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RESEARCH ARTICLE

Effects of biodegradable and polyethylene film mulches and their residues on soil bacterial communities

Chong Yang[1,2] · Yaozhu Huang[1,2] · Bibo Long[1,2] · Xuhua Gao[1]

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Abstract

To investigate the effects of plastic film mulches and their residual films after use on soil bacterial communities, mulching experiment and the subsequent residual film experiment were conducted on winter-planting potato field in two locations. During mulching experiment, treatments biodegradable film mulch (BM) and PE film mulch (PM) reduced soil nutrient regarding available nitrogen and available potassium, as well as microbial biomass carbon (MBC), but increased urease activity, as compared to treatment no film mulch (NM). Soil moisture was significantly elevated by mulching practices and correlated with more microbial phyla than the other tested soil properties, indicating its important role in shaping soil bacterial communities. In addition, mulching practices increased alpha diversity of soil bacteria, although location heterogeneity was observed. Network analyses showed that both treatments BM and PM promoted the interrelations within bacterial communities and harbored more keystone taxa than treatment NM. During residual film experiment, residual films from BM and PM were incorporated into soil after harvest of potato. Treatment residual biodegradable film (RBF) significantly increased the content of MBC and activity of β-glucosidase (BG) as compared to treatments residual PE film (RPF) and no residual film (NRF), and BG had the most correlations with microbial phyla among all the tested soil properties. Treatments RBF and RPF increased the relative abundance of some dominant bacterial phyla, including *Bacteroidetes*, *Actinobacteria*, and *Chlorofexi*, and enhanced the interrelations within bacterial community, whereas more keystone taxa were harbored by treatment RBF, due to the increase of keystone taxa in phyla *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, and *Proteobacteria*. These results indicate that the indirect effects of biodegradable and PE film mulch as a soil surface barrier on soil are similar, whereas their direct effects via incorporation into soil as residual films show specificity.

Keywords Biodegradable film mulch · PE film mulch · Residual biodegradable film · Residual PE film · Bacterial community

Introduction

The soil microbial communities play crucial roles in soil ecological processes, including maintenance of soil structure (Dong et al. 2017), mineralization of soil organic matter (Wang et al. 2020a), soil nutrient cycling (Bardgett and van der Putten 2014), and litter decomposition (Delgado-Baquerizo et al. 2016). In addition, soil microbiomes can stimulate plant growth through modulating plant flowering timing (Lu et al. 2018), promote plant diversity and productivity (van der Heijden et al. 2008), and enhance plant tolerance to various stresses such as abnormal temperature variation, drought, salinity (Lau and Lennon 2012), as well as pathogens and herbivores (Raaijmakers and Mazzola 2016; Howard et al. 2020). The soil microbial diversity has been considered an indicator of soil health and quality (Zheng et al. 2018). Thus, research on the effects of soil management on soil microbial communities has become a fundamental aspect of sustainable agriculture (Dong et al. 2017).

Soil organic carbon, moisture, temperature, vapor diffusivity, and presence of plant roots have been reported as important factors that affect the soil microbial community

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✉ Chong Yang
parker815@163.com

[1] Institute of Biological and Medical Engineering, Guangdong Academy of Sciences, Guangzhou 510316, China

[2] Guangdong Biomaterials Engineering Technology Research Center, Guangzhou 510316, China

composition (Drenovsky et al. 2004; Buyer et al. 2010; Li et al. 2017; Bandopadhyay et al. 2018). Thus, agricultural management practices, like mulching, can alter soil microbial diversity through modification of soil microenvironment (Bandopadhyay et al. 2018). Plastic mulch film, mostly made from low-density polyethylene (PE), has been extensively applied worldwide due to its low price, easy processibility, excellent chemical resistance, high durability, and flexibility (Kasirajan and Ngouajio 2012). PE film mulching (PM) can effectively improve crop yield through soil water conservation, soil temperature regulation, efficient use of soil nutrients, and weed control (Kader et al. 2017), thus influencing soil microenvironment. Dong et al. (2017) reported that PM increases the richness and diversity of soil microorganisms, due to its effect on elevating soil temperature and water content, as compared to no mulch. Farmer et al. (2017) also confirmed that PM plays a significant role in shaping microbial community composition. However, concerns on environmental pollution issues caused by application of PM in agriculture keep growing, as degradation of PE film is extremely slow under natural condition, and plastic fragments will remain in soil for decades. A recent survey on plastic pollution showed that the residual plastic films accumulated in soil reach up to 317.4 kg ha^{-1}, with a mean value of 34.0 kg ha^{-1} across croplands in China (Zhang et al. 2020). Accumulations of residual plastic films interfere with soil structure, soil water movement (Jiang et al. 2017; Bläsing and Amelung 2018), and rhizosphere bacterial communities (Qi et al. 2020), leading to inhibition of crop root distribution. Consequently, water and nutrient uptake of crops are disturbed, resulting in yield losses (Hu et al. 2020).

Biodegradable film mulch (BM) has been developed as an environmentally friendly alternative to PM (Yang et al. 2020). Biodegradable films have similar effects as PE films on crop production regarding mulching function (Wang et al. 2019) and can be completely catabolized into harmless products in a reasonable time frame, theoretically (Moreno and Moreno 2008). The toxicity of PBAT biodegradable films on *Allium cepa*, *Lactuca sativa*, and human cell line HepG2/C3A have been evaluated in a recent study, suggesting that the soil does not induce damage to the tested organisms before and after degradation of PBAT films (Souza et al. 2020). The knowledge about effects of BM on soil microbial communities is scarce. Bandopadhyay et al. (2018) divide these effects into two aspects: indirect effect as a soil surface barrier and direct effect via incorporation into soil. For indirect effect as mulch, BM presents lower soil temperature (Kader et al. 2017) and is more vapor-permeable (Touchaleaume et al. 2016) than PM, resulting in release of soil CO_2 (Zhang et al. 2015; Yu et al. 2016), which may contribute to the different effects between BM and PM on soil microbial communities. For direct effect, biodegradable film fragments left in field may physically modify soil before they are fully biodegraded (Bandopadhyay et al. 2018), resulting in alteration of soil microbial communities. Microplastics, possibly generated from mulching films as an emerging pollutant in terrestrial systems (Machado et al. 2018), can also alter microbial community composition and enzymatic activities in soil (Huang et al. 2019), thus acting as a distinct microbial habitat (Zhang et al. 2019). Small amounts of organic and inorganic components released from biodegradable films may also impact soil microbes, given that some compounds used in biodegradable plastics exhibited a concentration-dependent inhibition of plant growth (Martin-Closas et al. 2014). In addition, the growth of soil microbes in agricultural soil is usually carbon-limited, and the incorporated biodegradable films can be an input of carbon to soil, though the amount is very small (Lehmann and Kleber 2015).

In this study, polylactic acid/poly (butyleneadipate-co-terephthalate)-based biodegradable film and PE film were used as materials to compare their effects on soil. In order to maximize potential differences in environmental and soil conditions in this study, the experimental design was established at two locations. Two continuous experiments were conducted: (1) biodegradable and PE films were applied on winter-planting potato as mulch experiment; and (2) the residual films were then incorporated into soil after harvest for residual film experiment. The objective was to investigate the indirect effects of biodegradable and PE films as mulch and their subsequent direct effects as residual films, on soil properties, enzymatic activities, and bacterial communities. The associations in between bacterial communities and their relationship with soil environmental factors were identified by using network analyses.

Materials and methods

Experiment design

Experiment was performed in two locations (L1: 114°2′ E, 23°7′ N, and L2: 113°4′ E, 24°2′ N), Guangdong Province, China. The two study sites both have subtropical monsoon climates with an average annual precipitation of 1932.7 and 1906.2 mm, an average annual temperature of 21.8 and 21.1 °C, respectively. The soils at both study sites are classified as sandy loam. Winter-planting potato (*Solanum tuberosum* L.) was used as test crop. During the cropping season of winter-planting potato from November 8th, 2019 to March 7th, 2020, the average air temperatures were 18.5 °C and 17.4 °C, and total precipitations were 184 mm and 152 mm (less than 10% of annual rainfall), respectively at the two study sites.

The mulching experiment was designed with three treatments: (1) black biodegradable film mulch (BM)

with a film thickness of 0.012 mm, (2) black polyethylene (PE) film mulch (PM) with a film thickness of 0.008 mm, and (3) no mulch (NM). The biodegradable film was made from polylactic acid/poly (butyleneadipate-co-terephthalate). Both biodegradable and PE films were produced by Guangzhou Sweet Economic Development Co., Ltd, Guangdong, China. Each treatment had three replicates with plots area 18 m in length and 2 m in width as described by Yang et al. (2020). All of the agronomic managements were same as local winter-planting potato fields. Fertilizers were applied evenly on the field before planting with nitrogen, phosphorus, and potassium fertilizers 152, 106, and 135 kg ha^{-1}, respectively. After sowing, films (0.8 m in width) were applied on the soil surface by machine. After harvest of potato, PE films were broken into pieces by machine and incorporated into soil, while biodegradable films were incorporated into soil directly for the residual film experiment. Thus, the residual film experiment was also classified as three treatments: (1) residual biodegradable film (RBF), (2) residual PE film (RPF), and (3) no residual film (NRF).

Soil sampling

For the mulching experiment, soil samples were collected at 90 days after sowing of potato when biodegradable film started to degrade. Soil samples for the residual film experiment were taken at 300 days after sowing. Residual biodegradable films were dramatically degraded to a low level at 300 days after sowing, while residual PE films were barely reduced (Yang et al. 2020). Five soil ring samples (5 cm in diameter, 10 cm in depth) were randomly collected from each plot and pooled as a mixed sample, yielding 18 soil samples for each experiment (3 treatments × 3 replicates × 2 locations). These soil samples were homogenized and sieved for the following measurements.

Physicochemical analyses

Soil total organic carbon (TOC) was measured using wet oxidation (Bao 2000), and total nitrogen (TN) was assessed by the Kjeldahl method (Purcell and King 1996). Soil organic matter (SOM) was measured with $K_2Cr_2O_7$ oxidation–reduction titration method (Nelson and Sommers 1996). The content of soil available nitrogen (AN), phosphorus (AP), and potassium (AK) as well as soil pH was determined by using standard soil testing procedures (Bao 2000). Soil microbial biomass carbon (MBC) was determined using chloroform fumigation-extraction method (Vance et al. 1987). Soil moisture was determined by oven-drying soil samples at 105 ℃ for 48 h.

Assays on enzyme activities

β-glucosidase (BG) and acid phosphatase (ACP) were assayed using a fluorometric method with 4-methylumbelliferyl-β-D-glucopyranoside and 4-methylumbelliferyl-phosphate as substrate, respectively (Saiya-Corka et al. 2002). Urease (UR) activity was determined by using indophenol blue colorimetry method (Tabatabai 1994).

High-throughput sequencing of soil bacterial communities

Total DNA was extracted from soil samples using a Power Soil DNA Isolation Kit (MOBIO Laboratories) according to the manufacturer's protocol. The concentration and DNA quality were measured with an Eppendorf Biophotometer Plus (Eppendorf, Germany), and the extracted DNA was stored at − 20 °C for downstream analysis. For each sample, the primers 338F (5′-ACTCCTACGGGAGGCAGCA-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′) were used to amplify the V3-V4 region of the bacterial 16S rRNA gene. The DNA was amplified using two rounds of PCR. The PCR product from the first step was purified through VAHTS DNA Clean Beads (Vazyme, Nanjing, China). The PCR product from the second step was quantified by Quant-iT- dsDNA HS Reagent and pooled together for high-throughput sequencing using an Illumina Hiseq 2500 platform.

After removing adapters and low-quality reads, raw tags were obtained from the paired-end clean reads by using Fast Length Adjustment of Short reads (FLSAH, version 1.2.11) with a minimum overlap of 10 bp and mismatch error rates of 2% (Magočand Salzberg 2011). Trimmomatic (version 0.33) was then used to trim the raw tags (Bolger et al. 2014) and UCHIME (version 8.1) was applied to detect and remove chimera (Edgar et al. 2011) for clean tags. Operational taxonomic units (OTUs) were clustered at a threshold of 97% similarity using UPARSE (Edgar 2013). The tag sequence with the highest abundance was selected as its representative sequence.

Data visualization and statistical analysis

The bacterial representative sequences were aligned to the SILVA database (http://www.arb-silva.de/, Release132) and annotated using RDP Classifier version 2.2 with 0.8 confidence interval (Wang et al. 2007). The alpha diversity indices were analyzed using Mothur version 1.30 (Schloss et al. 2009) and compared among different treatments using Tukey's test. Non-metric multi-dimensional scaling (NMDS) was performed using R version 3.6.1. Correlation heatmaps based on the relevance between soil bacteria at the

phylum level and soil properties (Spearman with $p < 0.05$ and $r > 0.8$) were performed with data from two locations pooled together (Banerjee et al. 2019). The network analyses were conducted to investigate the co-occurrence patterns within the bacterial community members with relative abundances > 0.1% at the genus level using Cytoscape version 3.7.2 (Wang et al. 2020a). Keystone taxa could be identified using network analyses with high mean degree, high closeness centrality, and low betweenness centrality as criteria (Banerjee et al. 2018). OTUs with degree higher than 15, closeness centrality higher than 0.44, and betweenness centrality lower than 0.18 were selected as keystone taxa (Table S1). Analysis of variance (ANOVA) was conducted using R version 3.6.1, and significance was determined by Tukey's test ($p < 0.05$).

Results

Potato yield

The tuber yields of potato under different treatments were recorded in Fig. S1. Both treatments biodegradable film mulch (BM) and PE film mulch (PM) significantly increased the tuber yields of potato as compared to treatment no mulch (NM), with no difference observed between the two mulching treatments in location 1 (L1). Similar result was also found in location 2 (L2) during mulching experiment.

Soil physicochemical properties

Compared to treatment NM, BM performed similarly as PM on the increase of soil moisture during mulching experiment, while the soil moisture under the three treatments was significantly different during residual film experiment, ranking as residual PE film (RPF) > residual biodegradable film (RBF) > no residual film (NRF) in both locations (Table 1, Fig. S2). Available nitrogen (AN) and available potassium (AK) contents were significantly reduced by treatments BM and PM during mulching experiment in both locations, as compared to their respective treatment NM (Table 1, Fig. S2A). In addition, treatments BM and PM both decreased the microbial biomass carbon (MBC) contents during mulching experiment in L1 and L2, as compared to treatment NM (Table 1, Fig. S2A). The MBC content was significantly increased under treatment RBF, as compared to their respective treatment NRF in both locations (Table 1, Fig. S2B).

Soil enzymatic activities

During mulching experiment, no significant differences of β-glucosidase (BG) activities among the three treatments were observed in both locations (Fig. 1A). In contrast during residual film experiment, the BG activity was significantly enhanced by treatment RBF as compared to the other two treatments, with the activity under treatment RPF significantly higher than that under treatment NRF in L1, but no difference in L2 (Fig. 1B). The urease (UR) activities under treatments BM were significantly higher than that under treatment NM (Fig. 1C), whereas residual films significantly reduced the UR activities as compared to their respective treatment NRF in both locations (Fig. 1D). No differences of acid phosphatase activities were observed among the treatments through two experiments (Fig. 1E–F).

Bacterial community diversity

A total of 2,505,477 clean tags were obtained from 36 soil samples, generating 49,845 operational taxonomic units (OTUs). The unique and shared OTUs in the soil samples under three treatments at two locations across two experiments were shown in the Venn diagrams (Fig. S3). Compared to treatment NM, the numbers of OTUs unique in treatments PM and BM were 48 and 46 in L1, and 21 and 17 in L2. During residual experiment, the numbers of OTUs unique in treatments RPF and RBF were 8 and 15 in L1, and 18 and 23 in L2. Abundance-based coverage estimator (ACE) and Simpson indices were used to calculate the alpha diversity of soil bacteria. ACE index represents the community richness of bacteria, and Simpson index evaluates the bacterial community diversity. ACE index under treatments BM and PM was significantly increased, whereas Simpson index was significantly decreased, as compared to their respective NM in L1 (Fig. 2A and C). No significant differences of ACE or Simpson index between any two treatments of NM, BM, and PM were observed in L2 (Fig. 2A and C). There were no significant differences of ACE index among the three treatments in L1 during residual film experiment, whereas the ACE index under treatment RBF was significantly higher than that under treatment RPF in L2 (Fig. 2B). The Simpson index under treatments RBF and RPF was significantly lower than that under treatment NRF in L1, and in L2 treatment, RBF significantly reduced the Simpson index as compared to treatment NRF (Fig. 2D). Non-MetricMulti-Dimensional Scaling (NMDS) analyses on different treatments and two locations across two experiments showed that the treatments and locations formed distinct groups in the plotted ordination space during the two experiments (PERMANOVA, $p < 0.01$, Fig. 3, Fig. S4).

Soil bacterial taxa under different treatments

Soil bacterial phyla with top 10 relative abundances were *Proteobacteria*, *Actinobacteria*, *Chloroflexi*, *Acidobacteria*, *Firmicutes*, *Gemmatimonadetes*, *Bacteroidetes*,

Table 1 Soil properties under different treatments

Location	Treatment	TOC (g kg^{-1})	TN (g kg^{-1})	SOM (g kg^{-1})	AN (mg kg^{-1})	AP (mg kg^{-1})	AK (mg kg^{-1})	MBC (mg kg^{-1})	Moisture (%)	pH	C:N
L1	NM	15.56 ± 0.03b	1.32 ± 0.00b	24.46 ± 0.39b	171.33 ± 3.21a	338.33 ± 3.51a	441.67 ± 8.50a	315.24 ± 5.15c	10.32 ± 0.86c	5.19 ± 0.02c	11.80 ± 0.55a
L1	BM	15.47 ± 0.27b	1.31 ± 0.01b	24.34 ± 0.86b	100.67 ± 2.52d	332.67 ± 8.02a	415.67 ± 9.50b	288.66 ± 7.05d	15.32 ± 0.73b	5.61 ± 0.02b	11.85 ± 0.45a
L1	PM	15.96 ± 0.09b	1.31 ± 0.01b	24.08 ± 0.95b	116.67 ± 3.20c	347.67 ± 4.01a	355.67 ± 2.08d	280.29 ± 7.09d	16.25 ± 0.87b	5.42 ± 0.05b	12.18 ± 0.05a
L2	NM	16.74 ± 0.20a	1.34 ± 0.01a	26.37 ± 0.27a	137.33 ± 3.06b	288.67 ± 4.51b	451.33 ± 3.06a	387.60 ± 4.53a	15.66 ± 1.04b	6.28 ± 0.01a	12.46 ± 0.20a
L2	BM	16.62 ± 0.34a	1.36 ± 0.01a	26.17 ± 0.35a	116.00 ± 4.36c	264.33 ± 6.66c	406.67 ± 2.08c	356.56 ± 8.54b	17.17 ± 0.92ab	6.30 ± 0.03a	12.25 ± 0.30a
L2	PM	16.48 ± 0.14a	1.35 ± 0.01a	26.55 ± 0.21a	111.67 ± 6.51c	258.00 ± 4.58c	429.00 ± 6.56b	327.15 ± 8.70c	19.34 ± 0.89a	6.31 ± 0.04a	12.21 ± 0.13a
Location		***	***	***	**	***	NS	***	***	***	NS
Treatment		NS	NS	NS	***	**	***	***	***	**	NS
Location * treatment		*	*	NS	***	***	***	NS	*	***	NS
L1	NRF	15.68 ± 0.27b	1.31 ± 0.01b	25.69 ± 0.42b	85.77 ± 2.40a	351.67 ± 3.21a	392.00 ± 8.54a	217.71 ± 2.43d	18.09 ± 0.59e	5.54 ± 0.04c	11.95 ± 0.64a
L1	RBF	15.73 ± 0.40b	1.31 ± 0.01b	25.39 ± 0.32b	69.87 ± 2.60b	350.00 ± 7.21a	327.33 ± 6.03b	230.05 ± 9.53c	20.53 ± 0.29d	5.42 ± 0.01d	11.96 ± 0.22a
L1	RPF	15.66 ± 0.30b	1.32 ± 0.01b	25.55 ± 0.15b	72.03 ± 1.68b	346.33 ± 4.51a	292.33 ± 6.03c	207.58 ± 8.34d	23.89 ± 0.51ab	5.62 ± 0.03b	11.89 ± 0.51a
L2	NRF	16.51 ± 0.14a	1.35 ± 0.01a	27.08 ± 0.53a	83.00 ± 2.00a	220.00 ± 7.00b	392.00 ± 7.55a	255.91 ± 11.44b	21.90 ± 1.15c	6.47 ± 0.02a	12.23 ± 0.89a
L2	RBF	16.66 ± 0.14a	1.35 ± 0.01a	27.05 ± 0.01a	62.33 ± 1.15c	236.33 ± 10.07b	332.33 ± 3.21b	271.06 ± 13.51a	22.85 ± 0.60bc	6.41 ± 0.04a	12.31 ± 0.43a
L2	RPF	16.84 ± 0.17a	1.36 ± 0.01a	27.19 ± 0.31a	72.33 ± 0.58b	205.00 ± 8.00b	381.33 ± 11.71a	237.04 ± 7.36c	25.12 ± 0.69a	6.49 ± 0.06a	12.42 ± 0.57a
Location		***	***	***	***	***	***	***	***	***	NS
Treatment		NS	NS	NS	***	**	***	***	***	***	NS
Location * treatment		NS	NS	NS	***	*	***	NS	NS	**	NS

NS represents not significant; * represents significance at $p < 0.05$; ** represents significance at $p < 0.01$; *** represents significance at $p < 0.001$. Different letters represent significant differences between treatments

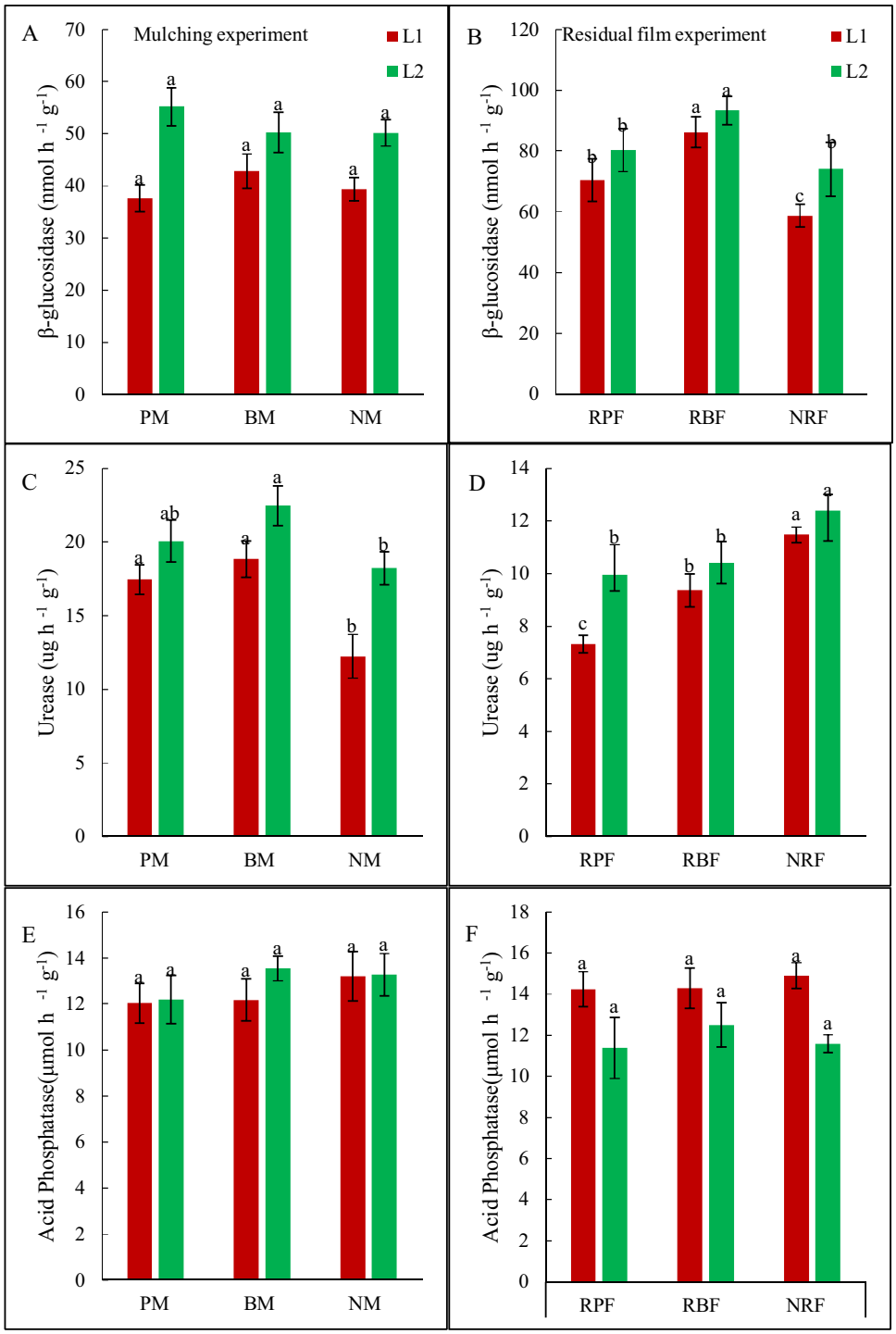

Fig. 1 Enzymatic activities under different treatments at two locations during mulching experiment and residual film experiment. **A** and **B** Activities of β-glucosidase; **C** and **D** activities of urease; **E** and **F** activities of acid phosphatase. NM, no mulch; BM, biodegradable film mulch; PM, PE film mulch; NRF, no residual film; RBF, residual biodegradable film; RPF, residual PE film. L1, location 1; L2, location 2. Different letters represent significant differences between treatments ($p < 0.05$). Error bars represent the standard deviations

Planctomycetes, *Verrucomicrobia*, and *Patescibacteria* across all treatments (Fig. 4, Fig. S5, Tables S2 and S3). As compared to treatment NM, the relative abundances of *Acidobacteria*, *Gemmatimonadete*, *Patescibacteria*, and *Verrucomicrobia* were increased, whereas *Actinobacteria* was decreased under treatments BM and PM in L1. In contrast, mulching practices enhanced the relative abundances of *Actinobacteria*, *Bacteroidetes*, and *Patescibacteria*, but reduced the relative abundances of *Acidobacteria*, *Gemmatimonadetes*, and *Verrucomicrobia* in L2. The relative abundances of *Bacteroidetes* under treatments RBF and RPF were significantly higher than that under treatment NRF in both locations. Treatment RBF significantly increased the relative abundances of *Acidobacteria* as compared to treatments RPF and NRF, with higher abundances under treatment RPF than that

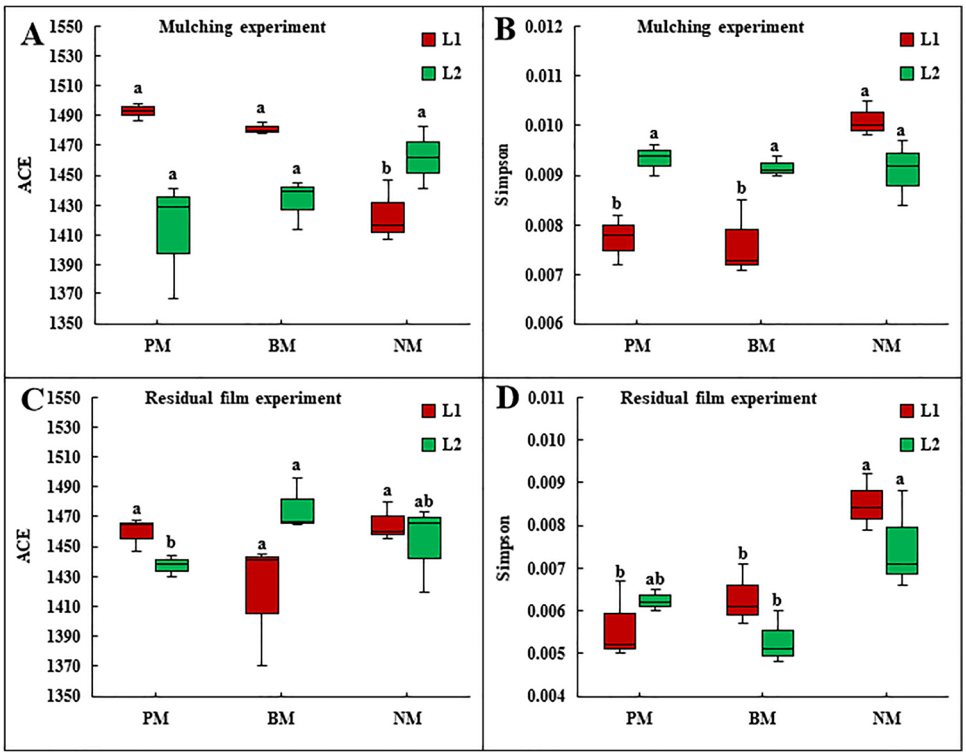

Fig. 2 Box plots of bacterial alpha-diversity under different treatments at two locations during mulching experiment and residual film experiment. **A** ACE index during mulching experiment; **B** Simpson index during mulching experiment; **C** ACE index during residual film experiment; **D** Simpson index during residual film experiment. NM, no mulch; BM, biodegradable film mulch; PM, PE film mulch; NRF, no residual film; RBF, residual biodegradable film; RPF, residual PE film. L1, location 1; L2, location 2. Different letters represent significant differences between treatments ($p < 0.05$)

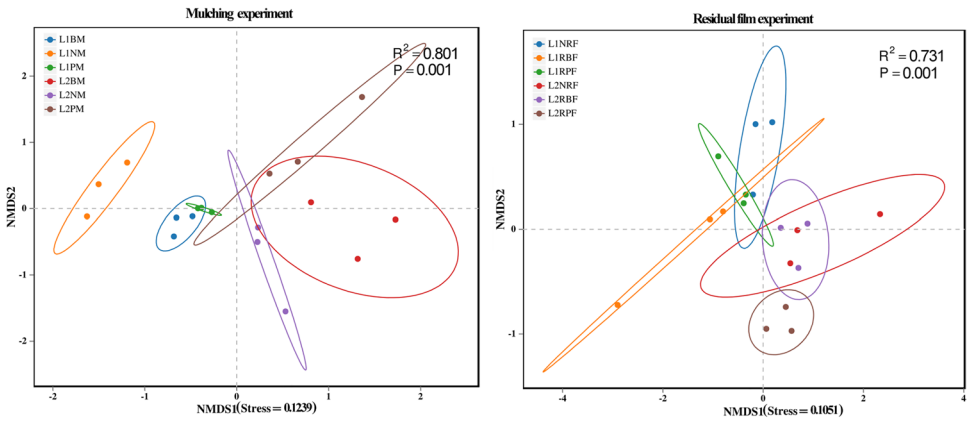

Fig. 3 Non-metric multi-dimensional scaling (NMDS) analyses under different treatments in two locations. **A** Mulching experiment; **B** residual film experiment. NM, no mulch; BM, biodegradable film mulch; PM, PE film mulch; NRF, no residual film; RBF, residual biodegradable film; RPF, residual PE film. L1, location 1; L2, location 2

under treatment NRF in L1 and no differences between the two treatments in L2. There were no significant differences of the relative abundances of *Actinobacteria* between treatments RBF and NRF in L1, but RBF and RPF in L2, and higher abundances under treatment RPF than treatment NRF were observed in both locations. The relative abundances of *Chloroflexi* under different treatments were ranked as RPF > RBF > NRF in both locations. The correlation heatmaps showed that soil moisture was significantly correlated with more bacterial phyla than the other tested soil properties during mulching experiment, whereas BG had the most correlations during residual film experiment (Fig. 5, Table S4). The redundancy analysis (RDA) showed that treatments BM and PM had more effects on soil moisture than treatment NM during mulching experiment, and treatment BM had more effects on BG than treatment PM during residual film experiment (Fig. S6).

Interactions between bacterial taxa in the network

Due to the difference of bacteria community structures across two experiments and three treatments, bacterial interaction networks based on genus level were constructed for each experiment and treatment (Fig. 6).The network under treatment NM consisted of 139 nodes and 763 edges, in contrast to 138 nodes and 951 edges under treatment BM and 144 nodes and 905 edges under

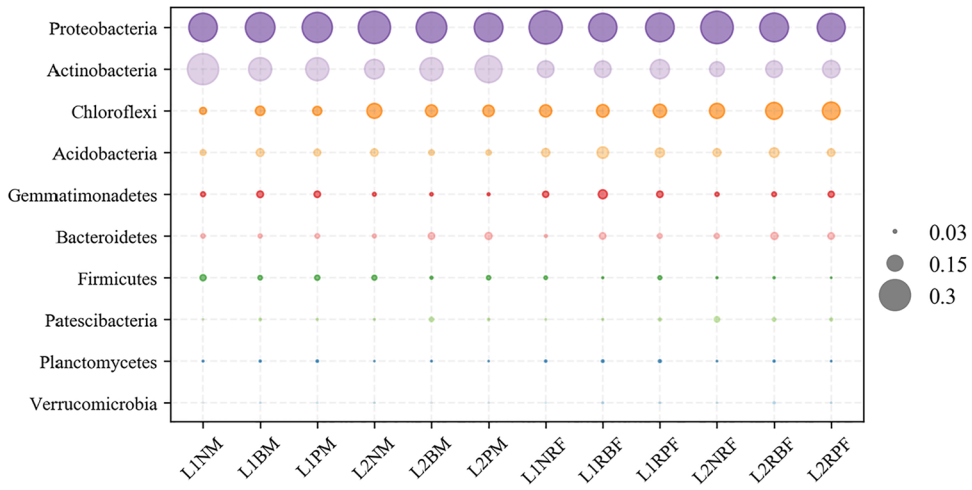

Fig. 4 Relative abundances of top 10 bacterial phyla under different treatments at two locations during mulching experiment and residual film experiment. NM, no mulch; BM, biodegradable film mulch; PM, PE film mulch; NRF, no residual film; RBF, residual biodegradable film; RPF, residual PE film. L1, location 1; L2, location 2

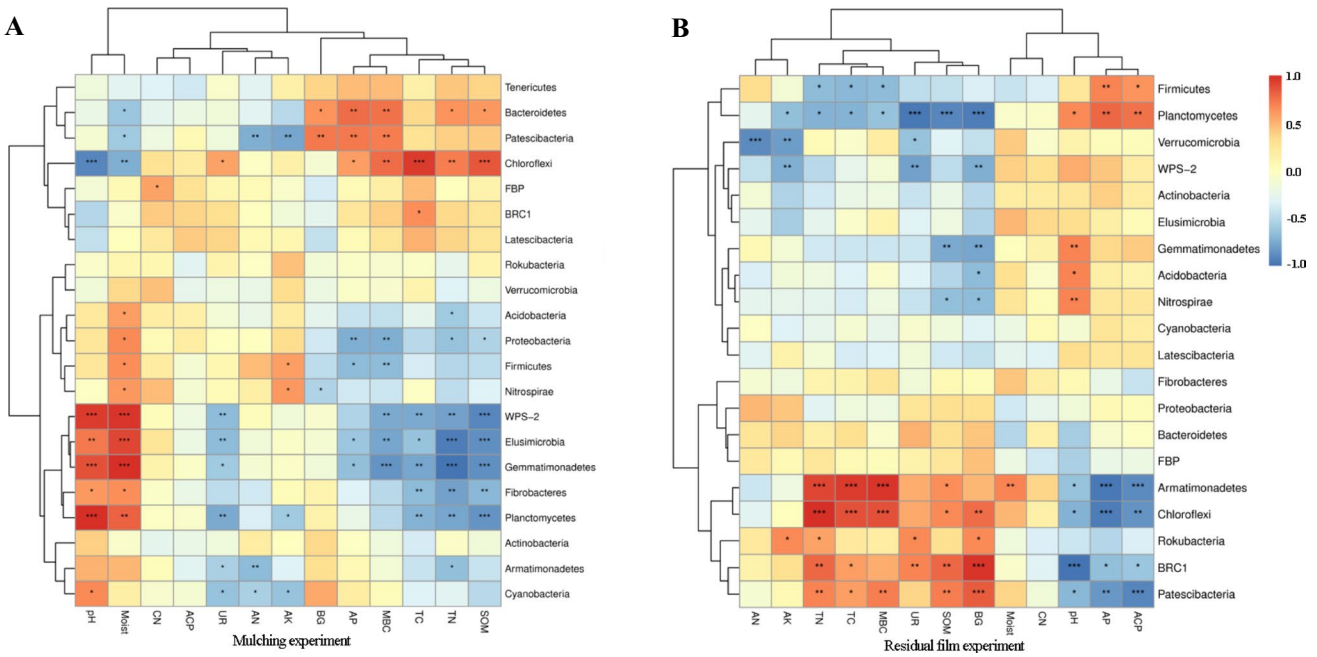

Fig. 5 Correlation heatmaps of soil bacteria at the phylum level with soil properties during mulching experiment and residual film experiment. Soil properties included pH, soil moist, soil total carbon (TC), soil total nitrogen (TN), C:N ratio, soil organic matter (SOM), microbial biomass carbon (MBC), available nitrogen (AN), available phosphorus (AP), available potassium (AK), β-glucosidase (BG), acid phosphatase (ACP), and urease (UR). Spearman's correlation coefficients between soil bacteria and soil properties were displayed with color gradient. Red represents positive correlation and blue represent negative correlation. **A** Mulching experiment; **B** residual film experiment. * represents significance at $p < 0.05$; ** represents significance at $p < 0.01$; *** represents significance at $p < 0.001$

treatment PM (Table 2). During the residual film experiment, more nodes were observed under treatment RBF (159) than that under treatments NRF (140) and RPF (142), while treatments RBF (1036) and RPF (1005) increased the edge numbers as compared to treatment NRF (797). The keystone taxa were also evaluated based on the degree, closeness centrality, and betweenness centrality of the networks. Treatments BM and PM harbored 37 and 40 keystone taxa, respectively as compared to 20 under treatment NM (Table 2). In contrast, 56 keystone taxa were discovered under treatment RBF as compared to 24 under treatment NRF and 26 under treatment RPF (Table 2). The networks without keystone taxa under film mulch (BM and PM) or residual film (RBF and RPF) treatments were similar to or even simpler than that under treatments NM or NRF, respectively (Fig. S7).

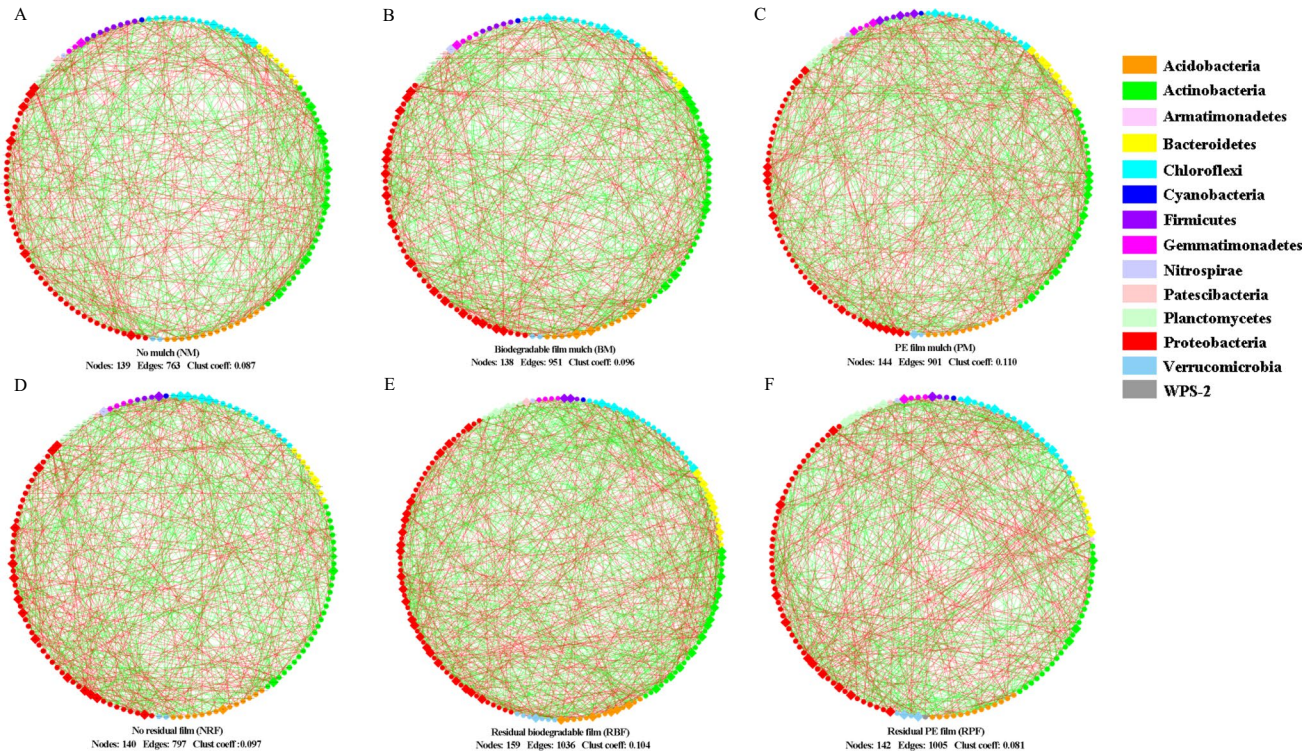

Fig. 6 Co-occurrence networks of bacterial communities at genus level under different treatments during mulching experiment and residual film experiment. **A** No mulch; **B** biodegradable film mulch; **C** PE film mulch; **D** no residual film; **E** residual biodegradable film; **F** residual PE film. Red and green lines represent significantly positive and negative links, respectively. Large diamond nodes indicate the keystone taxa in the network

Table 2 Numbers of nodes, edges, and keystone taxa under different treatments during two experiments

Treatment	Nodes	Edges			Keystone taxa
		Positive	Negative	Total	
NM	139	374	389	763	20
BM	138	390	561	951	37
PM	144	445	456	901	40
NRF	140	393	404	797	24
RBF	159	489	547	1036	56
RPF	142	392	613	1005	26

Discussion

Film mulches and their residues affect soil property

Both treatments biodegradable film mulch (BM) and PE film mulch (PM) were able to effectively increase soil moisture as compared to treatment no mulch (NM) (Table 1), likely due to reduction of evaporation under mulches (Zheng et al. 2017). Van Horn et al. (2014) reported that the bacterial community composition is altered in response to the addition of water. In our study, soil moisture was significantly correlated with more microbial members than the other investigated soil properties during the mulching experiment (Fig. 5A, Table S4), indicating its important effect on soil microbial diversity. During the residual film experiment, soil moisture under treatment residual PE film (RPF) was significantly higher than that under treatment residual biodegradable film (RBF) (Table 1). This is probably due to the dramatic degradation of RBFs to an extremely low level, while a large amount of RPFs were still remained in soil and had partial function as mulch at this time point (Yang et al. 2020). Microbial biomass carbon (MBC) is considered a key indicator of microbial activity (Munoz et al. 2017). Mulching practices significantly reduced MBC as compared to treatment NM (Table 1), which is consistent with the observations of Pi et al. (2017) and Wang et al. (2020b). The negative impact of the plastic film on MBC was also reported by Munoz et al. (2017), who attribute this to the less favorable soil condition after mulch. During the residual film experiment, MBC was significantly increased under treatment RBF as compared to treatments RPF and no residual film (NRF) (Table 1). This is probably because the degradation of RBFs provided metabolic substrates for microorganisms, thus facilitating their absorption of carbon (Wang et al. 2020b).

Film mulches and their residues alter soil enzyme activities

Soil microorganisms uptake organic monomers or mineral nutrients through synthesizing and excreting extracellular enzymes (Allison et al. 2010; Mooshammer et al. 2014). As extracellular enzymes are closely linked to the availability of environmental resources, they are considered good indicators for nutrient cycling in different ecosystems (Luo et al. 2017). Enzymes involved in carbon (β-glucosidase and β-galactosidase), nitrogen (urease), phosphorus (phosphatase), and sulfur (arylsulphatase) cycles are widely used to assess soil quality (Adetunji et al. 2017). In our case, the activities of β-glucosidase (BG), urease (UR), and acid phosphatase (ACP) were tested. During mulching experiment, there were no significant differences of BG activities between any two treatments of NM, BM, and PM in both locations (Fig. 1a). This was probably due to that plastic film mulch did not change SOM (Table 1), and BG is positively correlated with SOM on a global scale (Mariscal-Sancho et al. 2010). In contrast, BG activities under treatment RBF were significantly higher than that under treatments RPF and NRF in the two locations (Fig. 1b). BG activity greatly depends on the available substrates and the microorganisms that synthesize this enzyme (Wang and Liu 2006). Interestingly, BG had the most correlations with microbial phyla than the other tested soil properties during residual film experiment (Fig. 5, Table S4). Li et al. (2014) reported that BG could be used as a soil quality indicators, due to the fact that it was one of the most responsive soil properties to mulch and production systems. These results imply that decomposition of biodegradable films may provide organic substrates for BG and thus improve its correlations with associated microorganisms.

UR is the key enzyme for nitrogen mineralization. UR activity seems to be negatively regulated by available inorganic nitrogen, as reduced UR activity in agricultural systems has been shown with higher inorganic nitrogen availability (Bowles et al. 2014). Similarly in our study, mulching practices significantly increased the activities of UR as compared to treatment NM (Fig. 1c), whereas soil available nitrogen contents under treatments BM and PM were significantly lower than that under treatment NM (Table 1), probably due to the enhanced uptake of soil nitrogen by mulched plants, which may lead to the increase of potato tuber yield (Fig. S1). These results indicate that mulching practices may promote soil nitrogen mineralization and thus increase the UR activity. In contrast, during residual film experiment, treatments RBF and RPF significantly reduced UR activities as compared to treatment NRF (Fig. 1d). This may because plastic films potentially release additives into the soil, resulting in inhibition of soil enzyme activity (Ramos et al. 2015).

Film mulches and their residues shift soil bacterial community composition

Our field experiment revealed that both film mulches and film residues could alter the composition of the bacterial community in soil. Treatments BM and PM performed similarly on shaping the bacterial community at the phylum level, as compared to treatment NM (Fig. 4). This is probably due to that treatments BM and PM have similar effects on increasing soil temperature and conserving soil water (Yang et al. 2020). However, location differences in bacterial communities were observed during mulching experiment (Fig. 4). Soil conditions such as temperature, moisture, and pH play a pivotal role in modifying microbial communities (Fierer and Jackson 2006; Moore-Kucera et al. 2014; Rousk et al. 2010). In our study, the spatial variation in soil microbial communities might attribute to the significant differences of soil environment factors between the two locations (Table 1).

It has been reported that some members of *Bacteroidetes* can degrade cellulose (Naas et al. 2014), crude oil (Viñas et al. 2005), and other organic polymer compounds (Bauer et al. 2010). The increased abundances of *Bacteroidetes* under treatments RBF and RPF as compared to treatment NRF (Fig. 4) indicate that residual films possibly enrich degradation-related *Bacteroidetes*. However, some *Bacteroidetes* are pathogenic (Stewart et al. 2010) and the enrichment of these bacteria may threaten the health of agroecosystems (Zhang et al. 2019). The relative abundances of *Chloroflexi* under different treatments were ranked as RPF > RBF > NRF (Fig. 4, Tables S2 and S3B). Members of *Chlorofexi* have been found to tolerate extreme soil environments (Neilson et al. 2012) and the accumulation of *Chlorofexi* may indicate that residual films have caused stress on soil. It is well accepted that many members of *Actinobacteria* are involved in the decomposition of organic materials in soil (Nielsen et al. 2014) and some species can biodegrade polyethylene (PE) through the synthesis of hydrolytic enzymes (Abraham et al. 2017; Santo et al. 2013). *Actinobacteria* were enriched under treatment RPF in L1, and RPF and RBF in L2 (Fig. 4), suggesting their potential functions in degrading residual films. Interestingly, the relative abundance of *Acidobacteria* was significantly higher under treatment RBF than treatments RPF and NRF in both locations (Fig. 4). This might be explained by the relative lower soil pH under treatment RBF (Table 1). MacLean et al. (2021) proposed that the various steps of fragmentation and degradation of plastic materials, as well as assimilation and mineralization of plastic-derived carbon involve different microorganisms. Thus, researches on the degradation potential of microbial communities, rather than of single species, are needed.

Film mulches and their residues affect interactions between bacterial taxa in the network

Different soil microorganisms do not respond to environmental changes separately, but form complex association networks (Banerjee et al. 2019). Recent researches have shown that network analyses can effectively reflect microbe-microbe associations in response to environment (de Vries et al. 2018; Ramirez et al. 2018; Banerjee et al. 2019). In our study, the bacterial co-occurrence networks were constructed under different treatments (Fig. 6). During the mulching experiment, more edges under treatments BM and PM than that under treatment NM were observed (Table 2), which is in consistent with the result of Wang et al. (2020a) that mulching practices increase the total number of links in the microbial network. Similarly, there were more edge numbers under treatments RBF and RPF than that under treatment NRF (Table 2). These results may indicate that alteration of soil environment by external actions such as film mulch and incorporation of residual film into soil increase bacterial interactions.

Keystone taxa are the highly interacting taxa that have considerable influences on microbial composition and function irrespective of their abundance (Berry and Widder 2014; Banerjee et al. 2018; Herren and McMahon 2018). Both treatments BM and PM harbored almost double the number of keystone taxa as compared to treatment NM (Table 2), which can be attributed to the increase of keystone taxa in phylum *Proteobacteria* (Table S5). We speculate that soil moisture might be one of the major drivers of keystone taxa during mulching experiment, as soil moisture was significantly increased by mulching practices (Table 1) and was correlated with more microbial phyla, including *Proteobacteria*, than the other tested soil properties (Fig. 5, Table S4). The number of keystone taxa under treatment RBF was much higher than that under treatments RPF and NRF (Table 2), due to the increase of keystone taxa in phyla *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, and *Proteobacteria* (Table S5). Compounds released from degradation of RBFs might be the major driver of keystone taxa, as the direct input of carbon, additives and adherent chemicals into soil affect microbial communities (Bandopadhyay et al. 2018).

Conclusions

Mulching practices reduced soil nutrients as compared to treatment no mulch (NM), possibly through enhancing uptake of nutrients by mulched plants, leading to increase of urease activity and decrease of microbial biomass carbon content in soil. Mulching practices increased alpha diversity of soil bacteria, although location heterogeneity was observed. Soil moisture was significantly increased by mulching practices and played an important role in shaping soil bacterial communities, as it correlated with more microbial phyla than the other tested soil properties. In addition, mulching practices not only promoted the interrelations, regardless of positive or negative, within bacterial community, but also harbored more keystone taxa than treatment NM. After the films were incorporated into soil, β-glucosidase had the most correlations with microbial phyla among all the tested soil properties and was significantly promoted by treatment residual biodegradable film (RBF), suggesting its potential role in degradation. The relative abundance of some dominant bacterial phyla, including *Bacteroidetes*, *Actinobacteria*, and *Chlorofexi* with potential functions related to material degradation and/or soil stress, were increased by residual films. The interrelations within bacterial community were also enhanced by treatments RBF and residual PE film (RPF), whereas the number of keystone taxa under treatment RBF was doubled as compared to treatments RPF and no residual film (NRF), due to the increase of keystone taxa in phyla *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, and *Proteobacteria*. These results indicate that the indirect effects of biodegradable and PE films as mulch on soil are similar, whereas their subsequent direct effects as residual films show specificity, and incorporation of residual films into soil may cause stress, regardless degradable or non-degradable in a short term.

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Data availability Not applicable.

Declarations

Ethics approval The authors certify that this manuscript is original and has not been published and will not be submitted elsewhere for publication while being considered by Environmental Science and Pollution Research. The study has not been split up into several parts to increase the quantity of submissions and submitted to various journals or to one journal over time. No data has been fabricated or manipulated (including images) to support the established conclusions. No data, text, or theories reported by others have been presented as if they were our own.

Consent to participate The submission has been received explicitly from all co-authors. The authors whose names appear on the submission have contributed sufficiently to the scientific work and therefore share collective responsibility and accountability for the results.

Consent for publication The authors confirm that the publication of this manuscript has been approved by all co-authors and has been approved (tacitly or explicitly) by the responsible authorities at the institution where the work is carried out.

Competing interests The authors declare no competing interests.

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