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Plant biotype interacting grazing activity shapes grassland ecosystem functions

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Abstract

Grasslands play an essential role in maintaining the health of planet Earth, but many grasslands have lost their ecosystem services due to unsustainable management practices, such as overgrazing. Little is known about how grazing activity interacts with plant biotypes, impacting grassland ecosystem services. Here, we (1) assessed the relative performance of five plant biotypes in response to grazing activities and (2) determined the effectiveness of grazing exclusion in enhancing soil physiochemical properties in grasslands. The synthesis of 39,214 observations on plant-, soil-, and anthropogeny-related factors from 88 published studies revealed that grazing exclusion increased aboveground plant biomass accumulation by 100.4% (±4.2 SE), belowground biomass by 70.2% (±25.7), total soil C content by 21.4% (±1.7), and soil organic carbon (SOC) concentration by 14.3% (±0.8), on average, as compared to moderate-to-heavy (MtH) grazing. Plant biotypes responded to grazing activities differently; alpine meadows increased total soil C content by 107.2%, alpine steppes increased SOC by 52.2%, but desert steppes decreased total C content by 21.8% under the grazing exclusion. All plant biotypes reduced soil bulk density by 6.4%–19.4% under grazing exclusion. Soil microbial community diversity responded to grazing activities inconsistently, ranging from an 18% decrease to a 26% increase in soil microbial diversity compared to MtH grazing. We conclude that selecting appropriate plant biotypes alongside improved grazing management will enhance grassland ecosystem functions and services as plant biotypes affect aboveground and belowground biomass and interface with soil physiochemical properties.

KEYWORDS
bulk density, carbon cycling, grassland ecosystem services, microbial community diversity, plant composition, soil physiochemical property

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Li Wang and Shou-Jiang Feng contributed equally to the work reported here.

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INTRODUCTION

The global grasslands are approximately 3.4 billion ha, covering about 25% of the Earth's land surface (Ontl & Janowiak, 2017). Grasslands play an essential role in maintaining sustainable ecosystems on the Earth. However, a large proportion of global grasslands has lost ecosystem services mainly due to unsustainable management practices (Lin et al., 2022; Niu et al., 2021), such as intensified hay harvest (Jung et al., 2022), overexploitation (Guo et al., 2022), and eutrophication from fertilizer use and nitrogen (N) deposition (De Frenne et al., 2022). Also, several other factors affect grassland ecosystem functioning, including extreme weather events (Kang et al., 2022; Pei et al., 2021) and fluctuation in temperature and water availability due to climate change (Fan et al., 2021), invasive species (Ravi et al., 2022; Xing et al., 2021), insect and rodent infestation (Soubry et al., 2021), and habitat change (Warren et al., 2021).

Livestock grazing has been identified as a primary anthropogenic factor affecting grassland ecosystem services worldwide (Donovan & Monaghan, 2021; Teutscherova et al., 2021; Venter et al., 2021). Overgrazing—grazing for extended periods without sufficient vegetation recovery—causes a reduction in net primary production (Donovan & Monaghan, 2021; Wei et al., 2022), soil compaction as a result of animal trampling (Julich et al., 2022), the depletion of topsoil fertility and the reduction of water infiltration (Panahi et al., 2021), loss of soil organic carbon (SOC) (Medeiros et al., 2021), and heightened risks of soil erosion (Donovan & Monaghan, 2021; Panahi et al., 2021). In the past decades, relevant policies with strict regulations have been implemented in many regions/countries to regulate grazing activity and restore degraded grassland ecosystem services. In New Zealand, for example, substantial areas of alpine tall tussock grasslands have been restricted from grazing to reduce the negative impact on the ecosystem (Norton & Young, 2016). In northern China, the "grazing exclusion" policy has been implemented on severely degraded grasslands since the early 1990s to curb the degradation (Tai et al., 2021; Zhu et al., 2021). In southeastern Australia, best management practices have been implemented for decades to naturally recover deteriorated grasslands due to animal treading, which substantially improved physical properties of the soil, such as hydraulic conductivity, macropore volume, and bulk density (Drewry, 2006). In North America, improved grassland management is recognized as a fundamental natural approach to increasing carbon storage and mitigating climate change (Fargione et al., 2018; Griscom et al., 2017; Hewins et al., 2018). A recent meta-analysis synthesizing data from 45 studies on the northern Great Plains of North America showed that well-managed grazing activities enhanced soil C by 5.2% and soil N by 11.3%, increased litter decomposition by 26.8% and N mineralization by 22.3%, and increased soil mineral N concentrations by 47.7%–51.5%, relative to nongrazing systems (Wang et al., 2016).

Numerous studies have assessed how grazing exclusion impacts grassland ecosystem services compared with conventional moderate-to-heavy (MtH) grazing practices. A quick search of scientific literature (via Web of Science and Google Scholar) found 15,800 articles in referred international journals from 2013 to 2022 describing the effect of grazing on ecosystem functions and services. Of the publications, 28 articles synthesize the results hundreds of published studies using meta-analysis—an approach to systematically merge the findings of independent studies and determine overall effects across various studies (Akobeng, 2005; Shorten & Shorten, 2013). However, the conclusions on the general tendency of grassland ecosystems in response to grazing activities were inconsistent, inconclusive, or even controversial. For example, studies showed that the exclusion of grazing increased ecosystem services (Qin et al., 2021; Zhang et al., 2021), decreased part of the ecosystem services (Xiang et al., 2021), or had no influence on the ecosystem functions and services (Hao et al., 2021; Wang et al., 2021). These inconsistent results are probably attributable to the complexity of plant–soil–microbe–environment interactions.

Plant biotype is a crucial factor influencing grassland ecosystems (Lewis et al., 2014; Milne, 1998; Wang et al., 2022). Plant biotype can govern community assembly that influences aboveground biomass (Song et al., 2022) and belowground biomass (Klimesova et al., 2021; Sun et al., 2022) and interfaces with soil physiochemical and biological properties, such as microbial community structure (Rong et al., 2022) and stoichiometry (Liao et al., 2023) (Figure 1). Plant biotypes also influence microbial community richness, diversity, and plant–soil feedback (Abrahão et al., 2022; Bai et al., 2022; Li, Hooper, et al., 2021). However, information on plant biotypes interacting with grazing management that influences grassland ecosystem is missing in the scientific literature, which contributes to the inconsistent conclusions drawn by different published studies. This knowledge gap needs to be filled, so policymakers and land managers can better understand the underlying mechanisms of enhancing grassland ecosystem functions and services by identifying appropriate plant biotypes suitable for specific environments.

In this study, we use grasslands in northern China as the subject—one of the significant grassland ecosystems in the world servicing the global ecological environment and socioeconomics of the region and supporting diverse species of plants and animals (Kang et al., 2007).

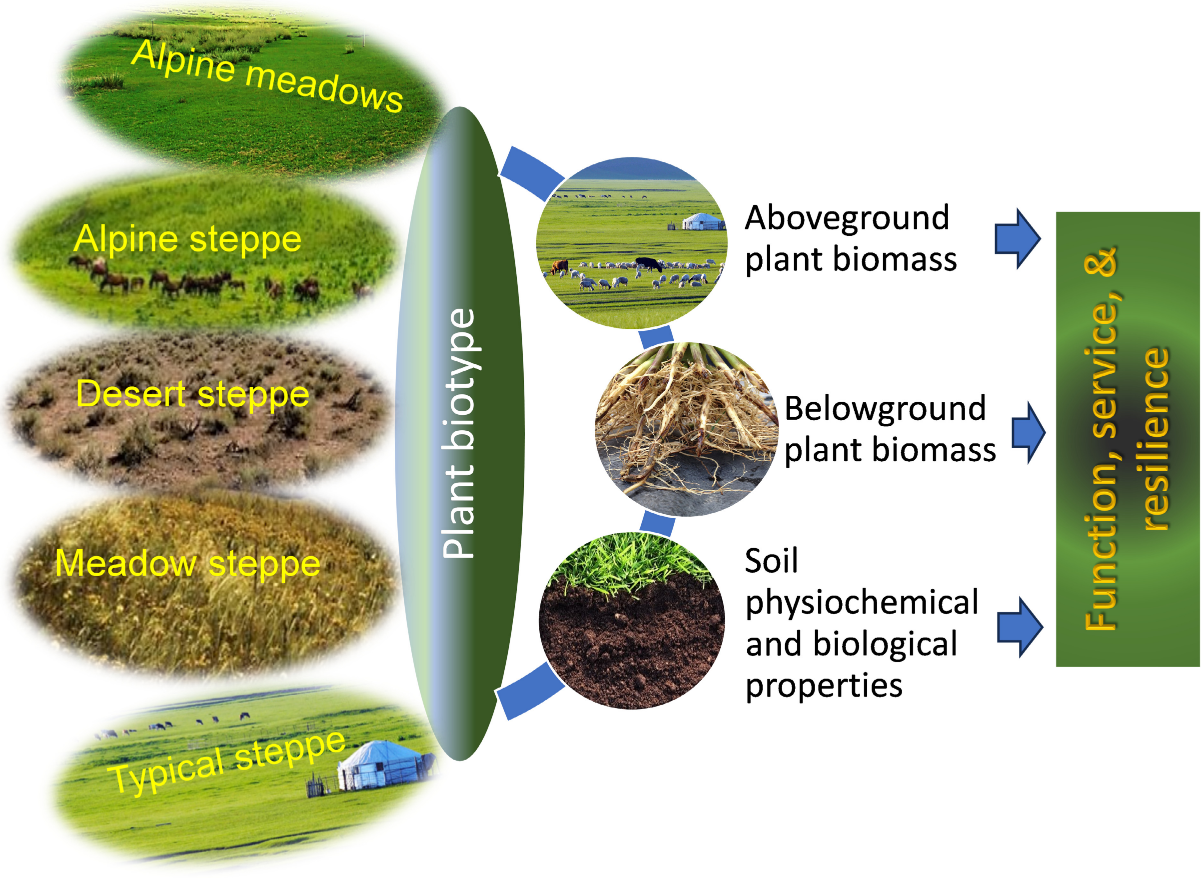

FIGURE 1 A schematic illustration of the study showing that plant biotype in grassland (i.e., alpine steppe, alpine meadow, meadow steppe, desert steppe, and typical steppe) in driving the ecosystem functions, services, and resilience by affecting plant aboveground and belowground biomass and soil physiochemical and biological properties. Photo credit: the authors.

Geographically, it includes those from the northeastern, central north, northwestern to the far west Qinghai-Tibetan Plateau (Figure 2). Plant biotypes are diverse, including alpine steppe, alpine meadow, meadow steppe, desert steppe, and typical steppe (Kang et al., 2007). Plant biotypic community, climate condition, and soil property can interactively affect grassland ecosystem services. As grasses grow, the dominant plants shift from sedge to forbs species in alpine meadow, whereas graminoid species shift to forbs in alpine steppe (Peng et al., 2020), and the intensity of the shift can vary with anthropogenic disturbances, such as grazing activity (Hao et al., 2021). In contrast, soil–plant interactions and species coexistence in both desert and typical steppes are mainly affected by water availability (Chen et al., 2022). Precipitation in July and August plays a critical role in driving net primary productivity of grasslands in the typical to desert steppe transition zone (Lv et al., 2022). During the extended drought period, the growth of shallow-rooted plants can be severely suppressed, and the degree of the influence can vary with soil properties (Tian et al., 2022).

Other plant biotypes, such as alpine typical steppe, alpine desert, and subalpine meadow, are primarily located above the forest zone in high-altitude areas. The vegetation of these grasslands is dominated by different plant species, including, but are not limited to, *Stipa baicalensis* Roshev., *Bothriochloa ischaemum* L., and *Cleistogenes mucronata* Keng in meadow steppe; *S. grandis* Smirn., *S. bungeana* Trin., and *Agropyron cristatum* L., in typical steppe; *S. gobica* Roshev., *S. breviflora* Griseb., and *C. songorica* Roshev., in desert steppe; and *S. purpurea* Grisebach., *Festuca kryloviana* Reverd., and *Artemisia salsoloides* L., in the alpine steppe.

The specific objectives of the study were to (1) assess the aboveground plant biomass, root biomass, and soil properties (including soil C stocks, soil N, P, soil moisture, temperature, pH, and bulk density) of five plant biotypes in response to grazing activities and (2) determine the effectiveness of grazing exclusion in maintaining and enhancing grassland ecosystem functions. To fulfill the objectives, we conducted a comprehensive literature review on the subject of interest (details in *Materials and methods*). We analyzed the results and assessed the

FIGURE 2 A schematic illustration of the study sites. The areas sampled represent about 390 million ha of grasslands, mainly consisting of the alpine steppe, alpine meadow, meadow steppe, desert steppe, and typical steppe.

effectiveness of grazing exclusion interacting with plant biotypes in grassland ecosystem services. The synthesis of in-depth analysis fills the identified knowledge gap and adds novel information to supplement the recent reviews on the relevant subjects conducted by peer researchers (Kang et al., 2007; Mayel et al., 2021; Mencel et al., 2022; Tessema et al., 2020).

MATERIALS AND METHODS

Systematic literature search

We performed a systematic review of the scientific literature using the pre-set criteria as follows: (1) research articles published from 2012 to the end of 2022 in referred scientific journals on the subject of interest and the journals are not on the 2022 version of warning list established by the Division of Science Citation Index journals, Chinese National Library. More information about the criteria for the generation of journal warming list is accessible (Zhang, Wei, et al., 2022); (2) the data were sourced from Web of Science, Google Scholar, ScienceDirect, and SpringerLink. Some other databases, albeit being rich in information, were not included this time to reduce unnecessary duplications; (3) a study carried out in replicated field experiments conducted for >2 years or at multiple sites in northern China only (Figure 2). Articles reporting the results from indoor or simulation studies were excluded; (4) the terms “grazing exclusion,” “exclusion of grazing,” or “non-grazing” were used as keywords in the literature search to ensure that the experimental design in the published articles contained a grazing exclusion treatment in comparison with other treatments; (5) the measurements reported in original articles contained at least four variables from the following list: category A, plant-related variables: (1) vegetation coverage, (2) aboveground plant biomass, (3) belowground biomass, and (4) plant diversity; and category B, soil-related variables: (5) SOC, (6) soil total C,

(7) soil total N, (8) available N, (9) soil total P, (10) available P, (11) C: N ratio, (12) soil pH, (13) temperature, (14) moisture, and (15) microbial community diversity (i.e., evenness, richness, and Shannon–Wiener diversity index). The requirement for a minimal set of variables in a single article helped to facilitate the determination of the potential association among variables.

Data extraction

The relevant data were extracted on a treatment-by-treatment basis from the selected articles focusing on the 4 plant-related and the 11 soil-related variables listed above. The extracted data were entered in an Excel "Master file," examined for accuracy, and standardized for measurement units across the different studies. For example, the units of SOC presented as grams per kilogram, kilogram per square meter, or percentage in the published articles were standardized to kilograms of C per hectare by each soil layer using the reported or estimated bulk density. A small percentage of articles reported soil organic matter values, which were converted to SOC using a 1.72 coefficient (Pribyl, 2010). "PlotDegitizer" (https://plotdigitizer.com/), a graph-to-data conversion program, was used to extract data points from figures presented in original articles. A careful scrutinization of the searched articles showed that 87 studies met the abovementioned pre-set criteria and reported the results from independent yet comparable experiments that were closely related to the subject of interest and fit the scope of our objectives.

Data set management and standardization

To determine the effectiveness of different grazing practices for each plant biotype, we compared the grazing exclusion with MtH grazing practices. In reviewed literature, the moderate ranged between 0.75 (Jiao et al., 2016) and 170 (Li, Li, et al., 2021) standardized sheep units per hectare, whereas heavy grazing ranged between 1.5 (Jiao et al., 2016) and 340 (Li, Li, et al., 2021) standardized sheep units per hectare. The standardized sheep units between studies differed hugely primarily due to local grassland conditions. Percent differences between the two grazing systems were calculated using the following equation (Equation 1):

$$\Delta d = \frac{x-y}{y} \times 100\%, \tag{1}$$

where Δd is the percent difference between grazing exclusion (x) and MtH grazing (y).

A positive value represents that grazing exclusion is superior to MtH grazing and vice versa. The scale, size, and scope of the experiments reported in original articles varied between studies. In some cases, the absolute value of a variable differed by a small amount, but the calculated percentage differed ginormous. The collected data for each variable were examined for the distribution frequency using the funnel plot asymmetry method (Borenstein, 2022), which gave an intuitive assessment of the data symmetricity, helping minimize potential publication bias (Byrne et al., 2022; Pham et al., 2001). In the case the graphic tests illustrated as a skewed, unnormal distribution pattern, the percentage data were transferred using the logarithm of the response ratio as follows (Equation 2):

$$\mathrm{Ln}(\Delta d) = \mathrm{Ln}\left(\frac{x-y}{y}\right) = \mathrm{Ln}(x-y) - \mathrm{Ln}(y), \tag{2}$$

where Δd is the percentage difference between (x) and (y) described in Equation 1 above.

For each variable, the means SD or SE is required in meta-analysis. If the SD of the mean for variable j (SD_j) was missing in the original articles, we estimated it using the average coefficient of variation $(\mathrm{CV}_{\mathrm{sdw}})$ of the SD in the entire database multiplied by the average value of the treatment (M_{avg}) (Equation 3) or the standard error (SE_j) multiples the square root of the number of replications ($\sqrt{n}$) (Equation 4), as follows:

$$\mathrm{SD}_j = \mathrm{CV}_{\mathrm{sdw}} \times M_{\mathrm{avg}}, \tag{3}$$

$$\mathrm{SD}_j = \mathrm{SE}_j \times \sqrt{n}. \tag{4}$$

The variables with neither SD nor SE presented in the original article were excluded in the data set.

Statistical analysis

Statistical analysis was performed using the STATA program (StataCorp, College Station, TX, USA) in two steps. First, the standardized data set was analyzed using the "proportional meta-analysis" (Barker et al., 2021) to determine the variability and heterogeneity across published studies and the significant differences between the two grazing systems (i.e., grazing exclusion vs. MtH grazing). The analysis determined the scale and trend of variability, overall means, and distribution patterns for each variable. The proportional meta-analysis is superior in handling percentage data (Barker et al., 2021) as compared to other meta-analysis methods available in world research communities. This model fits the requirements of the present study ideally because our focus was on the percent differences between the two grazing systems in plant- and soil-related variables. This analysis generated a pooled summary estimate and the variance for five key variables (Appendix S1: Table S1). *Z* and *p* values reveal significances in the null and *i* statistic test and Tau^2, respectively, quantified variability, and between-study variance of the underlying distribution of true effect sizes (Borenstein, 2022; Borenstein & Higgins, 2013). The significant differences between the two grazing systems are determined using fixed and random effects based on paired comparisons. However, the random effect results are considered more realistic and favorable as it reduces potential false effect caused by the observations in various studies (Akobeng, 2005; Borenstein, 2022).

The second step was to determine the plant biotype effect, which was treated as a subgroup factor in the analysis. Due to variable sizes in the experiment and treatment structure in the original articles, a weighted estimation approach was used to standardize percent differences among the five biotypes to improve the accuracy (Byrne et al., 2022). The weighted data were analyzed using one-way ANOVA, and the results are summarized in Appendix S1: Table S2. The degree of freedom (error or the corrected total) differed among variables because of the variable sizes of the data (number of years, sites, treatments, replicates) derived from diverse studies. A boxing plot was used to visualize variability between the two grazing systems for each plant biotype. One-way ANOVA determined the significant differences between plant biotypes with the weighted least square means (Krzywinski & Altman, 2014).

RESULTS

Grazing exclusion increased aboveground and belowground biomass

The synthesis of the analysis on the data set revealed that grazing exclusion practice significantly increased the quantity of biomass in aboveground and belowground plant parts, as compared to MtH grazing. The exclusion of grazing increased aboveground plant biomass by 100.4% (±4.2 SE), on average, which was significantly ($p < 0.01$) greater as compared to MtH grazing (Appendix S1: Table S1). The distribution pattern across various studies showed that about 4% of the paired comparisons between the two grazing systems had a negative value (Appendix S1: Figure S1), with grazing exclusion decreasing aboveground biomass accumulation in those rare cases. However, most of the paired comparisons showed a positive value in percent difference, some >460%, offsetting the small percentage of negative values. The huge variation in percent difference in aboveground biomass accumulation was primarily due to the data set originating from studies with various scales.

Grazing exclusion increased belowground biomass accumulation by 70.2% (±25.7), on average ($n = 992$ paired comparisons), significantly greater ($p = 0.016$) as compared to MtH grazing (Appendix S1: Table S1). The distribution pattern of belowground biomass accumulation showed that about 23% of the paired comparisons had a negative value (Appendix S1: Figure S2), with grazing exclusion lowering belowground biomass accumulation in those cases, as compared to MtH grazing. However, most paired comparisons had significantly positive percent differences in belowground biomass. Belowground biomass was measured from grasslands with diverse backgrounds, leading to a sizeable variation observed in the analysis.

Plant biotypes governed the magnitude of biomass increases

Plant biotypes affected aboveground biomass accumulation significantly ($p < 0.01$), with mean differences ranging from 126% to 460% among the five biotypes (Appendix S1: Table S2). Alpine steppes produced significantly greater amounts of aboveground biomass than the other biotypes. All five biotypes produced significantly greater aboveground biomass under grazing exclusion than MtH grazing, although large variability existed (Figure 3A). Similarly, the plant biotype affected belowground biomass accumulation significantly ($p < 0.01$), with all five biotypes increasing belowground biomass accumulation by 17.2% to 230.4% under grazing exclusion as compared to MtH grazing (Appendix S1: Table S2). Typical steppes had the greatest variation in percent differences among the five biotypes, with the rest showing a relatively small variability (Figure 3B).

The comparison of the two boxplots (Figure 3A,B) illustrated that plant biotypes performed significantly greater under grazing exclusion than under MtH grazing and that the magnitude of the response differed significantly among them. All five plant biotypes increased their aboveground biomass more substantially (average 247%) than increasing belowground biomass (average 72%) in response to grazing exclusion, except for typical steppes that increased aboveground and belowground biomass in a similar scale.

Plant biotypes shaped soil carbon stocks

Plant biotypes responded significantly to the two grazing systems ($p < 0.01$) in total soil C and SOC concentration.

Grazing exclusion increased total soil C by 21.4 ± 1.7% ($n = 619$ pairs) and SOC concentration by 14.3 ± 0.8% ($n = 11{,}223$ pairs), as compared to MtH grazing (Appendix S1: Table S1). The magnitude of the response differed between the five plant biotypes. Alpine meadows increased total soil C by 107%, whereas alpine and desert steppes decreased total soil C by 17.5% to 21.8% under grazing exclusion compared to MtH grazing (Appendix S1: Table S2). The boxplot (Figure 4A) shows that total soil C under meadow steppes and alpine meadows varied hugely in response to grazing activities, whereas the desert and alpine steppes had small variabilities in the response to grazing management. The diverse background of the original studies is attributable to the large variability.

Percent differences in SOC concentration were mostly positive, with a small proportion of the 11,223 paired comparisons having a negative value (Appendix S1: Figure S3), and in those cases, grazing exclusion practices reduced SOC concentration. On average, each of the five plant biotypes increased SOC concentration significantly ($p < 0.01$) under grazing exclusion as compared to MtH grazing (Appendix S1: Table S2). The magnitude of the effect on SOC concentration varied with plant biotype; alpine steppes increased SOC concentration by 52.2% with the greatest variability (Figure 4B). In comparison, alpine meadow increased SOC concentration by 17.7%, with the lowest variability.

The comparison of the two boxplots (Figure 4A,B) gave three key messages: (1) there was a considerable

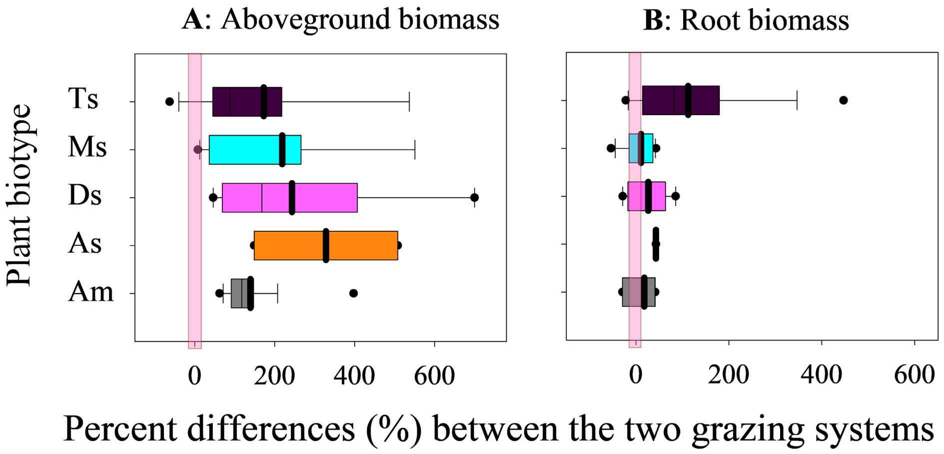

FIGURE 3 The boxplots showing percent differences between grazing exclusion and moderate-to-heavy grazing in (A) aboveground biomass and (B) belowground biomass for each of the five plant biotypes. The midline in each bar denotes the median; the whiskers represent the lower 25% and the upper 25% of scores; the box limits represent the interquartile range between the 25th and 75th percentile, and the data points outside the whiskers are the outliers. The semitransparent light pink line in each plot marks the points of zero percent difference. In this and the other boxplots throughout the article, a specific color was designated for each plant biotype to enhance the visual quality of the presentation. Am, alpine meadow; As, alpine steppe; Ds, desert steppe; Ms, meadow steppe; Ts, typical steppe.

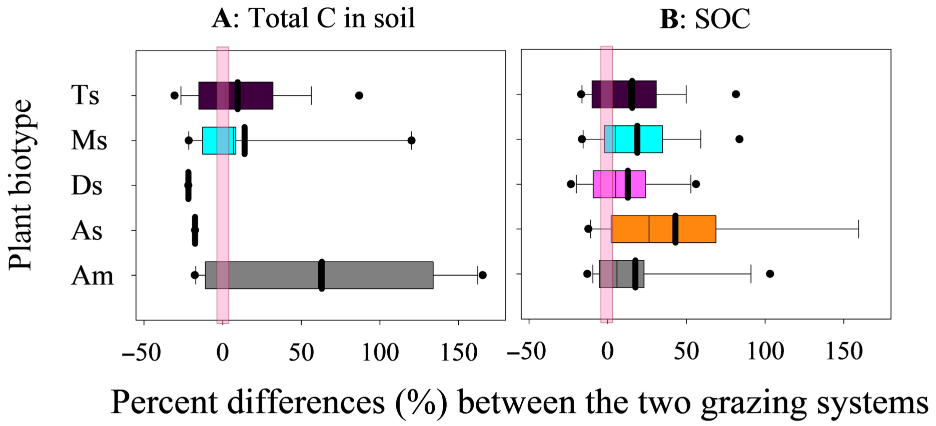

FIGURE 4 Percent differences between grazing exclusion and moderate-to-heavy grazing in (A) total C content in soils, and (B) soil organic carbon (SOC) concentration in soils, for each of the five plant biotypes. Plant biotypes abbreviations, features of the boxplots, and the semitransparent pink line are as in Figure 3.

variation in soil C stock among the five plant biotypes in response to grazing activities due to original studies with diverse backgrounds; (2) plant biotypes differed significantly in affecting soil C stocks; alpine meadow had the greatest increase in total soil C but the lowest increase in SOC concentration, whereas the opposite was true for alpine steppes which had the greatest increase in SOC concentration but decreased total soil C, with grazing exclusion; and (3) plant biotypes and grazing activities had significant, interactive effects on total soil C content and SOC concentration; grazing exclusion promoted alpine meadow and typical steppes, increasing both total soil C and SOC, but caused desert steppes and alpine steppes, decreasing total soil C by 17.5%–21.8%.

Plant biotypes and grazing interactively regulated fundamental soil properties

Grazing exclusion increased total soil N content by 51.9% and soil available N by 32.9%, on average, compared to MtH grazing (Appendix S1: Table S2). Plant biotypes significantly impacted total soil N, with alpine meadow increasing total soil N by 77.7%, alpine steppes increased by 23.7%, and the other three increased by 52%, on average. In contrast, plant biotype did not significantly impact soil available N ($p = 0.3570$), although the weighted least square means ranged between −14.8% for alpine steppes and +52.3% for alpine steppes meadow steppes under grazing exclusion (Appendix S1: Table S2). Boxplots (Figure 5A,B) show the variability among the five plant biotypes in response to grazing activities; alpine meadow had the greatest variability in total soil N and available N in response to grazing exclusion. The negative value in available soil N was noted for alpine steppes under grazing exclusion but did not differ from the other biotypes statistically.

Plant biotypes significantly impacted soil P status in response to grazing activities. Total P content in soil varied from −33% for typical steppes to +72% for meadow steppes. Available P concentration in soil varied from −20 for typical steppes to +21% for alpine steppes (Appendix S1: Table S2). The two boxplots (Figure 5C,D) show that typical steppes decreased total P and available P concentration, whereas alpine steppes increased both variables under grazing exclusion. The rest of the plant biotypes had an inconsistent response in soil P status to grazing management.

Grazing activities affected grassland bulk density consistently (Appendix S1: Figure S4). On average, grazing exclusion lowered soil bulk density by 2%–18% compared to MtH grazing (Figure 6A). Among the five biotypes,

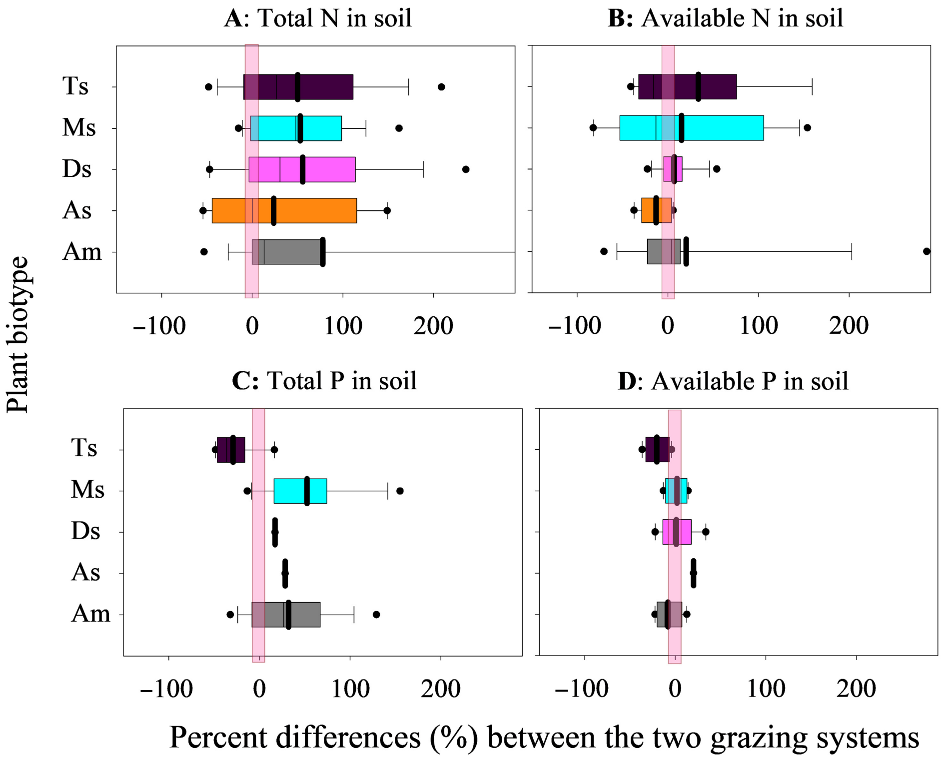

FIGURE 5 The boxplots showing the percent differences between grazing exclusion and moderate-to-heavy grazing in (A) total soil N content, (B) available N concentration, (C) total soil P content, and (D) available P concentration in soil, for each of the five plant biotypes. Plant biotypes abbreviations, features of the boxplots, and the semitransparent pink line are as in Figure 3.

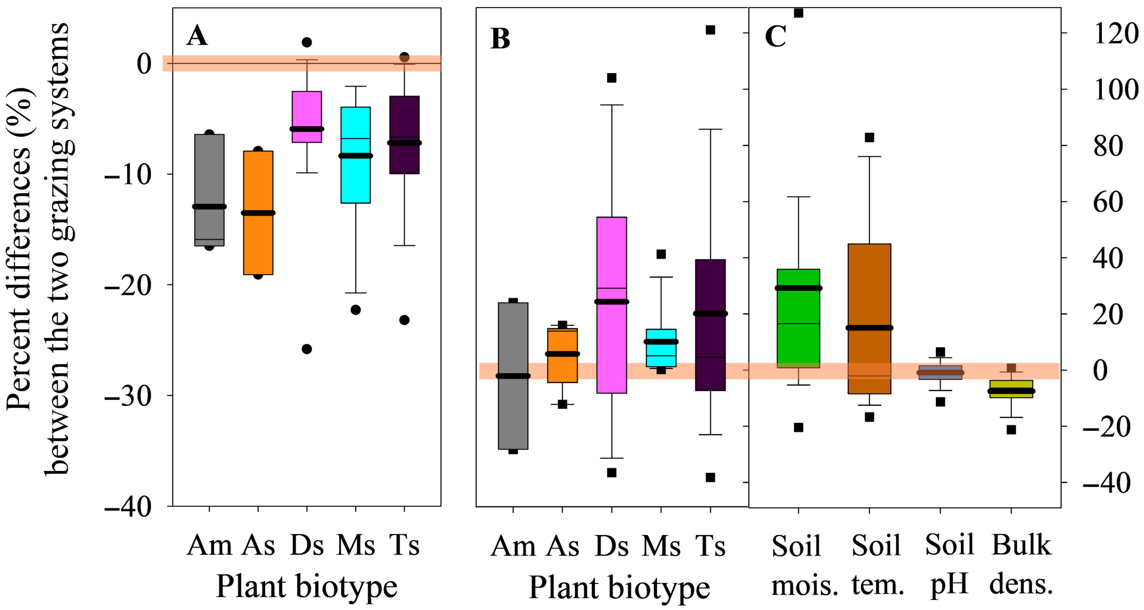

FIGURE 6 Percent differences (%) between grazing exclusion and moderate-to-heavy grazing in affecting (A) soil bulk density, (B) soil microbial community diversity, and (C) the relative magnitude of grazing influence on soil moisture (mois.), temperature (tem.), pH, and bulk density (dens.) averaged across various studies reviewed. Plant biotypes abbreviations, features of the boxplots, and the semitransparent pink line are as in Figure 3.

alpine meadow and alpine steppe decreased bulk density the most, whereas meadow steppe had the greatest variation in bulk density.

Grazing treatments had an inconsistent impact on soil microbial community diversity, ranging from an 18% decrease to a 26% increase in microbial diversity (Figure 6B). The effect varied with plant biotypes, with meadow steppes increasing soil microbial diversity with grazing exclusion, whereas the rest of the biotypes responded to grazing activities inconsistently. The impacts of grazing activities on the other soil properties were analyzed, including soil moisture, temperature, and pH (Figure 6C). The results showed that grazing exclusion improved soil moisture consistently and increased soil temperature in about 80% of the studies. Soil pH had none or little change with grazing activities.

DISCUSSION

Grassland ecosystem functions and services in response to anthropogenic activities, such as livestock grazing, can be evaluated using various methodologies (Zhan et al., 2020; Zhang & Xi, 2021), modeling (Klein et al., 2020; Li et al., 2022), or multiscale assessments (Taylor & Browning, 2021). In this project, we analyzed the distribution pattern of essential plant- and soil-related variables using the box-plotting method—a standardized way of illustrating the distribution of data with a five-number summary: “minimum,” first quartile [Q1], median, third quartile [Q3], and “maximum” (Potter et al., 2010). The preliminary analysis showed huge variations between original studies and among experimental treatments. The use of the proportional meta-analysis, a relatively newer meta-analysis method described by Barker et al. (2021), coupled with the box-plotting illustrations (Potter et al., 2010), provided a practical approach to analyze and summarize the multiyear, multisite results efficiently.

Plant biotype: A key driver to grassland ecosystem services

Grasslands contribute about 30% of the ecosystem’s carbon reserves globally (Henwood, 2017), playing a vital role in the global carbon cycle. In this study, we found that plant biotypes significantly affected total soil C content in grassland soils in response to grazing activity. A typical steppe dominant grassland ecosystem was highly sensitive to grazing activity, and the exclusion of grazing increased both aboveground and belowground biomass accumulation. In contrast, an alpine meadow dominant grassland ecosystem was relatively blunt (i.e., less sensitive to grazing activity) with little effect by the two different grazing systems. The wide range of variation between plant biotypes in response to grazing activity was probably due to the complex interactions between plant biotype and other factors or interplay among grazing intensity and environmental conditions (Buzhdygan et al., 2020). In addition, there exist "concomitant effects" among plant community, soil properties, and climate factors in a grassland ecosystem (Vidaller et al., 2022). In a substeppe plain in southeastern France, a change from millennia-old traditional herding to fenced, moderate-level grazing significantly increased plant biomass, species richness, and evenness while concomitantly changing vegetation (Vidaller et al., 2022). In a 34-year grazing exclusion grassland in China, the alternation of plant community changed nutrient cycling while concomitantly affecting nutrient resorption-induced ecosystem services (Zhang, Su, et al., 2022). In the semidesert–shrubland–grassland ecotone of northwestern China, the change in grazing intensity altered the relative abundance of Chloroflexi phylum, Deltaproteobacteria class, and Nitrospira class paralleled with plant community composition while concomitantly affecting soil chemical property (Wang et al., 2021). In the Eastern Carpathians in Ukraine, cattle density decreased plant species and functional diversity due to grazing while concomitantly increasing the proportion of undesirable species due to bare soil exposure (Buzhdygan et al., 2020). These examples show that plant biotype is a key driver affecting grassland ecosystem services, and the effectiveness can be complicated by soil fertility, the degree of degradation, the history of grassland management, and the climate conditions, among others.

Numerous studies have determined the effects of grazing activities on plant and soil properties (Abdalla et al., 2018; Eze et al., 2018; Hewins et al., 2018; Whitehead et al., 2018; Yan et al., 2020; Zhan et al., 2020). Using SOC as a specific example, a meta-analysis of 83 studies across different regional climates showed that grazing increased SOC stocks by 7.6% under moist–warm climates while decreasing SOC by 19% under moist–cool climates (Abdalla et al., 2018). Another meta-analysis of 341 data sets collected across global grasslands showed that grazing decreased SOC by 15.0%, with the greatest negative effect in the tropics (Eze et al., 2018). The existing scientific literature also shows that grazing typically increased grassland SOC storage in North America (Hewins et al., 2018; Wang et al., 2016), decreased SOC significantly in Chinese grasslands (Yan et al., 2020; Zhan et al., 2020; Zhou et al., 2017), and resulted in various outcomes in the European Union (Abdalla et al., 2018; Castillo-Garcia et al., 2022) and other regions/countries (Schipper et al., 2017; Whitehead et al., 2018). An important influencing factor—plant biotype—was missing in published studies. Our findings in the present study highlight that plant biotypes drive grazing effects on plant and soil properties. Specific features of plant community composition, diversity, and interaction with the history of grazing activities govern the grassland ecosystem functions and services—the novel information starts to fill the knowledge gap.

Mechanisms for grassland ecosystem functions and services

Sustainable grazing management is vital to conserve biodiversity and enhance the multiple ecosystem functions (Liu et al., 2019, 2022). Many published studies have shown inconsistent outcomes that the exclusion of grazing, compared to MtH grazing, increases ecosystem services (Qin et al., 2021; Zhang et al., 2021), reduces part of the ecosystem services (Xiang et al., 2021), or has no significant influence on ecosystem functions and service (Hao et al., 2021; Wang et al., 2021). Based on our in-depth analyses, coupled with findings by other researchers, we summarize the following "speculative" mechanisms responsible for the outcomes of grazing activities on grassland ecosystem services:

1. Grazing activity affects soil microbial biomass carbon—an essential component in soil C cycling. Grazing can increase (Gilmullina et al., 2020), decrease (Zhan et al., 2020), or have no influence (Rong et al., 2022) on the C component contributed by microbial biomass. Due to the complexity of the soil environment, structure, and dynamic process in a grassland ecosystem, the influence of grazing on soil C status and cycling can be complex. We find that plant biotypes play a critical role in influencing the magnitude of soil C cycling, which may require thorough investigations across multiple geographic sites with site-specific long-term experiments.
2. With continuous grazing, animal feeding on photosynthetic tissue brings a defoliation effect to inhibit photosynthesis (Shen et al., 2019), although this phenomenon can simultaneously stimulate root growth, leading to the rate of root biomass accumulation greater than that of aboveground biomass accumulation (Wang et al., 2018, 2020). The increased root:shoot ratio accelerates SOC accumulation (Wu et al., 2022). However, our analysis showed that grazing exclusion increased both aboveground and belowground biomass accumulation, leading to increased SOC.
3. Grazing exclusion ceased animal trampling and reduced soil compaction (Li, Hooper, et al., 2021), which improves soil structure and infiltration (Hargreaves et al., 2019). Reduced soil compaction favors microbial activities to stimulate nutrient cycling while fostering physical protection of SOC in the topsoil layers (Bondi et al., 2021; Zhang, Sun, et al., 2019).

4. Long-term grazing exclusion increases the input of plant litter which acts as the binding agent for soil aggregation, leading to a higher proportion of SOC in soil aggregates (Bai et al., 2020), which are required to form a heterogeneous structure of carbon-rich spots, "islands of fertility" (Ghiloufi & Chaieb, 2020; Lv et al., 2021), helping to redistribute organic materials from bare spots to patches. This effect may be interacted by plant biotype.
5. Light grazing is reported to affect the leaf area index, thus, affecting the interception of solar energy (Chang et al., 2020), leading to changes in plant biomass allocation; moderate grazing disturbs plant communities to promote the growth of less-active biotypes, offering a compensatory effect to biomass consumed by animal feeding and bringing positive herbivore–plant–soil feedbacks to preserve ecosystem functioning (Castillo-Garcia et al., 2022); heavy grazing increases the degree of surface exposure that causes soil moisture loss via evaporation, limiting the growth of the aboveground plant parts and reducing net primary production. Many North American studies reported that grazing brings numerous positive impacts on grassland ecosystems (Hewins et al., 2018; Liebig et al., 2010; Wang et al., 2016), whereas several meta-analyzes synthesizing hundreds of studies in Eurasia reported adverse effects of grazing on the ecosystems (Li et al., 2020; Ma et al., 2022; Zhan et al., 2020; Zhang, Xue, et al., 2019). The issue is the need for an internationally standardized "rating scale" of grazing intensity. For example, a "heavy grazing" rate in North America may be equivalent to a "light grazing" rate in Asia because stocking rates are usually much higher in Asia than in North America.
6. The risk of climate change-induced stresses, such as frequent drought, can be a high, low, or no-effect phenomenon on grassland ecosystems. Increased drought stress increases the vulnerability and risks of decreasing grassland net primary productivity (Wu et al., 2021) and reducing ecosystem services (Nandintsetseg et al., 2021); the opposite can be confirmed that rising atmospheric CO_2 under the scenario of global warming can increase net primary productivities (Sakalli et al., 2017) due to improved photosynthesis from the increased CO_2 source (Pastore et al., 2020); elevated temperature-induced sensitivity of soil N mineralization can be reduced with grazing exclusion strategies, helping prevent N losses in grasslands (Liu et al., 2020); or grasslands can be climate neutral because the increased CO_2 and N deposition increase net C sink (Chang et al., 2021). Our analyses shed a new light that plant biotype plays a vital role in the magnitude of climate-induced effects on fundamental physiochemical properties of grassland ecosystems. Selecting appropriate plant biotypes will enhance the grassland's adaptability to changing climate to improve ecosystem services.
7. Grazing shifted the soil's bulk density, moisture, temperature, and pH. Our analysis showed that excluding grazing significantly decreased bulk density, ranging from a decrease of 2%–18%, compared with MtH grazing. Soil bulk density is inversely proportional to SOC content, but the mechanisms of the inverse correlation are poorly understood. Based on our analysis and the reports by other researchers, we suggest that the mechanisms of the inverse correlation are mainly because (1) grazing exclusion allows high soil porosity to increase airflow permeability (Ajayi et al., 2021; Koppe et al., 2021)—a key factor favoring bulk density; (2) no animal feeding leads to more litter input to the soil to increase SOC; the higher the SOC, the lower the bulk density (Tessema et al., 2020); (3) little or no compaction improves water infiltration (Centeri, 2022), favoring soil microbial activities (Liu et al., 2019) contributing to SOC that decreases bulk density; and (4) the exclusion of grazing leads to an increase in the mass fraction of aggregates (Bai et al., 2020; Zhang, Sun, et al., 2019)—a structural unit important for soil bulk density. It is arguable that under grazing practice, livestock excrement inputs into the soil through organic matter, directly affecting bulk density. This hypothesis is based on the concept that about 30%–60% of the plant biomass consumed by livestock and 50%–70% of the nutrients recycled by livestock can be returned to the grassland. However, our results do not support this hypothesis, probably because increased soil compaction with animal trampling offset the beneficial effect of animal excrement on bulk density.

CONCLUSION

The synthesis shows that plant biotype, the core of plant community structure and diversity, is crucial in governing grassland ecosystems. Plant biotypes differ in their adaptation ability, net primary productivities, and the ability to resist abiotic and biotic stresses. Therefore, selecting appropriate plant biotypes is critical to maintaining and enhancing ecosystem functions and services. The outcome of plant biotypes affecting grassland ecosystems is complex because of factors like climate conditions, grazing history, and soil physiochemical properties. Overall, plant biotypes and grazing practices can modify grassland ecosystem functions and services. We suggest future research priorities to (1) establish long-term site-specific experiments to evaluate the features of different plant biotypes under diverse environmental conditions; (2) strengthen quantitative analysis and modeling to determine the adaptability of plant biotypes to climate change–induced stresses, such as drought; (3) assemble the plant community structure with diverse plant biotypes to maximize the use of climate change-induced, increased atmospheric CO_2 to improve photosynthesis and thus net primary productivities; and (4) focus on the plant–soil–microbe–environment–anthropogeny interactions affecting grassland ecosystem functions and services.

AUTHOR CONTRIBUTIONS

Li Wang and Yantai Gan conceived and designed the experiment. Shou-Jiang Feng, Dandi Sun, Junying Wang, and Yijia Wang conducted systematic reviews, data extraction, and data management. Soon-Jae Lee and Peina Lu were involved in data analysis and drafting the article. Yantai Gan and Li Wang wrote the article, and all authors contributed to article revisions and approved the submitted version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Gan, 2023) are available from Figshare: https://doi.org/10.6084/m9.figshare.24481201.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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