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# Contrasting pathways of carbon sequestration in paddy and upland soils

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## Abstract

Paddy soils make up the largest anthropogenic wetlands on earth, and are characterized by a prominent potential for organic carbon (C) sequestration. By quantifying the plant- and microbial-derived C in soils across four climate zones, we identified that organic C accrual is achieved *via* contrasting pathways in paddy and upland soils. Paddies are 39%–127% more efficient in soil organic C (SOC) sequestration than their adjacent upland counterparts, with greater differences in warmer than cooler climates. Upland soils are more replenished by microbial-derived C, whereas paddy soils are enriched with a greater proportion of plant-derived C, because of the retarded microbial decomposition under anaerobic conditions induced by the flooding of paddies. Under both land-use types, the maximal contribution of plant residues to SOC is at intermediate mean annual temperature (15–20°C), neutral soil (pH~7.3), and low clay/sand ratio. By contrast, high temperature (~24°C), low soil pH (~5), and large clay/sand ratio are favorable for strengthening the contribution of microbial necromass. The greater contribution of microbial necromass to SOC in waterlogged paddies in warmer climates is likely due to the fast anabolism from bacteria, whereas fungi are unlikely to be involved as they are aerobic. In the scenario of land-use conversion from paddy to upland, a total of 504 Tg C may be lost as $CO_2$ from paddy soils (0–15 cm) solely in eastern China, with 90% released from the less protected plant-derived C. Hence, preserving paddy systems and other anthropogenic wetlands and increasing their C storage through sustainable management are critical for maintaining global soil C stock and mitigating climate change.

**KEYWORDS**
biomarker approach, carbon sequestration, climate zone, lignin phenol, microbial necromass, paddy and upland

Xiangbi Chen and Yajun Hu contributed equally to this work.

## 1 | INTRODUCTION

Increasing soil organic carbon (SOC) sequestration through optimized agricultural management is a global priority for achieving food security and mitigating climate change (Lal, 2004; Schmidt et al., 2011). However, global cropland soils have lost 40–133 Pg C in relation to land-use change, intensive agriculture, and the associated disturbance and erosion (Pugh et al., 2015; Sanderman et al., 2017). One exception is that paddy soils, classified as Hydragric Anthrosols, are characterized by a prominent organic C sequestration potential, although subjected to intensive anthropogenic activities (Pan et al., 2004; Tian et al., 2015). SOC content in paddies is 12%–58% higher than adjacent agricultural upland (Guo & Lin, 2001). This is of great significance for increasing soil C stock and stabilizing climate, given the extensive area (167 million ha) covered by paddy fields globally (Liu et al., 2019).

While our knowledge about soil C sequestration has been significantly advanced by the recent conceptual and technological breakthroughs (Cotrufo et al., 2019; Lehmann et al., 2020), how soils can be managed to efficiently sequester C remains a huge research gap. Emerging evidence reveals that SOC storage depends on the retention of C derived from both plants and microorganisms (Schmidt et al., 2011; Sokol et al., 2019; Zhu et al., 2020). Partitioning SOC into plant- and microbial-derived C aids both in our understanding of the C formation pathways, as well as the mechanisms of SOC stability/persistence (Joergensen, 2018; Liang et al., 2017). Plant C inputs are the major energy source for microorganisms, and through microbial processing and assimilation, they can be converted into microbial-derived C (Liang et al., 2019; Sokol et al., 2019). Microbial-derived C can be physically protected in organo-mineral associations, because of its close proximity and interactions with the soil mineral matrix, and therefore it tends to be more stable than the unprocessed plant-derived C (Liang et al., 2017; Sokol et al., 2019). Microbial products of decomposition, mainly from necromass and other by-products, contribute significantly to stable SOC (Chen, Xia, et al., 2020; Cotrufo et al., 2013). Although considered less stable due to the lack of physical protection by minerals, plant residues may also accumulate and persist in soils under anaerobic conditions (Keiluweit et al., 2017). Consequently, the size and stability of the SOC pool are largely dependent on the retention of C from both plant and microbial origins (Kallenbach et al., 2016; Ma et al., 2018), which are strongly controlled by land use and the associated environmental conditions (Schmidt et al., 2011). During the past years, it has been well established that SOC of plant and microbial origins can be well assessed by lignin phenols and amino sugars, respectively (Crow et al., 2009; Liang et al., 2019; Ma et al., 2018).

Paddies with rice mostly grown under flooded lowland conditions make up the largest anthropogenic wetlands on earth (Kögel-Knabner et al., 2010; Pan et al., 2004). Paddy soils are widely distributed across tropical, subtropical, and temperate climate zones in Asia, and supply food for more than 50% of the world's population (Kögel-Knabner et al., 2010; Nguyen, 2005). Waterlogged paddy and well-drained upland fields are often located in close proximity, depending on the local topography (Cai, 1996). In anaerobic environments, the suppression of aerobic microbial activity and the consequent constrained production of pivotal enzymes, such as phenol oxidase and hydrolase, are proposed in $O_2$-limited conditions (Freeman et al., 2001). Hence, mineralization rates of organic substrates are much more slowly because of the thermodynamic constraints on microbial decomposition (Keiluweit et al., 2017). The formation of Fe-organic matter associations through organic compound adsorption or co-precipitation with Fe oxides induced by the frequent alternation of flooding and drying contributes to C preservation in paddy soils (Bi et al., 2021; Lalonde et al., 2012; Wang et al., 2017). Considering the diverse edaphic properties and climatic conditions, site-specific observations are insufficient to extrapolate the mechanism for greater long-term C sequestration in paddy than upland soils.

Here, we compared the biochemical origin and stability of SOC between paddy and upland soils at a continental scale. Paired paddy and upland soils were collected from four main grain-producing areas distributed in mid temperate, warm temperate, subtropical, and tropical climate zones across eastern China. Accumulated biomarkers of plant- and microbial-derived C, that is, lignin phenols and amino sugars, respectively, have been quantitatively assessed. Our results revealed the underlying mechanisms for the more efficient C sequestration in paddy than in adjacent upland soils.

## 2 | MATERIALS AND METHODS

### 2.1 | Soil collection

Four climate zones across eastern China were selected: mid temperate, warm temperate, subtropics, and tropics (Figure S1; Zheng et al., 2021). Both paddy and upland were widely distributed in each climate zone. The cropping systems in paddy fields were single-rice in both mid temperate and warm temperate, single- or double-rice in subtropics, and double- or triple-rice in tropics. The corresponding cropping systems in the upland fields were one season of crops, two seasons, two seasons, and two or three seasons, respectively, mainly including maize, soybean, wheat, canola, peanut, sweet potato, sugarcane (Table S1). The typical soils were Mollisols in mid temperate, Inceptisols in warm temperate, and Ultisols in both subtropics and tropics. The mean annual temperature (MAT) and precipitation (MAP) across the four climatic zones ranged from 4.1–24.2°C and 556–1955 mm (Table S1), respectively.

In each climate zone, 10 counties were selected based on the soil distribution map from the Resources and Environmental Science Data Center of the Chinese Academy of Sciences (http://www.resdc.cn/). In each county, soil samples (0–15 cm depth) from six paired adjacent paddy and upland fields were collected in the nongrowing season from December 2016 to May 2017. Soils of these sites were developed from the typical soil types and were distributed approximate 0.5 km apart. Based on field investigations, the current land-use type of the selected plots has remained stable for more

than 30 years. A total of 240 paired soil samples were collected, and each sample contained a mixture of six to eight surrounding soil cores within one plot. After removing visible plant roots and organic debris, soil samples were dried, ground, and passed through a 2-mm mesh sieve for soil pH and particle size distribution assessment. A portion of these soils was passed through a 0.15-mm mesh sieve for the SOC, total N, and biomarkers analysis. All samples were subjected to basic soil properties analysis. One pair of paddy and upland soils was randomly selected from each county and subjected to analysis of lignin phenols and amino sugar contents ($n$ = 10 in each climatic zone).

## 2.2 | Basic soil properties

SOC content was determined through a wet digestion method using potassium dichromate (Kalembasa & Jenkinson, 1973). Soil total N was determined using dry combustion with an elemental analyzer (Vario EL III, Elementar GmbH). Soil pH was determined in 1:2.5 (w/v) of soil and deionized water. Particle size distribution was assessed according to the method described by Miller and Schaetzl (2011). Briefly, 0.3–0.5 g soil was weighted and placed into a 25-ml glass vial. A quantity of 8 ml 50 g $L^{-1}$ sodium hexametaphosphate was added, and then the vials were left to stand for 2 h for upland soils and 16 h for paddy soils. Subsequently, all samples were placed in a 30 kHz ultrasonic bath for 15 min. The soil suspension was then added into a beaker containing 900 ml distilled water and measured by laser diffraction particle size analyzer (Mastersizer 2000, Malvern Instruments Ltd.). According to the soil taxonomy of the US Department of Agriculture (USDA), the particle size distribution was divided into three components comprising clay (<0.002 mm), silt (0.002–0.05 mm), and sand (0.05–2 mm).

## 2.3 | Analysis of lignin phenols and amino sugars

Lignin phenols were quantified by the alkaline CuO oxidation to release lignin monomers, followed by gas chromatography according to the method developed by Hedges and Ertel (1982). Briefly, 0.1–0.5 g soil was mixed with 500 mg CuO, 100 mg ammonium iron (II) sulfate hexahydrate [$Fe(NH_4)_2(SO_4)_2{\cdot}6H_2O$], 50 mg glucose, 0.4 ml internal standard (10 mg ethyl vanilline dissolved in 100 ml 2 M NaOH solution) and 15 ml of 2 M NaOH solution in Teflon vessel. All vessels were heated at 170°C for 2 h and then kept overnight at room temperature with continuous magnetic stirring. The oxidation products were transferred into a centrifuge tube with 10 ml water to rinse Teflon vessel and stirrer. After centrifugation (3000 rpm, 15 min), supernatant was transferred into another centrifuge tube, acidified to pH 1.8–2.2 with 6 M HCl and kept in the dark for 1 h. After centrifugation (4000 rpm, 25 min), supernatant was transferred into volumetric flask and made up to 100 ml with water. The solution was extracted with ethyl acetate and evaporated at rotary evaporator (temperature below 38°C). Residues were dissolved with 0.5 ml second internal standard solution, then transferred into a 3 ml derivative bottle and then dried under $N_2$ flux. Residues were dissolved with 50 μl pyridine and 100 μl N,O-bis-(trimethylsilyl) trifluoroacetamide (BSTFA), derivatized for 10 min at 60°C to yield trimethylsilyl (TMS) derivatives before quantification.

Microbial necromass was assessed by the analysis of amino sugars according to Zhang and Amelung (1996). The amino sugars extracted by the following procedures included the dead and living microbial origins with a slight contribution from living microbial biomass (Chen et al., 2018; Simpson et al., 2007). Approximately 0.15 g of air-dried soils (0.15 mm) was hydrolyzed with 10 ml 6 M HCl at 105°C for 8 h. An internal standard (myo-inositol) was added, and the solution was filtered and adjusted to pH 6.6–6.8 with a 0.4 M KOH solution, and then centrifuged (2000 $g$ for 10 min). The supernatant was freeze-dried, 5 ml methanol was added to dissolve the residues, and then the solution was dried by $N_2$ gas at 45°C. With the addition of quantitative standard (*N*-methyl glucosamine), amino sugars were transformed into aldononitrile derivatives by heating in 0.3 ml of a derivatization reagent containing 32 mg $ml^{-1}$ of hydroxylamine hydrochloride and 40 mg $ml^{-1}$ of 4-(dimethylamino)-pyridine in pyridine and methanol (4:1; v/v) at 75–80°C for 35 min. After cooling, the solution with 1 ml acetic anhydride was reheated at 75–80°C for 25 min for acetylation and then freeze-dried. Excessive derivatization reagents were removed by extracting with 1 M HCl and deionized water, and then the dichloromethane phase containing amino sugar derivatives were dried with $N_2$ gas at 45°C. Amino sugar derivatives were dissolved with 200 μl ethyl acetate-hexane (1:1) before quantification.

Derivatives of lignin phenols and amino sugars were analyzed by an Agilent 6890A gas chromatograph (Agilent Technologies) equipped with an HP-5 column (30 m × 0.25 mm × 0.25 μm) and a flame ionization detector. For lignin phenols, the $N_2$ flow rate was 1.5 ml $min^{-1}$. The column was heated from 100°C to 140°C at a rate of 8°C $min^{-1}$, and to 170°C at 4°C $min^{-1}$ and held for 5 min, and then to 300°C at a rate of 10°C $min^{-1}$ and held for 4 min. Injector and detector temperatures were kept at 300°C. For amino sugars, the $N_2$ flow rate was 0.6 ml $min^{-1}$. The temperature program was set as follows: 120°C held for 1 min, increased at 10°C $min^{-1}$ to 250°C and held for 2.5 min, increased at 20°C $min^{-1}$ to 270°C and held for 2 min. The injector and detector temperature was kept at 250°C. Quantification was achieved using internal standards to assess the recovery efficiency during extraction procedures. External quantification standards were used to normalize the response factor for different amino sugars and lignin phenols separately.

The amount of lignin phenols was calculated as the sum of vanillyl (V)-, syringyl (S)-, and cinnamyl (C)-type phenols. The ratios of C/V and S/V and acid/aldehyde ratios for V and S phenols ($(Ad/Al)_V$ and $(Ad/Al)_S$) indicate the degree of microbial alteration and oxidation of lignin (Kögel, 1986). According to Hautala et al. (1997), two thirds of the V phenols in lignin structures are not released by CuO oxidation, whereas S phenols are released with 90% efficiency. The release efficiency of C phenols is assumed as 100%. The plant-derived C in total SOC ($P$) is estimated by the following equation:

$$P = \frac{\left(\frac{V}{33.3\%} + \frac{S}{90\%} + C\right)}{8\% \times \mathrm{SOC}} \times 100\%$$

where *V*, *S*, and *C* represent the content of carbon in the V-, S-, and C-type phenols (g $kg^{-1}$), respectively. SOC represents the total SOC content (g $kg^{-1}$). Eight percent represents the minimum of lignin content in the plant residues of main crops (Burgess et al., 2002).

Amino sugars were summarized as glucosamine, galactosamine, and muramic acid. Muramic acid was used as biomarker for bacterial necromass (Parsons, 1981). Since glucosamine can be found both in fungal and bacterial cell walls (Glaser et al., 2004), fungal-derived glucosamine was calculated according to the molar ratio of glucosamine and muramic acid of 2:1 in bacterial cells (Chen et al., 2018; Engelking et al., 2007). Fungal and bacterial necromass were calculated by multiplying the content of fungal glucosamine by 9 and muramic acid by 45, respectively (Liang et al., 2019), and total microbial necromass C was the sum of fungal and bacterial necromass C (Sradnick et al., 2014).

## 2.4 | Data and statistical analysis

The differences of SOC-normalized biomarker content between paddy and upland soils in the same climate zone were tested using the paired-sample *t* test. The differences of SOC-normalized biomarkers among the four climate zones for the same land use were examined using one-way ANOVA, followed by Duncan's test ($p < 0.05$ as significant). Homogeneity of variances was tested by Levene's test, and normal distribution of residues was tested by the Shapiro test. Correlations of biomarkers with environmental parameters were tested after the natural-log transformation of nonnormally distributed data. If the normal distribution was not achieved after data transformation, two-tailed Spearman linear correlation was used instead. Correlations were considered to be significant at a level of $p < 0.05$. These statistical analyses were performed using SPSS 18.0 for windows (SPSS In.). The figures were plotted using Origin 8.5 (OriginLab).

Effects of environmental variables on the SOC-normalized contents of lignin phenols or amino sugars were assessed by random forest analysis. The variables indicating time-integrated environmental factors were selected, including climate (MAT in past 10 years), edaphic properties (clay/sand ratio, pH, SOC, total N and C/N ratio), and biotic characteristics of microbial necromass constituents (fungal glucosamine, bacterial muramic acid, and ratio of fungal glucosamine/bacterial muramic acid). Random forest models were specifically developed based on classification and regression tree (CART) methodology, which can handle nonlinear and nonadditive relationships (Breiman, 2001). The percentage increase of the mean squared error (%IncMSE) was reported to rank the relative importance of the environmental variables with the "randomForest" package in R (Liaw & Wiener, 2002). The significance of the effect of each environmental predictor on the response variable was reported using the 'rfPermute' package in R (Archer, 2016).

Structural equation modeling framework was applied to further investigate the direct and indirect effects of environmental variables on the SOC-normalized lignin phenols and amino sugars. To simplify the model, MAT as climate factor, the edaphic properties of pH and soil texture as clay/sand ratio, and the biotic factor as fungi/bacteria ratio were selected based on the screening factors from random forest models. The structural equation modeling (SEM) was carried out by the Amos 23.0 software package (Small Waters Corporation).

# 3 | RESULTS

## 3.1 | Lignin phenol and amino sugar accumulation in paddy and upland agricultural soils

SOC content in paddies was 78% higher than that in adjacent uplands across all climate zones (Figure 1a). The differences of SOC between paddy and upland soils were greater in warmer climates (tropics and subtropics, where SOC was 91%–127% greater in paddy than in upland) than in cooler climates (warm temperate and mid temperate with 39%–53% difference).

Lignin phenols accounted for 9–57 mg $g^{-1}$ SOC (Figure 1b) and were 3.3 times greater in paddy than in upland soils (Figure S2) ($p < 0.05$, with a nonsignificant exception in warm temperate). The highest levels of lignin phenols in paddy soils were found in subtropics, whereas in uplands, the highest levels occurred in warm temperate. Lignin constituents in both soils across all climate zones were dominated by V-type phenols (accounting for 46%–54% of total lignin phenols), followed by S- (37%–41%) and C-type phenols (7%–16%; Figure S3). The lignin phenols in paddy soils exhibited greater C/V ratios and lower acid/aldehyde ratios of S-type phenols, that is $(Ad/Al)_S$, than in upland soils (Figure 2).

In contrast, amino sugars, ranging from 30 to 94 mg $g^{-1}$ SOC in all samples, were lower in paddy than in upland soils across all climate zones ($p < 0.05$, Figure 1c; Figure S4b). The content of amino sugars was greater in warmer than in cooler climates in both croplands (Figure 1c), reflecting an increased degree of microbial processing with temperature. The contents of both fungal and bacterial biomarkers were lower in paddy than upland soils across all climate zones, with a greater difference for fungal biomarkers (37% lower in paddy) than bacterial biomarkers (27%; $p < 0.05$, Figure 3).

To trace the origins of SOC sequestration in paddy and upland soils, we calculated the plant residue-derived C and microbial necromass C using the biomarkers of lignin phenols and amino sugars, respectively (Figure 4; Figure S5). The amount of plant-derived C in paddies was 1.2–6.5 times that in uplands, whereas the corresponding value of microbial-derived C was only 0.7–1.4 times (Figure S5). Accordingly, 33%–54% of the SOC accumulated in paddy soils

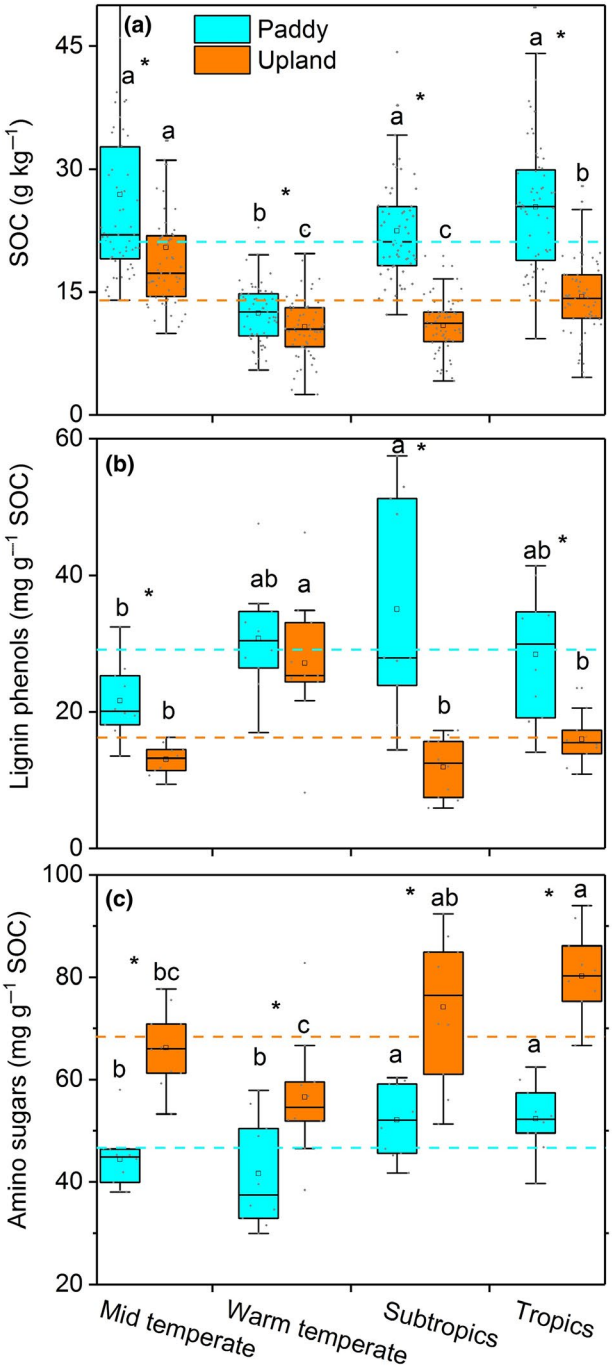



**FIGURE 1** Contents of soil organic C (SOC; a) and SOC-normalized lignin phenols (b) and amino sugars (c) in paddy and upland soils across the four climate zones. * represent significant differences at $p < 0.05$ between paddy and upland soils (paired-sample *t* test). Lowercase letters represent significant differences at $p < 0.05$ among the four climate zones within paddy or upland soils (one-way ANOVA with LSD test). The horizontal dashed lines show the average values (across four climates) for paddy (blue) and upland (orange) soils

derived from plant residues, whereas they only contributed 19%–42% in uplands (Figure 4). Concurrently, 28%–36% of SOC stored in paddies was microbial derived compared to 40%–59% in uplands (Figure 4).

### 3.2 | Divergent controls on lignin phenol and amino sugar accumulation in paddy and upland soils

Nine variables reflecting the effects of climate conditions, edaphic properties, and biotic parameters were used to explain the SOC-normalized contents of lignin and amino sugars (Figure 5). These variables used in the random forest models explained 13% and 35% of the total variance of lignin phenols, and 55% and 54% of the total variance of amino sugars in paddy and upland, respectively. The most important factors controlling the lignin phenols contents were clay/sand ratio, fungi, and MAT in paddies, and clay/sand ratio, pH, MAT, and bacteria in uplands (Figure 5a). The amino sugar accumulation in both soils was mainly dependent on pH and the constituents of microbial necromass (Figure 5b). Additionally, SOC, MAT, and total N influenced the amino sugars in uplands. Correlation analysis showed that neutral soil (pH~7.3), lower clay/sand ratio, and higher fungi/bacteria ratio in the microbial necromass were responsible for the higher accumulation of lignin phenols (Figure 6). In contrast, higher temperature (~24°C), lower soil pH (~5), higher clay/sand ratio, and lower fungi/bacteria ratio were favorable for accumulation of amino sugars (Figure 6; Table S2).

To identify and quantify the relationships between the SOC-normalized contents of lignin phenols and amino sugars and the main environmental variables, we further employed SEM. The validated SEMs mirrored the results from random forest models (Figure S6). For the lignin phenols in both croplands, MAT and pH had positive effects, whereas clay/sand ratio had negative effects. For the amino sugars, MAT and clay/sand ratio had positive effects, while pH showed negative effects.

## 4 | DISCUSSION

### 4.1 | Comparison of organic C content in paddy and upland soils

Greater SOC content in paddies than adjacent uplands was found in the upper soil horizons across all climate zones, regardless of agricultural managements and edaphic properties. The plow pan can hinder rice roots from penetrating into the subsurface of paddy, which secures more root-derived C in the surface layer of paddy relative to upland. This is evidenced by the greater differences of SOC between the surface and subsurface layers in paddy than in upland (Xie et al., 2007). The aboveground plant biomass input, 1.6–2 times greater in paddy rice than in upland wheat and maize (Chen, 2016; Liu et al., 2019), also contributes to the greater SOC in paddy soils. In addition, the $O_2$ limitation in paddy caused by flooding constrains microbial activity, and decreases the production of oxidative enzymes involved in plant residue decomposition (Huang & Hall, 2017) as well as other processes involving alternative electron acceptors to $O_2$ (Fan et al., 2020). As a result, an extended residence time of organic substances in paddy relative to upland can be expected (Keiluweit et al., 2016). The greater differences of SOC between paddy and upland in

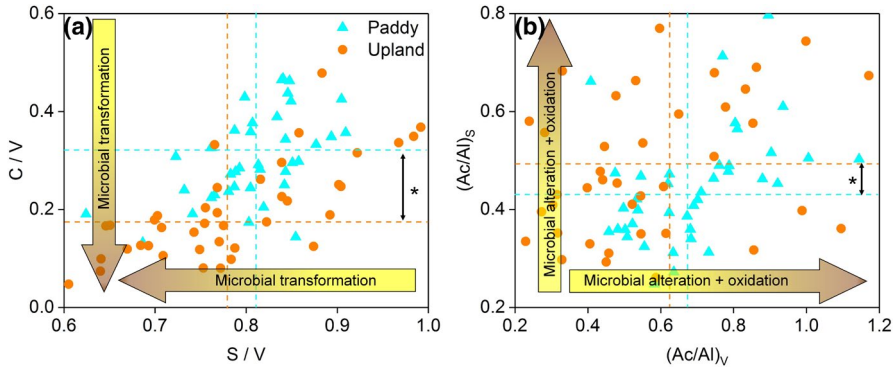



**FIGURE 2** Ratios of cinnamyl to vanillyl (C/V) vs syringyl to vanillyl (S/V) (a) and acid to aldehyde ratios of syringyl and vanillyl units $(Ac/Al)_S$ vs $(Ac/Al)_V$ (b) for lignin phenols in paddy and upland soils. Blue- and brown-dashed lines represent average values in paddy and upland soils, respectively. * across both dashed lines indicate significant differences between paddy and upland soils ($p < 0.05$, paired-sample *t* test). The stability and intensity of microbial transformation, alteration and oxidation of lignin increase with the direction of vertical and horizontal arrows, respectively

warmer than in cooler climates (Figure 1) might be attributed to the favorable climatic conditions in warmer climates (temperature, precipitation, light, etc.) that allow the double- or triple-cropping systems as compared to single- or double-cropping systems in cooler climates (Qiu et al., 2003). Consequently, the differences of C input in the forms of plant residues and rhizodeposits and the length of the flooding period will be greater in warmer climates.

## 4.2 | Contributions of plant- and microbial-derived C to SOC

By tracing plant- and microbial-derived C, we developed a conceptual diagram to elucidate the contrasting pathways of SOC formation in waterlogged paddy and well-drained upland soils and revealed the mechanism for greater SOC pool in paddy (Figure 7). SOC in paddy is characterized by a greater proportion of plant-derived C and less of microbial-derived C. Compared to the values reported by a limited number of studies using the same methodology, the contribution of microbial necromass to SOC in paddy in the present study (28%–36%; Figure 4) is generally lower than that in forest soils (33%–62%; Chen, Ma, et al., 2020; Ni et al., 2020), fertilized uplands (36%–86%; Li et al., 2020; Murugan & Kumar, 2013; Sradnick et al., 2014; Ye et al., 2019), and alpine grasslands (34%–53%; Ding et al., 2019). The weaker microbial anabolism caused by $O_2$ limitation in the mostly waterlogged paddy decreases the formation of microbial necromass, but prompts the retention of refractory components of plant residues (Figure 7). By contrast, 40%–59% of SOC was derived from microbial necromass in upland (Figure 4), demonstrating that a higher degree of microbial decomposition of plant residues resulted in a greater contribution of microbial-derived C to SOC, but a smaller SOC pool in upland than paddy soils (Figure 7). Consequently, the more efficient SOC sequestration in paddy than adjacent upland is largely attributed to its selective accumulation of plant-derived C, as directly reflected by the approximately 3.3 times larger stocks of lignin phenols in paddy relative to upland (Figures S2).

The distinct origins of SOC in paddy and upland soils have significant implications for their stability and vulnerability. It has been increasingly recognized that microbial-derived C may be more stable and persistent than plant-derived C because it is more likely to be physically protected in organo-mineral associations (Cotrufo et al., 2013; Sokol et al., 2019). We show that the sequestration of SOC in paddy is a result of enriched plant-derived labile C, whereas SOC in upland is more replenished by microbial-derived C (Figure 4). With regard to plant-derived C, the increasing $(Ad/Al)_V$ and $(Ad/Al)_S$ ratios of lignin phenols reflected an increasing degree of side chain oxidation, and the decreasing C/V and S/V ratios signified an increasing microbial transformation stage (Li et al., 2020; Ma et al., 2018). Therefore, the higher C/V and lower $(Ad/Al)_S$ ratios (Figure 2), representing a lower degree of oxidative decomposition (Kögel, 1986), suggest that the plant-derived C is less decomposed in paddy than upland soils. Concerning microbial-derived C, the bacterial biomarkers represented by muramic acid can be more susceptible to decomposition than their fungal counterparts after cell death (Nakas & Klein, 1979). Hence, the lower fungal glucosamine/bacterial muramic acid ratios in paddy soils relative to upland soils suggest a weaker stability of microbial-derived C in paddies (Figure 3c). Accordingly, the chemical constituents of both origins demonstrated that the SOC accumulating in paddy might be less stable and more vulnerable to further perturbations than in upland.

As suggested by Cotrufo et al. (2019), strategies aimed at increasing SOC should identify the contribution of both plant- and microbial-derived C. The latter is more stable when protected by mineral associations (mineral-associated organic matter), but it can saturate, whereas plant-derived C (particulate organic matter) is less protected in soil, but can accumulate indefinitely. Nevertheless, a switch from anaerobic to aerobic respiration, such as converting paddy to upland or reducing the regular flooding frequency of paddy, may cause a 10-fold increase in organic C mineralization rates (Keiluweit et al., 2017). Therefore, our findings have important implications for potential C loss under land-use changes. In the scenario of converting all paddies to uplands in eastern China, it is

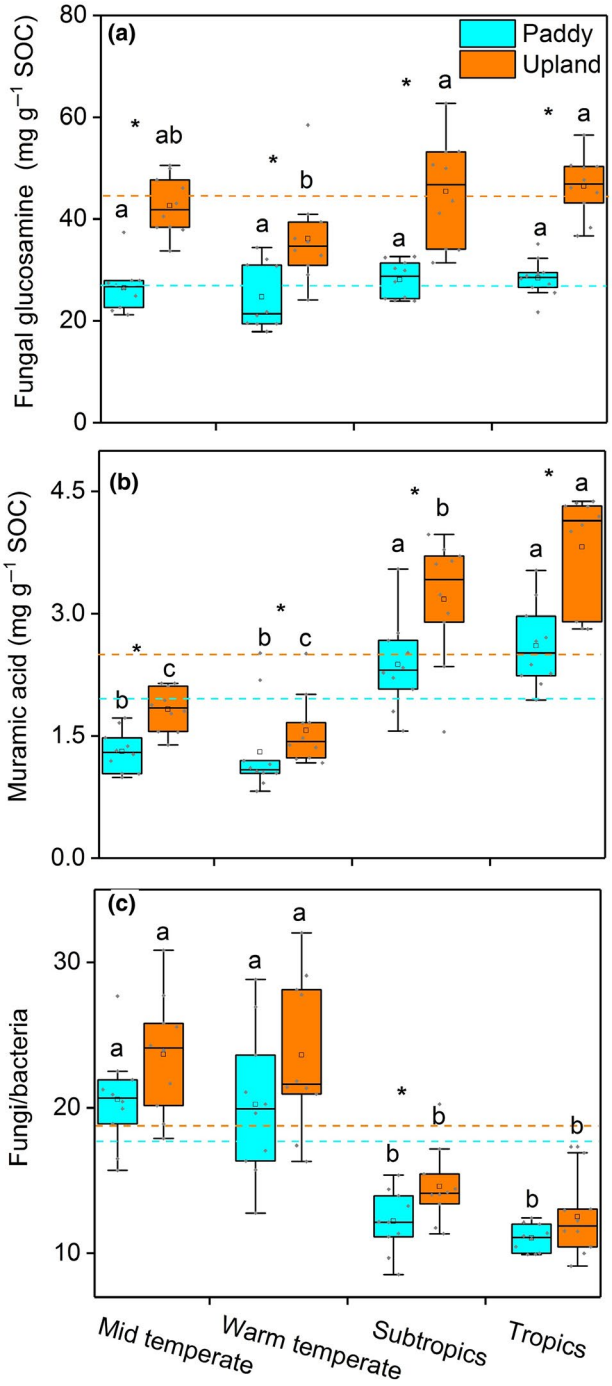



FIGURE 3 Contents of SOC-normalized fungal biomarkers (fungal glucosamine) (a) and bacterial biomarkers (muramic acid) (b) and ratio of fungal to bacterial biomarkers (c) in paddy and upland soils across the four climate zones. Lowercase letters indicate significant differences among the four climate regions for the same land use ($p < 0.05$, one-way ANOVA). * indicate significant differences between both lands ($p < 0.05$, paired-samples *t* test). The horizontal dashed lines show the average values (across four climates) for paddy (dashed blue) and upland (dotted orange) soils

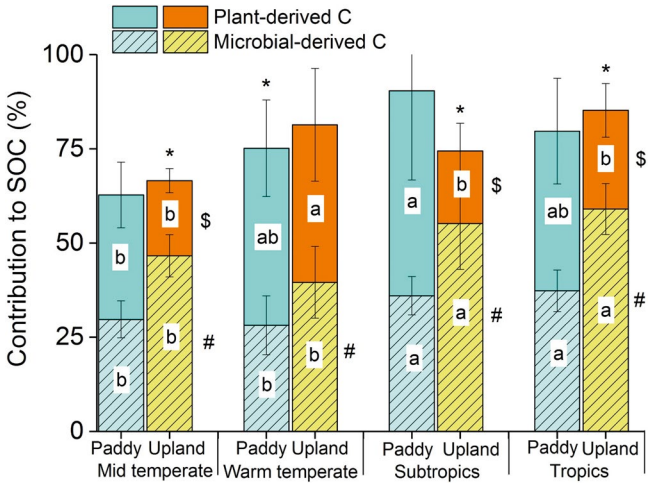
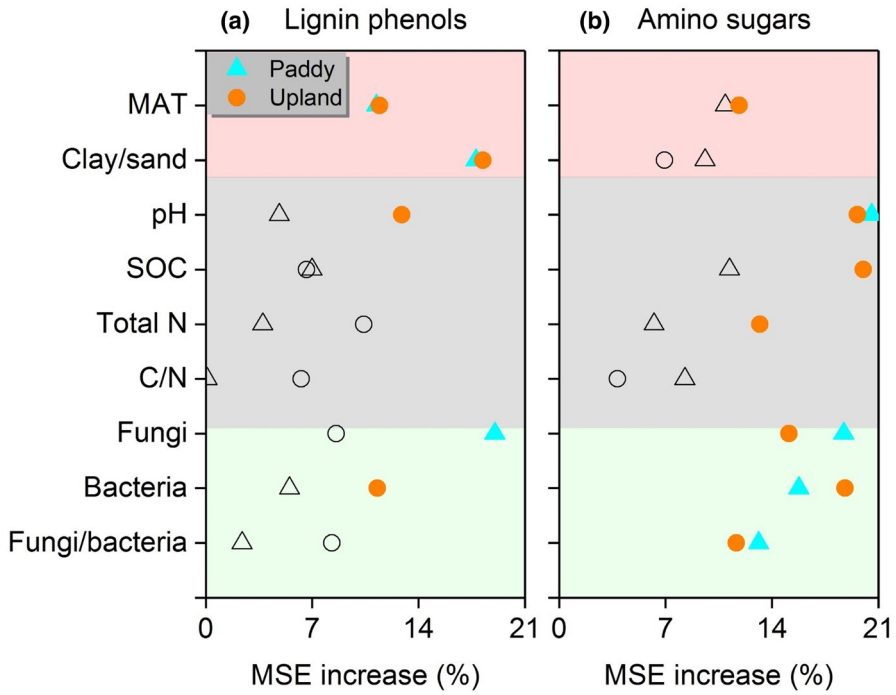



FIGURE 4 Contributions of plant- and microbial-derived C in total SOC in paddy and upland soils across the four climate zones. Lowercase letters indicate significant differences among the four climate regions for the same land use ($p < 0.05$, one-way ANOVA); $ indicate significant differences for the contribution from plant-derived C between paddy and upland soils for same pathways; # indicate significant differences for the contribution from microbial-derived C in SOC between paddy and upland soils; * indicate significant differences between the contributions from plant- and microbial-derived C in SOC for the same land-use within same climate zones ($p < 0.05$, paired-samples *t* test)

estimated that 504 Tg of C will be lost from the topsoil (0–15 cm; Table 1), which is equivalent to 13% of organic C stocks in surface soils of Chinese croplands (Yan et al., 2011). Approximately, 98% of total C loss occurs in warmer climates of the subtropics and tropics. Plant-derived C contributed to 90% of the total C loss, which is up to 406 and 48 Tg C in subtropics and tropics. In cooler climates, the conversion of paddy to upland may trigger a slight loss from plant-derived C, but partial of this loss may be offset by the accumulation of microbial-derived C (Table 1). This may attribute to the microbial transformation of plant residues and accumulation of microbial necromass (Cotrufo et al., 2013). Consequently, the land-use change between paddy and upland has minimal influence on the surface SOC stocks in cooler climates, but will likely cause a large SOC loss in warmer climates. As a result, preserving the subtropical and tropical paddy systems and other anthropogenic wetlands is critical to avoiding a substantial loss of SOC, mainly from the less protected plant-derived C.

### 4.3 | Environmental controls over SOC formation

Both paddy and upland soils showed relatively stable contents of amino sugars but wider variations of lignin phenols (Figure S4). Therefore, the role of microbial-derived C in SOC formation is more conservative since it is less dependent on environmental factors and agricultural managements (e.g., fertilization) than plant residues (Li et al., 2020). In contrast to the large heterogeneity of plant inputs, microbial necromass is relatively convergent, simple-structured, and tight in its C/N ratio (Cotrufo et al., 2019). The direct contribution of plant-derived C to SOC can be affected by diverse soil environmental




(c)

| | Explained variance (%) | |
|---|---|---|
| | Lignin phenols | Amino sugars |
| Paddy | 13 | 55 |
| Upland | 35 | 54 |

**FIGURE 5** Relative importance of independent variables for controlling SOC-normalized lignin phenols (a) and amino sugars (b) and their explained variance (c) in paddy and upland soils as identified by the percentage increase of the mean squared error (MSE%) using random forests models. Following variables were included: mean annual temperature (MAT) for climate; clay/sand ratio, pH, SOC, total N and C/N ratio for edaphic properties; fungal glucosamine, bacterial muramic acid, and ratio of fungal glucosamine/bacterial muramic acid for biotic characteristics of microbial necromass constituents. Significant factors ($p < 0.05$) are labeled as colored symbols

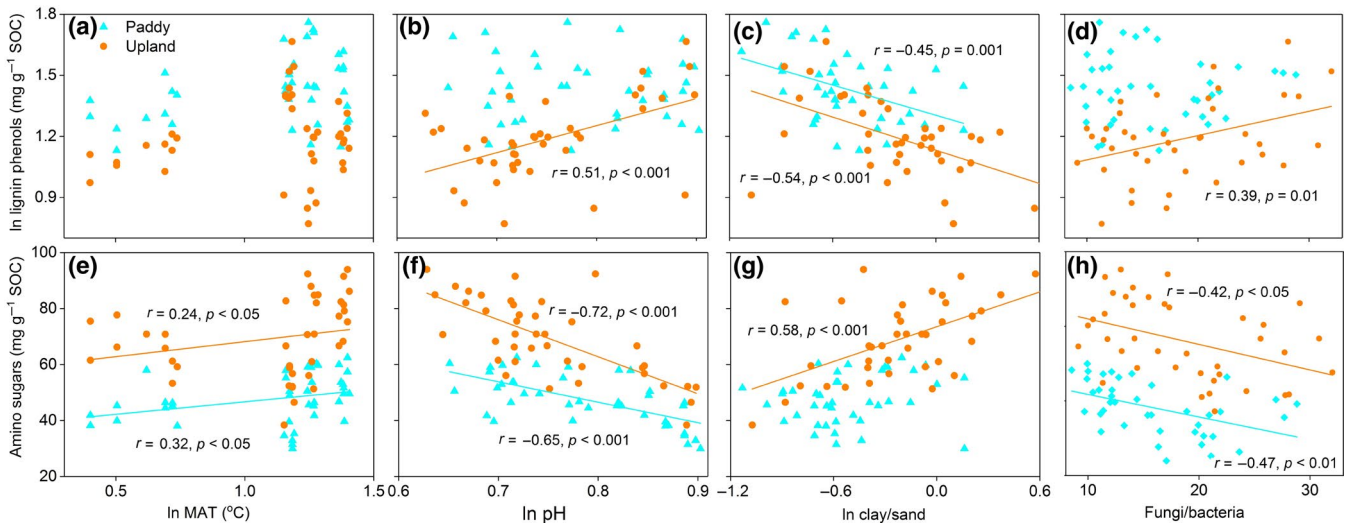



**FIGURE 6** Correlations of SOC-normalized lignin phenols and amino sugars with mean annual temperature (MAT), pH, clay/sand ratio, and fungi/bacteria ratio in necromass in upland (a, b, c, d) and paddy soils (e, f, g, h). Nonsignificant regressions ($p > 0.05$) are not presented

conditions, which could be more intensive in heterogeneous upland soils than in homogeneous paddy soils (Figure S4a).

Complementary patterns for plant- and microbial-derived C in response to MAT occur in upland but not in paddy (Figure 7). This indicates that both plant and microbial sources well explain the SOC sequestration in upland, but C accrual in paddy may be more involved some other sources. For example, the low-molecular-weight organic compounds (e.g., root exudates) which are directly adsorbed by soil minerals (Sokol et al., 2019) without microbial processing may exclude in the plant- and microbial-derived C in the present study. Generally, the more frequent cropping at higher temperature in $O_2$-limited paddy may retard the decomposition of plant residues owing

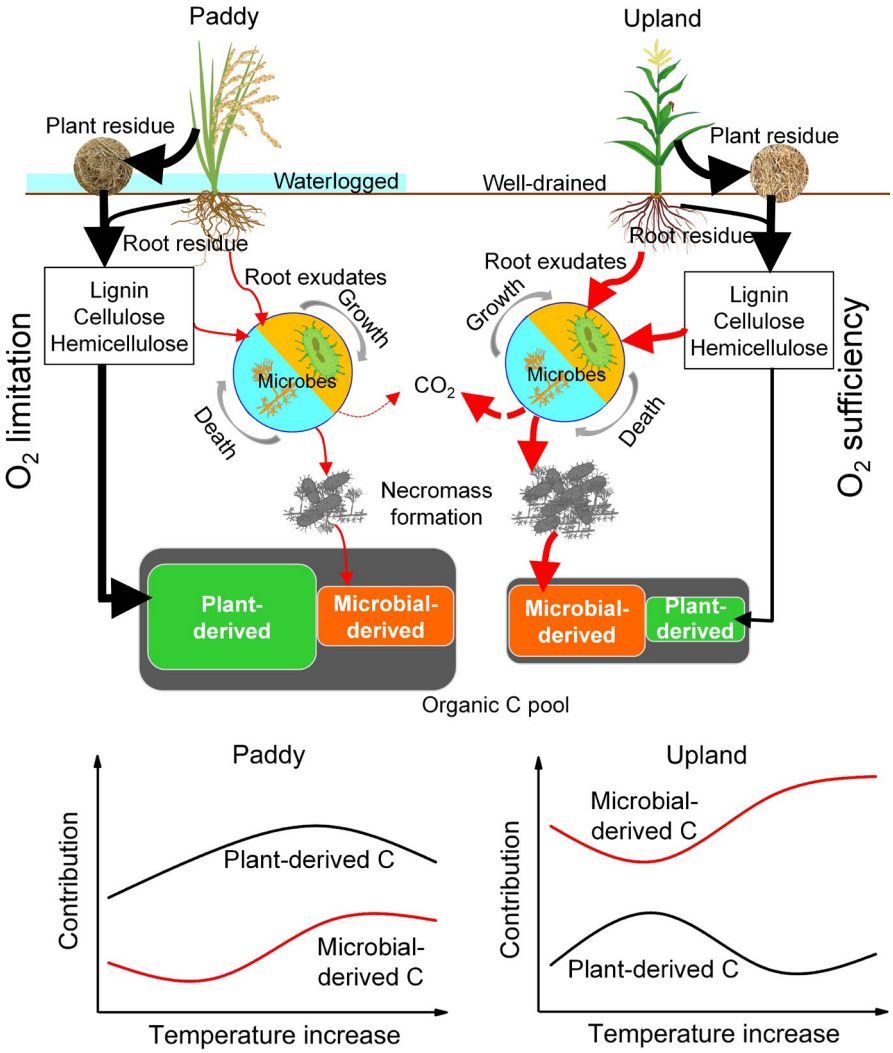



**FIGURE 7** Diagram illustrating the formation of SOC in waterlogged paddy and well-drained upland. Black and red arrows represent the pathways of plant- and microbial-derived C, respectively. The size of the arrows reflects the intensity of the pathways. The weaker microbial respiration ($CO_2$ release) in $O_2$-limited paddy than in $O_2$-sufficient upland was previously reported by Deng et al. (2021). The pool size of SOC in paddy is larger than that in upland. Paddy soil is enriched with greater proportion of plant-derived C, whereas upland soil is more replenished by microbial-derived C. Complementary patterns between plant- and microbial-derived C in response to MAT occur in upland but not in paddy soil

**TABLE 1** Estimated organic carbon (C) loss from topsoil (0–15 cm) due to the conversion of paddy to upland in the four climatic zones

| | Current average SOC (g $kg^{-1}$)[a] | | | Loss of C in the scenario of land-use conversion from paddy to upland (Tg)[c] | | |
|---|---|---|---|---|---|---|
| Climatic zone | Paddy | Upland | Area (kha)[b] | Total SOC | Plant-derived C | Microbial-derived C |
| Mid temperate | 27.6 | 21.0 | 857 | 9 | 7 | −4 |
| Warm temperate | 14.1 | 13.7 | 1,097 | −1 | 1 | −3 |
| Subtropics | 27.3 | 13.0 | 16,841 | 412 | 406 | 73 |
| Tropics | 25.4 | 14.4 | 3,655 | 84 | 48 | 13 |

[a]Current SOC content in paddy and upland was calculated based on the average values in each climatic zone ($n$ = 10).

[b]Data of area for each climatic zone were collected from the references of Mei et al. (1988).

[c]Loss of total SOC, plant- and microbial-derived C from topsoil in each climatic zone were calculated according to the equation: $T_{loss} = (A_{paddy} \times BD_{paddy} - A_{upland} \times BD_{paddy}) \times 15 \times S/10^4$, where $T_{loss}$ represents the loss of total C, or plant-derived C or microbial-derived C from topsoil in the scenario of paddy converted to upland (Tg; 1 Tg = $10^{12}$ g); $A_{paddy}$ and $A_{upland}$ are average contents of total C, or plant-derived C or microbial-derived C in current paddy and upland, respectively (g $kg^{-1}$); $BD_{paddy}$ and $BD_{upland}$ represent soil bulk density in paddy (1.20 g $cm^{-3}$) and upland (1.26 g $cm^{-3}$), respectively, which are calculated based on the relationships between soil bulk density and SOC, that is, equation I from Wu et al. (2003); 15 is soil depth (cm); $S$ is the area of paddy (kha); $10^4$ is used for unit conversion. Positive data represent C loss, whereas negative data indicate C accumulation.

to the prolonged soil submergence, but in $O_2$-sufficient upland, intensive cropping can accelerate the mineralization processes (Yu & Kuzyakov, 2021). This explains the highest contribution of plant residues to SOC at ~20°C in paddy soils but ~15°C in upland soils (Figures 1 and 6). Additionally, a higher temperature generally accelerates both microbial catabolism (mineralization to $CO_2$) and anabolism (biomass growth and proliferation; Ding et al., 2019; Ma et al., 2018). This strengthens the contribution of microbial necromass to SOC in warmer climates relative to cooler climates, with a greater increase in bacteria than fungi (Figure 3).

MAT could also affect the contribution of microbial necromass to SOC indirectly through its influence on soil pH, which decreases with increasing MAT across these four climate zones (Figure 6; Figure S6). A lower pH indicates stronger soil weathering and thus more abundant of the pedogenic minerals of Fe- and Mn oxides (Blume & Schwertmann, 1969; Koester et al., 2021). Since microbial living biomass and necromass are enriched in the organomineral associations (Ludwig et al., 2015), the microbial-derived C in SOC increases with lower soil pH and richer Fe- and Mn oxides (Cai et al., 2021). Additionally, at lower soil pH, hydronium ions enriched the surface sites of soil minerals and may satisfy the protonated state of carboxylic acid ($-COO^-$) groups to bind with negatively charged clay surfaces (Newcomb et al., 2017). Hence, considering the $-COO^-$ groups existing in muramic acid, lower pH could strengthen the stabilization of bacterial necromass via strong interactions of its $-COO^-$ groups with mineral surfaces.

The lignin phenols in SOC decreased with an increase in clay/sand ratio (Figure 6), which is consistent with previous reports (Thevenot et al., 2010). The contribution of plant-derived polysaccharides to SOC decreases from coarse- to fine-textured soils and in the same order as the increasing contribution from microbially synthesized polysaccharides (Guggenberger et al., 1994). This suggests less relative retention of plant-derived C and greater microbial-derived C with the increase in soil clay/sand ratio, regardless of land use (Figure 6). The progressive accumulation of amino sugars in SOC with increasing clay content reflects the pronounced association of microbial necromass with fine soil minerals (Zhang et al., 1999).

Partitioning the microbial necromass C into fungal and bacterial C helps to explain the divergent microbial pathways of SOC formation between paddy and upland (Six et al., 2006). It is noteworthy that the fungal biomarkers in SOC were similar across all climates, especially in paddy soils (Figure 3a; Figure S7a). The bacterial biomarkers in SOC, however, increased with MAT (Figure S7d), suggesting a greater role for bacterial participation in SOC formation in warmer climates. Therefore, the greater contribution of microbial necromass to SOC in warmer climates relative to cooler climates was predominantly a result of the greater anabolic activity of bacteria. The $O_2$ limitation in paddy relative to upland decreased the contribution from fungal necromass more than that of bacterial necromass (Figure 3), since fungi are aerobic, while many bacteria are more tolerant of anaerobic conditions (Moritz et al., 2009). Bacterial necromass is more susceptible to decomposition than fungal counterparts (Nakas & Klein, 1979), which could also explain the weaker accumulation of microbial-derived C in paddies than in uplands.

The contributions of plant residues and microbial necromass to SOC in response to environmental factors were similar between paddy and upland soils. However, the intensity of environmental factors affecting both pathways was weaker in paddy than in upland soils, especially for fungal necromass (Figure 6; Figure S7). Likely, $O_2$ limitation caused by flooding in paddies decreases particularly the sensitivity of aerobic fungal activity to diverse environmental conditions (Ou et al., 2019). As a whole, intermediate temperature range, neutral soil pH, and lower clay/sand ratio are beneficial to reinforcing the contribution of plant residues to SOC sequestration in both croplands, whereas higher temperature, lower soil pH, and higher clay content are favorable for strengthening the contribution from microbial necromass.

## 5 | CONCLUSIONS

Our continental-scale study provides several lines of quantitative evidence on the divergent pathways of SOC sequestration in paddy and upland soils and highlights the contrasting responses of plant- and microbial-derived C to cropland managements and environmental variables. Anaerobic conditions in paddies weaken the microbial transformation of plant residues, and thus paddy soils accumulate more C in the form of plant-derived C as compared with upland soils. In contrast, upland soils accumulate more microbial-derived C, and less from plant residues. Although paddies are more efficient in SOC sequestration, the stored C is less stable than that in uplands and can be prone to loss under changing land use. Relative to uplands, flooding in paddy fields decreases the sensitivity of SOC to diverse climatic conditions and edaphic properties. In warmer climates (subtropics and tropics), removal of the flooding stage, that is, a simple switch from anaerobic to aerobic conditions, likely will make the plant-derived C available for microbial decomposition and will trigger a substantial $CO_2$ pulse from the paddy soils and thus exacerbate climate change.

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### CONFLICT OF INTEREST

The authors declare no conflict of interest.

### AUTHOR CONTRIBUTIONS

X. C., Y. H., and Y. S. designed the study. X. C., Y. H., Y. X., and S. Z. collected the soil samples. D. H. provided the map of soil distribution and guided soil collection. Y. H., Y. X., S. Z., and C. M performed biomarker and geochemical analysis of all soil samples.

H. H. provided technical guidance of biomarker analysis. X. C. and Y. H. analyzed the data with help from Y. R., Z. Z., T. G., J. W., G. G., and Y. K. X. C. and Y. H. wrote the paper with inputs from all co-authors.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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