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META-ANALYSIS

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Grazing intensity significantly changes the C : N : P stoichiometry in grassland ecosystems

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Abstract

Aim: Livestock grazing can alter carbon (C), nitrogen (N) and phosphorus (P) cycles, thereby affecting the C : N : P stoichiometry in grasslands. In this study, we aimed to examine mechanisms underlying the impacts of grazing on grassland C : N : P stoichiometry, focusing on belowground processes and their linkages with aboveground vegetation properties.

Location: Global.

Time period: 1900–2018.

Major taxa studied: Grassland ecosystems.

Methods: We conducted a meta-analysis based on 129 published studies to synthesize the effects of grazing on the C : N : P stoichiometry of leaves, stems, litter, roots, microbial biomass, and soil in grassland ecosystems.

Results: Grazing significantly affected the C, N and P pools, and then the C : N : P stoichiometry in grassland ecosystems. Grazing effects on C : N : P stoichiometry varied strongly with grazing intensity. Specifically, heavy grazing decreased all C : N : P stoichiometry except litter N : P and root C : N ratios, while light and moderate grazing caused less negative or positive effects. Grazing effects on litter C : N ratio were negatively correlated with grazing effects on soil C : N ratios under light and moderate grazing, but this relationship was positive under heavy grazing. In contrast, grazing effects on root C : P and soil C : P were positively correlated under light and moderate grazing but negatively correlated under heavy grazing. Importantly, grazing significantly decreased the soil N pool by 10.0% but increased the soil P pool by 3.6%, indicating differential mechanisms for grazing impact on N and P cycles in grasslands.

Main conclusions: Our results strongly suggest that grazing intensity regulates the biogeochemical cycles of C, N and P in grassland ecosystems by affecting plant nutrient use efficiency and soil physicochemical processes. Therefore, incorporating grazing intensity into Earth system models may improve predictions of climate–grassland feedbacks in the Anthropocene.

KEYWORDS
carbon sequestration, ecosystem functioning, grasslands, grazing intensity, meta-analysis, stoichiometry

Miao He and Guiyao Zhou contributed equally to this work.

1 | INTRODUCTION

Grasslands cover approximately 40.5% of the Earth's land surface excluding Antarctica and Greenland (Hufkens et al., 2016), and provide numerous essential ecosystem services, including carbon (C) sequestration and climate regulation as well as economic benefits (Lal, 2004; Lecain, Morgan, Schuman, Reeder, & Hart, 2002; Wang & Fang, 2009). However, overgrazing threatens the biodiversity, functioning and stability of grassland ecosystems worldwide (Mcsherry & Ritchie, 2013). These negative impacts are largely mediated by the grazing effects on C, nitrogen (N) and phosphorus (P) cycling (Deng, Sweeney, & Shangguan, 2014; Derner, Briske, & Boutton, 1997; Liu, Kan, & Yang, 2015). Grazing-induced changes in C : N ratio have attracted much attention due to their impact on the availability of essential nutrients in grasslands (Zhou et al., 2017). As a critical element for plants and microorganisms, P is usually coupled with C and N, and linked to biological processes such as N fixation, organic matter decomposition, and plant photosynthesis (Delgado-Baquerizo, Maestre, & Gallardo, 2013; Walker & Syers, 1976). Therefore, understanding the responses of C : N : P stoichiometry to grazing is crucial for assessing human-induced impacts on ecosystem functions and developing sustainable strategies for grassland management.

Over the past half-century, numerous studies have suggested that long-term overgrazing might modify plant C sequestration, root exudation, and microbial activity, thereby affecting C–N–P cycling within root–microbe–soil systems (Delgado-Baquerizo et al., 2013; Zhou, Luo, Chen, He, et al., 2019). While grazing generally decreases C, N and P pools in leaves and litter (Bai et al., 2012), it has divergent effects on soil C, N and P pools (Knops, Bradley, & Wedin, 2002). However, most recent studies focused either on the aboveground or the belowground processes in response to grazing (Bai et al., 2012; Yang et al., 2018). Thus, stoichiometric links between above- and belowground processes in response to grazing remain uncertain, which may hamper our ability to predict global C–N–P dynamics in a changing environment.

The magnitude of grazing effects on C : N : P stoichiometry depends on grazing intensity, vegetation types and environmental factors (Derner et al., 1997; Mcsherry & Ritchie, 2013). Among these factors, grazing intensity may play the most essential role due to its influence on the plant community structure, soil microenvironment, and microbial diversity (Bello, Lepš, & Sebastià, 2010; Zhou et al., 2017). However, the effects of grazing intensity on C : N : P stoichiometry vary substantially among ecosystems. For example, Yang et al. (2018) found that light grazing decreased the soil C : N ratio in an alpine meadow, whereas heavy grazing increased it. Shrestha and Stahl (2008) found no change in soil C : N ratio in response to light grazing in a semi-arid sagebrush steppe. Moreover, heavy grazing decreased both soil C : P and N : P ratios in an upland grassland (Medina-Roldán, Pazferreiro, & Bardgett, 2012), but increased these ratios in meadow steppe, typical steppe and desert steppe (Bai et al., 2012). In spite of these efforts, the mechanisms underlying the effects of grazing intensity on C : N : P stoichiometry and the linkage between above- and belowground processes remain unclear. Therefore, it is necessary to integrate the available data on the response of C : N : P stoichiometry to various levels of grazing intensity.

In this study, we compiled a dataset of 3,610 paired comparisons from 129 published studies and conducted a meta-analysis to investigate the general response pattern of above- and belowground C : N : P stoichiometry to different grazing intensities. Specifically, our objectives were: (a) to examine global patterns of above- and belowground C : N : P stoichiometry in response to livestock grazing, (b) to explore links between grazing effects on above- and belowground C : N : P stoichiometry, and (c) to evaluate whether grazing effects on soil C : N : P stoichiometry depend on grazing intensity, climate, soil depth, and vegetation type.

2 | MATERIALS AND METHODS

2.1 | Data sources

We searched for peer-reviewed papers published before June 2018 in Web of Science and China Knowledge Resource Integrated Database (CNKI), using the following search terms: (grazing OR herbivory OR defoliation) and (C:N OR C:P OR N:P OR C:N:P) and (grassland OR pasture OR meadow). To be included in our dataset, studies had to meet the following six criteria: (a) the experiment was conducted in the field and included non-grazed plots and at least one grazing treatment, (b) experimental duration was longer than one growing season, (c) the initial climatic conditions, soil properties, and species compositions in the non-grazed and grazing treatments were the same, (d) all plots were free of grazing for at least 10 years prior to the start of the experiment, (e) the dominant species were clearly described and the grazing intensity was quantitatively and/or qualitatively reported, and (f) the mean, standard error (*SE*) or standard deviation (*SD*), and sample size (*n*) of the relevant variables could be extracted from the tables, digitized graphs or the text. We found 129 papers (Appendix: Data sources) meeting these criteria. Of these papers, 119 reported grazing effects on C : N ratios, 50 reported C : P ratios and 46 reported N : P ratios (Figure 1, Supporting Information Table S3).

Our database included 36 variables: above- and belowground C, N and P pools (i.e., C, N and P stocks in plant leaves, stems, litter and roots, microbial biomass and soil), and C : N : P stoichiometry (i.e., C : N, C : P and N : P ratios in plant leaves, stems, litter and roots, microbial biomass and soil). In total, there were 38, 11, 16, 34, 31 and 94 studies for leaves, stems, litter, roots, microbial biomass and soil, respectively. Data in the text and tables were directly extracted, and those in the figures were extracted by using GETDATA software (version 2.24, http://getdata-graph-digitizer.com). We also extracted and tabulated information on mean annual temperature (MAT), mean annual precipitation (MAP), elevation, grazing intensity, dominant species and soil depth. When MAT and MAP were not reported, we extracted them from the global climate database (http://www.worldclim.org/) according to the geographical coordinates.

Environmental variables included MAT with a range from −1.7 to 15 °C, MAP from 160 to 4,200 mm, and elevation from 300 to

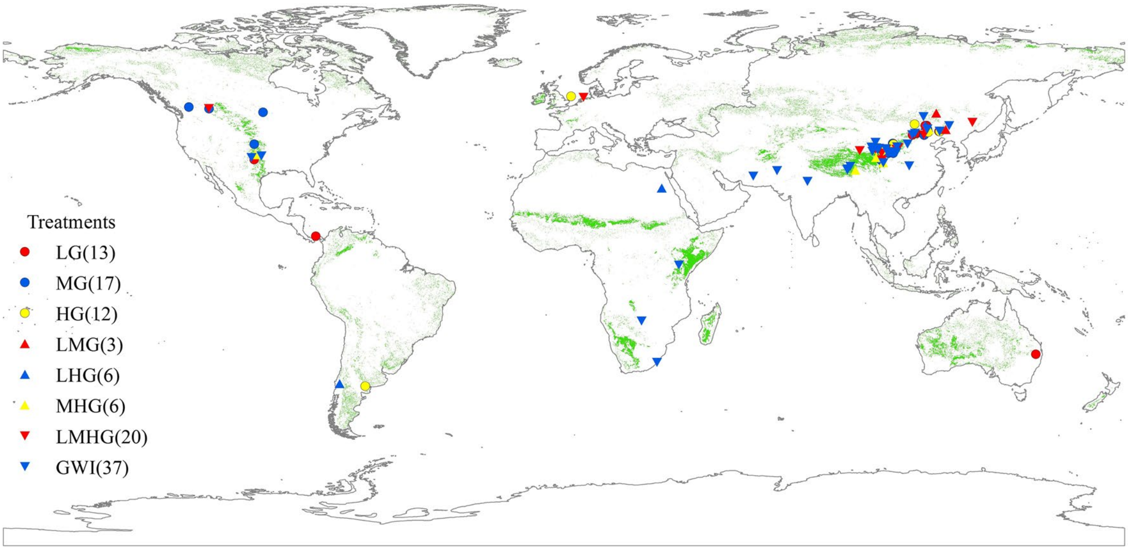

FIGURE 1 Global distribution of the grazing experimental sites used in this meta-analysis. The sites were spread over all continents except Antarctica, with most of them located in eastern Asia and North America. LG, MG and HG represent sites with light, moderate and heavy grazing treatments, respectively. LMG, LHG, MHG and LMHG represent the combinations of two or three grazing intensities (e.g., LMG includes both light and moderate grazing, LMHG includes all three grazing intensities). GWI represents the sites with no grazing intensity information. The base map represents the global distribution of grasslands

4,600 m. Grazing intensity was divided into un-grazed or fenced treatments (UG) as the control, light grazed (LG), moderate grazed (MG), and heavy grazed (HG) treatments. Because grasslands may differ in carrying capacity, it is difficult to set general criteria to classify studies according to grazing intensity. However, authors usually considered a light grazing intensity when livestock consume less than 20% of total plant biomass, a moderate intensity when livestock consume 20–50% of plants, and a heavy intensity when livestock overgraze grasslands (at least 50% of plants, Holechek & Galt, 2000; Yan, Zhou, & Zhang, 2013). Therefore, studies were classified according to grazing intensity using the authors' qualitative classification directly from papers or the references therein (Zhou et al., 2017), which represented the relative impacts of grazing on plants and were relatively comparable among studies. The studies were also grouped into C_3 and C_4 grasslands according to the dominant species, and into different MAT (< 0, 0–5 and > 5 °C), MAP (< 400, 400–800 and > 800 mm), elevation (< 1,500, 1,500–3,000 and > 3,000 m) and soil depth groups (< 15, 15–30 and > 30 cm).

2.2 | Data analysis

We used the same methods as Hedges, Gurevitch, and Curtis (1999) and Luo, Hui, and Zhang (2006) to quantify the responses of above- and belowground C, N and P contents and stoichiometry to grazing by using the response ratio (RR), which is the natural logarithm of the ratio between the mean value in grazing ($\overline{X}t$) to that in the control ($\overline{X}c$) for a concerned variable:

$$RR = Ln\left(\overline{X}t/\overline{X}c\right) \tag{1}$$

The variance (v) of the RR is estimated by:

$$v = \frac{s_t^2}{n_t\overline{X}_t^2} + \frac{s_c^2}{n_c\overline{X}_c^2} \tag{2}$$

where n_t and n_c indicate the sample sizes, and s_t and s_c are the standard deviations of the relevant variable in the grazing and control treatments, respectively. The average response ratio (RR_{++}) across a group of experiments was calculated as the weighted mean of individual RR (RR_i) with the weight (w) of each RR being the reciprocal of the variance (w = 1/v). The RR_{++} considered the precision of each individual study, which had the advantage compared to relative response (RR).

$$RR_{++} = \frac{\sum_{i=1}^{k} w_i RR_i}{\sum_{i=1}^{k} w_i} \tag{3}$$

where k represents the number of RRs. The standard error (SE) of RR_{++} was calculated by:

$$S\left(RR_{++}\right) = \sqrt{\frac{1}{\sum_{i=1}^{k} w_i}} \tag{4}$$

The 95% confidence interval (CI) for RR_{++} was RR_{++} ± 1.96 × $S(RR_{++})$. The influence of livestock grazing was considered significant if the 95% CI did not overlap zero (Luo et al., 2006). The percentage change of a variable was calculated as [exp (RR_{++}) – 1] × 100%. A t test was applied to examine the difference in RR_{++} between differential grazing intensities in groups with different climate (MAT, MAP), elevation, dominant species (C_3 and C_4), and soil depth. To validate the results from this meta-analysis, frequency

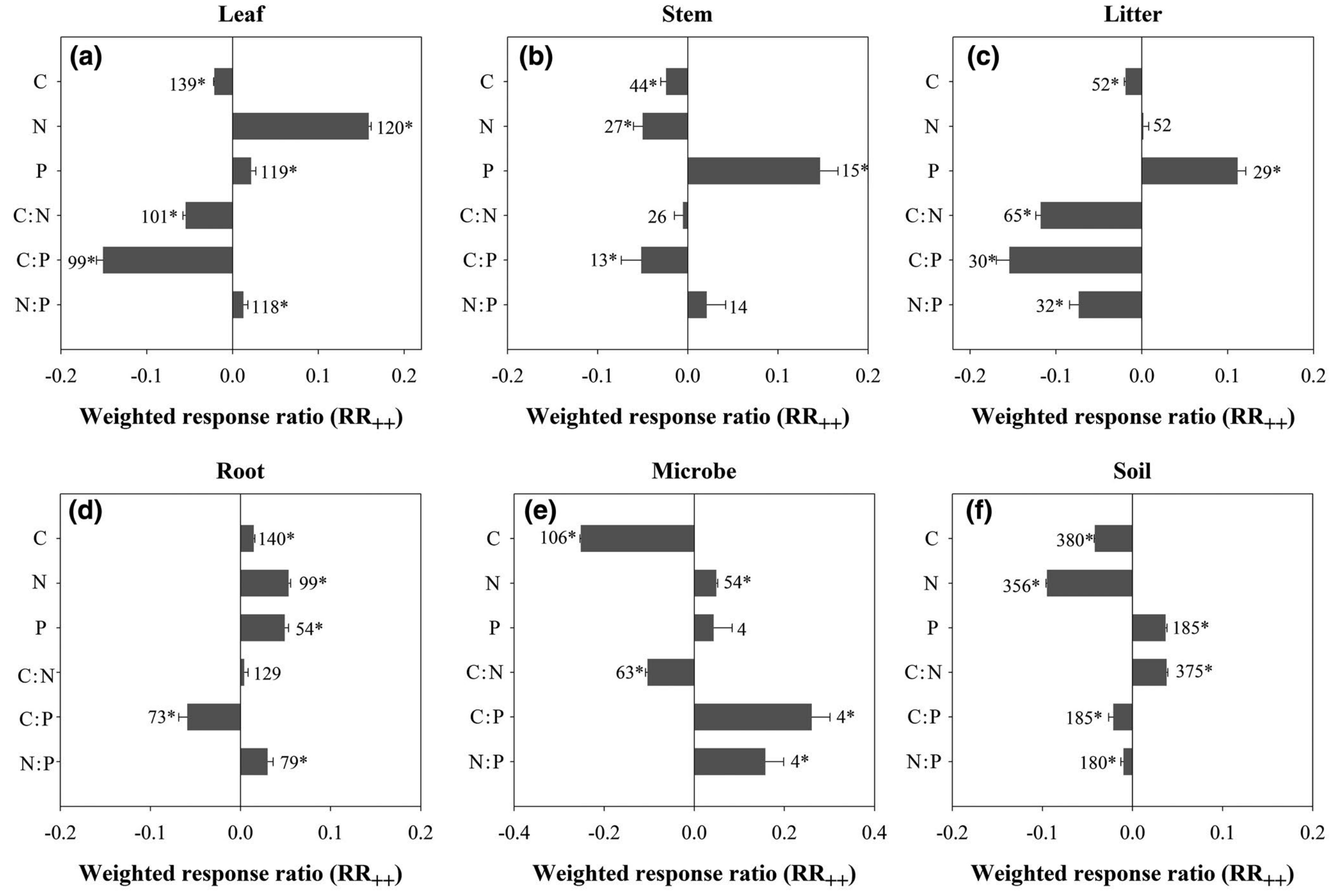

FIGURE 2 Effects of grazing on the C, N and P pools and C : N : P stoichiometry across different above- and belowground parts, including leaves, stems, litter, roots, microbial biomass and soil. Bars represent RR_{++} ± 95% confidence intervals. The vertical line is drawn at $RR_{++} = 0$. Asterisks (*) indicate the grazing effect on relevant variables are significant. Numbers for each bar indicate the sample size

distributions of RR ($n > 10$) of C : N, C : P and N : P ratios in leaves, stems, litter, roots, microbial biomass and soil were fitted with a Gaussian function (i.e., normal distribution):

$$y = \alpha \exp\left[-\frac{(x-\mu)^2}{2\sigma^2}\right] \quad (5)$$

where x is the RR of a target variable; y is its frequency (i.e., number of RR values); α is a coefficient showing the expected number of RR values at $x = \mu$; and μ and σ^2 are the mean and variance of the frequency distributions, respectively. Linear regressions were conducted to examine the relationships among C : N, C : P and N : P ratios in leaves, stems, litter, roots and soil.

3 | RESULTS

3.1 | Effects of grazing on above- and belowground C : N : P stoichiometry

Grazing significantly affected above- and belowground C : N : P stoichiometry in grassland ecosystems (Figure 2, Supporting Information Figure S1). On average, grazing decreased C pools in leaves, stems, litter, microbial biomass and soil by 2.1, 2.4, 1.9, 22.3 and 4.1%, respectively, but grazing increased root C pools by 1.5% (Figure 2). Grazing also decreased N pools in stems (−4.9%) and soil (−9.1%), but increased N pools in leaves, roots and microbial biomass by 17.2, 5.1 and 4.5%, respectively. In addition, grazing increased P pools in leaves (+2.2%), stems (+15.8%), litter (+11.8%), roots (+5.1%) and soil (3.7%).

Grazing-induced changes in C, N and P pools significantly affected the C : N : P stoichiometry in grassland ecosystems. Specifically, grazing decreased the soil N pool (−9.9%) more strongly than the soil C pool (−4.3%), leading to an increase in soil C : N ratio (+3.6%, Figure 2f, Supporting Information Figure S2). Grazing significantly decreased C : P ratios in leaves (−14.0%), stems (−5.0%), litter (−11.1%), roots (−5.8%) and soil (−3.9%), but increased microbial biomass C : P ratio by 29.8% (Figure 2). In addition, grazing significantly increased N : P ratios in leaves (+1.2%), roots (+3.1%) and microbial biomass (+17.1%), while it decreased N : P ratios in litter (−7.3%) and soil (−1.1%, Figure 2).

3.2 | Effects of grazing intensity on above- and belowground C : N : P stoichiometry

The response of aboveground C, N and P pools as well as their stoichiometry to grazing largely depended on grazing intensity (Figure 3,

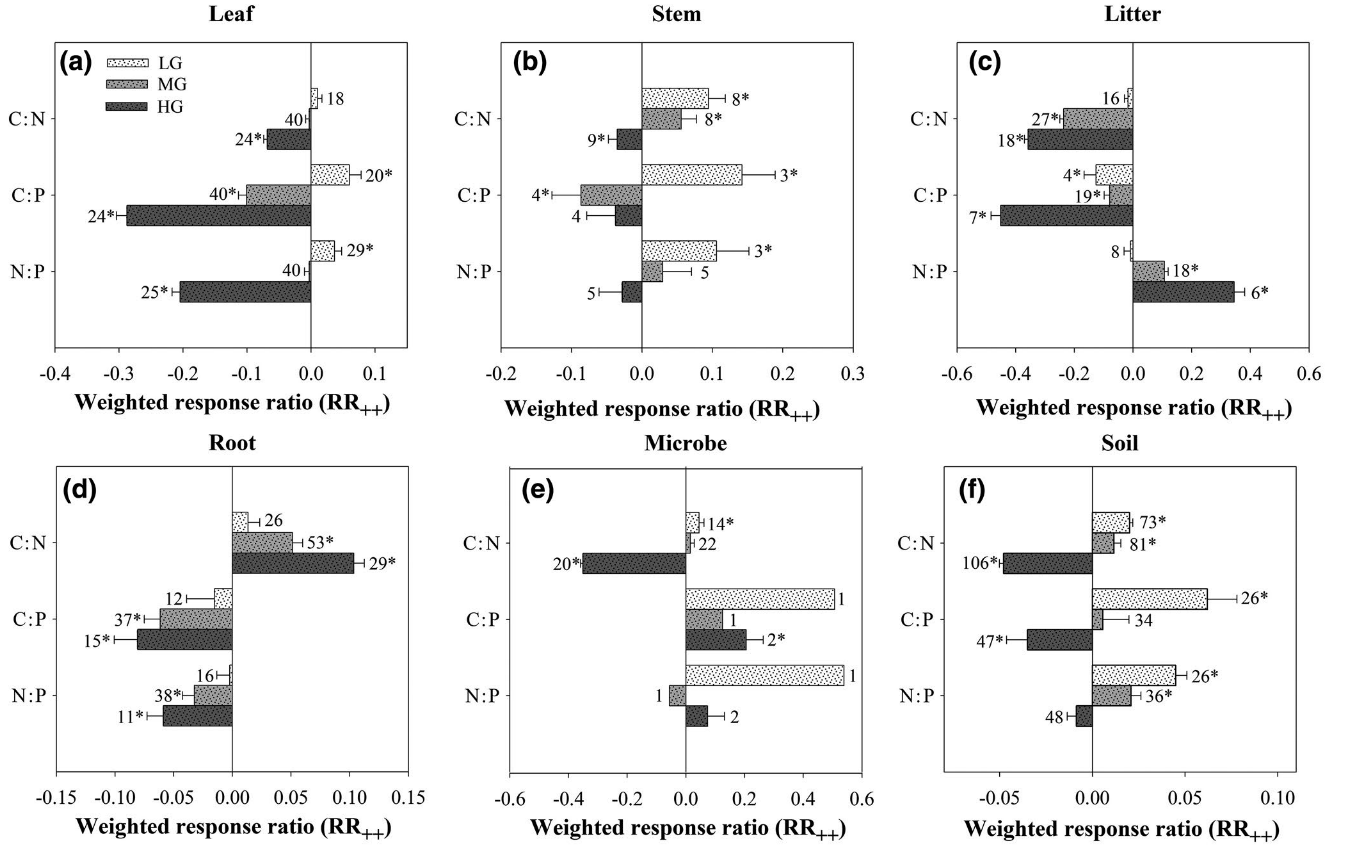

FIGURE 3 Influences of grazing intensity on C : N : P stoichiometry across different above- and belowground parts, including leaves, stems, litter, roots, microbial biomass and soil. Bars represent RR_{++} ± 95% confidence intervals. The vertical line is drawn at RR_{++} = 0. Asterisks (*) indicate the grazing effect on relevant variables are significant. Numbers for each bar indicate the sample size. LG = light grazing; MG = moderate grazing; HG = heavy grazing

Supporting Information Figure S2). Specifically, light grazing significantly increased leaf C : P and N : P ratios by 6.2 and 3.7%, respectively, while moderate and heavy grazing decreased C : P ratios by 9.6 and 25.0%, and N : P ratios by 0.3 and 18.5%, respectively (Figure 3a, Supporting Information Table S1). Light grazing significantly increased stem C : N, C : P and N : P ratios compared with moderate and heavy grazing (Figure 3b). In addition, heavy grazing decreased litter C : N and C : P ratios more strongly than light and moderate grazing (Figure 3c).

The responses of belowground C : N : P stoichiometry to grazing also varied with grazing intensity (Figure 3d–f). Light grazing did not significantly affect root C : N ratio, but moderate and heavy grazing increased it by 5.1 and 10.8%, respectively (Figure 3d). On the contrary, grazing significantly decreased root C : P and N : P ratios for all three intensities (i.e., light, moderate and heavy) but these effects became more severe with increased intensity (Figure 3d). Microbial C : N ratio increased under light grazing but decreased under heavy grazing, whereas the patterns in C : P and N : P ratios were uncertain due to small sample sizes (Figure 3e). For soil C : N : P stoichiometry, light grazing significantly increased C : N, C : P and N : P ratios by 2.0, 6.4 and 4.6%, but heavy grazing decreased these ratios by 4.7, 3.4 and 0.9%, respectively (Figure 3f). Moderate grazing significantly increased soil C : N and N : P ratios by 1.2 and 2.1%, respectively, but it did not affect soil C : P ratios.

Grazing intensity also affected the link between above- and belowground C : N : P stoichiometry (Figure 4). Grazing-induced changes in soil C : N ratio [RR(soil C : N)] were negatively correlated with changes in litter C : N under both light and moderate grazing, but a positive correlation was found under heavy grazing (Figure 4c). In contrast, RR(soil C : P) was positively correlated with RR(root C : P) under both light and moderate grazing, but a negative correlation was detected under heavy grazing (Figure 4d).

3.3 | Effects of other factors on soil C : N : P stoichiometry under grazing

Grazing effects on soil C, N and P pools also depended on MAT, MAP and elevation (Figure 5, Supporting Information Figure S3). Specifically, grazing increased soil C pools when MAT < 0 °C, but significantly decreased soil C pools in studies with MAT > 0 °C (Figure 5a). The responses of the soil N pool, soil P pool, and soil C : P and soil N : P ratios to grazing became weaker when MAT increased (Figure 5b–f, Supporting Information Table S2). Furthermore, grazing decreased the soil P pool by 4.2% when MAP < 400 mm, but increased soil P by 2.3% when MAP was 400–800 mm (Figure 5g). The average response of soil C : P and N : P ratios to grazing decreased

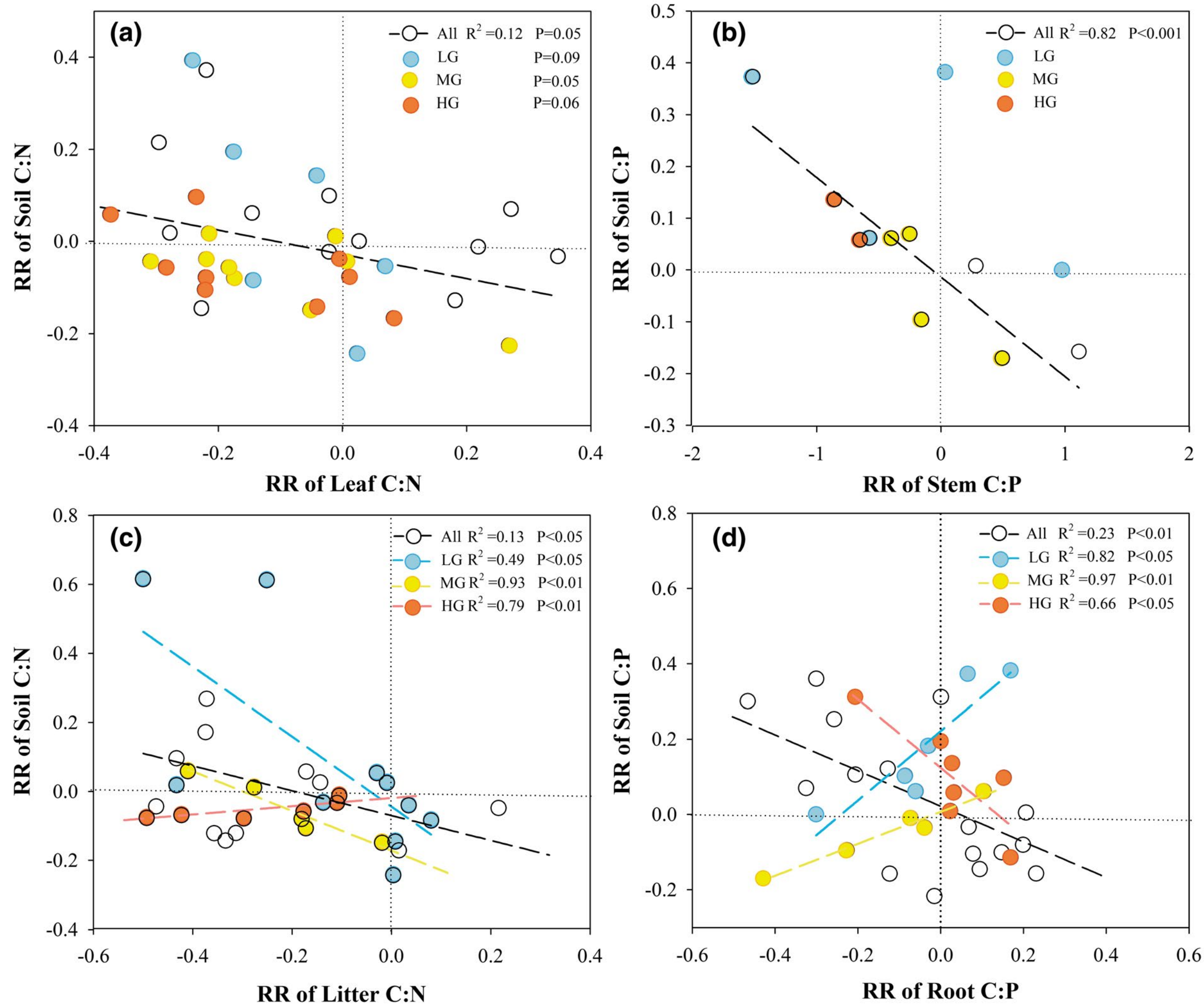

FIGURE 4 Relationships between the response ratios (RRs) of soil C : N ratio and leaf, litter C : N ratio, and the RR of soil C : P ratio and stem, root C : P ratio in different grazing intensities. LG = light grazing; MG = moderate grazing; HG = heavy grazing; All = all grazing intensities

with MAP (Figure 5k, l, Supporting Information Table S2). The response of the soil C pool to grazing shifted from positive to negative with increase in elevation, while the opposite trend was found for soil C : P ratio (Figure 5).

Soil depth and vegetation types (C3 versus C4) also affected the responses of soil C : N, C : P and N : P ratios under different grazing intensities (Supporting Information Figures S3–S5), but response patterns were uncertain due to the small sample sizes when the dataset was grouped into light, moderate and heavy grazing. Taken together, these changes support a conceptual framework in which grazing intensity determines the effects of livestock grazing on C : N : P stoichiometry in grassland ecosystems (Figure 6).

4 | DISCUSSION

Grazing is one of the main anthropogenic activities influencing the biogeochemical cycles of C, N and P in grassland ecosystems (Knops et al., 2002). Our analysis shows that grazing intensity affects above- and belowground C : N : P stoichiometry as well as their linkage across grasslands around the world. Our results showed that heavy grazing had significantly stronger effects on plant C : N : P stoichiometry than light and moderate grazing, and that the effects on soil C : N : P stoichiometry shifted from positive to negative with increasing grazing intensity (Figure 3). These patterns were closely associated with changes in above- and belowground C, N and P pools. Below, we will discuss how these results can be explained by grazing effects on plant ecophysiology, animal waste, microbial activity, and soil physicochemical environmental conditions (Figure 6).

4.1 | Effects of grazing intensity on aboveground C : N : P stoichiometry

The effects of grazing on leaf and litter C : N : P stoichiometry switched from positive to negative or became more negative with increasing grazing intensity, except for the N : P ratio in litter (Figure 3a, c). The decreased C : N, C : P and N : P ratios in plants could result from accelerated nutrient cycling or increased nutrient availability induced by livestock faeces and urine (Bai et al., 2012). Grazing increased the leaf

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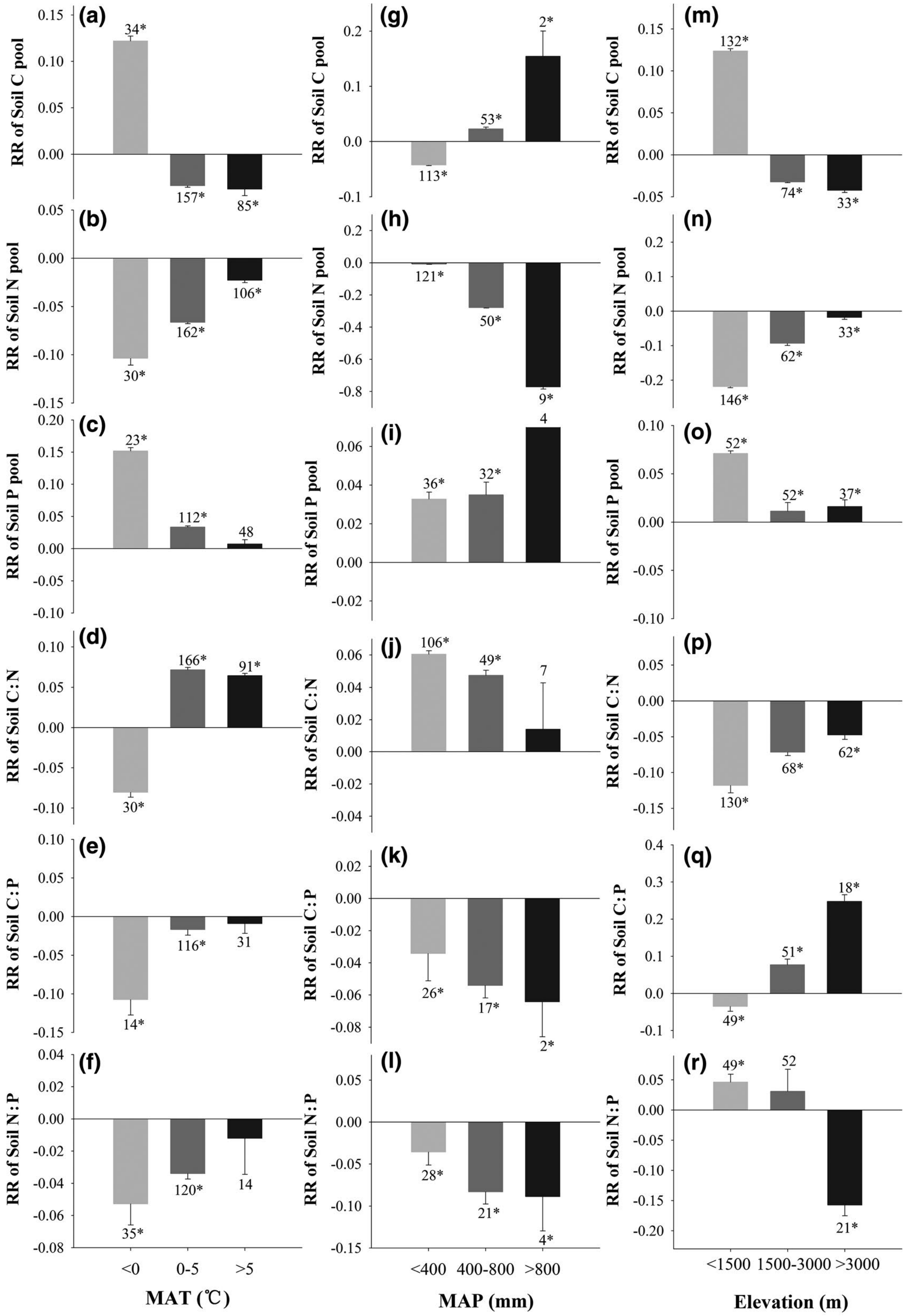

FIGURE 5 Effects of different environmental factors (mean annual temperature, MAT; mean annual precipitation, MAP; and elevation) on soil C : N : P stoichiometry. Bars represent RR_{++} ± 95% confidence intervals. Numbers for each bar indicate sample size. MAT is separated into < 0, 0–5 and > 5 °C, MAP is grouped into < 400, 400–800 and > 800 mm, while elevation is divided into < 1,500, 1,500–3,000, and > 3,000 m. Asterisks (*) indicate the grazing effect on relevant variables are significant. C, carbon; N, nitogen; P, phosphorus

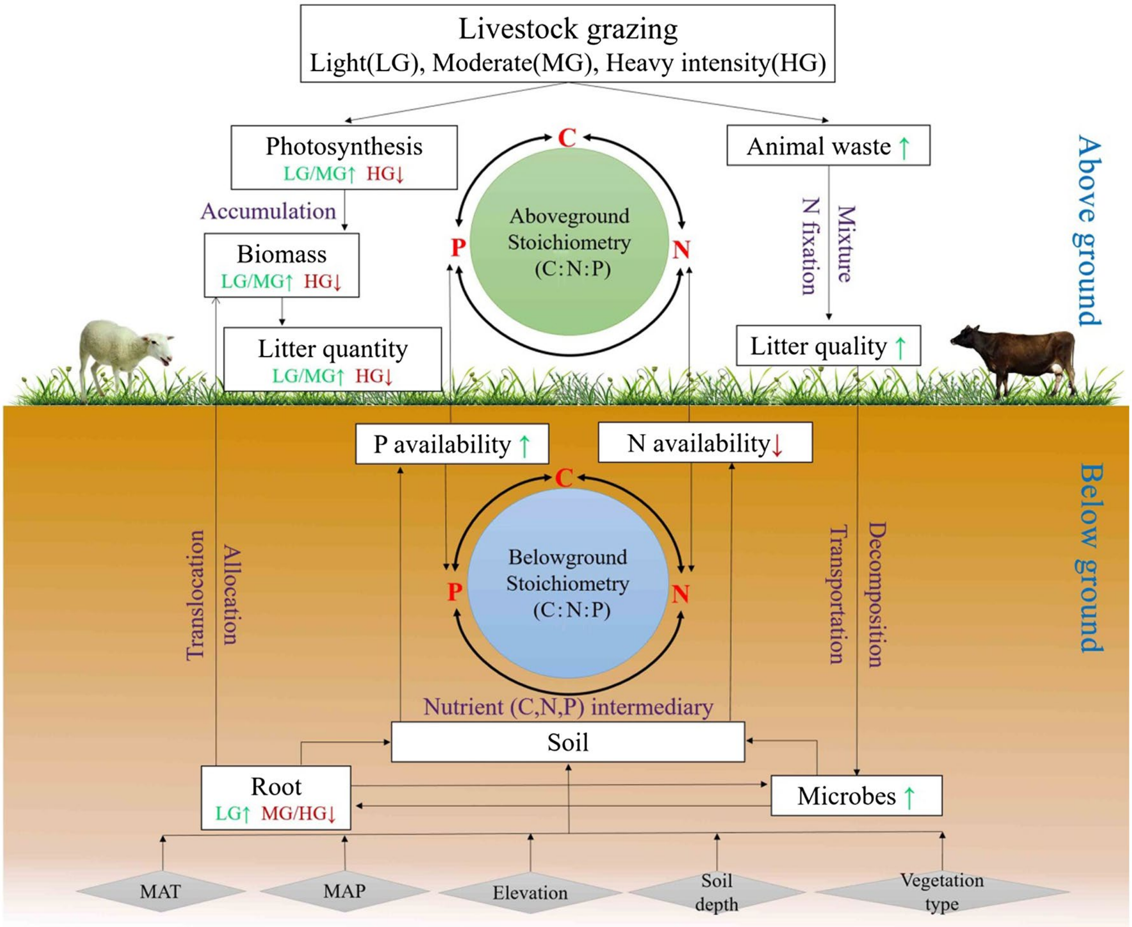

FIGURE 6 A conceptual diagram of the influence of different grazing intensities on processes controlling the above- and belowground C : N : P stoichiometry of grassland ecosystems. Nutrient pools include C, N and P content in above-and belowground plants, microbes and soil. Green upward arrows represent positive responses, red downward arrows negative responses. The positive or negative responses under different intensities are drawn based on the responses of C, N and P pools as well as our previous study (Zhou et al., 2017). LG = light grazing; MG = moderate grazing; HG = heavy grazing; MAT = mean annual temperature; MAP = mean annual precipitation

N pool but decreased the soil N pool (Figures 2, 6), suggesting that the decreased C : N ratio in leaves and litter with grazing were mainly due to the accelerated N cycling (Bai et al., 2012). However, the enhanced soil P pool under grazing (Figures 2, 6) largely caused the decreases in leaf C : P and N : P and litter C : P ratios, which might stem from both increased P use efficiency and soil P availability. The increase in litter N : P ratio under heavy grazing can probably be explained by plants failing to recycle N in time before grazing-induced defoliation (Avila-Ospina, Moison, Yoshimoto, & Masclaux-Daubresse, 2014). The changes in C : N : P stoichiometry of stems under light grazing were much larger than those of leaves and litter (Figure 3a–c), probably because leaves can absorb nutrients from stems to maintain an optimal stable C : N : P stoichiometry (Tang et al., 2018).

4.2 | Effects of grazing intensity on belowground C : N : P stoichiometry

The C : N : P stoichiometry of belowground processes was strongly regulated by grazing intensity. With increasing grazing intensity, effects on root C : P and N : P ratios became more negative, while effects on root C : N ratio became more positive (Figure 3a, d). The increased root C : N ratio may arise from grazing-induced C translocation to roots relative to N (Ritchie, Tilman, & Knops, 1998). This is a protective strategy, whereby plants allocate more non-structural carbohydrates to belowground organs to reduce C loss induced by overgrazing (Whigham & Simpson, 1978). Similar to the situations in leaves, the decreasing pattern in root C : P and N : P ratios with increasing grazing intensity might be due to enhanced N and P use efficiencies and increased soil P availability (Chapin, Matson, & Mooney, 2002).

The responses of soil C : N : P stoichiometry to grazing intensity have important implications for the development of sustainable strategies for grassland management. Our results showed that light grazing significantly increased the C : N, C : P and N : P ratios of soil but heavy grazing decreased these ratios (Figure 3f). The increases in soil C : N and C : P ratios under light grazing may result from grazing-induced increases in C-rich root exudates (Bardgett, Wardle, & Yeates, 1998). Heavy grazing with frequent livestock trampling and lower productivity may reduce both litter fall and root exudates, causing soil C and N loss (Figure 6; Derner et al., 1997; Heyburn, Mckenzie, Crawley, & Fornara, 2017). However, inputs of livestock urine and faeces may partly compensate N loss, resulting in a decreased C : N ratio under heavy grazing (Bai et al., 2012; Mcsherry & Ritchie, 2013). Moderate and heavy grazing decreased the soil N pool but increased the soil P pool (Figures 2, 6, Supporting Information Figure S2). These differences in grazing effects can possibly be explained by the mechanisms underlying N and P cycles. Whereas N can enter natural ecosystems through multiple routes, P derives mostly from mineral weathering (Peñuelas et al., 2013). Thus, we hypothesize that grazing increases soil P availability by stimulating rock weathering rates, possibly because of decreases in plant cover and increases in soil aridity and soil exposure (Delgado-Baquerizo et al., 2013; Eldridge & Delgado-Baquerizo 2017).

Microbes usually mediate the plant–soil feedback through mobilization and immobilization of nutrients, which may link the microbial C : N : P stoichiometry to soil stoichiometry (Bai et al., 2012). A previous study indicated a strong correlation between responses of microbial and soil C pools to grazing (Zhou et al., 2017). In this study, we also found that effects of grazing intensity on microbial C : N ratio were similar to those on soil C : N ratio (Figure 3e), suggesting that grazing affects these ratios through similar mechanisms, for example, grazing-induced root exudation, input of livestock urine and faeces, and trampling.

4.3 | Grazing intensity changed linkage between plant and soil C : N : P stoichiometry

Grazing intensity influences the relationship between plant and soil C : N : P stoichiometry (Bagchi & Ritchie, 2010; Liu et al., 2015). In this study, we found that correlations between the responses of litter and soil C : N ratios were negative under light and moderate grazing but became positive under heavy grazing (Figure 4c). These changes were probably due to the larger mixture of litter and soil with livestock urine and greater litter N fixation under heavy grazing than light and moderate grazing, enhancing microbial diversity and activity and stimulating the decay rate of litter (Knops et al., 2002).

Similarly, our results show that grazing-induced changes in soil C : P were positively correlated with changes in root C : P under both light and moderate grazing (Figure 4d). These results suggest a tight linkage between roots and soil under these grazing regimes due to increased root exudates and cascading effects on plant P uptake and then root P content (Bai et al., 2012; Gifford, & Marshall, 1973). However, this relationship became negative under heavy grazing, possibly because heavy grazing decreased soil C content but increased photosynthetic C allocation to roots (Klumpp et al., 2009). Alternatively, the cascade effect described above disappeared (Bai et al., 2012) and the excess P uptake by roots had a negative influence upon soil P.

Despite the correlations of soil stoichiometry with litter and root stoichiometry, soil C and N pools tended to respond more negatively to grazing than those of litter and roots (Figure 2). This suggests that grazing stimulated soil C and N loss through abiotic pathways. For example, livestock activities might change soil structure by disrupting aggregates and surface crust, leading to increased soil susceptibility to water and wind erosion and stimulating soil C and N losses (Neff, Reynolds, & Belnap, 2005). These effects may complicate the links between plants and soil, and provide another explanation as to why correlations between plant and soil stoichiometry changed with grazing intensities (Figure 4).

4.4 | Regulation of grazing effects on soil C : N : P stoichiometry by climate, soil depth and vegetation type

Climate, soil depth and vegetation type are known to affect the biogeochemical cycles of C, N and P (Mcsherry & Ritchie, 2013; Yuan & Chen, 2015), and might also affect the responses of these cycles to grazing. Responses of soil C : N : P stoichiometry to grazing increased with MAT but decreased with MAP (Figure 5). P limitation is more common in warmer biomes whereas N limitation is more common in colder biomes, explaining why grazing effects on soil N : P increased with MAT (Reich & Oleksyn, 2004). Grasslands in humid regions typically have greater plant productivity and higher microbial diversity than grasslands in arid regions (Bai et al., 2012), possibly explaining why grazing accelerated N cycling and decreased soil N stocks more strongly in humid regions. Because soil N can easily be leached with rainfall (Vitousek, Porder, Houlton, & Chadwick, 2010) as well as the grazing effects on soil P were relatively similar for humid and dry regions, grazing decreased soil N : P along the MAP gradient. As higher elevations are usually associated with lower temperature and greater precipitation, the increased responses of soil C : N and C : P ratios to grazing along the elevation gradient might be mainly explained by the effects of MAP, whereas the decreased responses of soil N : P might be due to the effects of MAT (Figure 5p–r).

Our results showed that grazing induced larger increases in soil C : N ratio in deeper soil compared to surface soil, due to weaker decreases in soil C stocks and stronger decreases in soil N stocks (Supporting Information Figure S2). Under grazing, frequent trampling activity in topsoil may largely destroy soil aggregates, accelerate decomposition of soil organic matter, and increase soil susceptibility to water and wind erosion (Neff et al., 2005), thereby causing larger decreases in soil C stocks but weak effects on soil N stocks compared to those in deeper soil. In addition, differences in root biomass distribution (Schuman, Reeder, Manley, Hart, & Manley, 1999) and microbial community composition (Shrestha & Stahl, 2008) within the plant–soil system may also affect the response of soil N and P pools and N : P ratios to grazing at different soil depths (Zhou et al., 2017).

Differential responses of C : N : P stoichiometry to grazing were also found between C3 and C4 plants. Unfortunately, most of the comparisons did not have sufficient data to draw a solid conclusion (Figure 6). With relatively larger sample size, grazing increased C : N ratios in C4 plants more strongly than in C3 plants. These results can possibly be explained by higher root-to-shoot ratios, higher root exudates, and tighter association with mycorrhizae to stimulate soil organic C storage in C4 grasslands (Mcsherry & Ritchie, 2013).

4.5 | Implications for future experiments and terrestrial ecosystem models

Understanding the effects of grazing intensity on the C : N : P stoichiometry of grassland ecosystems will help us improve grassland management and predict climate–biosphere feedbacks (Derner et al., 1997; Zhou, Luo, Chen, Hu, et al., 2019). Recent ecosystem models usually consider grazing effects through three primary processes (i.e., direct intake, excretion, and trampling; Chen et al., 2018), and apply livestock density and/or weight of livestock to indicate grazing intensity (Chen et al., 2019). In contrast, Earth system models (ESMs) simulate grazing by direct biomass removal (Erb et al., 2017), although the coupled C, N and P cycles have been incorporated into some models (Thum et al., 2019). Our results showed that grazing intensity significantly influenced plant and soil C : N : P stoichiometry as well as their linkage (Figures 3, 4). Furthermore, grazing might trigger the defence strategy of plants, shift the biomass allocation, and change plant nutrient use efficiency (Figure 6). These grazing-induced changes in C : N : P stoichiometry have not been incorporated into grazing models and ESMs (Thum et al., 2019). Integrating grazing effects on C : N : P stoichiometry into ESMs and validating these models against field observations may improve prediction of ecosystem functioning in grasslands worldwide (Bello et al., 2010).

Most of the studies included in this meta-analysis were conducted in the temperate grasslands in eastern Asia and Northern America (Figure 1). More experiments are needed to understand the impact of grazing on tropical savanna and boreal tundra. Moreover, field experiments are needed to provide mechanistic insight into grazing effects on C, N and P cycles. In addition to climate, soil depth, and vegetation type, management history might also regulate the response of C : N : P stoichiometry to grazing (Chapin et al., 2002; Zhou et al., 2017). Fortunately, both the grazed and ungrazed plots of most of the selected studies were free of grazing for at least for 10 years prior to the start of the experiment, minimizing the effect of land use history. Nevertheless, well-designed transect experiments might yield insights into grazing effects across large spatial scales and provide useful baselines for evaluating grazing effects in ESMs.

5 | CONCLUSIONS

Grazing is a key anthropogenic disturbance that strongly influences the ecosystem C, N and P cycles as well as their stoichiometry. Our analysis showed that heavy grazing generally had stronger effects on ecosystem C : N : P stoichiometry than light and moderate grazing, indicating substantial impacts of livestock disturbance on biogeochemical cycles of C, N and P in grassland ecosystems. The differential responses of soil N and P pools to grazing and their linkage between plants and soil suggested that soil physicochemical processes played an important role in regulating grazing effects. Experiments that are focused on belowground processes and experiments in tropical and boreal grasslands could deepen our understanding of the responses of ecosystems to grazing. Incorporating the effects of grazing intensity into the framework of next-generation ESMs may improve predictions on how human disturbance affects the functioning of grassland ecosystems.

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AUTHOR CONTRIBUTION

X. Zhou and G. Zhou designed and oversaw the research. G. Zhou and M. He collected and analysed the data, and wrote the first draft of the manuscript. All authors discussed and revised the manuscript together.

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DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository: https://doi.10.5061/dryad.xksn02vbc (He et al., 2019).

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BIOSKETCHES

Xuhui Zhou, **Junjiong Shao** and **Kees Jan van Groenigen** are career scientists mainly interested in the impacts of human activity on C, N and P dynamics of terrestrial ecosystems. **Miao He**, **Guiyao Zhou** and **Tengfei Yuan** are students in Prof. Zhou's research group.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX: DATA SOURCES

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