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Contrasting responses after fires of the source components of soil respiration and ecosystem respiration

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Wildfire is an important ecological disturbance that can have cascading effects on ecosystem carbon (C) fluxes. Ecosystem respiration (ER) and soil respiration (SR) account for two of the largest terrestrial C fluxes to the atmosphere, and they play critical roles in regulating C–climate feedbacks. Here, the responses of ER, SR and their source components to experimental burning in a meadow grassland on the Tibetan Plateau were investigated. Fire treatment increased ER by 9% but decreased SR by 15%. The contrasting post-fire responses of SR and ER can be explained by the behaviour of their source components; that is, fire increased aboveground plant respiration (R_{agb}) by 37%, but decreased heterotrophic respiration (HR) by 21%. Increases in ER and R_{agb} were mainly related to enhanced plant productivity, whereas smaller SR and HR were associated with reductions in microbial biomass and soil moisture. Accounting for the responses of ER, SR and their intrinsic components has advanced our understanding of how fire affects ecosystem C fluxes.

Highlights

- Fire treatment increased ecosystem respiration (ER) and aboveground plant respiration.
- Fire treatment decreased soil respiration (SR) and heterotrophic respiration (HR).
- Increases in ER and aboveground plant respiration were related to plant productivity.
- Reductions in SR and HR were caused by the suppressed microbial activity.

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1 | INTRODUCTION

Wildfire is one of the most important disturbances to ecosystems, and fires commonly occur after long-term drought and are exacerbated by high temperatures, especially in arid regions (Covington, 2000). The annual global burned area is estimated to be ~350 Mha (Giglio, Randerson & Werf, 2013), and the annual pyrogenic CO_2 emissions amount to approximately half of those from fossil fuel combustion (van der Werf et al., 2006). There is increasing evidence from field observations (Dore et al., 2010), meta-analyses (Holden & Treseder, 2013) and modelling (Kelly, Genet, McGuire, & Hu, 2016) that fire plays pivotal roles in affecting ecosystem C fluxes.

Ecosystem respiration (ER) and soil respiration (SR) are two of the largest C fluxes from terrestrial systems to the atmosphere (Luo & Zhou, 2006), but there is considerable debate about their post-fire responses. For example, SR was significantly larger in post-fire blocks than in control blocks in a study of an annual grassland in central coastal California (Strong, Johnson, Chiariello & Field, 2017), but SR was suppressed for the first 5 years after fire in the Amazon rainforest (Metcalfe et al., 2018). Even fewer studies have investigated the responses of ER post-fire, and these results are also highly contradictory. The current understanding of ER is largely based on estimates made from eddy covariance or SR measurements (Migliavacca et al., 2011). However, several recent studies suggest that the response of SR to fire is not necessarily a good predictor of the ER response (Chen et al., 2016). This is because the contribution of SR to ER can vary from 30 to 80% for ecological disturbances to different types of ecosystems (Luo & Zhou, 2006). This leads to the likelihood that a single observation of SR may be insufficient for evaluating the overall responses of ER post-fire. Therefore, a comprehensive and simultaneous evaluation of ER and SR in the same ecosystem is a better way to investigate post-fire ecosystem C fluxes.

The underlying mechanisms that control the post-fire responses of ER and SR are unclear. Ecosystem respiration and SR can be broadly divided into the source components of heterotrophic (HR) and autotrophic respiration (Luo & Zhou, 2006), but these components are regulated by an array of various biotic and abiotic factors (Czimczik, Trumbore, Carbone & Winston, 2006). For example, HR is a measure of the microbially mediated decomposition of litter and soil organic matter, which is closely related to soil microbial activity (Chen et al., 2017; Chen et al., 2018; Czimczik et al., 2006; Zhao et al., 2017). Autotrophic respiration, in contrast, is a measure of the metabolic activity of plants, which is mainly regulated by plant productivity (Chen et al., 2016), and is due to aboveground plant respiration and belowground plant respiration. Therefore, it is clear that better knowledge of the source components of SR and ER will advance the understanding of the overall responses of SR and ER post-fire.

The responses of plant functional type (PFT) biomass and microbial biomass after fire have been well studied (Wang et al., 2015), but their connections to ER, SR and their source components (HR, R_{agb} and R_{bgb}) remain to be explored. Plant functional types are groups of plants, such as graminoids, legumes and forbs, that share the same or similar adaptive traits for a specific function (Lipoma, Gurvich, Urcelay, & Díaz, 2016). Therefore, PFTs are important non-phylogenetic groups of species in terms of ecosystem function because they regulate biomass production and, thus, plant autotrophic respiration (Reichstein, Bahn, Mahecha, Kattge, & Baldocchi, 2014). For example, fire increased the dominance of tall, deep-rooted rhizomatous grasses in the Konza Prairie Biological Station, USA (Kirkman et al., 2014), which was expected to have critical effects on biomass production and vegetation C exchange (Smith et al., 2016).

Microbial biomass and activity are closely related to decomposition, which in turn is expected to have considerable effects on HR (Dooley & Treseder, 2012). This contention was supported by a recent meta-analysis, which showed that fire-induced changes in microbial biomass C were positively correlated with SR (Holden & Treseder, 2013). Thus, a better understanding of plant and microbial regulation of ER, SR and their source components will help us clarify the net responses of ER and SR post-fire.

The Tibetan Plateau is regarded as one of the most ecologically sensitive regions in the world, mainly because of its high elevation (>3,000 m), low temperature (Guo et al., 2018; Hu et al., 2015; Yang et al., 2018; Zhang et al., 2014) and large C stocks. Moreover, the Tibetan Plateau has also experienced an increasingly warmer and drier climate in the past three to five decades, which makes the region highly susceptible to wildfire. Here, we conducted a field study with prescribed burning on the Tibetan Plateau. Our objectives were to (a) investigate how ER, SR and their source components respond to fire treatments, and (b) determine which response mechanisms affect the various source components of ER and SR post-fire.

2 | MATERIALS AND METHODS

2.1 | Study site

The study site was located at the Haibei Grassland Ecological Monitoring Station (100°51′E, 36°57'N, 3,140 m), Haibei, Qinghai Province, China. Records from 1995 to 2013 show an annual mean temperature of 1.3 °C and an annual mean precipitation of 409 mm. Soils are classified as Cambisols in the UN Food and Agriculture Organization (Chen, Zhou, et al. 2017), and they have a pH of 7.8 and a bulk density of 1.0 g cm^{-3}. Detailed plant

community composition before and after fire is presented in Table S1. Other information associated with the study site may be found in Chen, Zhou, et al. (2017), Chen, Lou, et al. (2018) and Guo et al. (2018).

2.2 | Experimental design

The study was conducted at a winter grazing grassland that had a grazing intensity of approximately 0.5 yak and 2.5 sheep per hectare. The whole of the large site was fenced in 2008, 3 years before the fire treatment, to minimize heterogeneity to the extent possible. Twelve blocks (60 m × 30 m for each) were randomly selected in March 2011 and buffer zones at least 15-m wide were established between any two adjacent blocks. Six of the blocks were selected randomly and burned in April 2011. The fires were rapid, low-to-moderate in intensity and typical of wildfire on the Tibetan Plateau. All aboveground plants were removed by the fires. All measurements and samples in this study were repeatedly conducted across the following three growing seasons.

2.2.1 | Measurements of CO_2 fluxes

Circular aluminum frames were inserted into the centre of each block to provide a relatively flat base for the measurements of net ecosystem exchange and ecosystem respiration (ER). A transparent chamber was then attached to an LI-8100 gas analyser (LI-COR, Inc., Lincoln, NE, USA) to measure net ecosystem exchange. After those measurements were made, the chamber was covered with an opaque cloth to record ER (Figure S1). Two small fans were used to mix the air inside the chamber. Chamber-induced temperature increases were less than 0.2 °C, and thus too small to affect ER (Chen, Luo, et al., 2017).

Two types of collars (70 cm in height for heterotrophic respiration (HR) measurements and 5 cm in height for soil respiration (SR) measurements) were inserted into the soil close to the aluminum frames. The 70-cm collars cut all living roots and prevented new roots from growing, and thus the CO_2 released was considered representative of HR. To avoid overestimation of HR, the 70-cm collars were installed in April 2011, about 2 months before the first measurements of HR were made. Plants inside all collars were cut 1 or 2 days before the measurements. A chamber was attached to another LI-8100 analyser to measure SR and HR.

The measurements for CO_2 exchange lasted about 130–150 s, including an equilibration period of 10–30 s, which was required to reach a steady state. All CO_2 measurements were measured repeatedly using the same chamber in the same plot across the three growing seasons. Gross primary productivity was calculated as the sum of net ecosystem exchange and ER. Aboveground plant respiration

was calculated as the difference between ER and SR. Belowground plant respiration was the difference between SR and HR.

2.2.2 | Soil sampling

Fresh surface litter was removed before sampling. Soil samples were collected at a depth of 0–10 cm in August of each year from the control and burned blocks, with six replicates for each treatment. Within each block, three cores were collected and combined to make a composite sample. After sampling, large stones and all visible plant materials were removed, and then the samples were stored in a portable cooler and transported to the laboratory (at 4.0 °C) for subsequent analysis (usually within 2 weeks).

2.2.3 | Microbial biomass carbon and nitrogen

A chloroform fumigation method was used to measure microbial biomass C and nitrogen (N) (Chen et al., 2016). The concentrations of microbial biomass C and N were determined by taking the differences between C and N contents for soils before and after chloroform fumigation. Carbon and N contents were analysed with a TOC analyzer (Multi N/C 3100, Analytik, Jena, Germany). The concentrations were converted to a dry weight basis (mg kg^{-1} dry soil).

2.3 | Plant biomass

Plant biomass within the aluminum frames was estimated by a non-destructive method (Chen, Luo, et al., 2017; Klein, Harte, & Zhao, 2007); those measurements were made in August of each year. In brief, the plant biomass was estimated by documenting the cover and height for each plant functional type (Chen, Zhou, et al., 2017). Total aboveground biomass was calculated as the sum of biomass from all plant functional types. Belowground biomass samples were collected at a depth of 0–40 cm near the aluminum frames with a soil auger. Roots were washed manually to exclude soil and then dried at 65 °C for three days before weighing.

2.4 | Soil temperature and moisture

Soil temperature and soil moisture were measured at a depth of 10 cm and the data were stored on HOBO data loggers (HOBO U30, Onset Computer Corporation, Bourne, MA, USA). A thermocouple probe was used to measure soil temperature (12-Bit Temp Smart Sensor, Onset Computer Corporation). Soil moisture was measured with a concentric stainless-steel electrode (EC-5 Soil Moisture Smart Sensor,

Wareham, MA, USA). There was one paired soil temperature and soil moisture probe for each block.

2.5 | Data analysis

All original data were tested for normality using the Kolmogorov–Smirnov method. No variables required transformation in this study. Growing season averages for ER, SR and their source components were calculated from the monthly average values. All variables were measured repeatedly across the three growing seasons; therefore, a two-way repeated-measures analysis of variance (ANOVA) was used to assess the effects of fire treatment, year and their interactive effects on each variable. The criterion for statistical significance was set at a probability for chance occurrence of $p < 0.05$ (Webster, 2007). The null hypotheses were: (a) there were no differences between burned and unburned blocks and (b) there were no interactive effects of burning and year. If there were interactive effects of fire treatment and year, the differences in means for each year were tested by Fisher's least significant difference (LSD), which was determined using the within-plot residual mean square error of the repeated ANOVA. Residuals were examined for normality and the residual variances were examined for homogeneity for all variables. Pearson's correlation analysis was carried out to identify the relations between biotic and abiotic factors and ER, SR and their source components. Data analyses were carried out and figures were prepared with the R software program (aov function, cor.test function, LSD.test function in agricolae package, ggplot2 package, https://www.r-project.org/). All original data in this study are available from the open dataset (https://figshare.com/s/90ffe4666e35f86f1b10).

3 | RESULTS

3.1 | Biotic and abiotic factors after fire

Over the three growing seasons, fire treatment significantly increased soil temperature by 0.8 °C (Figure 1). Fire treatment decreased soil moisture by an average of 4, 3 and 3% for 2011, 2012 and 2013, respectively. In terms of microbial biomass, fire treatment significantly decreased microbial biomass C by 7%, but had no significant effect on microbial biomass nitrogen. Interactions between the effect of treatment with fire and year were observed for aboveground biomass, graminoid biomass and legume biomass (Table 1). In detail, fire treatment significantly increased aboveground biomass by 12, 22 and 19%, graminoid biomass by 11, 19 and 16%, and legume biomass by 20, 31 and 30% for 2011, 2012 and 2013, respectively, whereas fire treatment had no effect on forb biomass
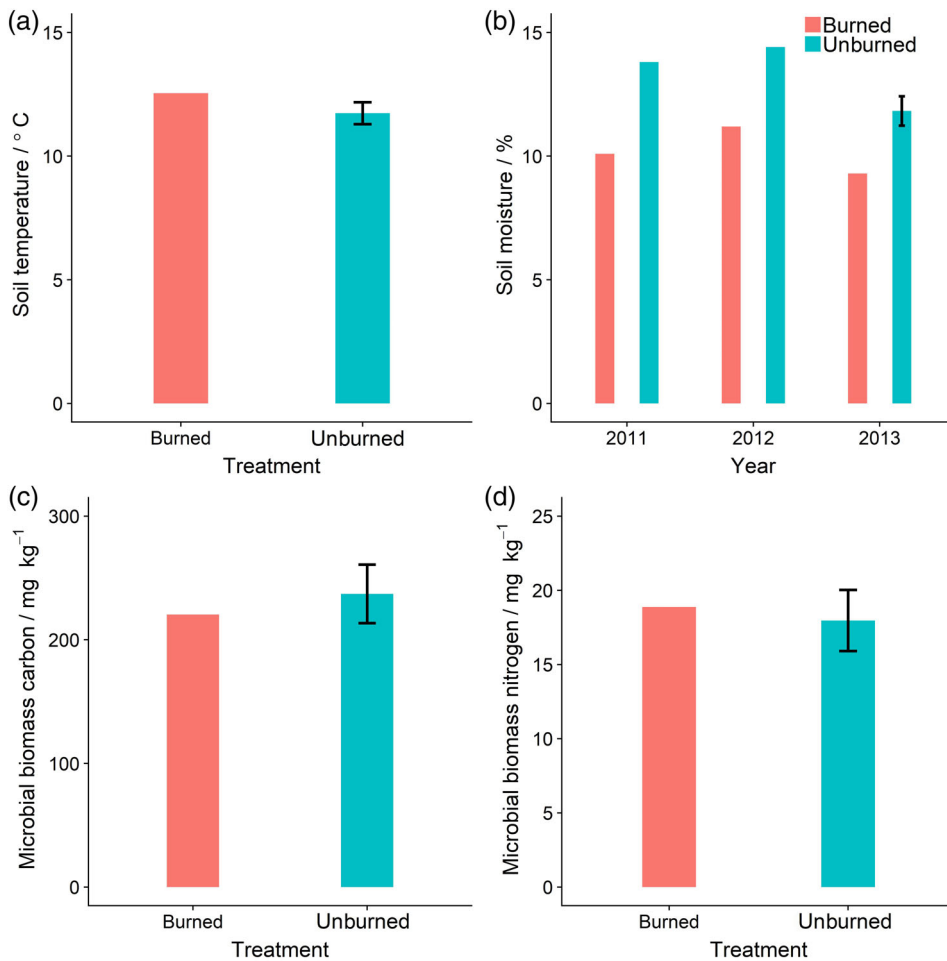
FIGURE 1 Arithmetic grand mean values of (a) soil temperature, (b) soil moisture, (c) microbial biomass carbon and (d) microbial biomass nitrogen in burned and unburned blocks. The error bars show standard errors determined from the residual mean square

(Figure 2 and Table S2). In addition, fire treatment also significantly increased belowground biomass by 41%.

3.2 | Responses of respiration to fire treatment

No interaction between the effect of fire and year was observed for ecosystem respiration (ER), soil respiration (SR) and belowground plant respiration (R_{bgb}) (Table 2). Across the three growing seasons, fire treatment increased ER by 9% on average, but decreased SR by 15% (Figure 3). Fire had no effect on R_{bgb}. Interaction between the effects of fire and year were observed for aboveground plant respiration (R_{agb}) and HR. Fire increased R_{agb} by 31, 47 and 33% in 2011, 2012 and 2013, respectively. Fire decreased HR by 26, 19 and 18% in 2011, 2012 and 2013, respectively.

On average, treatment with fire decreased the ratio of SR and R_{bgb} to ER (SR:ER and R_{bgb}:ER) and HR:SR by 24, 16 and 6%, but it increased the ratio of R_{agb}:ER and R_{bgb}:SR by 30 and 10%, respectively. Interactions between the effects of fire and year were observed for HR:ER. Treatment with fire decreased HR:ER by 32, 29 and 26% in 2011, 2012 and 2013, respectively (Figure 4).

3.2.1 | Factors affecting the responses of ecosystem respiration and soil respiration

Seasonal variations in ER, SR, HR, R_{agb} and R_{bgb} were all closely correlated with the seasonal patterns of soil temperature and soil moisture (Figures S2–S5). However, the observed changes in soil temperature and soil moisture could not fully account for the contrasting post-fire responses of ER and SR. The only observed relations were between fire treatment-induced changes in soil moisture and ER and HR (Figure S6). Pearson correlation analysis showed that changes in ER and R_{agb} were positively correlated with increases in plant functional type biomass and gross primary productivity (Figure 5). In contrast, reductions in SR and HR were closely coupled with the fire-induced changes in microbial biomass C and the ratio of microbial biomass C to N (Figure 6).

4 | DISCUSSION

4.1 | Contrasting responses of soil respiration and ecosystem respiration post-fire

The suppression of soil respiration (SR) post-fire is best explained by the negative responses in heterotrophic

TABLE 1 Two-way repeated-measures analyses of variance (ANOVA) for year, burn and their interactive effects on soil temperature and moisture, plant productivity and microbial biomass

Variables	Source	df	Sum of squares	Mean square	F	p
Ecosystem respiration	Burn	1	3.7	3.7	5.3	0.044
	Residual (main plots)	10	7.0	0.7		
	Year	2	10.4	5.2	63.9	< 0.001
	Year•burn	2	0.3	0.1	1.7	0.205
	Residual (repeated measures)	20	1.6	0.1		
Soil respiration	Burn	1	3.4	3.4	13.8	0.004
	Residual (main plots)	10	2.4	0.2		
	Year	2	2.7	1.37	35.0	< 0.001
	Year•burn	2	0.1	0.05	1.2	0.315
	Residual (repeated measures)	20	0.8	0.04		
Heterotrophic respiration	Burn	1	2.0	2.0	37.1	< 0.001
	Residual (main plots)	10	0.5	0.1		
	Year	2	0.7	0.34	36.9	< 0.001
	Year•burn	2	0.1	0.03	3.7	0.044
	Residual (repeated measures)	20	0.2	0.009		
Aboveground plant respiration	Burn	1	14.1	14.1	88.5	< 0.001
	Residual (main plots)	10	1.6	0.2		
	Year	2	3.8	1.9	45.2	< 0.001
	Year•burn	2	0.6	0.3	7.4	0.004
	Residual (repeated measures)	20	0.8	0.04		
Belowground root respiration	Burn	1	0.2	0.2	2.1	0.180
	Residual (main plots)	10	0.8	0.1		
	Year	2	0.8	0.4	7.7	0.003
	Year•burn	2	0.2	0.1	1.5	0.244
	Residual (repeated measures)	20	1.1	0.1		
Soil respiration/ecosystem respiration	Burn	1	0.15	0.15	250.6	< 0.001
	Residual (main plots)	10	0.006	0.0006		
	Year	2	0.02	0.01	18.6	< 0.001
	Year•burn	2	0.003	0.001	2.9	0.081
	Residual (repeated measures)	20	0.01	0.0005		
Heterotrophic respiration/ecosystem respiration	Burn	1	0.08	0.08	912.4	< 0.001
	Residual (main plots)	10	0.0008	0.00008		
	Year	2	0.011	0.006	19.6	< 0.001
	Year•burn	2	0.002	0.001	3.7	0.043
	Residual (repeated measures)	20	0.006	0.0003		
Aboveground plant respiration/ecosystem respiration	Burn	1	0.15	0.15	250.6	< 0.001
	Residual (main plots)	10	0.01	0.0006		
	Year	2	0.03	0.01	31.6	< 0.001
	Year•burn	2	0.003	0.001	2.9	0.081
	Residual (repeated measures)	20	0.01	0.0005		

TABLE 1 (Continued)

Variables	Source	df	Sum of squares	Mean square	F	p
Belowground plant respiration/ecosystem respiration	Burn	1	0.01	0.01	27.4	< 0.001
	Residual (main plots)	10	0.005	0.0005		
	Year	2	0.003	0.001	1.6	0.232
	Year•burn	2	0.004	0.002	2.6	0.103
	Residual (repeated measures)	20	0.02	0.0009		
Heterotrophic respiration/soil respiration	Burn	1	0.01	0.01	15.1	0.003
	Residual (main plots)	10	0.01	0.0007		
	Year	2	0.01	0.003	1.5	0.249
	Year•burn	2	0.01	0.01	3.3	0.059
	Residual (repeated measures)	20	0.04	0.002		
Belowground plant respiration/soil respiration	Burn	1	0.02	0.02	22.0	0.001
	Residual (main plots)	10	0.01	0.0007		
	Year	2	0.01	0.01	2.5	0.111
	Year•burn	2	0.01	0.005	2.4	0.12
	Residual (repeated measures)	20	0.04	0.002		

Note. df: degrees of freedom; *F*: *F* value of the two-way repeated measures ANOVA analysis. Significant difference is evaluated at $p < 0.05$. For very small values, more digits are retained.
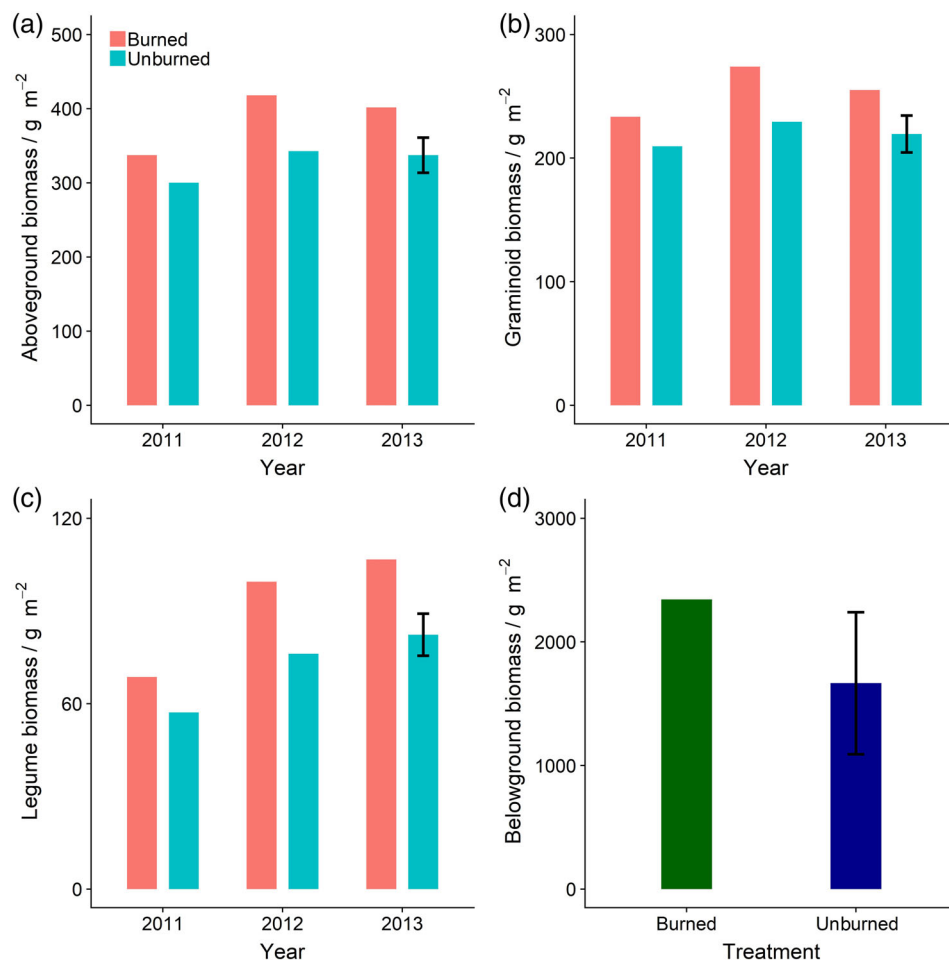
FIGURE 2 Grand mean values of (a) aboveground biomass, (b) graminoid biomass, (c) legume biomass and (d) belowground biomass in burned and unburned blocks. The error bars show standard errors determined from the residual mean square

TABLE 2 Two-way repeated-measures analyses of variance (ANOVA) of year, burn and their interactive effects on respiration and its components

Variable	Source	df	Sum of squares	Mean square	F	p
Soil temperature	Burn	1	5.9	5.9	76.5	< 0.001
	Residual (main plots)	10	0.8	0.1		
	Year	2	14.6	7.3	124.1	< 0.001
	Year•burn	2	0.2	0.1	1.8	0.189
	Residual (repeated measures)	20	1.2	0.1		
Soil moisture	Burn	1	89.5	89.5	92.1	< 0.001
	Residual (main plots)	10	9.7	1.0		
	Year	2	30.7	15.4	145.5	< 0.001
	Year•burn	2	2.1	1.1	10.0	0.001
	Residual (repeated measures)	20	2.1	0.1		
Aboveground biomass	Burn	1	31,182.0	31,182.0	37.7	< 0.001
	Residual (main plots)	10	8,271.0	827.0		
	Year	2	25,934.0	12,967.0	77.0	< 0.001
	Year•burn	2	2,298.0	1,149.0	6.8	0.006
	Residual (repeated measures)	20	3,368.0	168.0		
Graminoid biomass	Burn	1	10,809.0	10,809.0	52.6	< 0.001
	Residual (main plots)	10	2054.0	205.0		
	Year	2	5,491.0	2,745.7	40.9	< 0.001
	Year•burn	2	649.0	324.5	4.8	0.019
	Residual (repeated measures)	20	1,342.0	67.1		
Legume biomass	Burn	1	3,504.0	3,504.0	90.7	< 0.001
	Residual (main plots)	10	386.0	39.0		
	Year	2	6,657.0	3,328.0	239.7	< 0.001
	Year•burn	2	307.0	153.0	11.1	0.001
	Residual (repeated measures)	20	278.0	14.0		
Forb biomass	Burn	1	180.0	180.0	1.4	0.264
	Residual (main plots)	10	1,286.0	128.6		
	Year	2	247.8	123.9	3.3	0.057
	Year•burn	2	43.5	21.7	0.6	0.567
	Residual (repeated measures)	20	744.9	37.2		
Belowground biomass	Burn	1	4,127,177.0	4,127,177.0	60.3	< 0.001
	Residual (main plots)	10	684,352.0	68,435.0		
	Year	2	619,686.0	309,843.0	3.1	0.066
	Year•burn	2	141,394.0	70,697.0	0.7	0.502
	Residual (repeated measures)	20	1,979,192.0	98,960.0		
Microbial biomass carbon	Burn	1	2,536.0	2,535.9	8.2	0.017
	Residual (main plots)	10	3,093.0	309.3		
	Year	2	1913.0	956.3	5.7	0.011
	Year•burn	2	120.0	60.1	0.4	0.703
	Residual (repeated measures)	20	3,349.0	167.5		

TABLE 2   (Continued)

Variable	Source	df	Sum of squares	Mean square	F	p
Microbial biomass nitrogen	Burn	1	7.4	7.4	1.6	0.239
	Residual (main plots)	10	47.5	4.8		
	Year	2	12.5	6.3	4.9	0.018
	Year•burn	2	0.5	0.2	0.2	0.826
	Residual (repeated measures)	20	25.4	1.3		

Note. df: degrees of freedom; *F*: *F* value of the two-way repeated measures ANOVA analysis. Significant difference is evaluated at $p < 0.05$. For very small values, more digits are retained.

respiration (HR) because fire treatment had no significant effect on belowground plant respiration (R_{bgb}). We propose three possible mechanisms for the response of HR. First, reductions in SR and HR could be related to the suppression of decomposition because changes in those variables were accompanied by smaller microbial biomass C post-fire (Chen et al., 2015; Holden & Treseder, 2013). Changes in the ratio of microbial biomass C to N (MBC:MBN) were also correlated with the decreases in SR and HR following fire treatment, suggesting possible links between specific microbial communities and respiration (Dooley & Treseder, 2012; Wang et al., 2015). Second, reductions in soil moisture would be expected to suppress both HR and R_{bgb} (Holden, Berhe, & Treseder, 2015; Ren et al., 2018), particularly in a semiarid area such as the Tibetan Plateau. Indeed, there might have been more reductions in soil

moisture in early post-fire periods, because of the pronounced reduction in canopy cover and increase in evapotranspiration. Third, the depletion in labile substrates and the accumulation of charcoal after fire would suppress HR and R_{bgb} (Certini, 2005; Czimczik et al., 2006). One might expect that the relatively higher soil temperatures in burned blocks than in unburned ones would increase HR (Feng et al., 2017), but those positive effects were probably offset by reductions in soil moisture content or by the depletion of labile soil substrates.

An unexpected result of the study was that the fire treatments increased ecosystem respiration (ER). Together with the negative responses of SR following the fires, our results suggest that increases in ER post-fire were mainly the result of strong positive responses of aboveground plant respiration (R_{agb}) that were related to the accumulation of
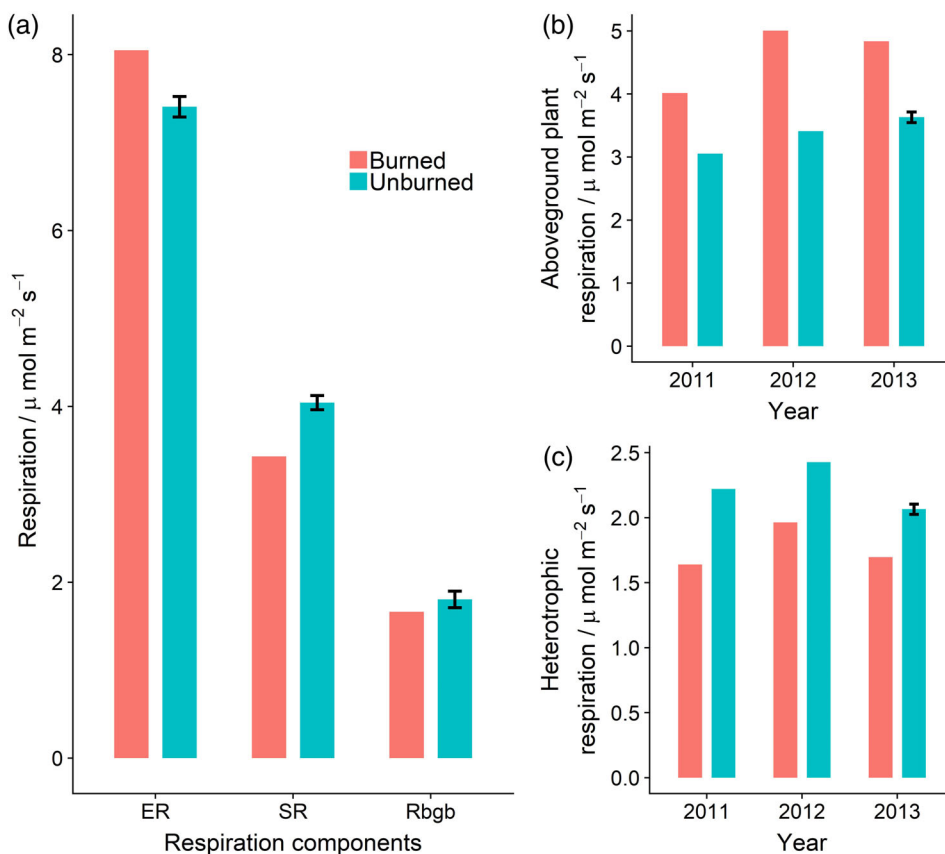
FIGURE 3   (a) Grand mean values of ecosystem respiration (ER), soil respiration (SR) and belowground plant respiration (R_{bgb}) in burned and unburned blocks. Annual mean values of (b) aboveground plant respiration and (c) heterotrophic respiration in burned and unburned blocks for 2011, 2012 and 2013, respectively. The error bars show standard errors determined from the residual mean square

FIGURE 4 (a) Grand mean proportions of respiration components to ecosystem respiration (ER) and soil respiration (SR) in burned and unburned blocks. (b) Annual mean proportions of heterotrophic respiration to ecosystem in burned and unburned blocks for 2011, 2012 and 2013, respectively. R_{agb}, aboveground plant respiration; R_{bgb}, belowground plant respiration. The error bars show standard errors determined from the residual mean square
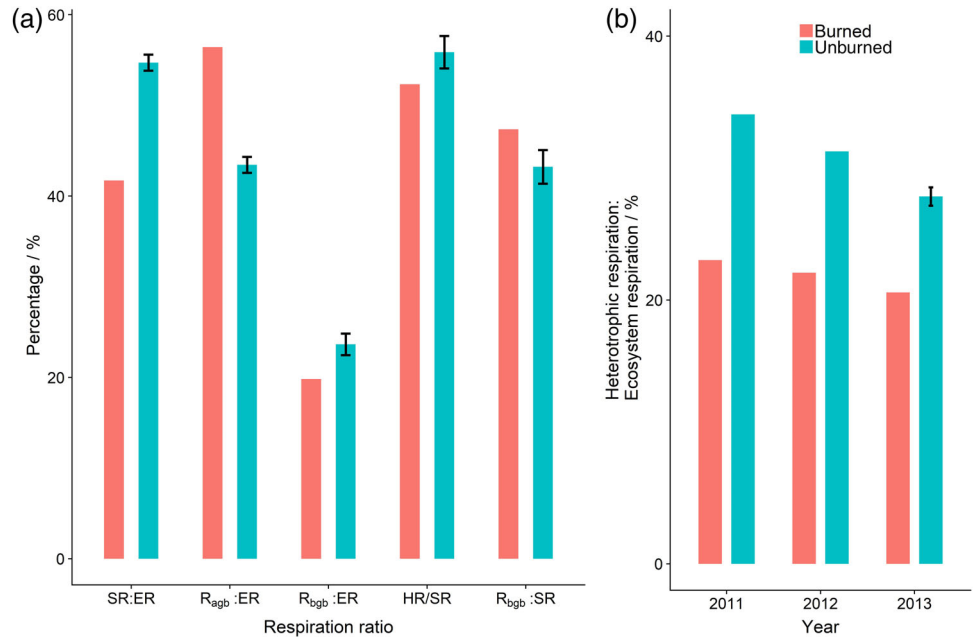
plant biomass and progressive changes in plant functional type (PFT) biomass. Changes in R_{agb} can be affected by plant growth and maintenance respiration (Luo & Zhou, 2006). Because of the initial large plant productivity following fire treatment, plant growth respiration was probably large (Nie, Bell, Wallenstein, & Pendall, 2015). This contention is supported by the positive correlation between gross plant productivity and R_{agb}. Meanwhile, reductions in soil moisture after fire treatment would also increase plant maintenance respiration (Rowland et al., 2015). Regardless of which process played the more important role, changes in plant productivity would have critical effects on both plant growth and maintenance respiration (Sitch et al., 2003). Future investigations of how

FIGURE 5 Relations between changes in plant functional type (PFT) biomass and corresponding changes in (a) ecosystem respiration (ER) and (b) aboveground plant respiration (R_{agb}). Relations between changes in gross primary productivity (GPP) and (c) corresponding changes in ER and (d) R_{agb}. Significant positive correlations were found between changes in ER and changes in aboveground biomass (AGB, $r = 0.618$, $p = 0.006$, $n = 18$), graminoid biomass ($r = 0.551$, $p = 0.018$, $n = 18$), legume biomass ($r = 0.792$, $p < 0.001$, $n = 18$) and GPP ($r = 0.824$, $p < 0.001$, $n = 18$). Significant positive correlations were found between changes in R_{agb} and changes in legume biomass ($r = 0.547$, $p = 0.019$, $n = 18$) and GPP ($r = 0.580$, $p = 0.012$, $n = 18$)
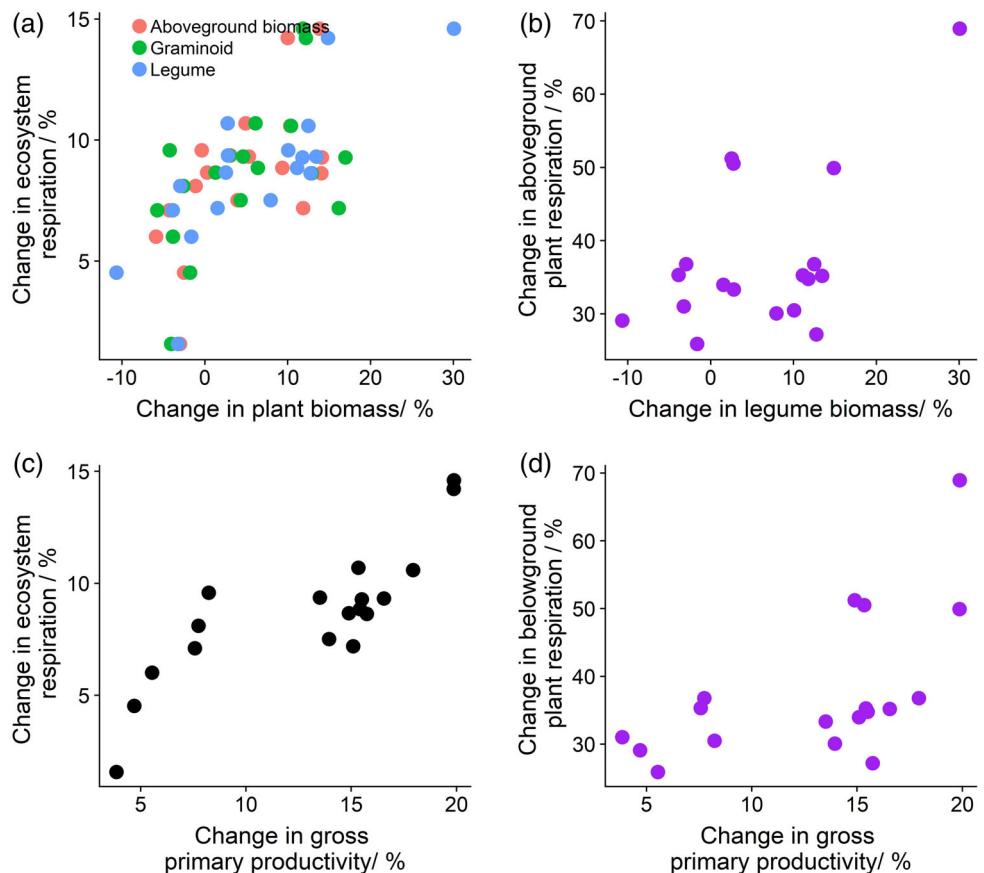
the compositions of plant communities change during ecosystem recovery and how PFTs affect plant productivity (Chen, Luo, et al., 2017) will lead to a better understanding of the post-fire responses of ER.

Fire treatments significantly increased the proportion of R_{agb} to ER (R_{agb}:ER) and decreased HR:ER. Aboveground plant respiration was an indicator of plant growth and biomass accumulation, whereas HR was a reflection of microbial activity (Luo & Zhou, 2006). Because of the larger value of R_{agb}:ER (56%) compared with HR:ER (22%), our results demonstrate that shifts in PFT biomass could have a greater effect than repressed microbial activity in regulating the overall responses of ER post-fire. Meanwhile, fire treatments generally decreased HR:SR and increased R_{bgb}:SR. Together with the suppressed SR after the fire treatments, our results indicate that microbial communities play critical roles in controlling the overall responses of SR post-fire.

4.2 | Ecosystem recovery

Our results highlight the critical roles of plant and microbial communities in determining the contrasting responses of ER and SR following fire treatment. Nevertheless, it has been reported that relatively rapid shifts in both plant and microbial community composition can occur in the early stages of post-fire ecosystem recovery (Pereira et al., 2016).

Therefore, it is plausible, if not likely, that long-term responses of ER, SR and their source components would differ from the patterns observed in this study. For example, SR was reduced significantly within the initial 2 years post-fire, but recovered to unburned levels 7 years after fire (Burke, Zepp, Tarr, Miller, & Stocks, 1997). Therefore, the stage of ecosystem recovery needs to be taken into consideration as we attempt to understand the full dynamics of ecosystem C fluxes post-fire.

4.3 | Environmental variability

There were significant year effects on ER, R_{agb}, R_{agb}:ER and HR:ER, suggesting that interannual environmental variation can affect ER and SR responses to fire (Table S2). Indeed, many environmental variables can potentially affect ER and SR, including precipitation and temperature (Thomey et al., 2011), evapotranspiration (Dore et al., 2010), photosynthesis (Cavaleri et al., 2017) and solar radiation (Fyllas et al., 2017). Clearly, more knowledge of the environmental regulation of ER and SR post-fire would advance our understanding of the underlying mechanisms that control C cycling after fire. Investigating which environmental factors controlled ER and SR post-fire was beyond the scope of this study, however, and long-term field
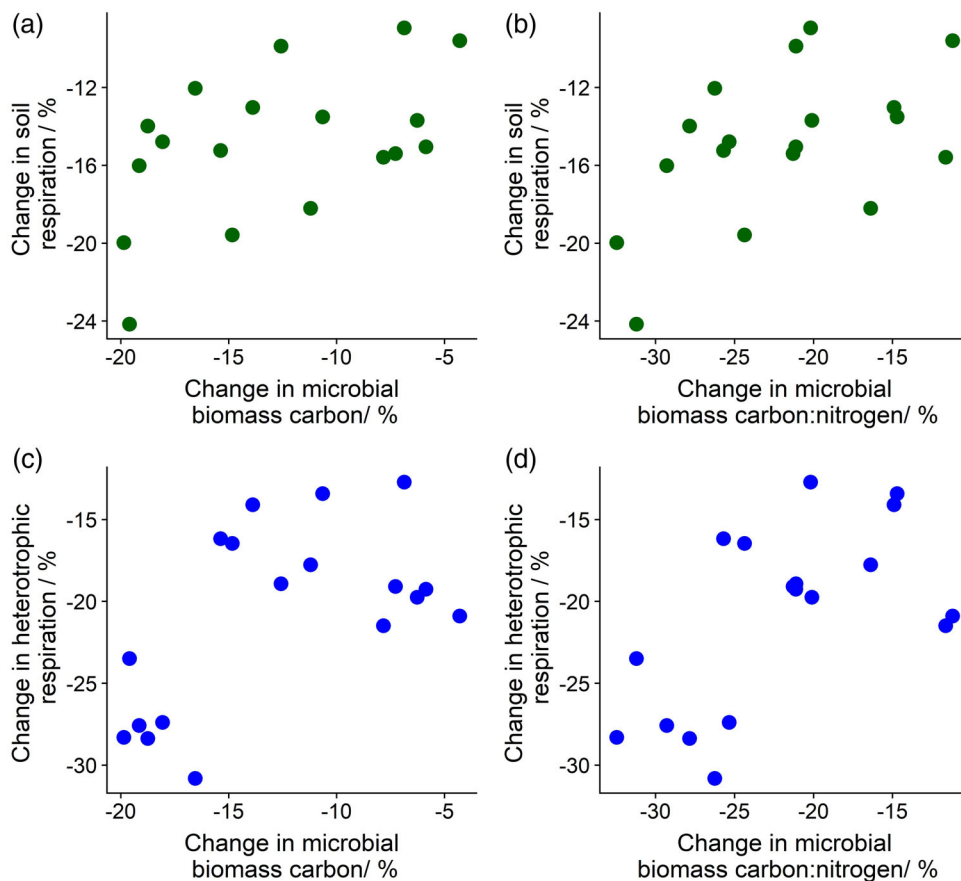
FIGURE 6 Relations between changes in soil respiration (SR) and corresponding changes in (a) microbial biomass carbon (MBC) and (b) the ratio of MBC to microbial biomass nitrogen (MBC:MBN). Relations between changes in heterotrophic respiration (HR) and corresponding changes in MBC and MBC:MBN (c and d). Significant positive correlations were found between changes in SR and changes in MBC ($r = 0.508$, $p = 0.031$, $n = 18$) and MBC:MBN ($r = 0.509$, $p = 0.031$, $n = 18$). Significant positive correlations were found between changes in HR and changes in MBC ($r = 0.580$, $p = 0.012$, $n = 18$) and MBC:MBN ($r = 0.598$, $p = 0.009$, $n = 18$)

observations should be conducted to determine what controls C fluxes as ecological systems recover from fire.

4.4 | Uncertainties

The effects of fire treatment on ecosystems are largely determined by specific features of the fire regimes, such as fire frequency, severity and intensity (Dore et al., 2010). This study showed the results from one controlled fire treatment only, and it was further limited to the relatively early stages of recovery post-fire. Moreover, it has been reported that the responses of ER, SR and their source components can vary depending on timing, season and duration of fire regimes (Katherinep, Danield, & Erics, 2006). Fire regimes can also be altered by human activities and by global climate change (Turetsky et al., 2011); these complications make projections of the effects of fire on ecosystem C fluxes challenging, but they do deserve study nevertheless.

Despite the fact that the root exclusion method used in our study has been used in numerous studies previously (Chen et al., 2016; Luo et al., 2017), there are some uncertainties associated with this procedure. First, dead root decomposition cannot be entirely eliminated even though root exclusion was carried out several months before the first measurements of HR. Second, clipping of aboveground plants could result in relatively higher soil temperatures but lower soil moisture than the control blocks. Third, because of reduced inputs of fresh C and root exudates, the root exclusion method could cause some differences in microbial communities and extracellular enzyme activities compared with the undisturbed system. Finally, there were some uncertainties in the estimation of R_{agb} and R_{bgb} because of the propagation of errors.

5 | CONCLUSIONS

These results demonstrate contrasting responses of ecosystem respiration and soil respiration and also different responses of their source components in the early stage post-fire. However, this information is not considered adequately in the current land surface models because there is a lack of direct field observations. If the different responses of respiration components hold true over large scales or over broad types of ecological disturbances, the current model projections could be greatly improved by considering this information. Different components of respiration are regulated by various biotic and abiotic factors, which suggests that a holistic understanding of fire-induced changes in both plant and microbial properties is warranted in future research priorities, for a better understanding of C exchange in post-fire ecosystems. The unique high-altitude region of the Tibetan Plateau is of great concern in terms of changing climate and ecosystem disturbance, but future comparisons with other ecosystems will be useful for a more comprehensive evaluation of how wildfire affects C cycling.

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SUPPORTING INFORMATION

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

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