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Grazing intensity significantly affects belowground carbon and nitrogen cycling in grassland ecosystems: a meta-analysis

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Abstract

Livestock grazing activities potentially alter ecosystem carbon (C) and nitrogen (N) cycles in grassland ecosystems. Despite the fact that numerous individual studies and a few meta-analyses had been conducted, how grazing, especially its intensity, affects belowground C and N cycling in grasslands remains unclear. In this study, we performed a comprehensive meta-analysis of 115 published studies to examine the responses of 19 variables associated with belowground C and N cycling to livestock grazing in global grasslands. Our results showed that, on average, grazing significantly decreased belowground C and N pools in grassland ecosystems, with the largest decreases in microbial biomass C and N (21.62% and 24.40%, respectively). In contrast, belowground fluxes, including soil respiration, soil net N mineralization and soil N nitrification increased by 4.25%, 34.67% and 25.87%, respectively, in grazed grasslands compared to ungrazed ones. More importantly, grazing intensity significantly affected the magnitude (even direction) of changes in the majority of the assessed belowground C and N pools and fluxes, and C : N ratio as well as soil moisture. Specifically,light grazing contributed to soil C and N sequestration whereas moderate and heavy grazing significantly increased C and N losses. In addition, soil depth, livestock type and climatic conditions influenced the responses of selected variables to livestock grazing to some degree. Our findings highlight the importance of the effects of grazing intensity on belowground C and N cycling, which may need to be incorporated into regional and global models for predicting effects of human disturbance on global grasslands and assessing the climate-biosphere feedbacks.

Keywords: carbon sequestration, CO_2 emission, heavy grazing, mineralization, soil microbial biomass

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Introduction

Grassland ecosystems cover approximately 40% of the terrestrial lands and provide important ecosystem services including carbon (C) sequestration and climate regulation as well as economic and recreational values (Lecain *et al*., 2002; Lal, 2004; Piao *et al*., 2009; Wang & Fang, 2009). Global grasslands store 10–30% of soil organic C (SOC) with a sequestration rate of 0.5 Pg C yr^{-1} and harbor more than 10% of terrestrial biomass C (Follett & Reed, 2010; Qiu *et al*., 2013). Currently, a majority of grasslands are experiencing overgrazing (Salvati & Carlucci, 2015), which not only threatens the biodiversity and stability of grasslands, but also alters ecosystem structure and functioning, leading to increased C and N losses (Knops & Tilman, 2000; Stavi *et al*., 2008; Fornara *et al*., 2011; Liu *et al*., 2015).

Over the past 40 years, a large number of studies have been conducted to examine the responses of aboveground processes to grazing in grassland ecosystems, which have considerably improved our understanding of the mechanisms underlying the grazing effects (Bai *et al*., 2012; Stahlheber & D'Antonio, 2013; Dean *et al*., 2015). For example, intermediate grazing could contribute to sustain plant species diversity and ecosystem stability, while no grazing may decrease diversity of equilibrium community (i.e., intermediate disturbance hypothesis, Connell, 1978; Sasaki *et al*., 2009). Aboveground biomass often increased by intermediate grazing compared to that by light and heavy

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grazing, due to the fact that medium grazing resulted in a higher species diversity than no or low grazing (Connell, 1978; Yan *et al*., 2013; Gong *et al*., 2014). However, effects of grazing on belowground C and N storage remain uncertain due to methodological difficulties and spatial heterogeneity (Holland & Detling, 1990; Henderson *et al*., 2004; Liu *et al*., 2015).

Currently, numerous studies have investigated the responses of belowground C and N cycles to livestock grazing, showing contradictory results, especially on SOC with decrease (He *et al*., 2011; Liu *et al*., 2015), increase (Knops & Tilman, 2000; Bai *et al*., 2012) and no effect (Bagchi & Ritchie, 2010). In addition, root biomass under grazing treatment was approximately 1.5 times higher than those under grazing exclusion (Gong *et al*., 2014). In contrast, livestock grazing led to significant decreases in MBC and MBN, while TN in the topsoil remained constant compared to ungrazed grassland (Wen *et al*., 2013). To clarify the inconsistency among individual studies, Mcsherry & Ritchie (2013) conducted a meta-analysis to examine grazing effects on soil C in grasslands and found that grazing increased SOC under heavier intensities in C_4-dominated grasslands and decreased it in C_3-dominated grasslands, probably due to increases in fine and shallow roots of C_4 grasses.

Contradictory responses of belowground C and N processes to grazing may be associated with the differences in grazing intensities, grazing duration or climatic conditions (Mcsherry & Ritchie, 2013). Grazing intensity may be the major driving factor in influencing belowground C and N processes because grazing intensity alters plant community structure, soil microenvironment, and soil microbial diversity and activity (McNaughton *et al*., 1988; Manley *et al*., 1995; Stavi *et al*., 2008). However, effects of grazing intensity on belowground C and N dynamics are also contradictory. For example, Schuman *et al.* (1999) found that neither light nor heavy grazing could significantly change total plant biomass and soil C and N pools. In contrast, Lin *et al.* (2010) and Liu *et al.* (2012) found that light grazing stimulated both soil C and N sequestration, while moderate and heavy grazing enhanced soil C and N losses in both typical and desert steppes. In addition, Yan *et al.* (2013) showed that soil C and N pools decreased with increased grazing intensity in a semiarid grassland, China. Therefore, it is necessary to compile all the available data to reveal the patterns and mechanisms of belowground C and N responses to different grazing intensities.

In this study, a meta-analysis was conducted on 622 paired comparisons from 115 experimental studies to evaluate the responses of belowground C and N cycles to grazing intensities. Specifically, our objectives were to (i) examine global patterns of belowground C and N responses to livestock grazing; (ii) assess effects of grazing intensities on the belowground C and N dynamics; and (iii) investigate regulation of the environmental factors on soil C pools (SCP) and soil N pools (SNP) alteration in response to grazing.

Materials and methods

Data sources

Peer-reviewed journal articles published before October 2015 were searched using Web of Science and China Knowledge Resource Integrated Database (CNKI) with the following search term combinations: (grazing or herbivory or defoliation) and (carbon or nitrogen) and (grassland or pasture or meadow). To avoid bias in publication selection, the following five criteria were set to select studies: (i) Experiments were conducted in the field and had at least one pair of data (under control and treatment); (ii) grazing regimes were clearly defined with both quantitative and/or qualitative descriptions for grazing intensity, experimental duration (DUR) and livestock type (i.e., cattle, sheep or others); (iii) to avoid short-term noise, experiments with durations less than one growing season were excluded; (iv) initial environmental and climate conditions, soil parameters and species compositions in the control and treatments were the same; (v) the mean, standard error (SE) or standard deviation (SD) and sample size (n) of selected variables (see below for the detailed description) in control and treatment groups could be extracted directly from tables, digitized graphs or contexts. In total, 115 published papers (of 2000), among which 71 addressed soil C, 52 addressed soil N and 44 were associated with both belowground C and N cycles under different grazing conditions, were selected (Fig. 1, Appendix S1 and Table S1).

The selected study had at least one of 19 response variables to be included in the database. The database included belowground C and N pools [C and N stocks in soil, litter, root and microbial biomass], C : N ratio [i.e., soil C : N (SCN), root C : N (RCN), litter C : N (LCN), microbial C : N ratio (MCN)], fluxes [i.e., soil respiration (Rs), soil net N mineralization (SNNM) and soil net N nitrification (SNNN)] and related soil parameters such as soil bulk density (BD), soil moisture (SM), soil temperature (ST), soil pH and soil depth. In total, 19 variables related to belowground C and N cycling were selected in the database. The number of studies for the following variables included carbon pools (n = 68), nitrogen pools (n = 55), C : N ratio (n = 38), fluxes (n = 18) and environmental conditions (n = 41). All the data were extracted from figures and tables in selected published papers. Meanwhile, environmental variables including latitude, mean annual temperature (MAT), mean annual precipitation (MAP) were recorded directly from papers or cited papers, or in case that the MAT and MAP were not reported in studies, extracted from the global climate database (http://www.worldclim.org/) using site geographical coordinates information.

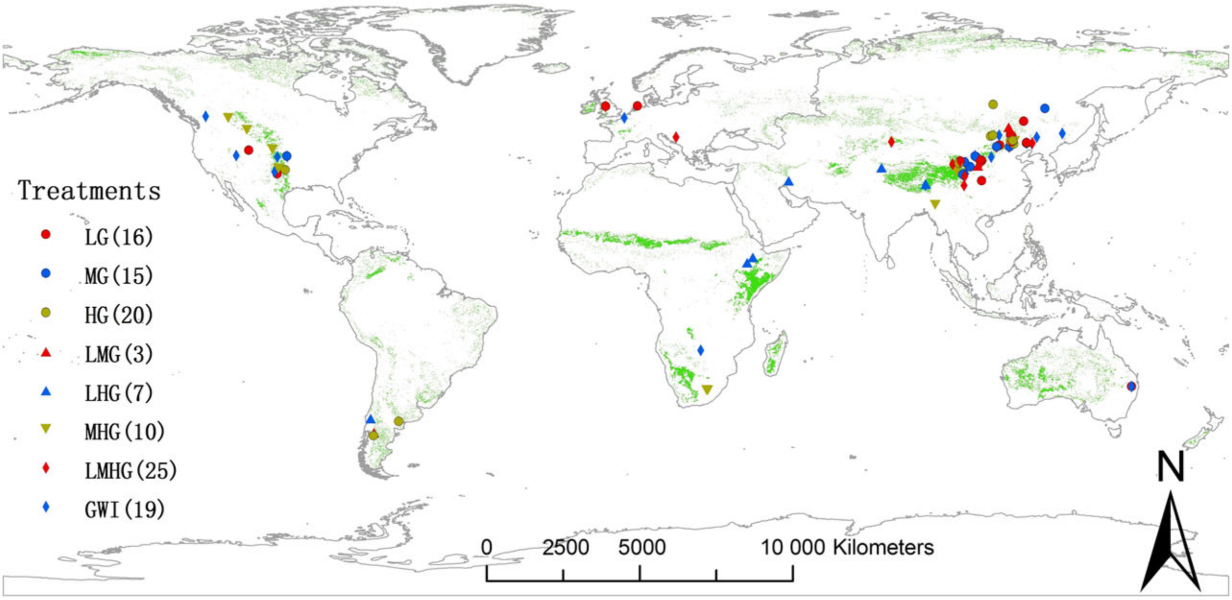

Fig. 1 Global distribution of grazing experiments used in this meta-analysis. Most studies were conducted in eastern Asia. LG, MG and HG represent sites with light, moderate and heavy grazing treatments, respectively. LMG, LHG, MHG and LMHG represent the combinations of two or three grazing intensities (e.g., LMG includes both light and moderate grazing; LMHG includes all three grazing intensities). GWI represents the sites with no grazing intensity information. Based map with green color represents the distribution of global grasslands.

To test the differences in responses of belowground C and N cycling to grazing, the chosen 19 variables were then grouped into five categories including carbon pools, nitrogen pools, C : N ratio, fluxes and environmental variables. This study used the soil and root data at the depth of 0–100 cm, which were divided into 0–15 cm and >15 cm due to the limited data when soil depth was >30 cm. Environmental variables included MAT between −0.1° and 18.3°, MAP between 145 and 860 mm and latitude between 42.1°S and 52.3°N (Fig. 1). The study sites were considered as arid/semiarid and semihumid/humid climate when MAP was <400 mm and ≥400 mm, respectively. Grazing duration varied between 0.4 and 30 years. Grazing intensity was divided into ungrazed or fenced treatments (UG) as the control, light grazed (LG), moderate grazed (MG) and heavy grazed (HG) treatments based on the authors' qualitative classification directly from papers or cited papers, as diverse grasslands may have the different carrying capacity in the specific study area. Livestock type was classified into cattle and sheep. The spatiotemporal variations of belowground C and N responses were examined with climatic factors, grazing duration and soil depth.

Data analysis

We followed the methods used by Hedges *et al.* (1999) and Luo *et al.* (2006) to calculate the response ratio (RR) of belowground C and N processes to grazing. RR is defined as natural log of the ratio of the mean value of a concerned variable in the grazing treatment group ($\overline{X}_t$) to that in the control group ($\overline{X}_c$) to represent the magnitude of changes of belowground C and N processes as below:

$$\mathrm{RR} = \mathrm{Ln}(\overline{X}_t/\overline{X}_c) \tag{1}$$

where $\overline{X}_t$ and $\overline{X}_c$ are the means in the treatment and control groups, respectively. The variance (v) of RR is estimated by:

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

where n_t and n_c represent the sample sizes, and s_t and s_c are the standard deviations of the concerned variable in the treatment and control groups, respectively. The reciprocal of variance ($w = \frac{1}{v}$) was considered as the weight (W) of each RR.

The means of response ratio (RR_{++}) are calculated from individual RR of each paired comparison between the control and grazing treatments, RR_{ij} ($i = 1,2,\ldots,m$; $j = 1,2,\ldots,k$) with the weight of each RR. Here, m is the numbers of groups (e.g., different intensity, climate type, livestock type or soil depth), and k is the number of comparisons. The mean response ratios were calculated using the following equation:

$$\mathrm{RR}_{++} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij}\mathrm{RR}_{ij}}{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij}} \tag{3}$$

The weighted standard error (SE) was

$$S(\mathrm{RR}_{++}) = \sqrt{\frac{1}{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij}}} \tag{4}$$

The 95% confidence interval (95% CI) is $\mathrm{RR}_{++} \pm 1.96\ S(\mathrm{RR}_{++})$ (Zhang *et al.*, 2015a). We applied a *t*-test to examine the significance of variation in each variable between the control and treatment, and the difference in RR_{++} between grazing intensity, climate type, grazing type and soil depth. The effect of livestock grazing was considered to be significant if the 95% CI of a response variable did not overlap zero (Luo *et al.*, 2006). The percentage changes of variables were calculated on the basis of $[\exp(RR_{++}) - 1] \times 100\%$. Frequency distributions of RR ($n > 25$) of belowground C and N pools were plotted to validate the results from the meta-analysis by a Gaussian function (i.e., normal distribution) using Eqn (5) in SIGMAPLOT software (Systat Software Inc., San Jose, CA, USA).

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

where x is RR of a variable; y is the 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 mean and variance of the frequency distributions of RR, respectively. Pearson correlation analyses were performed to examine the relationships between the response ratio of SCP and SNP with environmental conditions (i.e., grazing duration, latitude, MAT and MAP).

Results

Effects of grazing on belowground C and N pools and fluxes

The mean response ratios (RR_{++}) of the 19 variables to grazing related to belowground C and N cycles and environmental variables were all significantly different from zero ($P < 0.05$; Fig. 2). On average, grazing significantly decreased C pools in bulk soils, root, soil microbes and litter by 10.28%, 13.72%, 21.62% and 8.93%, respectively, and N pools by 13.38%, 4.40%, 24.40% and 10.39%, respectively (Fig. 2; Table S2). Among the variables, microbial biomass C and N showed the largest decrease in response to grazing compared to other variables (Fig. 2). In contrast, soil and root C : N ratios increased under grazing whereas microbial biomass and litter C : N ratios decreased under grazing compared to the control (Fig. 2). Grazing also significantly increased soil respiration (Rs), soil net N mineralization and soil net N nitrification by 4.25%, 30.63% and 12.88%, respectively (Fig. 2; Table S2). In addition, grazing increased soil bulk density (BD), soil pH and temperature but decreased soil moisture (Fig. 2).

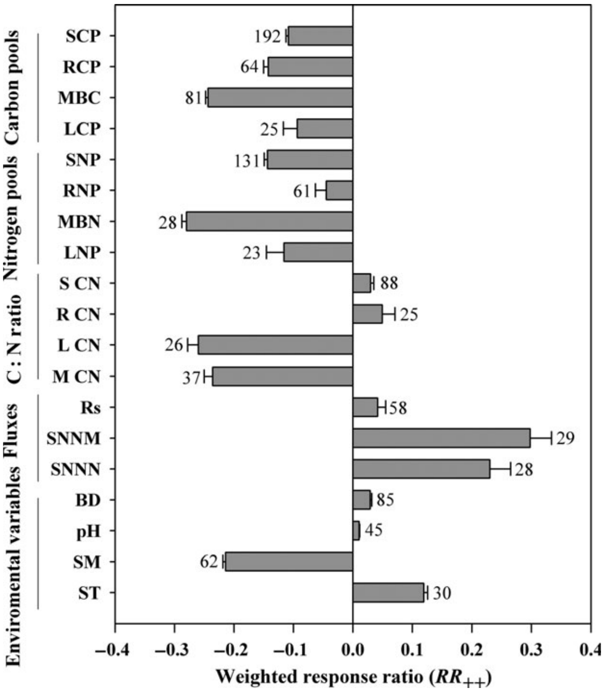

Fig. 2 Weighted response ratio (RR_{++}) of 19 variables related to carbon and nitrogen cycling in response to grazing. Bars represent 95% confidence intervals. The vertical line was drawn at $RR_{++} = 0$. Numbers for each bar indicate the sample size. SCP, soil carbon pool; RCP, root carbon pool; MBC, microbial biomass carbon; LCP, litter carbon pool; SNP, soil nitrogen pool; RNP, root nitrogen pools; MBN, microbial biomass nitrogen; LNP, litter nitrogen pool; SCN, soil C : N ratio; MCN, microbial biomass C : N ratio; RCN, root C : N ratio; Rs, soil respiration; SNNM, soil net mineralization; SNNN, soil net N nitrification; BD, bulk density; SM, soil moisture; ST, soil temperature.

Effects of grazing intensity on belowground C and N pools and fluxes

Grazing intensity significantly affected the responses of belowground C and N processes to livestock grazing (Fig. 3; Table S2). Heavy grazing decreased soil C and N pools more than those of light and moderate grazing with two exceptions observed in SNNN and RCN. Specifically, light grazing increased SCP and SNP by 0.78% and 3.24%, respectively ($P < 0.01$, Fig. 3; Table S2). However, moderate and heavy grazing significantly decreased SCP by 3.45% and 9.92%, and SNP by 8.41% and 13.04%, respectively, resulting in a decreasing trend in effects of light to heavy grazing on soil C : N ratio (SCN, Fig. 3). The responses of RCP, LCP and MBC to grazing were significantly correlated with RR (SCP) but with different slopes under three intensities (Fig. 4). Specifically, the significant relationships of RR (SCP) with RR (RCP) decreased from light intensity ($R^2 = 0.75$) to heavy intensity ($R^2 = 0.37$, Fig. 4b). However, the most significant correlation between RR (SCP) and RR (MBC) was found in moderate intensity compared with light and heavy intensities (Fig. 4b, d). In addition, RR (SCP) showed a significant negative correlation with the response of bulk density to grazing, but was positively correlated with pH (Fig. S2).

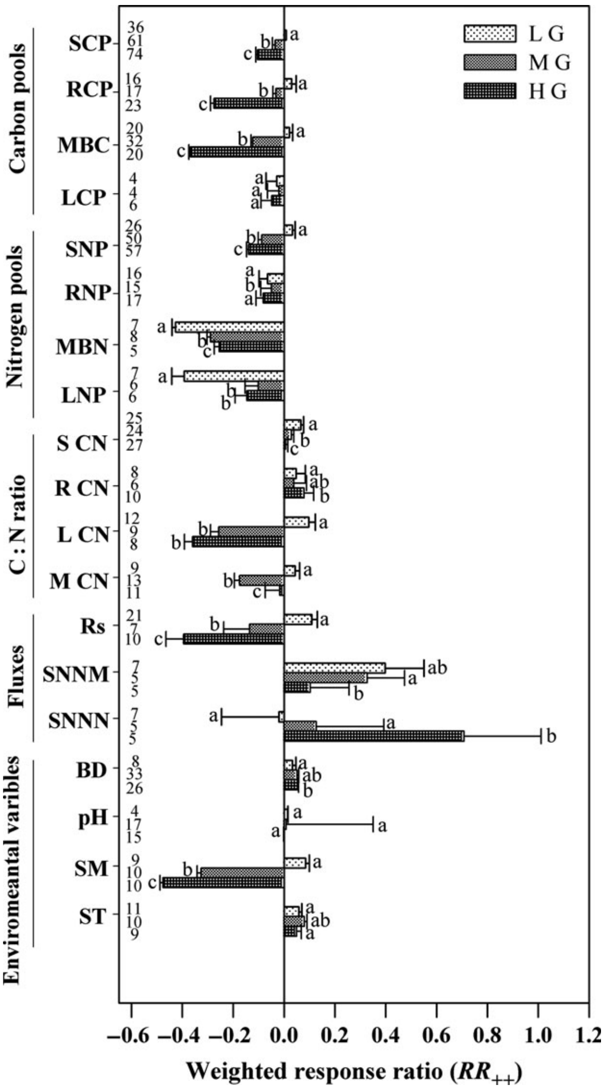

Fig. 3 Weighted response ratio (RR_{++}) of 19 variables related to carbon and nitrogen cycles in response to different grazing intensity. Bars represent RR_{++} ± 95% confidence intervals. The vertical line was drawn at $RR_{++} = 0$. Numbers for each bar indicate the sample size. Symbols *a, b* and *c* represent the significant differences among three grazing intensities for the responses of selected variables to grazing. SCP, soil carbon pools; RCP, root carbon pools; MBC, microbial biomass carbon; LCP, litter carbon pools; SNP, soil nitrogen pools; MBN, microbial biomass nitrogen; LNP, litter nitrogen pools; RNP, root nitrogen pools; SCN, soil C : N ratio; MCN, microbial biomass C : N ratio; RCN, root C : N ratio; Rs, soil respiration; SNNM, soil net mineralization; SNNN, soil net N nitrification; BD, bulk density; SM, soil moisture.; ST, soil temperature. LG, light grazing; MG, moderate grazing; HG, heavy grazing.

Similarly, light grazing increased root C pool (RCP) and litter C : N ratio (LCN) by 2.99% and 10.14%, respectively, while moderate and heavy grazing decrease RCP by 3.17% and 24.1% and LCN by 22.61% and 30.18%, respectively. The increasing magnitudes also occurred for responses of microbial biomass C (MBC) to grazing from light to heavy intensity (Fig. 3). However, microbial biomass N (MBN) and litter N pool (LNP) showed the larger decreases in response to light grazing compared with those to moderate and heavy grazing. In addition, responses of litter C pool (LCP), root N pool (RNP) and root C : N ratio (RCN) to different grazing intensities did not vary ($P > 0.05$).

For belowground C and N fluxes, the weighted response ratio of Rs [RR_{++} (Rs)] differed significantly among grazing intensities ($P < 0.05$, Fig. 3). Rs increased by 11.53% under light intensity, whereas moderate and heavy intensities decreased Rs by 12.7% and 32.6%, respectively. The weighted response ratios of SNNM [RR_{++} (SNNM)] decreased by 48.87–10.85% from light to heavy grazing intensities. However, light grazing did not affect the response ratios of SNNN [RR_{++} (SNNN)], but moderate and heavy grazing intensities significantly increased [RR_{++} (SNNN)] by 13.43% and 103.06%, respectively.

Effects of environmental factors, livestock type and soil depth on soil C and N pools under grazing

Grazing disturbance decreased RCP, SNP and RNP greater in semihumid/humid regions than those in arid/semiarid regions. Similarly, the weighted response ratio of Rs [RR_{++} (Rs)] in semihumid/humid regions was 0.099 ± 0.023 ($P < 0.01$; Fig. 5a), which was slightly higher than those in arid/semiarid regions with 0.011 ± 0.017 ($P > 0.05$). However, MBC and LCP exhibited the larger negative effects in response to grazing under arid/semiarid regions compared to those under semihumid/humid regions. In contrast, SNNM, SNNN and ST increased positively in arid/semiarid regions under grazing compared to those of semihumid/humid regions (Fig. 5a). Different livestock type and soil depth showed different magnitudes of changes (even direction) for many of the considered variables (Fig. 5b, c). For example, the response of SCP, SNP, RCP and RNP under sheep grazing showed a greater decrease than those under cattle grazing. Response of MBC to grazing was positive at the depth of <15 cm, but negative at the depth of >15 cm.

Climate type, livestock type and soil depth also affected the overall magnitude and even direction of the weighted response ratios of SCP, SNP and SCN under different grazing intensities (Fig. 6). For example, both SCP and SNP significantly decreased with increasing intensity in semihumid/humid regions, whereas moderate and light intensity exhibited positive effects on SCP and SNP, respectively, in arid/semiarid regions. Decreased SCP was highest under heavy grazing, followed by light and moderate ones, irrespective

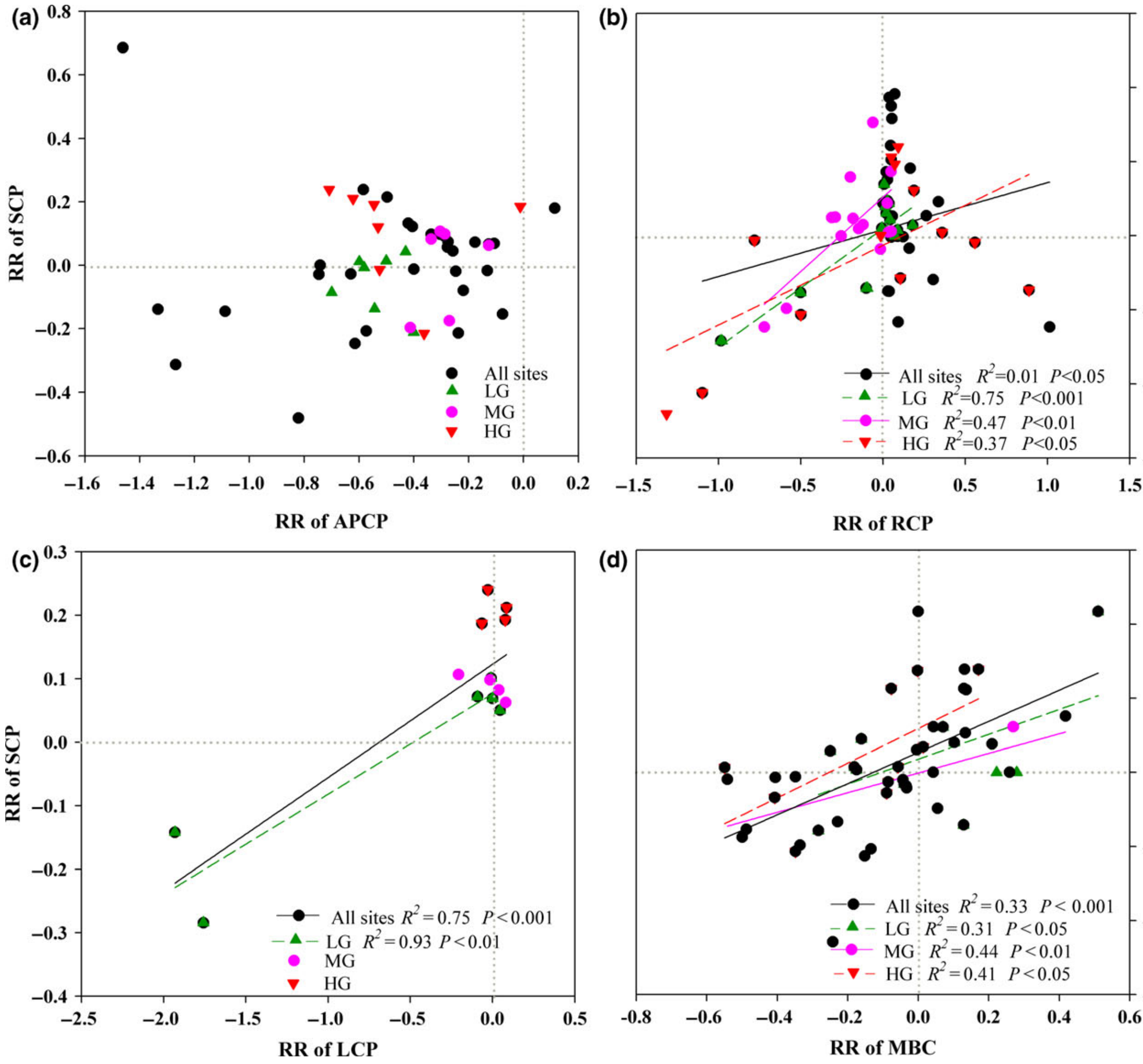

Fig. 4 Relationships of response ratios (RR) of soil carbon pools (SCP) with aboveground carbon pools (APCP, a), root carbon pools (RCP, b), litter carbon pools (LCP, c) and microbial biomass carbon pools (MBC, d). All sites represented the data for all intensities and some with no intensity information – black closed circles; LG, light grazing intensity – green closed triangles; MG, moderate grazing intensity – purple closed circles; HG, heavy grazing intensity – red closed triangles.

of cattle or sheep grazing. SNP exhibited positive effects under light grazing at the soil depth of >15 cm, while moderate and heavy intensity at the same depth had the opposite trends (Fig. 6).

Our meta-analysis also showed that grazing duration and MAT displayed significant correlations with RR (SCP) and RR (SNP, Fig. 7; Table S3). Both RRs of SCP and SNP to grazing decreased with increasing grazing duration, with a larger decrease for SCP (Fig. 7a, b). The MAP exhibited a significant correlation with the response of SCP (P < 0.05), but it was not correlated with response of SNP to grazing (Fig. 7; Table S3). Similarly, the latitude showed a significantly negative correlation with RR (SCP), but no correlation with RR (SNP) was observed (Table S3). In addition, the responses of SCP to grazing exhibited a significant positive correlation with RR (SNP). Therefore, all of these changes showed a conceptual framework in which there were positive or negative effects of livestock grazing on belowground C and N cycles in grazed ecosystems (Fig. 8).

Discussion

Grazing-induced decreases in belowground C and N pools and fluxes

Grazing by domestic livestock is one of the major human activities that significantly affects the C and N

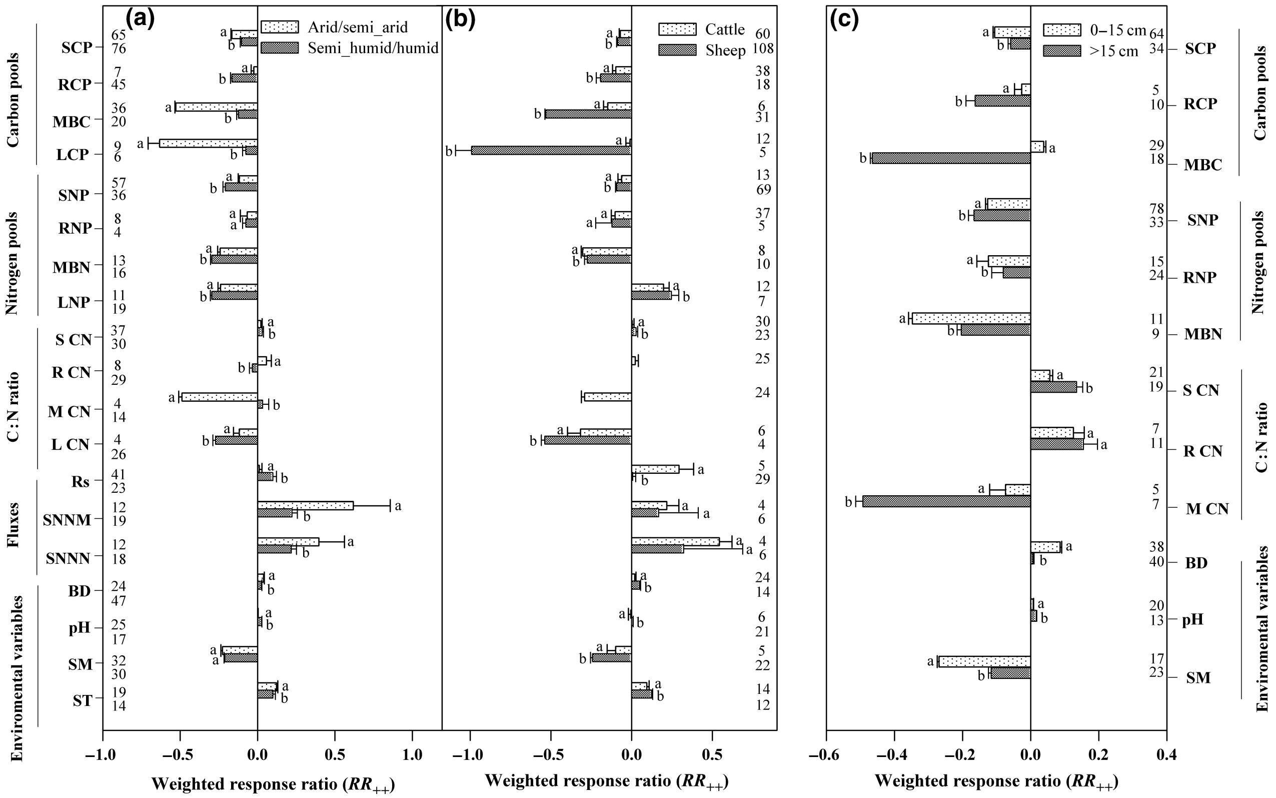

Fig. 5 Weighted response ratio (RR_{++}) of 19 variables related to carbon and nitrogen cycles in response to arid/semiarid – white columns and semihumid/humid – gray columns (a), cattle grazing – white columns and sheep grazing – gray columns (b), 0–15 cm – white columns and >15 cm – gray columns (c). Bars represent RR_{++} ± 95% confidence intervals. The vertical line was drawn at $RR_{++} = 0$. Numbers for each bar indicate the sample size. Symbols *a* and *b* represents the significant differences among two categories (panel a, arid/semiarid vs. semihumid/humid climate; panel b, cattle vs. sheep grazing; panel c, soil depth of 0–15 cm vs. >15 cm) for the responses of selected variables to grazing. SCP, soil carbon pools; RCP, root carbon pools; MBC, microbial carbon; LCP, litter carbon pools; SNP, Soil nitrogen pools; MBN, microbial nitrogen; LNP, litter nitrogen pools; RNP, root nitrogen pools; SCN, soil C : N ratio; MCN, microbial C : N ratio; RCN, root C : N ratio; Rs, soil respiration; SNNM, soil net mineralization; SNNN, soil net N nitrification; BD, bulk density; SM, soil moisture.; ST, soil temperature.

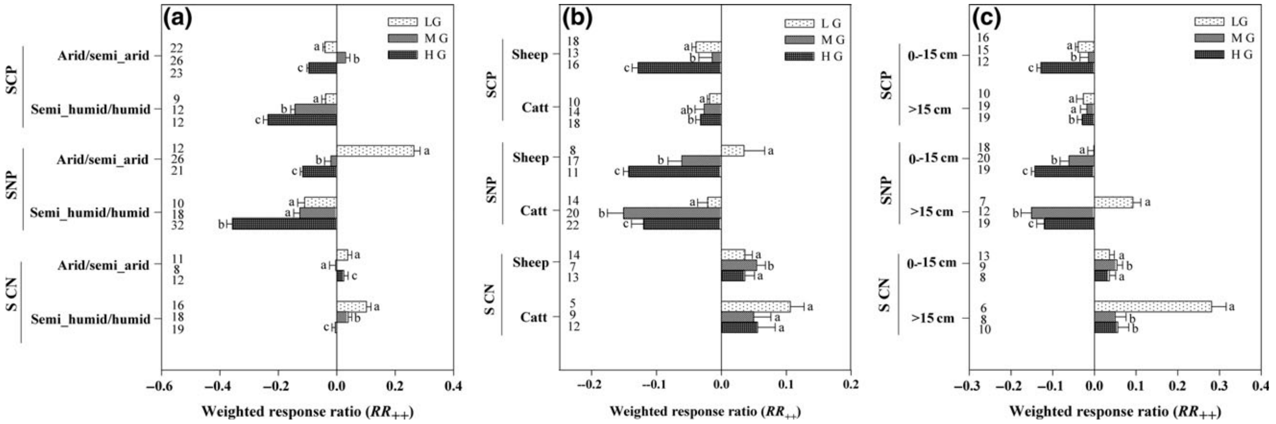

Fig. 6 Weighted response ratio (RR_{++}) of soil carbon pools (SCP), soil nitrogen pools (SNP), and soil C : N ratio (SCN) in different grazing intensities with respect to climate type (a), livestock type (b), and soil depth (c). Bars represent RR_{++} ± 95% confidence intervals. The vertical line was drawn at $RR_{++} = 0$. Number values for each bar indicate the sample size. Symbols *a*, *b* and *c* represents the significant differences among three grazing intensities for the responses of selected variables to grazing.

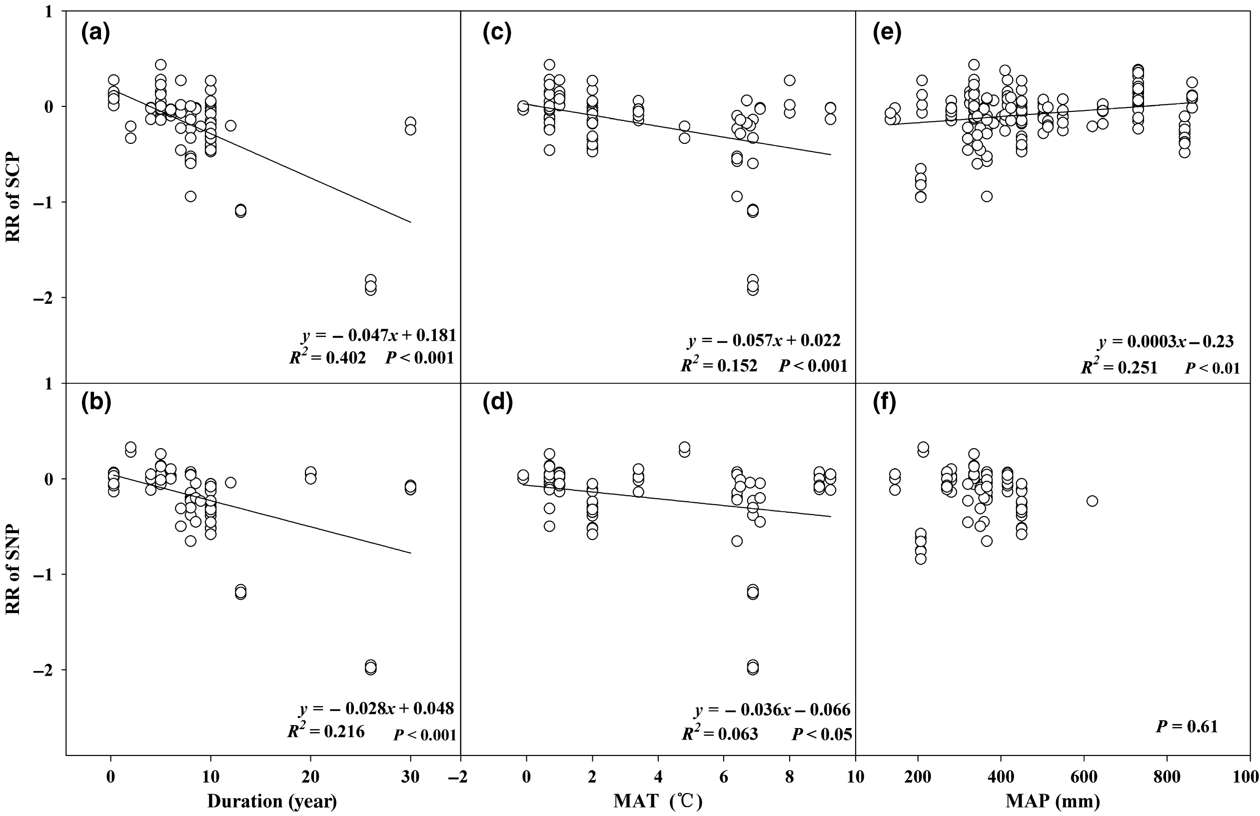

Fig. 7 Relationships of grazing duration (a, b), mean annual temperature (MAT, c, d) and mean annual precipitation (MAP, e, f) with response ratios (RR) of soil carbon pools (SCP, a, c, e) and soil nitrogen pools (SNP, b, d, f).

cycles in grassland ecosystems (Knops *et al.*, 2002; Wu *et al.*, 2014). Our meta-analysis showed that grazing decreased the C and N pools in soils, belowground plants, microbes and litters (Figs 2 and 8; Table S2). The decreased C and N pools may be attributed to the decreased aboveground plant production due to plant removal induced by livestock grazing (Frank & Groffman, 1998; Bagchi & Ritchie, 2010). Specifically, grazing decreased aboveground biomass leading to reduced litterfall and litter mass, which was also supported by our meta-analysis (Liu *et al.*, 2015). Plant damage and removal by livestock grazing are also likely to decrease root elongation and biomass (Bagchi & Ritchie, 2010), resulting from the reduced C allocation to roots (Mcsherry & Ritchie, 2013). Changes in litter and root biomass decreased soil bacterial community and diversities (Knops *et al.*, 2002) and then microbial biomass and soil C pool (Bai *et al.*, 2015a). It has been shown that C inputs from root production and biomass may have a significant effect on soil C storage compared to aboveground biomass (Russell *et al.*, 2009; Lu *et al.*, 2011). Our results also found that the grazing-induced decreases in SCP were linearly correlated with that in root C pool (RCP) but not with that in aboveground inputs (Fig. 4a, b). In addition, livestock disturbance activities can change soil structure, aggregates and surface crust, leading to increased soil susceptibility to water and wind erosion and enhancing soil C and N loss (Neff *et al.*, 2005).

Our results indicated a decrease in soil microbial biomass in grazed areas. The decreased belowground C and N pools under grazing in our study were consistent with those from previous studies in many American and Chinese grasslands (Mcsherry & Ritchie, 2013; Liu *et al.*, 2015). Decrease in C inputs led by grazing has shown to negatively affect microbial N immobilization and then lowered N stocks in soils (Schuman *et al.*, 1999; Knops *et al.*, 2002; Luo *et al.*, 2006), as the C cycling is closely coupled by N cycling (Bai *et al.*, 2015b).

Effects of grazing intensity on belowground C and N processes

Grazing intensity affected belowground C and N cycles with different magnitudes and even directions in a large number of individual studies (Schuman *et al.*, 1999; Savadogo *et al.*, 2007; Liu *et al.*, 2012). Using a

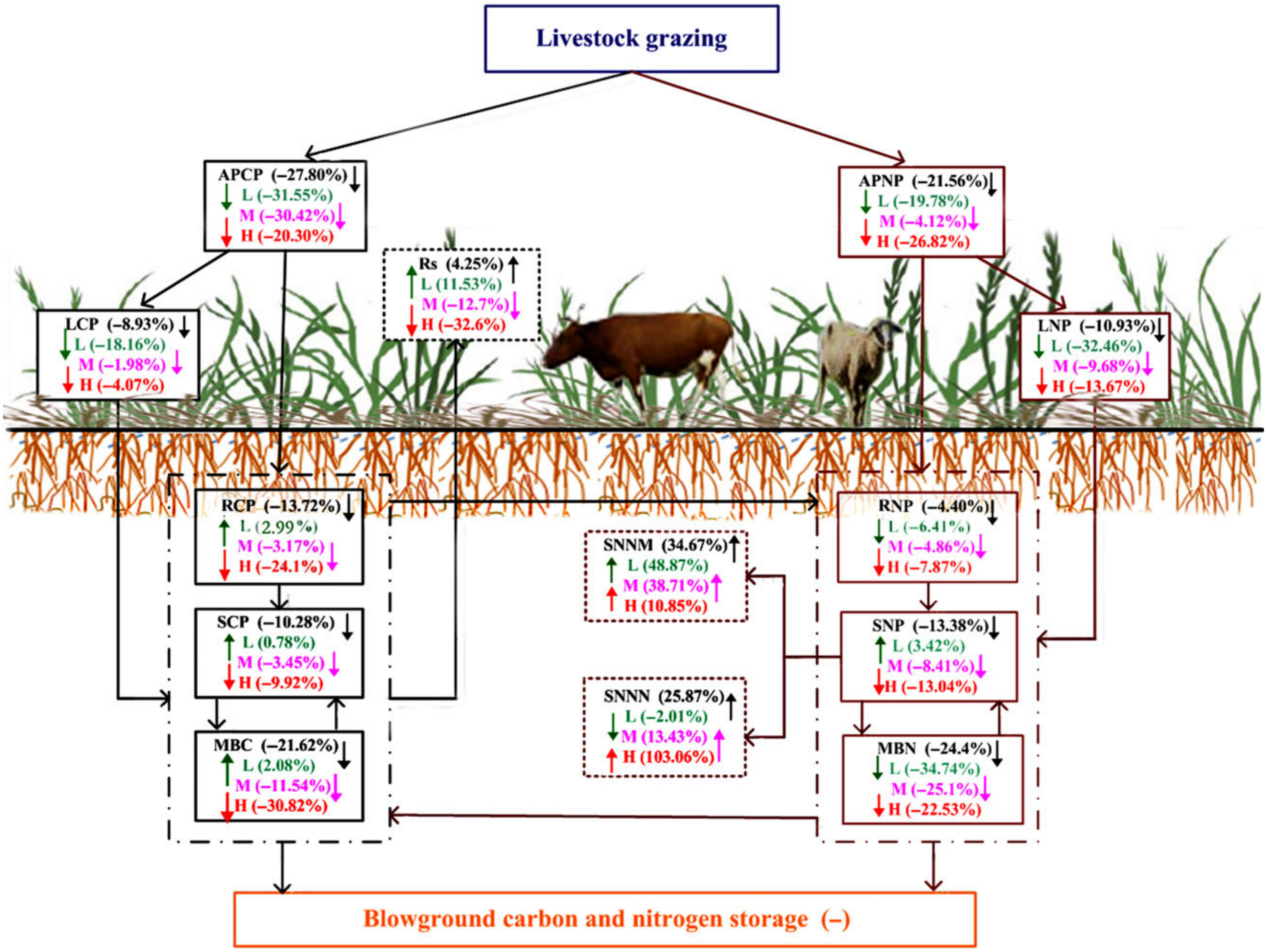

Fig. 8 Potential mechanisms of belowground C and N processes in response to livestock grazing. The numbers refer to percentage change ($e^{RR++} - 1$) × 100% of belowground C and N variables in response to grazing. SCP, soil carbon pools; RCP, root carbon pools; MBC, microbial carbon; LCP, litter carbon pools; SNP, soil nitrogen pools; MBN, microbial nitrogen; LNP, litter nitrogen pools; RNP, root nitrogen pools; APCP, aboveground plant carbon pools; APNP, aboveground plant nitrogen pools. APCP and APNP data were provided in supporting information. L, light grazing intensity presented with green color; M, moderate grazing intensity presented with purplish color; H, heavy grazing intensity presented with red color. ↑, positive response to livestock grazing; ↓, negative response to livestock grazing.

meta-analysis method, we found that light intensity significantly enhanced SCP and SNP, while moderate and heavy intensity exhibited the opposite trends (Figs 3 and 8; Table S2), which was similar to the results from Lin *et al.* (2010) and Liu *et al.* (2012) in typical and desert steppes, respectively. The increased above-belowground biomass induced by light grazing (including livestock foraging) stimulated more photosynthetically fixed C inputs to belowground roots, leading to increased root exudates and root biomass (Mcsherry & Ritchie, 2013; Liu *et al.*, 2015; Zhang *et al.*, 2015a). Increased root exudates in soil may enhance C accumulation and further stimulate N inputs into soils (Derner *et al.*, 1997). Due to the increased root biomass and soil C accumulation, light grazing also significantly stimulated soil respiration (Reicosky, 1997; Baker *et al.*, 2007; Gong *et al.*, 2014). Our meta-analysis showed that light grazing increased soil moisture, which may be due to increased ground cover and decreased soil compaction under light grazing compared to moderate and heavy grazing (Thomey *et al.*, 2011; Zhang *et al.*, 2015b). Increased soil moisture and temperature would also stimulate plant growth and microbial activities, leading to increased Rs (Savadogo *et al.*, 2007).

Both moderate and heavy grazing, however, significantly decreased SCP and SNP (Figs 3 and 8; Table S2), which was consistent with many previous studies (Parton *et al.*, 1987; He *et al.*, 2011; Wu *et al.*, 2012). The decreased SCP and SNP may arise from decreased C inputs through plant removal by livestock and decreased litter mass as well as RCP and microbial biomass (Detling *et al.*, 1979; Schuman *et al.*, 1999; Knops *et al.*, 2002). Similarly, Rs also exhibited negative responses to moderate and heavy grazing (Figs 3 and 8; Table S2), largely resulting from a decrease in RCP and the limited substrate availability, which largely reduced root and microbial respiration, respectively (Kuzyakov & Cheng, 2001; Ryan & Law, 2005). Moderate and heavy grazing probably also depressed soil infiltrability and nutrient availability, inhibiting plant biomass accumulation and microbial activity (Savadogo *et al.*, 2007). In addition, the faster soil evaporation with poor ground cover under heavy grazing lowered soil moisture, which might also further explain decreased Rs (Savadogo *et al.*, 2007; Stavi *et al.*, 2008; Thomey *et al.*, 2011).

Similarly, our results found that light grazing increased litter C : N ratio, but both moderate and heavy grazing significantly decreased litter C : N ratio (Figs 3 and 8; Table S2). The increased aboveground biomass under light grazing may increase accumulation of both fallen litter and dieback of the aboveground biomass, leading to increased litter C : N ratio (Li *et al.*, 2008; Lin *et al.*, 2010). Lower N circulation rate under light grazing would also contribute to increased litter C : N ratio in grassland ecosystems (Holland *et al.*, 1996; Li & Chen, 1998; Pineiro *et al.*, 2009). Litter C : N ratio, however, significantly decreased under moderate and heavy grazing (Figs 3 and 8; Table S2), probably resulting from large mixture with livestock feces by livestock trampling and/or litter N fixation under moderate and heavy grazing (Knops *et al.*, 2002; Neff *et al.*, 2005; Liao *et al.*, 2008).

Grazing-induced changes in SCP may be related to alteration of RCP, LCP and MBC (Knops *et al.*, 2002; Bagchi & Ritchie, 2010; Liu *et al.*, 2015). In our study, we found that grazing intensity significantly affected the relationships of RR (SCP) with C pools (e.g., RCP, LCP and MBC). Positive correlation between RR (SCP) and RR (RCP) under light grazing was more significant than those under moderate and heavy intensities (Fig. 4b), suggesting that RCP was more important in affecting the SCP under light grazing with increased photosynthetically C inputs (Liu *et al.*, 2015). RR (MBC) was also positively correlated with RR (SCP) at the ecosystem scales with the largest significant effect under moderate grazing ($R^2 = 0.44$, $P < 0.01$), which probably resulted from abundant root exudates under moderate grazing that may increase microbial activity (Zhao *et al.*, 2014). The litter C transfer and transport may cause a positive correlation between RR (SCP) and RR (LCP) under light intensity (Bai *et al.*, 2012) but with large uncertainty due to the limited numbers of samples (Fig. 4c).

Factors regulating the responses of belowground C and N processes to grazing

Environmental factors (both MAP and MAT), climate type, livestock type and grazing duration have shown to affect plant performance and belowground C and N dynamics (Mcsherry & Ritchie, 2013). Grazing-induced decreases in RCP were more significant in semihumid/humid than arid/semiarid climate regions, which may be related to faster root turnover in wetter regions compared to those in the drier regions (Chapin *et al.*, 2002). We found that changes in the weighted response ratio of MBC were consistent with those of LCP (Fig. 5), which were supported by the close relationship between LCP and MBC in terrestrial ecosystems (Su *et al.*, 2005). Grazing significantly decreased the MBC and LCP in arid/semiarid climate, where lower productivity was more responsive to grazing disturbance compared to those in semihumid/humid condition. In addition, the larger decrease from litter inputs by grazing may considerably weaken MBC in arid/semiarid climate (Osem *et al.*, 2004; Liu *et al.*, 2012; Shi *et al.*, 2013). Furthermore, Rs in semihumid/humid regions increased more than that in arid/semiarid regions, which might be associated with existing high net ecosystem productivity (Xia *et al.*, 2009) and high microbial activity (Zhou *et al.*, 2009) in the wetter regions than those in the drier regions.

The response of belowground C and N cycles to grazing did not show a similar trend at different soil depths (0–15 vs. >15 cm; Fig. 5). Differences in foraging selectivity by livestock usually lead to the variation of species composition and community structure, inducing the difference of C and N inputs/outputs in grazed ecosystems (Knops *et al.*, 2002). At different depths, thus, grazing-induced spatial variations of root biomass distribution (Schuman *et al.*, 1999) and different sensitivity to environments (Holland & Detling, 1990) within plant–soil system probably caused response differences of belowground C and N cycles to livestock grazing.

A weak correlations between RR (SCP) and MAP were observed in this study (Fig. 7; Table S3), which was consistent with Mcsherry & Ritchie (2013) and Hu *et al.* (2016). As plant productivity and microbial activity in wetter areas are usually greater than those in drier climate, the actual responses of SCP to grazing may have been masked, causing weak correlation between SCP and MAP (Raich & Schlesinger, 1992; Williams *et al.*, 2000; Luyssaert *et al.*, 2007). In our study, despite the fact that there was a weak correlation between *RR* (SCP) and MAP, MAT was negatively correlated with RR (SCP) and RR (SNP) (Fig. 7; Table S3; $P < 0.001$). Grasslands in tropical and temperate regions have high MAT and greater microbial activity than those in boreal regions with the low-MAT (Chapin *et al*., 2002). The higher microbial activity in high-MAT regions can usually accelerate decay of soil organic matter and increase turnover rate, and then lower the SCP and SNP more in those grazed ecosystems, resulting in the negative correlation between MAT and RR (SCP) or RR (SNP). On the other hand, soil temperature, water content and their interactions fundamentally determine the temporal dynamics of C cycle in grassland ecosystem, especially Rs (Wang *et al*., 2006).

Soil organic C showed a significant negative correlation with bulk density, which was in line with a previous grassland mesocosm study (Fig. S2, Steffens *et al*., 2008). The compacted soil by livestock trampling may destroy soil aggregates and then stimulate organic matter decomposition as well as increasing accessibility to wind erosion (Hamza & Anderson, 2005; Neff *et al*., 2005), resulting in the lower SCP. However, a positive correlation between SCP and pH was observed in this study. Low pH condition favors fungal communities, which would stimulate the decomposition of recalcitrant organic matter and then decrease SCP in grazed grassland ecosystems (Brodie *et al*., 2002; Jensen *et al*., 2003).

Implications for grassland management and model development

Overgrazing has been a primary contributor to grassland degradation and desertification, which not only decreases biodiversity and stability of grassland ecosystems but also threatens global C and N balance and further contributes to accelerate climate change in the future (Lal, 2004; He *et al*., 2011; Mcsherry & Ritchie, 2013). Our results may provide some insights to explain to what extent belowground C and N cycles respond to grazing at a global scale. Thus, this study offers recommendations for development and improvement of land-surface models as well as design of manipulative experiments in the future, at least in three aspects as follows.

First, the majority of current studies were distributed in temperate climate, especially in eastern Asia and northern America. Thus, more long-term manipulative experiments in cold and hot regions, especially in Africa and Australia, need to be conducted to examine the effects of grazing on belowground C and N cycles at temporal and spatial scales. Experimental duration of livestock grazing in most studies was less than 10 years; hence, there is a need to undertake studies over one decade to better understand the effects of grazing on belowground C and N cycling.

Second, the response of belowground C and N cycles to livestock disturbance differed among light, moderate and heavy grazing intensities. However, current land-surface models usually do not differentiate the effects of grazing intensities on belowground C and N cycles (Lal, 2004; Henderson *et al*., 2015; Tagesson *et al*., 2015), which often creates a great challenge to the prediction of future feedbacks between the climate and the C cycle. Future land-surface models may need to differentially treat with grazing intensity in order to develop more precise process-based mechanism for forecasting the feedback of grassland ecosystems to climate change.

Third, the responses of SCP [RR (SCP)] and SNP [RR (SNP)] to livestock grazing were negatively correlated with MAT (Fig. 7). The response ratios of SCP and SNP to grazing in warmer biomes were clearly higher than those in the low range (Fig. 7), suggesting that sensitivity of RR (SCP) and RR (SNP) to grazing changed with MAT. These results indicate the importance of conducting transect studies of livestock grazing along the MAT gradient to better examine the effects of grazing on C and N cycling when other environmental variables (e.g., precipitation and soil) do not affect the explication of spatial patterns (Mcsherry & Ritchie, 2013; Zhou *et al*., 2014). Therefore, these relationships can be incorporated into land-surface models to improve the prediction about livestock grazing-regulated response of terrestrial ecosystems C and N cycles if they are validated in transect and other studies.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Frequency distributions of response ratios (RR) of soil carbon pools (SCP, a), soil nitrogen pools (SNP, b), belowground plant carbon pools (RCP, c), root nitrogen pools (RNP, d) microbial biomass carbon (MBC, e) and microbial biomass nitrogen (MBN, f) to livestock grazing.
Figure S2. Relationships of response ratios (RR) of soil carbon pools (SCP) with bulk density (BD, a) and pH (b).
Table S1. Response ratio (RR) and number of data sets (in parentheses) of 19 variables extracted from each of the papers.
Table S2. Percentage of change concerned variables in responses to livestock grazing.
Table S3. Correlation analysis of environmental variables with each other and with response ratio of SCP [RR(SCP)] and SNP [RR(SNP)] of surface soil (<15 cm).
Appendix S1. A list of 115 papers from which the data were extracted for this meta-analysis.