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Key Points:
- We present the first large-scale study of solvent-extractable SOM compounds in the alpine and temperate grasslands of China
- Carbohydrates and plant-derived compounds are better preserved in the alpine relative to temperate grassland soils
- Solvent-extractable compounds are mainly regulated by plant input in alpine grasslands and by decay processes in temperate grasslands

Supporting Information:
- Supporting Information S1
- Data Set S1

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Large-Scale Distribution of Molecular Components in Chinese Grassland Soils: The Influence of Input and Decomposition Processes

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Abstract Chinese grasslands hold a third of the national soil organic carbon (OC) stocks but remain poorly investigated in terms of soil molecular components and their distribution patterns. Such information is important for understanding mechanisms governing grassland soil OC dynamics and its response to global changes. Here employing solvent-extractable compounds as a group of widely used biomarkers, we present a large-scale study on the distribution of different soil OC components (including plant- and microbial-derived carbohydrates and aliphatic and cyclic lipids) in the surface soils of Chinese grasslands, spanning from temperate grasslands in the arid/semiarid regions to alpine grasslands on the Qinghai-Tibetan Plateau. We show that alpine grassland soils are more enriched with carbohydrates and plant-derived compounds relative to the temperate counterparts due to temperature-inhibited decomposition. While plant belowground biomass plays a key role in explaining the spatial variation of compounds in the alpine grasslands, climatic variables do in the temperate region. In particular, aliphatic lipids accumulate with increasing mean annual temperature in the temperate grasslands due to a preferential decay of labile soil OC, whereas they decrease in the alpine grasslands owing to dilution by an enhanced plant input of nonlipid components. Collectively, these results demonstrate different mechanisms governing the distribution of solvent-extractable compounds in grassland soils, with climate-mediated decomposition processes dominating in the temperate grasslands and plant inputs being more important in the alpine region. In the context of climate change, alterations to soil OC input and decomposition processes may have varied impacts on soil carbon cycling in these two regions.

1. Introduction

Grasslands are one of the most widely distributed ecosystems on Earth and play a crucial role in the global terrestrial carbon cycle (White et al., 2000). China's grasslands are the third largest in the world and cover 41.7% of the national land surfaces, ranging from temperate grasslands in the arid and semiarid regions of northern China to alpine grasslands on the Qinghai-Tibetan Plateau (QTP) (Fang et al., 2010; Kang et al., 2007; Yang et al., 2010). Organic carbon (OC) stored in the soil organic matter (SOM) of grasslands accounts for approximately one third of soil OC stock in China (Yang et al., 2010). Therefore, soil OC dynamics in China's grasslands have attracted considerable attention in recent decades (Fang et al., 2010; Liu et al., 2017; Wang, Sistla, et al., 2016; Yang et al., 2010).

Previous studies have revealed distinct soil OC distribution patterns and environmental influences in the alpine versus temperate grasslands of China. The QTP, with an average altitude of 4,000 m above sea level, is the largest high-altitude ecosystem in the world. Alpine grasslands on the QTP are characterized by high belowground biomass (BGB) (Fan et al., 2008; Liu et al., 2012), prevailing low temperatures and widespread frozen soils (Baumann et al., 2009; Shang et al., 2016), leading to an enhanced preservation of SOM (Liu et al., 2012; Shang et al., 2016; Yang et al., 2010). In contrast, temperate grasslands are

developed under an arid and semiarid climate with precipitation recognized as a critical factor in controlling primary production and microbial activity (Bai et al., 2004; Chen et al., 2015; Wang, Sistla, et al., 2016). Soil OC in the temperate grasslands tends to decrease with increasing temperature (Wang, Sistla, et al., 2016; Yang et al., 2010), as temperature increase enhances microbial decomposition more than plant detrital production in this water-limited ecosystem (Wang, Sistla, et al., 2016; Yang et al., 2010). Nonetheless, grasslands in both regions are shown to be highly susceptible to climatic and environmental changes (Chen et al., 2013; Liu et al., 2012), which may result in grassland degradation and alterations to carbon exchanges between soil and the atmosphere (Baumann et al., 2009; Wang, Sistla, et al., 2016; Yang et al., 2010). However, most of the current studies have relied on bulk measurements of total soil OC and nitrogen (N) contents to examine SOM dynamics. It remains largely unknown whether SOM molecular composition differs between the alpine and temperate grasslands, thereby potentially causing distinct responses to environmental change. Since SOM consists of heterogeneous mixtures of plant-, microbe-, and animal-derived residues with different physicochemical properties and environmental stabilities (Kögel-Knabner, 2002; Schmidt et al., 2011), investigations on the molecular components may reveal intrinsic changes to SOM and are hence indispensable for understanding soil OC dynamics under climate or land use changes (Feng et al., 2008; Pisani et al., 2016; Rushdi et al., 2016; Zhao et al., 2014).

Source-specific biomarkers can provide unparalleled insight into the molecular components of SOM as well as its biological origins, contributing important perspectives on the dynamic change of SOM composition (Feng & Simpson, 2011; Kaiser et al., 2002; Otto & Simpson, 2005). Among the myriad of organic constituents preserved in soils, solvent-extractable compounds, including carbohydrates, alkanoic acids, alkanols, alkanes, steroids, and terpenoids, may yield information on the relative contribution of plants versus microbes as well as on the relative abundance of compounds with varied degradabilities (Feng & Simpson, 2007; Kaiser et al., 2002). Over the past few decades, solvent-extractable compounds have been applied to examine SOM dynamics in response to changing environmental conditions, such as climate (Feng et al., 2008; Naafs et al., 2004; Rushdi et al., 2016), vegetation shifts (Jandl et al., 2006; Wiesenberg et al., 2010; Zocatelli et al., 2014), and land use changes (Pisani et al., 2016; Zhao et al., 2014). It is found that solvent-extractable aliphatic lipids that are relatively resistant to decomposition tend to accumulate with higher temperatures (Feng et al., 2008; Pisani et al., 2014) and at low soil pHs (Bull et al., 2000; Nierop et al., 2005). In contrast, solvent-extractable carbohydrates that are labile tend to peak in grassland soils during spring to late summer, suggesting their accumulation with increasing primary production (Medeiros et al., 2006; Rushdi et al., 2016). However, the majority of these studies have focused on site-specific experiments or small-scale investigations, which encompass a limited range of environmental gradients to fully investigate variables regulating the distribution of different SOM components. Large-scale or regional investigations on the distribution of solvent-extractable compounds may shed new light on the key processes or mechanisms governing SOM preservation in natural grasslands and/or under different climatic zones.

Here we take advantage of the wide distribution of grasslands in China and conduct a large-scale investigation of solvent-extractable compounds in the surface soils of different types of grasslands. The objectives of this study are (1) to compare and contrast the relative abundance and composition of solvent-extractable compounds in the alpine versus temperate grassland soils and (2) to investigate the key environmental variables and mechanisms affecting the distribution of different solvent-extractable compounds in these two regions. Our working hypotheses are the following: (1) labile SOM components (e.g., solvent-extractable carbohydrate) and plant-derived compounds are better preserved in alpine grassland soils due to temperature-constrained decomposition, while aliphatic lipids may be enriched in temperate grassland soils relative to other soil organic carbon components owing to a preferential decay of labile SOM; and (2) given varied environmental conditions in the alpine versus temperate grasslands, the distribution of solvent-extractable compounds may be governed by different mechanisms and/or environmental variables in these two regions. Our study area extends from temperate grasslands on the arid and semiarid Mongolian Plateau to alpine grasslands on the QTP and include a total of 114 soil samples. The wide range of environmental gradients and intensive sampling scheme allow a comprehensive evaluation of the distribution patterns as well as their influencing factors for the solvent-extractable compounds in China's grassland soils.

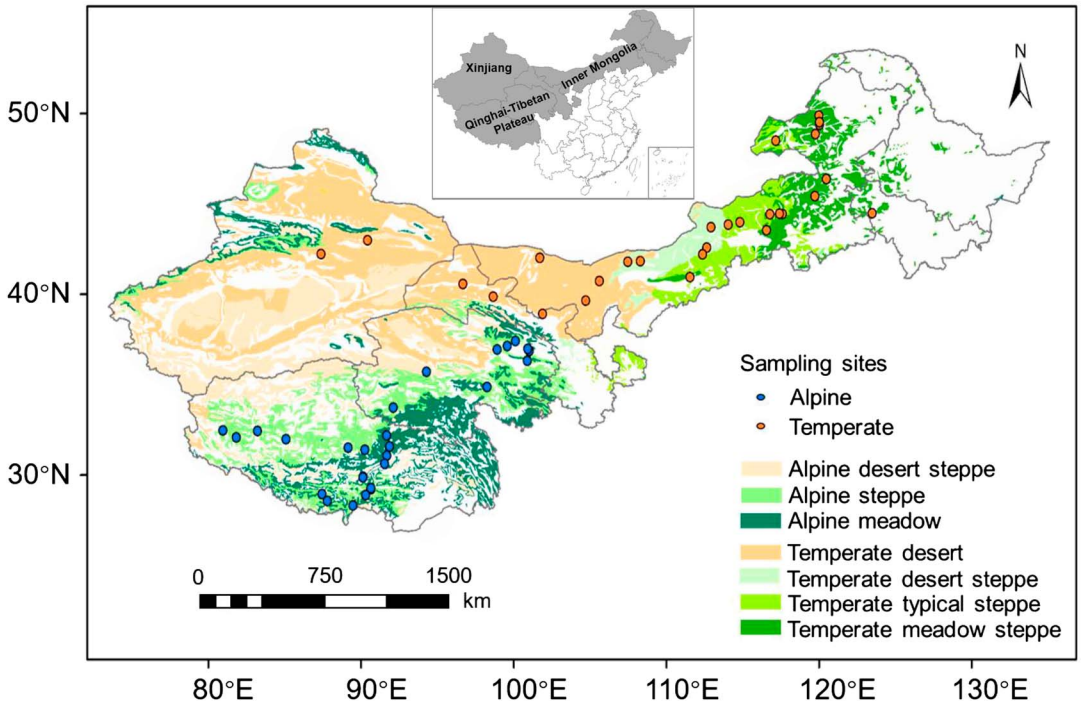

Figure 1. Location of sampling sites in the grassland-dominated transects of northern China underlain by China's vegetation map (1:10000000).

2. Materials and Methods

2.1. Study Area

The study area encompasses a 3,200 km transect of alpine grasslands on the QTP and a 4,700 km transect of temperate grasslands in the arid and semiarid regions of northern China (Figure 1 and Table S1 in the supporting information). The former transect extends from northeastern Qinghai Province to southern and western Tibet, ranging from 3,066 to 5,418 m in elevation. Mean annual temperature (MAT) ranges from −4.6 to 7.8°C along this transect (Table 1), with the lowest mean monthly temperature in January and the highest in July. Mean annual precipitation (MAP) varies between 147 and 446 mm (Table 1), with 90% occurring in May to September. Soil types in this transect include Leptosols, Gleysols, Cambisols, and Phaeozems according to

Table 1
Environmental Properties and Surface Soil Characteristics of the Sampling Sites in the Alpine and Temperate Grasslands (Mean ± Standard Error)

	Alpine grasslands				Temperate grasslands				Temperate desert (n = 9)
	AM (n = 37)	AS (n = 16)	ADS(n = 10)	Average (n = 63)	TMS (n = 15)	TS (n = 14)	TDS (n = 13)	Average (n = 42)	
Elevation (m)	4,592 ± 83	3,963 ± 182	4,169 ± 127	4,365 ± 78	889 ± 117	1,073 ± 39	1,243 ± 41	1,059 ± 50	1,203 ± 102
MAT (°C)	−0.45 ± 0.42	−0.13 ± 0.52	3.02 ± 1.16	0.18 ± 0.37	−0.72 ± 0.51	1.28 ± 0.17	3.78 ± 0.25	1.34 ± 0.35	8.43 ± 0.37
MAP (mm)	291 ± 11	316 ± 16	332 ± 38	304 ± 10	387 ± 8	313 ± 14	202 ± 6	304 ± 13	85 ± 11
AGB (g m^{-2})	86 ± 9	123 ± 19	26 ± 7	86 ± 8	245 ± 24	183 ± 16	65 ± 13	169 ± 16	15 ± 4
BGB (g m^{-2})	3,327 ± 400	660 ± 96	402 ± 85	2,152 ± 290	1,053 ± 95	1,376 ± 233	840 ± 151	1,095 ± 100	38 ± 22
Clay (%)	5.7 ± 0.4	2.7 ± 0.7	1.8 ± 0.6	4.3 ± 0.4	0.69 ± 0.15	0.44 ± 0.07	0.50 ± 0.06	0.55 ± 0.06	0.98 ± 0.44
Silt (%)	31.5 ± 2.9	34.9 ± 4.1	16.7 ± 3.6	30.0 ± 2.2	41.9 ± 4.3	27.7 ± 2.9	24.4 ± 2.2	31.7 ± 2.2	29.6 ± 7.5
Sand (%)	62.8 ± 3.3	62.4 ± 4.3	81.5 ± 3.9	65.6 ± 2.4	57.2 ± 4.2	71.8 ± 2.9	74.5 ± 2.0	67.4 ± 2.2	68.0 ± 7.8
pH	7.0 ± 0.1	8.2 ± 0.1	8.2 ± 0.1	7.5 ± 0.1	7.1 ± 0.2	8.0 ± 0.1	8.4 ± 0.1	7.8 ± 0.1	8.4 ± 0.2
OC (%)	4.84 ± 0.37	2.35 ± 0.31	0.81 ± 0.15	3.57 ± 0.31	3.01 ± 0.29	1.31 ± 0.11	0.49 ± 0.04	1.66 ± 0.20	0.16 ± 0.03
N (%)	0.37 ± 0.03	0.24 ± 0.03	0.12 ± 0.02	0.30 ± 0.02	0.27 ± 0.03	0.15 ± 0.01	0.06 ± 0.00	0.16 ± 0.02	0.02 ± 0.01
OC/N	13.5 ± 0.5	10.6 ± 0.8	7.8 ± 1.3	11.9 ± 0.5	11.5 ± 0.4	9.0 ± 0.2	8.8 ± 0.2	9.8 ± 0.3	7.7 ± 0.7
Al_d (%)	0.14 ± 0.01	0.07 ± 0.02	0.05 ± 0.01	0.10 ± 0.01	0.06 ± 0.01	0.03 ± 0.00	0.04 ± 0.01	0.05 ± 0.00	0.01 ± 0.00
Fe_d (%)	1.06 ± 0.05	0.78 ± 0.15	0.58 ± 0.11	0.91 ± 0.05	0.49 ± 0.05	0.37 ± 0.04	0.43 ± 0.06	0.43 ± 0.03	0.28 ± 0.03

Note. AM: alpine meadow; AS: alpine steppe; ADS: alpine desert steppe; TMS: temperate meadow steppe; TS: temperate typical steppe; TDS: temperate desert steppe; MAT: mean annual temperature; MAP: mean annual precipitation; AGB: aboveground biomass; BGB: belowground biomass; OC: soil organic carbon; N: soil nitrogen; OC/N: ratio of OC to N; Al_d: dithionite-extractable aluminum; and Fe_d: dithionite-extractable iron.

IUSS Working Group WRB (2006). Three dominant vegetation types in this transect are alpine meadow (dominated by *Kobresia pygmaea, Kobresia humilis,* and *Kobresia tibetica*), alpine steppe (dominated by *Stipa purpurea, Carex lanceolata,* and *Stip subsessiliflora*), and alpine desert steppe (dominated by *Oxytropis ochrocephala*, etc.).

The temperate grassland transect extends from east to west across the Inner Mongolia, Gansu, and Xinjiang Provinces with elevations ranging from 147 to 2,664 m. MAT ranges from −3.4 to 11.0°C along this transect, while MAP ranges from 38 to 436 mm (Table 1) with 80% of the precipitation occurring in the growing season from May to August. Soil types in this transect include Arenosols, Kastanozems, and Chernozems according to IUSS Working Group WRB (2006). There are four vegetation types from east to west: temperate meadow steppe (dominated by *Leymus chinensis*, *Stipa baicalensis*, and *Carex pediformis*), temperate typical steppe (dominated by *Stipa grandis*, *Leymus chinensis,* and *Achnatherum sibiricum*), temperate desert steppe (dominated by *Stipa klemenzii*, *Agropyron michnoi,* and *Cleistogenes squarrosa*), and temperate desert (dominated by *Oxytropis aciphylla* and *Ceratoides latens*).

2.2. Soil Sampling and Biomass Survey

A total of 57 sites with minimal anthropogenic disturbances and grazing acitivities was selected for soil sampling and biomass survey along the two transects (29 sites in alpine grasslands and 28 sites in temperate grasslands) during the summer (July to August) of 2011–2012. At each site (10 m × 10 m), aboveground biomass (AGB) were harvested from five random plots (1 m × 1 m) to the ground level. BGB was sampled by taking 5 soil cores (diameter of 7 cm) at a depth of 10 cm from each of the 5 plots. Roots retrieved from the soil cores were immediately placed in a cooler and transported back to the laboratory, where they were soaked in deionized water and cleaned of soil particles using a 0.5 mm sieve. All biomass samples were oven-dried at 65°C to a constant weight for AGB and BGB measurement. As dead roots were not removed during sampling, living root biomass was estimated at a living-to-total root biomass ratio of 56% or using a fixed ratio of living to dead root mass of 1.167 (Jing et al., 2015). This ratio is comparable to others calculated for Chinese alpine meadows, steppe, and desert shrublands in other studies (1.14–1.29), which do not seem to differ among different vegetation types in the grasslands (Hu et al., 1990; Wei et al., 2012; Wen et al., 2013).

Surface soil samples (0–10 cm) were collected by taking three additional random soil cores (diameter of 7 cm) from each of the five plots (1 m × 1 m) at every site. The three cores were mixed in situ as one composite sample. After homogenization and removal of stones and visible roots, the soils were passed through a 2 mm sieve and air-dried for subsequent chemical analyses. Organic matter contained within the sieved soils is defined as SOM in our paper. Although visible plant roots and litter were handpicked in the preparation, the soil sample may contain some light-density materials such as poorly decomposed plant debris. For this study, three soil samples were selected for 16 alpine and 10 temperate grassland sites each, while two soil samples were selected for another 2 alpine and 3 temperate grassland sites each. For the remaining 26 sites, soils from 3 plots were mixed in equal proportions to constitute a single representative sample due to limited sample availability and logistic reasons (Table 1). As a result, a total of 114 surface soil samples from 57 sites was included for our analysis. Soil bulk density was measured with volumetric sampling using a standard container with a volume of 100 cm^3. Bulk density was calculated as the ratio of the oven-dried soil mass to the volume of the container.

In addition, whole-plant samples were collected in the summer (July–August) of 2016 to compare the chemical composition of the dominant vegetation, including five species in the alpine grasslands (*Kobresia pygmaea*, *Kobresia humilis*, *Kobresia tibetica*, *Carex moorcroftii,* and *Oxytropis ochrocephala*) and five species in the temperate grasslands (*Leymus chinensis*, *Stipa grandis*, *Agropyron michnoi*, *Cleistogenes squarrosa,* and *Achnatherum sibiricum*). The average coverage of the five dominant species is 10–60% in the alpine grasslands (Liu et al., 2016; Wang, Yi, et al., 2016) and 5–50% for the temperate grassland (Chen & Wang, 2000; B. Li et al., 1988). The leaves and roots of fresh plants were separated in situ after sampling and kept at 4°C before returning to the laboratory. After cleaning, the plant tissues were oven-dried at 65°C and crushed with a ball mill prior to chemical analysis.

2.3. Soil and Plant Physiochemical Analyses

Total carbon and N contents of soil and plant samples were measured by combustion using an elemental analyzer (Vario EL III, Elementar, Hanau, Germany). Soil OC content was calculated by subtracting inorganic

carbon from total carbon, with the former analyzed volumetrically by reaction with hydrochloric acid. To check the quality of our soil OC data, we selected 12 soil samples from the temperate grasslands with low OC contents (Table S2) that are allegedly more prone to bias by the subtraction method (Bisutti et al., 2004; Walthert et al., 2010) and compared their OC contents measured by the subtraction and fumigation methods. For the latter, dried soils were fumigated with 37% hydrochloric acid for 72 h and the excessive acid vapor was subsequently removed by sorbing to sodium hydroxide pellets under vacuum for 24 h (Harris et al., 2001). The treated soils were oven-dried (65°C) before measuring soil OC by combustion using an elemental analyzer. The alpine soils were not included in this preliminary test due to limited sample availability. Results of the bootstrap (based on 1,000 bootstrap samples) paired *t* test showed that there was no significant difference in the OC contents measured by the two methods ($p = 0.810$; $n = 12$). Furthermore, the OC contents measured by both methods were highly correlated and fell on the 1:1 line (Figure S1). Based on these results, we conclude that the soil OC data measured by subtraction (volumetrical) method were acceptable in our study.

Soil pH was measured using a pH meter at a soil: water ratio of 1:2.5 (*w*:*v*). Soil texture was examined by laser diffraction using Malvern Mastersizer 2000 (Malvern Instruments Ltd., UK) after removal of organic matter and calcium carbonates (Sun et al., 2011). Reactive iron (Fe_d) and aluminum (Al_d) were extracted from soils using the citrate-bicarbonate-dithionite method according to Mehra and Jackson (1960). Fe_d and Al_d included both crystalline and poorly crystalline Fe and Al oxides, and their contents were determined on an inductively coupled plasma-atomic emission spectrometer (ICP-AES; ICAP6300, Thermo Scientific, USA).

2.4. Extraction and Analysis of Solvent-Extractable Biomarkers

Solvent-extractable compounds were extracted and analyzed as described by Feng and Simpson (2007) and Dai et al. (2016). Briefly, ~0.1 g of plant materials (leaves and roots, separately) or 5–8 g of dried soils were sonicated for 15 min with 30 mL of dichloromethane, dichloromethane:methanol (1:1, *v*:*v*) and methanol, respectively. The combined extracts were filtered through combusted glass fiber filters (Whatman GF/F) and evaporated almost to dryness using rotary evaporation. The extracts were further cleaned through a silica gel column (0.5 cm in inner diameter (i.d.)), with hydrocarbon and polar compounds eluting with 15 mL of hexane and 10–15 mL of methanol, consecutively. The hydrocarbon fraction was not included in this study due to the presence of an unresolved complex mixture in many of the grassland soil extracts, preventing accurate compound quantifications. Hence, solvent-extractable compounds refer to the polar fraction throughout this paper. An internal standard (C_{19} *n*-alkanoic acid) was added to the polar fraction. Aliquots of the extracts were dried in a stream of nitrogen gas and converted to trimethylsilyl derivatives by reacting with 40 μL of N,O-bis-(trimethylsilyl) trifluoroacetamide, 10 μL of pyridine, and 50 μL dichloromethane for 3 h at 70°C. Individual compounds were identified and quantified on a Trace GC 1310 gas chromatograph coupled to an ISQ mass spectrometer (Thermo Fisher Scientific, USA) using a DB-5MS column (30 m × 0.25 mm i.d., film thickness, 0.25 μm) for separation. The temperature increased from 65°C (initial hold time 2 min) to 300°C at a rate of 6°C min^{-1} with helium as the carrier gas (1.2 mL min^{-1}). The mass spectrometer was operated in an EI mode at a 70 eV ionization energy and scanned from 50 to 650 amu. Quantification was achieved by comparison with the internal standard. Analytical errors were typically <10% based on replicate analysis of the same soil sample.

To estimate the fraction of solvent-extractable OC in soil OC, we further summarized and quantified all (nonsolvent) peaks in the GC chromatogram, assuming a similar response factor for all compound classes and a carbon content of 65% for the unidentified extractable compounds (similar to the mean carbon content of all identified compound classes). In total, solvent-extractable compounds accounted for 0.1–4.3% of soil OC in the studied grasslands (Figure S2). These yields are comparable to those measured by weighing dried solvent extracts for the Canadian prairie grassland soils (0.5–2.5%) (Feng & Simpson, 2007; Otto & Simpson, 2005). Of all the solvent-extractable compounds, approximately 41 ± 3% were identifiable, equivalent to 0.03–0.91% of soil OC (Figure S2). Admittedly, the investigated biomarkers make up only a small fraction of soil OC, because the majority (up to 80%) of soil OC is believed to have undergone complex interaction with each other and/or minerals during diagenesis and is molecularly uncharacterized or not extractable (Hedges et al., 2000). Nonetheless, a key part of the uncharacterized OC is considered to derive from the same carbon source (s) as the extractable biomarkers (Hedges et al., 2000). In other

words, the source and diagenesis information carried by biomarkers may be treated as conservative reflections of the behavior of soil OC components of similar origins (Kögel-Knabner, 2002; Feng & Simpson, 2011; Schmidt et al., 2011).

2.5. Plant Input and Preservation Percentage of Solvent-Extractable Biomarkers

To account for plant input variations of each compound class in the alpine versus temperate grasslands given varied net primary productivity (NPP) as well as plant compound concentrations, we estimated plant inputs of each compound class as below:

$$\text{Input} = [C_L \times 1/(1+R) + C_R \times R/(1+R)] \times \text{NPP}/1,000, \quad (1)$$

where input is the plant input of compounds (carbohydrates, aliphatic lipids, and cyclic lipids, respectively) in the units of g m^{-2} yr^{-1}; C_L and C_R is the OC-normalized compound concentrations (mg g^{-1} OC) in the leaves and roots of the dominant species, respectively; R is the ratio of belowground to aboveground biomass at each sampling site; NPP is the net primary productivity (g C m^{-2} yr^{-1}), obtained for each sampling site from the Numerical Terradynamic Simulation Group Data (http://www.ntsg.umt.edu/data) with a 1 km resolution (Table S1).

To further estimate the fraction of NPP that gets preserved in the surface soils as total solvent-extractable or plant-derived compounds, we calculated the preservation percentage using the following equation:

$$\text{Preservation percentage} = \frac{M \times \rho \times h}{\text{NPP} \times t} \times 100\%. \quad (2)$$

In equation (2), M is the concentration of total solvent-extractable or plant-derived compounds in the soil (including $>C_{20}$ even-numbered *n*-alkanoic acids and *n*-alkanols, sucrose, and cyclic lipids other than ergosterol and cholesterol for the latter) in the units of μg C g^{-1} soil (with the carbon content of different compounds being accounted for: that is, 44, 80, and 84% for carbohydrates, aliphatic lipids, and cyclic lipids, respectively, while a mean value of 65% is assumed for the unidentified extractable compounds similar to all identified compound classes); ρ is the soil bulk density (g cm^{-3}); h is the thickness of soil (cm) and is 10 cm in this study; NPP is in the units of g C m^{-2} yr^{-1}, obtained from the same source as equation (1) (Table S1); t is the time (year) for plant OC to accumulate in the surface soil (0–10 cm) under a steady state condition, approximated as the turnover time of surface soil OC and estimated to be 64 years in the alpine grasslands (Yu et al., 2017) and 30 years in the temperate grasslands (L. H. Li, et al., 1998).

2.6. Climatic Data and Statistical Analysis

To examine climatic effects on the distribution of solvent-extractable compounds, we compiled a complementary list of climatic variables across the grassland transects by extracting MAT and MAP from the WorldClim Global Climate Data (http://www.worldclim.org/) with a spatial resolution of 0.0083° (approximately 1 km^2 at the equator). Differences in the concentration of solvent-extractable compounds or other soil properties were examined using independent sample *t* tests between the alpine and temperate grassland soils and using one-way analysis of variance followed by posthoc analysis (Dunnett's test) for varied vegetation types. The results were confirmed using general linear model with "vegetation types" as random effects. Redundancy analysis (RDA) combined with ordinary least squares regression was performed to assess the relationship of solvent-extractable compounds with climatic (i.e., MAT and MAP), plant (i.e., AGB and BGB), and edaphic variables (i.e., soil pH, OC, N, sand, Al_d, and Fe_d contents). Partial correlation tests were used to examine the effect of MAT and plant biomass (including AGB and BGB) on the concentration of solvent-extractable compounds with the other variables being controlled. Compound concentrations were natural log-transformed before analysis, and normal distribution of transformed data was confirmed using Shapiro-Wilk test. To ensure that the statistical results obtained using log-transformed data are relevant for the original, nontransformed data, we also performed all the statistical analyses on the original, nontransformed data. To show how close our sample mean is to the population mean, standard error is used for all figures, while statistical results are based on the standard deviation. Differences and correlations were considered to be significant at a level of $p < 0.05$.

Table 2
The Organic Carbon (OC), Nitrogen (N) Contents and OC/N Ratios in the Dominant Plants From the Alpine and Temperate Grasslands

		Leaf			Root		
Grassland type	Dominant plant species	OC (%)	N (%)	OC/N	OC (%)	N (%)	OC/N
Alpine	*Oxytropis ochrocephala*	42.00	2.88	14.58	38.53	1.80	21.42
	Kobresia tibetica	42.96	1.66	25.82	46.28	0.42	109
	Carex moorcroftii	43.33	2.08	20.84	41.69	1.04	40.14
	Kobresia humilis	43.18	2.24	19.31	44.30	0.50	87.83
	Kobresia pygmaea	43.11	2.65	16.28	45.77	0.67	67.94
Temperate	*Agropyron michnoi*	43.44	1.96	22.18	31.70	0.97	32.81
	Stipa grandis	44.98	2.08	21.66	29.82	0.91	32.64
	Cleistogenes squarrosa	42.98	2.56	16.81	32.40	0.62	52.28
	Leymus chinensis	43.56	2.38	18.29	34.97	0.85	41.24
	Achnatherum sibiricum	44.73	2.41	18.53	28.57	0.77	37.32

3. Results and Discussion

3.1. Bulk Properties of Soils and Plants

The investigated surface soils had a coarse texture dominated by sand (66.5 ± 1.7%, mean ± s.e., standard error) and silt (30.6 ± 1.6%; Table 1), consistent with poor soil development in these regions (Fang et al., 2010; Kang et al., 2007). Soil pH ranged from 5.8 to 8.8 and was comparable in the alpine (7.5 ± 0.1) and temperate grasslands (7.8 ± 0.1; $p > 0.05$; Table 1). The Fe_d and Al_d contents in the alpine grassland soils (0.91 ± 0.05% and 0.10 ± 0.01%, respectively) were similar to those reported in other grassland or agricultural soils (Dethier et al., 2012; Doetterl et al., 2015) but were significantly higher than in the studied temperate grassland soils (0.43 ± 0.03% and 0.05 ± 0.00%, respectively; $p < 0.05$, Table 1).

Soil OC and N contents were both significantly higher in the alpine grasslands (3.57 ± 0.31% and 0.3 ± 0.02%, respectively) than in the temperate ones (1.66 ± 0.20% and 0.16 ± 0.02%, respectively; $p < 0.01$). This result is consistent with the higher OC contents in the roots of the dominant plants in the alpine (43.31 ± 1.29%) than temperate grasslands (31.49 ± 0.98%; $p < 0.05$, $n = 5$) despite comparable OC contents in the leaves of dominant plants in these two grasslands (42.92 ± 0.21% and 43.94 ± 0.34%, respectively; $p > 0.05$, $n = 5$; Table 2). A strong positive correlation was observed between soil OC and N contents ($r = 0.949$; $n = 105$; $p < 0.001$), suggesting that N was primarily associated with SOM (Liu et al., 2012). The OC/N ratios were higher in the alpine grasslands (11.9 ± 0.5) than in the temperate grasslands (9.8 ± 0.3; $p < 0.01$; Table 1). The higher OC/N values in the surface soils of alpine versus temperate grasslands may be attributed to an inhibited degradation of SOM in the cold region (Baumann et al., 2009; Fang et al., 2010; Liu et al., 2012), since the OC/N ratio typically decreases with the degradation of plant-derived organic matter and shows values of approximately 10 in well-developed grasslands (Cleveland & Liptzin, 2007; Tian et al., 2010). Alternatively, although both roots and leaves of the investigated five dominant plants had comparable OC/N ratios between the alpine and temperate grasslands (Table 2), higher OC/N ratios were previously reported in plant fine roots (but not leaves) in the alpine (49.01 ± 2.36) than temperate grasslands (39.47 ± 1.16) (Geng et al., 2017). Hence, the higher OC/N ratios of alpine grassland soils may be partly attributed to the higher OC/N ratio of alpine versus temperate plant roots as well.

By comparison, soils in the temperate deserts had the lowest contents of soil OC, N, OC/N, Fe_d, and Al_d contents ($p < 0.05$; Table 1) and a similar soil pH and coarse texture compared with the grasslands, which are consistent with previous studies (Shi et al., 2012; Wang et al., 2010). The lowest soil OC, N contents, and OC/N ratios may be caused by a much lower plant input (e.g., low AGB and BGB; Table 1) in the deserts (Shi et al., 2012), while the lower Fe_d and Al_d contents can be attributed to the lower chemical weathering rates and age of soils as well as parent materials in the temperate desert (Wang et al., 2010).

3.2. Composition and Sources of Solvent-Extractable Compounds in Soils and Plants

Solvent-extractable compounds contained aliphatic lipids, carbohydrates, and cyclic lipids in the investigated soils and plants. Among them, aliphatic lipids were the most abundant component in all soils except from the alpine desert steppe, accounting for 55 ± 2%, 69 ± 2%, and 86 ± 3% of the identified compounds in the alpine

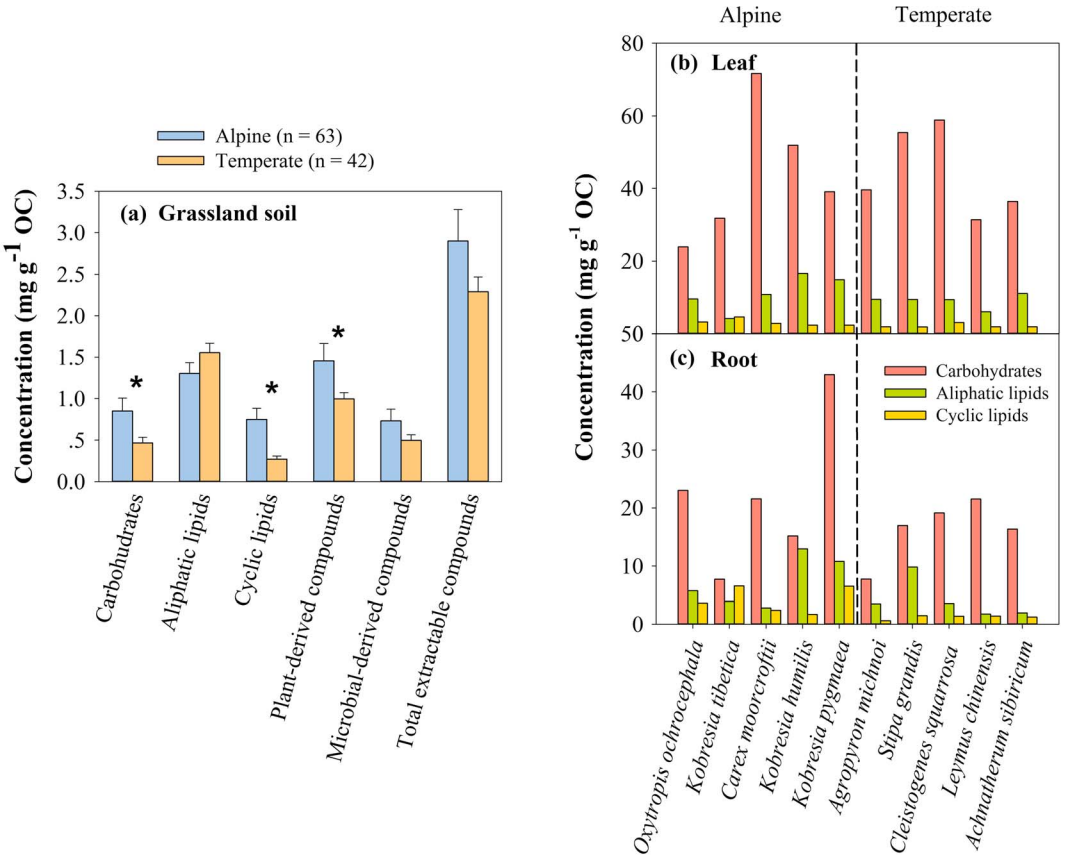

Figure 2. Organic carbon (OC)-normalized concentrations of solvent-extractable compounds in the surface (a) soils, (b) leaves, and (c) roots of the dominant plants in the alpine and temperate grasslands. Error bars represent standard error of mean. Asterisk denotes significant difference between alpine and temperate grassland soils ($p < 0.05$).

grassland, temperate grassland, and temperate desert soils, respectively (Figures 2a and 3). By comparison, plant tissues contained a much smaller proportion of aliphatic lipids in the identified compounds, being 9–26% (17 ± 2%) in the leaves and 7–43% (23 ± 4%) in the roots. The dominance of even-numbered long-chain ($>C_{20}$) *n*-alkanoic acids and *n*-alkanols in soils is in agreement with the literature (Jandl et al., 2006;

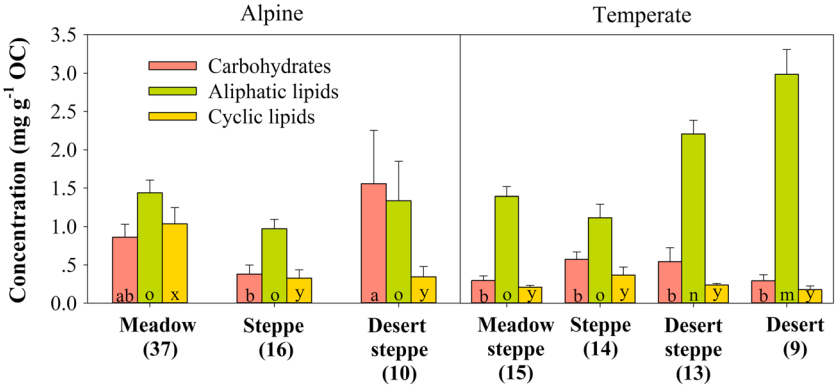

Figure 3. Organic carbon (OC)-normalized concentrations of solvent-extractable compounds in the surface soils under different vegetation types. Error bars represent standard error of mean with the number of samples indicated in the parenthesis. Different letters indicate differences between the vegetation types: a and b for carbohydrates, m and o for aliphatic lipids, and x and y for cyclic lipids ($p < 0.05$).

Otto & Simpson, 2005; Wiesenberg et al., 2010), suggesting major lipid inputs from the overlying vegetation. Branched alkanoic acids (*iso*-C_{15} and *iso*-C_{17}) were detected at trace amounts in all soil samples, which are mainly biosynthesized by bacteria and fungi (Otto & Simpson, 2005, and references therein). In addition, minor contributions of unsaturated *n*-alkanoic acids (including $C_{16:1}$,$C_{18:1}$ and $C_{18:2}$) were found in the soil, which were in higher abundances in plant tissues and represented relatively fresh inputs from plants as well as microbes due to the high degradability of unsaturated acids (Moucawi et al., 1981; Wiesenberg et al., 2010).

Carbohydrates identified in the plant tissues included sucrose, glucose, mannitol, galactose, and xylitol, with sucrose being the most abundant (accounting for 32 ± 2% and 42 ± 4% of the identified compounds in leaves and roots, respectively). Consistent with previous studies (Kögel-Knabner, 2002; Otto & Simpson, 2005), carbohydrates were the dominant solvent-extractable compounds in plant tissues, representing 65–86% of the identified compounds in the leaves and 42–87% in the roots (Figures 2b and 2c). By comparison, carbohydrates only accounted for 29 ± 2%, 16 ± 1%, and 8 ± 2% of the identified compounds in the soils of alpine grasslands, temperate grasslands and temperate deserts, respectively (Figures 2a and 3). In addition to the above mentioned carbohydrates, trehalose occurred in significant amounts in all soils, contributing up to 84 ± 2% of the identified carbohydrates (ranging from 61 ± 3% in alpine meadows to 98 ± 1% in temperate desert steppes). Trehalose has also been identified as the predominant carbohydrate in the grassland and agricultural soils from Western Canada (Otto & Simpson, 2005), Oregon (Medeiros et al., 2006; Rushdi et al., 2016), and California (Rogge et al., 2007; Simoneit et al., 2004). As a reserve carbohydrate and stress protectant, trehalose occurs in a wide range of organisms, such as fungi, bacteria, and insects, but is only rarely found in plants (Müller et al., 1995; Wingler, 2002). Its high abundance in the soil likely indicates an important contribution from soil microbes (Feng & Simpson, 2007; Otto & Simpson, 2005). By contrast, sucrose, the primary carbohydrate found in the overlying vegetation, was detected in small amounts in soils (8.7 ± 1.4% and 1.0 ± 0.5% for the alpine and temperate grasslands, respectively). This observation suggests that soil carbohydrates were mainly composed of microbial products (such as trehalose) instead of plant-derived sugars that are easy to be consumed by soil microbes (Otto & Simpson, 2005; Rogge et al., 2007; Rushdi et al., 2016).

Cyclic lipids (including steroids and triterpenoids) accounted for 3–36% and 5–24% of the identified compounds in plant tissue and soil samples, respectively (Figure 2). Among these, plant-derived steroids (i.e., campesterol, stigmasterol, β-sitosterol, stigmasta-3,5-dien-7-one, and sitosterone) occurred in relatively high abundances in grassland soils (comprising $>$75% of total cyclic lipids), confirming major inputs of plants to soil lipids along the transects. Plant-derived triterpenoids (oleanolic acid and ursolic acid) were also found in both plant tissues and surface soils. In addition, cholesterol (a nonplant steroid found in soil fauna, fungi, and algae) (Otto & Simpson, 2005; Rogge et al., 2007) and ergosterol (a viable fungal biomarker) (Högberg, 2006) were detected in trace amounts in both alpine and temperate grassland soils, indicating minor contributions of microbes to soil cyclic lipids.

To further distinguish contribution from varied biological origins, we grouped the identified compounds into components exclusively derived from plants or microbes. Microbial-derived compounds included branched alkanoic acids (*iso*-C_{15} and *iso*-C_{17}), trehalose, ergosterol, and cholesterol. Plant-derived compounds consisted of long-chain ($>C_{19}$) even-numbered *n*-alkanoic acids and *n*-alkanols, sucrose, and cyclic lipids other than ergosterol and cholesterol. Other solvent-extractable compounds (such as short-chain *n*-alkanoic acid and *n*-alkanols, and other carbohydrates) are not source specific (Otto & Simpson, 2005; Rogge et al., 2007) and hence not included. Plant-derived compounds made up 49.1 ± 1.9%, 43.5 ± 1.3%, and 22.9 ± 3.1% of all identified compounds in the alpine grassland, temperate grassland, and temperate desert soils, respectively, while microbial-derived compounds represented 21.4 ± 1.9%, 21.0 ± 1.7%, and 10.6 ± 2.0% in the corresponding soils, respectively (Figures 2a and 3). The mean ratio of plant- versus microbial-derived compounds (plant/microbe ratio) was 3.6 ± 0.3, 3.3 ± 0.4, and 3.5 ± 0.2 in the alpine grassland, temperate grassland, and temperate desert soils, respectively.

3.3. Distribution and Preservation of Solvent-Extractable Compounds in Soils of Varied Grassland Types

To compare the concentration and distribution of solvent-extractable compounds in different grassland soils, we categorized the samples based on the region (alpine versus temperate grasslands) as well as vegetation

types, that is, alpine meadow, alpine steppe, alpine desert steppe, temperate meadow steppe, temperate typical steppe, and temperate desert steppe. In addition, temperate desert was also included to represent soils developed under extreme aridity. The comparison revealed several interesting observations.

First of all, despite their varied OC contents (Table 1), the alpine and temperate grassland soils had similar amounts of total solvent-extractable compounds per unit of soil OC ($p > 0.05$; Figure 2a), ranging from 0.38 to 12.88 mg g^{-1} OC. This result is consistent with the similar abundances of solvent-extractable compounds in the leaves (Figure 2b) and roots (Figure 2c) of the dominant plants in the corresponding grasslands. Using equation (1), we calculated the upper and lower ranges for plant inputs of each compound class at every sampling site, assuming a 100% coverage by the dominating plant species typical for each vegetation type with the highest and lowest compound concentrations measured for the dominant species, respectively. As shown in Figure S3, the upper and lower ranges of plant inputs were overall similar for each compound class between the alpine and temperate grasslands, except that the lower range for carbohydrate inputs was lower in the alpine than temperate grasslands ($p < 0.05$). This result indicates that plant inputs of each compound class were generally similar (or could be even lower for carbohydrates) in the alpine relative to temperate grassland. However, the abundance of different compound groups varied significantly between the alpine and temperate grassland soils (Figure 2a). Consistent with our hypothesis, the former was more enriched with carbohydrates, cyclic lipids, and plant-derived compounds ($p < 0.05$), while total aliphatic lipids and microbial-derived compounds had similar concentrations in both grassland soils (Figure 2a). The enrichment of cyclic lipids in the alpine grassland soils may be associated with the higher OC-normalized concentration of cyclic lipids in the roots of the dominant plants in the alpine relative to temperate grasslands ($p < 0.05$; Figure 2c). By comparison, given a similar concentration and plant inputs of carbohydrates in the plants of temperate and alpine grasslands ($p > 0.05$; Figures 2b, 2c, and S3), the higher abundances of carbohydrates and plant-derived compounds in the alpine grassland soils likely reflect a lower decomposition stage of organic matter, leading to an accumulation of both labile components (i.e., carbohydrates) (Miltner & Zech, 1998; Otto & Simpson, 2005) and nonprocessed plant carbon. This conclusion is consistent with the higher OC contents and OC/N ratios in the alpine grasslands.

Among different vegetation types, alpine meadow had the highest concentration of cyclic lipids in the surface soils ($p < 0.05$; Figure 3). This may be explained by the high concentration of cyclic lipids in the roots of the dominant plants in the alpine meadow (*Korresia pygmaea*, *Kobresia humilis,* and *Korresia tibetca*; Figure 2c) as well as its higher BGB (Table 1). By comparison, the abundance of total carbohydrates was comparable in the alpine desert steppe soils to that in the alpine meadow soils ($p > 0.05$) but significantly higher than those in the alpine steppe and all temperate soils ($p < 0.05$; Figure 3). As trehalose was the dominant form of soil carbohydrates across this transect and had the highest abundance in the alpine desert steppe ($p < 0.05$), the high abundance of total carbohydrates in the soils of this vegetation type may be attributed to the high accumulation of trehalose as an antifreeze and antidrought protectant in soil microbes under cold and dry conditions (De Vries et al., 2012; Gorham, 1991). Also, in agreement with our hypothesis, the higher abundance of aliphatic lipids in the temperate desert and temperate desert steppe soils ($p < 0.05$; Figure 3) can be attributed to their preferential accumulation at warmer and drier climate (as discussed in the next section) (Pisani et al., 2014), since aliphatic lipids had similar abundances in the dominant plants of temperate relative to alpine grasslands (Figures 2b and 2c).

According to equation (2), the preservation percentage ranged from 0.02 to 3.52% for total solvent-extractable compounds and 0.002–0.585% for the plant-derived compounds. Although only a tiny fraction of annual NPP is preserved as plant-derived compounds in the surface soils, the long-term preservation of these compounds may account for a quite considerable fraction of annual NPP given the long accumulation time of surface soil OC (30–64 years) (L. H. Li et al., 1998; Yu et al., 2017). Overall, the preservation percentages of solvent-extractable and plant-derived compounds show very similar spatial patterns (Table 3). The preservation percentage was significantly higher in the alpine (0.58 ± 0.10 and 0.093 ± 0.015% for solvent-extractable and plant-derived compounds, respectively; $n = 63$) than temperate grassland soils (0.12 ± 0.01 and 0.028 ± 0.003%, respectively; $n = 42$; $p < 0.01$), mainly due to the much higher values in the alpine meadows (Table 3). This result is consistent with the higher abundance of plant-derived compounds in the alpine than temperate grassland soils (Figure 2) and confirms a better preservation of plant-derived organic matter in the alpine grasslands.

Table 3
Soil Bulk Density, Net Primary Productivity (NPP), Concentration and Preservation Percentage of Solvent-Extractable and Plant-Derived Compounds in the Surface Soils of the Alpine and Temperate Grasslands (Mean ± Standard Error, s.e.)

				Concentration (μg C g^{-1} soil)		Preservation percentage (%)	
Grassland type	Vegetation type	Soil bulk density (g cm^{-3})	NPP (g C m^{-2} yr^{-1})	Total extractable compounds	Plant-derived compounds	Total extractable compounds	Plant-derived compounds
Alpine (n = 63)	AM (n = 37)	0.90 ± 0.03 a	95.3 ± 7.9 a	470.25 ± 78.44 a	80.95 ± 15.04 a	0.84 ± 0.15 a	0.132 ± 0.023 a
	AS (n = 16)	1.09 ± 0.05 b	115.0 ± 18.2 b	73.32 ± 19.38 b	16.13 ± 5.21 b	0.19 ± 0.06 b	0.032 ± 0.009 b
	ADS (n = 10)	1.40 ± 0.08 c	59.8 ± 14.1 a	25.45 ± 5.50 b	3.09 ± 0.64 b	0.21 ± 0.08 b	0.041 ± 0.018 b
Temperate (n = 51)	TMS (n = 15)	1.09 ± 0.05 b	227.6 ± 6.4 c	75.52 ± 8.35 b	19.22 ± 2.54 b	0.13 ± 0.02 b	0.038 ± 0.007 b
	TS (n = 14)	1.33 ± 0.04 c	178.3 ± 9.1 d	58.43 ± 17.13 b	11.76 ± 4.15 b	0.11 ± 0.02 b	0.020 ± 0.003 b
	TDS (n = 13)	1.48 ± 0.04 cd	93.6 ± 8.1 a	22.03 ± 1.49 b	4.46 ± 0.26 b	0.13 ± 0.01 b	0.025 ± 0.002 b
	TD (n = 9)	1.60 ± 0.01 d	23.3 ± 6.5 e	16.51 ± 2.70 b	1.00 ± 0.24 b	1.18 ± 0.43 a	0.046 ± 0.013 b

Note. Letters indicate different levels among vegetation types ($p < 0.05$). Preservation percentage is calculated using equation (2). Abbreviations are defined in the footnotes of Table 1.

3.4. Environmental Influences on the Distribution of Solvent-Extractable Compounds

To further examine environmental influences contributing to the varied distribution of solvent-extractable compounds in the alpine and temperate grasslands, RDA models were first built based on the OC-normalized concentrations of different compound groups and environmental parameters (Figure 4). Temperate deserts were excluded due to the small number of samples. The first two axes displayed in the biplot diagram of RDA explain 56.5% and 46.4% of the variance in the alpine and temperate grassland soils, respectively, indicating good explanation power of the models. BGB, MAT, MAP, soil pH, and Al_d content are the most important variables contributing to compound variations in the alpine grasslands, while MAT, MAP, and AGB are the most important factors in the temperate grasslands (Figure 4), implying varied environmental controls on the distribution of solvent-extractable compounds in these two regions. In both grasslands, carbohydrates and microbial-derived compounds cluster together in the first quadrant as trehalose is the dominant component in both groups (Figure 4). By comparison, aliphatic lipids are clustered together with plant-derived compounds in the fourth quadrant due to the predominance of the latter in the former compound groups (Figure 4). RDA analysis using original, nontransformed data yielded similar results (Figure S4). Therefore, linear correlations were subsequently conducted to compare environmental effects on the concentration of carbohydrates versus aliphatic and cyclic lipids (excluding plant- and microbial-derived compounds) to avoid redundancy. Variables showing high correlations (i.e., $|r| > 0.7$) within the same environmental category in both regions are also excluded, including soil N content (correlated with soil OC), MAP (correlated with MAT), and Fe_d (correlated with Al_d). The comparison revealed varied distribution trends for the alpine and temperate grasslands as well as for different compound groups.

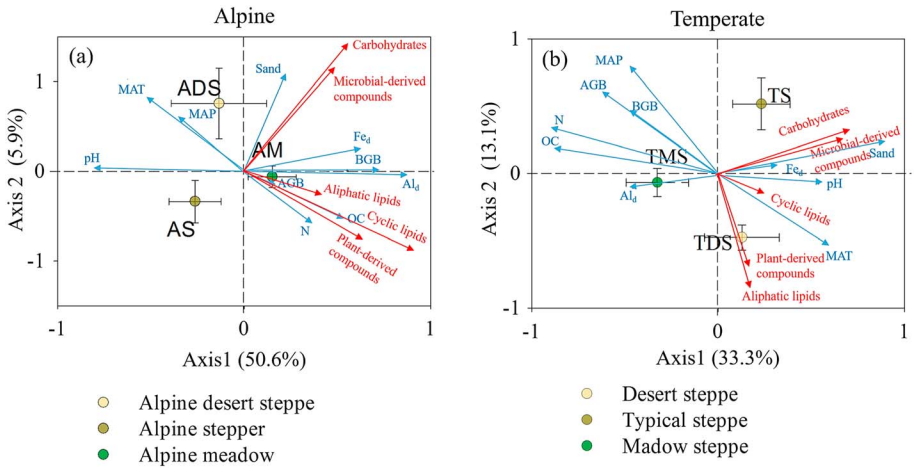

Figure 4. Ordination biplot diagram from redundancy analysis (RDA) displaying the effect of environmental factors on the concentration variations of solvent-extractable compounds in the (a) alpine and (b) temperate grasslands of China. Abbreviations are defined in the footnotes of Table 1. Data are natural log-transformed to ensure normal distribution.

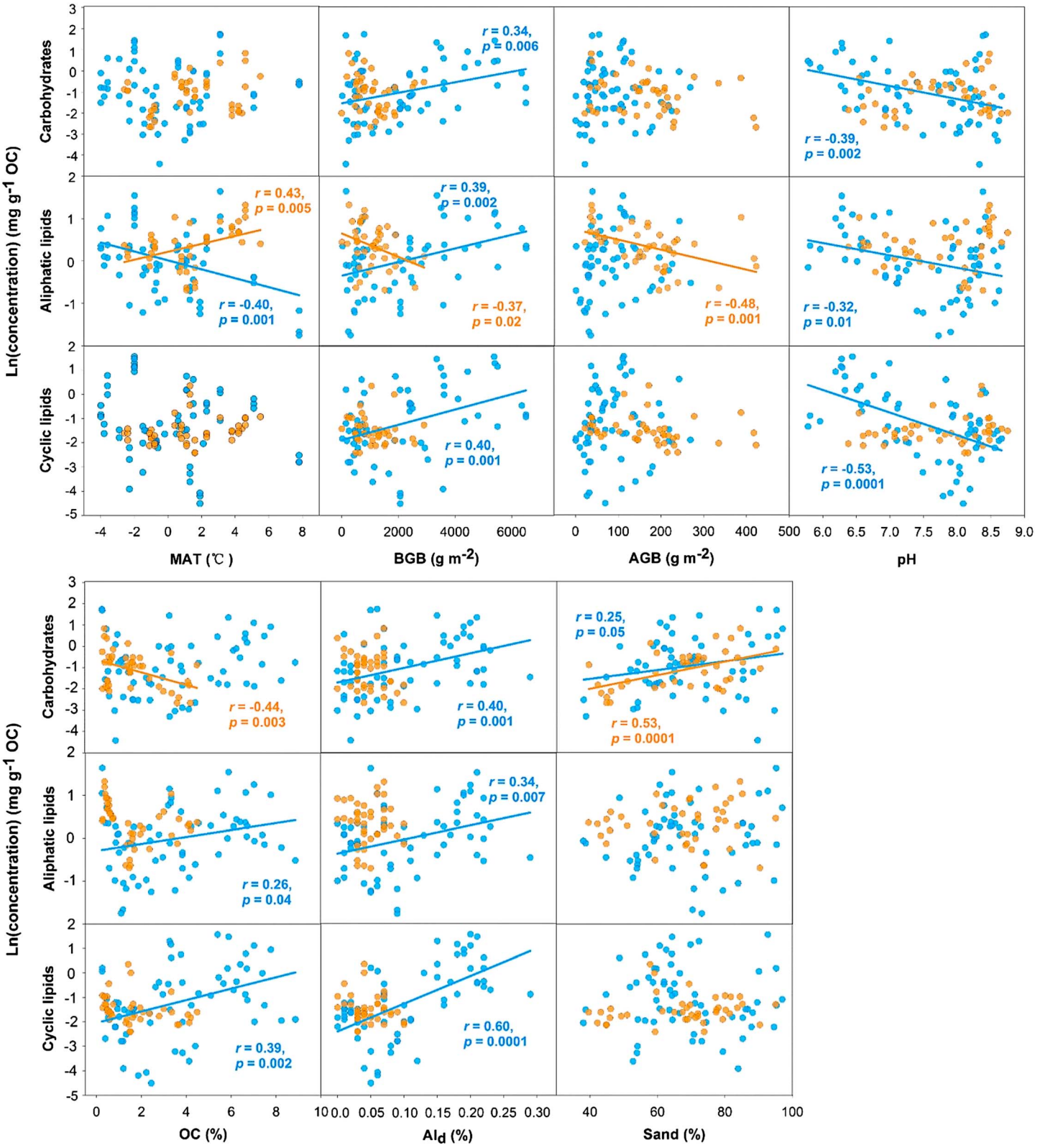

Figure 5. Relationships of the organic carbon (OC)-normalized concentrations of different compound groups and environmental variables in the alpine (blue dots) and temperate (orange dots) grassland soils of China. Concentrations are natural log-transformed. Blue and orange lines indicate correlations for the alpine and temperate grasslands, respectively ($p < 0.05$). Abbreviations are defined in the footnote of Table 1. Original data used in this figure are listed in supporting information Table S1.

First of all, all compound groups decrease with increasing soil pH in the alpine grassland soils ($p < 0.05$; Figure 5). The preferential preservation of lipids has been widely reported in acidic soils (Bull et al., 2000; Naafs et al., 2004; Nierop et al., 2005; Rosenberg et al., 2003) due to inhibited microbial activity (Bull et al., 2000; Nierop et al., 2005). While soils in this study have neutral to alkaline pHs, a similar pH influence seems to be operative for soil lipids in the alpine grasslands. By comparison, the influence of soil pH on the preservation of soil carbohydrates is rarely reported. The negative relationship between pH and carbohydrates in the alpine grasslands is partly attributed to the negative correlation between trehalose and soil pH ($p < 0.05$), in accordance with an increased fungal biomass (indicated by ergosterol) at lower soil pHs in the alpine grasslands ($p < 0.05$). This result contrasts with the findings by Naafs et al. (2004) and Nierop et al. (2005) where microbial-derived compounds decreased with decreasing soil pH, attributed to a declining microbial population and activity at low pHs. The discrepancy is mainly caused by the difference of soil pH, ranging from 3.8 to 6.9 in the referred studies (Naafs et al., 2004; Nierop et al., 2005) as opposed to 5.8–8.7 in the alpine grasslands of our study. As found by Fierer and Jackson (2006) and De Vries et al. (2012), soil microbial biomass peaked around pH 6 in a wide array of ecosystem types (spanning forest and grassland) in the United States and in the UK grassland soils and showed a decreasing trend in the pH range of 6–9, corroborating our result. In contrast, soil pH does not have a significant effect on any compound groups in the temperate grasslands ($p > 0.05$; Figure 5), suggesting that other environmental variables may play a more important role (in accordance with the RDA result).

Other than soil pH, both Al_d contents and BGB have strong positive effects on the abundance of all compound groups in the alpine grassland soils ($p < 0.05$; Figures 4 and 5). The former trend can be attributed to the strong sorption capacity of reactive Al oxides for soil aliphatic components (Cloy et al., 2014; Fleury et al., 2017; Mikutta et al., 2006; Ulrich et al., 1988) and carbohydrates (Cloy et al., 2014; Miltner & Zech, 1998), contributing to their enhanced preservation in the soil. By comparison, the latter trend is, to a large extent, a reflection that plant roots are a key source of solvent-extractable compounds in the alpine grassland soils and that such input signals are not significantly altered by decomposition processes, which are inhibited by low temperatures in the alpine regions (Baumann et al., 2009; Liu et al., 2017). This conclusion also supports the RDA result and is consistent with the findings by Liu et al. (2012) that BGB is the main source for soil OC in the topsoil of alpine grasslands on the QTP, given their much higher ratios of BGB:AGB compared with temperate grasslands (Table 1). Notably, the Al effect is not observed in the temperate grasslands ($p > 0.05$; Figure 4) due to the extremely low Al_d contents in the temperate relative to alpine grasslands ($p < 0.05$; Table 1). Furthermore, in sharp contrast to the alpine grasslands, aliphatic lipids display a negative relationship with both BGB and AGB in the temperate grassland soils ($p < 0.05$; Figure 5). We hence postulate that decomposition rather than input processes dominates the distribution of aliphatic lipids in the temperate grasslands (which is further supported by the discussion below).

Contrasting relationships are also observed for the solvent-extractable compounds with MAT and soil OC contents between the alpine and temperate grasslands (Figure 4). With an increase in MAT, aliphatic lipids decrease in the alpine grassland soils but increase in the temperate ones ($p < 0.01$; Figure 5). This finding supports our hypothesis for the varied influence of the decomposition and input processes in these two grasslands, as increasing temperature is known to enhance both SOM degradation and plant inputs to the soil (Davidson & Janssens, 2006). In the temperate grasslands where increasing temperature induce soil OC loss due to accelerated microbial decomposition (Yang et al., 2010), aliphatic lipids become enriched relative to soil OC due to their chemical recalcitrance and a preferential decay of more labile SOM components (such as carbohydrates and proteins) (Otto & Simpson, 2005; Pisani et al., 2014) at higher temperatures. Conversely, in the alpine grasslands where increasing MAT induce soil OC increase under stimulated plant growth (Liu et al., 2017; Yang et al., 2010), the abundance of aliphatic lipids is mainly diluted by an enhanced input of nonlipid (possibly labile) components rather than altered decomposition processes, as degradation of labile components is relatively inhibited at low temperatures.

To disentangle the effects of plant input and decomposition processes mediated by temperatures, a partial correlation analysis was conducted. In the alpine grasslands, carbohydrates, aliphatic and cyclic lipids remain positively correlated with BGB when the effect of MAT is controlled for ($p < 0.01$; Table 4). However, correlations between aliphatic lipids and MAT are weakened when BGB is controlled for ($p = 0.02$; Table 4). In addition, aliphatic lipids are no longer correlated with soil pH or Al_d content when BGB is controlled for ($p > 0.05$;

Table 4
Values of r From Partial Correlation Tests Between Solvent-Extractable Compounds in Grassland Soils (Excluding Deserts) and Key Environmental Variables With Certain Variables Being Controlled

Tested variable	Alpine (n = 63)			Temperate (n = 42)			Controlled variable
	Carbohydrates	Aliphatic lipids	Cyclic lipids	Carbohydrates	Aliphatic lipids	Cyclic lipids	
MAT	−0.04	−0.40**	−0.21	0.24	0.43**	0.25	None
	0.10	−0.30*	−0.07	0.20	0.36*	0.23	BGB
	−0.03	−0.38**	−0.19	0.12	0.34*	0.16	AGB
BGB	0.34*	0.39**	0.40**	−0.17	−0.37*	−0.11	None
	0.36*	0.28*	0.35*	−0.11	−0.29	−0.04	MAT
	0.34*	0.27*	0.24	−0.14	−0.26	−0.06	MAP
AGB	0.04	0.17	0.10	−0.25	−0.48**	−0.22	None
	0.03	0.10	0.06	−0.16	−0.32*	−0.10	MAT
	0.03	0.15	0.07	−0.22	−0.09	−0.10	MAP
pH	−0.39**	−0.32*	−0.53**	0.27	0.13	0.25	None
	−0.39**	−0.34*	−0.54**	0.13	−0.42**	0.08	MAT
	−0.38**	−0.29*	−0.54**	0.23	−0.24	0.17	MAP
	−0.25	−0.14	−0.41**	0.24	0.05	0.23	BGB
	−0.39**	−0.33*	−0.54**	0.18	−0.10	0.17	AGB
Al_d	0.40**	0.34**	0.60**	−0.25	−0.02	−0.20	None
	0.41**	0.47**	0.67**	−0.21	0.22	−0.14	MAT
	0.39**	0.28*	0.58**	−0.18	0.17	−0.12	MAP
	0.30*	0.21	0.52**	−0.21	0.10	−0.18	BGB
	0.40**	0.31*	0.59**	−0.18	0.16	−0.14	AGB

Note. ** and * indicate significant correlations at $p < 0.01$ and <0.05, respectively. Abbreviations are defined in the footnote of Table 1. Data are natural log-transformed to ensure normal distribution.

Table 4), suggesting a dominant impact of BGB in the alpine grasslands. In contrast, in the temperate grasslands, aliphatic lipids are not correlated with plant biomass (AGB or BGB) when MAT is controlled for ($p > 0.05$; Table 4). However, aliphatic lipids remain positively correlated with MAT ($p < 0.05$; Table 4) when plant biomass is controlled for. Thus, these results further support our hypothesis that climate-mediated decomposition processes control the preservation and distribution of aliphatic lipids in the temperate grasslands, while plant input has a stronger impact in the alpine grasslands.

Furthermore, both aliphatic and cyclic lipids increase with soil OC in the alpine grassland soils ($p < 0.05$; Figure 5), reflecting coupled variation of soil OC and lipid components under the main influence of BGB inputs ($p < 0.05$). Conversely, carbohydrates decrease with increasing soil OC in the temperate grassland soils ($p < 0.05$; Figure 5), possibly due to dilution by other SOM components such as microbial-processed degradation products (Fierer et al., 2009).

Finally, sand content is positively correlated with carbohydrates in the temperate grasslands ($p < 0.05$), while this trend is only marginally significant in the alpine grasslands ($p = 0.05$; Figure 5). This observation seems to suggest a better preservation of carbohydrates in coarse-textured soils that are characterized by a lower microbial activity (De Vries et al., 2012; Fierer & Jackson, 2006). This trend is not observed for lipids, suggesting varied preservation mechanisms for the labile, microbial-dominated carbohydrates versus chemically resistant, plant-dominated lipids in the soil. The above results (both Pearson and partial correlations) were checked by similar analyses of original, nontransformed data, which yielded highly consistent results (Tables S2 and S3 and Figure S4). Therefore, the analysis of both nontransformed and log-transformed data using three independent statistical methods supports our findings.

4. Conclusions and Implications for Soil OC Preservation

This study presents the first broad-scale investigation on the composition and distribution of solvent-extractable compounds (including carbohydrates and aliphatic and cyclic lipids) in surface soils across the alpine and temperate grasslands of China. Although the investigated biomarkers make up only a tiny fraction (0.03–0.91%) of soil OC, they represent 41 ± 3% of the solvent-extractable OC. Given the long accumulation time of soil OC in these grasslands (30–64 years), the latter is a nonnegligible fraction of NPP preserved in the soil in the long term. More importantly (as mentioned previously), the source and diagenesis information

carried by biomarkers may be treated as conservative reflections of the behavior of soil OC components of similar origins (Feng & Simpson, 2011; Kögel-Knabner, 2002; Schmidt et al., 2011).

Consistent with our hypothesis, distinct composition was observed in the investigated SOM components between the two regions. The alpine grassland soils were more enriched with carbohydrates, cyclic lipids, and plant-derived compounds relative to the temperate grasslands despite similar plant inputs, reflecting a better preservation of labile components (i.e., carbohydrates) and nonprocessed plant carbon due to inhibited SOM decomposition at low temperatures. In contrast, aliphatic lipids were more concentrated in the temperate desert and temperate desert steppe soils due to their selective accumulation with the decay of labile compounds. Using both RDA and regression analyses, we also demonstrate different mechanisms governing the distribution of solvent-extractable compounds in the soils of the two regions. While plant biomass (BGB) and soil properties (pH and Al_d content) have important effects on compound concentrations in the alpine grasslands together with climatic variables (MAT and MAP), the latter play a dominant role in the temperate grasslands. In particular, contrasting relationships are observed for the solvent-extractable compounds with MAT, soil OC contents, and (partly) plant biomass between the alpine and temperate grasslands. While aliphatic lipids accumulate with increasing MAT and decreasing OC in the temperate grasslands due to the preferential decay of more labile SOM, they tend to decrease with increasing MAT in the alpine grasslands owing to dilution by an enhanced plant input of nonlipid components. Collectively, these results suggest that plant input is the dominant factor governing the distribution of solvent-extractable compounds in the alpine grasslands, while climate-mediated decomposition processes control their spatial variations in the temperate grasslands. Such information is difficult (if not impossible) to tease apart with bulk OC analysis. Hence, the solvent-extractable biomarkers measured in this study provide new information on the relative contribution of plants versus microbes as well as on the varied fate of soil OC components in contrasted grasslands.

Another important finding of this study is that plant roots (BGB) exert a dominant influence on the distribution of solvent-extractable components in the alpine grassland soils but not in the temperate counterparts and that surface soils in these two regions have varied response to climatic variations. This result suggests that soil OC and plant biomass may be decoupled in their response to climate change depending on the region: alterations to soil OC content and composition may not reflect vegetation (especially aboveground biomass) changes under global change. With the predicted warming of the QTP and arid and semiarid regions in China, it is interesting to speculate the stabilization and dynamics of SOM and how these changes may manifest themselves or be detected using the molecular tracers described in this study. With a projected warmer and wetter climate (Chen et al., 2013, and references therein), the QTP is anticipated to experience increased grass productivity (Yang et al., 2010), which may lead to enhanced plant carbon input into soils and better preservation of labile and plant-derived SOM in the alpine grasslands. By comparison, in the arid and semiarid temperate grasslands, increase in plant biomass is limited by enhanced evapotranspiration associated with drier climate (Bai et al., 2004). Together with enhanced decomposition associated with increased MAT (Bai et al., 2004; Yang et al., 2010), these changes may result in increased decomposition of labile SOM, leading to a selective accumulation of aliphatic SOM.

As the complex chemistry of SOM and its interactions with the environmental parameters limit our ability to predict feedbacks between soil OC and climate change (Kögel-Knabner, 2002; Schmidt et al., 2011), the broad spectrum of solvent-extractable compounds provides a powerful means to attribute source and fate of these various OC pools. Overall, our findings add a novel facet of information on soil carbon characteristics in the grasslands of China and highlight the contrasts of key mechanisms (or variables) influencing distribution of solvent-extractable OC in the alpine versus temperate grassland soils. In the context of climate change, alterations to the input and decomposition processes may have varied impacts on soil carbon cycling in these two regions. Teasing apart mechanisms governing the varied influence of aboveground and belowground inputs on SOM will also provide key information for predicting future soil OC dynamics.

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