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Differential responses of soil bacterial community and respiration to plastic film and straw mulching in a maize field

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Abstract

Soil respiration (R_s), driven by microbial activity, is influenced by mulching practices. However, the microbial mechanisms underlying the divergent effects of various mulching practices on R_s remain inadequately understood. To address this knowledge gap, a three-year (2019-2021) maize field study was conducted to evaluate three treatments: no mulching (CK), plastic film mulching (PM), and straw mulching (SM). This study assessed the effects of these practices on the alpha diversity and structure of the bacterial community and R_s, and explore the roles of soil abiotic and biotic factors in driving R_s. The results indicated that PM decreased bacterial alpha diversity (as indicated by OTUs, Chao1, and Shannon indices), whereas SM significantly increased it. Furthmore, PM and SM significantly altered the bacterial community, with PM enriching oligotrophs (*e.g.*, *Chloroflexi* and *Firmicutes*), while SM enriching copiotrophs (*e.g.*, *Proteobacteria and Acidobacteriota*). Cumulative R_s under PM varied interannually, increasing in 2019 and 2020 but decreasing by 9.1% in 2021. In contrast, SM consistently stimulated cumulative R_s by 31.8–72.4%. Correlation and redundancy analysis identified soil temperature (ST) and NH_4^+-N as key factors shaping the bacterial community, negatively affecting alpha diversity. Structural equation modeling revealed that NH_4^+-N, NO_3^--N, bacterial alpha and beta diversity exerted a greater total effect on R_s, with NH_4^+-N and ST indirectly affect R_s via alpha and beta diversity, respectively. Overall, PM suppressed R_s in 2021 mainly by reducing bacterial alpha diversity and altering community structure under high ST in the summer, whereas SM promoted R_s via enhanced soil NH_4^+-N content, increased bacterial alpha diversity, and recruitment of taxa involved in soil carbon cycling. This study elucidated the contrasting microbial pathways through which different mulching practices affect R_s in summer maize cropping systems.

Keywords: Plastic film mulching · Straw mulching · Bacterial community · Soil respiration

Introduction

Carbon dioxide (CO_2) is a major greenhouse gas and the primary contributor to global warming (IPCC 2021). Soil respiration (R_s) plays a key role in the terrestrial carbon cycle, with slight alternations it can significantly impact atmospheric CO_2 concentrations (Crow et al. 2009). Cropland is a vital component of terrestrial ecosystem, and greatly susceptible to human disturbances (Farina et al. 2017).

Changes in field management practices can modify the soil environment, thereby affecting R_s (Lal 2004). Hence, it is imperative to study the response of R_s to different field management practices.

R_s is a complex biochemical process, including the decomposition of soil organic matters (SOM) and plant residues, as well as the respiration by live roots and rhizosphere microorganisms (Subke et al. 2006). Biotic and abiotic factors, such as soil temperature, moisture, nutrient availability, microbial activity, and plant growth, predominantly regulate R_s (Davidson and Janssens 2006; Lenka and Lal 2013; Knowles et al. 2015). Soil hydrothermal conditions and substrate availability significantly influence the growth of plant roots, thus impacting root respiration (Janssens et al. 2001; Schipper et al. 2014). Furthermore, these soil micro-environmental factors also affect the activity of soil enzymes involved in SOM decomposition (Chen et al. 2018a), primarily produced by microbes (Carreiro et al. 2000). Therefore, changes in microbial communities can alter soil enzymes activity, ultimately affecting R_s (Chen et al. 2018a). Several studies have explored the response of R_s to field management from the perspective of soil microbial communities (Jiang et al. 2021; Zhang et al. 2022; Guo et al. 2024). For instance, in a temperate vineyard, reduced fertilizer and water input decreased R_s, which was attributed to the decreased abundance of Proteobacteria and Bacteroidetes (Zhang et al. 2022).

Plastic film mulching (PM) and straw mulching (SM) have been widely used in arid, semi-arid, and sub-humid areas, owing to the significant yield improving ability (Kader et al. 2017). Some studies have investigated the effects of PM and SM on soil biotic (Dong et al. 2018; Mendonça et al. 2021) and abiotic factors (Fu et al. 2019; Zhao et al. 2022). A meta-analysis based on 536 observations showed that PM significantly increased soil microbial alpha diversity (OTU richness, Chao1 and Shannon indices), but decreased beta-diversity (Li et al. 2020). SM has been reported to alter the soil bacterial community structure by promoting the growth of copiotrophs, such as Proteobacteria and Acidobacteria (Fu et al. 2019; Liu et al. 2021). In addition, a lot of studies have investigated the response of R_s to PM and SM, but the findings were inconclusive (Xu et al. 2020; Zhang et al. 2023). Majority of studies have showed that PM improved the soil hydrothermal environment and accelerated the mineralization of SOM, thereby promoting R_s and enhancing CO_2 emissions (Cuello et al. 2015; Li et al. 2019). However, it has also been showed that PM reduced CO_2 emissions from the soil (Li et al. 2011), or had no significant effect on CO_2 emissions (Okuda et al. 2007). Similarly, SM has been reported to enhance (Lenka and Lal 2013), have no effect (Wang et al. 2021), or reduce (Hu et al. 2013) R_s. Moreover, most studies have attributed the discrepancies in these results to soil abiotic factors or plant growth (Lenka and Lal 2013; Xu et al. 2020),

neglecting the soil biotic factors. Therefore, although the effect of PM and SM on soil microbial communities have been previously reported (Fu et al. 2019; Liu et al. 2022), systematic and complete analyses, especially on the response of soil bacterial communities and R_s to PM and SM, are still lacking. In our previous research, PM was observed to reduce R_s during summer, whereas SM elicited a significant enhancement (Luo et al. 2023). In the present study, we aim to explain the mechanisms underlying these divergent R_s responses by examining the differential impacts of PM and SM on soil microbial communities.

In this study, a field experiment was performed over three maize growing seasons to clarify the effects of PM and SM on soil physiochemical properties, soil bacterial communities, and R_s. The objectives of this study were: (1) to assess the effects of PM and SM on soil bacterial community diversity and structure; (2) to determine the relationships among soil physiochemical properties, bacterial communities, and R_s; and (3) to explore the key factors in driving R_s under PM and SM. We hypothesized that: (1) soil bacterial community diversity and structure would be significantly influenced by the changes in soil physiochemical properties under PM and SM; and (2) PM and SM can affect R_s by altering soil bacterial communities.

Materials and Methods

Study site

The field experiment was carried out during three maize growing seasons of 2019, 2020, and 2021 at the Northwest A&F University experimental station in Yangling, located in southern Loess Plateau of China (34°20'N, 108°24'E, elevation 521 m). This region experiences a sub-humid climate, characterized by a mean daily temperature of 14.3 °C and a mean annual precipitation of 593 mm, based on the period of the past 30 years (1992–2021). Daily temperature and precipitation during the three maize growing seasons were recorded by an automatic weather observation station (HOBO event logger, USA) at the experimental site (Fig. 1). The soil in the experimental area had a silty clay loam texture (17% clay, 75% silt, and 8% sand) in the 0–10 cm soil layer. Basic soil properties (0–20 cm) were measured at the beginning of experiment and are as follows: bulk density of 1.37 g cm^{-3}, field capacity of 27.92%, pH of 8.20, soil organic carbon (SOC) of 9.78 g kg^{-1}, total nitrogen (TN) of 0.98 g kg^{-1}, soil NO_3^--N content of

5.73 mg kg^{-1}, and soil NH_4^+-N content of 1.51 mg kg^{-1}.

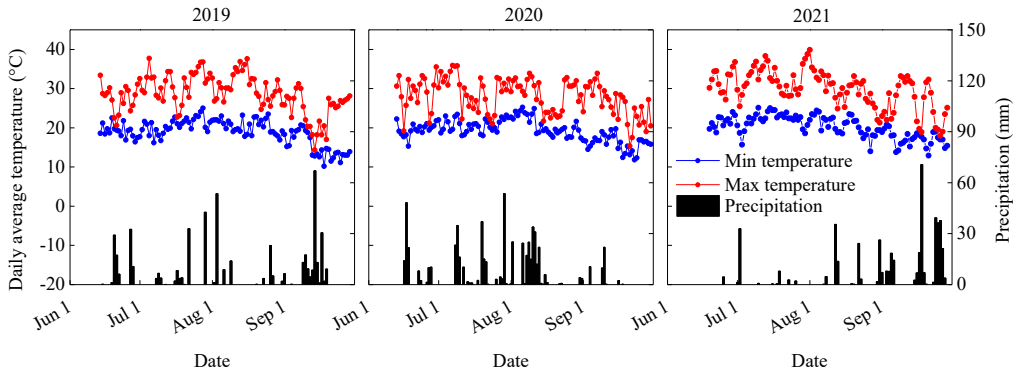


Fig. 1 Daily precipitation, min air temperature, and max air temperature during the maize growing seasons in 2019, 2020, and 2021.

Experimental design and field management

The experiment was arranged in a completely randomized block design, and comprised three treatments: (a) the control with no mulching over the soil surface (CK), (b) plastic film mulching (PM), and (c) straw mulching (SM) (Fig. 2). Each plot had a net area of 30 m^2 (6–m long and 5–m wide), and all treatments were replicated three times. For the PM treatment, the transparent plastic film had a thickness of 0.01 mm, which covered the entire soil surface. Maize seeds were planted into holes dibbled through the mulch and into the soil. The plastic film was removed after harvest and replaced immediately before the next crop was planted. For the SM treatment, wheat straw (4000 kg ha^{-1} season^{-1}) was chopped into residue lengths of approximately 10 cm, and mulched evenly on the soil surface after the maize planting. Maize was planted in mid-June and harvested in early October. The maize received fertilizer at a rate of 225 kg N ha^{-1} and 90 kg P_2O_5 ha^{-1} each season, with no K fertilizer or irrigation.



Fig. 2 A schematic diagram illustrating different mulching treatments: (a) CK, the control with no mulching, (b) PM, plastic film mulching, and (c) SM, straw mulching.

R_s measurement

The flux of R_s was measured in situ using closed static chambers and gas chromatography. At the

beginning of the experiment, the stainless-steel base (50–cm long, 50–cm wide, and 20–cm high) with grooves at the top were inserted into the center of each plot. Weeds in and around the base were manually removed periodically 24 h prior to gas sampling. A chamber with a height of 50–cm was inserted to the base groove before collecting the gas sample. The grooves were filled with water to create a closed environment. The surface of the gas chamber was covered with foam plates to minimize temperature changes inside the chamber. An electronic thermometer was installed on the top of the chamber to measure the air temperature inside. To ensure mixing of air, a small fan was installed in the chamber headspace, and a polyvinyl chloride gas channel with a three-way stopcock was installed on the outer side panel. Gas samples were collected using a syringe (60 mL) between 9:00 and 11:00 am every 7–10 days. The frequency of gas sampling was increased to daily for a week following fertilizer application or heavy precipitation events. Samples were collected at 0, 10, 20, and 30 min after the chamber was closed. Gas samples were analyzed by gas chromatography (Agilent 7890B, Agilent Technologies, Inc., USA) within 24 h (Chen et al. 2017).

The R_s flux was calculated using the following formula:

$$R_S = H\frac{MP}{R(273+T)}\frac{dC}{dt} \quad (1)$$

where R_s is soil respiration flux (mg CO_2-C m^{-2} h^{-1}), H is the height of the chamber (m), M is the molar mass of CO_2 (g mol^{-1}), P is air pressure (Pa), R is the gas constant (8.314 Pa m^3 mol^{-1} K^{-1}), T is the air temperature inside the chamber (°C), dC/dt is the linear change ratio of gas concentration versus time (μL L^{-1} h^{-1}).

The cumulative R_s was calculated as:

$$M = \sum_{i=1}^{n}\frac{(F_{i+1}+F_i)\times(t_{i+1}-t_i)\times 24}{2\times 100} \quad (2)$$

where M is the cumulative R_s (kg CO_2-C ha^{-1}), F is the R_s flux value (mg CO_2-C m^{-2} h^{-1}), t is the sampling day (d), and i is the sampling time.

Soil sampling and property measurements

Soil temperature and moisture measurements were synchronized during the gas collection processes. Soil temperature at a depth of 5 cm was manually recorded using alcohol-in-glass thermometers (Hongxing Instruments Factory, China). Soil moisture content (0 to 10 cm) was determined by drying soil samples at 105 °C for 24 h, followed by conversion to water-filled pore space (WFPS) (Ding et al.

2007). During key maize growing stages in 2021, namely emergence (VE), sixth-leaf (V6), silking (R1), and maturity (R6), topsoil samples (0–20 cm) were collected from five locations within each plot using a 5–cm diameter soil drill, arranged in an "S" shape pattern. These five soil samples were then sifted through a 2–mm sieve to remove the roots and large debris, and subsequently combined to create a composite sample. A portion of the composite sample was placed in a sterile plastic bag and stored at –80 °C for DNA extraction. Another portion was extracted with 2 mol L^{-1} KCl solution (25 mL) for analyzing NO_3^--N and NH_4^+-N contents by a Continuous Flow Analytical System (AA3, Seal, Germany). The remaining portion was air-dried for pH measurement by a pH meter (PHS-3C, China).

DNA extraction, quantitative real-time PCR (qPCR), and MiSeq sequence analysis

DNA extraction from soil samples was conducted using the E.Z.N.A.® soil DNA Kit (Omega Bio-tek, USA), following the manufacturer's instructions. Subsequently, the concentration of the extracted DNA was estimated and standardized on a 1.0% agarose gel using a NanoDrop 2000 UV–vis spectrophotometer (Thermo Scientifc, USA). Bacterial abundance was determined via *quantitative real-time PCR* (*qPCR*) utilizing the primer pairs 338F (5'-ACTCCTACGGGAGGCAGCAG-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3') (Castrillo et al. 2017). The gene amplifications were carried out in an ABI 7500 Real-Time PCR System (Applied Biosystems, USA) under the following conditions: initial denaturation at 95 °C for 5 min, followed by 35 cycles of denaturation 95 °C for 30 s, annealing at 58 °C for 30 s, and extension at 72 °C for 1 min. All qPCR reactions were performed in triplicate. Standard curves were generated using a ten-fold serial dilution of the plasmid DNA containing the target gene. The gene copy numbers were then calculated per gram of dry soil (Sun et al. 2015).

The hypervariable V3–V4 region of the bacterial *16S rRNA* gene was amplified using the primers 338F/806R with a T100 Thermal Cycler PCR thermocycler (BIO-RAD, USA). The PCR reaction mixture consisted 4 μL 5×Fast Pfu buffer, 2 μL dNTPs (2.5 mM), 0.8 μL of each primer (5 μM), 0.4 μL Fast Pfu polymerase, 10 ng of template DNA, and ddH_2O to a final volume of 20 μL. PCR amplification conditions were as follows: initial denaturation at 95 °C for 3 min, followed by 27 cycles of denaturation at 95 °C for 30 s, annealing at 55 °C for 30 s, extension at 72 °C for 45 s, and single extension at 72 °C for 10 min, with a final hold at 4 °C. The PCR products were then extracted from a 2% agarose gel and purified using the PCR Clean-Up Kit (YuHua, China) according to manufacturer's instructions. The purified products were quantified using Qubit 4.0 (Thermo Fisher Scientific, USA). The obtained PCR

amplicons were sequenced on an Illumina MiSeq PE250 platform (Illumina, USA) at Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China). Sequence data were submitted to the National Center for Biotechnology Information (NCBI) under accession number BioProject PRJNA1101230.

The raw data obtained from high-throughput sequencing was quality-filtered by fastp version 0.19.6 (Chen et al. 2018b) and merged by FLASH v. 1.2.7 (Magoč and Salzberg 2011). These optimized sequences were then clustered into operational taxonomic units (OTUs) at a 97% similarity level using UPARSE 7.1 (Edgar 2013). The taxonomy of each OTU representative sequence was classified using RDP Classifier version 2.2 (Wang et al. 2007). To assess the richness and diversity of the bacterial communities, metrics such as observed OTUs, Chao1, Shannon indices, and Good's coverage were evaluated using MOTHUR v. 1.30.1 (Schloss Patrick et al. 2009).

Statistical analysis

An analysis of variance (ANOVA) followed by *LSD* test ($P < 0.05$) was conducted to assess the impacts of mulching practices on soil physiochemical properties, gene copies, alpha diversity indices, the relative abundances of bacterial phyla and class, and total R_s. The ANOVA analyses and Pearson correlation coefficient between R_s and soil bacterial phyla were performed using SPSS 20 (SPSS Inc., USA). The changes in beta diversity of bacterial communities were determined by non-metric multidimensional scaling (NMDS) based on Bray-Curtis distance, with significance evaluated by permutation tests using the "Adonis" function in the Vegan 2.5-3 package (https://www.rproject.org/). Pearson's correlation heatmaps were generated to assess correlations among soil physiochemical properties, bacterial *16S rRNA* gene copies, and alpha diversity indices using Origin 2023b (https://www.originlab.com). Redundancy analysis (RDA) was employed to explore the relationships between soil physiochemical properties and bacterial community compositions at phylum level. The RDA results were visualized using CANOCO 5.0 (Craig 2015). Variation partitioning analysis (VPA) was conducted to partition the effects of soil physiochemical properties (e.g., ST, WFPS, NO_3^--N, NH_4^+-N, and pH) and bacterial composition (represented by the soil bacterial community composition with relative abundance greater than 1% at phylum level) on R_s. VPA was performed using the "varpart" function of the "vegan" package. Structural equation modeling (SEM) was carried out using AMOS 24.0 (IBM Corp., USA) to analyze the direct and indirect relationships among soil physiochemical properties, soil bacterial alpha and beta diversity, and R_s. The least significant path between two factors was deleted

during SEM construction, with the model re-estimated until it achieved acceptability (Wang *et al.*, 2018). The χ^2 test, comparative fit index (CFI), goodness-of-fit index (GFI), and Akaike information criterion (AIC) values were utilized to assess overall model goodness of fit ($p > 0.05$ for χ^2; closer to 1 for CFI and GFI indicates better model fit; and the lowest AIC indicates the best fit) (Schermelleh-Engel et al. 2003).

Results

Soil physiochemical properties

Soil temperature at a 5-cm depth showed similar seasonal variation trends across different mulching treatments (Fig. 3a–c). The peak soil temperature generally occurred in mid-July, with the highest values of 36.3 °C in 2019, 30.9 °C in 2020, and 38.3 °C in 2021, which were all observed in PM. Consequently, PM increased the average soil temperature over the three maize growth seasons by 1.8 °C, while SM decreased the average soil temperature by 1.8 °C, as compared with CK. Soil WFPS at 0–10 cm varied from 19.1% to 69.2% during the three maize seasons, and largely depended on rainfall (Fig. 3d–f). In comparison with CK, the average WFPS across the three maize seasons under PM and SM was increased by 11.8% and 11.6%, respectively.

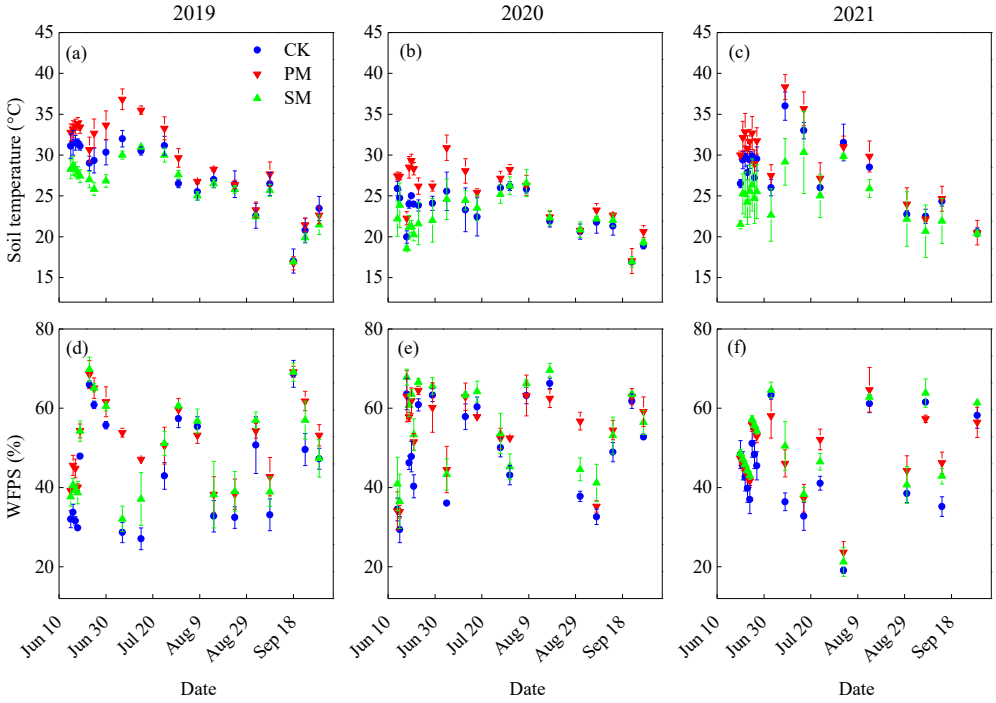


Fig. 3 Soil temperature at a depth of 5–cm and soil moisture (water-filled pore space, WFPS) within 0–10 cm layer

during the maize growing seasons of 2019, 2020, and 2021. The error bars denote the standard deviation from the mean (n = 3). CK, the control with no mulching; PM, plastic film mulching; SM, straw mulching.

Soil NO_3^--N contents at V6 and R1 stages were notably higher than at VE and R6 stages (Table 1), likely due to heavy rainfall before the sampling during the V6 and R1 stages. As compared with CK, both PM and SM significantly increased soil NO_3^--N contents ($P < 0.05$) at the VE stage; while PM still significantly increased soil NO_3^--N content, but SM significantly decreased it ($P < 0.05$) at the V6 stage. Soil NH_4^+-N contents at V1 and V6 stages were markedly higher than at R1 and R6 stages (Table 1), resulting from the fertilization at sowing. At the VE stage, the soil NH_4^+-N content under PM and SM was 1.38 and 1.90 times higher than that under CK, respectively. At the R1 stage, the soil NH_4^+-N content under SM was 3.6 times higher than that under CK, with no difference between PM and CK. Soil pH across all treatments ranged from 7.81 to 8.19 (Table 1). At V6, R1, and R6 stages, the pH under PM and SM were significantly lower than that under CK ($P < 0.05$).

Table 1 Soil NO_3^--N content, NH_4^+-N content, and pH at 0–20 cm layer during the 2021 maize season.

Growth Stage	Treatment	NO_3^--N (mg kg^{-1})	NH_4^+-N (mg kg^{-1})	pH
VE	CK	16.24±2.35b	15.95±2.67c	8.19±0.02a
	PM	32.44±8.08a	21.96±3.51b	7.95±0.05ab
	SM	40.80±5.37a	30.26±1.21a	7.81±0.21b
V6	CK	191.77±0.10c	13.59±1.14a	8.13±0.01a
	PM	254.64±4.02a	12.85±0.24a	7.92±0.02b
	SM	230.22±6.88b	12.56±0.37a	7.97±0.04b
R1	CK	89.57±8.34a	2.03±0.43b	8.12±0.03a
	PM	94.00±11.54a	3.51±1.09b	7.90±0.07b
	SM	74.13±15.15a	7.30±3.04a	7.97±0.04b
R6	CK	10.09±3.94a	2.60±0.14a	8.15±0.03a
	PM	9.14±4.09a	3.15±0.86a	7.87±0.05c
	SM	9.41±3.23a	3.39±0.71a	7.97±0.06b

Note: Values represent the mean ± standard deviation (n = 3). Different lowercase letters at each growth stage indicate significant differences at $P < 0.05$. VE, emergence; V6, sixth-leaf; R1, silking; R6, maturity. CK, the control with no mulching; PM, plastic film mulching; SM, straw mulching.

Soil bacterial abundance

Bacterial abundance is measured by gene copy number. The range of gene copies for soil bacteria was 0.88–5.05×10^9 copies g^{-1} dry soil (Fig. 4a). At V6 and R6 stages, PM decreased the gene copies by 47.3% ($P > 0.05$) and 61.3% ($P < 0.05$) respectively, but increased the gene copies ($P > 0.05$) at VE and R1 stages, compared with CK. The gene copies under SM were higher than those under CK at VE, V6,

and R1 stages ($P > 0.05$).

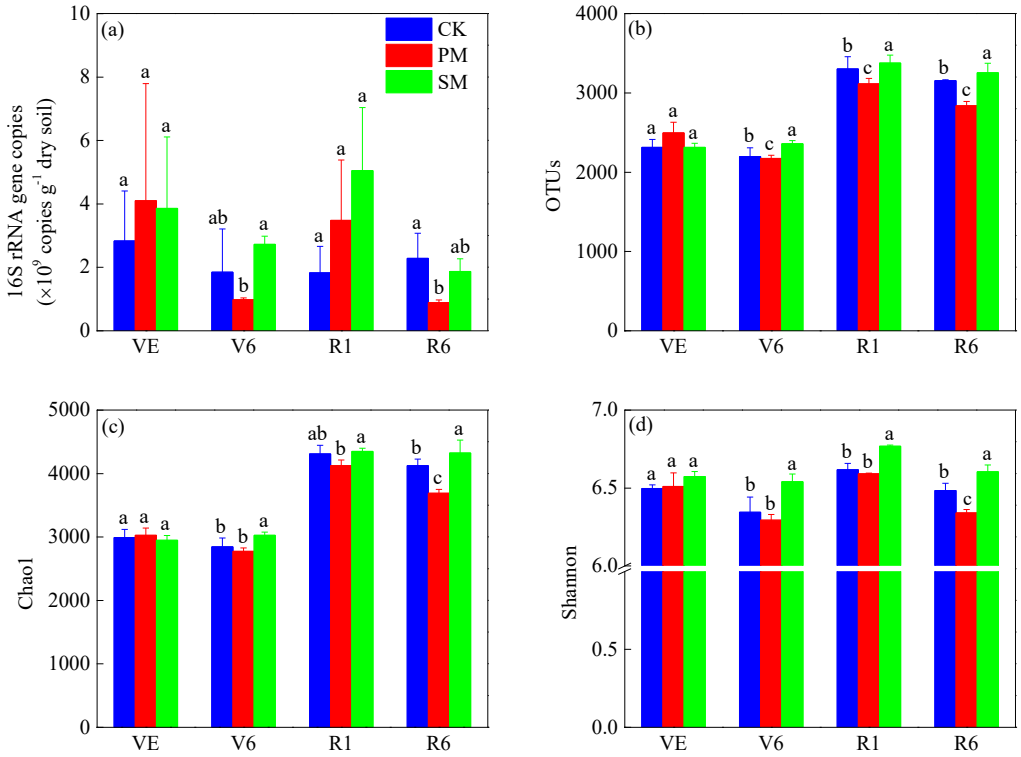


Fig. 4 Soil bacterial *16S rRNA* gene copies (a), Chao1 index (b), and Shannon index (c) during the 2021 maize season. Bars represent standard deviations (n = 3). Different lowercase letters within the same column indicate significant differences at $P < 0.05$. VE, emergence; V6, sixth-leaf; R1, silking; R6, maturity. CK, the control with no mulching; PM, plastic film mulching; SM, straw mulching.

Soil bacterial diversity and community composition

Following quality filtering and resampling, the number of bacterial OTUs for all treatments ranged from 2229 to 2737 based on 97% sequence similarity (Fig. 4b). At V1, R1, and R6 stages, in comparison with CK, PM significantly decreased OTUs ($P < 0.05$), while SM significantly increased OTUs ($P < 0.05$). Chao1 and Shannon indices under PM were slightly lower than those under CK at V6 and R1 ($P > 0.05$), which such decreases reached to the significant level at R6 ($P < 0.05$) (Fig. 4c–d). At V1, R1, and R6 stages, Chao1 and Shannon indices under SM were significantly higher than those under CK and PM ($P < 0.05$). Neither PM nor SM significantly affected OTUs, Chao1, or Shannon indices at the VE stage ($P > 0.05$).

Non-metric multidimensional scaling (NMDS) analysis was conducted to explore the variations in bacterial structure among different mulching practices (Fig. 5). The NMDS plot revealed distinct clustering of CK, PM, and SM, indicating significant influences of PM and SM on soil bacterial community structure. The cluster representing PM was positioned further from the CK cluster than SM

along the first coordinate axis, suggesting a greater impact of PM on soil bacterial community structure. In addition, the PERMANOVA test (R = 0.71, P = 0.001) corroborated the NMDS results, indicating significant effects of mulching practices on bacterial community structures.

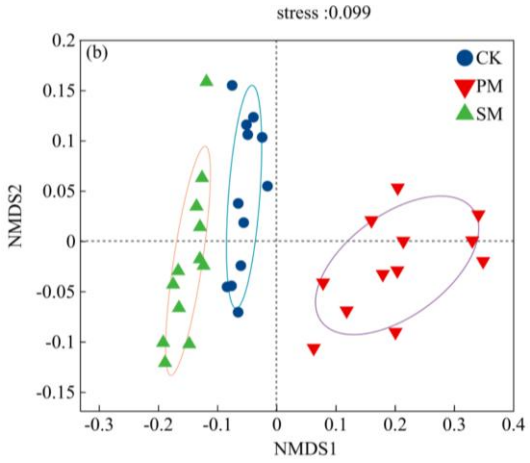


Fig. 5 Non-metric multi-dimensional scaling (NMDS) analysis of soil bacterial community at OTU level based on Bray-Curtis distance. CK, the control with no mulching; PM, plastic film mulching; SM, straw mulching.

In all samples, the predominant bacterial phyla were *Actinobacteriota* (25.4–39.5%), *Proteobacteria* (15.9–24.6%), *Chloroflexi* (11.2–25.0%), *Acidobacteriota* (4.3–22.3%), and *Firmicutes* (2.3–10.7%) (Fig. 6). Compared with CK, PM significantly increased the relative abundance of *Chloroflexi* and *Firmicutes* by 25.3–42.5% and 44.8–113.4% ($P < 0.05$) respectively, but decreased the relative abundance of *Acidobacteriota*, *Bacteroidota*, and *Nitrospirota* by 7.3–38.7%, 7.7–42.2%, and 22.4–39.3%, respectively. SM, as compared with CK, increased the relative abundance of *Proteobacteria* and *Acidobacteriota* ($P > 0.05$), but decreased *Firmicutes* ($P < 0.05$). Moreover, SM significantly boosted the relative abundance of *Bacteroidota* by 16.9–52.5% than CK ($P < 0.05$). At the class level, *Actinobacteria*, *Alphaproteobacteria*, *Chloroflexia*, *Thermoleophilia*, *Vicinamibacteria*, *Gammaproteobacteria*, *Bacilli*, and *Gemmatimonadetes* were dominant (relative abundance > 5%). The relative abundance of *Thermoleophilia* was higher under PM but lower under SM, as compared with CK.

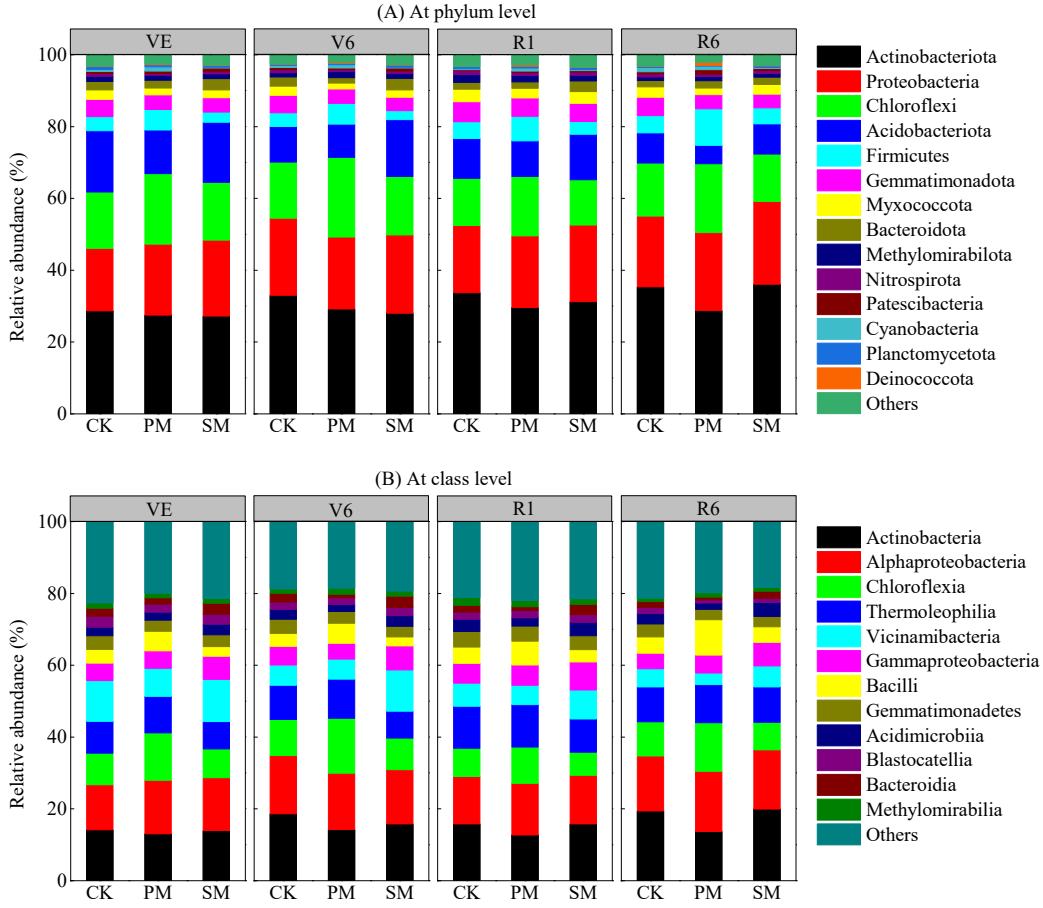


Fig. 6 Bacterial community composition at phylum (A) and class (B) levels under different treatments. VE, emergence; V6, sixth-leaf; R1, silking; R6, maturity. CK, the control with no mulching; PM, plastic film mulching; SM, straw mulching.

Soil respiration (R_s)

R_s flux ranged from 25.4 to 379.6 mg C m^{-1} h^{-1} across the three maize growth seasons (Fig. 7a–c). The average R_s flux across all the treatments during 2021 growing season (136.8 mg C m^{-1} h^{-1}) was notably lower than that during the 2019 (150.7 mg C m^{-1} h^{-1}) and 2020 (158.2 mg C m^{-1} h^{-1}) seasons. In comparison with CK, the cumulative R_s under PM was significantly increased by 20.6% ($P < 0.05$) and 7.9% ($P > 0.05$) in 2019 and 2020, respectively, but decreased by 9.1% ($P > 0.05$) in the 2021 (Fig. 7d–f). SM significantly increased the cumulative R_s by 31.8%, 39.3%, and 72.4% in 2019, 2020, and 2021 ($P < 0.05$), respectively, compared with CK.

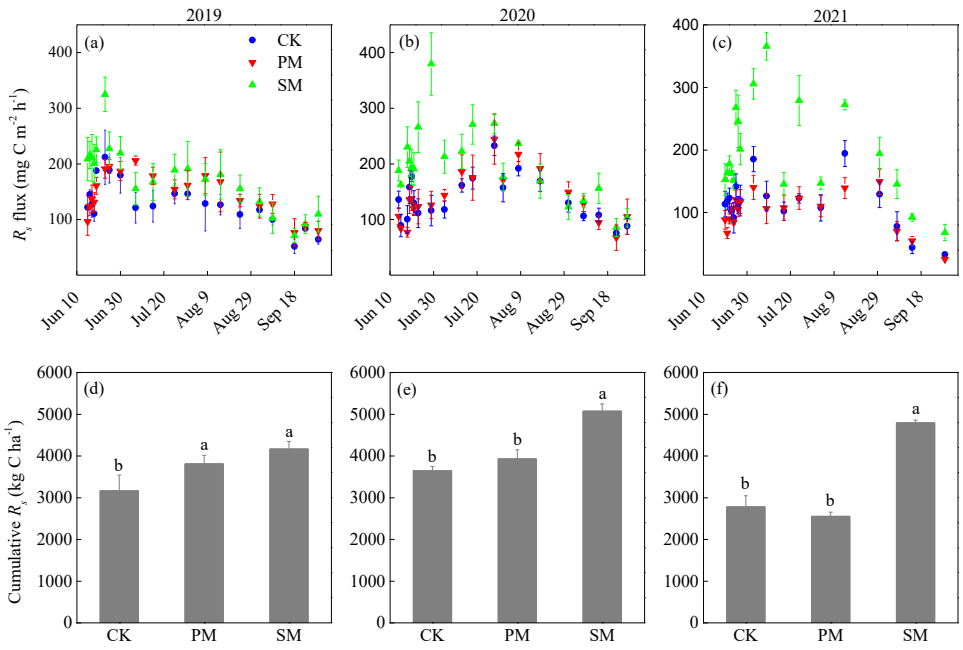


Fig. 7 Soil respiration (R_s) flux (a–c) and cumulative R_s (d–f) under different treatments during the maize growing seasons of 2019, 2020, and 2021. The error bars denote the standard deviation from the mean (n = 3). Different lowercase letters in each panel indicate significant differences ($P < 0.05$) among treatments according to the *LSD* test. CK, the control with no mulching; PM, plastic film mulching; SM, straw mulching.

Relationships among soil physiochemical properties, bacterial community, and R_S

Correlation analysis revealed a positive correlation between *16S rRNA* gene copies and NH_4^+-N (Fig. 8). On the contrary, OTUs, and Chao1 index showed negative correlations with ST and NH_4^+-N ($P < 0.05$), but positive correlation with WFPS ($P < 0.05$). In addition, RDA was employed to investigate the influence of soil physiochemical factors on soil bacterial community compositions at phylum level (Fig. 9). The soil physiochemical properties elucidated 31.11% of the total variation in soil bacterial community composition, with RDA1 and RDA2 explaining 23.04% and 8.07% of the variance, respectively. Notably, *Chloroflexi* and *Firmicutes* had positive correlations with soil temperature. While *Acidobacteriota* and *Bacteroidota* positively correlated with NH_4^+-N, but *Actinobacteriota* and *Firmicutes* negatively correlated with NH_4^+-N.

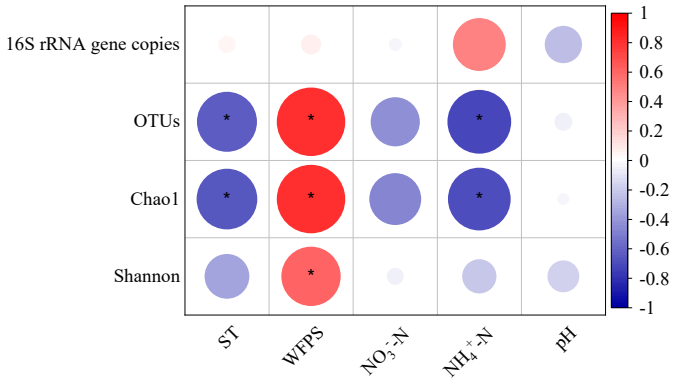


Fig. 8 Correlation analysis of soil bacterial *16S rRNA* gene copies and alpha diversity and soil physiochemical properties. *, significance level at $P < 0.05$; ST, soil temperature; WFPS, soil water-filled pore space.

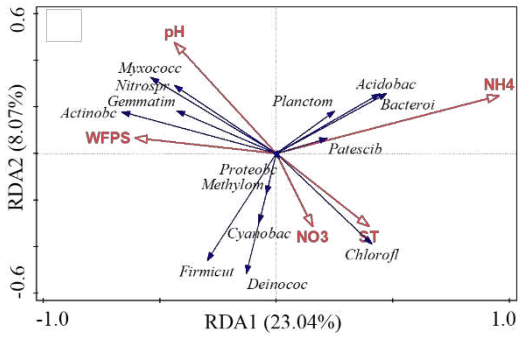
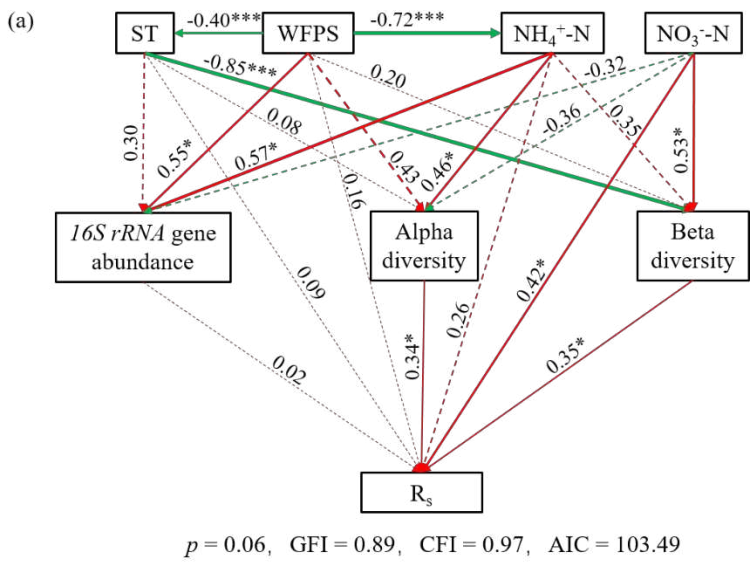
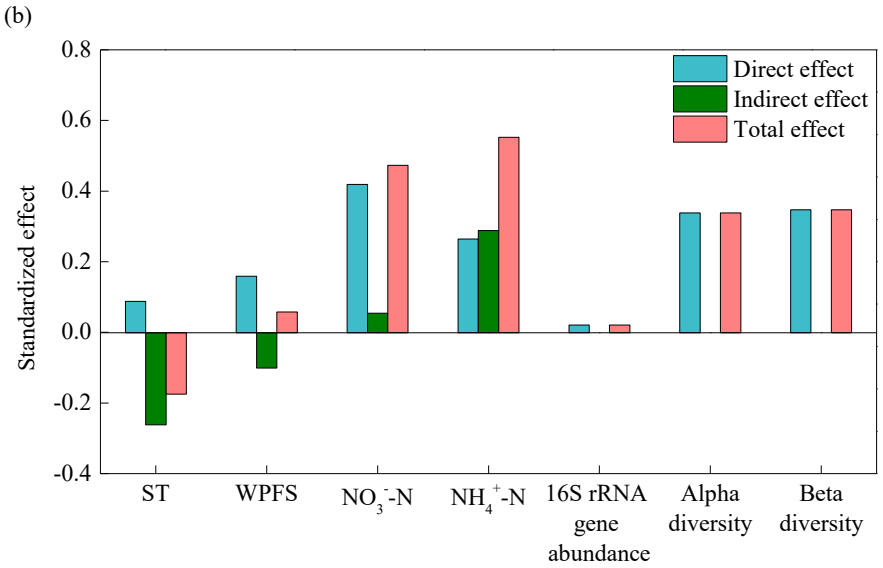


Fig. 9 Redundancy analysis (RDA) of bacterial community compositions (at phylum level) and soil physiochemical properties. ST, soil temperature; WFPS, soil water-filled pore space.

A structural equation model was constructed to delve deep into the direct, indirect, and total effects of soil physiochemical properties and bacterial characteristics on R_s (Fig. 10). The SEM results showed that NH_4^+-N (0.55), NO_3^--N (0.47), bacterial beta diversity (0.35), and bacterial alpha diversity (0.34) had greater total effect on R_s. Notably, NH_4^+-N not only directly influenced R_s, but also indirectly influenced bacterial alpha diversity. In addition, soil temperature indirectly affected R_s by affecting bacterial beta diversity.



330



331

332 **Fig. 10** Direct or indirect effects of soil temperature (ST), soil water-filled pore space (WFPS), bacterial *16S rRNA*
333 gene abundance, alpha diversity, and beta diversity on soil respiration (R_s) (a) using structural equation model (SEM).
334 Standardized direct, indirect, and total effects of ST, WFPS, gene abundance, alpha diversity, and beta diversity on
335 R_s (b) based on SEM. *16S rRNA* gene abundance was represented by *16S rRNA* gene copies; alpha diversity was
336 represented by OTUs, Chao1, and Shannon indices; beta diversity was represented by NMDS1. Numbers closed to
337 the arrows are standardized path coefficients; asterisks following the numbers indicate significant levels: *** $P <$
338 0.001, and * $P < 0.05$. Red and green arrows represent positive and negative relationships, respectively. Solid and
339 dashed arrows represent significant and insignificant relationships, respectively. The line width of the arrows
340 indicates the correlation strength.

341 The correlation between R_s and bacterial community composition was investigated (Table 2), owing
342 to the significant impact of soil bacterial beta diversity on R_s indicated by the SEM results. At the phylum
343 level, R_s showed negative correlations with the relative abundances of *Chloroflexi*, *Firmicutes*,
344 *Cyanobacteria*, and *Deinococcota* ($P < 0.05$), but positive correlations with the relative abundances of

Acidobacteriota, *Bacteroidota*, *Methylomirabilota*, *Nitrospirota*, and *Planctomycetota* ($P < 0.05$).

Table 2 Correlation coefficient between soil respiration (R_s) and soil bacterial community compositions (at phylum level)

Classification level	Name	Correlation coefficient
Phylum	*Actinobacteriota*	-0.18
	Proteobacteria	-0.06
	Chloroflexi	-0.33*
	Acidobacteriota	0.58**
	Firmicutes	-0.65**
	Gemmatimonadota	0.19
	Myxococcota	0.27
	Bacteroidota	0.52**
	Methylomirabilota	0.55**
	Nitrospirota	0.36*
	Patescibacteria	-0.33
	Cyanobacteria	-0.59**
	Planctomycetota	0.48**
	Deinococcota	-0.61**

Note: ** and * represent significant levels at $P < 0.01$ and $P < 0.05$, respectively.

Discussion

Effects of PM and SM on soil bacterial abundance and alpha diversity

The alpha diversity of soil bacteria serves as a crucial indicator of soil health (Delgado-Baquerizo et al. 2016). The Chao1 index assesses species richness and the Shannon index evaluates both species richness and evenness (Xie et al. 2022). In arid and semi-arid regions, PM has been found to significantly increase soil bacterial abundance and alpha diversity, primarily due to improvements in soil hydrothermal conditions and nutrient environments (Dong et al. 2017; Huang et al. 2019). However, it has been reported that the humid environment fostered by PM promotes fungal growth (Qin et al. 2017), which in turn can limit bacterial proliferation (Fu et al. 2019). In addition, the exceptionally high soil temperatures under PM may have a sterilizing effect, reducing the bacterial abundance and diversity (Farmer et al. 2018; Luo et al. 2019). In this study, the OTUs, Chao1, and Shannon indices of bacteria were negatively correlated with soil temperature (Fig. 8), suggesting that increased soil temperatures were detrimental to bacterial survival. PM significantly decreased bacterial alpha diversity (i.e., OTUs, Chao1, and Shannon indices) during the 2021 maize season, possibly because of the harmful effect of extremely high soil

363 temperature (above 38 °C) under PM. As for SM, it can provide abundant sources of carbon and nitrogen
364 for soil microorganisms, thus increase bacterial abundance and richness (Somenahally et al. 2018). In
365 this study, SM significantly increased bacterial alpha diversity, which was attributed to the improved soil
366 nutrient status as well as the cooling effect of SM during the summer. Although it has been reported that
367 SM had no significant effect on soil bacterial diversity but increased fungal diversity (Fu et al. 2019),
368 owing to the more efficiently decomposing and utilizing carbon than bacteria (Waring et al. 2013), fungal
369 community diversity was not investigated in this study. The effects of PM and SM on the diversity of
370 fungal communities shall be taken into consideration in future studies. In addition, soil disturbance
371 caused by tillage shall also be considered, since it may mask the effects of mulching practices on soil
372 bacteria (Li et al. 2020). This could potentially explain why PM and SM did not significantly affect soil
373 bacterial abundance and diversity at the VE stage.

374 **Effects of PM and SM on soil bacterial community compositions**

375 In this study, *Actinobacteriota*, *Proteobacteria*, *Chloroflexi*, and *Acidobacteriota* were dominant,
376 consistent with findings from other agricultural dryland studies (Fu et al. 2019; Luo et al. 2022).
377 *Actinobacteriota* were categorized as slow-growing oligotrophs that thrive in low-nutrient environments
378 (Pascault et al. 2013). *Proteobacteria*, known as fast-growing copiotrophs, were stimulated in nutrient-
379 rich soils (Eilers et al. 2010). SM provided a rich source of carbon for *Proteobacteria*, thus increased its
380 relative abundance (Fig. 6), which is consistent with previous research (e.g., Fu et al. 2019; Huang et al.
381 2019; Tian et al. 2022). *Chloroflexi* were anaerobic oligotrophs, characterized by slow growth rates (Qian
382 et al. 2022). The higher relative abundance of *Chloroflexi* under PM was probably caused by the anoxic
383 environment created by PM, as compared with CK and SM. *Firmicutes*, another major phylum, can
384 produce spores to withstand nutrient deficiencies and extreme environmental conditions (Trivedi et al.
385 2013). The increased relative abundance of *Firmicutes* under PM may be attributed to the fact that the
386 high soil temperatures accelerate the decomposition of soil organic matter, resulting in nutrient deficiency
387 during the later stages of maize growth.

388 **Influence of bacterial community and soil physicochemical properties on R_s**

389 Abiotic and biotic factors play crucial roles in R_s (Nazaries et al. 2015). In this study, R_s was
390 significantly influenced by both soil physiochemical properties and bacterial communities (Fig. 10).

Among soil physiochemical properties, soil available N had a greater impact on R_s as compared with soil temperature and moisture (Fig. 10). Soil available N can alter plant root characteristics (e.g., root biomass and root length density), thereby affect root respiration, which is a component of R_s (Tu et al. 2011). In addition, soil available N can influence R_s by shaping the soil microbial communities (Fig. 10), which is consistent with Sushko et al. (2019). Soil temperature and moisture are typically considered as key abiotic factors controlling soil respiration (Davidson and Janssens 2006). In this study, soil temperature had a negative effect on R_s, which diverges from a few previous studies (e.g., Lloyd and Taylor 1994; Davidson and Janssens 2006). This discrepancy might be attributed to the exceptionally high soil temperature during the summer of 2021 (38.3 °C), largely exceeding the optimal range for soil bacteria and thereby inhibiting the decomposition of soil organic matter (Schipper et al. 2014). Soil moisture (WFPS) had minor effect on R_s, possibly due to adequate precipitation throughout the experiment period (500 mm for 2019, 608 mm for 2020, 466 for 2021, and 354 mm for the average for the last 30 years). Soil bacteria are considered as essential drivers of soil carbon cycling (Lemanceau et al. 2015). In this study, the diversity and structure of soil bacterial community, rather than bacterial abundance, regulated R_s (Fig. 10), which is in agreement with Wang et al. (2022). Previous studies have noted *Acidobacteriota*'s capacity to decompose soil organic carbon (Cleveland et al. 2007; Rawat et al. 2012; Banerjee et al. 2016). Similarly, *Bacteroidota* are the initial metabolizer of soil organic matter, breaking down lignocellulose into short-chain fatty acids (Dodd et al. 2011). These roles may possibly explain the positive correlation observed between R_s and the relative abundances of *Acidobacteriota* and *Bacteroidota* (Table 2). In addition, *Chloroflexi* is able to fix carbon (Hug et al. 2013), and *Firmicutes* prefer to survive in an anaerobic environment (Ma et al. 2020). Since the decomposition of organic matter by microbes to produce CO_2 primarily occurs under aerobic conditions, *Firmicutes* may have a limited role in this process (Ma et al. 2020), which may result in their negative correlations with R_s.

Mulching practices have a significant impact not only on soil physiochemical properties, but also on the diversity and structure of soil bacterial communities, and ultimately influence R_s. PM is able to increase available nitrogen levels in the soil and promote early-stage root development, thereby improve root respiration (Li et al. 2019). However, prolonged exposure to increased soil temperatures, anoxic conditions, and nutrient depletion induced by PM can diminish bacterial diversity and favor the proliferation of oligotrophic bacteria such as *Chloroflexi* and *Firmicutes*. These bacteria are less efficient in mineralizing SOM, leading to reduced soil CO_2 emissions (Hug et al. 2013; Ma et al. 2020). This

phenomenon likely contributed to the observed reduction in R_s under PM in 2020 (Fig. 7). In contrast, SM can supply abundant nutrients for bacterial activity, fostering a diverse soil bacterial community dominated by copiotrophic bacteria such as *Acidobacteriota* and *Bacteroidota*. This enrichment of copiotrophic bacteria enhanced the decomposition of straw and SOM, thereby promoted R_s (Banerjee et al. 2016). Therefore, mulching practices might play a critical role in shaping soil bacterial communities, which in turn affect R_s dynamics through their metabolic activity and interactions with soil physiochemical conditions.

Conclusion

This study showed that the differential effects of mulching practices on R_s were related to their impacts on soil biotic and abiotic factors. The effect of PM on R_s was observed to have inter-annual variability. In hot summers, higher soil temperatures under PM, combined with nutrient deficiency in the late growth stage of maize, can decrease soil bacterial abundance and alpha diversity. This environment under PM also favored the proliferation of oligotrophic bacteria such as *Chloroflexi* and *Firmicutes*, while suppressed the growth of copiotrophic bacteria such as *Acidobacteriota*, both resulting in decreasing R_s. On the contrary, SM created favorable soil temperature and nutrient conditions, thus increased the abundance and alpha diversity of soil bacterial community. This facilitated the growth of *Proteobacteria*, *Acidobacteriota*, and *Bacteroidota*, which made SM capable of decomposing SOM and thus increasing R_s. Our study highlights the significant role of bacterial community composition and soil properties in R_s and suggested that the carbon cycle of agricultural field could be influenced by the soil bacteria under different mulching practices.

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Author contributions Xiaoqi Luo: conceived the idea, performed the experiments, and wrote the original draft of the manuscript; Nanping Lin and Naijiang Wang: collected the data, analyzed the data and prepared the figures; Benhua Sun: Supervised the experiments and data analysis; Yunfei Tuo and Jianqiang Li: reviewed and edited the manuscript; Haixin Chen and Hao Feng: designed the experiments,

reviewed the manuscript, and supervised the project. All authors read and approved the final manuscript.

Data availability 16S rRNA gene sequences were deposited to the National Center for Biotechnology Information (NCBI) under the project accession number PRJNA1101230. The physicochemical properties and soil respiration of the soil will be made available on request.

Declarations

Competing interests The authors declare that they have no conflict of interest.

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675