Environmental Science and Pollution Research (2018) 25:9904–9914
https://doi.org/10.1007/s11356-018-1323-9

RESEARCH ARTICLE

Rhizospheric effects on the microbial community of e-waste-contaminated soils using phospholipid fatty acid and isoprenoid glycerol dialkyl glycerol tetraether analyses

Mengke Song[1,2] · Zhineng Cheng[1] · Chunling Luo[1,2] · Longfei Jiang[1] · Dayi Zhang[3] · Hua Yin[4] · Gan Zhang[1]

Received: 18 July 2017 / Accepted: 17 January 2018 / Published online: 26 January 2018

Abstract

We performed the study of rhizospheric effects on soil microbial community structure, including bacteria, fungi, actinomycete, and archaea, at an electronic waste (e-waste) recycling site by analyzing the phospholipid fatty acid (PLFA) and isoprenoid glycerol dialkyl glycerol tetraether (GDGT) contents. By comparing PLFA and isoprenoid GDGT profiles of rhizospheric and surrounding bulk soils of 11 crop species, we observed distinct microbial community structures. The total PLFA concentration was significantly higher in rhizospheric soils than in non-rhizospheric soils, whereas no obvious difference was found in the total isoprenoid GDGT concentrations. The microbial community structure was also different, with higher ratios of fungal-to-bacterial PLFAs (F/B) and lower relative abundance of Gram-positive bacteria in rhizospheric soils. The extent of rhizospheric effects varied among plant species, and *Colocasia esculenta* L. had the greatest positive effects on the total microbial biomass. Dissolved organic carbon and pH were the main environmental factors affecting the microbial community represented by PLFAs, while the archaeal community was influenced by copper and zinc in all soils. These results offer a comprehensive view of rhizospheric effects on microbes in heavy metal and persistent organic pollutant co-contaminated soil, and provide fundamental knowledge regarding microbial ecology in e-waste-contaminated soils.

Keywords e-waste · Phospholipid fatty acid (PLFA) · Isoprenoid glycerol dialkyl glycerol tetraether (isoprenoid GDGT) · Rhizospheric soil · Microbial community

Introduction

Improper disposal of electronic waste (e-waste), including discarded electrical and electronic devices, is motivated by profits and results in high concentrations of persistent organic pollutants (POPs) and heavy metals leaching into e-waste-dismantling sites and their surrounding environments. POPs and heavy metals can exert pressure on soil microbes, decreasing microbial abundance, richness, and diversity (Bourceret et al. 2016; Liu et al. 2015; Song et al. 2015b). Field studies have shown that e-waste pollution altered indigenous microbial community structure by enriching microbes related to POP degradation (Liu et al. 2015; Tang et al. 2014; Tang et al. 2013; Zhang et al. 2010). Variations in microbial communities are caused by different environmental factors related to soil type and location, including soil physicochemical properties and the presence of heavy metals and organic pollutants (Liu et al. 2015; Tang et al. 2013; Zhang et al. 2010).

Responsible editor: Diane Purchase

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11356-018-1323-9) contains supplementary material, which is available to authorized users.

✉ Chunling Luo
clluo@gig.ac.cn

[1] Guangzhou Institute of Geochemistry, Chinese Academy of Sciences, Guangzhou 510640, China

[2] College of Natural Resources and Environment, South China Agricultural University, Guangzhou 510642, China

[3] School of Environment, Tsinghua University, Beijing 100084, China

[4] College of Environment and Energy, South China University of Technology, Guangzhou 510006, China

Microbial communities can be restored with the aid of planting vegetation in contaminated soils (Haichar et al. 2008; Hur et al. 2011). Plants secrete ~20% of their photosynthetic products into the soils, encouraging microbial growth, microbial interactions, and genetic exchange, especially in soils surrounding the roots, which explains why the rhizosphere is a hot spot of microbial activity (Tkacz et al. 2015). The higher abundance of bacteria and archaea in rhizoplanes than in bulk soil has been verified by analyzing archaeal and bacterial tetraether membrane lipid contents (Ayari et al. 2013). In addition, rhizospheric microorganisms are sensitive to plant species, plant age, and location within the root system (Deng et al. 2018). Root exudate composition varies among individual plants, which, as a result, develop different microbial communities in the vicinity of their roots (Berg and Smalla 2009; Corgie et al. 2003; Costa et al. 2006; Somers et al. 2004; Haichar et al. 2008).

At contaminated sites, rhizospheric microbial diversity benefits from root exudates and pollutant dissipation via degradation, root adsorption, and plant accumulation (Corgie et al. 2003; Wenzel 2009). Gradients in bacterial and archaeal contents have been observed in rhizospheric soils contaminated with polycyclic aromatic hydrocarbons (PAHs), with higher numbers of heterotrophic bacteria located closer to the roots (Corgie et al. 2003; Ma et al. 2015). By analyzing phospholipid fatty acid (PLFA) concentrations, the total microbial biomass (i.e., bacteria and actinomycetes) in the rhizosphere of rice was higher than that of bulk soils at e-waste-contaminated sites (Chen et al. 2014). Similarly, in the rhizospheres of poplars grown near waste mine tailings, the richness and diversity of bacteria and archaea were higher than those of bulk soils (Hur et al. 2011). In a pot experiment on polychlorinated biphenyl (PCB) degradation, the rhizospheric microbial biomass depended on the plant species, and higher PLFA concentrations were observed in *Cucurbita*-amended treatments (Qin et al. 2014). The diversity and succession of microbial communities including bacteria, fungal, and archaea varied among plant species to different extents (Hur et al. 2011; Thion et al. 2012; Deng et al. 2018). However, few field studies have compared the whole microbial community structure (e.g., bacteria, fungi, actinomycetes, and archaea) between rhizospheric soils of different typical crops grown at the same e-waste-contaminated site.

In this study, we conducted an in-depth and comprehensive survey using PLFA and isoprenoid glycerol dialkyl glycerol tetraether (GDGT) analyses to determine the microbial assemblages of the rhizospheric and surrounding bulk soils of 11 typical crops contaminated by in situ crude e-waste recycling activities. PLFA and isoprenoid GDGT are specific membrane lipids derived from bacteria and archaea, respectively, and often used as biomarkers to characterize the abundance and diversity of microbes in various environmental samples due to the high reproducibility and low detection limit. In addition, PLFA reflects the active microbes in soils, owing to the fast decomposing after cell death, and is valuable for timely observing the microbial response to environmental conditions (Ayari et al. 2013; Chen et al. 2014; Huguet et al. 2006; Smets et al. 2016). By profiling the whole microbial populations, including bacteria, fungi, actinomycetes, and archaea, we aimed to (1) investigate the composition and diversity of the whole microbiota in the rhizospheric soils of different crops at a crude e-waste recycling site and (2) elucidate how the rhizosphere influences the soil microbial community. This study extends our knowledge of the effects on soil microbial communities of crop rhizospheres, which will benefit the restoration of agricultural ecosystems co-contaminated with heavy metals and POPs.

Material and methods

Sample collection

The study site is located in Longtang Town, Guangdong Province, south China (23° 34′ N, 113° 0′ E), as shown in our previous study (Wang et al. 2014b). Sampling was conducted in June, 2012. After gently pulling plants from soils, the soil fraction strongly adhering to the roots (< 2 mm to roots) was collected as rhizospheric soils. Bulk soils located with 5–10 cm distance from the root system were collected as "non-rhizospheric soils." Totally, the soils of 11 plant species were collected, including *Oryza sativa* L., *Lactuca sativa* L., *Arachis hypogaea* L., *Glycine max* L., *Ipomoea aquatica* Forsk., *Vignaunguiculata* (L.) Walp, *Colocasia esculenta* L., *Zea mays* L., *Solanitm melongena* L., *Ipomoea batatas* (L.) Lam., and *Gynura cusimbua* (D. Don) S. Moore. The four replicates of each sample were combined as one soil sample both for rhizospheric and non-rhizospheric soils. They were immediately placed on ice and transported to laboratory. After homogenization and sieving through 2-mm mesh, all the soils were stored at −20 °C until further analysis.

Chemical analysis

Soil pH was measured using a pH meter in 1:2.5 (*w*/*v*) KCl (1 mol/L) suspensions. Soil total organic carbon (TOC) and total nitrogen (TN) were measured using an elemental analyzer (Vario EL-III, Elementar, Hanau, Germany) as described previously (Cheng et al. 2014). Soil dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) were determined according to Cheng's method using TOC-VCPH analyzer (Shimadzu, Japan) (Cheng et al. 2014). The total heavy metal concentrations including copper, lead, and zinc were determined by ICP-AES (Perkin–Elmer Optima 3300 DV) after strong acid digestion with 4:1 concentrated HNO_3 and $HClO_4$ (*v*/*v*) (Luo et al. 2005).

The analysis of PCBs and polybrominated diphenyl ethers (PBDEs) was carried out as previously described (Syed et al. 2013; Wang et al. 2011a, b). Briefly, following the addition of surrogate standards including PCB-30 and PCB-198, all freeze-dried soil samples were Soxhlet-extracted and purified using multilayer alumina/silica column. After concentrated to 20 μL, the eluate was spiked with C^{13}-PCB141 as the internal standard prior to instrumental analysis. GC-EI-MS (Agilent GC7890 coupled with 5975C MSD) equipped with a Varian capillary column (50 m × 0.25 mm i.d., and 0.25 μm film thickness) was used for 32 PCB congeners analysis. The determination of PBDEs was performed with a GC-ECNI-MS (Agilent GC7890 coupled with 5975C MSD) equipped with a DB5-MS capillary column (30 m × 0.25 mm i.d., and 0.25 μm film thickness). QA/QC was performed as described by Wang et al. (2011b) and Syed et al. (2013). The recoveries for PCB-198 and PCB-209 were 84.1 ± 14.5 and 87.8 ± 9.7%, respectively. The reported data were not corrected by the surrogate recoveries. All concentrations were normalized to dry soil weight.

PLFA analysis

PLFA analysis was performed using the method by Frostegard et al. (1993) and Yang et al. (2013). In brief, phospholipids were extracted directly from freeze-dried soils (3.0 g) by using solvent buffer (chloroform:methanol:citrate = 1:2:0.8, *v*/*v*/*v*), and fractionated on silica-bonded phase columns (Supelco, Bellofonte, PA, USA) into neutral, glycolipids, and phospholipids (polar) by elution consecutively with chloroform (10 mL), acetone (10 mL), and methanol (10 mL), respectively. The phospholipids fraction was then subjected to a mild alkaline methanolysis to form fatty acid methyl esters (FAME). After drying, FAME were re-dissolved in hexane, spiked with methyl nondecanoate (19:0) as an internal standard, and analyzed using GC-MS (Agilent GC7890 coupled with 5975C MSD) with a DB5-MS capillary column (30 m × 0.25 mm i.d., and 0.25 μm film thickness).

Total PLFAs, the sum of extracted PLFAs, were used to represent the total microbial biomass including bacteria, fungi, and actinomycetes in soils. PLFA i15:0, a15:0, 15:0, i16:0, i17:0, a17:0, 17:0, cy17:0, 16:1ω5, 16:1ω7, 16:lw9, 18:1ω7, and cy19:0 were used to assess the bacterial biomass (Frostegard et al. 1993). PLFA 16:lω5c, 16:1ω9, 18:1ω9c, 18:2ω6, and 20:4 characterized the fungal biomass (Yang et al. 2013). PLFA i15:0, a15:0, i16:0, i17:0, a17:0, and 10Me16:0 were presented in Gram-positive (GP) bacteria, and PLFA 16:1ω7c, 17:1ω8, cy17:0, 18:1ω7c, and cy19:0 were attributed to Gram-negative (GN) bacteria (Qin et al. 2014). PLFA 10Me 16:0, 10Me 17:0, and 10 Me18:0 were used as the indicator of actinomycetes (Chen et al. 2014). To conduct a more thorough analysis, we selected four indicators representative of soil microbial structures, including the ratios of fungal PLFAs to bacterial PLFAs (F/B), GN bacterial PLFAs to GP bacterial PLFAs (GN/GP), cyclopropyl PLFAs to monoenoic precursors (cyc/pre), and isomeric PLFAs to anisomeric PLFAs (I/A).

GDGT analysis

Freeze-dried and homogenized soils (5.0 ± 0.1 g) were sequentially extracted with methanol (MeOH), dichloromethane (DCM)/MeOH (1:1, *v*/*v*), and DCM via ultra-sonication (3 × 15 min). After centrifugation, all the extracts were combined and concentrated to 1–2 mL by rotary evaporation. The extracts were then purified and separated over an activated silica gel column by elution with *n*-hexane/DCM (9:1, *v*/*v*) and DCM/MeOH (1:1, *v*/*v*), respectively (Jia et al. 2012). The polar fraction containing isoprenoid GDGTs was collected and dried with gentle N_2 gas. The residue was then re-dissolved in hexane/propanol (99:1, *v*/*v*), filtered through a 0.45-μm PTFE filter, and injected with C_{46}GDGT as the internal standard (Huguet et al. 2006) prior to instrumental analysis.

Isoprenoid GDGT analysis was performed on an Agilent 1200 HPLC/6410 TripleQuad MS instrument equipped with a Prevail Cyano column (2.1 × 150 mm, 3 μm diameter particles; Grace, USA) as described by Jia et al. (2012) and Schouten et al. (2007). Quantification was performed by integrating the peak areas of $[M + H]^+$ ions and the internal synthetic C_{46}GDGT standard (Huguet et al. 2006). Isoprenoid GDGTs were used to represent the archaeal biomass.

Statistical analysis

Statistical analyses were performed using SPSS 18.0 and various R packages. All the concentrations of DOC, DON, heavy metals, PCBs, PBDEs, PLFAs, and GDGTs were reported on dry soil weight. The independent samples *t* test was carried out to test the significant difference in physiochemical properties, PCBs, PBDEs, and the concentration and relative abundance of PLFAs and GDGTs between the rhizospheric and non-rhizospheric soils. Statistical significance was determined at the 95% level ($p < 0.05$). Principal component analysis (PCA) of soil PLFAs and GDGTs was performed using SPSS 18.0. Redundancy analysis (RDA) by R package vegan with the Monte Carlo test of environmental variable significance was used to analyze the relationship between soil properties and microbial communities.

Results

Soil physicochemical characteristics

Table S1 lists the soil properties. The pH of the rhizospheric soils ranged from 3.03 to 5.88 and was generally lower than that of the non-rhizospheric soils. The rhizospheric soils

contained higher levels of TOC (1.13–3.60%), TN (0.09–0.29%), and DOC (90.0–274 mg/kg) and carbon-to-nitrogen ratio (C/N, 10.3–12.7). Among the occurrence of heavy metals and POPs in e-waste-contaminated soils, copper (Cu), lead (Pb), zinc (Zn), PCBs, and PBDEs were the dominant toxic pollutants in contaminated farmland and were targeted in the present study (Liu et al. 2015; Wang et al. 2011a, b). Cu, Pb, and Zn had higher concentrations in the rhizospheric soils (152 ± 5.0, 88.9 ± 9.0, and 114 ± 10.8 mg/kg) compared with non-rhizospheric soils (117 ± 9.0, 77.7 ± 6.1, and 99.9 ± 9.8 mg/kg). The results showed that PCBs and PBDEs accumulated in the rhizospheric soils with concentrations of 137 ± 10.8 and 156 ± 13.9 mg/kg, respectively. The pH, TOC, C/N, TN, DOC, total PCBs, and total PBDEs of the rhizospheric soils differed significantly from those of non-rhizospheric soils (independent sample *t* tests; $p < 0.05$).

Microbial community profile identified with PLFA and GDGT analyses

In total, 43 PLFAs were detected in all samples, comprising PLFAs with chain lengths of 13 to 26 carbon atoms, which included saturated PLFAs, monounsaturated PLFAs, polyunsaturated PLFAs, methylated PLFAs, and cyclopropyl PLFAs. Of the 43 PLFAs, 20 accounted for ~93% of the total microbial biomass in both rhizospheric and non-rhizospheric soils, of which 18:1w9cis and 18:2w6cis represented fungi; i16:0, a17:0, 16:1w7t, i15:0, 15:0, 18:1w7cis, and 17:0 represented aerobic bacteria; and cyc17 and cyc19:0 represented anaerobic bacteria.

Figure 1a presents the concentrations of PLFAs grouped by their corresponding microbes. The average concentrations of PLFAs representing total microbes, total bacteria, fungi, actinomycetes, GP bacteria, GN bacteria, and aerobic bacteria were higher in rhizospheric soils than in non-rhizospheric soils (Fig. 1a). The relative abundances of GP bacteria, total bacteria, and fungi differed significantly between the rhizospheric and non-rhizospheric soils, with a higher relative abundance of fungi and lower relative abundance of GP and total bacteria in the rhizosphere (Fig. 1b). Besides, GN bacteria were more abundant than GP bacteria in rhizospheric soils but not in non-rhizospheric soils, which has been reported previously in soils contaminated with heavy metals or POPs (Thompson et al. 1999; Ying et al. 2006). Both in rhizospheric and non-rhizospheric soils, the relative abundance of bacterial, actinomycetes, and fungal PLFAs accounted for ~65, ~5, and ~15% of the total PLFAs, respectively. Around 50% of the total PLFAs were derived from aerobic bacteria, much higher than those from anaerobic bacteria (~4%). Compared with the non-rhizospheric soils in

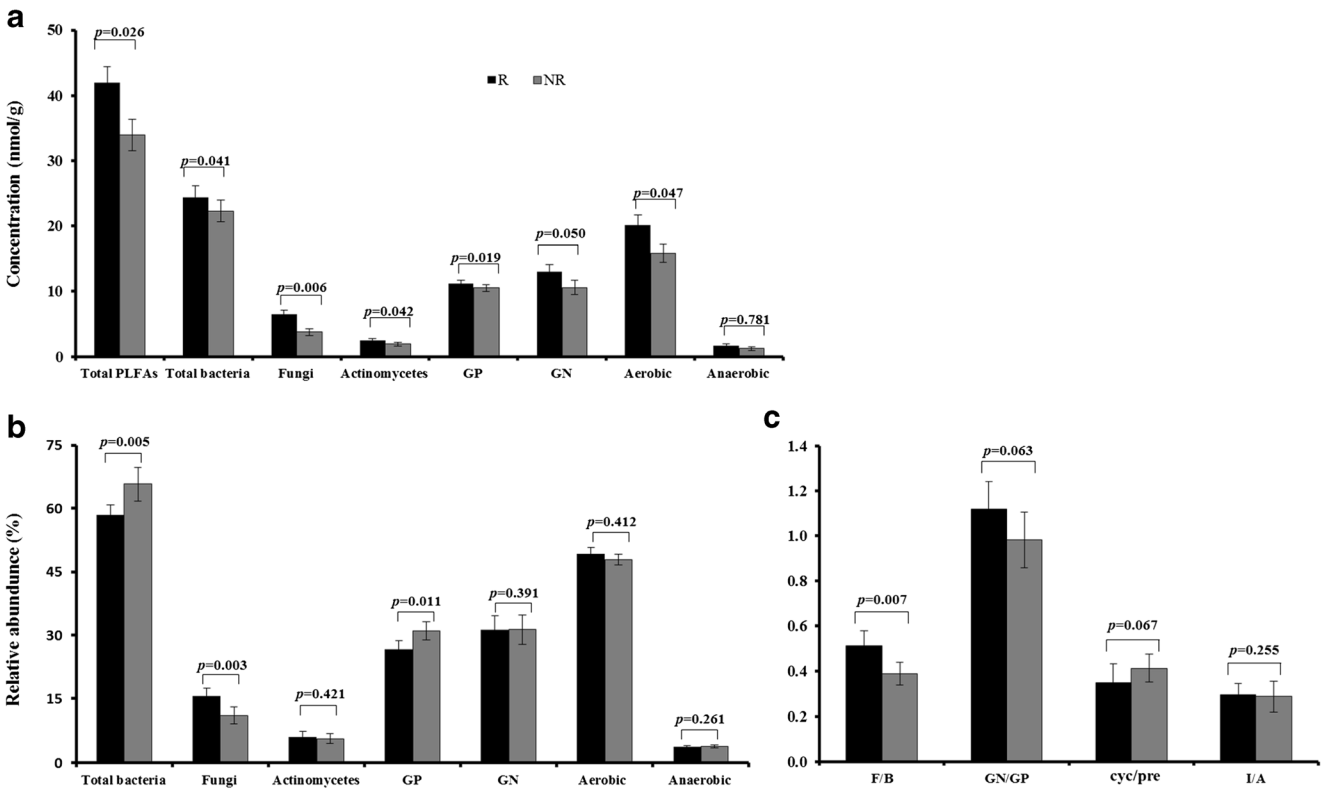

Fig. 1 Microbial community composition and structure profiled by PLFAs. **a** PLFA concentrations in soils. **b** Relative abundance of PLFAs in soils. **c** Indicators of microbial community structure. *R* rhizospheric soils, *NR* non-rhizospheric soils. All data are presented with mean ± SE (standard error, $n = 11$)

this study, the rhizospheric microbial community had higher F/B, GN/GP, and I/A ratios and lower cyc/pre ratios, but only F/B differed significantly ($p = 0.007$) (Fig. 1c). Higher F/B ratios have been suggested to be indicative of more sustainable agroecosystems, in which organic matter decomposition dominates the provision of plant nutrients for crop growth (de Vries et al. 2006). Meanwhile, higher F/B ratios are often observed in the rhizospheres of grassland and forests without intense management (Grayston et al. 2001; Pollierer et al. 2015). Microbes produce more anisomeric and cyclopropyl PLFAs under stress, such as starvation and the presence of heavy metals, leading to elevated cyc/pre and decreased I/A ratios (Frostegard et al. 1993; Pollierer et al. 2015).

In this study, the abundance of archaea was represented by the sum of isoprenoid GDGTs including crenarchaeol (Cren), crenarchaeol isomer (Cren'), GDGT-0, GDGT-1, GDGT-2, and GDGT-3 (Ayari et al. 2013). Although the total archaea amount (33.9 ng/g) was higher in rhizosphere, no obvious difference was observed for the mean concentrations of total archaea and the relative abundance of each GDGT subgroup between the rhizospheric and non-rhizospheric soils (Fig. 2a). In all the soils, the relative abundance of Cren derived from *Thaumarchaeota* was the highest among the six GDGTs, accounting for almost 50% of the total GDGTs (Fig. 2b) (Leininger et al. 2006). This was followed by GDGT-0, which is the main cell membrane component of *Euryarchaeota* (Shen et al. 2011), with relative abundances of 27.4 and 25.4% in the rhizospheric and non-rhizospheric soils, respectively (Fig. 2b).

Relationship between microbial biomass, indicators, and environmental factors

The correlation between microbial biomass, indicators, and environmental factors was analyzed using a Pearson correlation analysis (Table 1). In both rhizospheric and non-rhizospheric soils, the amount of GDGTs was significantly positively correlated with TN ($p = 0.001$), TOC ($p = 0.005$), DOC ($p = 0.004$), Zn ($p < 0.001$), and Pb ($p = 0.001$). The concentrations of total ($p = 0.027$) and subgroup PLFAs, including total bacteria ($p = 0.005$), GP bacteria ($p = 0.005$), and GN bacteria ($p = 0.027$) PLFAs, were positively correlated with C/N. In addition, GP bacteria PLFAs had significantly positive correlation with TOC ($p = 0.030$). No significant correlation was observed between fungal biomass and the environmental factors. However, F/B was affected differently by various environmental factors, negatively correlated with pH ($p = 0.004$) and PCBs ($p = 0.011$) but positively correlated

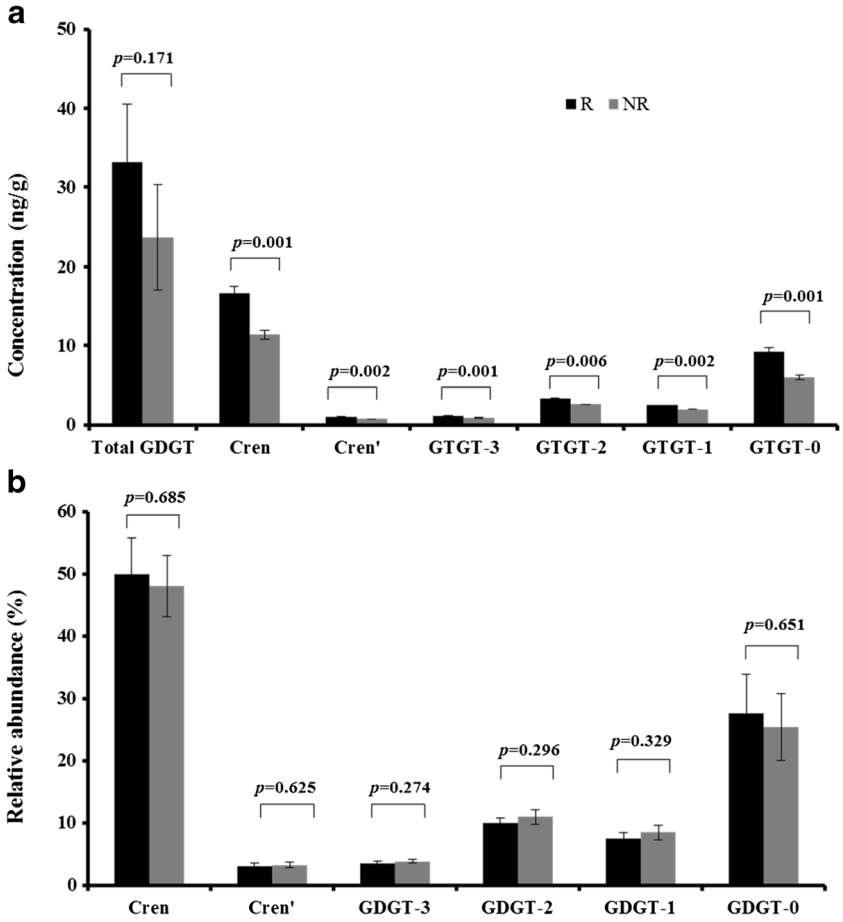

Fig. 2 Archaeal community composition and structure profiled by isoprenoid GDGTs. **a** GDGTs concentrations in soils. **b** Relative abundance of individual GDGT in soils. *R* rhizospheric soils, *NR* non-rhizospheric soils. Cren and Cren' refer to thaumarchaeol and thaumarchaeol regio isomer, respectively. All data are presented with mean ± SE (standard error, $n = 11$)

Table 1 Pearson correlation coefficient between isoprenoid GDGTs, PLFAs subgroups and environmental factors

	pH	TN	TOC	C/N	DOC	DON	PCBs	PBDEs	Cu	Pb	Zn
GDGT	−.224	.669**	.576**	−.332	.589**	−.071	.171	.090	0.256	0.636**	0.686**
PLFA											
Total	−.226	.254	.345	.470*	.252	−.096	−.225	.030	−0.332	−0.114	−0.226
Total bacteria	−.076	.264	.383	.580**	.177	−.112	−.093	.121	−0.326	−0.238	−0.245
Fungi	−.373	.303	.359	.326	.409	−.101	−.372	−.039	−0.351	0.053	−0.174
GP bacteria	−.194	.343	.464*	.572**	.327	−.214	−.084	.163	−0.411	−0.257	−0.312
GN bacteria	−.075	.195	.294	.490*	.089	−.039	−.143	.028	−0.246	−0.176	−0.181
Actinomycetes	−.505*	.346	.362	.109	.568**	−.393	−.160	.189	−0.236	0.061	−0.188
Indicator											
F/B	−.587**	.217	.170	−.114	.585**	−.080	−.533*	−.173	−0.262	0.422	−0.016
cyc/pre	−.498*	−.168	−.213	−.340	.025	−.109	−.241	−.178	0.178	0.016	−0.143
I/A	−.459*	.052	.072	.146	.306	−.055	−.483*	−.142	−0.191	0.126	−0.190
GN/GP	.322	−.019	.039	.316	−.218	.098	.136	.045	0.066	−0.084	0.118

**Correlation is significant at the 0.01 level (two-tailed).*Correlation is significant at the 0.05 level (two-tailed)

with DOC ($p = 0.004$). I/A was negatively correlated with pH ($p = 0.032$) and PCBs ($p = 0.023$). The cyc/pre ratio was only influenced by pH ($p = 0.018$), which exhibited a negative correlation.

The results of the Pearson correlation analysis of soil physicochemical properties and individual PLFAs are presented in Table S2. The amount of each PLFA, except 16:1w7c, was positively correlated with TOC ($p < 0.05$) and TN ($p < 0.05$). Additionally, DOC had a significantly positive relationship with the major PLFAs. However, no significant correlation was observed between metals, PCBs or PBDEs, and individual PLFAs.

Relationship between microbial community structure and environmental factors

PCA score plot of soil PLFAs and isoprenoid GDGTs (Fig. S1) showed the different microbial community between rhizospheric and non-rhizospheric soils for each plant species, which was suggestive of rhizospheric effects on soil microbes. For communities represented by PLFAs, the first principal component (PC1) explained 39.52% of the variation, while the second principal component (PC2) explained 32.00%. For isoprenoid GDGTs, 82.13% of the variation was explained by PC1 (51.15%) and PC2 (30.98%). In addition, the Shannon-Wiener diversity (H) index, which directly indicates the apparent diversity of a microbial community, was calculated from the PLFA and GDGT results. The H index in this study suggested that the rhizospheric and non-rhizospheric soils had similar levels of microbial diversity ($p > 0.05$).

The relationships between microbial community structure, indicated by the PLFA profiles, and the environmental factors were investigated using RDA (Fig. 3). The targeted environmental factors explained 75.30% of the variance in community structure. Based on the Monte Carlo method, pH was the most important factor affecting the microbial community, explaining 21.40% ($p = 0.001$) of the PLFA composition, followed by DOC which accounted for 14.60% ($p = 0.015$). Notably, pH was negatively and strongly correlated with the PLFAs 18:1w9c and 18:2w6 representing fungi, whereas PCBs had negative correlation with the PLFA 17:0 (*Arthrobacterium*).

Correlation analysis between the environmental factors and archaeal community structure is shown in Table 2. PC1 (51.15%) was negatively correlated with Cu ($p < 0.05$) and Zn ($p < 0.01$) concentrations, but no significant correlation was observed between PC2 and any environmental factors,

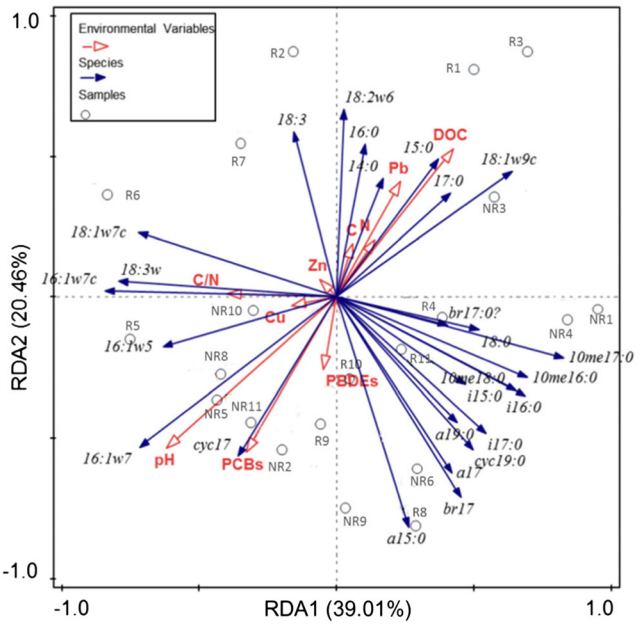

Fig. 3 Redundancy analysis triplots showing relationships between soils with different planting (black circles), environmental factors (hollow red arrows), and PLFAs (solid blue arrows). *R* rhizospheric soil, *NR* non-rhizospheric soil. Numerals following NR or R represent plant species. 1: *Oryza sativa* L.; 2: *Lactuca sativa* L.; 3: *Arachis hypogaea* L.; 4: *Glycine max* L.; 5: *Ipomoea aquatica* Forsk.; 6: *Vignaunguiculata* (L.) Walp; 7: *Colocasia esculenta* L.; 8: *Zea mays* L.; 9: *Solanitm melongena* L.; 10: *Ipomoea batatas* (L.) Lam.; 11: *Gynura cusimbua* (D. Don) S. Moore

Table 2 Pearson correlation between principal components of PCA for isoprenoid GDGTs and environmental factors in all the soils

PCA component	pH	TN	TOC	C/N	DOC	DON	PCBs	PBDEs	Zn	Cu	Pb
PC1 (51.15%)	0.327	− 0.304	− 0.211	0.141	− 0.167	0.016	− 0.145	0.002	− 0.570**	− 0.521*	− 0.401
PC2 (30.98%)	− 0.216	− 0.004	0.067	0.187	0.151	− 0.231	− 0.171	0.349	− 0.136	0.067	− 0.259

**Correlation is significant at the 0.01 level (two-tailed).*Correlation is significant at the 0.05 level (two-tailed)

indicating that soil properties, Pb, and organic pollutants had little influence on archaeal community structure.

Influence of plant species on the microbial community

The rhizospheric effects of different plant species on microbial biomass were represented by C_R/C_N (Table 3). Most plants enhanced the biomass of bacteria, actinomycetes, and archaea ($C_R/C_N > 1$), although the increases were dependent on plant species. The biomass of bacteria, actinomycetes, fungi, and archaea was the most improved by *Colocasia esculenta* L. with the highest C_R/C_N, followed by *Oryza sativa* L. Although *Arachis hypogaea* L., *Glycine max* L., and *Vigna unguiculata* (L.) Walp increased the C_R/C_N of PLFAs, they had $C_R/C_N < 1$ for GDGTs, indicating a decrease in archaeal populations. In the rhizospheric soils of *Zea mays* L. and *Solanum melongena* L., the microbial biomass represented by PLFAs decreased ($C_R/C_N < 1$).

Table 3 illustrates the influence of plant species on the microbial indicators (GN/GP, F/B, cyc/pre, and I/A). All the C_R/C_N ratios for F/B were at least 1.0, which is indicative of a sustainable rhizosphere (de Vries et al. 2006). Most cyc/pre ratios, which reflect environmental stress, were lower in the rhizospheric soils ($C_R/C_N < 1$), except for *G. max*, *Z. mays*, *S. melongena*, and *Gynura cusimbua* (D. Don) S. Moore, suggesting that the growth of some plant species relieved this stress. Most GN/GP ratios were higher in the rhizospheric soils, except those associated with *C. esculenta*, *S. melongena*, and *G. cusimbua*, while all C_R/C_N ratios for I/A were near 1.0 and were not affected significantly by plant species.

Discussion

To explore the rhizospheric effects on microbial communities in e-waste-contaminated soils, we performed the first analysis of the microbial composition, using PLFA and isoprenoid GDGT, between the rhizospheric and non-rhizospheric soils of 11 typical crops. Both the soil physicochemical features and microbes were affected by the rhizosphere to different extents, depending on the plant and microbial species. In general, the rhizospheres contained higher microbial biomass and different microbial communities due to the changes in the soil properties owing to the rhizospheric effects, which is consistent with the positive effects of plants on the microbial community reported in previous studies (Berg and Smalla 2009; Qin et al. 2014).

In this study, planting crops altered the soil physicochemical properties. The pH of the rhizospheric soils was lower than that of the non-rhizospheric soils, confirming the acidifying action of roots on the surrounding soils (Hinsinger et al. 2003; Massaccesi et al. 2015). The higher contents of TOC, TN, and DOC in the rhizospheric soils resulted from the exudation of labile carbon compounds, the debris of roots, and the improvement of organic matter cycling (Dijkstra et al. 2013; Massaccesi et al. 2015). The present study observed the accumulation of toxic organic pollutants in the rhizosphere, which is consistent with the increased PCBs and PBDEs in the contaminated farmland soils over time (Liu et al. 2015). Higher

Table 3 C_R/C_N value of different indicators of microbial community in soils

Plant	GDGT	PLFA						Indicator			
		Total	GP bacteria	GN bacteria	Total bacteria	Actinomycetes	Fungi	GP/GN	F/B	cyc/pre	I/A
Oryza sativa L.	3.26	2.6	1.9	3.0	2.6	1.4	3.2	1.6	1.3	0.4	1.2
Lactuca sativa L.	1.05	1.2	0.8	1.1	1.0	0.9	1.9	1.3	1.8	0.8	1.1
Arachis hypogaea L.	0.88	1.5	1.1	1.5	1.4	1.1	2.3	1.4	1.7	0.7	1.1
Glycine max L.	0.43	1.1	1.0	1.2	1.1	1.0	1.3	1.2	1.1	1.2	1.1
Ipomoea aquatica Forsk.	2.05	1.1	1.0	1.2	1.1	1.1	1.1	1.2	1.1	0.8	1.1
Vignaunguiculata (L.) Walp	0.81	1.2	0.8	1.3	1.0	0.8	1.6	1.7	1.5	0.7	0.9
Colocasia esculenta L.	59.50	15.3	16.3	22.1	14.7	15.9	17.7	0.9	1.0	0.9	0.8
Zea mays L.	0.86	0.8	0.8	0.8	0.8	0.8	1.0	1.0	1.2	1.2	1.0
Solanitm melongena L.	1.27	0.8	0.8	0.7	0.8	1.1	1.0	0.8	1.2	1.5	1.1
Ipomoea batatas (L.) Lam.	1.60	1.1	1.0	1.0	1.0	0.9	1.2	1.1	1.2	0.9	1.0
Gynura cusimbua (D. Don) S. Moore	1.15	2.4	2.6	2.0	2.3	2.4	2.4	0.8	1.1	1.4	1.0

PCB and PBDE concentrations in rhizospheric soils were attributed to the activation and desorption of the abundant adhered compounds in aged contaminated soils due to the root exudates as observed previously (Liste and Alexander 2000; Wang et al. 2016; Wang et al. 2014b).

The PLFA and isoprenoid GDGT analyses provided a comprehensive view of the microbial compositions of the rhizospheric and non-rhizospheric soils. In both soils, bacteria were more abundant than fungi, and archaea represented by isoprenoid GDGTs were much less abundant than other microbes represented by PLFAs, regardless of plant species, indicating that the altered habitats in the rhizosphere remained more suitable for bacteria and did not discriminate sufficiently to alter the rank of these microbes. The same trend was observed previously in the rhizospheres of plants located in PAH-metal co-contaminated soils, as well as in many uncontaminated sites, where bacteria were approximately tenfold more abundant than fungi (Bourceret et al. 2016; Liang et al. 2016). Moreover, aerobic bacteria dominated the microbial communities, especially in the rhizospheric soils, and *Pseudomonas* (represented by 18:1w7c) was one of the predominant microbes, which benefited from the enhanced soil aeration, and DOC, PCBs, and PBDEs in the rhizosphere owing to the rhizospheric effects described above (Martin et al. 2014; Thomas et al. 1996). *Pseudomonas* is known for its powerful ability to metabolize organic matters, including PAHs, toluene, phenols, and PCBs, and is frequently identified in PAH- and PCB-contaminated soils (Liu et al. 2015; Song et al. 2015a). Of the microbes represented by isoprenoid GDGTs, *Thaumarchaeota* and *Euryarchaeota* dominated archaeal communities in both the rhizospheric and non-rhizospheric soils, consistent with previous results showing their high abundance in archaeal populations from soils, peats, and sediments (Schouten et al. 2013; Shen et al. 2011). Our results indicated their strong adaptability to various environmental factors and possible contribution to the growth of plants and other microbes via nitrogen and carbon fixation (Leininger et al. 2006). *Thaumarchaeota* is often used as a biomarker to characterize and quantify ammonia-oxidizing archaea (Leininger et al. 2006). *Euryarchaeota* species include methanoarchaea that can oxidize methane in the absence of oxygen (Schouten et al. 2013).

By further comparing the profiles of PLFA and isoprenoid GDGT subgroups between rhizospheric and non-rhizospheric soils, we observed significant rhizospheric effects on microbial biomass. The concentrations of total PLFAs, PLFA subgroups (i.e., bacteria, fungi and actinomycetes), total GDGTs, and GDGT subgroups were higher in the rhizospheric soils. The increase in PLFAs might be attributed to the lower pH and higher TOC, C/N, and DOC (Table 1), which was indicated in a previous study of PAH-metal co-contaminated soils (Bourceret et al. 2016). Regarding GDGTs, the increased biomass in the rhizospheric soils might be attributed to the higher TN, TOC, DOC, Pb, and Zn in rhizosphere (Table 1), which differentiated from the results of several studies that archaea were mainly affected by pH, temperature, and Cu concentration (Deng et al. 2018; Schouten et al. 2013; Wang et al. 2014a); however, our results are supported by the positive correlation between archaeal abundance and organic matters in agricultural soils (Shen et al. 2011). The discrepancy between our results and those of previous studies may be attributed to the minimal differences in pH, temperature, and Cu concentration between rhizospheric and non-rhizospheric soils in this study, which might be too small to significantly influence archaeal biomass.

We observed the rhizospheric effects on microbial community structure. The relative abundance of fungal PLFAs was higher in rhizospheric soils than in non-rhizospheric soils, while the bacterial PLFAs followed the opposite trend, resulting in higher F/B ratios in rhizospheric soils where the microbial community possessed a stronger capacity to degrade organic matters and a higher tolerance to environmental pressures (Chen et al. 2014; de Vries et al. 2006). In this study, the F/B ratio was negatively correlated with soil pH, which was consistent with previous studies showing that fungi were more adaptive to acidic conditions (Steenwerth et al. 2008) and had higher abundance in rhizospheric soils where the soil pH was decreased by roots secreting organic acids (Deng et al. 2018). Similar results were reported by Pietri and Brookes (2009) who found that the F/B ratio was higher in more acidic soils. The relative abundance of GP bacteria PLFAs in rhizospheric soils was lower than that in non-rhizospheric soils. The significant negative correlation between PCBs and *Arthrobacterium* (17:0), one of the predominant GP bacteria observed in this study, might explain the lower relative abundance of GP bacteria PLFAs in rhizospheric soils, in which PCB concentrations were higher than in non-rhizospheric soils. Thompson et al. (1999) also observed a decrease in GP bacteria in dichlorobenzene-contaminated sediments. Comparing to the non-rhizospheric soils not affected by root exudates, the lower cyc/pre ratio in rhizospheric soils indicated less influence of environmental stress, which might be resulted from the elevated DOC. Chen et al. (2014) showed that the cyc/pre ratio was significantly lower in rice rhizospheric soils than non-rhizospheric soils, implying the increased contents of nutrients and bioavailability of PCBs in rhizosphere. Overall, the rhizospheric effects improved the soil microflora, which possibly benefited from the improved growth conditions in the e-waste-contaminated soils due to the increasing available nutrients in root-associated niches.

Unlike the microbial community represented by PLFAs, the community structure of archaea, represented by isoprenoid GDGTs, was only slightly affected by plant species, with no significant difference in the relative abundances of total and subgroup GDGTs between the rhizospheric and non-

rhizospheric soils. Although the archaeal distribution in this study was significantly correlated with soil Zn and Cu concentrations (Table 2), no obvious difference in these two metals was observed between rhizospheric and non-rhizospheric soils, and the selective stimulation of archaea in the rhizosphere was not observed. Several studies have reported that archaea were significantly affected by Zn and Cu with decreased archaeal populations in soils contaminated by these heavy metals (Liu et al. 2014; Mertens et al. 2009). The limited difference in heavy metal contents between rhizospheric and non-rhizospheric soils in the present study might result from the discriminated effects of root exudates on metals, for example, forming metal chelates in rhizospheric soils increases the availability of heavy metals, while the organic acids secreted by root decrease the heavy metal contents by accelerating metal mobility (McGrath et al. 1997; Seguin et al. 2004). The relative abundance of *Thaumarchaeota* as the dominant archaeal species in this study might be affected by soil DON, because *Thaumarchaeota* are ammonia-oxidizing archaea and often obtain energy via ammonia oxidation (Ayari et al. 2013). However, there was no significant difference in the DON content between the rhizospheric and non-rhizospheric soils, which might lead to the similar isoprenoid GDGT levels in this study.

The rhizospheric effects on the biomass and composition of the microbial community varied among plant species. The C_R/C_N of total PLFAs, isoprenoid GDGTs, individual PLFAs, GN/GP, F/B, cyc/pre, and I/A differed among the rhizospheric soils of the 11 plant species studied. The different rhizospheric effects on total PLFAs and individual PLFAs were probably caused by the different amount of root exudates produced by each plant species as carbon and nitrogen sources, consistent with previous results in the uncontaminated soils (Berg and Smalla 2009; Sliwinski and Goodman 2004). It was also indicative in the significant correlation between PLFAs and the C/N ratio in the present soils (Table 1). The changes in F/B and I/A in the present study were the combination effects of pH and PCBs contents, dependent on the different capability of each plant species to produce compounds such as organic acids and accumulate toxic PCBs (Martin et al. 2014). Besides, it is well known that the organic compounds secreted by root can change the speciation and activity of metals by dissolving, chelating, and deoxidizing, which are specific for each plant family or species and then result in the different metal levels in the rhizospheres of plants studied in this work (McGrath et al. 1997; Seguin et al. 2004). Herein, the significant correlation between isoprenoid GDGTs and the specific amount of Zn and Pb in the rhizospheric soils of the studied plants might contribute to the different rhizospheric effects on archaea, similar with the previous study on the rhizosphere of poplar growing near waste mine tailings that rhizospheric microbial communities were driven by Zn and Pb amounts depending on the poplar types (Hur et al. 2011).

Conclusion

From this study, it was clear that both the biomass and composition of microbes in e-waste-contaminated soils were affected by the rhizosphere. Planting crops enhanced the microbial biomass in the rhizosphere, and such influence was more profound on bacteria and fungi than archaea, owing to the stronger rhizospheric effects on the PLFAs profiles than isoprenoid GDGT. The soil microbial community structure represented by PLFAs was affected significantly by pH and DOC, while the isoprenoid GDGT profiles were significantly correlated with the Zn and Cu content. These results indicated that, altered by planting, soil properties were the main factors influencing bacterial and fungal communities in e-waste-contaminated soils and resulted in the differences of microbial community between rhizospheric and non-rhizospheric soils. The distinctive rhizospheric effects among plant species were attributing to the discriminating change of these environmental factors. The study contributes to our comprehensive understanding of rhizospheric effects on soil bacteria, fungi, actinomycete, and archaea, which is helpful for further remediation of e-waste-contaminated soils.

Funding This study was supported by the Scientific and Technological Planning Project of Guangzhou, China (No. 201707020034), the National Natural Science Foundation of China (Nos. U1501234 and 41673111), and the China Postdoctoral Science Foundation (2015 M582430).

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