass (g m^{-2}). Three 10 cm diameter soil cores were also collected, to a depth of 20 cm, from each quadrat using a root auger, and the roots in each soil core cleaned and dried at 45 °C and weighed and expressed as g m^{-2}. Aboveground and belowground biomass was collected in the same area for C, N and P analyses.

Soil samples were collected by taking three 5 cm diameter soil cores from the 0–10 cm, 10–20 cm and 20–40 cm depths from each quadrat with a soil auger. The three cores from each quadrat were combined, air dried, hand sorted to remove rocks and visible plant material, and the soil ground to pass through a 2 mm sieve for use in soil physicochemical analyses. Soil pH was measured in 1:2.5 (soil: water) suspension using a pH meter (Mettler Toledo, Shanghai, China). Rock volume was measured to correct for soil C, N and P pools. Bulk density of the surface 10 cm was determined with a 100 cm^3 corer after correction for rock volume. Soil cores were oven-dried at 105 °C to constant weight. Total organic C in soil and plant samples was analysis on a liquiTOC analyzer (Elementar, Hanau, Germany). Total N in plant and soil samples was determined following Kjeldehl digestion by a Nitrogen Analyzer System (Kjeltec 2300 Auto System II, Foss Tecator AB, Höganäs, Sweden), and total P in soil and plant samples determined by the H_2SO_4-$HClO_4$ fusion method (Sparks et al. 1996). The soil texture was determined using Laser Particle Size Analyser (S3500, Microtrac, America), and divided into clay (< 2 um), silt (2–50 um) and sand (50–2000 um) according to the USDA system (Soil Survey Staff 1951). To assess the effects of grazing and mowing on functional group composition, we classified all plants into five functional groups based on life forms (perennial grasses, perennial forbs, perennial rhizomatous grasses, shrubs and semi-shrubs, annuals; after Bai et al. 2012).

Statistical analyses

All analyses were based on site-level data. We calculated an average multifunctionality index (MF) assigning each of the 32 attributes to a particular function (Table 1), obtained as the average standardised (*z*-score) values across the different ecosystem functions (Maestre et al. 2012). This index has good statistical properties and is a straightforward and easily interpretable measure of multifunctionality (Lefcheck et al. 2015). The index

Table 1 The relationship between different attributes and functions. #not included as an ecosystem service in Fig. 2

Services	Functions	Attribute
Provisioning	Plant productivity	Aboveground biomass
		Belowground biomass
		Plant foliage cover
Biodiversity	Plant diversity	Alpha diversity
		Pieleu's index
		Evenness index
		Simpson index
		Beta diversity
		Gamma diversity
		Cover CV
		ShannonWeiner index
Supporting	Water resources	Soil Water
	Nutrient cycling	Soil N 0-10 cm
		Soil N 10-20 cm
		Soil N 20-40 cm
		Soil P 0-10 cm
		Soil P 10-20 cm
		Soil P 20-40 cm
	Nutrient uptake	Root N
		Root P
		Root C
		Plant N
		Plant P
		Plant C
Regulating	Carbon stocks	Soil organic carbon 0-10 cm
		Soil organic carbon 10-20 cm
		Soil organic carbon 20-40 cm
Soil properties	Soil acidification	Soil pH
	Soil density#	Soil bulk density

is an averaging method, and attempts to summarize multifunctionality so that high values equate with high values of many, but not necessarily all, attributes (Garland et al. 2020). We also report results on individual function to aid interpretation.

Differences in multifunctionality of aboveground and belowground attributes for the three land use practices, and the seven ecosystem services/functions for each of the three land use types were tested using Oneway ANOVA. A Least Significant Difference (LSD) test was used to identify those land uses that differed significantly using SPSS 22 (IBM, Chicago, IL, USA) software. We used a linear model to examine the relationships among selected aboveground and belowground attributes for the three land use practice categories, after using standard diagnostic tests (G-G plots, homogeneity of residuals) in the R statistical package (R Core Team 2019). Correlations among all aboveground and belowground attribute (Table S1) were analysed separately, for each landuse type, using the R statistical package. To account for different sample sizes among the three land use types, we randomly selected 56 sites from each of the grazed (original n = 186) and mown (original n = 127) sites.

Results

Multifunctionality of aboveground and belowground attributes was greater at mown sites than those at grazed, either alone or in combination with mowing (Fig. 1a & b). Similar results were found for individual groups of functions, except nutrient uptake and acidification (soil pH; Fig. 2). We also found a general association between aboveground and belowground multifunctionality (r = 0.27, $P < 0.001$; Fig. 1c).

Compared with mowing, we found significantly lower values in nine of the 15 aboveground attributes, and only two values that were greater (plant N, shrub cover) when sites were grazed. Half of the attributes whose values were lower under grazing had even lower values when grazing was combined with mowing (Fig. 3, Table S1). For belowground attributes, values of soil C, N and P were all lower under grazing in all soil layers, even down to 40 cm (Fig. 4, Table S1). Despite the lower, grazing-induced values of soil C and nutrients, we found no grazing-induced changes in root C, N or P.

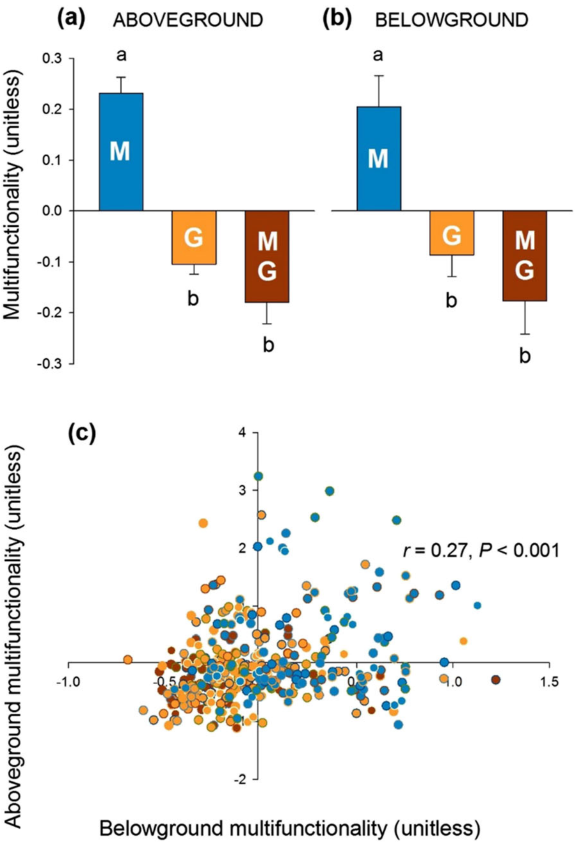

Fig. 1 Multifunctionality of (**a**) aboveground and (**b**) belowground attributes for the three land use types and (**c**) the relationship between above- and belowground multifunctionality. Different letters indicate a significant difference in multifunctionality among the land use types at $P < 0.05$. M = mowing, G = grazing, MG = mowing plus grazing

When we explored the correlation among multiple separate belowground and aboveground functions, we found some strong differences and similarities among the three land use practices. In particular, the intense land use scenario (grazing combined with mowing) decoupled the correlations among belowground and aboveground functions compared with that of single functions (mowing only or grazing only; Fig. 5). For example, there were 39 significant correlations under mowing, and this declined to 23 when sites were both mown and grazed (Fig. 5). The richness, cover and biomass of perennial forbs were generally positively correlated with all belowground attributes under mowing, but these correlations declined markedly under grazing and all but disappeared when sites were mown and grazed. Conversely, plant C, N and P were uncorrelated with soil P, at all three depth under grazing, but

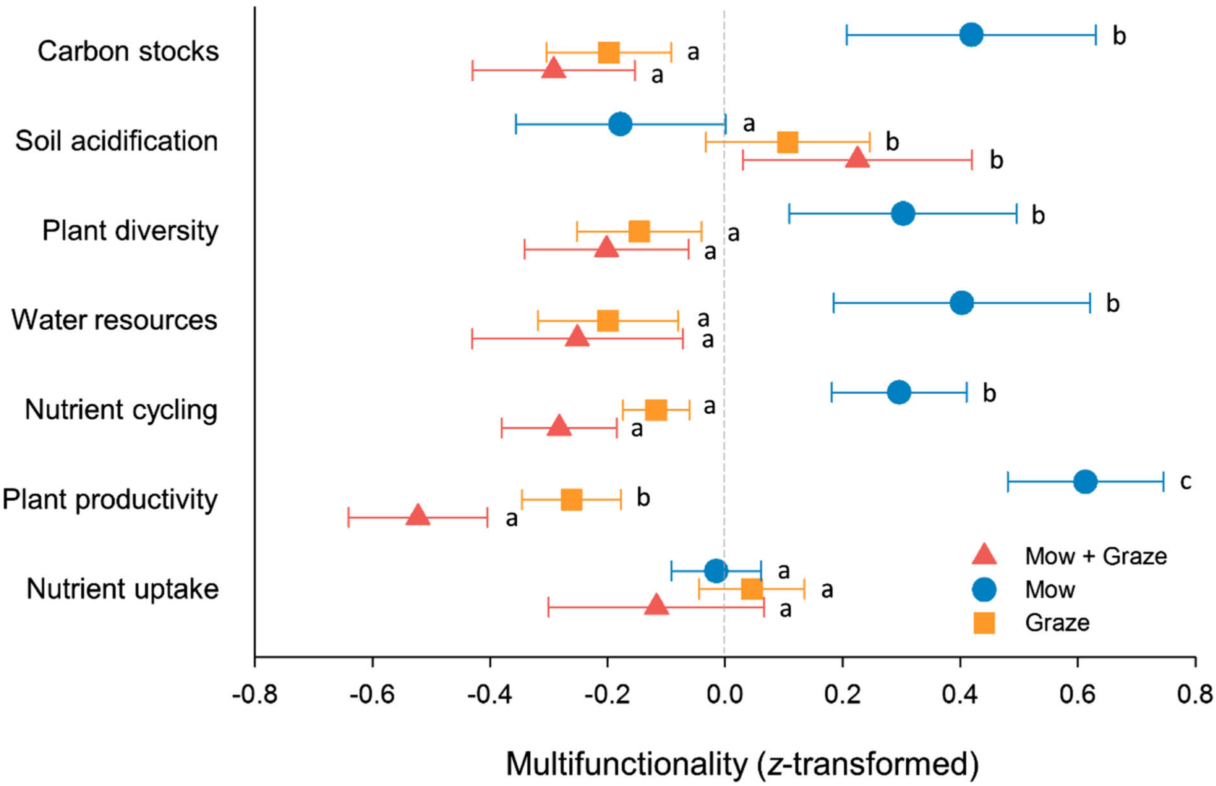

Fig. 2 Mean (± 95% CI) multifunctionality for seven ecosystem services/functions for each of the three land use types. Within a function, different letters indicate a significant difference at $P < 0.05$

when sites were grazed, and/or mown, correlations were highly positive. There were few if any correlations for annual plants and shrubs across all land use types. Perennial grass richness cover and biomass showed some negative correlations with root N under grazing but not under any other land uses. Finally, there were few correlations for shrubs, with soil P at depth being positively correlated with shrub richness, but only under the mowing plus grazing land use (Fig. 5).

Discussion

Our study provides compelling evidence of lower multifunctionality of most aboveground and belowground attributes when sites are grazed, with or without mowing, than sites under only the mowing land use. Further, there were significant reductions in most aboveground and belowground attributes when sites were grazed. Although grazing resulted in a reduction in soil C, N and P, we found no grazing-induced effects on root C, N or P. Importantly, subjecting sites to the most intense land use practice (both land uses combined) resulted in a decoupling of the correlations among belowground and aboveground functions compared with single land use practices. Overall, our study reinforces the notion that mowing results in better ecological outcomes in terms of sustaining soil processes in the semi-natural Eurasian grassland, consistent with previous studies (Wahlman and Milberg 2002; TäLle et al. 2015). Our results can provide a scientific basis for policy decisions regarding appropriate land uses to sustain soil functions and therefore healthy, productive grasslands.

Grazing impacts on functions exceed those from mowing

Land use change due to increasing intensity of anthropogenic activity is a major driver of ecosystem functions (Allan et al. 2015; Chillo et al. 2016). Grazing and mowing have similar direct effects on plant production, with non-selective reductions in productivity and cover (Baoyin et al. 2014). Unlike mowing, grazing is highly

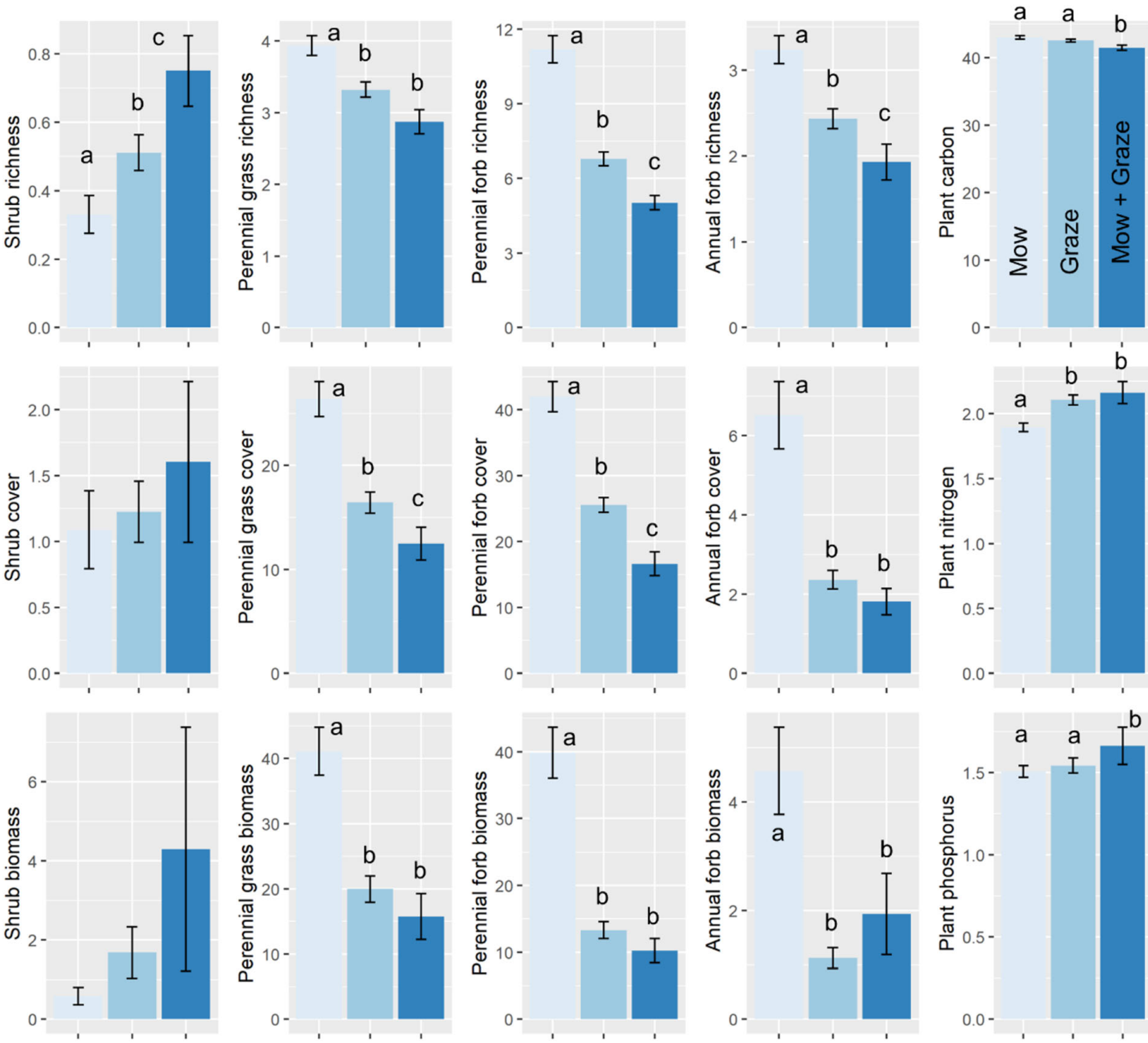

Fig. 3 Mean (± SE) values of aboveground plant attributes under the three land uses (Mowing, Grazing, and Mowing+Grazing). For a particular attribute, different superscripts indicate a significant difference among land uses. Richness values expressed as the number of species per site, plant cover, nitrogen, phosphorus and nitrogen values in %, biomass values in g m^{-2}. There were no significant differences for shrub cover and shrub biomass

selective (Zhu et al. 2020), often more intense and sustained, and rather than a one-off process. Despite some positive effects in specific areas and for certain attributes (e.g., Lu et al. 2017), grazing often leads to reductions in plant richness (Allan et al. 2015) and a range of physical effects on the soil surface (Eldridge et al. 2016). These indirect effects can lead to changes in the amount and distribution of dung and litter (Eldridge et al. 2015), reduced decomposition, declines in soil stability, and long-term reductions in soil functions (Daryanto et al. 2013). In general, the effects of mowing combined with grazing on functions were similar to those from grazing only, suggesting that mowing already grazed sites does not result in additive negative impacts on functions.

Our results indicate that, compared with mowing, most aboveground attributes were significantly reduced when sites were grazed (Fig. 2, Table S1). Reductions in plant richness and productivity under grazing have been demonstrated in other grassland systems in Switzerland (Peter et al. 2009), Italy (Catorci et al. 2014) and Sweden (TäLle et al. 2015), to name a few. As well as its

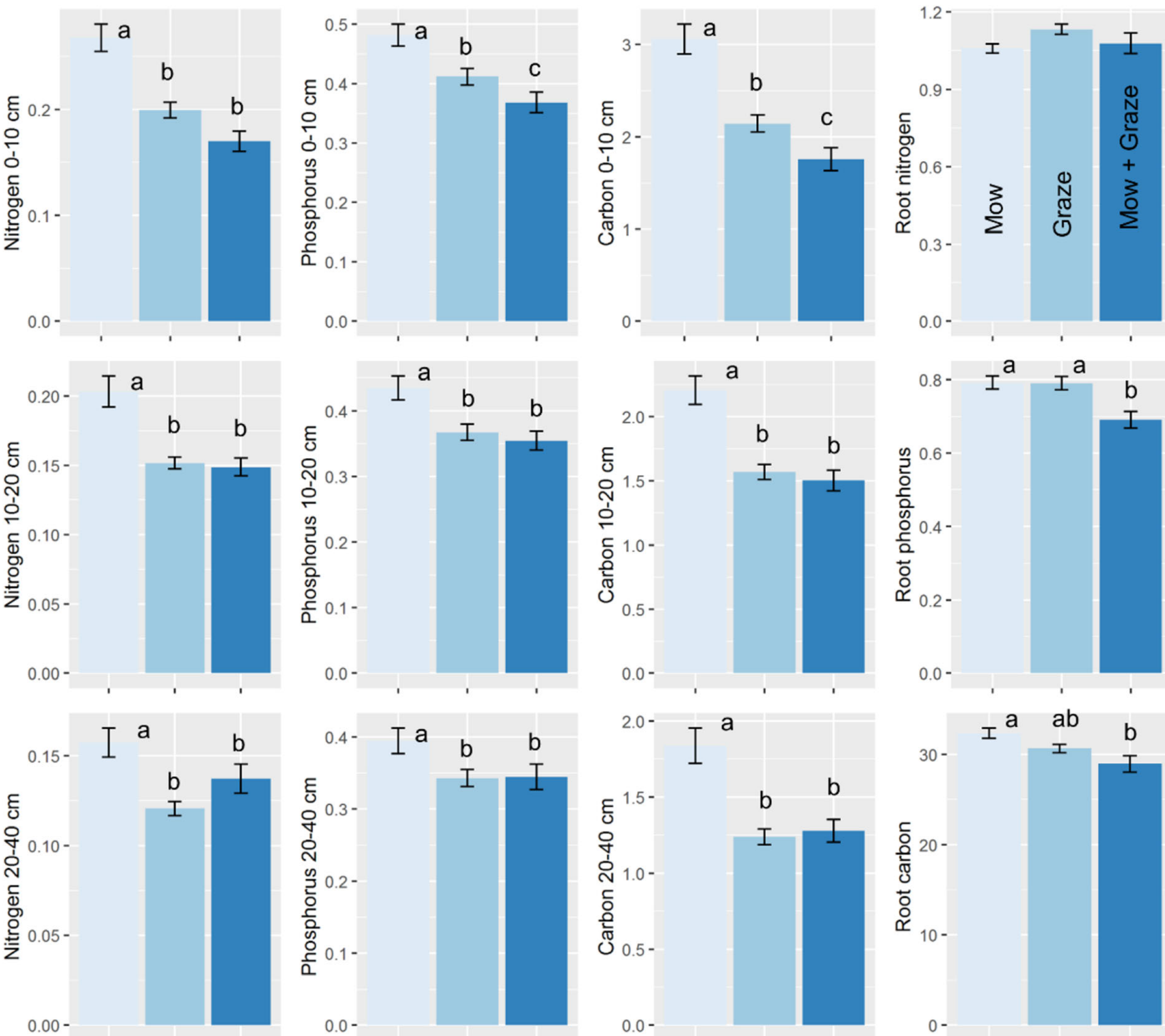

Fig. 4 Mean (± SE) values of belowground plant attributes under the three land uses (Mowing, Grazing, and Mowing+Grazing). For a particular attribute, different superscripts indicate a significant difference among land uses. All values are expressed as %. There were no significant differences in root nitrogen among the three land uses

effects on aboveground systems, grazing also affects belowground processes, directly, by altering soil physicochemical properties such as soil bulk density, and soil C, N and P concentrations (Teague et al. 2011; Walter et al. 2013) and indirectly, by altering plant nutrient use efficiency, vegetation cover, and soil community structure and diversity (Mayfield et al. 2010; He et al. 2019).

Our results showed that, compared with mowing, grazing significantly reduced soil C, N, and P contents across all depths (Table 1), consistent with previous findings from temperate steppe systems (Avila-Ospina et al. 2014; Tang et al. 2018). Our results are novel because most previous studies have focused on the very surface of the soil. We found that the negative impacts of grazing compared with mowing in C, N and P reach at least the top 40 cm of soil. Frequent livestock trampling destroys biological soil crusts and reduces soil aggregation, resulting in soil C, N and P loss (Heyburn et al. 2017; Zhou et al. 2017). Overgrazing is known to alter plant rooting patterns and C:N:P stoichiometry within the rhizosphere (Rumpel et al. 2015; Zhou et al. 2019). While large amounts of P and N are returned to the soil in dung and urine (Senapati et al. 2014), grazing has been shown to decouple C from N and P (Delgado-

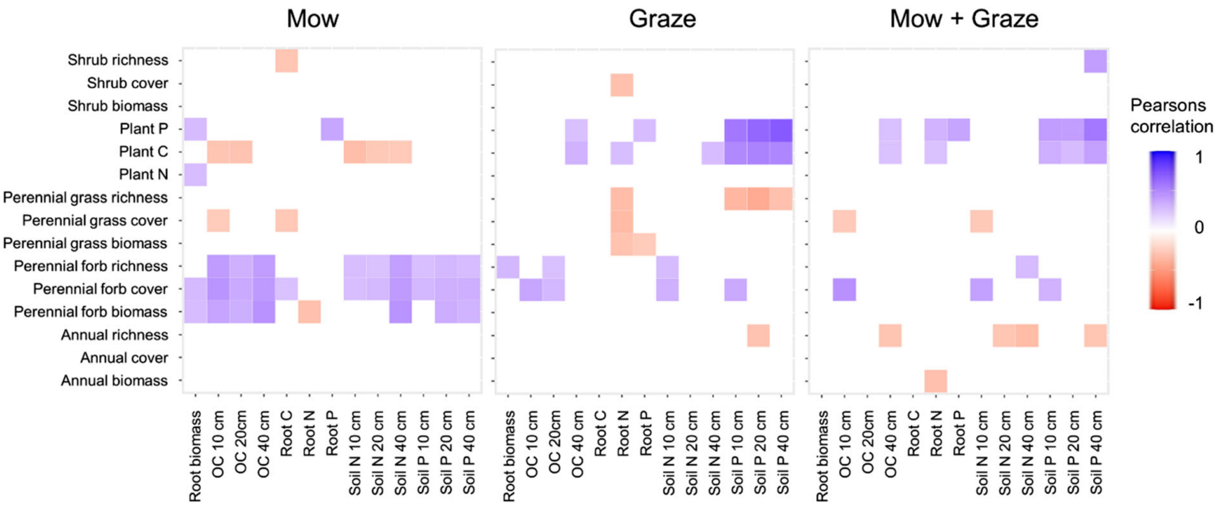

Fig. 5 Correlations among aboveground and belowground attributes for Mow, Graze and Mow + Graze landuses. Only significant ($P < 0.05$) correlations are shown

Baquerizo et al. 2013). Dung is a source of labile C, N and P, which may increase microbial biomass (Rumpel et al. 2015), and the heavy grazing pressure can increases N and P losses (Jouquet et al. 2011). Mowing may stimulate a rapid changing in the amount of organic matter (soil C, N, P) that is stored in the soil through the compensatory growth (Wang et al. 2020; McSherry and Ritchie 2013). Long-term grazing can reduce the capacity of plants to fix N and P in grasslands (Schuman et al. 1999; Yang et al. 2017). Mown sites were not grazed in order to maximise the accumulation of available pasture (Ruthrof et al. 2013). This leads to an accumulation of surface litter and soil organic matter (Hou et al. 2019). Vegetation restoration and litter accumulation may reduce nutrients loss due to erosion of soil, which may also contribute to the higher C, N and P content in mowing sites than in grazing sites, including those mown and grazed (Yang et al. 2017).

Aboveground and belowground processes decoupled under grazing

We might expect to find strong correlations between soil C, N and P and aboveground productivity, given the strong links between soil nutrients and productivity (Heyburn et al. 2017; Deyn 2017). We found that these relationships were positive under the least disturbed land use (mowing), but only for forbs (Fig. 5). However, total plant C was weakly negatively correlated with soil C and N, and these correlations were not restricted to the immediate surface 10 cm (Fig. 5). Grazing however, either singly or in combination with mowing, had two major effects. First, it decoupled any positive relationship between forbs and soil C, N and P, and second, soil P became positively associated with plant C and P. Thus, our results suggest that mowing is a less aggressive land use driver when it comes to disconnecting the multiple relationships between plant and soil properties. However, grazing impacts largely decouple the natural associations between plant communities and soil properties. Ecosystem connectivity is often associated with ecosystem properties responding in a different manner to a given driver.

Grazing can also indirectly affect interactions among plants through changes in soil physical and chemical properties, litter breakdown and soil microbial community (Herrera Paredes et al. 2016; Yao et al. 2018), with shifts in functional composition of the soil biota (Casper and Castelli 2007; Bardgett and Wardle 2010). Consistent with the interactions among plants and soil, plant roots and litter are important linkages connecting plant and soil material and energy conversion. Grazing can also affect root tissue chemistry by altering carbon allocation and nutrient uptake (Jaramillo and Detling 1988; Weemstra et al. 2016), and lead to changes in root breakdown and therefore C (Semmartin et al. 2004; Semmartin and Ghersa 2006). This can alter microbial communities associated with the rhizosphere (Wardle et al. 2004). Herbivory may influence organic matter decomposition and nutrient cycling rates by changing the quality of plant litter entering the soil through both above and belowground pathways (Wardle et al. 2002; Semmartin et al. 2008). Moreover, grazing could either accelerate or retard nutrient release from litter by altering decomposition rates (Sankaran and Augustine 2004; Zhou et al. 2017).

We acknowledge that, in this study, we did not identify differences in grazing management strategies or practices among sites that were either grazed or grazed and mown. Differences in herbivore densities, timing, frequency, herd and flock makeup, and overall management style could influence the effects of grazing on our separate response variables and overall multifunctionality. We also recognise that a crude characterisation of grazing as grazed or ungrazed (Davies and Boyd 2020) may not reflect true management styles used in the Hulun Buir grassland. However, notwithstanding this caveat, we still found that grazing had substantial impacts on many aboveground and belowground attributes. Future studies including specific grazing management strategies may well identify even greater effects of grazing on some attributes. Finally, we also acknowledge two caveats of our study. First, part of the decoupling under grazing and mowing could be an artefact of low species richness in the grazed and mown sites. Given that this is study is observational, a more definitive test of this decoupling would need to involve experimentally testing changes in function after manipulation of plant species richness. Second, it is conceivable that differences in the effects of grazing and mowing could be due to legacy effects of these treatments. Implicit in our study is that environmental conditions are consistent across the treatments in the Hulun Bair grassland and that sites have an equal likelihood of being mowed, grazed or mowed and grazed. While we made every attempt to sample sites with similar abiotic conditions, it is possible that some sites differed slightly in their abiotic signature as a result of historic lands uses imposed over thousands of years.

Concluding remarks

Our work provides novel evidence of strong correlations among aboveground and belowground functions under the single mowing land use practice. Further, more intense land use practices where mowing is combined with grazing led to a decoupling of biotic and abiotic functions. Compared with the continuous grazing or mowing plus grazing land uses, mowing can provide benefits such as the retention of litter and vegetation, increasing species richness and diversity, and a more functional soil surface due to reduced physical disturbance to the surface. In particular, our research results suggest that overgrazing will not only affect aboveground diversity and productivity, but might also have deleterious belowground effects, which are likely to have feedback effects on plant diversity and productivity. Our work provides the basis for an improved understanding of how land use affects grassland ecosystem functions. This is a priority if we are to maintain healthy productive grasslands on which the herdsmen of the Hulun Buir steppe depend for their livelihoods.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-021-04970-5.

Acknowledgements This work was supported by the National Natural Science Foundation of China (41971061) and International (Regional) Cooperation and Exchange Program of The National Natural Science Foundation of China (32061123005). M.D-B. was supported by the European Union's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie Grant Agreement No 702057 (CLIMIFUN) and by a Large Research Grant from the British Ecological Society (Grant Agreement No. LRA17\1193, MUSGONET).

References

Allan E, Manning P, Alt F, Binkenstein J, Blaser S, Blüthgen N, Böhm S, Grassein F, Hölzel N, Klaus VH, Kleinebecker T, Morris EK, Oelmann Y, Prati D, Renner SC, Rillig MC, Schaefer M, Schloter M, Schmitt B, Schöning I, Schrumpf M, Solly E, Sorkau E, Steckel J, Steffen-Dewenter I, Stempfhuber B, Tschapka M, Weiner CN, Weisser WW, Werner M, Westphal C, Wilcke W, Fischer M (2015) Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. Ecol Lett 18:834–843

Avila-Ospina L, Moison M, Yoshimoto K, Masclaux-Daubresse C (2014) Autophagy, plant senescence, and nutrient recycling. J Exp Bot 65:3799–3811

Bai Y, Wu J, Clark CM, Pan Q, Zhang L, Chen S, Wang Q, Han X (2012) Grazing alters ecosystem functioning and C:N:P stoichiometry of grasslands along a regional precipitation gradient. J Appl Ecol 49:1204–1215

Baoyin T, Li FY, Bao Q, Minggagud H, Zhong Y (2014) Effects of mowing regimes and climate variability on hay production of *Leymus chinensis* (Trin.) Tzvelev grassland in northern China. Rangel J 36:593–600

Bardgett RD, Wardle DA (2010) Aboveground-belowground linkages, biotic interactions, ecosystem processes, and global change. Oxford series in ecology and evolution. Oxford University Press, New York, USA

Blüthgen N, Simons N, Jung K, Prati D, Renner S, Boch S et al (2016) Land use imperils plant and animal community stability through changes in asynchrony rather than diversity. Nat Commun 7:10697

Cai Y, Wang X, Tian L, Zhao H, Xuyang LU, Yan Y (2014) The impact of excretal returns from yak and Tibetan sheep dung on nitrous oxide emissions in an alpine steppe on the Qinghai-Tibetan plateau. Soil Biol Biochem 76:90–99

Casper BB, Castelli JP (2007) Evaluating plant–soil feedback together with competition in a serpentine grassland. Ecol Lett 10:394–400

Catorci A, Cesaretti S, Malatesta L, Tardella FM (2014) Effects of grazing vs mowing on the functional diversity of sub-Mediterranean productive grasslands. Appl Veg Sci 17: 658–669

CENMN (Comprehensive Expedition in Nei Mongol, Ningxia, Chinese Academy of Sciences) (1985) Nei Mongol Vegetation. Science Press, Beijing

Chillo V, Ojeda RA, Capmourteres V, Anand M (2016) Functional diversity loss with increasing livestock grazing intensity in drylands: the mechanisms and their consequences depend on the taxa. J Appl Ecol 54:986–996

Daryanto S, Eldridge DJ, Throop HL (2013) Managing semi-arid woodlands for carbon storage: grazing and shrub effects on above- and belowground carbon. Agric Ecosyst Environ 169: 1–11

Davies KW, Boyd CS (2020) Grazing is not binomial (i.e., grazed or not grazed): a reply to Herman. BioSci 70:6–7

Delgado-Baquerizo M, Maestre FT, Gallardo A, Bowker MA, Wallenstein MD, Quero JL, Ochoa V, Gozalo B, García-Gómez M, Soliveres S, García-Palacios P, Berdugo M, Valencia E, Escolar C, Arredondo T, Barraza-Zepeda C, Bran D, Carreira JA, Chaieb M, Conceição AA, Derak M, Eldridge DJ, Escudero A, Espinosa CI, Gaitán J, Gatica MG, Gómez-González S, Guzman E, Gutiérrez JR, Florentino A, Hepper E, Hernández RM, Huber-Sannwald E, Jankju M, Liu J, Mau RL, Miriti M, Monerris J, Naseri K, Noumi Z, Polo V, Prina A, Pucheta E, Ramírez E, Ramírez-Collantes DA, Romão R, Tighe M, Torres D, Torres-Díaz C, Ungar ED, Val J, Wamiti W, Wang D, Zaady E (2013) Decoupling of soil nutrient cycles as a function of aridity in global drylands. Nature 502:672–676

Deyn GBD (2017) Plant life history and above–belowground interactions: missing links. Oikos 126:497–507. https://doi.org/10.1111/oik.03967

Eldridge DJ, Beecham G, Grace J (2015) Do shrubs reduce the adverse effects of grazing on soil properties? Ecohydrology 8:1503–1513

Eldridge DJ, Poore AGB, Ruiz-Colmenero M, Letnic M, Soliveres S (2016) Ecosystem structure, function and composition in rangelands are negatively affected by livestock grazing. Ecol Appl 26:1273–1283

Garland G, Banerjee S, Edlinger A, Oliveira EM, Herzog C, Wittwer R, Philippot L, Maestre FT, van der Heijden MGA (2020) A closer look at the functions behind ecosystem multifunctionality: a review. J Ecol 109:600–613. https://doi.org/10.1111/1365-2745.13511

Gao L, Kinnucan HW, Zhang Y, Qiao G (2016) The effects of a subsidy for grassland protection on livestock numbers, grazing intensity, and herders' income in Inner Mongolia. Land Use Policy 54:302–312

Habel JC, Dengler J, Janišová M, Török P, Wellstein C, Wiezik M (2013) European grassland ecosystems: threatened hotspots of biodiversity. Biodivers Conserv 22:2131–2138

Han Y, Zhang Z, Wang C, Jiang F, Xia F (2012) Effects of mowing and nitrogen addition on soil respiration in three patches in an oldfield grassland in Inner Mongolia. J Plant Ecol 5:219–228

He M, Zhou G, Tengfei Y, Groenigen KJV, Zhou X (2019) Grazing intensity significantly changes the C:N:P stoichiometry in grassland ecosystems. Glob Ecol Biogeogr 29:355–369. https://doi.org/10.1111/geb.13028

Herrera Paredes S, Lebeis SL, Bailey JK (2016) Giving back to the community: microbial mechanisms of plant–soil interactions. Funct Ecol 30:1043–1052

Heyburn J, McKenzie P, Crawley MJ, Fornara DA (2017) Long-term belowground effects of grassland management: the key role of liming. Ecol Appl 27:2001–2012

Hou SL, Lü XT, Yin JX, Yang JJ, Hu YY, Wei HW et al (2019) The relative contributions of intra- and inter-specific variation in driving community stoichiometric responses to nitrogen deposition and mowing in a grassland. Sci Total Environ 20:887–893

Jaramillo V, Detling JK (1988) Grazing history, defoliation, and competition: effects on shortgrass production and nitrogen accumulation. Ecology 69:1599–1608

Jouquet P, Boquel E, Doan TT, Rocoy M, Orange D, Rumpel C, Duc TT (2011) Do compost and vermicopost improve marcornutrient retention and plant growth in degraded tropical soils? Compost Sci Utiliz 19:15–24

Lefcheck JS, Byrnes JEK, Isbell F, Gamfeldt L, Griffin JN, Eisenhauer N, Hensel MJS, Hector A, Cardinale BJ, Duffy JE (2015) Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nat Commun 6:6936

Lu X, Kelsey KC, YanY SJ, Wang X, Cheng G, Neff JC (2017) Effects of grazing on ecosystem structure and function of alpine grasslands in Qinghai–Tibetan plateau: a synthesis. Ecosphere 8:e01656. https://doi.org/10.1002/ecs2.1656

Maestre FT, Quero JL, Gotelli NJ, Escudero A, Ochoa V, Delgado-Baquerizo M, Garcia-Gomez M, Bowker MA, Soliveres S, Escolar C, Garcia-Palacios P, Berdugo M, Valencia E, Gozalo B, Gallardo A, Aguilera L, Arredondo T, Blones J, Boeken B, Bran D, Conceicao AA, Cabrera O, Chaieb M, Derak M, Eldridge DJ, Espinosa CI, Florentino A, Gaitan J, Gatica MG, Ghiloufi W, Gomez-Gonzalez S, Gutierrez JR, Hernandez RM, Huang X, Huber-Sannwald E, Jankju M, Miriti M, Monerris J, Mau RL, Morici E, Naseri K, Ospina A, Polo V, Prina A, Pucheta E, Ramirez-Collantes DA, Romao R, Tighe M, Torres-Diaz C, Val J, Veiga JP, Wang D, Zaady E (2012) Plant species richness and ecosystem multifunctionality in global drylands. Science 335:214–218

Mayfield MM, Bonser SP, Morgan JW, Aubin I, Mcnamara S, Vesk PA (2010) What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. Glob Ecol Biogeogr 19:423–431

McSherry ME, Ritchie ME (2013) Effects of grazing on grassland soil carbon: a global review. Glob Chang Biol 19:1347–1357

NSBC (National Statistical Bureau of China). China Statistical Yearbook (2019) China statistical press: Beijing, China

Ochoa-Hueso R, Piñeiro J, Power SA (2019) Decoupling of nutrient cycles in a Eucalyptus woodland under elevated CO2. J Ecol 107:2532–2540

Peter M, Gigon A, Edwards PJ, Lüscher A (2009) Changes over three decades in the floristic composition of nutrient-poor grasslands in the Swiss alps. Biodivers Conserv 18:547–567

R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org/

Risch AC, Ochoa-Hueso R, van der Putten WH, Bump JK, Busse MD, Frey B, Gwiazdowicz DJ, Page-Dumroese DS, Vandegehuchte ML, Zimmermann S, Schütz M (2018) Size-dependent loss of aboveground animals differently affects grassland ecosystem coupling and critical functions. Nat Commun 9:3684

Rumpel C, Crème A, Ngo PT, Velásquez G, Mora ML, Chabbi A (2015) The impact of grassland management on biogeochemical cycles involving carbon, nitrogen and phosphorus. J Soil Sci Plant Nut 15:353–371

Ruthrof KX, Fontaine JB, Buizer M, Matusick G, McHenry MP, Hardy GESJ (2013) Linking restoration outcomes with mechanism: the role of site preparation, fertilisation and revegetation timing relative to soil density and water content. Plant Ecol 214:987–998

Sankaran M, Augustine DJ (2004) Large herbivores suppress decomposer abundance in a semiarid grazing ecosystem. Ecology 85:1052–1061

Schönbach P, Wan H, Gierus M, Bai Y, Müller K, Lin L, Susenbeth A, Taube F (2011) Grassland responses to grazing: effects of grazing intensity and management system in the Inner Mongolia steppe. Plant Soil 340:103–115

Schuman GE, Reeder JD, Manley JT, Hart RH, Manley WA (1999) Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecol Appl 9: 65–71

Semmartin M, Aguiar MR, Distel R, Moretto AS, Ghersa CM (2004) Litter quality and nutrient cycling affected by grazing-induced replacements in species composition along a precipitation gradient. Oikos 107:149–161

Semmartin M, Garibaldi LA, Chaneton EJ (2008) Grazing history effects on above- and below-ground litter decomposition and nutrient cycling in two co-occurring grasses. Plant Soil 303: 177–189

Semmartin M, Ghersa CM (2006) Intra-specific changes in plant morphology, associated with grazing, and effects on litter quality, carbon and nutrient dynamics during decomposition. Austral Ecology 31:99–105

Senapati N, Chabbi A, Gastal F, Smith P, Mascher N, Naisse C (2014) Net carbon storage measure in a mowed and grazed temperate sown grassland shows potential for carbon sequestration under grazed system. Carbon Manag 5:131–144

Soil Survey Staff (1951) 'Soil survey manual. USDA Agric. Hand Book 18.' (Govt. Printing Office: Washington DC, USA)

Sparks DL, Page AL, Loeppert PA, Soltanpour PN, Tabatabai MA, Johnston CT & Sumner ME. (1996). Methods of soil analysis part 3: chemical methods. Soil science Society of America and American Society of Agronomy, Madison, WI

TäLle M, Fogelfors H, Westerberg L, Milberg P (2015) The conservation benefit of mowing vs grazing for management of species-rich grasslands: a multi-site, multi-year field experiment. Nord J Bot 33:761–768

Tang Z, Xu W, Zhou G, Bai Y, Li J, Tang X, Chen D, Liu Q, Ma W, Xiong G, He H, He N, Guo Y, Guo Q, Zhu J, Han W, Hu H, Fang J, Xie Z (2018) Patterns of plant carbon, nitrogen, and phosphorus concentration in relation to productivity in China's terrestrial ecosystems. P Natl Acad Sci USA 115: 4033–4038

Teague WR, Dowhower SL, Baker SA, Haile N, Conover DM (2011) Grazing management impacts on vegetation soil biota and chemical physical and hydrological properties in tall grass prairie. Agric Ecosyst Environ 141:310–322

Tilman D, Balzer C, Hill J, Befort BL (2011) Global food demand and the sustainable intensification of agriculture. Proc Natl Acad Sci U S A 108:20260–20264

Travers SK, Eldridge DJ, Val J, Oliver I (2019) Rabbits and livestock grazing alter the structure and composition of mid-storey plants in a wooded dryland. Agr Ecosyst Environ 277:53–60

Wahlman H, Milberg P (2002) Management of semi-natural grassland vegetation; evaluation of long-term experiment in southern Sweden. Ann Bot Fenn 39:159–166

Walter J, Hein R, Beierkuhnlein C, Hammerl V, Jentsch A, Schädler M, Schuerings J, Kreyling J (2013) Combined effects of multifactor climate change and land-use on decomposition in temperate grassland. Soil Biol Biochem 60:10–18

Wang X, Li FY, Wang Y, Liu X, Cheng J, Zhang J, Baoyin T, Bardgett RD (2020) High ecosystem multifunctionality under moderate grazing is associated with high plant but low bacterial diversity in a semi-arid steppe grassland. Plant Soil 448:265–276. https://doi.org/10.1007/s11104-020-04430-6

Wardle DA, Bardgett RD, Klironomos JN, Setala H, van der Putten WH (2004) Ecological linkages between aboveground and belowground biota. Science 304:1629–1633

Wardle DA, Bonner KI, Barker GM (2002) Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. Funct Ecol 16:585–595

Weemstra M, Mommer L, Visser EJW, Ruijven J, Kuyper TW, Mohren GMJ, Sterck FJ (2016) Towards a multidimensional root trait framework: a tree root review. New Phytol 211: 1159–1169

Yang Z, Baoyin T, Minggagud H, Sun H, Li FY (2017) Recovery succession drives the convergence, and grazing versus fencing drives the divergence of plant and soil N/P stoichiometry in a semiarid steppe of Inner Mongolia. Plant Soil 420:1–12

Yao X, Zhang N, Zeng H, Wang W (2018) Effects of soil depth and plant-soil interaction on microbial community in temperate grasslands of northern China. Sci Total Environ 630:96–102

Ye XH, Pan X, Cornwell WK, Cornelissen JHC, Dong M (2013) Decoupling of above and belowground C and N pools within predominant plant species stipa grandis along a precipitation gradient in Chinese steppe zone. Biogeoences Discussions 10:4995–5013

Zhou G, Luo Q, Chen Y, Hu J, He M, Gao J et al (2019) Interactive effects of grazing and global change factors on soil and ecosystem respiration in grassland ecosystems: a global synthesis. J Appl Ecol 56:2007–2019

Zhou G, Zhou X, He Y, Shao J, Hu Z, Liu R, Zhou H, Hosseinibai S (2017) Grazing intensity significantly affects belowground carbon and nitrogen cycling in grassland ecosystems: a meta-analysis. Glob Chang Biol 23:1167–1179

Zhu YJ, Delgado-Baquerizo M, Shan D, Yang XH, Liu YS, Eldridge DJ (2020) Diversity-productivity relationships vary in response to increasing land-use intensity. Plant Soil:1–10

Zhu YJ, Shan D, Wang BZ, Shi ZJ, Yang XH, Liu YS (2019) Floristic features and vegetation classification of the Hulun Buir steppe in North China: geography and climate-driven steppe diversification. Glob Ecol Conserv 20:e00741