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Divergent responses of ecosystem respiration components to livestock exclusion on the Qinghai Tibetan Plateau

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Abstract

Grazing exclusion (GE) is an effective method for protecting degraded grasslands, and it can profoundly affect ecosystem carbon (C) cycles. Ecosystem respiration (ER), which includes both autotrophic and heterotrophic respiration (HR), accounts for the largest land-to-atmosphere C fluxes. How ER responds to GE is still unclear, however, and to investigate this, a controlled GE experiment was conducted at a meadow grassland near Qinghai Lake, China. Animal exclusion enhanced ER and aboveground plant respiration (R_{agb}) by 10.5% and 40.1%, respectively, but it suppressed soil respiration by 12.4% and HR by 17.6%. Positive responses of ER and R_{agb} were linked to increased aboveground biomass, particularly graminoids biomass. Negative responses of soil respiration and HR were associated with GE-induced changes in microbial biomass C and nitrogen. These results show that grassland responded in complex ways to GE and that ER and its components were regulated by both abiotic and biotic factors. Moreover, the divergent responses of respiration components have important implications for models of terrestrial C cycles and climate under enhanced human activities and changes in land use.

KEYWORDS

ecosystem respiration, livestock grazing, meadow grassland, microbial biomass, plant functional types

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1 | INTRODUCTION

Grazing exclusion (GE) has become one of the most commonly used ecological management methods in recent decades, and it is widely considered to be an effective way of protecting the land from degradation throughout the world (Harris, 2010; Paz-Ferreiro, Medina-Roldán, Ostle, Mcnamara, & Bardgett, 2012). By using fences to prevent the damaging effects of grazing, GE is also considered a simple but effective restoration method for degraded grasslands across the world. In this regard, the Chinese central government invested more than 160 million US dollars on a project called 'returning grazing lands to grasslands' in 2004 (Dong et al., 2007; Shao et al., 2016). There is growing evidence that GE can significantly increase plant productivity, alter plant community structure, and change soil properties (Lkhagva, Boldgiv, Goulden, Yadamsuren, & Lauenroth, 2013; Riedel, Bernues, & Casasus, 2013; Tarhouni, Ben Hmida, & Neffati, 2017). Changes in ecosystem processes caused by GE are expected to have substantial impacts on carbon (C) fluxes (Frank & Groffman, 1998; Metcalfe & Olofsson, 2015; Zhao et al., 2017; Zhou et al., 2017), but studies into these relationships are still limited, especially in the cold and remote Tibetan Plateau.

Ecosystem respiration (ER) plays pivotal roles in affecting C fluxes from terrestrial ecosystems to the atmosphere, but the effects of GE on ER are still unclear (Chen et al., 2017; Guo et al., 2018; Hu et al., 2016; Liebig, Kronberg, Hendrickson, Dong, & Gross, 2013; Liu, Zang, & Chen, 2016; Sharkhuu et al., 2016). One reason for this is that ER can be divided into various subcomponents, including heterotrophic respiration (HR), aboveground (R_{agb}), and belowground (R_{bgb}) plant autotrophic respiration (Chen, Luo, Xia, Shi, et al., 2016; Sagar, Li, Singh, & Wang, 2017; Zhao et al., 2017), and these components respond to GE in complex ways (Sharkhuu et al., 2016; Villanueva-López, Martínez-Zurimendi, Ramírez-Avilés, Aryal, & Casanova-Lugo, 2016). For instance, GE can increase ER due to the growth of biomass, and so positive effects can be caused by GE-induced increases in autotrophic respiration (Sharkhuu et al., 2016; Zhao, Li, Li, Tian, & Zhang, 2016). On the other hand, GE can decrease ER by lowering soil temperature and reducing the inputs of animal wastes that provide nutrients for the plants (Hou et al., 2016; Ren, Chen, et al., 2017; Wei et al., 2016; Zhao, Li, et al., 2016). GE can affect HR through its effects on microbial activities, and this was reported to be the main driver of the negative responses of ER to GE (Hou et al., 2016; Wei et al., 2016; Zhao, Li, et al., 2016). The gaps in our understanding of the mechanisms responsible for the effects of GE on the various components of ER have limited our ability to evaluate the impact of animals on C fluxes and to assess the potential benefits of GE for grassland management.

GE can influence ER both directly and indirectly (Figueiredo et al., 2016; Gao et al., 2017; Jerome et al., 2014; Zhou et al., 2017). First, the GE-induced accumulation of both aboveground biomass (AGB) and belowground biomass (BGB) can lead to higher plant growth respiration and plant maintenance respiration (Koncz et al., 2015; Wang, Wu, Liu, Yang, & Hao, 2015), and this is likely to cause higher ER in GE plots than in grazed plots. Second, GE can affect ER through changes in microbial activity and community composition, particularly the heterotrophic components (Liebig et al., 2013; Zhao et al., 2017). This is largely due to the effects of GE on chemical inputs from animals (Boon, Robinson, Chadwick, & Cardenas, 2014), changes in soil physical and chemical properties (Mekuria & Aynekulu, 2013; Pulido, Schnabel, Lozano-Parra, & González, 2016), and the proportion of C allocation belowground (Falk, Schmidt, & Strom, 2014; Liebig et al., 2013). In addition, variations in soil microclimate induced by GE (particularly, soil temperature and soil moisture) were also reported to have substantial impacts on ER on the cold and arid Tibetan Plateau (Chen, Shi, & Cao, 2015; Luo et al., 2015; Zhao, Luo, Li, Li, & Tian, 2016). The responses of various components of ER to GE are driven by complex interacting mechanisms, and the current understanding of the effects of GE on ER is limited because of these interactions (Hou et al., 2016; Sharkhuu et al., 2016; Wei et al., 2016; Zhao, Li, et al., 2016; Zhao, Luo, et al., 2016). Therefore, it is important to understand the specific responses and underlying mechanisms that link the various components of ER to GE.

The Tibetan Plateau has an average elevation of more than 3,000 m, and it is one of the highest elevated plateaus in the world and also one of the largest in area, covering more than 2,500,000 km^2. Indeed, it has been called the 'Roof of the World' and the 'Third Pole of the World'. There is growing evidence that the Tibetan Plateau affects the Asian summer monsoon because of its large area and high elevation, and this in turn influences regional and global climate dynamics (Boos & Kuang, 2010; Hu et al., 2015; Liu & Dong, 2013). More important, the Tibetan Plateau is among one of the most environmentally sensitive regions in our changing world (partly due to its low temperature), and it is currently undergoing accelerated land degradation owing to enhanced anthropogenic activities, including pressure from livestock grazing (Harris, 2010; Lehnert, Meyer, Meyer, Reudenbach, & Bendix, 2014). Degradation of the alpine grasslands not only affects the pastoral livelihoods of local populations but also leads to other environmental problems that may exacerbate both current and future global climate change (Mcsherry & Ritchie, 2013; Zhang et al., 2014). Therefore, there is an urgent need to develop effective and sustainable restoration methods for degraded grasslands.

In recent decades, GE has become widely used on the Tibetan Plateau to rejuvenate degraded grasslands (Chen, Zhou, et al., 2016; Luo et al., 2015; Mekuria, Langan, Noble, & Johnston, 2017), but it is still unclear how GE might affect the various components of ER. We therefore designed a controlled grazing and fencing experiment near Qinghai Lake on the Tibetan Plateau to address these issues. Our aims were (a) to investigate how endogenous components of ER respond to grazing and GE and (b) to identify the underlying drivers for the responses of ER and its components to GE.

2 | STUDY SITE AND METHODS

2.1 | Study site

The multiyear, field grazing and fencing experiment was conducted at a site near Qinghai Lake in Haiyan County, Qinghai Province, China (100°51′20″E, 36°57′35″N, 3,130 m), which had been used as winter grazing pasture for more than 20 years and is under the control of the

China Meteorological Administration. The temperature and precipitation were relatively high during the growing seasons, and it was windy during the nongrowing seasons with extremely low temperatures and dry conditions. The average annual precipitation from 1995 to 2012 was 408.5 mm, and the average annual air temperature was 1.3 °C. Based on the soil classification scheme of the Food and Agriculture Organization of the United Nations (IUSS Working Group, 2015), the soil was classified as cambisol, and it is mountain brown in the Chinese soil classification scheme. The soil pH was 7.77, and soil bulk density was 0.95 g cm^{-3}. A list of the dominant plant species can be found in Table S1, and other detailed information related to the study area can be found in Chen et al. (2017), Chen, Luo, Xia, Shi, et al. (2016), and Guo et al. (2018).

2.2 | Experimental design

In October 2007, we established 12 random blocks (60 m × 30 m) at the study site, and buffer zones (~10-m wide) were set up between any two adjacent blocks. Animal grazing was then totally excluded from six of the 12 blocks by mesh fencing, and these were designated as the GE blocks, whereas the other six blocks were still under the traditional winter free grazing. The livestock grazing intensity was about 1.41 tropical livestock units (about 0.5 yak and 2.5 sheep per hectare; Chen, Zhou, et al., 2016). Field measurements were taken during two consecutive growing seasons (2012 and 2013), and therefore, the duration of GE was 4 or 5 years.

2.3 | Measurements of respiration fluxes

Aluminum frames (0.5 m on each side and with a height of 0.05 m) were inserted into the center of each block when the controlled GE experiment was conducted to prevent air leakage when the measurements were made. An opaque glass chamber (0.5 m × 0.5 m × 0.5 m) was placed inside the frames and attached to a LI-8100 gas analyzer (LI-COR, Inc., Lincoln, NE, USA) to measure ER. Two small electric-fans were installed in the chambers to fully mix the air inside the chamber during the ER measurements (Farquhar, Firth, Wetselaar, & Weir, 1980; Pumpanen, Ilvesniemi, Perämäki, & Hari, 2003).

For the measurements of soil respiration (SR) and HR, two types of polyvinylchloride collars were buried in each block adjacent to the aluminum frames at the start of the experiment. The heights of polyvinylchloride collars for HR were 0.7 m, and those for SR were 0.05 m, and both collars were 0.1 m in internal radius. Aboveground plants inside the collars were cut to the ground at least 1 or 2 days before the measurements. To measure the gas fluxes, a survey chamber which was cyclonical in shape, 0.1 m in internal radius, and had a height of 0.15 m was connected to a LI-COR Li-8100 gas analyzer (Chen et al., 2017; Pregitzer, Burton, King, & Zak, 2008). The measurement for each respiration component lasted ~120–150 s, including an initial 10–25 s needed to reach a steady state. Variations of air temperature inside the chambers during the measurements were usually <0.2 °C and thus insufficient to affect the CO_2 fluxes (Niu, Sherry, Zhou, & Luo, 2013). The CO_2 accumulation in chambers also was small enough that it did not alter the respiration fluxes. ER, SR, and HR were measured twice each month on sunny days from April to October during each of growing season. R_{agb} was calculated as the difference between ER and SR, that is, R_{agb} = ER − SR, whereas R_{bgb} was R_{bgb} = SR − HR.

2.4 | Soil microclimate

Electronic HOBO data storage units (16-bit Smart sensors, Onset Computer Co., Pocasset, USA) were used to record soil temperature and moisture at a depth of 0.1 m at 5-min intervals during the two growing seasons. A thermocouple probe was used to measure soil temperature, whereas soil volumetric moisture was quantified by two concentric stainless steel electrodes. Soil temperature and moisture were measured simultaneously for each grazing and GE block; thus, there were in total 12 probes used for temperature and moisture measurements.

2.5 | Plant productivity

One of the primary goals for the study was to investigate the seasonal and monthly responses of ecosystem C fluxes to GE, and therefore, the biomass within the aluminum frames could not be harvested before the experiments were completed. The AGB and plant functional type biomass (PFT, graminoids biomass, legumes biomass, and forbs biomass) were thus estimated by a method that did not involve clipping of the vegetation inside the frames (Chen, Luo, Xia, Wilcox, et al., 2016; Flombaum & Sala, 2007; Klein, Harte, & Zhao, 2007; Tucker, 1980). In brief, we first selected 54 plots (0.5 m × 0.5 m) near the frames that had plant communities similar to those within the frames. The cover, height, basal diameter, abundance, number of leaves, and leaf area (when possible) were carefully recorded for each plot in August of 2012. After recording the plant functional traits for the 54 plots, we clipped the aboveground plants in them and separated the clippings by PFT, and those biomass samples were then oven dried at 65 °C for 3 days before weighing.

We conducted stepwise multiple regression analysis with PFTs' biomass as the dependent variable and plant functional traits (cover, height, basal diameter, abundance, number of leaves, and leaf area) as independent variables. The results of those analyses indicated that plant height and cover were the best predictors of plant biomass (Table S2). Following this method, we estimated the PFT's biomass within the aluminum frames by recording the height and cover for each PFT. Monthly variations of BGB (with a depth of 0.4 m) were measured near the aluminum frames by using a soil auger with a radius of 0.02 m. Roots were picked from the soils by hand and then washed to remove soil particles. These roots were then oven dried at 65 °C for 3 days. Average values of AGB, PFTs' biomass, and BGB were calculated from the monthly averages.

2.6 | Soil sampling methods

Fresh surface litter and other extraneous materials, such as stones and animal bones were removed before sampling the soils. A soil auger (0.02 m in radius) was used to manually collect samples from each of the 12 blocks once per month during the growing season (May to October) in both 2012 and 2013. The sampling depth was 0–10 cm. After removing all large plant matter and any stones, the soil samples were then stored in a portable refrigerated box at 4 °C and transported to the laboratory for the further analysis.

2.7 | Microbial biomass carbon and microbial biomass nitrogen

A chloroform fumigation method was used to measure soil microbial biomass C (MBC) and microbial biomass nitrogen (MBN; Chen, Luo, Xia, Shi, et al., 2016; Vance, Brookes, & Jenkinson, 1987). Briefly, we took two soil subsamples (~10 g for each) from each soil collected from the field study site. One of these subsamples was fumigated with $CHCl_3$ for 24 hr, and the other one was not fumigated, and afterwards, both soil samples were extracted for 1 hr with 0.5 M K_2SO_4 using a shaker. Carbon and nitrogen (N) contents of both subsamples were measured with a TOC/TN Analyzer (Analytik Jena TOC Analyser multi N/C 3100). The differences in C and N content for the soil subsamples with and without fumigation were designated as the MBC and MBN. Correction factors of 0.45 for MBC and 0.54 for MBN were used to account for possible incomplete extraction of the subsamples. In addition, soil water content was measured for each soil by oven drying the original fresh soils (at 105 °C for 30 hr), and those results were used to convert the MBC and MBN results to a dry mass basis (mg kg^{-1} dry soil).

2.8 | Data analysis

Monthly average values were calculated for ER and various components of ER based on the diurnal measurements, and average values during the growing seasons for the same variables were calculated from their monthly average values. Repeated measures analyses of variance (ANOVAs) were used to evaluate the impacts of GE, measuring date (the specific date within each growing season), and the potential interactions between GE and date on ER and its components (with a level of significance of $p < .05$). The impacts of GE, year, and the possible interactive impacts of GE and year on the annual values of AGB, PFTs' biomass, BGB, MBC, MBN, MBC/MBN, soil temperate and moisture, ER, the components of ER, and the contribution of each component to ER were evaluated by two-way factorial ANOVAs analysis ($p < .05$). Linear regression and multiple stepwise regression analysis were used to test for possible relationships between GE-caused variations in the various components of ER and the corresponding changes in MBC, MBN, PFTs' biomass, soil temperature, and soil moisture. The regression models were evaluated by the Akaike information criterion (Akaike, 1974; Burnham & Anderson, 2004).

3 | RESULTS

3.1 | Effects of livestock grazing on microclimate, plant productivity, and microbial biomass

GE significantly (two-way factorial ANOVA analysis, Table 1) reduced the soil temperature at a depth of 10 cm by an average of 0.65 ± 0.01 °C during the two growing seasons (Figure S1). More specifically, compared with the grazed plots, the soil temperature in GE plots was lower by 0.48 ± 0.01 °C in 2012 and 0.82 ± 0.02 °C in 2013. Across the two growing seasons, the exclusion of livestock grazing significantly increased soil moisture by a mean value of 12.2% when compared with the grazed blocks, with an increase of 9.9% in 2012 and 14.4% in 2013. There were significant differences between years for soil moisture and temperature, and there were significant interactive effects of year and GE on soil temperature (Table 1).

Relative to the grazed blocks, GE significantly enhanced AGB by 44.3% through the two consecutive growing seasons, with increases in legume biomass of 40.3% and graminoid biomass of 53.5% (Figure 1). In more detail, the respective increases in biomass for 2012 and 2013 were 51.6% and 55.5% for graminoids; 40.2% and 40.4% for legumes, and 44.0% and 44.7% for AGB, respectively. No effect of year or its interaction with GE was found for AGB or PFTs' biomass (apart from significant year effects on forb biomass). In addition, the GE in this study had no effects on BGB or forb biomass, even when evaluated for each year separately (Table 1).

GE significantly reduced MBC by 9.3% over the two growing seasons (9.4% in 2012 and 9.2% in 2013; Figure 1). There were significant year effects on MBC, with a relatively larger decrease in 2012 than 2013 (Table 1). GE had no effect on MBN and MBC/MBN, even when evaluated separately for the two growing seasons. In addition, no interactive effect of GE versus year was found for MBC, MBN, or MNC/MBN (Table 1).

3.2 | Impacts of livestock exclusion on the components of ER

Overall, GE significantly increased ER by 10.5% and R_{agb} by 40.1% over the two growing seasons, but GE decreased SR and HR by 12.4% and 17.6%, respectively (Figure 2). Two-way ANOVAs indicated that there were no effects of year (apart from R_{bgb}) and no interactive effect of year and GE for ER and its components (Table 1). The significant effects of GE on ER, R_{agb}, SR, and HR still held true when each of the two growing seasons were analyzed by repeated measures ANOVAs (Table 2). In addition, GE had no effects on R_{bgb}, even when evaluated for the individual years.

GE significantly increased R_{agb}/ER by an average of 26.4%, with increases of 23.5% for 2012 and 29.5% for 2013 (Figure 3), and R_{agb}/ER varied from 0.35 to 0.67 for both the grazed and GE blocks over the two growing seasons. For the two growing seasons combined, GE also significantly decreased SR/ER, HR/ER, R_{bgb}/ER, and HR/SR by 19.3%, 23.7%, 14.2%, and 5.5%, respectively. Additionally, no interactive effect of year and GE was found for the proportion of each component normalized to ER (Table 1).

3.3 | Factors regulating ER components to livestock exclusion

High soil moisture and temperature were linked to the relatively large values of respiration components during the two growing seasons (Figure S2). Nonetheless, GE-caused variations in soil temperature and moisture were not directly correlated with GE-induced changes in respiration. The increases in ER and R_{agb}, however, were significantly related to the increment in AGB after GE, particularly the large increases in the ratio of graminoid biomass to AGB (Figure 4).

TABLE 1 Results of two-way factorial ANOVA analysis (*F* values) of livestock exclusion (GE), year (Y), and their interactive effects (GE:Y) on ecosystem respiration (ER), soil respiration (SR), heterotrophic respiration (HR), aboveground plant respiration (R_{agb}), and belowground plant respiration (R_{bgb})

Effect	*df*[a]	ER	SR	HR	R_{agb}	R_{bgb}
GE	1	45.432**	30.986**	111.116**	257.068**	2.555
Y	1	3.302	10.675*	0.318	1.292	14.806*
GE:Y	1	0.302	0.214	0.156	1.736	0.115
	df	SR/ER	HR/ER	R_{bgb}/ER	R_{agb}/ER	HR/SR
GE	1	212.563**	261.619**	22.518**	212.563**	9.582*
Y	1	4.619*	7.785*	13.252*	4.619*	16.704*
GE:Y	1	1.466	0.019	1.162	1.466	0.165
	df	ST[b]	SM[b]	MBC[b]	MBN[b]	MBC/MBN[b]
GE	1	216.924**	53.730**	87.209**	0.258	2.401
Y	1	228.878**	243.723**	7.369*	0.42	0.001
GE:Y	1	22.282**	0.496	0.001	0.011	0.006
	df	AGB[b]	G[b]	L[b]	F[b]	BGB[b]
GE	1	278.449**	257.169**	216.751**	2.906	0.871
Y	1	2.853	0.118	0.131	62.607**	0.002
GE:Y	1	0.171	0.284	0.001	0.001	0.374

Note. Differences between treatments are evaluated at $p < .001$ (denoted by double asterisks, **) and $p < .05$ (denoted by single asterisk, *).

[a]*df* stands for degrees of freedom.

[b]See Figures 1–3 for keys to abbreviations.

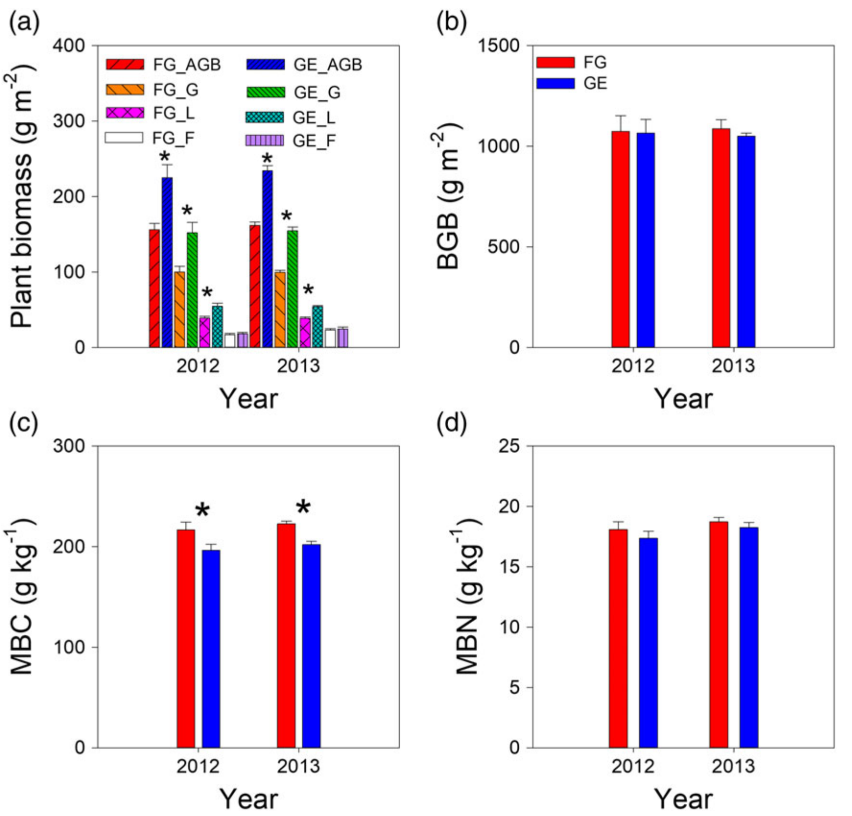

FIGURE 1 Annual variations of (a) total above-ground biomass (AGB) and plant functional type biomass (see key below), (b) belowground biomass (BGB), (c) microbial biomass carbon (MBC), and (d) microbial biomass nitrogen (MBN) for both free grazing (FG) and grazing exclusion (GE) blocks. Data presented in the figure are annual mean values calculated from the month means during the growing season ± standard errors (*n* = 6). Differences between FG and GE are evaluated at $p < .05$, and significant differences are denoted by asterisks. FG_AGB = total aboveground biomass for FG blocks; FG_G = graminoid biomass for FG blocks; FG_L = legume biomass for FG blocks; FG_F = forb biomass for FG blocks; GE_AGB = total aboveground biomass for GE blocks; GE_G = graminoid biomass for GE blocks; GE_L = legume biomass for GE blocks; GE_F = forb biomass for GE blocks [Colour figure can be viewed at wileyonlinelibrary.com]

Reductions in SR and HR that occurred after GE were significantly related to the GE-induced changes in MBC and MBC/MBN (Figure 5).

Stepwise multiple regression analysis showed that ER and its components were affected by both biotic and abiotic factors (Table 3). The GE-induced changes in ER were mainly related to AGB, soil temperature, and soil moisture (F = 6.700, R^2 = 0.264), whereas SR and HR were significantly related to AGB, MBC, and soil temperature (F = 11.310, R^2 = 0.377; F = 11.340, R^2 = 0.378). In addition, R_{agb} was closely associated with soil moisture and AGB

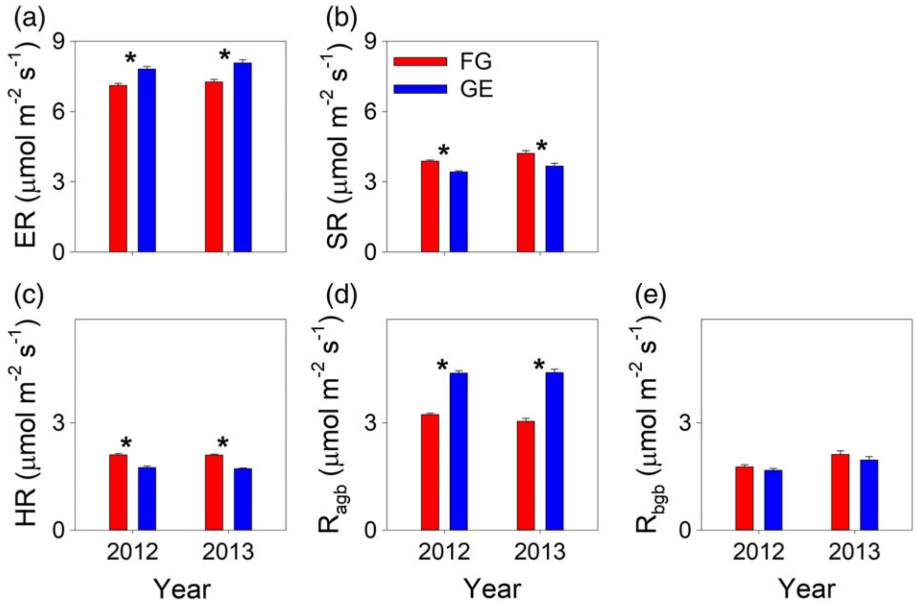

FIGURE 2 Mean values for (a) ecosystem respiration (ER), (b) soil respiration (SR), (c) heterotrophic respiration (HR), (d) aboveground plant respiration (R_{agb}), and (e) belowground root respiration (R_{bgb}) for free grazing (FG) and livestock grazing exclusion (GE) blocks in 2012 and 2013. Data presented in the figure are annual mean values ± standard errors (*n* = 6). Significant differences ($p < .05$) between FG and GE are denoted by asterisks [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Results from repeated measure ANOVA analysis (F values) of grazing exclusion (GE), measuring date (D), and their combined effects (GE:D) on ecosystem respiration (ER), soil respiration (SR), heterotrophic respiration (HR), aboveground plant respiration (R_{agb}) and belowground plant respiration (R_{bgb})

	df[a]	ER	SR	HR	R_{agb}	R_{bgb}
Year: 2012						
GE	1	24.496**	44.765**	36.461**	187.857**	1.809
D	11	484.080**	232.011**	127.476**	268.054**	56.210**
GE:D	11	1.494	1.783	1.734	6.282	0.282
Year: 2013						
GE	1	18.722**	11.188*	91.289**	88.970**	1.250
D	11	168.218**	73.369**	44.223**	128.790**	38.198**
GE:D	11	0.961	0.662	1.552	4.782	0.179

Note. Differences between treatments are evaluated at $p < .001$ (denoted by double asterisks, **) and $p < .05$ (denoted by single asterisk, *).

[a]*df* stands for degrees of freedom.

($F = 8.304$, $R^2 = 0.226$), and R_{bgb} was significantly related to soil moisture and BGB ($F = 3.407$, $R^2 = 0.131$).

4 | DISCUSSION

Two consecutive years of observations showed that GE had contrasting effects on various components of ER in a meadow grassland near Qinghai Lake, and those effects were driven by the differing responses of the system's respiratory subcomponents. Specifically, the GE-induced increase in ER can be explained by the fact that the positive responses of R_{agb} more than compensated for the GE-induced decreases in HR (Figures 2 and 3). The positive effects of animal exclusion on R_{agb} were closely associated with the GE-induced increases in AGB, particularly the large increases in graminoid biomass. Meanwhile, the negative responses of HR and SR to GE were mainly related to changes in soil MBC and MBC/MBN (Figures 4 and 5). Even though our results provide novel insights into the differing ways in which the various components of ER responded to GE, the underlying mechanisms that caused the changes in each component are still not fully understood and merit further study.

4.1 | Stimulation of ER by GE

The stimulation of ER by GE has been documented in previous studies conducted in a wide range of ecosystems (Chen, Luo, Xia, Wilcox, et al., 2016; Li et al., 2005; Sharkhuu et al., 2016; Zhao, Luo, et al., 2016). Even so, there are several exceptions showing that GE may have no effect or even negative impact on ER (Hou et al., 2016; Wei et al., 2016). A closer look at the previous studies showed that the responses of ER to GE were driven by differing responses of the components of ER to GE, and several potential mechanisms were

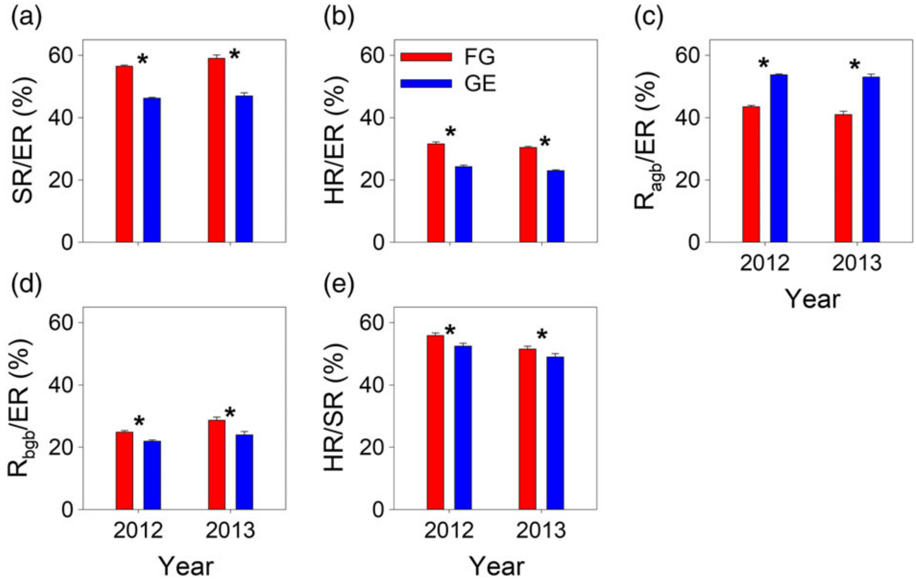

FIGURE 3 (a–e) Contributions of selected components to ecosystem respiration (ER) and soil respiration (SR) under free grazing (FG) and livestock grazing exclusion (GE) in 2012 and 2013. Data presented are annual mean values ± standard errors (n = 6). Significant differences (p < .05) between FG and GE are denoted by asterisks. See Figure 2 for explanation of abbreviations [Colour figure can be viewed at wileyonlinelibrary.com]

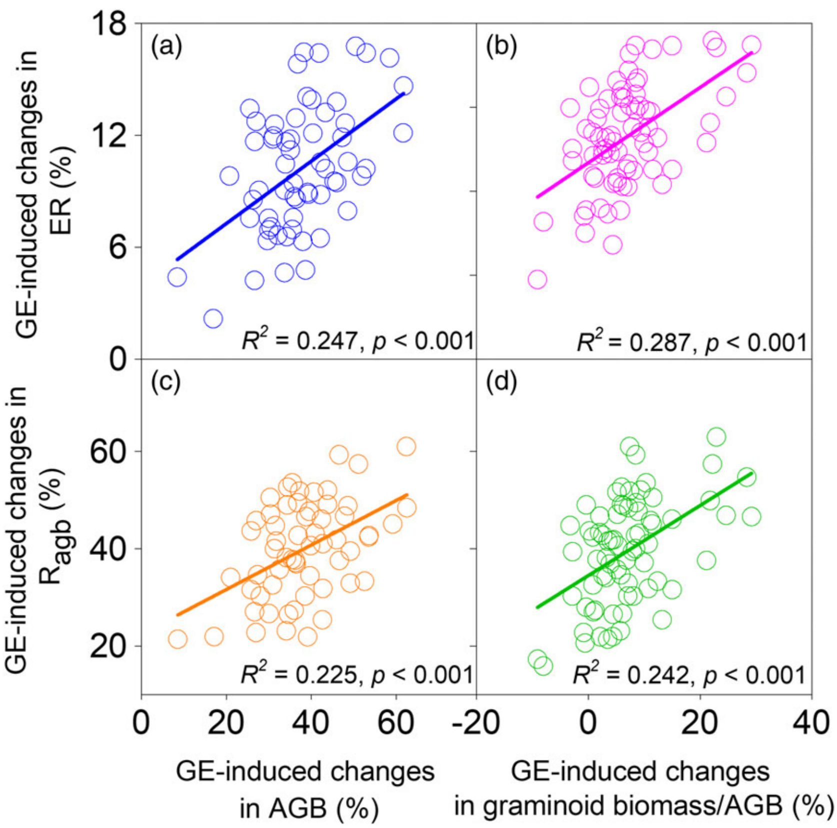

FIGURE 4 Linear regressions of the changes in ecosystem respiration (ER) caused by grazing exclusion (GE) versus GE-induced changes in (a) aboveground biomass respiration and (b) the proportion of graminoid biomass to aboveground biomass (AGB) and regressions of GE-induced changes in aboveground plant respiration (R_{agb}) versus GE-induced changes in (d) aboveground biomass respiration and (e) the proportion of graminoid biomass to AGB [Colour figure can be viewed at wileyonlinelibrary.com]

likely involved (Hou et al., 2016; Wei et al., 2016; Zhao, Li, et al., 2016). For example, Zhao, Li, et al. (2016) suggested that the GE-induced reduction of HR in a swamp meadow may have overridden the positive response of R_{agb} and that lowered the overall ER. Thus, it is critically important to determine how various components of ER respond to GE because that information is needed to understand—and eventually build models of—the underlying processes that control the production of CO_2 and cycling of C in grassland ecosystems.

The stimulation of ER following GE in our study is best explained by the effects of GE on R_{agb}. Apart from the increases in plant growth that resulted from the exclusion of livestock grazing, GE-induced changes in PFTs' biomass also may lead to higher R_{agb} (Figure 4). Indeed, it can be seen that these two variables are often related

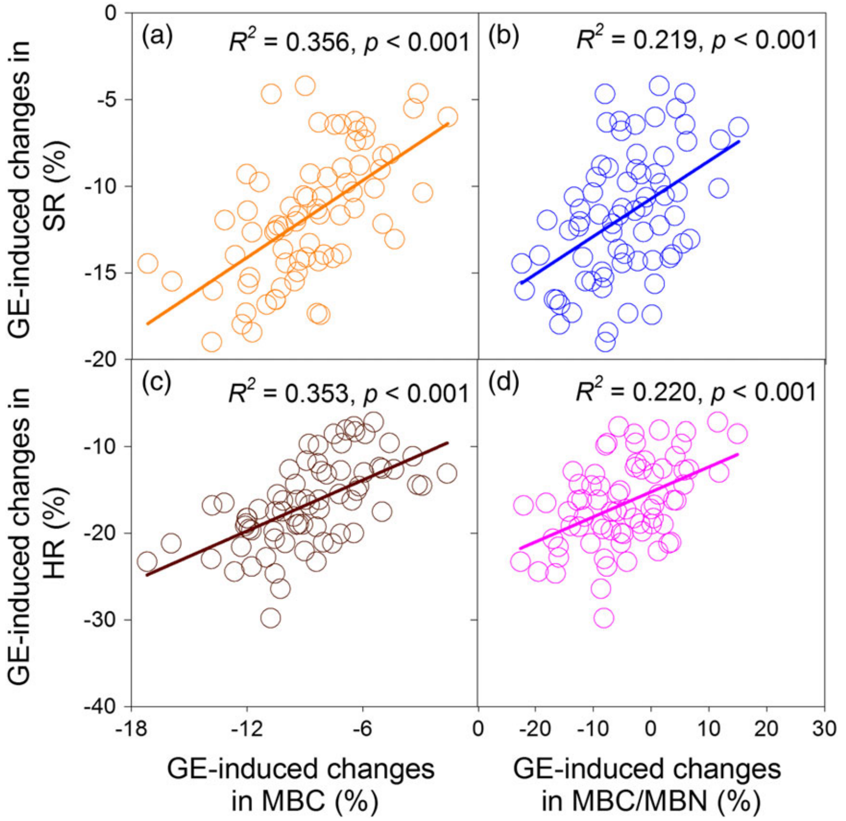

FIGURE 5 Linear regressions of grazing exclusion (GE)-induced variations in soil respiration (SR) versus GE-induced changes in (a) microbial biomass carbon (MBC) and (b) the ratio of MBC to microbial biomass nitrogen (MBC:MBN) and GE-induced variations heterotrophic respiration (HR) versus GE-induced variations in (c) MBC and (d) MBC: MBN [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Stepwise multiple regression analysis of the variations in ecosystem respiration (ER) and its components that caused by livestock grazing exclusion with the corresponding changes in soil temperature (ST), soil moisture (SM), aboveground biomass (AGB), belowground biomass (BGB), microbial biomass carbon (MBC) across the two growing seasons

	Variables[a]						
	ST	SM	AGB	BGB	MBC	R^2	*F*
ER	+	+	+			0.264	6.700**
SR	+		+		+	0.377	11.310**
HR	+		+		+	0.378	11.340**
R_{agb}		+	+			0.226	8.304**
R_{bgb}		+		+		0.131	3.407*

Note. + indicates selected variables by the models, differences between treatments are evaluated at p < .001 (denoted by double asterisks, **) and p < .05 (denoted by single asterisk, *).

[a]See Figures 1–3 for keys to abbreviations.

because changes in PFTs can be associated with the increased AGB (Figure S3) (Chen, Luo, Xia, Wilcox, et al., 2016; Májeková et al., 2016). Changes of this nature can increase plant growth respiration and plant maintenance respiration (Heskel et al., 2016; Luo, 2007; Pilkington et al., 2015), especially during the early stages of GE (Renou-Wilson, Muller, Moser, & Wilson, 2016). Another possible explanation is that changes in plant communities can affect soil substrate availability and soil microbial communities. Although both of these factors have been shown to affect respiration (Chen, Luo, Xia, Wilcox, et al., 2016; Xu et al., 2015), studies of their potential effects at our site were beyond the scope of the current project. Nonetheless, the results already obtained do provide evidence for potential links between GE-induced changes in PFTs' biomass and ER, and these findings highlight the potential importance of graminoids for CO_2 production in meadow grasslands and the need for future research into the underlying relationships between plant communities and respiration.

Monthly changes in ER and its components covaried with the temporal patterns of soil moisture and temperature (Figures S1 and S4). GE significantly reduced soil temperature but raised soil moisture, presumably due to the changes induced in canopy cover and surface albedo, and this is another potentially important reason for the observed changes in the components of ER (Paz-Ferreiro et al., 2012; Wei et al., 2016; Zhao, Luo, et al., 2016). The results are consistent with those from the stepwise multiple regression models, which showed that GE-induced changes in ER and its components were most closely connected with the changes in soil microclimate factors caused by fencing (Table 3). Given the strong impacts of soil microclimate parameters on ER and its components, future long-term studies should be designed to explore the combined impacts of climate change (e.g., climatic warming, drought, and perturbations of precipitation) and livestock grazing on ecosystem C fluxes.

4.2 | GE-induced reductions in SR

GE significantly decreased SR at our grassland site, and similar effects have been reported in studies of other ecosystems (Frank, Liebig, & Hanson, 2002; Hou et al., 2016; Zhou et al., 2017). Nonetheless, the underlying mechanisms for these effects are still under debate, and GE also was shown to have the opposite effect of increasing SR in other studies (Hou et al., 2016; Liu et al., 2016; Rong, Ma, Johnson, & Yuan, 2015; Wang, Ji, Hou, & Schellenberg, 2016). SR is the sum of HR and R_{bgb}, and these in turn are affected by a suite of underlying factors, including soil microclimate parameters and microbial activity (Chen, Luo, Xia, Shi, et al., 2016; Feng et al., 2017). Thus, the differential responses of the components of SR to GE observed in our study do provide some fresh insights into the impacts of GE on SR, but details of the interactions await further research.

The repression of SR under GE is best accounted by the negative response of HR because there was no effect of GE on R_{bgb} (Tables 1 and 2). Reductions in MBC, which reflects microbial abundance, activity, and respiration (Chen, Luo, et al., 2015; Ren et al., 2018; Zhao et al., 2017) may be an important means by which GE can cause negative responses in HR and SR. Indeed, MBC was positively correlated with HR and SR (Figure 5), and there are several reasons why GE may have led to reductions in MBC: These include the exclusion of nutrient inputs from the grazing animals (Wang, Wang, et al., 2016), the accumulation of old and hard decomposable surface litter (Ren, Zhao, et al., 2017; Stark, Mannisto, Ganzert, Tiirola, & Haggblom, 2015), the depletion of labile soil substrates (Creamer et al., 2016), and the reduction in soil temperature (Chen, Shi, & Cao, 2015). Another explanation is that the minor changes in MBC/MBN, an effective proxy of possible changes in microbial community composition and physiology, could contribute to the variations in SR and HR (Figure 5). Although we lack hard evidence showing that changes in microbial abundances, communities, or physiology play important roles in the response of SR to GE, our findings imply that the effects of microbial ecology should be included in follow up studies of the effects of GE on SR (Zhao et al., 2017).

GE had no effect on R_{bgb}, and this is consistent with the nonsignificant responses of BGB to GE (Figures 1 and 2). Some short-term GE studies have shown similar results (Koerner & Collins, 2014), but long-term GE would probably increase BGB because this has been shown in previous studies (Kauffman, Thorpe, & Brookshire, 2004; Koerner & Collins, 2014; Zhou et al., 2017). Moreover, R_{bgb} is more closely related to fine root production rather than total BGB (Bahn, Knapp, Garajova, Pfahringer, & Cernusca, 2006), and longer term GE treatments probably would have larger positive effects on the fine root production than short-term exclusions (Kauffman et al., 2004; Makita, Hirano, Sugimoto, Tanikawa, & Ishii, 2015). The present study was not designed to investigate the details of how R_{bgb} and BGB responded to GE, and a different experimental design involving long-term observations would be needed to address those questions.

4.3 | Contributions of each component to ER under GE

GE significantly altered the contributions of each component to ER; for example, GE profoundly increased R_{agb}/ER and HR/SR but decreased SR/ER and HR/ER (Figure 3). The proportions of each component to ER and SR were within the ranges of previous studies nearby (Chen, Luo, Xia, Shi, et al., 2016; Jiang et al., 2013). These results imply that the effects of GE on ER could be increasingly determined by the responses of R_{agb} to GE. Similarly, the responses of SR to GE would be driven by the GE-induced changes in HR (Gong et al., 2014; Wei et al., 2016). Both plant productivity and PFTs' biomass were affected by GE, and those changes evidently affected both R_{agb} and ER even though no significant correlations were found for HR and SR and changes in PFTs' biomass (Table 3). The fact that R_{agb}/ER was much larger than HR/ER supports the hypothesis that GE-induced changes in plant communities play more important roles in affecting ER than GE-induced changes in microbial activities.

4.4 | Implications

Our results provide novel insights into how GE affects ER and how the components differ in their responses to GE. It is noteworthy that the differential responses of ER components to GE are not well captured by current Earth system models (Carbone et al., 2016; Hashimoto et al., 2015), and therefore, important information on what controls C output is not included in these models (Bond-Lamberty et al., 2016). Moreover, the various components of ER are regulated by fundamentally different mechanisms; for example, positive responses of R_{agb} are driven by the GE-induced changes in the PFTs' biomass, whereas the negative responses of HR are caused by the reductions in MBC and changes in MBC/MBN (Figures 4 and 5). Model projections of ecosystem C fluxes would no doubt be improved if they could take into account the responses of the components of ER to GE, especially because the relative contributions of each component to ER evidently are altered by GE.

5 | CONCLUSIONS

The Tibetan Plateau has been perturbed by human activities, and the effects of livestock grazing on this fragile ecosystem are highly complicated and just beginning to be understood. Our results show dissimilar responses of the major components of ER to GE, providing fresh insights into the impacts of GE on ER. GE significantly increased R_{abg} and ER, mainly due to GE-induced shifts in PFTs' biomass and increases in AGB, but GE decreased SR and HR due to reductions in MBC and changes in the MBC/MBN in soils. These results imply that the various processes that are affected by GE and drive the respiratory ecology are likely regulated by different mechanisms. Therefore, models of land use change and ecosystem C cycles could be improved by taking into account these divergent responses of the endogenous components of ER.

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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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