



# Diversity-productivity relationships vary in response to increasing land-use intensity

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## Abstract

**Background and aims** Theoretical and experimental evidence, predominantly from temperate grasslands, demonstrates strong support for a positive relationship between biodiversity and ecosystem functioning. This relationship is likely to be affected by land use drivers that remove vegetation, and/or disturb the soil surface. Our study aimed to examine the links between land use intensity and plant richness, and potential effects on productivity and function.

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**Methods** We examined the impact of mowing, grazing, and mowing plus grazing, on the relationship between plant diversity, and two measures of function; above-ground biomass and soil carbon. Our focus was on Eurasian grasslands, which support a high diversity of plant species, millions of people and their livelihoods, and where livestock grazing and mowing are predominant land uses. We used structural equation modelling to examine the effects of these land use drivers at 371 sites across 100,000 km<sup>2</sup> of northern China.

**Results** Mown sites supported a greater number of plant species than sites that were either grazed, or grazed and mown. Increasing plant richness was associated with greater aboveground biomass and soil carbon when sites were either mown or grazed, but these relationships disappeared when the two land use drivers were combined. Relationships among plant diversity and two measures of function were maintained when we accounted for the spatial differences between sites.

**Conclusion** Our results demonstrate that additional land use pressure imposed when mowing and grazing are applied together can decouple the positive associations between plant richness and functions. An understanding of these potential effects is important if we are to adopt strategies, such as destocking or reduced mowing, to maintain diverse grassland ecosystems, and their services and functions.

**Keywords** Grasslands · Inner Mongolia · Sheep grazing · Livestock disturbance · Mowing · Plant diversity · Ecosystem functions

## Introduction

Theoretical and experimental evidence over the last decades provides support for a strong positive relationship between plant diversity and key ecosystem functions such as plant production and soil organic carbon (SOC; Diaz et al. 2009; Hooper et al. 2012). These biodiversity-ecosystem function relationships have been, for example, largely studied in temperate European systems where reductions in diversity are known to have marked reductions in function (Hector et al. 1999, 2001; Kirwan et al. 2007). Global studies have demonstrated that diverse grasslands lead to more stable plant productivity and soil carbon sequestration (Grace et al. 2016; Wang et al. 2019b). Such a relationship is expected to be highly vulnerable to global change drivers, but studies evaluating how the biodiversity-ecosystem function relationships changes across different ecological contexts are lacking.

We know relatively little about how diversity-productivity relationships might be affected by disturbance, particularly different land-use types that involve either herbivory (e.g. mowing), a combination of herbivory (mowing) and surface disturbance (grazing), or more intensive landuses that combine both mowing and grazing (Fig. 1a). Temperate Eurasian grasslands have evolved under a long history of biomass removal (Fischer and Wipf 2002; Kristin et al. 2017) and have been maintained for thousands of years by intensive mowing and grazing by livestock (Socher et al. 2012), which are likely to have a strong influence on how diverse plant communities function. Studies from Eurasian grasslands indicate that mowing and grazing, individually, can have significant effects on plant diversity in temperate grasslands (Zhou et al. 2019; Smith et al. 2018). While the effects on grassland biodiversity of grazing or mowing, with or without fertilization, have been examined (Yang et al. 2012; Socher et al. 2012; Kristin et al. 2017), little is known about the potential additive effects of combining both land use drivers on plant richness and grassland functions such as primary productivity and soil function, and how this might likely influence biodiversity-ecosystem function relationships. An understanding of the links between the two important land use drivers and biodiversity-productivity relationship is critically important if we are to manage Eurasian grasslands sustainably as the planet moves towards a hotter and drier climate, and grazing increases to feed a larger global population.

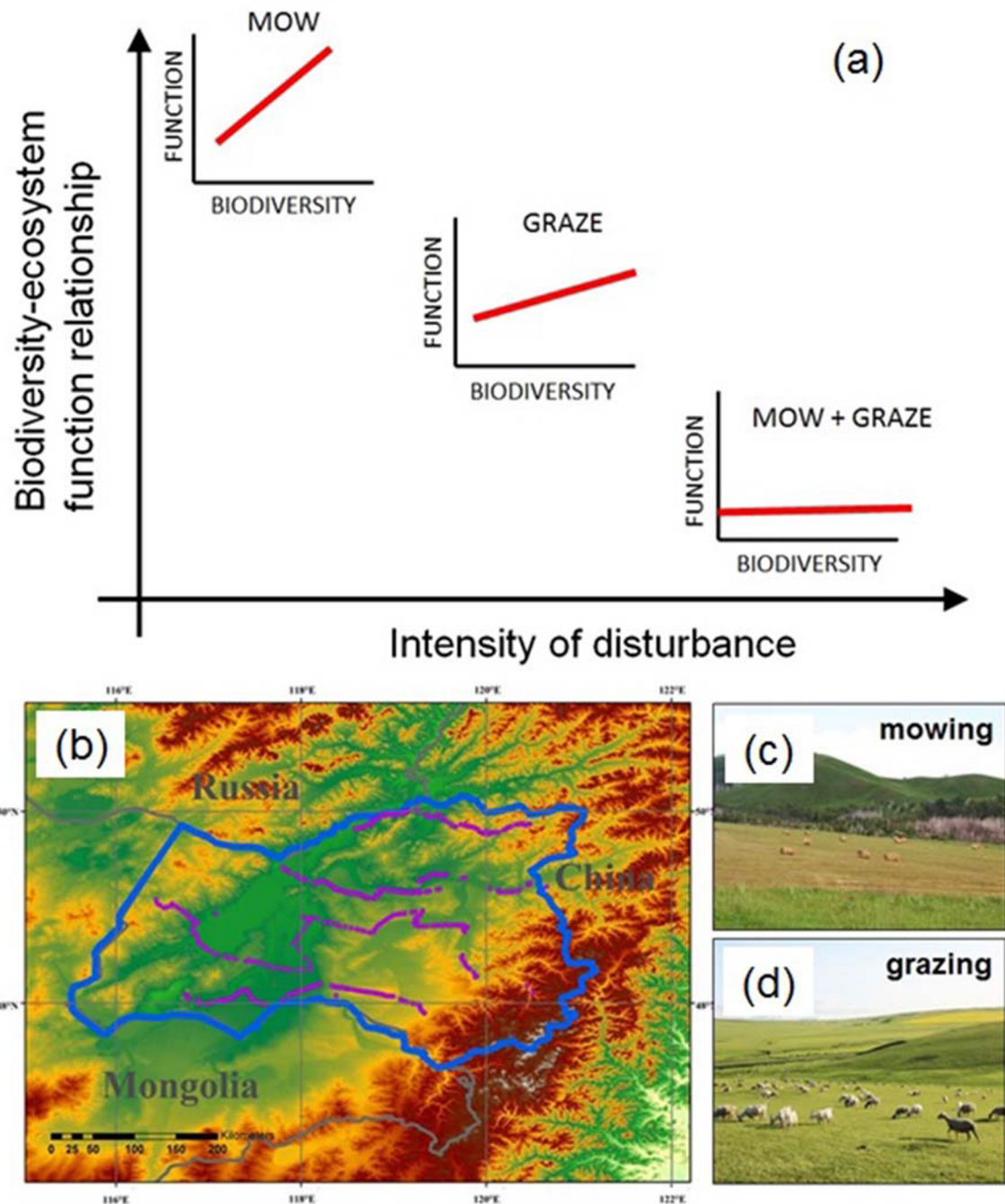
Mowing and grazing have markedly different effects on grassland ecosystems. Mowing is non-selective, resulting in a uniform removal of plant biomass with little or no surface disturbance (Socher et al. 2012). Mowing can enhance niche complementarity, allowing more species to capture light and nutrients (Mason et al. 2011; Moineau et al. 2018), and stimulating increases in species diversity and ecosystem functioning (Mason et al. 2011). Conversely, though it supports the livelihoods of millions of peoples worldwide (Petz et al. 2014; Eldridge and Manuel 2018), grazing can also have substantial negative effects on ecosystem structure, composition and function (Eldridge et al. 2016), leading to changes in plant community composition, reductions in soil health and reduced hydrological functions. Unlike mowing, grazing is highly selective, combining the selective removal of vegetation with physical disturbance to the soil surface (Fig. 1a). Livestock-induced disturbance to the soil surface creates gaps in the vegetation, promoting the establishment and persistence of annual, exotic and light-demanding species (Köhler et al. 2016; Rupprecht et al. 2016).

In this study we examined the relationships between plant richness, and two essential functions: aboveground plant biomass and soil organic carbon in grasslands, under three land uses that represent a gradient from low to intensive across a large area of Eurasian grasslands in Inner Mongolia. We had three hypotheses; First, we expected that mown sites, which represent sites under the least intensive land use, should support the greatest plant richness, given that mowing will reduce the influence of large biomass plants, potentially releasing subordinate species from competition. Second, we expected that the relationship between richness, and both productivity and function, would be strongest under mowing, because grazing has both herbivory and soil disturbance effects. Finally, we expected that when grazing and mowing were combined in these grassland sites, any positive relationships between richness and productivity-function would disappear.

## Methods

### Site description

The study was located in the Hulun Buir grassland, Inner Mongolia Autonomous Region, P.R. China across an area of about 100,000 km<sup>2</sup>, between 47°05′–53°20′N and 115°31′–123°00′E. The study area lies among China,

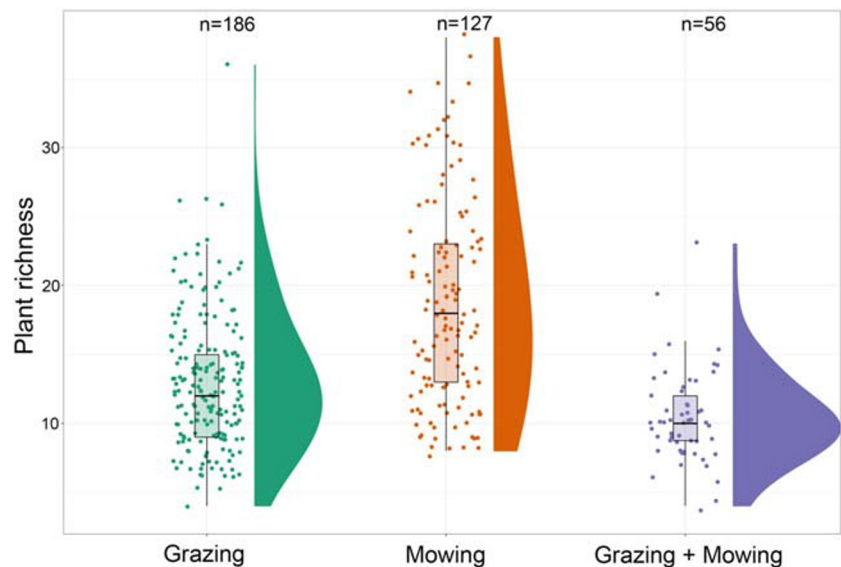


**Fig. 1** (a) Biodiversity-ecosystem function relationship with predicted changes with increasing intensity of land use. (b) Map of the research area in Inner Mongolia China showing the location of the four west-east transects, and images of plots that are (c) mown or (d) grazed

Mongolia and Russia (CENMN 1985; Zhang et al. 2011; Zhu et al. 2019) (Fig. 1b). The Hulun Buir grassland comprise relatively flat, vast and undulating high plains, and the dominant management uses are mowing (Fig. 2b),

grazing (Fig. 2c), and the combination of mowing and grazing. In the Hulun Buir grassland, grazing is carried out year-round (except during the banned period in May), and mowing is generally carried out in late August, at the

**Fig. 2** Box and raincloud plots of plant richness for grazing, mowing and grazing + mowing land-use types



end of the grassland growing season. The semiarid continental climate is characterized by mean annual precipitation of 250–350 mm and mean annual temperature ranging from 0 to 3 °C, mean growing season (May to September) temperatures from 14 to 18 °C, and mean winter temperatures from –20 to –18.5 °C. Rainfall declines from the northeast to the southwest, and approximately 80% is concentrated between June and September. The frost-free period ranges from 85 to 155 days. The temperature in the southwest is higher than in the northeast, with an annual sunshine period of 2650–3000 h (Zhang et al. 2011; Huhe et al. 2014; Liu et al. 2014). The perennial rhizomatous grass *Leymus chinensis*, the perennial bunchgrass *Stipa grandis*, and the perennial sedge *Carex duriuscula* dominate typical steppe communities (Zhu et al. 2019). The major soil types of this region are chernozems and chestnuts (CENMN 1985). We recorded 193 species across the 371 sites. Of these, 11% were grasses and the remainder forbs and shrubs. The most common grass species were *Carex duriuscula* (65% of sites), *Leymus chinensis* (58%) and *Stipa grandis* (44%). Plant cover ranged from 8 to 85%.

#### Sampling procedures

We sampled the grassland community in July and August 2017 and 2018, along four west-east transects of about 400 km. Transects ran from the eastern end of the western foothills of the Great Khingan Mountains to the western end of the China-Mongolia border, and plots

were distributed relatively evenly along these transects every 2–3 km, except in urban, disturbed areas, rivers and lakes. In total, 371 sites were selected away from roads (> 100 m) in homogeneous and natural steppe vegetation (Fig. 1b). The land use of each site was verified by interviewing local pastoralists. Within each site, we established three 1 m × 1 m quadrats separated by distances of >10 m) within which we measured the total cover, and cover, density and height of every vascular plant species. We also recorded the location (latitude, longitude) and environmental data such as altitude, aspect, slope angle, bedrock, topographic position, and whether the grassland was grazed, mown or both. Since almost all the grassland in Hulun Buir is allocated to local farmers for either grazing or hay production, natural ‘control’ areas are largely non-existent across the study area. All the plants in each quadrat were clipped, dried to a constant weight at 80 °C, and weighed to calculate aboveground biomass. Three 5 cm diameter soil cores were collected, to a depth of 15 cm from each quadrat using a soil auger. Samples were combined, air dried, and visible plant material and roots removed and the soil ground to pass a 0.5 mm sieve. Total soil carbon (C) was analyzed on a C-N analyzer (CN-2000, LECO Inc., St. Joseph, MI).

#### Statistical analyses

All analyses were based on site-level data. We used a linear mixed effect model, with transects as random



effects, to examine potential differences in plant richness between the three land use categories, after using standard diagnostic tests (G-G plots, homogeneity of residuals) in the R statistical package (Vers. 3.6.2; R Core Team 2019). A Least Significant Difference (LSD) test was used to identify those land uses that differed significantly. We then used regression analysis to examine potential relationships between plant richness and both soil carbon and aboveground plant biomass in R. We tested both linear and nonlinear models and used AIC to select the most parsimonious model.

Finally, we used Structural Equation Modelling (SEM; Grace 2006) to analyze the effects of different land-use types (grazing, mowing, grazing + mowing) on site-level plant richness, or plant cover, and ecosystem functions (soil organic carbon and aboveground biomass). We developed separate models for each land-use type. Structural equation modelling was used because it allowed us to partition direct and indirect effects of one variable upon another and to estimate the strengths of these multiple effects (Eldridge et al. 2018).

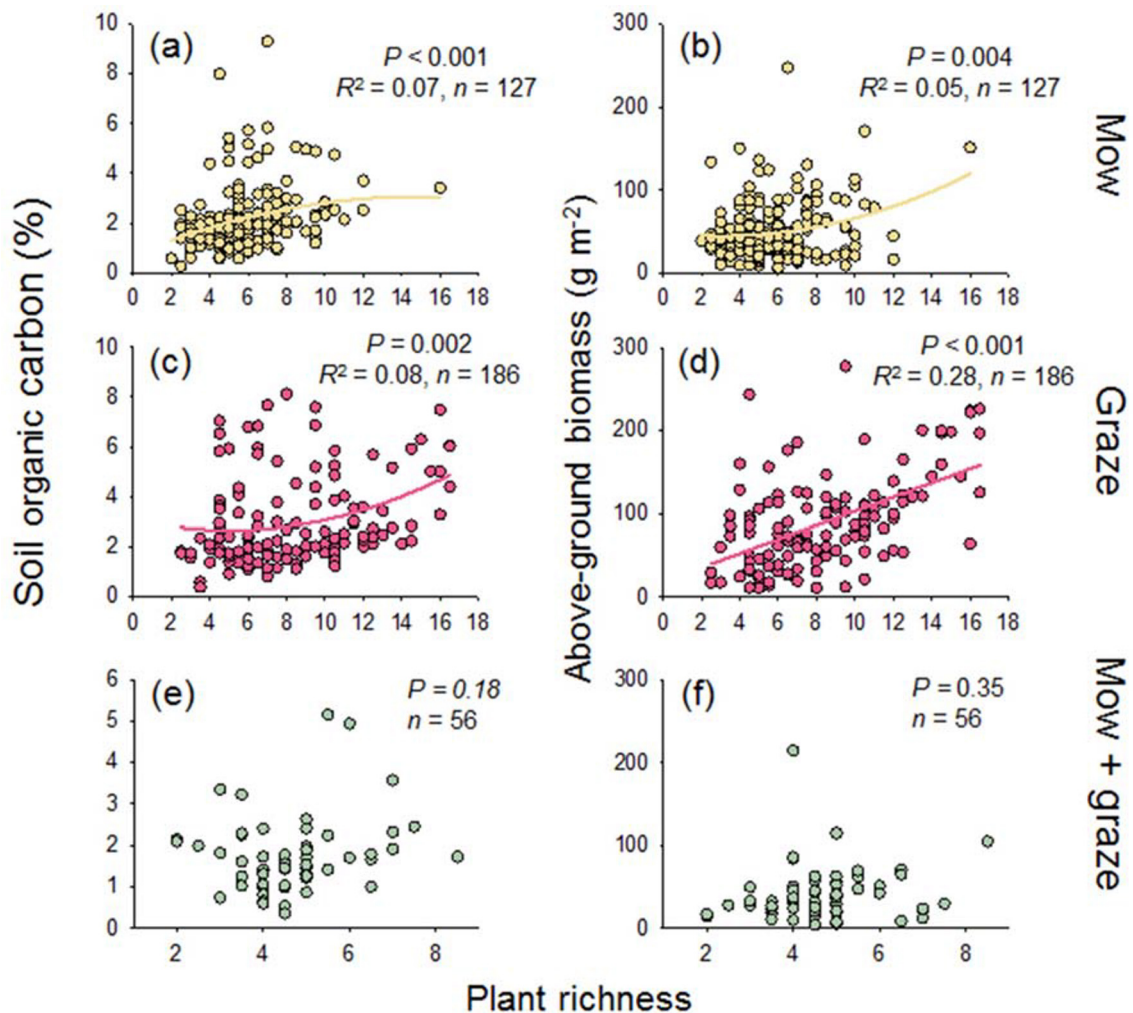
We fitted three SEMs where we examined the relationships among location (latitude, longitude), plant richness (at the site level), and two measures of function (aboveground plant biomass, soil organic carbon). Our a priori model predicted that plant richness directly influences both biomass and soil carbon, after accounting for the effects of location i.e. the location of all study sites. To account for any spatial correlation in our data, we expressed location as a composite variable made up of latitude, cosine longitude and sine longitude. Both measures of function, biomass and soil carbon, were allowed to covary (double headed arrow). Separate models using either untransformed or transformed ( $\log_{10}$ ) data revealed that models using untransformed data were superior ( $AIC < 2$ ). The a priori model was compared with the variance-covariance matrix to assess an overall goodness-of-fit, using the  $\chi^2$  statistic. The goodness of fit test estimates the probability of the observed data given the a priori model structure (Appendix S1), indicating whether the models are highly plausible causal structures underlying the observed correlations. Because our a priori model was a good fit to our data (low  $\chi^2$ , high Goodness of Fit Index [GFI] and high Normal Fit Index [NFI] or low root mean square error of approximation [RMSEA]) we made no post hoc alterations to the model, allowing us to interpret the path coefficients of the model and the  $P$  values. Our analyses with the AMOS 22 (IBM, Chicago, IL, USA) software.

## Results

Our results indicated a significant effect of landuse on plant richness ( $F_{2,365.6} = 43.1$ ,  $P < 0.001$ ; Fig. 2), with greater plant richness under mowing than either the grazing or mowing plus grazing. Moreover, we found positive associations between plant richness, and aboveground biomass and soil carbon, for mowing and grazing alone. Non-linear models best described the relationships between richness and soil carbon for mown and grazed sites, and for the relationship between richness and biomass for mown sites. However, these relationships broke down across locations wherein both mowing and grazing were applied simultaneously. For example, increasing plant richness was associated with increasing soil carbon (Fig. 3a;  $R^2 = 0.07$ ) and aboveground biomass (Fig. 3b;  $R^2 = 0.28$ ) across mown sites, and similar, though weaker trends, across grazed sites (soil carbon,  $R^2 = 0.07$ , Fig. 3c; biomass:  $R^2 = 0.04$ , Fig. 3d). However, when sites were both mown and grazed, these relationships were non-significant (Figs. 3e-f). When we examined effects of cover on functions, it was less sensitive to changes in the intensity of land use drivers (Fig. S2).

### Direct and indirect effects among plant richness and functional variables

Our structural equation modelling provided further evidence that, in locations being grazed and mowed simultaneously, the relationship between plant richness and ecosystem functions collapses (Fig. 4). However, when mowing or grazing are applied separately, we still found positive associations between richness and ecosystem functions. For instance, plant richness had strong positive effects on plant biomass under mowing, but the strength of the effect declined under grazing. We found a weak effect of richness on soil carbon, but only under grazing. When we modelled the effects of plant cover on carbon and biomass, given the reported strong relationship between cover and biomass (e.g. Röttgermann et al. 2000), we found that, unlike the results for richness, the strong positive effects on biomass were retained, irrespective of treatment (Fig. S2). These results were maintained when we accounted for the spatial differences among the sites i.e. differences in latitude and longitude, in our models.



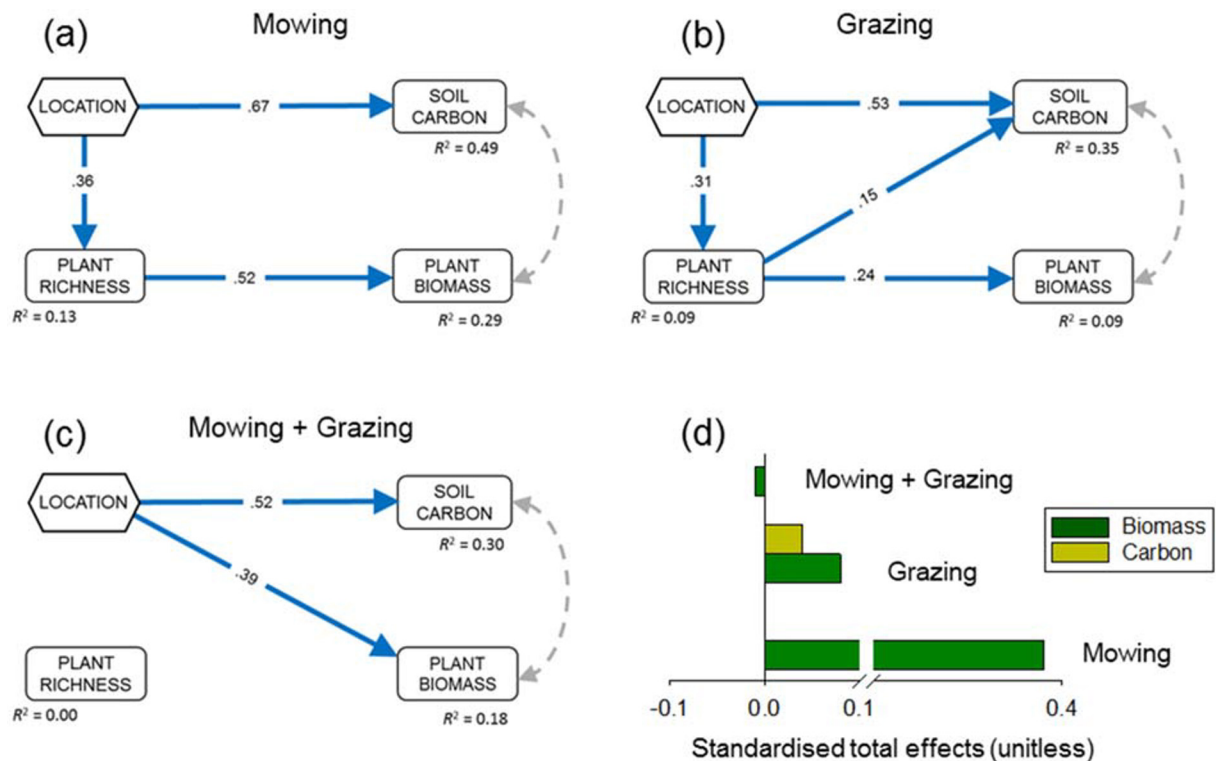
**Fig. 3** Relationships between plant richness, and soil organic carbon (%) and aboveground biomass (m<sup>-2</sup>) for mowing, grazing, and grazing + mowing land-use types

## Discussion

Using an extensive sampling network of 371 sites across 100,000 km<sup>2</sup> of northern China, one of the largest remaining grasslands on Earth, we show that locations under two land-use drivers, mowing and grazing, had lower levels of plant richness than those locations including either mowing or grazing applied alone. More importantly, the correlations among plant richness and aboveground and below-ground functions declined with increasing land-use intensity i.e. from mowing, through grazing, to combined mowing and grazing. 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

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

Plant richness has been shown to play an important role in maintaining productive, functional and resilient temperate and alpine grasslands (Kuzyakov and Domanski 2002; Yun and Wesche 2016) and dryland ecosystems globally (Maestre et al. 2016). Increasing richness is linked to a greater number of plant functional types (grasses, forbs, shrubs), and would be expected to support a greater diversity of litter, and root types with a greater range of organic exudates (Bezemer et al. 2006) and more biomass (Deyn et al. 2011). A more diverse plant community would also be expected to produce more varied litter with different decomposition rates



**Fig. 4** Structural equation model depicting the effects of the location (latitude, cosine longitude, sine longitude), plant richness, soil organic carbon and plant biomass under (a) mowing, (b) grazing, (c) grazing + mowing treatment, and (d) the standardized total effects of the three land-use types on biomass and soil carbon.

and chemistries (e.g., wide ranges of C:N ratios; Bardgett and Wardle 2013). These attributes all likely contribute to the strong positive relationships between plant richness and ecosystem function. Our results accord with these positive biodiversity-function associations where single land-use types occur, but highlight the fact that these critically important associations are highly vulnerable and can disappear when multiple land use management practices (grazing + mowing) are applied simultaneously.

Regular mowing is used to maintain grassland biodiversity (Collins et al. 1998; Prober et al. 2007) and has been an integral component of semi-natural grassland management in Europe and China for thousands of years (Hansson and Fogelfors 2000). We found that plant richness and function were positively related under mowing, but the explanatory power of the relationship was relatively weak. Mowing can increase population and community stability in temperate grassland ecosystem (Yang et al. 2012), and mowing has also been

shown to lead, indirectly, to increases in plant species richness (Benot et al. 2014; Kotas et al. 2017; Chai et al. 2019) via compensatory growth (Kitchen et al. 2009; Wan et al. 2016), removal of dead plant material that enhances plant establishment, resulting in greater productivity and diversity (Yang et al. 2019; Zhang et al. 2018; Zhou et al. 2019). Mowing would be expected to release subordinate plant species from competition by reducing the biomass of taller dominant plants (Smith et al. 2018; Liu et al. 2018) and can increase the capacity of plants to buffer the negative effects of N enrichment on diversity (Zheng et al. 2017; Yang et al. 2019). Compared with mowing plus grazing, the most obvious effect of mowing is to reduce aboveground biomass, indiscriminately, irrespective of plant palatability (Fu and Shen 2017). In our study, grazing reduced plant richness compared with mowing, and compared with mown sites, the explanatory power on plant biomass was substantially diminished (Fig. 4a and b). Interestingly, however, we also found a weak correlation

between richness and soil C under grazing but not under mowing (Fig. 4). The most parsimonious explanations relate to mechanistic differences between locations affected by both land use drivers.

We found that in locations when grazing and mowing were applied together, the effects of richness on soil C and plant biomass were decoupled compared with the same association in either mowed or grazed locations (Fig. 4c). Furthermore, grazed and mown sites had lower plant richness than either land use alone (Fig. 2). The expected effect of both mowing and grazing is to remove biomass indiscriminately (mowing), selectively remove palatable or sensitive plants, disturb the soil surface, increase erosion, alter soil hydrological processes (Prober et al. 2007; Socher et al. 2013; Eldridge et al. 2016), change soil microbial food webs (Wang et al. 2019a) and influence soil fungal functional groups (Eldridge and Manuel 2018). It is possible that the lack of a significant relationship between richness and function at sites that were both mown and grazed might be an artefact of the low range in plant richness values resulting from the effects of a combined treatments. Low intensity management of high diversity grasslands can lead to potentially high forage production (Weigelt et al. 2009), and mowing has been shown to increase population and community stability in temperate grasslands (Yang et al. 2012). Intensive grazing combined with mowing has been shown to reduce not only plant richness, but the richness of lichens, grasshoppers and butterflies (Allan et al. 2014). Thus mowing combined with grazing will remove aboveground plant reserves, reducing belowground processes (Socher et al. 2012; Kristin et al. 2017; Larreguy et al. 2017), and selectively remove species that might perform specific functions and services such as N fixation, hydrological function, or those associated with specific microbial functions of decomposition (Soliveres et al. 2012; Allan et al. 2014; Boch et al. 2016; Kruse et al. 2016). Mowing can also reduce structural heterogeneity by preferentially removing taller plants (Tälle et al. 2016; Valkó et al. 2012) allowing herbivores access to smaller, less grazing-tolerant species. Overall, therefore, it is not unexpected that combining both land-use types reduces richness more than either land-use driver separately, thereby weakening the linkages between richness and critical ecosystem functions.

## Concluding remarks

A better understanding how mowing and grazing, together, affect plant community structure and ecosystem function is urgently needed to ensure the sustainable management of large areas of the world's grasslands. Our work provides novel evidence that the combination of two land uses was sufficient to decouple the essential associations between biodiversity and ecosystem functions in one of the largest remaining grasslands of Earth. In particular, our research indicates that grazing combined with mowing will likely reduce plant richness and alter the positive effects of plant richness on C sequestration and grassland productivity. This is likely to be more important as Earth experiences a drier and more variable climate. Under such a scenario, producers will be forced to increase stocking rates to maintain their livelihoods, on a land base that is declining due to degradation of existing grasslands. Given that both mowing and grazing are economically fundamental for people living in the studied ecosystems, our work suggests that in Hulun Buir grasslands, management practices including single land use drivers are likely to maintain the positive effects of biodiversity on ecosystem functions, while maintaining livestock productivity.

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**Authors' contributions** X. Yang, Y. Liu and D.J. Eldridge designed the research; Y. Zhu and D.J. Eldridge performed the research; Y. Zhu and D. Shan contributed data; Y. Zhu and D.J. Eldridge analyzed the data; Y. Zhu, D.J. Eldridge and M. Delgado-Baquerizo wrote the paper; all authors contributed to editing the manuscript.

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