




Effects of livestock grazing on grassland carbon storage and release override impacts associated with global climate change

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Abstract

Predicting future carbon (C) dynamics in grassland ecosystems requires knowledge of how grazing and global climate change (e.g., warming, elevated CO₂, increased precipitation, drought, and N fertilization) interact to influence C storage and release. Here, we synthesized data from 223 grassland studies to quantify the individual and interactive effects of herbivores and climate change on ecosystem C pools and soil respiration (Rs). Our results showed that grazing overrode global climate change factors in regulating grassland C storage and release (i.e., Rs). Specifically, grazing significantly decreased aboveground plant C pool (APCP), belowground plant C pool (BPCP), soil C pool (SCP), and Rs by 19.1%, 6.4%, 3.1%, and 4.6%, respectively, while overall effects of all global climate change factors increased APCP, BPCP, and Rs by 6.5%, 15.3%, and 3.4% but had no significant effect on SCP. However, the combined effects of grazing with global climate change factors also significantly decreased APCP, SCP, and Rs by 4.0%, 4.7%, and 2.7%, respectively but had no effect on BPCP. Most of the interactions between grazing and global climate change factors on APCP, BPCP, SCP, and Rs were additive instead of synergistic or antagonistic. Our findings highlight the dominant effects of grazing on C storage and Rs when compared with the suite of global climate change factors. Therefore, incorporating the dominant effect of herbivore grazing into Earth System Models is necessary to accurately predict climate–grassland feedbacks in the Anthropocene.

KEYWORDS

C-climate feedback, drought, elevated CO₂, increased precipitation, N fertilization, soil respiration, warming

1 | INTRODUCTION

The grassland biome is the largest terrestrial ecosystem type, covering up to 40% (59 million km²) of the world's ice-free land area (Hufkens et al., 2016) and storing 10%–30% of the global soil organic

carbon (SOC; Follett & Reed, 2010). Consequently, changes in grassland carbon (C) dynamics would have profound effects on the global C balance (Follett & Reed, 2010; IPCC, 2013). Currently, grassland C dynamics are strongly impacted by grazing (McSherry & Ritchie,

2013; Zhou, Zhou, He, et al., 2017a) and global climate change (e.g., warming, elevated CO₂, increased precipitation, drought, N fertilization; Yuan & Chen, 2015; Zhou, Zhou, Shao, et al., 2016a; Zhou, Zhou, Nie, et al., 2016b). Because most global grasslands are grazed (Salvati & Carlucci, 2015), grazing is an important control on global C processes, including C storage and release (Frank & Groffman, 1998; McSherry & Ritchie, 2013). In addition, a variety of factors associated with global climate change (e.g., warming, drought) also alters grassland C dynamics in diverse ways (Bradford et al., 2016; Yuan & Chen, 2015). Knowledge of the individual and interactive effects of grazing and global climate change factors on C dynamics remain rudimentary but is vital to assess the climate–biosphere feedbacks in the future (Davidson & Janssens, 2006; McSherry & Ritchie, 2013).

Over the past 20 years, numerous studies had been conducted to explore the effects of grazing on C-cycle processes in grassland ecosystems, which have substantially enhanced our understanding of the potential mechanisms underlying how grasslands respond to grazing (Dean, Kirkpatrick, Harper, & Eldridge, 2015). For example, the intermediate disturbance hypothesis suggests that moderate grazing maintains higher ecosystem diversity, while lower or higher grazing decreases species diversity in subhumid grasslands with long evolutionary history of grazing (Cingolani, Noymeir, & Díaz, 2005; Connell, 1978; Katja et al., 2009). Milchunas *et al.*'s generalized model (MSL model) predicts that different grazing intensities have distinct equilibrium outcomes, and the grazing effects on biodiversity are associated with the coevolutionary history between vegetation and large herbivores and mean precipitation (Cingolani et al., 2005; Gillson & Hoffman, 2007). Global meta-analyses further revealed that herbivores had diverse effects on plant diversity and soil C storage dependent on grazing intensity, frequency of precipitation, soil texture, and dominant plant species (Herrero-Jáuregui & Oesterheld, 2018; McSherry & Ritchie, 2013).

Predicting future grassland dynamics requires that the effects of grazing are considered in combination with the impacts of global climate change factors on grasslands (Luo et al., 2004). The combined effects may lead to a positive or negative C-climate feedback, which may amplify or diminish grazing effects (Milchunas, Lauenroth, Burke, & Detling, 2008; Parsons, Leafe, Collett, Penning, & Lewis, 1983). Several studies have synthesized the net effects of global climate change factors on ecosystem C storage and release at the global scale (Luo, Hui, & Zhang, 2006; Yuan & Chen, 2015; Chen et al., 2018). For example, Zhou, Zhou, Shao, et al. (2016a) and Zhou, Zhou, Nie, et al. (2016b) indicated that increased precipitation significantly stimulated soil respiration (Rs), whereas drought largely suppressed above- and belowground plant C pools (BPCP) of grasslands. Warming stimulated Rs by 12% in the early stages, but the simulation was offset by the effects of microbial acclimation and warming-induced drought over time (Wang et al., 2014). The recent meta-analysis of Zhou, Zhou, Shao, et al. (2016a) found that the combination of global climate change factors induced a greater positive effect on Rs than that of any single factor. However, the relative importance of grazing and global climate change factors and their combined effects in regulating C storage and release remains

unclear, which may hamper us in predicting global C dynamics and understand climate–biosphere feedbacks.

Additionally, previous studies found that the interactive effects of multiple global climate change factors on C pools were often additive rather than synergistic or antagonistic (Crain, Kroeker, & Halpern, 2008; Yuan & Chen, 2015). For example, additive effects of elevated CO₂ and warming on grassland soil C storage and Rs were often observed (Yue et al., 2017; Zhou, Zhou, Shao, et al., 2016a; Zhou, Zhou, Nie, et al., 2016b). However, the form of interactions (e.g., synergistic, additive, or antagonistic) between grazing and global climate change factors is not known (Chapin, Matson, & Mooney, 2002; Yuan & Chen, 2015). In addition, aboveground plant C pool (APCP) is likely more sensitive to grazing than global climate change factors compared with other C pools, because of the reduction of leaf biomass by herbivory and the expected reduction in C allocation to belowground structures (McSherry & Ritchie, 2013; Yuan & Chen, 2015; Zhou, Zhou, Zhang, et al., 2017b). Therefore, it is necessary to examine available data to gain an understanding of how grazing and climate change will drive future grassland C dynamics around the globe.

Meta-analyses use findings from individual studies on a common theme to draw general conclusions (Gurevitch, Koricheva, Nakagawa, & Stewart, 2018) and have been increasingly applied to understand grassland C dynamics (Lu et al., 2013; McSherry & Ritchie, 2013). In this study, we conducted a comprehensive analysis of data extracted from 223 multiple-factor studies to examine the individual and interactive effects of grazing and global climate change factors on above and belowground plant, soil and microbial C pools, and C fluxes from the soil to the atmosphere (Rs). Our objectives were to (a) address individual versus combined effects of grazing and global climate change factors on soil and plant C pools and Rs; (b) investigate whether the interactive effects of grazing and global climate change factors on C pools and Rs are additive, synergistic, or antagonistic.

2 | MATERIALS AND METHODS

2.1 | Data compilation

Web of Science and *Google Scholar* (1900–2017) searches yielded more than 2,500 peer-reviewed journal articles about the combined effects of grazing (G) and global climate change (i.e., elevated CO₂ [E], warming [W], N fertilization [N], drought [D], increased precipitation [P]). The selected studies had at least one of five response variables related to C storage and release. These variables were above- and belowground plant carbon pools (APCP & BPCP), soil carbon pool (SCP), microbial biomass C pool (MBC), and soil respiration (Rs). The C pools were C stocks in soil, above- and belowground plants, and microbial biomass. The studies also included the related soil parameters such as pH, soil bulk density (BD), soil moisture (SM), and soil temperature (ST). To avoid publication bias, the following six criteria were used to select studies: (a) At least a full-factorial design was used to examine the effects of grazing and

global climate change factors, including elevated CO₂, nitrogen addition, warming, increased precipitation, and/or drought. (b) At least one of the selected variables (i.e., above- and BPCP, APCP & BPCP; soil C pool (SCP); and microbial biomass C, MBC; soil respiration, Rs) was examined in all treatments and the control at the same temporal and spatial scales. (c) Initial environmental and climate conditions, ecosystem type, soil parameters, and dominant species composition in the control and treatments were the same. (d) The grazing difference between the control and treatments in the site had lasted for ten or more years; both enclosure studies and comparisons of differently grazed areas were included. (e) The methods used for elevated [CO₂] [e.g., free-air CO₂ enrichment or open top chamber (OTC)], warming (e.g., infrared heater, soil heating cable, or OTC), nitrogen addition, drought (e.g., rain exclusion shelter), and irrigation treatments were clearly described, and the experimental duration was longer than one growing season. (f) The mean, standard error (SE) or standard deviation (SD) and sample size (n) of selected variables (see below for the detailed description) in the control and treatment groups could be extracted directly from tables, digitized graphs, or contexts. Because there were only three studies that examined interactions of three treatments (1 for grazing + warming + N fertilization, GWN; 2 for grazing + increased precipitation + N fertilization, GPN), only studies including two treatments were included in the analysis. In total, 64 published papers with 223 multifactor studies were selected (see Supporting Information Appendix S1 and Figure 1).

The APCP and BPCP at 0–50 cm depth were determined by plant biomass as described in Lu et al.(2013) and Zhou et al.(2018). Plant biomass was sampled while grazing was occurring. Soil C efflux (i.e., Rs) included autotrophic and heterotrophic respiration. Herbivore species identity and grazing intensity were extracted directly from papers or cited ones. Studies that included sheep, cattle, and other herbivore species numbered 78, 21, and 124, respectively. The number of studies with grazing intensity was 28, 58, and 31 for light, moderate, and heavy intensity, respectively. The experimental duration (0.5–8 years) of each study was extracted from the paper. Environmental variables, including latitude, longitude, mean annual temperature [MAT], mean annual precipitation [MAP]), also were taken directly from the papers. In cases in which MAT and MAP were not reported, they were extracted from a global climate database (<http://www.worldclim.org/>) using the geographical coordinates of the study sites.

2.2 | Meta-analysis

2.2.1 | Individual and combined effects

The individual effect of grazing or a global climate change factor and the combined factors (e.g., grazing + one global climate change factor, G + GC; or combination between two different global climate change factors, GC + GC) on a C response variable was defined as the natural logarithm of the response ratio (LnRR):

$$\text{LnRR} = \ln\left(\frac{X_t}{X_{\text{ctrl}}}\right) \quad (1)$$

where X_t and X_{ctrl} were the means of the treatment and control pairs, respectively (Crain et al., 2008; Vilà et al., 2011). Descriptions of how variance (v) and weight (w) of each RR and the weighted mean LnRR (LnRR₊₊) calculated are provided in the Supporting Information Appendix S1. The effect of an individual treatment or combination of treatments on a variable was significant if the 95% CI did not overlap with zero. If the sample size was less than 20, a resampling bootstrapping method was used to obtain the 2.5% and 97.5% CIs based on 5,000 iterations (Janssens et al., 2010).

Before each analysis, we used Kendall's Tau method to test for publication bias (Møller & Jennions, 2001). If the mean effect was significantly different from zero (i.e., indicating the existence of publication bias), Rosenthal's fail-safe number, which was applicable to both fixed-and random effects models, was calculated by METAWIN 2.1 Software to estimate whether our conclusion was likely to be affected by the nonpublished studies (Rosenberg, Adams, & Gurevitch, 2000). The relationships of environmental variables (e.g., MAP, MAT, latitude) and experimental duration with LnRR were assessed by conducting meta-regressions. The percent change of each variable was calculated as $[\exp(\text{RR}_{++}) - 1] \times 100\%$, and the effect was significant if the 95% CI did not overlap zero. We also plotted RR frequency distributions to display variability among individual and combined studies. Frequency distributions of RR for a response variable were assumed to be normal and were fitted with a Gaussian function (i.e., normal distribution) in SIGMAPLOT software (Systat Software Inc., CA, USA) using the following equation.

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

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.

2.2.2 | Interactive effects

To further explore the interactive effects of two treatments on grassland C pools and release, Hedge's d was employed to calculate the interaction effect size according to the method described by Gurevitch and Hedges (2001). The effect size of an interaction between A and B (d_i) was calculated by.

$$d_i = \frac{(X_{AB} - X_A) - (X_B - X_C)}{2s} J(m) \quad (3)$$

where X_C , X_A , X_B , and X_{AB} were means of a variable in the control, treatment groups A and B and their combination (A + B), respectively. s and m were the pooled standard deviation and degrees of freedom, respectively, which were estimated by.

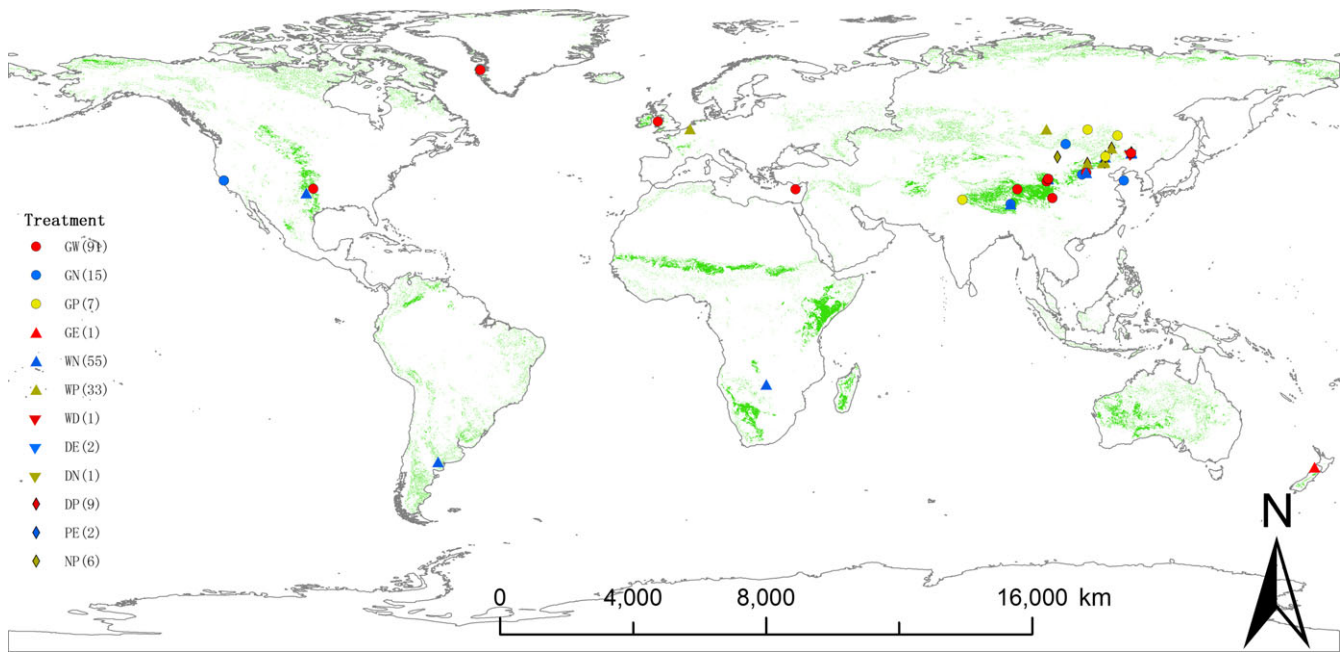


FIGURE 1 Global distribution of 223 multifactor studies selected in this meta-analysis. Numbers in parentheses is the actual number of samples with different factorial designs. G, W, N, E, P and D represent grazing, warming, N fertilization, elevated CO₂, increased precipitation and drought, respectively. The distribution of global grasslands is in green. GW, grazing + warming; GN, grazing + N fertilization; GP, grazing + increased precipitation; GE, grazing + elevated CO₂; WN, warming + N fertilization; WP, warming + increased precipitation; WD, warming + drought; DE, drought + elevated CO₂; DN, drought + N fertilization; DP, drought + increased precipitation; PE, increased precipitation + elevated CO₂; NP, N fertilization + increased precipitation [Colour figure can be viewed at wileyonlinelibrary.com]

$$s = \sqrt{\frac{(n_c - 1)(s_c)^2 + (n_A - 1)(s_A)^2 + (n_B - 1)(s_B)^2 + (n_{AB} - 1)(s_{AB})^2}{n_c + n_A + n_B + n_{AB} - 4}} \quad (4)$$

$$m = n_c + n_A + n_B + n_{AB} - 4 \quad (5)$$

where n_A , n_B , n_C , n_{AB} were the sample sizes, and s_A , s_B , s_C , and s_{AB} were the standard deviations of the treatment (s_A , s_B) and control groups (s_C), and their combinations (s_{AB}), respectively. $J(m)$ was a correction term for small sample bias (Hedges & Olkin, 1985), which was calculated by

$$J(m) = 1 - \frac{3}{4m - 1} \quad (6)$$

The variance of d_i (v_2) of main and interaction effects was estimated by.

$$v_2 = \left[\frac{1}{n_c} + \frac{1}{n_A} + \frac{1}{n_B} + \frac{1}{n_{AB}} + \frac{d_i^2}{2(n_c + n_A + n_B + n_{AB})} \right] / 4 \quad (7)$$

The weighted mean d_i (d_{++}) was calculated by

$$d_{++} = \frac{\sum_{i=1}^m \sum_{j=1}^k W_{ij} d_{ij}}{\sum_{i=1}^m \sum_{j=1}^k W_{ij}} \quad (8)$$

where i was the number of groups, k was the number of comparisons in the i th group and w was weight, which was calculated as the reciprocal of the variance ($1/v_2$). The 95% CI of RR_{++} and d_{++} was calculated as $RR_{++} \pm C_{w/2} \times s$ (RR_{++}) and $d_{++} \pm C_{w/2} \times s$ (d_{++}), respectively, where $C_{w/2}$ was the two-tailed critical value of the

standard normal distribution. Similar to the calculation of CI of individual and combined effects, a bootstrapping method was used to resample when the sample size was less than 20.

Based on the above calculations, the interaction between two treatments was classified as additive, synergistic, and antagonistic (Crain et al., 2008). If the 95% CI overlapped with zero, the interactive effect was additive (Zhou, Zhou, Shao, et al., 2016a; Zhou, Zhou, Nie, et al., 2016b). For pairs of variables whose individual effects were either both negative or one negative and one positive, an interaction effect < 0 was synergistic and > 0 was antagonistic. In cases where the individual effects were both positive, an interaction effect > 0 was synergistic and < 0 was antagonistic. To reduce uncertainty when sample size was small, we only present results for cases with ≥ 8 studies between grazing and a global climate change factor (i.e., GW, GN, GP) or between a pair of global climate change factors (i.e., WN, WP, WD, ED, DP). Note that we did not find any studies that included pairwise combinations of GD or GE.

3 | RESULTS

3.1 | Individual and combined effects of grazing and global climate change factors

Both grazing and global climate change factors significantly affected the C storage and release in grassland ecosystems (Figure 2; Supporting Information Table S1). Grazing exerted negative effects on all ecosystem C pools and soil respiration (Rs), with decreases in

APCP, BPCP, SCP, microbial biomass C (MBC), and Rs by 19.1%, 6.4%, 3.1%, 10.0%, and 4.6%, respectively (Figure 2; Supporting Information Figures S4 and S5; Supporting Information Table S1). In contrast to grazing, most global climate change factors increased APCP. Specifically, warming, elevated CO₂, N fertilization, and increased precipitation increased APCP by 2.1%, 38.7%, 32.6%, and 34.0%, respectively (Figure 2a; Supporting Information Table S1). Elevated CO₂ and increased precipitation stimulated BPCP by 12.3% and 12.6%, respectively (Figure 2b). Warming had no significant effect on BPCP when considered individually or in combination with other global climate change factors (Figure 2b; Supporting Information Table S1). SCP was significantly increased by nitrogen fertilization (+3.9%) and increased precipitation (+3.8%), and reduced by warming (−2.0%) in the multifactor studies (Figure 2c; Supporting Information Table S1). The response of Rs to global climate change factors was more sensitive than SCP and was increased by warming (+2.1%), N fertilization (+38.7%), elevated CO₂ (+32.6%), and increased precipitation (+34.0%), while decreased by drought (−14.4%).

The combination of grazing and a global climate change factor also significantly affected C storage and release in grassland ecosystems (Figure 2; Supporting Information Figure S4). We found that the combined effects of grazing + warming (GW) and grazing + N fertilization (GN) influenced BPCP by −16% and +39%, respectively. BPCP was unaffected by grazing + increased precipitation (GP), although there was high uncertainty because of the small sample size. Grazing + warming (GW) decreased Rs (−2%), whereas it increased SCP (+4.7%). Both GW and GP had little effect on APCP, but GN increased APCP (+19.5%) and GW enhanced MBC (+27.7%, Figure 2; Supporting Information Figure S4; Supporting Information Table S1).

Interestingly, grazing and global climate change factors generally had opposite impacts on C storage and release when pairwise-factor results were pooled (Figure 3; Supporting Information Figure S1). Grazing had markedly negative effects on APCP, BPCP, SCP, and Rs. Global climate change factors (GC) jointly increased APCP, BPCP, and Rs by 6.5%, 15.3%, and 3.4%, respectively, but had no significant effect on SCP (Figure 3; Supporting Information Table S1). Although global climate change factors significantly increased C pools, the combination of those factors and grazing (G + GC) qualitatively changed the direction of the responses, resulting in declines in APCP, SCP, and Rs by 4.0%, 4.7%, and 2.7%, respectively (Figure 3; Supporting Information Table S1). In addition, dominant effects of grazing on soil environmental parameters (e.g., pH, BD, SM, and temperature) over global climate change factors were also observed (Supporting Information Figures S5–S8).

3.2 | Interactive effects of grazing and global climate change factors

The interactive effects between pairs of factors (e.g., G + GC, GC + GC) include additive, synergistic, and antagonistic ones. We found that interactive effects of pairwise combinations of G + GC and

GC + GC on C pools (e.g., APCP, BPCP, SCP, MBC) and Rs were mostly additive (Figure 4). The antagonistic interactions between grazing and global climate change factors (G + GC) on APCP (19.2%) appeared more than synergistic ones (10.6%). However, synergistic G + GC interactions on BPCP were more common than the antagonistic interactions (10%).

Additive interactions dominated all combinations of grazing and a global climate change factor (e.g., GW, GN, & GP) on the C pools and Rs (Figure 5). For example, the interactive effect between grazing and warming on APCP, MBC, and Rs was additive, except for SCP and BPCP, which were antagonistic (Figure 5). Similar to C pools, additive effects were more common on SM and temperature, as shown by the frequency distribution of interaction types among individual observations (Supporting Information Figure S8).

3.3 | Regulation of environmental variables

The response ratio (RR) of SCP to grazing, global climate change factors, and their combination had different relationships with MAT, MAP, experimental duration, and latitude (Figure 6). Specifically, the response of SCP to grazing was negatively correlated with MAT, experimental duration and latitude, but not with global climate change factors (Figure 6).

Changes in SCP with G + GC were negatively correlated with MAT, experimental duration, and latitude. The response of SCP to both grazing and global climate change factors was negatively correlated with MAP ($R^2 = 0.36$, $p < 0.05$), and their combination (G + GC) significantly enhanced the negative response of SCP to MAP ($R^2 = 0.54$, $p < 0.05$) (Figure 6).

Taken together, the results showed that the effect of grazing on C storage and release overrode impacts associated with global climate change in grassland ecosystems (Figure 7). Specifically, grazing significantly decreased C storage (i.e., APCP, BPCP, MBC, and SCP) and release (i.e., Rs) in grassland ecosystems whereas global climate change factors increased these variables besides SCP. However, the combination of grazing and global climate change factors qualitatively decreased APCP, SCP, and Rs but had no effect on BPCP and MBC (Figure 7).

4 | DISCUSSION

4.1 | Effects of grazing and single global climate change factors

Understanding the effects of grazing and global climate change factors on C storage and release is crucial to better predict and assess global climate-C cycle feedbacks (Chapin et al., 2002; Wang & Wesche, 2016; Yuan & Chen, 2015). Our meta-analysis showed that grazing significantly decreased C pools in above- and belowground plant, microbe, and soil as well as soil C release (i.e., soil respiration, Rs; Figures 2 and 7). The decreased C pools and Rs might be attributed to the decreased aboveground–belowground biomass induced by livestock grazing (Knops, Bradley, & Wedin, 2002; Milchunas &

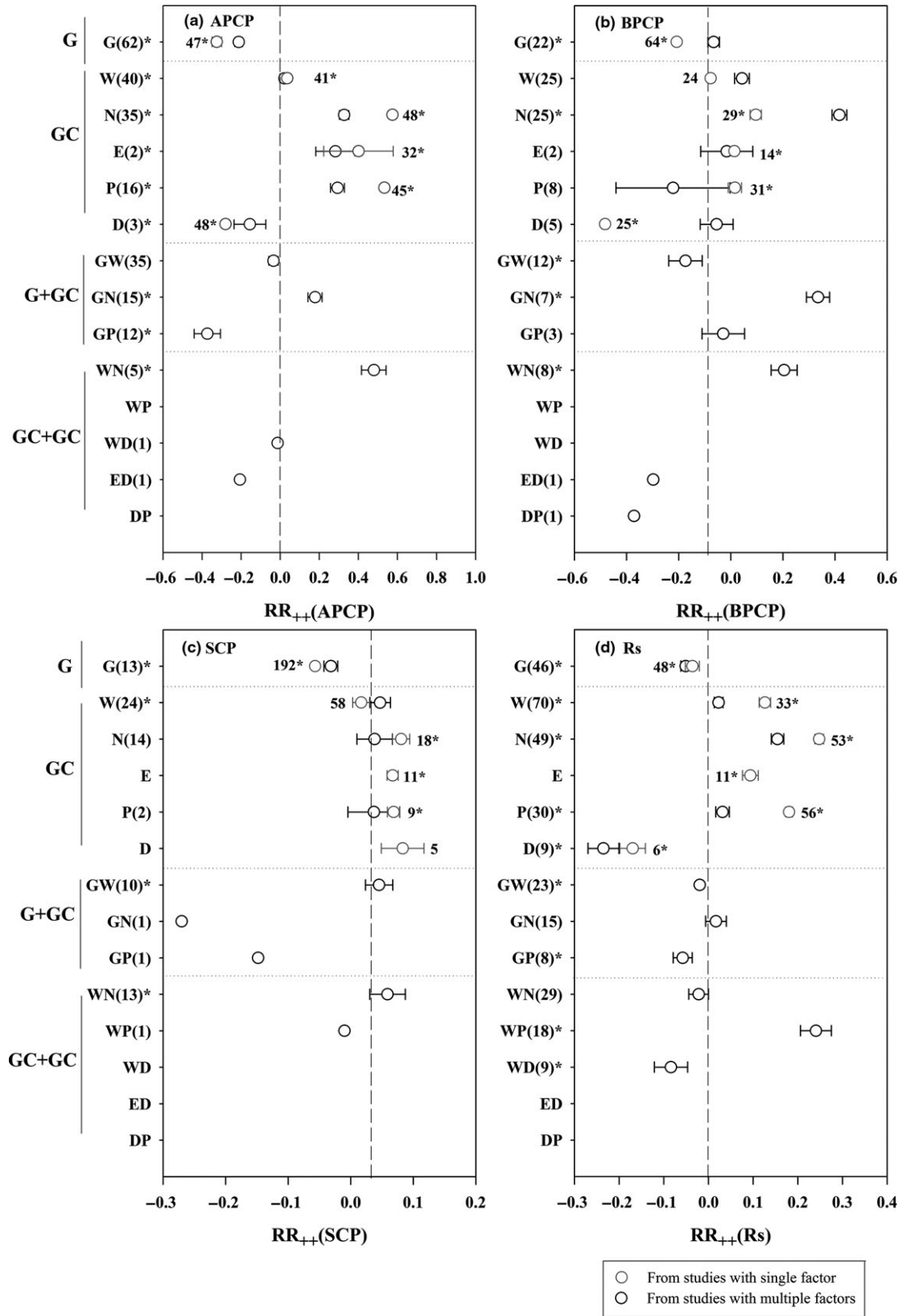


FIGURE 2 Weighted response ratio (RR_{++}) of aboveground plant carbon (APCP, a), belowground plant carbon pools (BPCP, b), soil carbon pool (SCP, c) and soil respiration (Rs, d) to the effects of a single factor and the combination of two factors. Bars represent 95% confidence intervals. The horizontal line denotes $RR_{++} = 0$. G, W, N, E, P and D represent grazing, warming, N fertilization, elevated CO_2 , increased precipitation and drought, respectively. GW, grazing + warming; GN, grazing + N fertilization; GP, grazing + increased precipitation; WN, warming + N fertilization; WP, warming + increased precipitation; WD, warming + drought; ED, elevated CO_2 + drought; DP, drought + increased precipitation. Note: no grazing + drought (GD) and grazing + elevated CO_2 (GE) were included in our database

FIGURE 3 Weighted response ratios of aboveground plant carbon (APCP, a), belowground plant carbon pools (BPCP, b), soil carbon pool (SCP, c) and soil respiration (Rs, d) in response to single factor and combined studies. Bars represent 95% confidence intervals. The horizontal line refers to $RR_{++} = 0$. Numbers for each bar indicate the sample size. G, grazing; GC, all single-global climate change factors treatments; G + GC, grazing combined with a global climate change factor; GC + GC, two combined global climate change factors [Colour figure can be viewed at wileyonlinelibrary.com]

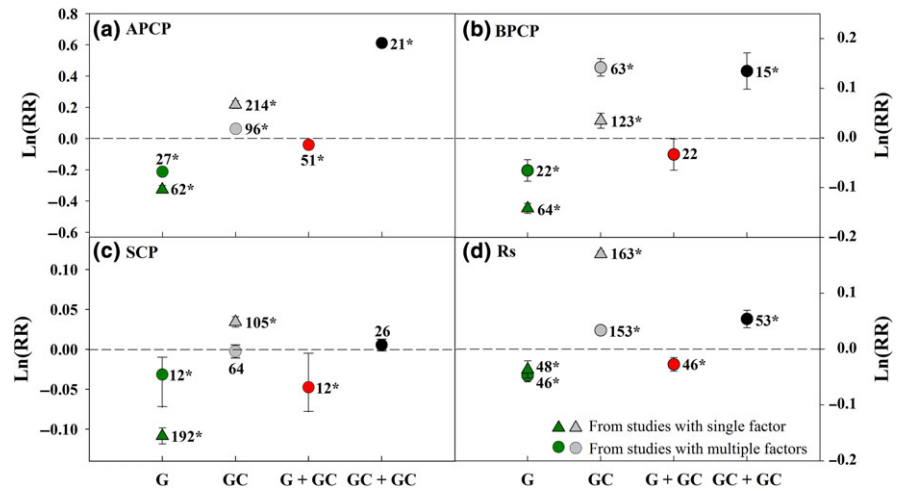
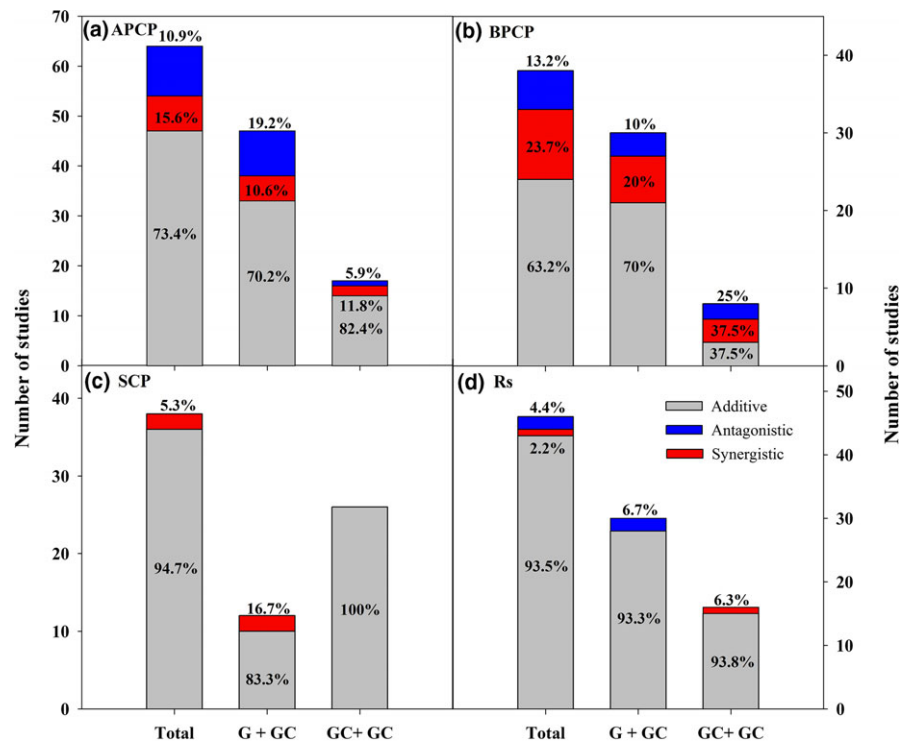


FIGURE 4 Frequency distribution of interaction types in individual studies with two-factorial designs for aboveground plant carbon (APCP, a), belowground plant carbon pools (BPCP, b), soil carbon pool (SCP, c) and soil respiration (Rs, d). G + GC, grazing combined with a global climate change factor; GC + GC, two combined global climate change factors [Colour figure can be viewed at wileyonlinelibrary.com]



Lauenroth, 1993). Generally, grazing decreases C allocated to roots, leading to reduced root biomass and soil C content, which is supported by previous studies (Burke et al., 2008; Wang & Wesche, 2016; Zhou, Zhou, He, et al., 2017a). It has been shown that the disturbed soil structure and surface crust by grazing may accelerate C loss from the plant-soil-microbe system due to enhanced soil susceptibility to water and wind erosion (McSherry & Ritchie, 2013; Neff et al., 2005). In addition, lower plant cover caused by grazing would also promote evaporation and lower SM, resulting in decreased microbial diversity and Rs (Savado, Sawadogo, & Tiveau, 2007).

On average, our results showed that warming, elevated CO₂, N fertilization, and increased precipitation significantly increased APCP, BPCP, SCP, and Rs, while drought exhibited negative effects on

those variables (Figure 2). Drought generally impedes plant growth due to the reduction of canopy photosynthesis and nutrient uptake from soil by decreased SM and relative humidity in grassland ecosystems (Davidson & Janssens, 2006; Knapp & Smith, 2001; Ru, Zhou, Hui, Zheng, & Wan, 2018). The decreased canopy photosynthesis induced by drought may also reduce root biomass due to depressed supply of photosynthetic products to roots, resulting in decreased microbial biomass, a smaller SCP, and lower Rs (Knapp & Smith, 2001; Liu et al., 2016; van Groenigen et al., 2017). Among individual global climate change factors, N fertilization caused the largest stimulation in BPCP compared with other factors (Figure 2a), likely due to its stimulatory effect on photosynthesis (Jiang, Deng, Bloszies, Huang, & Zhang, 2017; Poorter & Nagel, 2000). N fertilization-

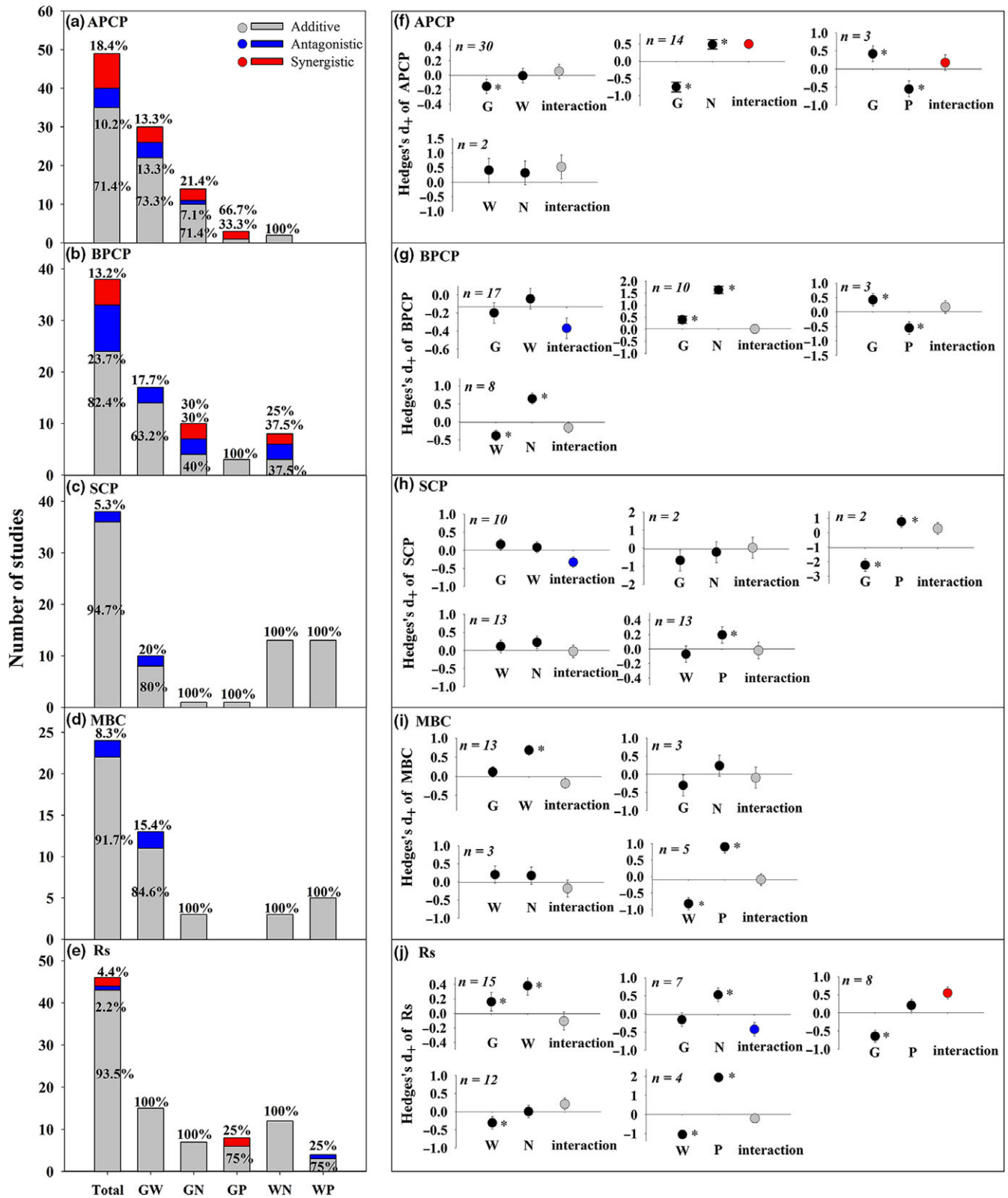


FIGURE 5 Frequency distribution of interaction types in individual studies with two-factorial designs for aboveground plant carbon (APCP, a), belowground plant carbon pools (BPCP, b), soil carbon pool (SCP, c), microbial biomass carbon (MBC, d) and soil respiration (Rs, e). G, W, N, E, P and D represent grazing, warming, N fertilization, elevated CO₂, increased precipitation and drought, respectively. GW, grazing + warming; GN, grazing + N fertilization; GP, grazing + increased precipitation; WN, warming + N fertilization; WP, warming + increased precipitation. Asterisk in panel f, g, h, i and j indicated statistical significance ($p < 0.05$) [Colour figure can be viewed at wileyonlinelibrary.com]

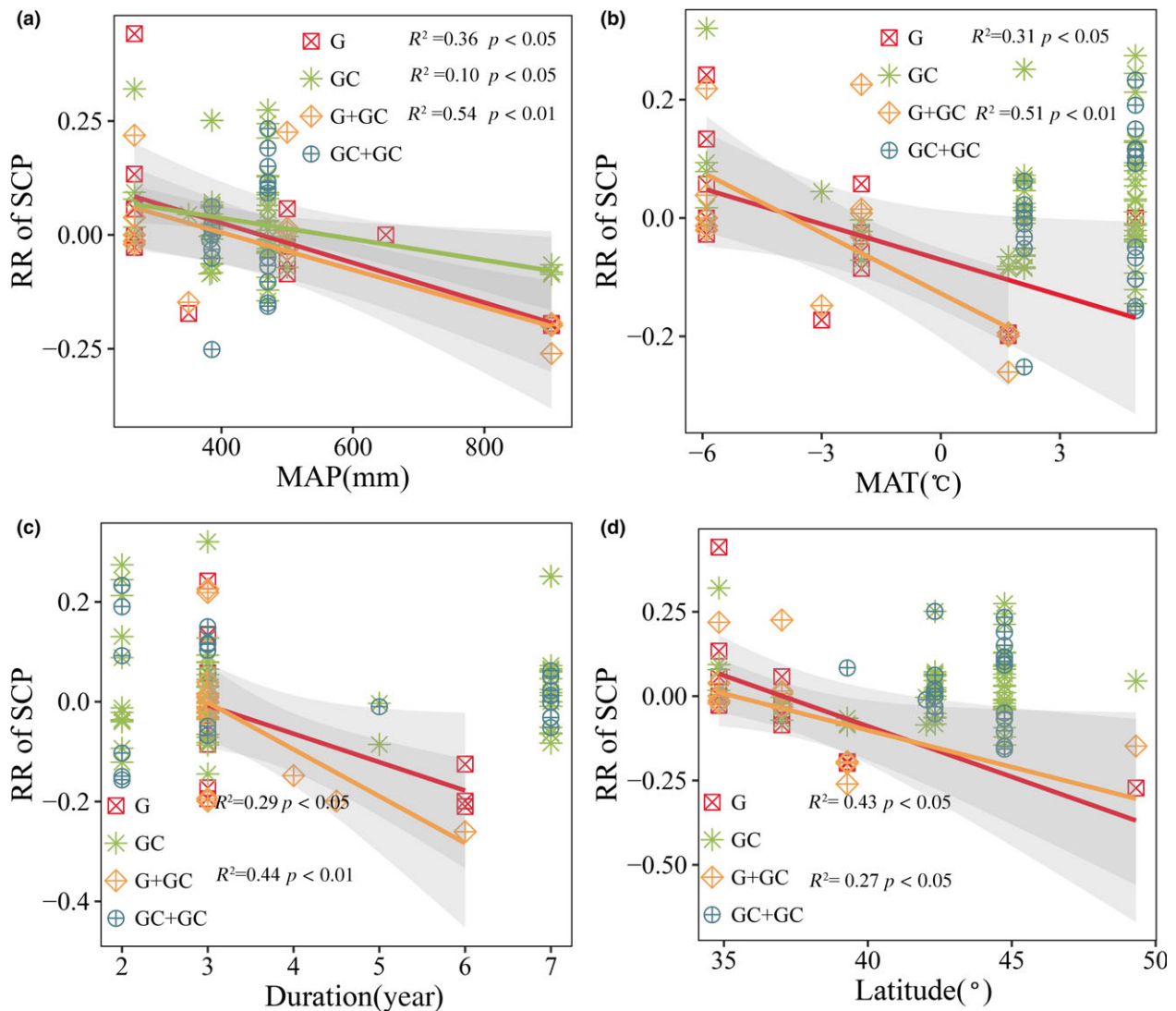


FIGURE 6 Relationships of response ratios (RR) of soil carbon pools (SCP) with mean annual precipitation (MAP, a), mean annual temperature (MAT, b), experimental duration (c) and latitude (d) in single factor and combined studies. The black dots mean the observations and the gray shaded areas represent 95% confidence intervals. G, grazing; GC, all single-global climate change factors treatments; G + GC, grazing combined with a global climate change factor; GC + GC, two combined global climate change factors

induced increase in C allocation to roots with higher root/shoot ratio would contribute to increase water and nutrient absorption (Högberg et al., 2001; Poorter & Nagel, 2000).

4.2 | Combined and interactive effects of pairs of factors

Since global climate change involves simultaneous shifts in multiple environmental factors (e.g., elevated CO₂, warming, increased precipitation, drought, nitrogen fertilization), understanding the combined environmental effects is important to predict future grassland C cycling and its effects in the Anthropocene (Crain et al., 2008; Harrison, Gornish, & Copeland, 2015; Mueller et al., 2016; Yuan & Chen, 2015). In this study, we found that warming + N fertilization (WN) significantly enhanced APCP, BPCP, and SCP, while

warming + drought (WD) exhibited the opposite effect on Rs ($p < 0.05$; Figure 2). These results indicated that the effect of warming on C storage and release was largely dependent on the associated factors (e.g., drought, N fertilization). The warming-induced changes in plant phenology (e.g., earlier leaf bud burst, prolonged growing season) and increased soil N availability would stimulate plant growth and net primary productivity (NPP; Sherry et al., 2007; Vitousek & Howarth, 1991). Warming in combination with N fertilization stimulated plant growth, leading to increased APCP and BPCP (Figure 2; Lu et al., 2013; Zhou et al., 2017a). Increased C inputs from root production and biomass may have significant positive effect on soil C storage (Figure 7; Chapin et al., 2002; McSherry & Ritchie, 2013). However, warming associated with drought is likely to lead to a decline in SM, causing negative effects on root growth and microbial activity (Lu et al., 2013; Wang et al., 2014). A drought-

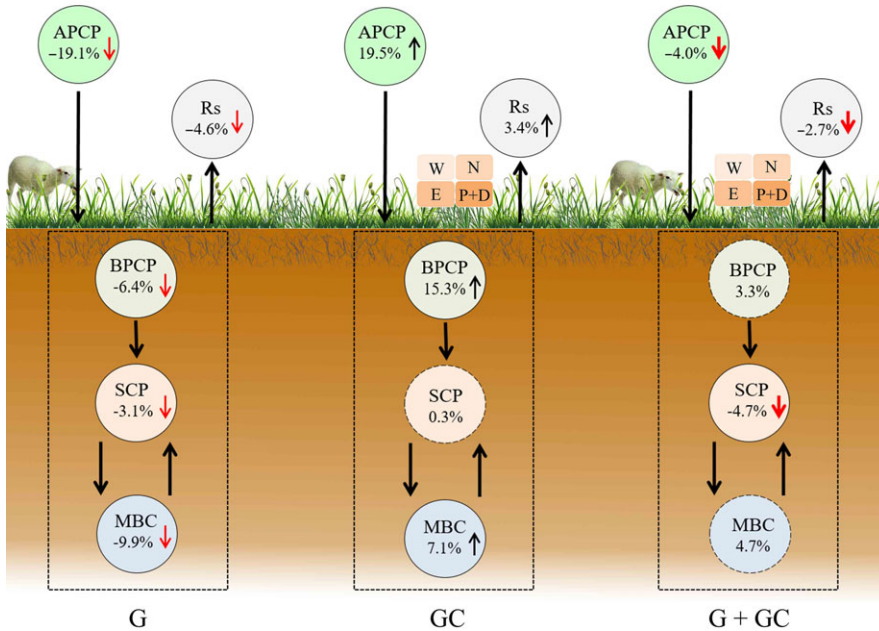
Global change (Warming, N addition, Elevated CO₂, Increased precipitation, Drought)

FIGURE 7 Potential mechanisms of grassland C dynamics in response to livestock grazing (a), global climate change factors (b), and their combination (c). The numbers refer to percentage change ($e^{RR^{++}} - 1$) \times 100% of C variables in response to different treatments. Global climate change factors included warming, N fertilization, elevated CO₂, increased precipitation and drought. SCP, soil carbon pool; BPCP, belowground plant carbon pool; MBC, microbial biomass carbon and Rs, soil respiration. G, grazing; GC, all single-global climate change factors treatments; G + GC, grazing and a global climate change factor; GC + GC, all pairwise combinations of global climate change factors. Green upward arrows represent positive responses, red downward arrows negative responses. Dashed circles represent nonsignificance

induced decrease in SM could further exacerbate water limitation caused by warming, which would impede plant growth and microbial decomposition and lower Rs (Wang et al., 2014; Zhou, Zhou, Shao, et al., 2016a; Zhou, Zhou, Nie, et al., 2016b).

Warming and increased precipitation induced positive effects on C storage and Rs. However, the combination of each of those factors with grazing reduced C pools and Rs (Figure 2; Lu et al., 2013; Wang et al., 2014). The positive effects of increased precipitation on APCP and Rs may be partially offset under a grazing regime, especially in moist region. Increased precipitation stimulates plant productivity that would increase plant biomass, especially in semi-arid and arid grasslands (Poulter et al., 2014; Sirimarco, Barral, Villarino, & Littera, 2018). However, grazing + increased precipitation (GP) significantly decreased APCP because the magnitude of plant material removed by grazing was greater than the stimulated production by increased precipitation (Figure 2; Chapin et al., 2002; Zhou, Zhou, He, et al., 2017a). Although increased precipitation enhanced Rs by stimulating plant photosynthesis, and thus root respiration and microbial activity (Liu et al., 2016), Rs was strongly reduced by the combination of grazing and increased precipitation (GP; Figure 2d). This might be largely due to decreased aboveground biomass, increased water and nutrient losses, and inhibited plant production induced by grazing, overwhelming the positive effects of increased precipitation (Figure 7; Liu et al., 2016; Zhou et al., 2017a). In contrast, GN increased APCP, BPCP, and Rs (Figure 2). The increased plant C pools and Rs may have been a function of light grazing increasing photosynthetic rates, which may have been strengthened by the positive effect of N fertilization in N-limited grasslands (Liu & Greaver, 2010; Zhou, Zhou, He, et al., 2017a).

Our results showed that interactions between pairs of global climate change factors and between grazing and various global climate change factors were predominantly additive (Figures 4 and 5). For

example, interactions between grazing and warming were mostly additive, except on SCP and BPCP, which were antagonistic. The lower soil water availability induced by grazing due to the faster soil evaporation with lower ground covers could be enhanced when combined with warming (GW), further reducing plant growth and microbial activity (Savadojo et al., 2007; Wang et al., 2014; Zhou, Zhou, He, et al., 2017a). Suppressed plant growth by GW decreased photosynthetically fixed C inputs to belowground roots, leading to reduced root biomass and then soil C storage (Knops et al., 2002; Savadojo et al., 2007). Similarly, the interactive effect of grazing and increased precipitation on C storage and release was also largely additive, and only synergistic with reference to Rs (Figure 5j). Lower SM under grazing would be offset by increased precipitation, thus mitigating the grazing-induced declines in plant biomass, microbial activity, and Rs (Liu et al., 2016; McSherry & Ritchie, 2013; Zhou, Zhou, Shao, et al., 2016a; Zhou, Zhou, Nie, et al., 2016b). In this case, the negative grazing effect on Rs would be smaller in the combined treatment than in the individual grazing treatment. Taken together, the general additive interactions indicate that it will be necessary to consider the combined impacts of grazing and global climate change factors to understand how grassland C processes will vary in the future.

4.3 | Dominant effects of grazing on grassland C storage and release

Livestock grazing usually inhibits leaf photosynthesis and primary production, overwhelming the compensatory or overcompensation effects induced by various types of environmental change to some degree (Chapin et al., 2002; Parsons et al., 1983; Zhou, Zhou, He, et al., 2017a). Our results showed that grazing led to greater effects

than global climate change factors on C storage and release in grassland ecosystems (Figures 2, 3 and 7). Grazing reduces grass biomass to a greater extent than two global change factors: warming and N fertilization, which increased plant growth (McNaughton, 1994; McSherry & Ritchie, 2013; Yuan & Chen, 2015). Plant removal by grazing reduces leaf and root biomass, leading to reduced litter input and shifts in soil bacterial communities and soil C processes (Figure 7; Knops et al., 2002; Zhou, Zhou, Zhang, et al., 2017b). Although some global climate change factors (e.g., N fertilization, elevated CO₂) stimulate plant production and microbial activity according to results of this study, grazing largely offset those positive effects, likely by decreasing substrate supply (e.g., photosynthetically fixed C inputs, soil organic matter) and increasing water limitation (Chapin et al., 2002; Pan et al., 2016; Zhou, Fu, Zhou, Li, & Luo, 2013).

The important role of grazing in governing C storage and release was also evident when inspecting the interactions between grazing and global climate change factors (G + GC). In this study, we found that GW exhibited a substantial predominance of additive interaction on APCP, BPCP, SCP, MBC, and Rs. Although the overall interactive effects of GW were additive, antagonistic interactions are relatively more important than synergistic ones in regulating C storage and release (Figures 5a5–7e). In water-limited grasslands, the reduced water availability caused by warming likely decreased root biomass and the soil microbial community, leading to lower BPCP and Rs when combined with grazing (Peters, Cleland, & Mooney, 2006). It has been shown that warming markedly altered plant phenology, inducing earlier leaf bud burst and advanced flowering, which may modify forage quality (e.g., cellulose, glucose, leaf C:N) and plant community (Barbehenn, Chen, Karowe, Karowe, & Spickard, 2004; Peters et al., 2006; Sherry et al., 2007). The altered forage properties induced by warming may change the feeding preferences of herbivores, further magnifying the dominant negative effects of grazing in governing C storage and release in livestock favored grasslands (McNaughton, 1994; Peters et al., 2006).

4.4 | Factors regulating the responses of C storage and release to grazing and global climate change

Dominant effects of grazing on grassland C cycle compared to global climate change factors were also observed with respect to the relationships of the response ratio of the SCP [RR (SCP)] with several environmental factors (e.g., MAP, MAT and latitude) and experimental duration. In this study, we found that, for each of the single global climate change factors, RR (SCP) was unrelated to experimental duration (GC; Figure 6c). The lack of the relationships may be linked to the pooling of several factors together and that, when separately analyzed, the individual factors could have either increasing or decreasing trends over time. For example, Zhou et al. (2013) and Liu et al. (2016) indicated that SOC stock exhibited a downward trend with increasing experimental duration in response to N fertilization, but it increased with duration under precipitation changes. However, significant negative correlations between RR (SCP) and environmental variables were observed when global climate change factors were

combined with grazing (G + GC), which may be attributed to the negative effects induced by grazing. In the presence of grazing, we also found a negative relationship with the RR (SCP) and MAT. Greater MAT will increase microbial activity, accelerate soil organic matter decomposition, and then lead to the negative relationship between RR (SCP) with MAT under both grazing and its combination with global climate change factors (Zhou, Zhou, He, et al., 2017a). In addition, increasing grazing duration may degrade grassland, resulting in less soil organic matter and available nutrients, and thereby inhibit plant growth (McSherry & Ritchie, 2013). Since MAT usually declines with latitude, the higher microbial activity in low latitude regions can usually stimulate biogeochemical cycle of labile C supply and then lower SCP under grazing and its dominated ecosystems than those in low latitude regions with the low-MAT (Chapin et al., 2002; Zhou, Zhou, He, et al., 2017a). Therefore, the correlations between SOC and environmental variables under global climate change factors combined with grazing showed a similar response pattern with these under grazing.

4.5 | Implications for land-surface models and future experiments

Grazing and global climate change both control grassland C processes, which may lead to a positive or negative climate–biosphere feedbacks (Follett & Reed, 2010; McSherry & Ritchie, 2013). In this study, we found that the effects of grazing on grassland C storage and release overrode those effects of factors associated with global climate change. Specifically, we found that global change factors increased aboveground carbon pools and Rs. Yet, the consequences were the opposite when the impact of grazing was also included: both aboveground C pools and Rs decreased when global climate changes occurred simultaneously with grazing. Our study may provide insights about how grazing and global climate change factors interact to drive grassland C cycling that will be helpful to incorporate in Earth System Models, as well as design of manipulative experiments in the future.

First, grazing intensity has been shown to impact key grassland C processes (McSherry & Ritchie, 2013). The effect of stocking rate on grassland production also is regulated by environmental fluctuations, especially water availability (Gillson & Hoffman, 2007). How the interaction of grazing and global climate change factors may be influenced by grazing intensity needs further study as well as the effects of C₄-dominated and C₃-dominated plants, which have been shown to affect the response of grassland C dynamics to grazing (McSherry & Ritchie, 2013; Xu et al., 2015). However, how the responses of C storage and release to the combination of grazing and global climate change factors are contingent on species composition is poorly unknown. These knowledge gaps impede a complete understanding of how grazing affects grassland C dynamics.

Second, our results indicate that different combinations of grazing and global climate change factors have disparate effects on grassland C processes (Figures 4 and 5). However, current land-surface models usually do not differentiate the effects of grazing with

different global climate change factors (e.g., warming, increased precipitation and elevated CO₂, Cingolani et al., 2005), which impedes predictions of how ecosystems will respond to future environmental change. Differential responses of C storage and release to grazing combined with different global climate change factors are therefore required in Earth System Models to better understand the climate–grassland feedbacks in the Anthropocene.

Third, the majority of studies included in our dataset were distributed in North America and eastern Asia (especially in China; Figure 1). Thus, more studies from other regions (e.g., Africa and Australia) should be conducted in order to develop a more comprehensive understanding of how grazing and global climate change factors influence grasslands. The longest experiments in our database were less than 8 years. The lack of large and complete datasets from long-term studies likely limits our ability to better understand long-term effects of grazing and environmental changes expected in the future. Hence, studies over one or more decades should be undertaken to better explore the effects of grazing and global climate change on C storage and release.

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SUPPORTING INFORMATION

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

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