

## RESEARCH ARTICLE

# Grazing and global change factors differentially affect biodiversity-ecosystem functioning relationships in grassland ecosystems

Miao He<sup>1,2</sup>  | Yuhan Pan<sup>1,3</sup>  | Guiyao Zhou<sup>1</sup>  | Kathryn E. Barry<sup>2</sup>  | Yuling Fu<sup>1</sup>  | Xuhui Zhou<sup>1,4</sup> 

<sup>1</sup>Center for Global Change and Ecological Forecasting, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, China

<sup>2</sup>Ecology and Biodiversity, Department of Biology, Institute of Science, Utrecht University, Utrecht, The Netherlands

<sup>3</sup>School of Life Sciences, Nanjing University, Nanjing, China

<sup>4</sup>Northeast Asia Ecosystem Carbon Sink Research Center (NACC), Center for Ecological Research, Key Laboratory of Sustainable Forest Ecosystem Management-Ministry of Education, School of Forestry, Northeast Forestry University, Harbin, China

## Correspondence

Yuling Fu and Xuhui Zhou, School of Ecological and Environmental Sciences, East China Normal University, 500 Dongchuan Road, Shanghai 200241, China.

Email: [yifu@re.ecnu.edu.cn](mailto:yifu@re.ecnu.edu.cn) and [xhzhou@des.ecnu.edu.cn](mailto:xhzhou@des.ecnu.edu.cn)

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## Abstract

Grazing and global change (e.g., warming, nitrogen deposition, and altered precipitation) both contribute to biodiversity loss and alter ecosystem structure and functioning. However, how grazing and global change interactively influence plant diversity and ecosystem productivity, and their relationship remains unclear at the global scale. Here, we synthesized 73 field studies to quantify the individual and/or interactive effects of grazing and global change factors on biodiversity-productivity relationship in grasslands. Our results showed that grazing significantly reduced plant richness by 3.7% and aboveground net primary productivity (ANPP) by 29.1%, but increased belowground net primary productivity (BNPP) by 9.3%. Global change factors, however, decreased richness by 8.0% but increased ANPP and BNPP by 13.4% and 14.9%, respectively. Interestingly, the strength of the change in biodiversity in response to grazing was positively correlated with the strength of the change in BNPP. Yet, global change flipped these relationships from positive to negative even when combined with grazing. These results indicate that the impacts of global change factors are more dominant than grazing on the belowground biodiversity-productivity relationship, which is contrary to the pattern of aboveground one. Therefore, incorporating global change factors with herbivore grazing into Earth system models is necessary to accurately predict climate-grassland carbon cycle feedbacks in the Anthropocene.

## KEYWORDS

biodiversity conservation, carbon sequestration, changed precipitation, grassland stability, N deposition, warming

## 1 | INTRODUCTION

Grassland ecosystems cover about 25% of global land area and account for more than 20% of global productivity (Alkemade et al., 2013; Gholizadeh et al., 2017). These grasslands are often managed through livestock grazing, which not only provides 16% of the demand of meat and dairy products for human beings, but also has significant impacts on ecosystem structure and services (Bakker et al., 2006; FAO, 2006). Currently, overgrazing of these grasslands

is common, but simultaneously these grasslands are under pressure from global change (e.g., elevated CO<sub>2</sub>, warming, nitrogen deposition and altered precipitation; IPCC, 2013; Smith et al., 2010). Both grazing and global change may influence biodiversity, ecosystem functioning, and the relationship between the two (Asner et al., 2004; Herrero & Thornton, 2013; Sala et al., 2000). Although biodiversity-ecosystem functioning (BEF) relationships vary greatly with logarithmic, exponential, or bell-shaped curves (Cardinale et al., 2011; Isbell et al., 2017; Oba et al., 2001), how grazing and global change

factors interact to alter BEF relationship remains unclear, especially at the global scale, which greatly hampers the model prediction of climate-carbon cycle feedbacks in grassland ecosystems.

Over the past half century, numerous studies have explored the impacts of grazing on grassland BEF relationships (Bardgett & Van Der Putten, 2014; Tälle et al., 2016). For example, livestock directly graze aboveground plant biomass, yet moderate grazing maintains ecosystem diversity (intermediate disturbance hypothesis; Cingolani et al., 2005). In addition, the feeding preference of livestock changes the dominance of plant species in grassland community, causing a change in plant composition (Bendix et al., 2017; Klein et al., 2007; Pereira & Walpole, 2010). Grazing also likely reduces interspecific competition and thereby plant community structure (Mu et al., 2016). The changes in community composition and structure under grazing may induce diverse changes to the link between biodiversity and ecosystem functioning. Therefore, BEF relationships might be significantly influenced by livestock grazing.

Global change is occurring simultaneously with other anthropologic disturbances (e.g., grazing), which may have considerable effects on grassland BEF relationship in contradictory ways (Jing et al., 2015; Yuan & Chen, 2015). Warming may prolong plant growing seasons and contribute to more photosynthetic carbon accumulation, likely resulting in increases of both aboveground net primary productivity (ANPP) and aboveground NPP (BNPP; Huang et al., 2018; Sherry et al., 2007; Vitousek & Howarth, 1991). At the same time, plant species loss induced by warming may indirectly decrease ANPP, which probably decouples BEF relationships by causing contradictory changes in plant diversity and productivity (García et al., 2018). In addition, increased precipitation, nitrogen enrichment, and elevated CO<sub>2</sub> may stimulate plant growth and boost productivity due to water and nutrient supplement (Jamieson et al., 2013; Reich, 2009). Alternatively, they may reduce plant diversity due to lessened need for niche differentiation (Eskelinen & Harrison, 2015). These diverse impacts on diversity and productivity might result in larger (Cardinale et al., 2011; Hector et al., 1999), smaller (Mitchell et al., 2002; Zavaleta et al., 2010), or no change on BEF relationships (Byrnes et al., 2014; Hooper & Vitousek, 1997).

Similarly, the interactive effects of grazing and global change on plant diversity, ecosystem productivity, and their relationship are diverse. Interactions of different treatments include additive (different treatments take effect without interacting with each other), synergistic (different treatments facilitate each other when taking effect), and antagonistic (different treatments go against each other when taking effect). Previous syntheses have shown that the effect of grazing on grassland aboveground and belowground carbon pools overpower the influence of global change factors (Zhou, Luo, Chen, He, et al., 2019). Meanwhile, grazing and global change may interactively affect carbon storage, with additive interactions for most studies instead of synergistic or antagonistic ones (Zhou, Luo, Chen, Hu, et al., 2019). In addition, aboveground biomass might be more sensitive to livestock grazing than belowground biomass because aboveground plant organs are more directly impacted by grazing, and the grazing-induced changes in belowground biomass

are mainly due to reduction in carbon allocation from aboveground parts (Mcsherry & Ritchie, 2013; Zhou et al., 2016). Furthermore, global changes, such as nitrogen deposition, significantly alter soil nutrient condition, resulting in changes in belowground biomass (Harpole et al., 2016; He et al., 2020). Therefore, understanding the combined effects of grazing and global change factors on grassland BEF relationship is fundamental to better predict the carbon cycle and thereby climate feedbacks around the globe.

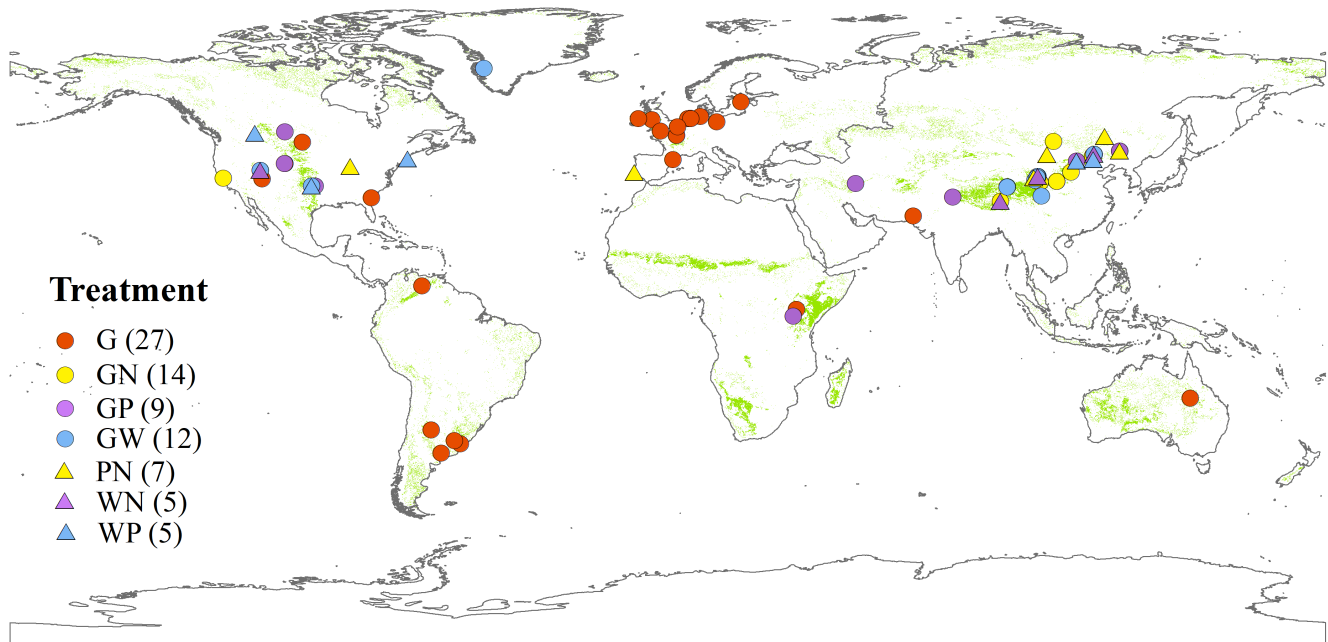
In this study, we compiled data from 73 studies to investigate the responses of BEF to grazing and selected global change factors. Specifically, our objectives were to (i) explore the individual and/or interactive effects of grazing and global change factors (i.e., warming, nitrogen addition, and altered precipitation) on biodiversity and ecosystem functioning and (ii) evaluate the effects of grazing, global change factors, and their paired combinations on aboveground and belowground BEF relationships.

## 2 | MATERIALS AND METHODS

### 2.1 | Data compilation

We searched for articles published before February 2020 using Web of Science and the China Knowledge Resource Integrated Database (CNKI) with the following search terms: (grazing or clipping or herbivory or defoliation) and (warming or increased temperature or nitrogen deposition or nitrogen addition or increased precipitation or decreased precipitation) and (evenness or richness or biodiversity) and (plant or soil or biomass or ANPP or BNPP). It should be noted that our initial literature search did not return any studies that manipulated CO<sub>2</sub> fertilization and grazing or drought and grazing. To avoid bias in publication selection, we had six criteria for study inclusion: (1) Experiments were conducted in the field and had at least one pair of data in both control and treatment groups to examine the effects of grazing and global change factors, including warming, nitrogen deposition/addition, and increased precipitation; (2) at least one of the selected variables (i.e., species richness, evenness, ANPP, and BNPP) was examined in all controls and treatments at the same temporal and spatial scale; (3) initial environmental and climate conditions, ecosystem type, and dominant species composition in the controls and treatments were the same; (4) the control plots should have had grazing excluded or fenced for more than 10 years if it once was grazed; (5) the methods used for nitrogen deposition/addition, warming (e.g., infrared heater, soil heating cable, or open top chamber) and irrigation treatments were clearly described, and experimental duration was longer than one growing season; and (6) the mean, standard error (SE) or standard deviation (SD) and sample size (*n*) of the selected variables (see below for the detailed description) in the control and treatment groups could be extracted directly from tables, digitized graphs or the article text. In total, 73 published papers were selected (Figure 1; Table S1).

The number of datasets for the following variables included species richness (*n* = 358), evenness (*n* = 87), ANPP (*n* = 558),



**FIGURE 1** Global distribution of multifactor studies selected for this meta-analysis. The number in parentheses is the actual number of studies with different factorial designs. G, grazing; GN, grazing + nitrogen addition; GP, grazing + increased precipitation; GW, grazing + warming; PN, increased precipitation + nitrogen addition; WN, warming + nitrogen addition; WP, warming + increased precipitation. The distribution of global grasslands is in green (Latham et al., 2014). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

and BNPP ( $n = 303$ ). All the data were extracted from the text and/or tables in selected published articles. If data was only reported in figures, we extracted the data using the GETDATA software (version 2.24, <http://getdata-graph-digitizer.com>). We also recorded latitude, longitude, mean annual temperature (MAT), and mean annual precipitation (MAP) for each of the selected papers. Data on MAT and MAP were obtained from the WorldClim database ([www.worldclim.org](http://www.worldclim.org)) if they were not reported in the article.

## 2.2 | Meta-analysis

### 2.2.1 | Individual and combined effects

The individual effect of grazing or a single global change factor on variables of biodiversity or ecosystem functioning was defined as the response ratio (RR)

$$RR = \ln\left(\frac{X_t}{X_c}\right), \quad (1)$$

where  $X_t$  and  $X_c$  were the means of the treatment and control, respectively (Crain et al., 2008; Vilà et al., 2011). While the variance ( $v$ ) of RR is estimated by

$$v = \frac{s_t^2}{n_t \bar{X}_t^2} + \frac{s_c^2}{n_c \bar{X}_c^2} \quad (2)$$

in which  $n_t$  and  $n_c$  indicate the sample sizes, and  $s_t$  and  $s_c$  are the standard deviations of the target variable in the grazing treatment and control groups, respectively.

The weight ( $w$ ) of each RR was represented by the reciprocal of the variance ( $w = \frac{1}{v}$ ). In order to correct for the effect of sample size, we calculated the weighted response ratio ( $RR_{++}$ ) from the single RR of each individual comparison between the control and treatment,  $RR_{ij}$  ( $i = 1, 2, \dots, m$ ;  $j = 1, 2, \dots, k$ ), and the weight of each RR ( $w_{ij}$ ), in which  $m$  stands for the numbers of groups (e.g., different intensities, climate types, livestock types, dominate species or soil depth) and  $k$  represents the number of comparisons. The weighted response ratio was computed with the following equation:

$$RR_{++} = \frac{\sum_{i=1}^m \sum_{j=1}^k w_{ij} RR_{ij}}{\sum_{i=1}^m \sum_{j=1}^k w_{ij}}. \quad (3)$$

The weighted standard error (SE) was calculated by:

$$S(RR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^m \sum_{j=1}^k w_{ij}}} \quad (4)$$

$RR_{++} \pm 1.96S(RR_{++})$  is the 95% confidence interval (95% CI; Zhang & Zhang, 2014). 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 5000 iterations (Janssens et al., 2010).

The combined effect of the multi-factors (grazing + one single global change factor, G + C; or two different global change factors

combined, C+C) was calculated using the same method as the individual effect, but with raw data from plots that crossed two treatments instead of plots under individual grazing or global change treatment, and the effect size was compared to the non-treatment plots.

Before each analysis, we used Kendall's Tau method to test for publication bias (Møller & Jennions, 2001). The percent change of each variable was calculated as  $[\exp(RR_{++}) - 1] \times 100\%$ , and the effect was significant if the 95% CIs did not overlap with zero. We also plotted RR frequency distributions to display the 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 the SigmaPlot software (SYSTAT Software Inc., CA, USA) using the following equation:

$$y = \alpha e^{-\frac{(x-\mu)^2}{2\sigma^2}}, \quad (5)$$

where  $x$  is the RR of a variable;  $y$  is the frequency (i.e., number of RR values);  $\alpha$  is a coefficient showing the expected number of RR values at  $x = \mu$ ; and  $\mu$  and  $\sigma^2$  are mean and variance of the frequency distributions of RR, respectively.

### 2.3 | Interactive effects

To further explore the interactive effects of two treatments on grassland biodiversity and ecosystem functioning, we used Hedges'  $d$  to calculate the interactive effect size according to the method described by Gurevitch & Hedges (2001). Hedges'  $d$  is sensitive to differences in sample standard deviation but has higher precision for detecting null effects compared to the log response ratio (Gurevitch et al., 2000; Lajeunesse & Forbes, 2003).

The effect size of an interaction between A and B ( $d_i$ ) was calculated by

$$d_i = \frac{(X_{AB} - X_A) - (X_B - X_C)}{2s} J(m), \quad (6)$$

where  $X_C$ ,  $X_A$ ,  $X_B$ , and  $X_{AB}$  were means of a variable in the control (C), 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

$$s = \sqrt{\frac{(n_c - 1)(s_c)^2 + (n_A - 1)(s_A)^2 + (n_B - 1)(s_B)^2 + (n_{AB} - 1)(s_{AB})^2}{n_c + n_A + n_B + n_{AB} - 4}}, \quad (7)$$

$$m = n_c + n_A + n_B + n_{AB} - 4, \quad (8)$$

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 ( $s_A$ ,  $s_B$ ), control groups ( $s_C$ ), as well as their combinations ( $s_{AB}$ ), respectively.  $J(m)$  was a correction

term for small sample bias (Hedges & Olkin, 1985), which was calculated by

$$J(m) = 1 - \frac{3}{4m - 1} \quad (9)$$

The variance of  $d_i$  ( $v_2$ ) of main and interactive effects was estimated by

$$v_2 = \left[ \frac{1}{n_c} + \frac{1}{n_A} + \frac{1}{n_B} + \frac{1}{n_{AB}} + \frac{d_i^2}{2(n_c + n_A + n_B + n_{AB})} \right] / 4 \quad (10)$$

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

$$d_{++} = \frac{\sum_{i=1}^m \sum_{j=1}^k w_{ij} d_{ij}}{\sum_{i=1}^m \sum_{j=1}^k w_{ij}}, \quad (11)$$

where  $m$  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  $RR_{++} \pm 1.96 \times s(RR_{++})$  and  $d_{++} \pm 1.96 \times s(d_{++})$ , respectively. Similar to the calculation of CI of individual and combined effects, a bootstrapping method was used to resample when the sample size was  $<20$ .

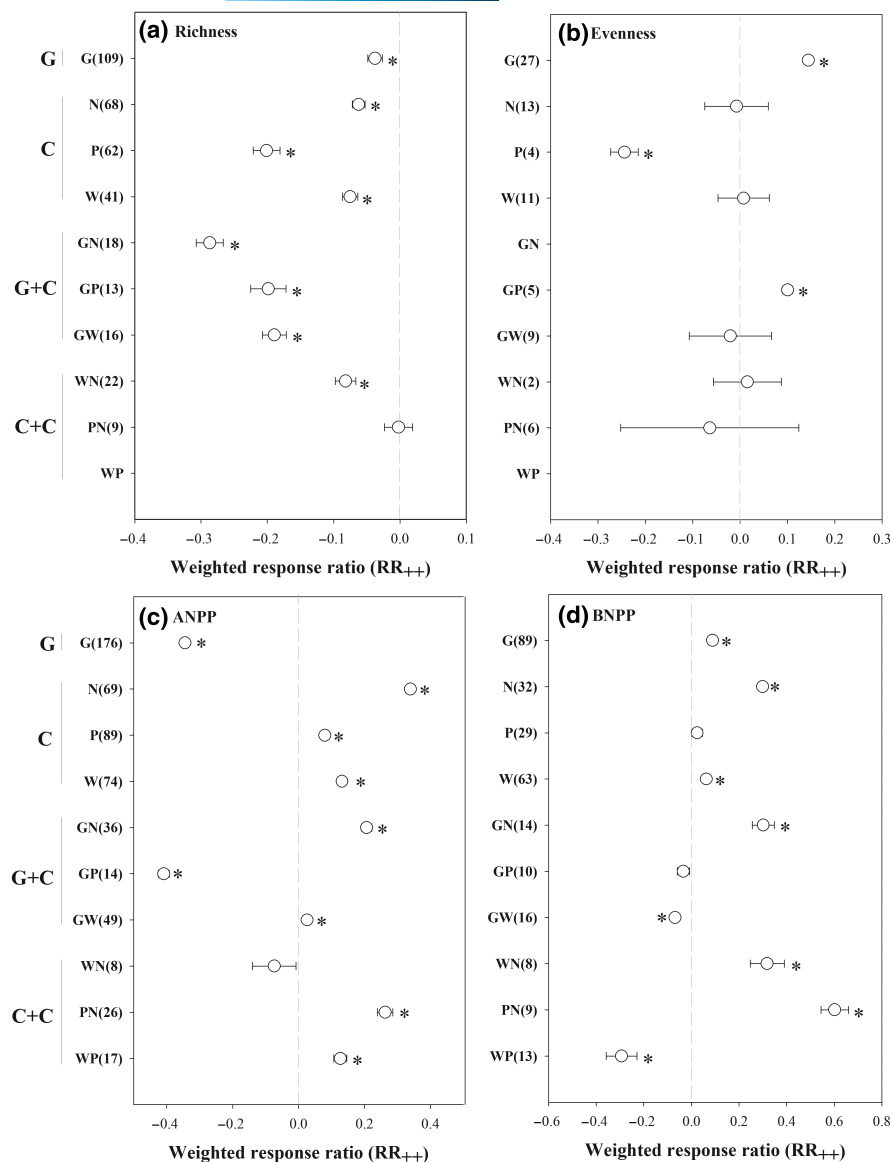
Based on the above calculations, the interaction between two treatments was classified as additive, synergistic, or antagonistic (Crain et al., 2008). If the 95% CI overlapped with zero, the interactive effect was identified as additive (Zhou et al., 2016). In cases where the individual effects were either both negative or one negative and the other positive, an interactive effect size  $<0$  was considered synergistic and  $>0$  was considered antagonistic. In cases where the individual effects were both positive, an interactive effect size  $>0$  was considered synergistic and  $<0$  was considered antagonistic.

## 3 | RESULTS

### 3.1 | Individual effects of grazing and global change factors

Both grazing and global change factors have significant effects on biodiversity and ecosystem functioning, with negative impacts for plant richness (Figures 2 and 3; Table S2). Specifically, grazing (G) decreased richness by 3.7% and ANPP by 29.1%, but increased evenness by 15.5% and belowground net primary productivity (BNPP) by 9.3% (Figures 2 and 3; Table S2). On average, global change factors (C) decreased richness by 8.0% and evenness by 15.1%, but increased ANPP and BNPP by 13.4% and 14.9%, respectively (Figure 3). Nitrogen addition (N) reduced richness by 6.0%, but increased ANPP and BNPP by 40.4% and 34.9%, respectively. Increased precipitation (P) reduced richness by 18.2% and evenness by 21.7%, stimulated ANPP by 8.3%, and did not affect BNPP. Warming (W) increased ANPP and BNPP by 14.1%





**FIGURE 2** Weighted response ratio ( $RR_{++}$ ) of richness (a), evenness (b), aboveground primary productivity (ANPP, c) and belowground primary productivity (BNPP, d) to a single factor or the combination of two factors. G, W, N, and P represent grazing, warming, nitrogen addition, and increased precipitation, respectively. GN, grazing + nitrogen addition; GP, grazing + increased precipitation; GW, grazing + warming; WN, warming + nitrogen addition; PN, increased precipitation + nitrogen addition; WP, warming + increased precipitation. C, all single global change factors treatments; G + C, grazing combined with a global change factor; C + C, two global change factors combined. Asterisks indicated statistical significance ( $p < .05$ ). Bars represent 95% confidence intervals. The vertical line shows  $RR_{++} = 0$ . The numbers in parentheses indicate the sample size.

and 6.5%, respectively, decreased richness by 7.2%, and did not influence evenness (Figure 2; Table S2).

### 3.2 | Combined and interactive effects of grazing and global change factors

On average, the combined effects of grazing and global change factors (G + C) remarkably reduced plant richness by 20.1% (Figure 3; Table S2). Specifically, grazing + nitrogen addition (GN) decreased richness by 24.9% but increased ANPP by 22.9% and BNPP by 35.2%. Grazing + increased precipitation (GP) reduced plant richness by 18.0% and ANPP by 33.6% but did not affect evenness and BNPP.

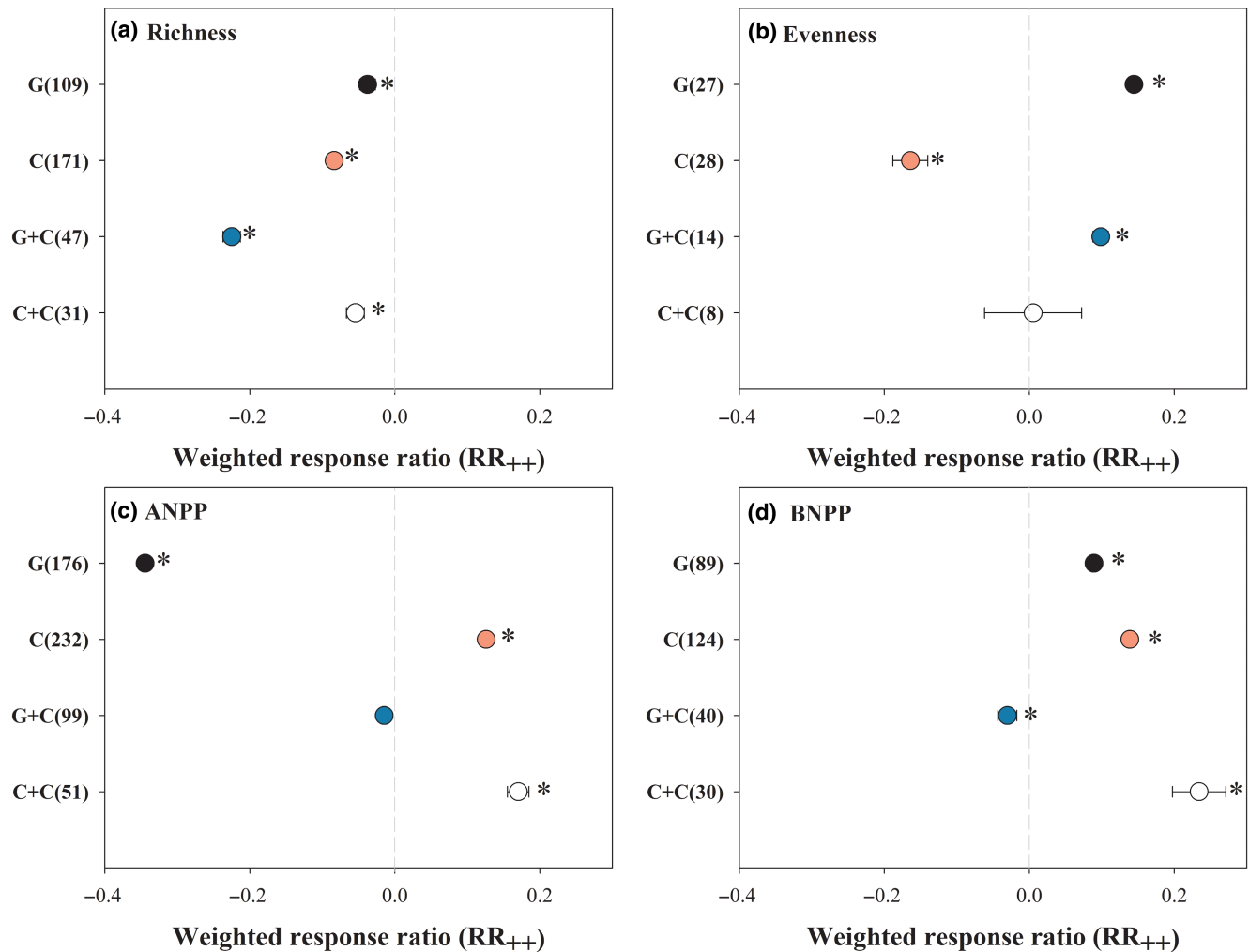
In addition, grazing + warming (GW) decreased richness by 17.3% and BNPP by 6.6%, but increased ANPP by 2.6% and did not affect evenness. Among global change factors, warming + nitrogen addition (WN) decreased richness by 7.9%, while increased precipitation + nitrogen addition (PN) increased both ANPP and BNPP

by 30.0% and 81.5%, respectively. Warming + increased precipitation (WP) increased ANPP by 13.5% but decreased BNPP by 25.4% (Figure 2; Table S2).

Grazing and global change factors (e.g., GN, GW, GP) had largely additive interactions with richness, ANPP, and BNPP (Figure 4). The combination of global change factors (e.g., WN and PN) exhibited similar additive influences on richness (Figure 4a) but not evenness and productivity. Alternatively, the interaction of increased precipitation and nitrogen addition (PN) was antagonistic on evenness while warming and nitrogen addition (WN) had a synergistic effect on ANPP (Figure 4f,g).

### 3.3 | BEF relationships in response to grazing and global change factors

The responses of biodiversity to both individual (grazing; global change) and combined factors (grazing + global change; global



**FIGURE 3** Weighted response ratios ( $RR_{++}$ ) of richness (a), evenness (b), aboveground net primary productivity (ANPP, c) and belowground net primary productivity (BNPP, d) in response to single factor and combined studies. G, grazing (black); C, all single global change factors treatments (red); G + C, grazing combined with a global change factor (blue); C + C, two global change factors combined (white). Asterisks indicate statistical significance ( $p < .05$ ). Bars represent 95% confidence intervals. The vertical line refers to  $RR_{++} = 0$ . The numbers in parentheses indicate the sample size. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

change+global change) led to changes in ecosystem functioning (Figures 2 and 5). Specifically, response ratios of ANPP ( $RR(ANPP)$ ) were positively related to the effect of biodiversity ( $RR(Richness)$ ), while response ratios of BNPP ( $RR(BNPP)$ ) were negatively correlated with  $RR(Richness)$ ; Figure 5a). In contrast,  $RR(Richness)$  was positively correlated with  $RR(ANPP)$  but negatively correlated with  $RR(BNPP)$  under global change (Figure 5b). The combination of grazing and global change resulted in negative linear relationships between  $RR(Richness)$  and  $RR(ANPP)$  as well as between  $RR(Richness)$  and  $RR(BNPP)$ ; Figure 5c).

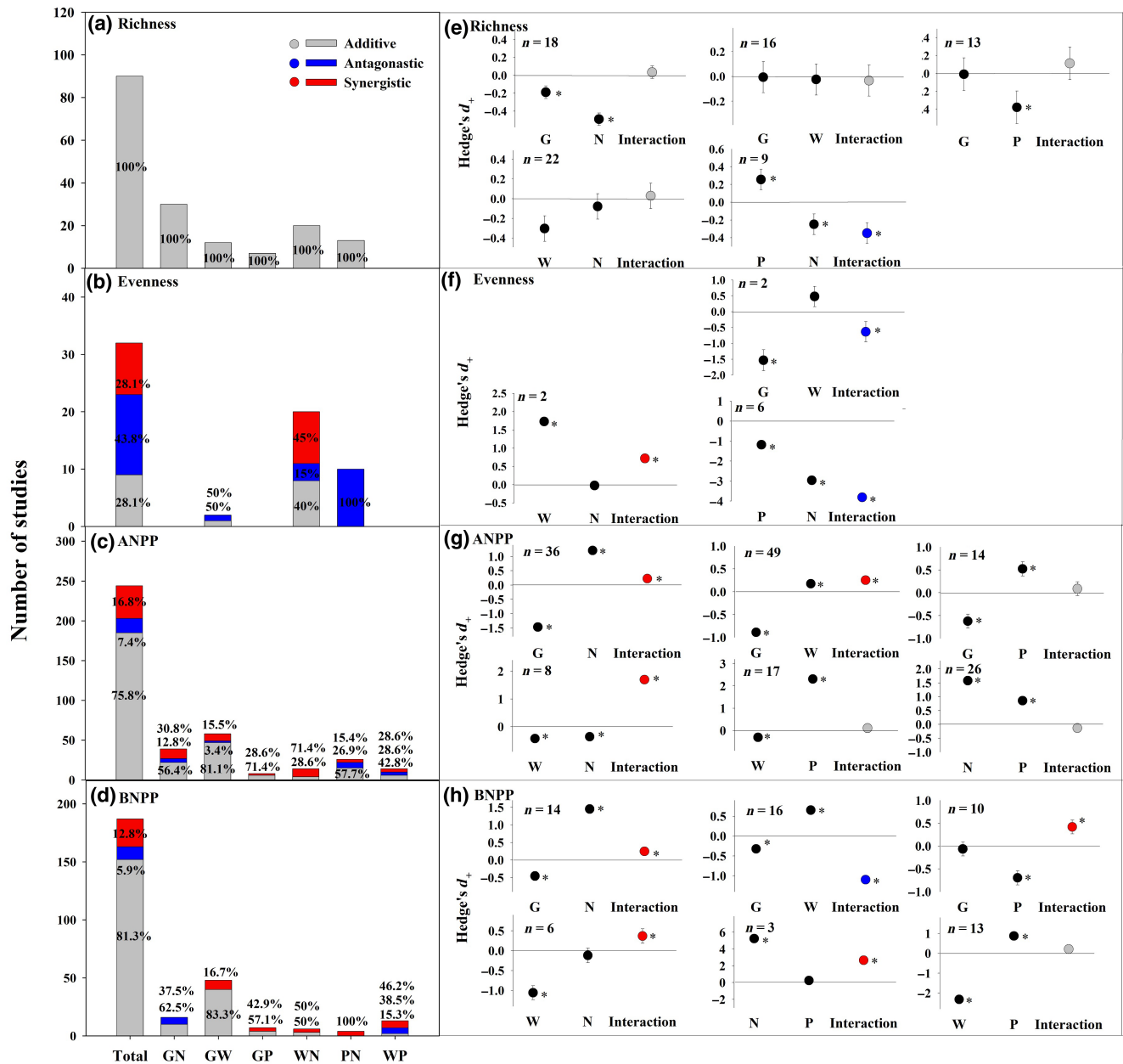
The linkage between response of richness and response of productivity differed significantly in the magnitude and direction on aboveground and belowground parts under grazing, global change or grazing+global change (Figure 5). Specifically, the relationship between  $RR(Richness)$  and  $RR(BNPP)$  had varying responses especially when compared to the relationship between  $RR(Richness)$  and  $RR(ANPP)$  under grazing or global change (Figure 5a,b).  $RR(Richness)$

and  $RR(ANPP)$  were less strongly correlated than  $RR(Richness)$  and  $RR(BNPP)$  under the combined effect of grazing+global change (Figure 5c).

## 4 | DISCUSSION

### 4.1 | Individual effects of grazing and single global change factors

Understanding the effects of grazing and global change factors on biodiversity and ecosystem functioning is crucial to evaluate and predict the responses of grassland biodiversity-ecosystem functioning relationship (BEF) in natural ecosystems (García et al., 2018; Milchunas et al., 1998). Our meta-analysis found that grazing decreased plant richness and ANPP, but increased evenness and BNPP (Figures 2 and 3). Grazing-induced decrease in



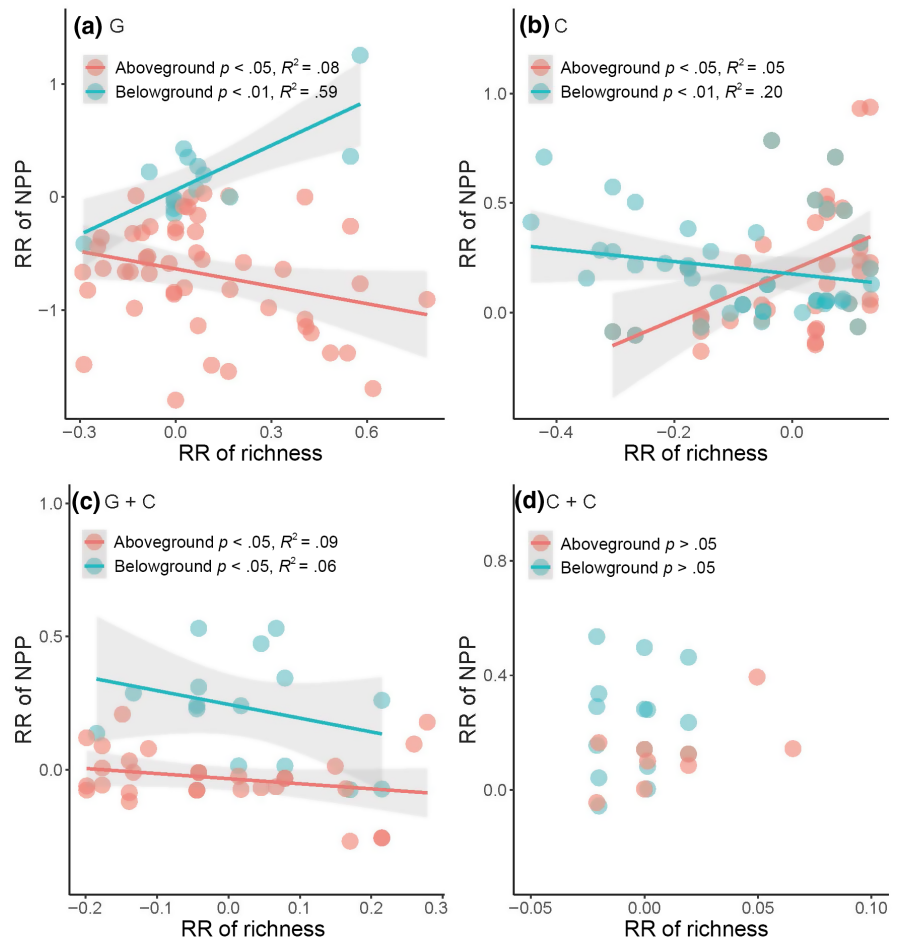
**FIGURE 4** Frequency distribution of interaction types (a–d) and interactive effects (e–h) of the two paired treatments on: Richness (a and e), evenness (b and f), aboveground primary productivity (ANPP, c and g) and belowground primary productivity (BNPP, d and h). G, W, N, and P represent grazing, warming, nitrogen addition, and increased precipitation, respectively. The numbers in parentheses indicate the sample size ( $n$ ). Asterisks indicated statistical significance ( $p < .05$ ). If the 95% CI overlapped with zero, the interactive effect was considered additive (gray). In cases where the individual effects were either both negative or one negative and the other positive, an interactive effect  $< 0$  was considered synergistic (red) and  $> 0$  was considered antagonistic (blue). In cases where the individual effects were both positive, an interactive effect size  $> 0$  (red) was considered synergistic and  $< 0$  was considered antagonistic (blue). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

plant richness might be attributed to herbivorous diet preference and therefore the continuous ingestion of certain species, resulting in a selective effect on plant community composition (Detling et al., 1979; Provenza et al., 2003; Schuman et al., 1999). The increased evenness caused by grazing might be due to that livestock mainly graze aboveground biomass of dominant species, leading to higher resource accessibility for other plant species (Clark et al., 2013; Svanbäck & Bolnick, 2006). Grazing decreased ANPP by removing aboveground plant biomass, but the reallocation of

carbon to belowground organs may be one of the reasons for the increase in BNPP (Mcsherry & Ritchie, 2013).

Our results showed that warming and nitrogen addition decreased richness, but exerted positive influences to both ANPP and BNPP (Figure 2). Warming-induced decreases in richness may be attributed to the exclusion of certain species with relatively low thermal tolerance (Klein et al., 2004), resulting in the homogenization of community structure and an increase in evenness (Wang et al., 2014). The warming-induced increases in aboveground and

**FIGURE 5** Relationships of response ratios (RR) of richness with aboveground net primary productivity (ANPP, red) and belowground net primary productivity (BNPP, blue) in single factor and combined factors studies. G, grazing; C, all single global change factors treatments; G + C, grazing combined with a global change factor; C + C, two global change factors combined. The dots represent the observations and the grey shaded areas represent 95% confidence intervals. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



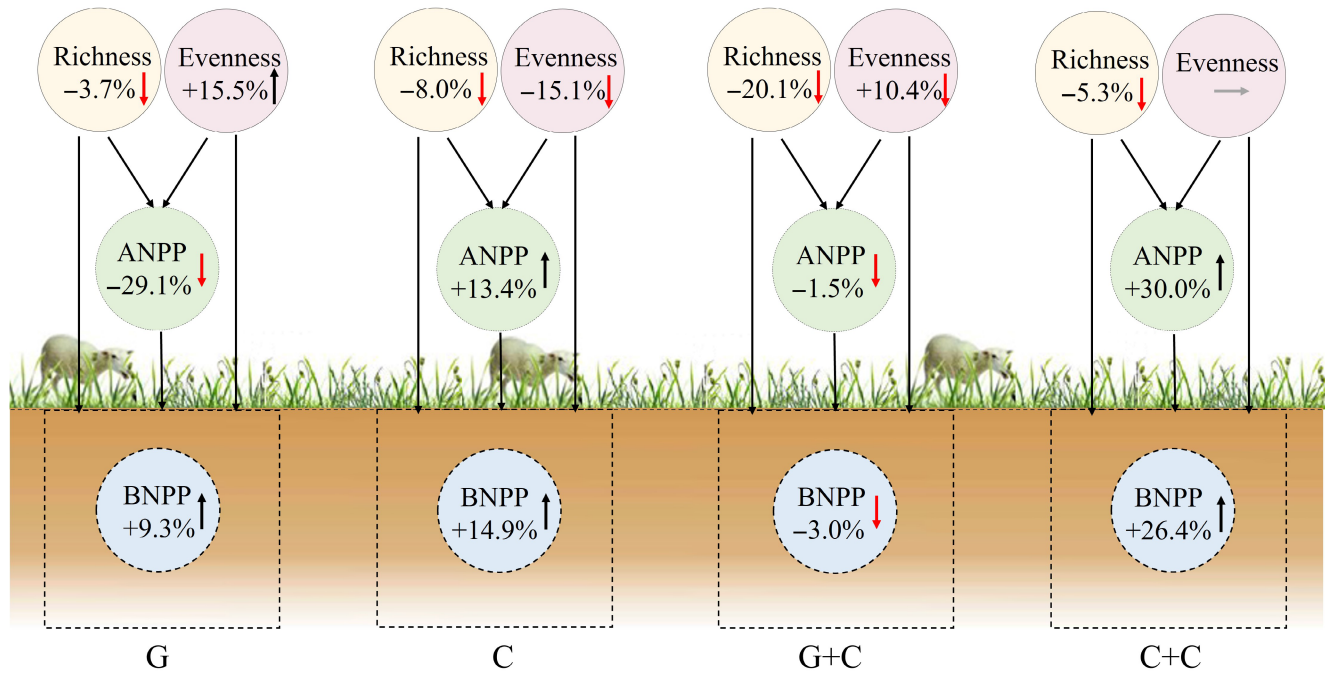
belowground productivity were consistent with previous global syntheses (Lu et al., 2013). Warming increased soil nutrient availability via nitrogen mineralization, which may stimulate plant nitrogen uptake and then photosynthesis, promoting growth of shoots and roots (Jiang et al., 2018). In addition, warming will alter plant phenology (e.g., advanced flowering and prolonged growing season), which may further enhance plant growth and promote aboveground as well as belowground productivity as a consequence (Arft et al., 1999; Liu et al., 2022; Sherry et al., 2007). Nitrogen addition caused the largest stimulation on ANPP and BNPP compared with other individual global change factors (Figure 2). Previous studies have demonstrated that nitrogen addition increases plant photosynthesis, leading to more fixed carbon inputs to aboveground and belowground components of ecosystems (Poorter & Nagel, 2000). Meanwhile, the enhanced aboveground and belowground productivity caused by nitrogen addition may also result from the increased nutrient absorption (Nordin et al., 2001).

## 4.2 | Interactive effects of grazing and global change factors

The interactive effects of grazing and global change factors on biodiversity and ecosystem functioning are vital for mapping and

assessing ecosystem services (Jing et al., 2015; Yuan & Chen, 2015). In this study, we found that grazing + global change decreased richness and BNPP, but enhanced evenness (Figure 3). The interactions of grazing + global change and global change + global change were primarily additive, indicating combined treatments taking effect together without interaction (Figure 4). For example, both grazing and increased precipitation respectively reduced grassland richness (Figures 2a and 4e). The selective effect of livestock grazing may decrease interspecific competition, and the plant community under increased precipitation may be more sensitive to resource limitation due to more leaching, both contributes to greater species loss (Clark et al., 2013; Svanbäck & Bolnick, 2006). Conversely, grazing + warming synergistically increased aboveground productivity (Figure 4g), which could be attributed to that the increased temperature promotes decomposition and lessens soil aggregate compaction caused by livestock. This decreased compaction then allows higher nutrient uptake and compensates for the direct removal of biomass by grazing (Detling et al., 1979; Nosalewicz & Lipiec, 2014; Schuman et al., 1999).

Our study also found an overall additive interaction of paired factors on richness (Figure 4e,f). This may derive from niche partitioning among species, which means that individual species tend to be restricted by the least available resource (Liebig's law of the minimum), thus responding to the change in resource limitation



**FIGURE 6** Conceptual diagram of the influence of grazing and global change factors on processes controlling the biodiversity and ecosystem functioning. G, grazing; C, global change factors; G + C, grazing combined with a global change factor; C + C, two global change factors combined; ANPP, aboveground net primary productivity and BNPP, belowground net primary productivity. Black upward arrows represent positive responses, red downward arrows represent negative responses, grey flat lines represent non-significant responses. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

(Pekin et al., 2012). Nitrogen addition increases the dominance of nitriphile species because reduced nitrogen limitation causes plants to compete more for other limited resources, such as light or water (Hautier et al., 2009; Siebenkäs & Roscher, 2016). Nitrogen and grazing on preferred species combined (Clark et al., 2013) may therefore lead to species turnover and richness decrease (Figure 4e). Interestingly, an antagonistic interaction on evenness was found under increased precipitation + nitrogen addition (Figure 3), possibly due to the higher sensitivity of plants to nitrogen addition in humid than arid environment (Johansson et al., 2012; Zhang et al., 2013).

### 4.3 | BEF relationships in response to grazing and/or global change factors

Global change-induced change in  $RR(ANPP)$  was positively correlated with  $RR(Richness)$  but this relationship was negative under grazing + global change (Figure 5b,c). Global change, such as nitrogen deposition, might relieve plants' resource limitation, thus promoting aboveground productivity (Figure 5b; Guerrero-Ramírez et al., 2017; Harpole et al., 2016; Reich, 2009). However, the environmental alteration (e.g., pH changes) induced by nitrogen addition might drive the exclusion of plant species, which may bring down the increase of aboveground productivity due to a positive relationship between richness and productivity (Figure 51; Gao et al., 2018; Prager et al., 2017). On the other hand, continuous trampling by livestock grazing may directly affect aboveground plant organs, resulting in a larger decrease on ANPP, especially in communities that are

mainly dominated by livestock-preferred species (Figure 5a; Bendix et al., 2017; Klein et al., 2007; Mu et al., 2016). Meanwhile, grazing may also change the distribution pattern of subsurface carbon by accelerating carbon allocation in plants (Luan et al., 2014; Mcsherry & Ritchie, 2013), resulting in a negative correlation between  $RR(ANPP)$  and  $RR(Richness)$ . Taken together, although the relationship between  $RR(Richness)$  and  $RR(ANPP)$  was positive under global change, the negative impact of grazing brought that relationship under grazing + global change to be negative, indicating that grazing is more dominant than global change in aboveground BEF relationships.

The relationship between  $RR(BNPP)$  and  $RR(Richness)$  was positive under grazing, but was negative under the combined influence of grazing + global change, which aligns with the individual impact of global change factors (Figure 5). This indicated that global change dominated the response of belowground richness-productivity relationships when combined with grazing. The continuous grazing and trampling of livestock can increase soil compaction and then influence soil aggregates, which might suppress soil respiration and biomass accumulation (Bai et al., 2010; He et al., 2020; Schlesinger, 1996). In addition, livestock mainly graze on the most abundant grasses in grasslands, leading to increases in evenness as well as interspecific competition and thus a positive correlation between  $RR(BNPP)$  and  $RR(Richness)$ ; Provenza et al., 2003; Schuman et al., 1999). However, global change factors (e.g., warming) might increase activity of soil microorganisms and animals, resulting in faster breakdown of soil aggregates and soil organic carbon decomposition, which increases BNPP despite biodiversity loss (Jonasson et al., 1999; Klein et al., 2004; Wang et al., 2014). Moreover, global



change factors might favor those species that were suppressed by grazing via providing resource supply, resulting in an overall negative correlation between RR(BNPP) and RR(Richness) under the combined effect of grazing + global change (Jing et al., 2015; Liu et al., 2022).

#### 4.4 | Implications for future models and experiment design

Understanding the impacts of grazing and global change factors on grassland biodiversity and ecosystem functioning may help improve our prediction for future grassland dynamics (Alkemade et al., 2013; Mcsherry & Ritchie, 2013). In this study, we found that grazing and global change factors differentially influenced BEF relationships, and the effects on aboveground and belowground BEF relationships are in opposite trend (Figure 6).

First, our results showed that grazing-induced changes in richness were positively correlated with changes in BNPP, but were negatively correlated under the combination of grazing and global change factors. In contrast, RR(ANPP) was negatively correlated with RR(Richness) under grazing, but positively under global change and grazing + global change (Figure 5). These results suggested that the effects of grazing are more dominant in aboveground organs while global change dominates the impact in belowground BEF. However, current land surface models do not fully consider the combination effects of grazing and global change on grassland BEF responses, which limits predictions on how grasslands respond to future environmental change. The differential response of aboveground and belowground BEF to grazing combined with global change factors should be included in future Earth system models to better understand grassland-climate feedbacks under human disturbance.

Second, grazing intensity may significantly affect aboveground and belowground carbon cycling globally (Zhou et al., 2016). The effect of livestock grazing on ecosystems functioning was also regulated by environmental fluctuations, such as water and nutrient availability (Jamieson et al., 2013; Reich, 2009). Therefore, whether and how the effect of grazing and global change factors on grassland BEF could be regulated by grazing intensity remains unclear. Meanwhile, the responses of ecosystems functioning to grazing, global change, and their combinations varied with different environmental variables such as MAT and MAP (He et al., 2020; Zhou, Luo, Chen, Hu, et al., 2019).

Third, most of the studies included in our dataset were distributed in temperate regions (e.g., North America and Eastern Asia, Figure 1). Our findings have, therefore, little capacity to predict the response of BEF relationships to grazing and global change in the tropics and Africa. Furthermore, our selected studies were largely shorter than 3 years. This short duration may also influence our findings (Zhou, Luo, Chen, Hu, et al., 2019). The lack of large and complete datasets from long-term studies likely limits our ability to better understand the long-term effects of grazing and change factors on grassland BEF relationships. In addition, elevated CO<sub>2</sub> may preserve biodiversity loss but promote productivity when combined

with nitrogen addition (Reich, 2009). However, we did not find studies that cross CO<sub>2</sub> fertilization treatment and grazing to see their combined impact to grassland BEF.

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#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad Digital Repository at <https://doi.org/10.5061/dryad.8w9ghx3q3>.

#### ORCID

Miao He  <https://orcid.org/0000-0002-1851-9797>

Yuhan Pan  <https://orcid.org/0000-0002-8334-4946>

Guiyao Zhou  <https://orcid.org/0000-0002-1385-3913>

Kathryn E. Barry  <https://orcid.org/0000-0001-6893-6479>

Yuling Fu  <https://orcid.org/0000-0001-6286-8866>

Xuhui Zhou  <https://orcid.org/0000-0002-2038-9901>

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#### SUPPORTING INFORMATION

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

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