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RESEARCH ARTICLE

Intrinsic microbial temperature sensitivity and soil organic carbon decomposition in response to climate change

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Abstract

Soil microbes are essential for regulating carbon stocks under climate change. However, the uncertainty surrounding how microbial temperature responses control carbon losses under warming conditions highlights a significant gap in our climate change models. To address this issue, we conducted a fine-scale analysis of soil organic carbon composition under different temperature gradients and characterized the corresponding microbial growth and physiology across various paddy soils spanning 4000 km in China. Our results showed that warming altered the composition of organic matter, resulting in a reduction in carbohydrates of approximately 0.026% to 0.030% from humid subtropical regions to humid continental regions. These changes were attributed to a decrease in the proportion of cold-preferring bacteria, leading to significant soil carbon losses. Our findings suggest that intrinsic microbial temperature sensitivity plays a crucial role in determining the rate of soil organic carbon decomposition, providing insights into the temperature limitations faced by microbial activities and their impact on soil carbon-climate feedback.

KEYWORDS
climate change, growth curve, molecular mixing model, respiration, soil organic carbon composition, temperature gradients

Sen Li and Manuel Delgado-Baquerizo contributed equally to this study.

1 | INTRODUCTION

Soil organic carbon (SOC) is a crucial renewable resource that provides essential ecosystem services such as food and fiber production, climate and water regulation, soil fertility restoration, and biodiversity conservation (Lal, 2016; Tiessen et al., 1994; Trumbore, 1997). As a primary carbon reservoir, soil holds more carbon than both the atmosphere and terrestrial vegetation, with even small losses of organic carbon from soil significantly impacting atmospheric CO_2 concentrations under climate change (Eglinton et al., 2021; Lal, 2004; Soong et al., 2021). However, the extent to which microbes and SOC respond to warming is uncertain due to gaps in understanding the decomposition dynamics of SOC compounds (van Gestel et al., 2018). SOC comprises diverse biomolecules derived from plant and microbial degradation, with minor contributions from abiotic processes (Nelson & Baldock, 2005; Zosso et al., 2023).

The complexity of SOC is underscored by its composition of diverse biomolecules derived from plant and microbial degradation. As global warming intensifies, understanding how different SOC molecules respond to elevated temperatures and the mechanisms driving these responses becomes increasingly important (Cheng et al., 2017; Crowther et al., 2016). Studies have shown that lipids and sugars within subsoils accumulate under warming conditions, while the decomposition of lignin is accelerated due to priming effects (Jia et al., 2019). The turnover of lipids and black carbon exhibits limited sensitivity to thermal fluctuations and is largely influenced by soil mineralogy, whereas the degradation of lignin is predominantly driven by temperature (Jia et al., 2023). However, contrasting views exist on the temperature sensitivity of SOC decomposition, with some suggesting that recalcitrant fractions are unresponsive to temperature changes (Giardina & Ryan, 2000), while others propose that labile SOC pools are less sensitive than recalcitrant ones (Lefèvre et al., 2013) or that both pools share similar sensitivities (Conen et al., 2006). As such, it has become increasingly imperative to delineate the ways in which climatic warming impacts different SOC components and to unravel the underlying processes.

Soil serves as a vast source of microbial diversity, with intricate microbial communities contributing significantly to soil-climate feedback (Banerjee & van der Heijden, 2022). The most diverse soil microbes are adaptable to changing environmental conditions due to their short generation times, large populations, and high mutation rates (Chase et al., 2021; Matulich et al., 2015). Although soil microorganisms have a wide temperature range for adaptation at the community level, the optimal growth temperatures vary among different types of microorganisms (Ratkowsky et al., 1982). Based on the suitable temperature range for growth, microorganisms can be classified into psychrophilic (<20°C), mesophilic (<45°C), and thermophilic (>100°C) types (Nedwell, 1999). However, the influence of temperature-responsive microbes on SOC decomposition under a changing climate remains unclear. Disturbances to soil microbial communities due to warming could lead to accelerated organic matter breakdown through increased microbial respiration and growth, potentially contributing to a positive feedback mechanism to climate change (Nottingham et al., 2022; Soong et al., 2021). Microbial physiological traits such as growth efficiency play a crucial role in SOC dynamics, given that microbes can contribute significantly to SOC, ranging from 30% to 80% (Kallenbach et al., 2016). Understanding microbial growth characteristics is essential for monitoring cellular activity and forming the basis of microbial community functionality (Mai et al., 2021; Peleg et al., 2007). While the importance of microbial diversity in carbon cycling under warmer conditions has been emphasized, debates persist regarding the temperature sensitivity of microbial growth and metabolic processes (García-Palacios et al., 2021; Wu et al., 2022). Comprehensive analyses are necessary to elucidate the interplay between temperature, microbial physiological processes, and changes in soil carbon.

Paddy fields, which are the world's largest artificial wetlands, globally feed more than half of the world's population (Kögel-Knabner et al., 2010). The variations between anaerobic and aerobic conditions in paddy soils promote organic carbon accumulation, resulting in higher carbon stocks in paddy soils than in dryland soils (Chen et al., 2021; Liu et al., 2021; Wu, 2011). Understanding the mechanisms that govern SOC dynamics in paddy soils is crucial for preserving global soil carbon reservoirs and mitigating climate change. In this study, we analyzed various paddy soils spanning 4000 km in China using ^{13}C solid-state magic-angle spinning NMR spectroscopy at five thermal regimes (8, 15, 20, 25, and 35°C). We also characterized the corresponding soil microbial growth and physiology. We hypothesized that the accelerated carbon loss due to warming is closely related to the temperature response of soil microorganisms. Our findings provide direct evidence for the role of temperature-sensitive microbes in carbon-climate feedback.

2 | MATERIALS AND METHODS

2.1 | Site description and field sampling

We collected 429 soil samples from 39 paddy fields across 13 regions of China (19.72° N to 47.82° N, 110.01° E to 126.97° E) between June and October 2013 (Table S1). Soil samples collected for this study represent five distinct soil types: neutral black soil, alkaline fluvo-aquic soil, hydromorphic paddy soils, acidic red soil, and submergenic paddy soil. These samples are derived from regions with four different crop rotations: single-crop rice, rice–wheat rotation, double- and triple-cropping of rice. Moreover, the study sites are distributed across two main climate zones as per the Koppen classification system: the humid subtropical climate and the continental climate. This diversity in soil types, crop rotations, and climate zones enables us to comprehensively assess the impact of environmental factors on soil microbial communities. The mean annual temperature ranges from 1.5 to 23.8°C, and the mean annual precipitation varies from 400 to 2215 mm. At each site, we established three separate 100 m × 100 m plots, and within each plot, we used an "L-shaped"

sampling pattern to collect 11 topsoil cores, each with a depth of 0–15 cm. Each topsoil core was obtained using a sampling tube with a diameter of 2.5 cm. From these, we randomly selected five soil cores within each plot and combined them to create a composite sample of approximately 500 g, which served as one replicate. This process was repeated independently for each of the three plots at each site, resulting in three replicate soil samples per site. The soils were then transported to the laboratory in sterile bags on dry ice. Soils were passed through a 2 mm mesh to remove roots and stones, adjusted to 60% of the water-holding capacity (WHC), and preincubated for 1 week before use.

2.2 | Short-term incubation experiment

The chosen temperatures reflect the diverse thermal environments that soil microorganisms encounter across China. The annual average temperature range varies from 1.5 to 23.8°C in China. Microorganisms in these environments can generally be categorized into two groups based on their temperature preferences: psychrophiles and mesophiles. Psychrophiles thrive in colder conditions with optimal growth between −20 and 20°C, whereas mesophiles prefer warmer temperatures with growth optima ranging from 20°C to approximately 45°C. Our study aimed to encompass a representative range of temperatures that would elicit differential responses from these microbial communities. Based on previous studies (Chen et al., 2020; Tian et al., 2022; Zhang et al., 2023), we incubated 200 g of field soil, maintained at 60% of its WHC, within 500 mL containers at five different temperatures: 8, 15, 20, 25, and 35°C. These temperatures were selected to span the range from colder to warmer conditions, allowing us to observe the behavior and adaptability of soil microorganisms across this spectrum. The samples were incubated for a period of 4 weeks to assess the impact of temperature on microbial activity and community structure.

2.3 | Respiration measurements

To investigate the effects of temperature on soil carbon dioxide (CO_2) emissions, 10 g of soil was weighed into a specimen cup and placed in a mason jar equipped with a septum for headspace gas sampling. The soil moisture was adjusted to 60% of the WHC for each replicate, and the samples were incubated for 7 days at five different temperatures (8, 15, 20, 25, and 35°C), with three replicates conducted under each temperature regime. To measure the CO_2 concentration, t_0 gas samples were taken 10 min after the lid was closed. Headspace gas samples were then collected every 24 h using a 15 mL syringe and analyzed using a LI-Cor 6262 (LI-Cor Biosciences Inc. Lincoln, USA). The accumulated CO_2 was estimated by comparing the CO_2 values from t_0 to t_{24} h. After gas sampling, the mason jars were opened for 20 min to release the accumulated CO_2 and achieve atmospheric CO_2 concentration equilibrium before being closed again. This process was repeated over the 7-day incubation period.

2.4 | Microbial physiology assays

We utilized an automated microbiology growth curve analysis system to assess microbial growth. Initially, 1 g of fresh soil sample was combined with 50 mL of Luria–Bertani (LB) medium and vortexed. Subsequently, 25 μL of the prepared bacterial cultures were mixed with 175 μL of LB medium and transferred to sterile microplates. The microbial growth of each soil sample was estimated with three laboratory replicates, leading to a total of 585 assays (13 sites × 3 soil replicates × 5 temperature regimes × 3 laboratory replicates). The microplates were covered with lids and placed in the Bioscreen C Automated Microbiology Growth Curve Analysis System (Oy Growth Curve Ab Ltd., Turku, Finland) to monitor the optical density (OD) at 600 nm under five temperature conditions (8, 15, 20, 25, and 35°C). Considering the growth patterns of microorganisms, we employed classical microbial growth models to obtain bacterial growth parameters such as generation time, lag phase time, and maximum growth rate, which are referred to as microbial physiological traits. In brief, we fitted the OD values with the corresponding incubation temperatures using the following equation:

$$y = \frac{a}{1 + \exp\left(\frac{(x - x_0)}{b}\right)}, \quad (1)$$

where y represents the OD value at a specific temperature, x denotes the incubation temperature, and a, b, and x_0 are the parameters obtained through fitting. Parameter b signifies the generation time, while x_0 denotes the lag phase time.

The maximum growth rate can be calculated as the maximum slope of the logarithmic phase, which is represented by the following equation:

$$y = A2 + \frac{A1 - A2}{1 + \left(\frac{x}{x_0}\right)p}, \quad (2)$$

where y represents the OD value at a given temperature, $A1$ is the initial value, $A2$ is the final value, p is the maximum growth rate, and x_0 is the time of the maximum growth rate.

2.5 | Solid-state ^{13}C nuclear magnetic resonance assays

The molecular structure of SOC was determined using nuclear magnetic resonance (NMR) analysis. Prior to NMR analysis, 195 soil samples (13 sites × 3 soil replicates × 5 temperature regimes) were preprocessed with hydrofluoric (HF) acid to eliminate interference from Fe^{3+} and Mn^{2+}. Initially, 5 g of air-dried soil was mixed with 50 mL of HCl in a 100 mL sealed centrifuge tube and shaken for 1 h. Following centrifugation, the supernatant was discarded, and the residues were rinsed eight times with a HF acid solution (10%) using ultrasonication. Each sample was then washed four times with

distilled water, dried at 40°C in an oven, ground, and passed through a 60-mesh sieve before further analysis.

Solid-state magic-angle spinning NMR measurements were performed using ^{13}C cross polarization/total sideband suppression (CP/TOSS) and CP/TOSS with dipolar dephasing experiments on a Bruker AVANCE400 spectrometer (Bruker BioSpin GmbH, Karlsruhe, Germany) equipped with a 4 mm sample rotor at 100 MHz (Mao et al., 2012). The following parameters were used for all NMR measurements: an observed frequency of 5 kHz, a CP time of 1 ms, a 1H 90° pulse length of 4 ms, and a recycle delay of 0.8 s. Four-pulse TOSS was applied before detection, and two-pulse phase-modulated decoupling was used to achieve optimal resolution. CP/TOSS combined with 40 ms dipolar dephasing was employed to obtain a subspectrum containing nonprotonated carbons and mobile groups. Spectral quantification was carried out by measuring each chemical shift region in the background of the baseline correction: 0–45 ppm (alkyl C), 45–60 ppm (N-alkyl/methoxy C), 60–95 ppm (O-alkyl C), 95–110 ppm (Di-O-alkyl C), 110–145 ppm (aromatic C), 145–165 ppm (phenolic C), and 165–210 ppm (carbonyl C). The relative abundances of six molecular SOC constituents, including carbohydrates, proteins, lignin, lipids, carbonyls, and char, were estimated by applying a molecular mixing model to seven integrated spectral regions (Nelson & Baldock, 2005). The elemental concentrations of C and N as constraints were measured in the HF-treated soils via elemental analysis.

2.6 | DNA extraction

DNA was extracted from 2 g of fresh soil for each replicate, amounting to a total of 195 soil samples (13 sites × 3 soil replicates × 5 temperature regimes), using a well-established method (Zhou et al., 1996). The quality and quantity of the extracted DNA were assessed using a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA) and a Qubit 3.0 fluorometer (Thermo Fisher Scientific, USA), respectively. The extracted DNA was then stored at −80°C until further analysis.

2.7 | Accurate amplicon-based sequencing and data processing

Absolute quantification of 16S rRNA amplicon sequencing was performed by Genesky Biotechnologies Inc., Shanghai, China. Nine different spike-in sequences with identical conserved regions to those of 16S rRNA genes and hypervariable regions substituted by stochastic sequences were artificially synthesized and combined with the sample DNA (Maghini et al., 2023; Tourlousse et al., 2017). The V4-V5 region of the bacterial 16S rRNA gene and spike-ins were amplified using the general primers 515F (5′-GTG CCA GCM GCC GCG G-3′) and 907R (5′-CCG TCA ATT CMT TTR AGT TT-3′) (Huber et al., 2006). Accurate 16S absolute quantification sequencing was carried out using an Illumina NovaSeq 6000 sequencer (Illumina San Diego, CA, USA). Strong linear correlations between spike-in amount and read count were observed for dose–response curves based on multiple spike-in standards with varying input concentrations in a single mixture (Table S2).

The raw sequence reads were processed using QIIME2 (Bolyen et al., 2019). DADA2, wrapped by QIIME2, was employed to generate a feature table using q2-vsearch after the filtering of adaptor sequences and the removal of low-quality reads, ambiguous nucleotides, and barcodes (Callahan et al., 2016). The representative sequences were classified by the feature classifier against the Ribosomal Database Project (RDP) (version 11.5) (Cole et al., 2014). The spike-in sequences were identified, and the read counts were calculated. Each sample's standard curve was generated by comparing the read counts to the spike-in copy number. The absolute copy number of each ASV per sample was calculated using the read counts of the corresponding ASVs, and the spike-in sequences were filtered before further analysis.

2.8 | Classification of cold-preferring and warm-preferring bacteria

Cold-preferring bacteria, including both psychrophiles and psychrotrophs, are capable of growth at 0°C. Psychrophiles exhibit optimal growth at temperatures ≤15°C. Psychrotrophs, a subgroup within psychrophiles, can also proliferate at 0°C, yet their optimal growth temperature is closer to the mesophilic range near room temperature (15–25°C). Conversely, warm-preferring bacteria (mesophiles) thrive within a broader temperature spectrum, ranging from 20 to 45°C, with an optimal growth temperature between approximately 30–39°C. Thus, cold-preferring bacteria demonstrate increased temperature sensitivity compared to their warm-preferring counterparts (Moon et al., 2023).

Using the Threshold Indicator Taxa Analysis (TITAN) approach, as introduced by Baker and King (2010), we identified bacterial taxa characteristic of "cold-preferring" and "warm-preferring" groups. The TITAN method operates by selecting indicator species highly responsive to temperature gradients based on z scores for specific taxonomic groups. Subsequently, thresholds for temperature gradients were determined by analyzing the response patterns of these indicator species. After confirming their accuracy and reliability, these thresholds were applied to categorize taxa into negative [z−] and positive [z+] groups, tracking the cumulative community response of taxa experiencing decline or increase. Finally, taxa identified as z− and z+ were classified as cold-preferring and warm-preferring bacteria, respectively.

2.9 | Statistical analysis

Since the data were not completely independent, we employed linear mixed-effect models to investigate the relationships between warming and C functional groups, C molecules, microbial diversity, microbial physiological traits, and the soil respiration rate using the lme4 R package (Bates et al., 2015). In the model, warming was considered a fixed effect, while sampling site was considered a random effect

(*y*~warming+(1|site)). The effect sizes were expressed as regression coefficients in the models, and *p*-values were obtained through Wald type II χ^2 tests using the car R package (John & Sanford, 2019). Bacterial diversity (Shannon index), Procrustes analysis, and the Mantel test were estimated using the vegan R package (Oksanen et al., 2022). Bacterial composition was represented by the first axis of principal coordinate analysis and calculated using the "vegdist" function of the ape R package (Paradis & Schliep, 2019). To evaluate the extent to which the microbial community modified the temperature sensitivity of the soil respiration rate and microbial growth in soils, we fitted an exponential model to the soil respiration rate and microbial growth separately at 13 sites using the R package ggtrendline (v1.0.3) (Mei et al., 2022). The Q10 value was calculated as follows:

$$R = a \times \exp^{b \times T}, \tag{3}$$

$$\mathrm{Q10} = \exp^{10 \times b}, \tag{4}$$

where *R* is the soil respiration rate or microbial growth at a specific temperature, *T* is the incubation temperature, and *a* and *b* are modeling parameters. To investigate the relationships between C molecules and environmental variables, we employed linear mixed-effects models. In these models, the sampling site was considered to have a random intercept effect. The correlations between each individual molecule and environmental variables were calculated using the "r.squaredGLMM" function of the MuMIn R package, which tests the marginal coefficient of determination, providing insight into the variance explained by the fixed effects in the linear mixed-effects model (Barto, 2023). Structural equation modeling (SEM) was applied to investigate the direct and indirect effects of temperature, bacterial diversity, the temperature sensitivity of soil respiration ($Q10_{SR}$) and microbial growth ($Q10_{BG}$), including generation time, lag phase time and maximum growth rate, on C release using the R packages piecewiseSEM and nlme (Lefcheck & Freckleton, 2015; Pinheiro et al., 2022). In the prior model, warming-induced C losses by changing soil microbial activity via the temperature sensitivity of microbial growth and respiration, which can be altered by temperature-sensitive microbial diversity (Figure S5). Principal component analysis (PCA) was performed to create new variables for C molecules using the predictors significantly correlated with C molecules, and the first component of PCA was employed in the construction of the structural equation model (Table S7). The goodness of fit of the SEM was assessed using Fisher's *C*, the Akaike information criterion, and the whole-model *p*-value.

3 | RESULTS

3.1 | Thermal response of SOC fractions

To verify the sensitivity of soil carbon loss to temporary warming, we conducted a soil microcosm experiment and analyzed the molecular composition of SOC using ^{13}C solid-state magic-angle spinning NMR spectroscopy. Our results revealed significant changes in the molecular composition of SOC (Figure S1). The analysis revealed a decrease in the abundance of O-alkyl C and an increase in the abundance of alkyl C due to warming, while the other five groups of organic matter components—Methoxy C, Di-O-alkyl C, aryl C, and O-aryl C—exhibited no significant changes under the influence of elevated temperatures (Table S3). Furthermore, the degree of SOC decomposition was greater in humid continental climates than in humid subtropical climates. This was due to a greater increase in alkyl C and decrease in O-alkyl C in soils from humid continental climates (alkyl: $\beta = .0485$, $p < .001$; O-alkyl: $\beta = -.0277$, $p < .05$) than in soils from humid subtropical climates (alkyl: $\beta = .0257$, $p < .01$; O-alkyl: $\beta = -.0320$, $p < .001$).

We then employed the molecular mixing model to evaluate alterations in the molecular components of organic matter in soils based on the distribution of ^{13}C NMR signal intensity across all samples. Our results revealed that increasing temperatures led to a decrease in carbohydrate content of 0.026% in soils from humid continental climates ($\beta = -.0261$, $p < .05$) and 0.030% in soils from humid subtropical climates ($\beta = -.0302$, $p < .001$) (Figure 1a). Conversely, there was an increase in lipids of 0.039% in soils from humid continental climates ($\beta = .0392$, $p < .001$), which was greater than the 0.027% increase in soils from humid subtropical climates ($\beta = .0270$, $p < .001$) (Figure 1a). Moreover, warming also resulted in a reduction in protein in soils in humid subtropical regions ($\beta = -.0211$, $p < .05$). The molecular mixing model implied that warming caused alterations in the molecular composition of SOC. Furthermore, significant differences were observed between humid continental and humid subtropical climate zones.

3.2 | Temperature sensitivity of soil microbes

Given the role of microbes in biochemical cycling, we hypothesized that soil C losses are associated with the response of soil microbial communities to warming. To explore the temperature sensitivity of soil microorganisms, we categorized soil microbes into cold-responsive and warm-responsive types using TITAN (Figure 1b). Our results showed that humid continental climate regions had a greater prevalence of cold-preferring bacteria (2%) than humid subtropical regions. Warming had distinct effects on the composition of temperature-sensitive microorganisms, with a reduction in the absolute abundance of cold-preferring microorganisms in humid continental regions (0.0136% to 0.0396%) and an increase in the absolute abundance of warm-preferring bacteria in humid subtropical regions (0.0140% to 0.0334%) (Figure 2). The species showing higher temperature sensitivity primarily belonged to the phyla Bacteroidetes ($\beta = -.0396$, $p < .001$) and Firmicutes ($\beta = .0334$, $p < .001$). As expected, warming had a significant negative impact on the diversity of cold-preferring bacteria (humid continental climate: $\beta = -.0304$, $p < .01$; humid subtropical climate: $\beta = -.0228$, $p < .001$) (Figure 3a). These findings suggest that warming led to a notable decrease in both the richness and diversity of cold-preferring bacteria, particularly in humid continental regions where they were disproportionately abundant.

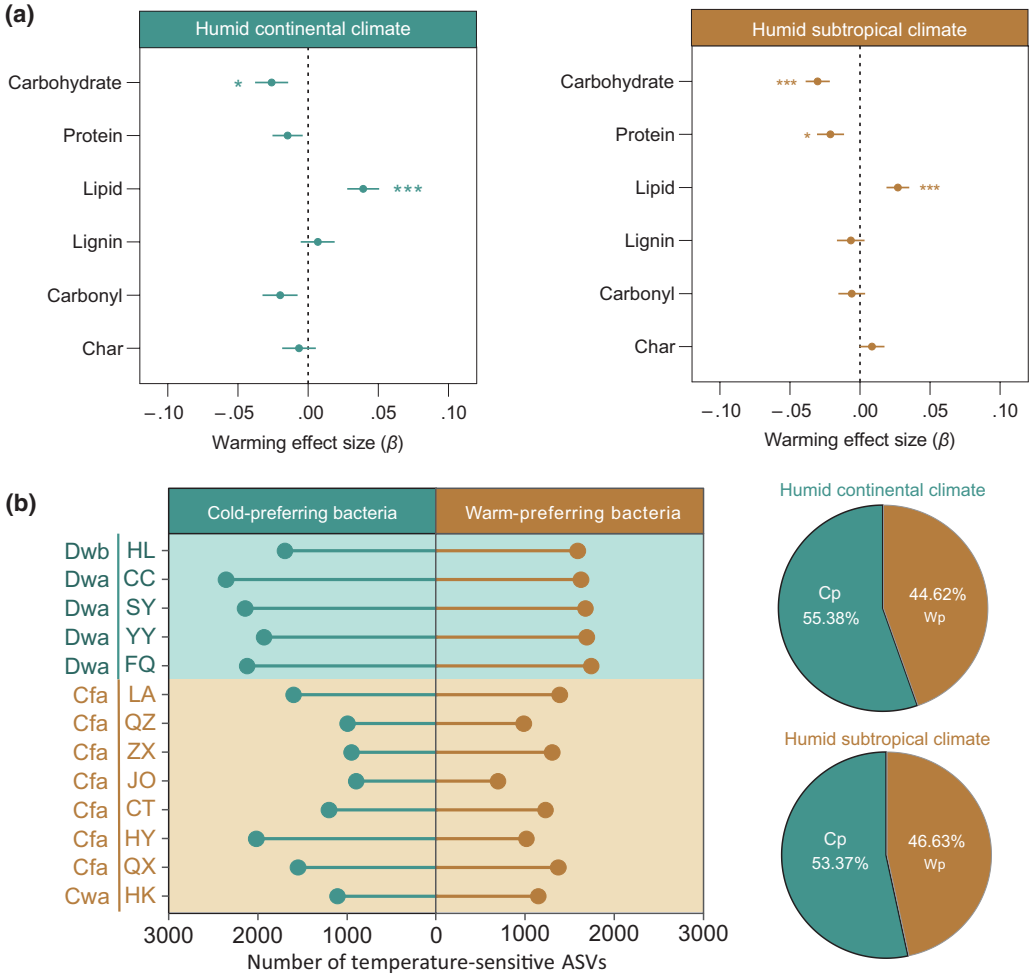

FIGURE 1 Effects of warming on C molecules and soil bacteria. (a) Effect size of warming on soil C molecules in the humid continental and humid subtropical climates of China. $^{*}p < .05$, $^{***}p < .001$. (b) Number of cold- and warm-preferring bacteria in paddy soils of China and the percentage of cold- and warm-preferring bacteria in the humid continental and humid subtropical climates of China. Humid continental climate (Dwa and Dwb in the Köppen climate classification); Humid subtropical climate (Cwa and Cfa in the Köppen climate classification). Cp, cold-preferring bacteria; Wp, warm-preferring bacteria.

Our experimental study on the physiological characteristics of soil microbial community growth confirmed that microorganisms in humid continental regions were more susceptible to temperature increases (Figure S2). As the temperature increased, the rates of soil respiration and maximum growth exhibited exponential growth, while the generation time and lag phase time of soil bacteria showed the opposite trend (Figure S3). The response of respiration to warming was stronger in humid continental regions than in humid subtropical regions, and microbial growth exhibited a greater effect in low-latitude regions (Figure 3a). We also observed a negative correlation between cold-preferring bacterial diversity and soil respiration (Figure S4).

3.3 | Factors driving SOC decomposition

We further assessed whether warm-induced alterations in microbial activity impact soil C losses. Our results showed a strong linkage between microbial growth and the composition of SOC, particularly carbohydrates and lipids (Figure 3b). Additionally, we observed a positive correlation between soil respiration and lipids only in the humid continental regions (Figure 3b). We calculated the temperature sensitivity (Q10) of microbial respiration and growth (Tables S4 and S5). Consistent with our earlier findings, soils in humid continental climates had greater temperature sensitivity to soil respiration but lower temperature sensitivity to microbial growth than soils in humid subtropical regions. The response of SOC to warming was primarily driven by the sensitivity of microbial growth and respiration (Figure S4; Table S6).

To further investigate the drivers of soil C loss between humid continental and humid subtropical climate soils, we conducted SEM analyses using the presumed relationships (Figure S5). Our results showed that warming had a negative effect on the diversity of cold-preferring bacteria, while no warming effects were observed for warm-preferring bacteria (Figure 4). Additionally, the Q10 of soil microbial growth and respiration was negatively

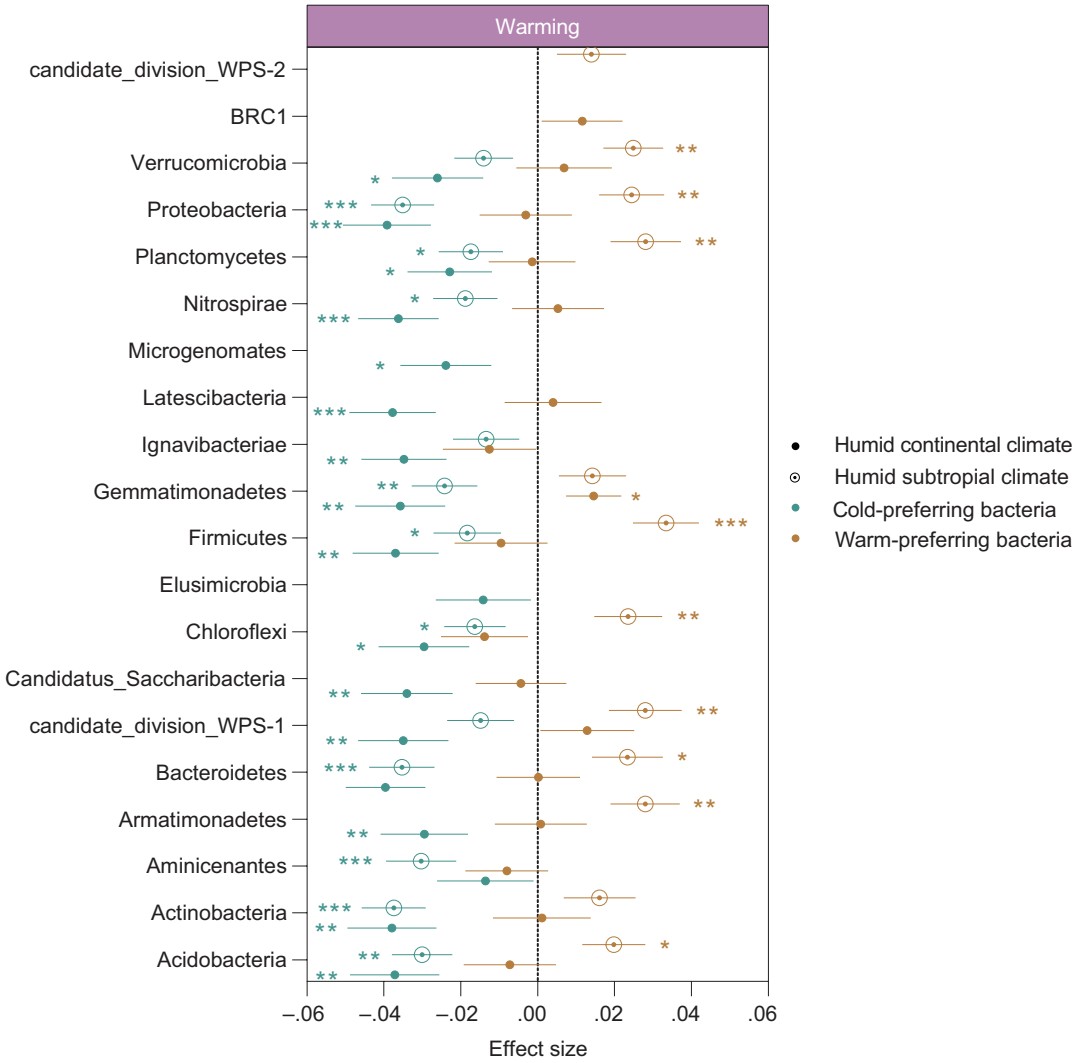

FIGURE 2 Effects of warming on temperature-sensitive bacteria. Effect sizes of warming on the absolute abundance of major bacterial taxa at the phylum level based on linear mixed-effects models. Statistical significance is based on Wald type = II χ^2 tests. The data are presented as the means ± SDs of the estimated effect sizes. $^*p < .05$, $^{**}p < .01$, $^{***}p < .001$.

correlated with cold-preferring bacterial diversity in humid continental regions (Figure 4a). These findings indicate that climate warming leads to a reduction in the diversity of cold-preferring bacteria in soils of humid continental climates, resulting in changes in the Q10 of soil microbial growth and respiration. This is the main factor contributing to the promotion of soil C losses. In contrast, the relationships between cold-preferring bacterial diversity and the Q10 of soil microbial growth and respiration were significantly positive in humid subtropical climates (Figure 4b). Furthermore, our results indicated that soil C losses were primarily regulated by the Q10 of soil respiration in humid subtropical regions. These findings demonstrate that cold-preferring bacterial diversity plays a predominant role in regulating SOC decomposition under climate warming in humid continental regions (Figure S6), while soil C losses are primarily driven by the Q10 of microbial growth in humid subtropical regions. This could be attributed to the long-term adaptation of microbes to temperature changes in these regions.

4 | DISCUSSION

Understanding the impact of climate change on SOC turnover and its underlying mechanisms is a crucial issue in climate research (Cavicchioli et al., 2019; Jansson et al., 2023; Tiedje et al., 2022). However, the role of temperature-sensitive microorganisms in soil carbon-climate feedback remains a significant uncertainty (Frey et al., 2013; Rousk et al., 2012). Our findings provide insights into the significance of these microorganisms by revealing dynamic changes in SOC molecular components and intrinsic soil microbial traits. In this study, we noted a reduction in labile O-alkyl C, primarily originating from carbohydrates, under warming conditions within humid subtropical and continental climatic zones (Figure 1a). This process provides evidence that decomposition drives terrestrial C cycling and that warming accelerates the decomposition of SOC. Due to the higher average temperature in humid subtropical climate zones than in continental climate zones, this long-term climatic legacy of the soil leads to a greater degree of decomposition of easily degradable

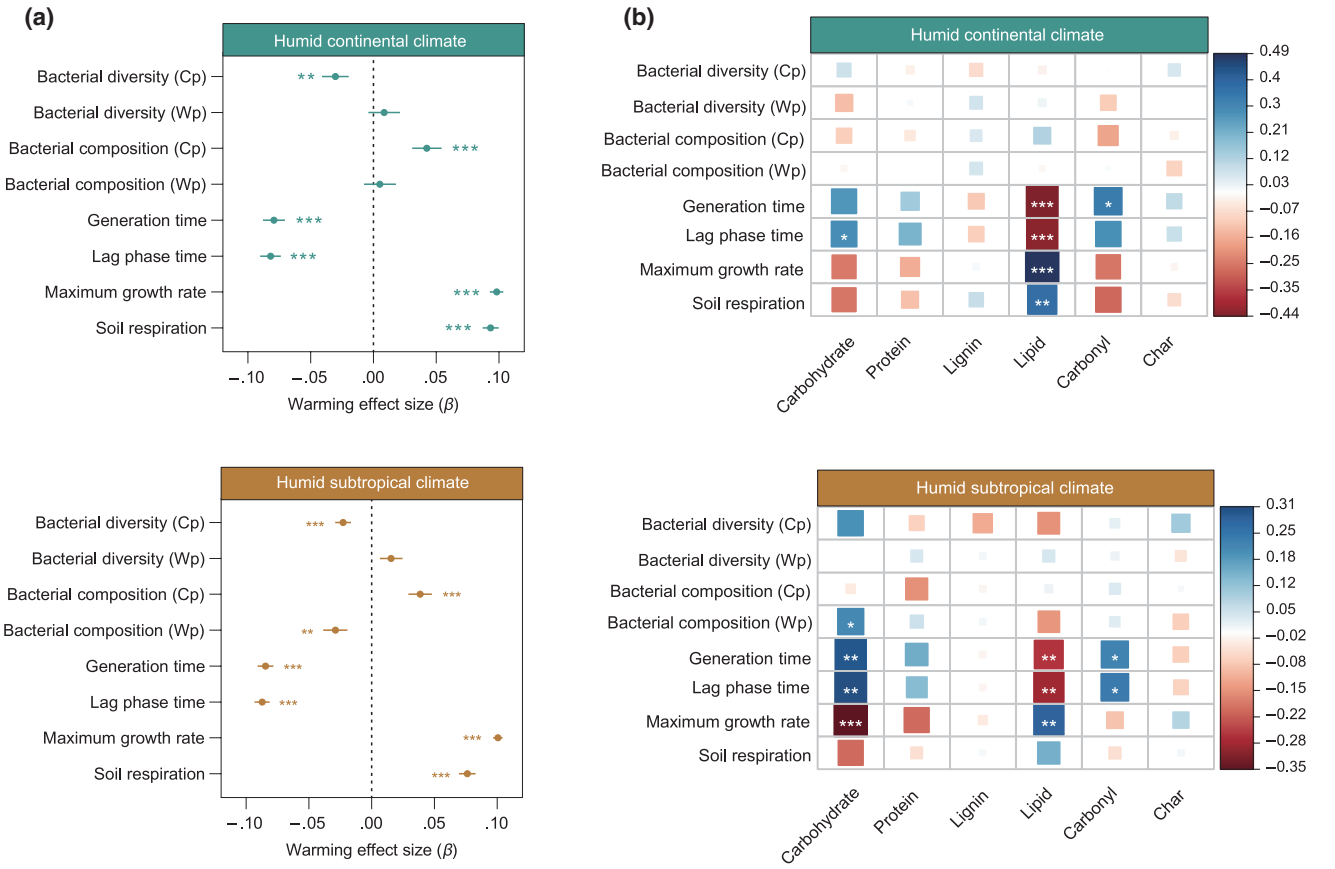

FIGURE 3 Correlations between environmental variables and C molecules. (a) Effects of warming on soil C molecules and the soil microbial community based on linear mixed-effects models in humid continental and humid subtropical climates of China. Effect sizes of warming on the microbial diversity and composition, soil respiration rate and microbial growth (generation time, lag phase time, and maximum growth rate) in the linear mixed-effects models. The values represent the means ± standard errors of the effect sizes. (b) Correlations between environmental variables and C molecules in the humid continental and humid subtropical climates of China. The color shows the correlation coefficient measured by the linear mixed-effects model. Statistical significance is supported by Wald type II χ^2 tests. The *p*-values were adjusted by the false discovery rate. $^*p < .05$, $^{**}p < .01$, $^{***}p < .001$. Cp, cold-preferring bacteria; Wp, warm-preferring bacteria.

carbon in humid subtropical climate zones. Simultaneously, the elevated temperatures resulted in a rise in the levels of recalcitrant alkyl C and lipids (Figure 1a; Table S3). Using NMR carbon spectroscopy, alkyl C can be categorized into microbial-derived (0–31 ppm) and plant-derived (31–45 ppm) alkyl C, based on structural differences (Audette et al., 2021). Our findings indicate that the increase rate of alkyl C with temperature from microbial origins was faster than that from plant sources (Figure S7). This phenomenon could be attributed to the process of microbial carbon pumps, as microbial controls on soil C dynamics primarily responsible for decomposing SOC can also drive C sequestration by producing stable SOC through an iterative process of life activities, resulting in alterations to the molecular composition of SOC (Liang et al., 2017; Qiu et al., 2023). Our incubation experiments showed that continental soils exhibit a more substantial increase in alkyl C (i.e., recalcitrant C) compared to subtropical soils. Furthermore, the ratio of alkyl to O-alkyl C, which serves as an indicator for the stability of SOC decomposition, is notably higher within humid continental climate zones. Consequently, climate warming could potentially alter the stability of SOC pools, facilitating a redistribution of soil C among various reservoirs, and implying enhanced conservation prospects in high-latitude areas (Manlick et al., 2024).

The stability of SOC is influenced by a variety of environmental factors (Ofiti et al., 2023). Our findings indicate that pH and initial SOC content were the primary factors explaining the variation in SOC decomposition and microbial activities across our sampled soils (Figure S8). This suggests that initial soil properties play a crucial role in determining the subsequent dynamics of soil carbon and microbial activity under different environmental conditions. Soil microorganisms exhibit distinct geographical distribution characteristics and are influenced by various factors, with climatic conditions serving as one of the key determinants of their distribution (Labouyrie et al., 2023; Patel et al., 2023). Cold-preferring microorganisms were more prevalent in humid continental climates compared to humid subtropical regions, where species favoring warmer conditions were more common (Figure 1b). Soil microbial activity is dependent on temperature conditions within the soil, and most microorganisms thrive within a specific temperature

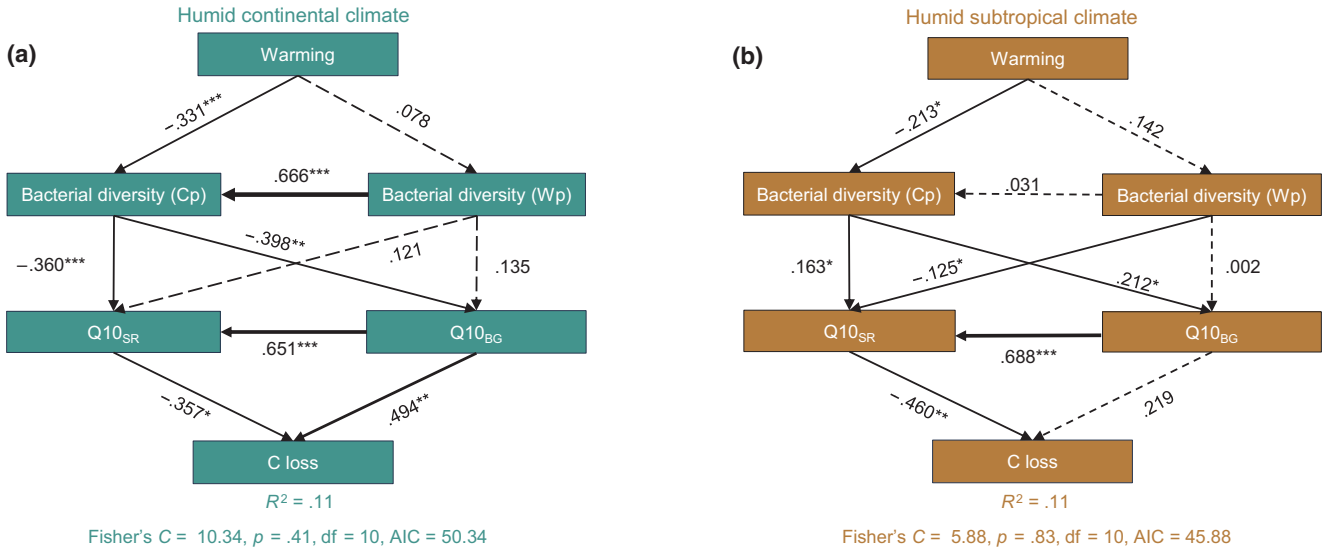

FIGURE 4 Environmental drivers of C losses according to structural equation modeling. Models for the relationships among the variables in the humid continental (a) and humid subtropical climates (b) of China. The solid and dotted lines represent significant and nonsignificant relationships, respectively. The arrow width shows the strength of the relationship. Numbers embedded in the arrows are standardized path coefficients. C loss is the first component from the principal component analysis performed on the basis of the molecular composition of soil organic carbon. R^2 indicates the proportion of variance explained. Bacterial alpha diversity represented by Shannon diversity in cold- and warm-preferring bacterial communities. $Q10_{(BG)}$, the temperature sensitivity of bacterial growth, is a composite variable that includes the temperature sensitivity of generation time, lag phase time, and maximum growth rate. $Q10_{(SR)}$ is the temperature sensitivity of soil respiration, $^*p < .05$, $^{**}p < .01$, $^{***}p < .001$. AIC, Akaike information criterion; Cp, cold-preferring bacteria; Wp, warm-preferring bacteria.

range (Cavicchioli et al., 2019). The growth and activity of most microorganisms are constrained by increased temperatures that exceed their optimal range (Barton et al., 2016). This propensity was particularly pronounced among cold-preferring microorganisms in humid continental climates, with a larger fraction of these organisms exhibiting an adverse reaction to increased temperatures. This phenomenon can be attributed to the extended winter periods and the typical cold soil environment characteristic of such regions (Rantanen et al., 2022). In comparison with Firmicutes, Bacteroidetes displayed a heightened sensitivity to temperature fluctuations in contrast to Firmicutes, which exhibited the inverse response (Figure 2). Similarly, warming reduced the abundance of Bacteroidetes and increased that of Firmicutes, which was also observed in the gut microbiota (Zhang et al., 2022). Further analysis confirmed that the optimal growth range for cold-preferring microorganisms was lower than that for warm-preferring microorganisms. This disparity was chiefly characterized by a substantial decrease in the diversity of microorganisms adapted to lower temperatures under conditions of increased warmth, whereas those adapted to higher temperatures maintained relative stability (Figure 3). Experiments with soil bacterial cultures have further demonstrated that bacterial species from humid continental climates exhibit greater sensitivity to shifts in temperature compared to those from humid subtropical climates (Figure S2).

The intrinsic temperature sensitivity of soil microbes is challenging to alter over time scales ranging from weeks to decades, despite their rapid adaptability under harsh conditions (Alster et al., 2023; Walker et al., 2018). Microbial physiological processes are sustained by changes in microbial biomass, which are influenced by the intrinsic temperature sensitivity of soil microbes (Karhu et al., 2014; Simon et al., 2020). The heightened sensitivity of microbial respiration activity to warming in continental soils stems primarily from the composition of bacterial communities. Our data indicate that humid continental climates host a greater proportion of cold-preferring bacteria (2%) than humid subtropical regions (Figure 1). Given the enhanced temperature sensitivity of cold-preferring bacteria in continental soils, the thermal adaptation of microbial respiration in subtropical regions may impose constraints on potential fluctuations in respiratory rates (Tian et al., 2022). Hence, under warming conditions, microbial respiration activity is more pronounced in humid continental climates than in humid subtropical climates. While the respiration rate of microorganisms is less affected by optimal temperatures compared to their growth rate, it significantly escalates under warming conditions. Conversely, the microbial growth rate decreases subsequent to reaching the optimal temperature. Therefore, it can be inferred that microorganisms with increased temperature sensitivity in respiratory activities might exhibit diminished sensitivity to growth rates in humid continental climate regions (Figure 3; Figure S2). This may be the primary factor underlying the higher rate of SOC decomposition in cooler regions than in warmer regions. The intrinsic microbial temperature sensitivity can cause a transient warming effect on the attenuation of soil carbon storage. Warming-induced perturbations in SOC are driven by alterations in microbial activity, stemming from the temperature-sensitive responses of microbial growth and respiration (Figure 4). In the

future, a theoretical framework is needed to elucidate the complex interactions between temperature, microbial communities, and soil carbon dynamics. It is expected that by harnessing engineered microorganisms, the adverse effects of climate change can be alleviated in the future (Jansson et al., 2023).

Overall, our study highlights that short-term warming affects SOC decomposition by enhancing microbial growth and respiration, which is primarily governed by the diversity of cold-preferring bacteria. Due to temperature variations in different climate zones, the inherent temperature sensitivity of microorganisms varies significantly, and an increase in temperature causes most microorganisms to exceed their optimal growth range. Our research underscored the importance of the inherent temperature sensitivity of soil microorganisms in influencing the relationship between soil carbon and climate feedback, a subject that has been increasingly garnering scientific interest. Additionally, we intend to incorporate them into land surface models by providing reliable laboratory evidence of their occurrence. By concentrating on these key areas of research, we can better comprehend and address the challenges posed by climate change and its impact on our planet's ecosystems.

AUTHOR CONTRIBUTIONS

Sen Li: Data curation; formal analysis; investigation; validation; visualization; writing – original draft; writing – review and editing. **Manuel Delgado-Baquerizo:** Investigation; writing – original draft; writing – review and editing. **Jixian Ding:** Data curation; investigation; methodology; validation; writing – review and editing. **Han Hu:** Data curation; investigation; writing – review and editing. **Weigen Huang:** Data curation; formal analysis; investigation; methodology; validation; writing – original draft; writing – review and editing. **Yishen Sun:** Data curation; investigation; writing – review and editing. **Haowei Ni:** Investigation; writing – review and editing. **Yanyun Kuang:** Investigation; validation; writing – review and editing. **Mengting Maggie Yuan:** Data curation; investigation; methodology; writing – original draft; writing – review and editing. **Jizhong Zhou:** Conceptualization; methodology; writing – review and editing. **Jiabao Zhang:** Conceptualization; supervision; writing – review and editing. **Yuting Liang:** Conceptualization; formal analysis; funding acquisition; project administration; supervision; validation; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The raw sequence data for this study were submitted to the NCBI Sequence Read Archive (SRA) with accession number BioProject PRJNA866844. All data needed to evaluate the conclusions in the paper are presented in the paper and/or the Supporting Information. The data that support the findings of this study are openly available in figshare at http://doi.org/10.6084/m9.figshare.25996651. Incubation and respiration data are available in Figshare at https://doi.org/10.6084/m9.figshare.25996651.v1.

STATISTICS AND GRAPHICS

The data were statistically analyzed and graphically presented using the R 4.2.1 statistical environment (https://cran.r-project.org/).

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SUPPORTING INFORMATION

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

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