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Soil microbial community changes in response to the environmental gradients of urbanization in Guangzhou City

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Abstract

Soil microbes play important roles in many terrestrial ecological processes. Rapid urbanization causes drastic changes in land use and land cover, thus forming a heterogeneous environmental gradient and directly or indirectly affecting the composition and function of soil microbial communities. To investigate the effects of rapid urbanization on soil microbial community composition and function, we analyzed soil microbial communities by quantifying phospholipid fatty acids among the land cover categories (rural forests, urban low-impacted forest fragments, urban high-impacted forest fragments, and urban parks) in Guangzhou. We found that soil microbial communities differed across this urbanization gradients. Specifically, compared to the rural forest ecosystems, the biomass of Actinobacteria and gram-positive bacteria in urban high-impacted forest fragments ecosystems were 53.8% and 31.23% greater, respectively, while the biomass of Actinobacteria and gram-positive bacteria in urban park ecosystems were 67.8% and 37.45% greater respectively. Microbial communities of rural forests and urban low-impacted forest fragments, characterized by lower urbanization intensity, were dominated by the microbial groups, 19:0cy, i16:0, i15:0, 15:0, 18:0 (bacterial biomarkers), 18:2ω6c (fungal biomarkers), and 10Me17:0 (Actinobacterial biomarkers), whereas the urban park and urban high-impacted forest fragments, characterized by higher urbanization intensity were dominated by the microbial groups, 18:1ω5c, 18:1ω7c, cy17:0, i17;0, a17:0, 16:1ω9c, a15:0, i14:0 (bacterial biomarkers), 16:1ω5c (fungal biomarkers), and 10Me16:0 (Actinobacterial biomarkers). Fungal biomass was positively correlated with soil pH and the metal comprehensive index, whereas bacteria were only positively correlated with soil organic matter. Soil pH, organic matter, total nitrogen content and the heavy metal comprehensive index were all positively correlated with total soil microbial biomass and Actinobacterial biomass. These results suggest that rapid urbanization caused land use and land cover changes that significantly affect soil microbial community composition, and urbanization impacts soil properties which then affect soil microbes.

Keywords Urbanization · Intensity · Soil microbial community · PLFAs

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Introduction

Urbanization changes land use and land cover patterns, creating environmental gradients across urban, suburban, agricultural and natural ecosystems. This can cause ecological problems, such as, the sharp decline of arable land, soil compaction, soil pollution, and reduced biodiversity (Chen 2007; Larson 2013; Lopez et al. 2018; Lu et al. 2015). Conserving urban green spaces has a positive effect on the sustainable development of cities; these spaces act as carbon sinks, mitigate the heat island effect, and help address other negative ecological impacts of urban development, while simultaneously supporting ecological, economic and social development of cities (Ning et al. 2016).

Soil is a foundational element of urban ecosystems, providing residents with various ecological services such as food supply, pollutant purification, and water conservation. Urbanization changes the soil and inevitably affects the supply and maintenance of soil ecological services (O'Riordan et al. 2021; Pereira et al. 2018). Soil microorganisms are the most biologically active part of the soil ecosystem and, they play a critical role in regulation of the biogeochemical cycles (Ha et al. 2008). Soil microorganisms mediate many ecological processes in soil, such as carbon sequestration, nitrogen fixation, and organic matter decomposition. Microorganisms also are of vital importance to the degradation of soil pollutants (Condron et al. 2010; Kuypers et al. 2018; Sofi et al. 2016; Wardle et al. 2004). Soil microorganisms further participate in processes, such as litter decomposition and nutrient turnover (Klimek et al. 2016; Li 2015; Veresoglou et al. 2015). Soil microorganisms are highly sensitive to environmental changes, and the composition of soil microbial communities varies across different ecosystems. In general, soil microbial biomass in natural ecosystems (forests and grasslands) is higher than that in urban ecosystems (Rai et al. 2018b; Wang et al. 2017; Zhao et al. 2012), whereas the diversity of soil microorganisms can sometimes be higher in urban ecosystems (Tan et al. 2019). Changes in the soil environment from urbanization and human activity have drastically affected the composition and distribution of soil microorganisms, which consequently alters the function and ecosystem services provided by these microbes (Demina et al. 2018; Rai et al. 2018a, 2021; Zhu et al. 2017).

Important environmental factors that are affected by urbanization and then impact soil microbial communities include soil properties (such as soil texture, organic carbon, moisture, nutrients, pH, and temperature), vegetation coverage, and presence of pollutants (Frossard et al. 2017), though key influencing factors differ in different landscapes (Grimm et al. 2008; Pastor and Hernandez 2012; Zhang et al. 2003). In comparison, cropland soil microbial communities are also affected by crop strains, tillage practices and fertilizer application (Wang et al. 2016). Rapid urbanization and construction activities, such as soil turning, compaction and sealing, can significantly change soil properties, and alter the composition, structure, and diversity of microbial communities. Further, anthropogenic pollution eventually enters the soil, and strongly affects the soil microbial community (Pickett and Cadenasso 2009). For example, soil pollution by heavy metals and polycyclic aromatic hydrocarbons can negatively impact soil bacterial communities (Parajuli et al. 2017; Singh et al. 2019). Significant changes in the microbial community can affect human health; thus, it is necessary to explore the relationships among soil properties, pollutants, and soil microbial communities in urban-impacted areas where urbanization and human activity are abundant. In this study, we collected soil samples from Guangzhou, South China, along a gradient of urbanization to determine whether the microbial community structure in soils is influenced by urbanization and to identify the key soil properties that affect soil microbial community composition and function. We hypothesized that (1) soil microbial communities differ significantly among the land cover categories, and (2) soil organic matter and soil pH are the main factors affecting urban soil microbial communities.

Materials and methods

Research area and soil sampling

This study was conducted in Guangzhou, Guangdong Province, South China, which is one of the central urban areas in the Guangdong-Hong Kong-Macao Greater Bay Area. The climate of this area is consistent with that of a subtropical marine monsoon climate, with annual average precipitation of 1623.6—1899.8 mm and an average annual temperature of 28.6 °C. The soil is classified as latosolic red soil in natural ecosystems.

To accurately determine the long-term effects of urbanization intensity, it is necessary to sample areas with relatively stable soil environments. We carried out a preliminary selection of urban ecosystems based on satellite imagery along arterial roads across the study area (Yu et al. 2021). We ultimately selected 42 urban and rural forests as the sampling plots (Fig. 1). Each site was classified into one of four ecosystem types according to their location, vegetation cover, amount of anthropogenic solid waste, dominant plant type, and management intensity. The four ecosystem types with increasing urbanization intensity were rural forests (8 sites), urban low-impacted forest fragments (15 sites), urban

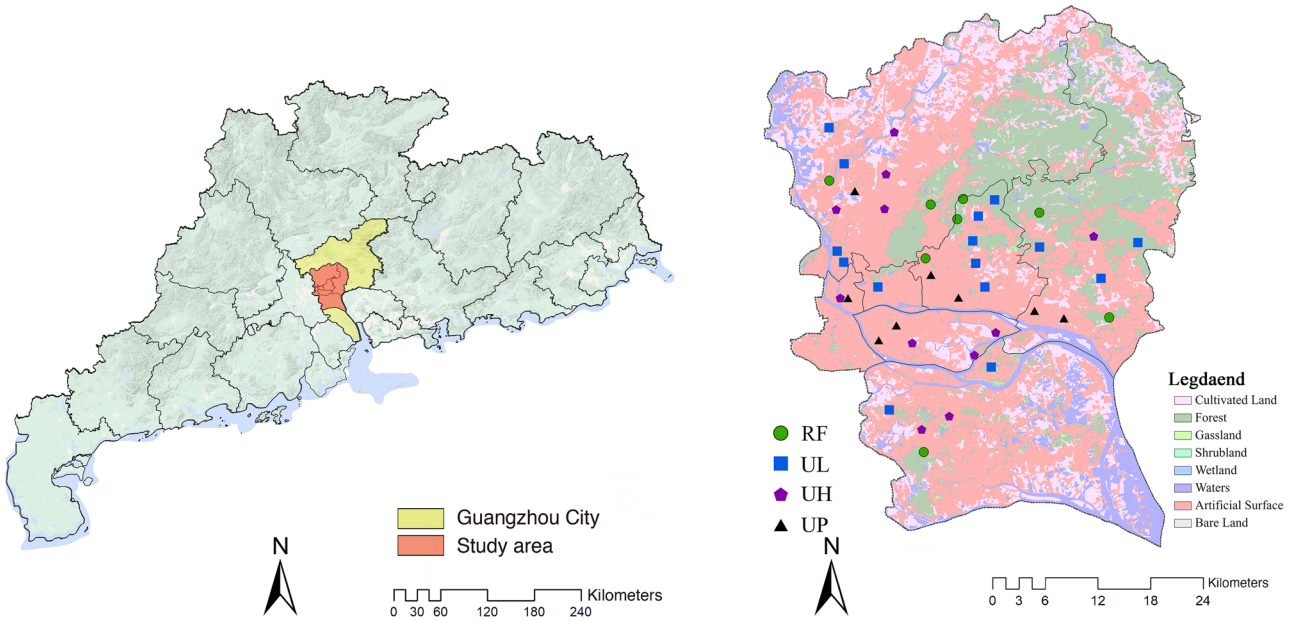

Fig. 1 Locations of study areas in Guangdong Province and location of the 42 sampling sites in downtown and adjacent regions in Guangzhou City

high-impacted forest fragments (11 sites), and urban parks (8 sites). Rural forests were characterized by woodlands at least 5 km away from urban roads and buildings, whereas urban forests referred to fragmented woodlands surrounded by urban structures. Urban low-impacted forest fragments were mostly located in hilly areas and were less disturbed by humans than urban high-impacted forest fragments or parks. Urban high-impacted forest fragments were usually small in area and close to urban buildings; consequently, soil in urban high-impacted forest fragments was commonly polluted by waste generated from human activities (such as plastics, wires, paper, bricks, and clothing). Urban parks were managed ecosystems in which trees or grasses were often trimmed, watered, and fertilized; decomposing leaves were removed from the ground; and soil might have been turned over and contaminated with solid waste. Specific classifications are listed in Table S1. The latitudinal and longitudinal coordinates of all sample sites were recorded using a GPS. At each sampling site, topsoil samples (0–10 cm) were collected using a steel auger (5 cm diameter) from five randomly selected sites and then collated into a composite sample. Soil sampling sites avoided buildings, roads and trees, and the distance between each sampling point was more than 5 m. One subsample of fresh soil was brought to the laboratory and passed through a 2 mm sieve within 7 days. Roots, rocks, and visible residues were manually removed, then the samples were air-dried at room temperature, ground, and sieved into 100-mesh (0.149 mm) particles for future analysis. Another subsample of fresh soil was immediately brought to the laboratory and freeze-dried to determine soil phospholipid fatty acids (PLFAs).

Laboratory analysis

Soil pH was measured using a 1: 2.5 soil: water suspension using the potentiometric method (Pansu and Gautheyrou 2006). The soil organic carbon (SOC) was measured using the H_2SO_4-$K_2Cr_2O_7$ oxidation method (Yeomans and Bremner 1988). Soil total nitrogen (TN) was quantified using the Kjeldahl acid digestion method (Williams and Fehsenfeld 1991). Heavy metal concentrations (Zn, Cu, Cd, and Pb) were analyzed after digestion in a mixture of nitric acid, perchloric acid, and hydrogen peroxide (US-EPA 1996). The soil heavy metal comprehensive index (*CPI*) was calculated using the following equation (Li et al. 2008):

$$P_i = \frac{C_i}{S_i}$$

$$CPI = \sqrt{\frac{\left(\frac{1}{n}\sum_{i=1}^{n} P_i\right) + [\max(P_i)]^2}{2}}$$

where P_i is the pollution index of heavy metal "i", C_i (mg kg^{-1}) is the quantity of heavy metal i, S_i (mg kg^{-1}) is the environmental background value of Guangzhou City (Zhuo et al. 2009), and *CPI* is the comprehensive pollution index. Soil properties are shown in Table S2.

PLFA extraction and analysis

Soil samples were analyzed using extraction and characterization of microbial PLFAs to quantify microbial abundance and assess microbial community structure (Luo et al. 2016). Four grams of freeze-dried soil was extracted using a solution of 1: 2: 0.8 ratio of chloroform: methanol: citric acid buffer, and the phospholipids in the extraction were separated after elution using methanol on a silica column. The separated phospholipids were methylated with a 0.2 mol/l KOH methanolysis solution and the fatty acid methyl esters (FAMEs) were subsequently formed and collected. Considering methyl nonadeconoate 19:0 as internal standards, the FAMEs were analyzed using a capillary gas chromatography (Agilent 6850 Series, Agilent Technologies Inc., USA) equipped with an FID detector and using an Agilent 19091B-102 column (25 m × 200 μm × 0.33 μm). The FAMEs were identified and quantified using the MIDI system (MIDI Inc., USA), and the total or individual amounts of PLFA were calculated based on of the quantity of FAMEs (nmol g/1). Each group in the microbial community was described as the sum of the corresponding PLFAs. Gram-negative bacterial (GNB) biomass was represented by 17:0cy, 19:0cy, 16:1ω9c, 18:1ω7c, 18:1ω9c; gram-positive bacterial (GPB) biomass was represented by i14:0, i15;0, i16:0, a15:0, i17;0, a17:0; bacterial (B)biomass was represented by 17:0 cy, 19:0 cy, 16:1ω9c, 18:1ω7c, 18:1ω9c, i14:0, i15;0, i16:0, a15:0, i17;0, a17:0, 14:0,15:0,16:0, 17:0,18:0; fungal (F) biomass was represented by 16:1ω5c and 18:2ω6c; and Actinobacteria (A) biomass was represented by 10Me16:0, 10Me17:0, 10Me18:0 (Bååth 2003; Bossio and Scow 1998; Frostegård et al. 2011).

Statistical analysis

Principal Component Analysis (PCA) and Non-metric multidimensional scaling (NMDS) were conducted using the vegan package in R (Oksanen et al. 2017). Permutational multivariate analysis of variance (PERMANOVA) was employed in the Past (PAleontological STatistics) 3 software (Oslo, Norway) to explore the influence of urbanization on the microbial community (Hammer et al. 2001). Other statistical analyses were performed using IBM SPSS Statistics v.21 (© 1989–2012 International Business Machines Corp., USA). Figures were plotted using OriginPro 2016 (© 1991–2015 OriginLab Corporation, USA).

Results

Soil microbial biomass and community structure

Total soil microbial, fungal, bacterial and GNB biomass were not significantly different among the land cover categories; however, the biomass of Actinobacteria and GPB in urban high-impacted forest fragments and urban parks were significantly higher than those in rural forests (Fig. 2a, Table S3). Compared to the rural forest ecosystems, the biomass of Actinobacteria and GPB in urban high-impacted forest fragments was greater by 53.8% and 31.23%, respectively, and the biomass of Actinobacteria and GPB in urban park ecosystems was greater than that of rural forests by 67.8% and 37.45%, respectively. There was no significant difference in the ratio of fungi to bacteria among the land cover categories; however, the ratio of GPB to GNB in urban low-impacted forest fragments was significantly higher than that in rural forests (Fig. 2b, Table S3).

Soil microbial distribution characteristics and influencing factors

Principal component analysis (PCA) of the relative abundance of different microbial groups (normalized, accounting for 73.1% of the variation; Fig. 3a) and the relative abundance of individual phospholipid fatty acids (normalized, accounting for 70.95% of the variation; Fig. 3b) roughly separated microbial abundance by land cover. Permutational multivariate analysis of variance (PERMANOVA) confirmed that the relative abundances of different microbial groups ($F = 2.946$, $P = 0.020$) and individual phospholipid

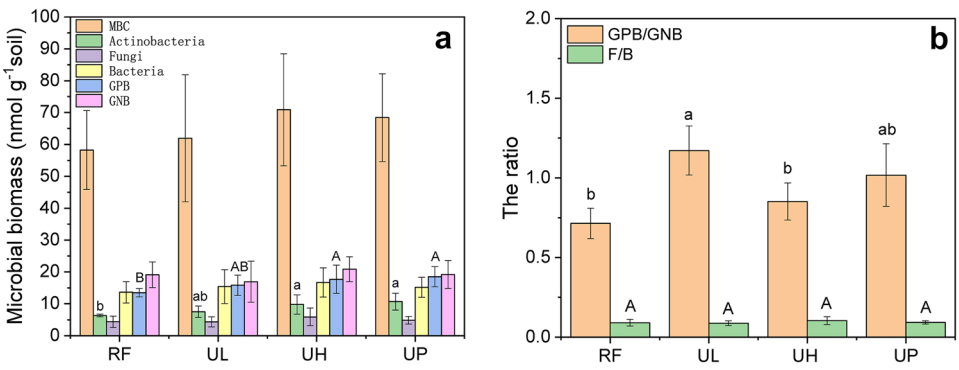

Fig. 2 Soil microbial biomass of different groups (**a**) and microbial community structure (**b**) among the land cover categories Values are presented as mean ± standard deviation. Different lowercase or uppercase letters indicate the significant difference among different urbanization intensities ($P < 0.05$)

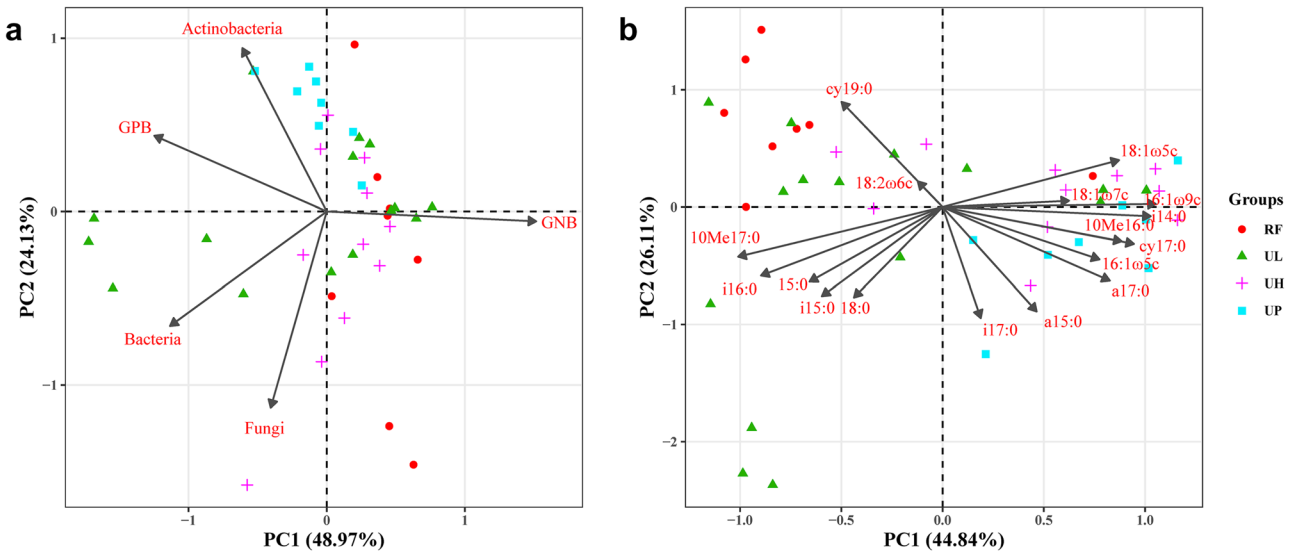

Fig. 3 Principal component analysis (PCA) of microbial community composition (%) among the land cover categories. **a**: the relative abundance of different microbial groups, **b**: the relative abundance of individual phospholipid fatty acids

fatty acids ($F=4.402$, $P=0.001$) were significantly different between the four gradients of urbanization. The microbial communities of rural and urban low-impacted forest fragments, characterized by lower urbanization intensity were dominated by the microbial groups 19:0 cy, 10Me 17:0, i16:0, i15:0, 15:0, and 18:0 (which were mainly classified as the Actinobacterial and bacterial biomarkers), whereas the urban parks and urban high-impacted forest fragments, which are characterized by higher urbanization intensity, were dominated by microbial groups 18:1ω5c, 18:1ω7c, 16:1ω9c, 10Me 16:0, i14:0, cy17:0, 16:1ω5c, i17;0, a17:0, and a15:0 (which were mainly classified as gram-negative bacterial and fungal biomarkers). Nonmetric multidimensional scaling (NMDS) analysis of the relative abundance of different microbial groups and soil properties showed that fungal biomass was mainly affected by soil organic matter (SOM) content and pH, whereas the proportions of Actinobacteria and bacteria were correlated with CPI (Fig. 4a). Non-metric multidimensional scaling (NMDS) analysis was also used to explore the relationships between the relative abundance of microbial communities, individual phospholipid fatty acids, and soil properties. The results indicated

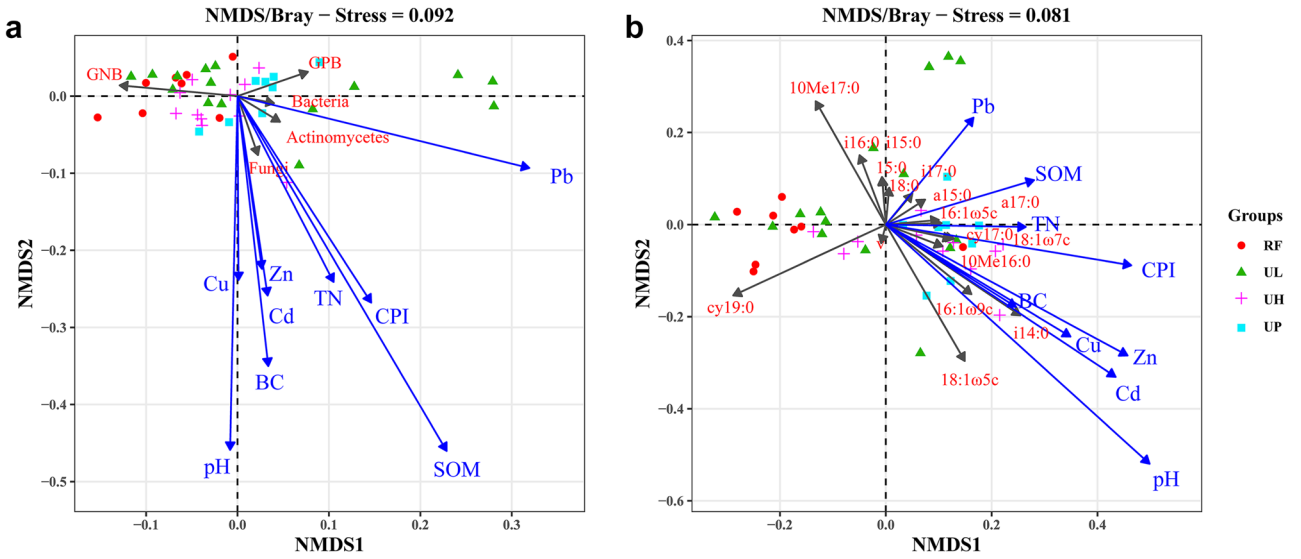

Fig. 4 Non-metric multidimensional scaling (NMDS) biplot of microbial community composition (%) and soil properties; **a**: the relative abundance of different microbial groups, **b**: the relative abundance of individual phospholipid fatty acids

that 16:1ω9c, 18:1ω5c, and i14:0 (described as bacterial biomarkers) had a significant relationship with soil pH, which might indicate that bacteria are more susceptible to soil pH than fungi and Actinobacteria (Fig. 4b).

Linear relationships between soil microbial biomass and soil properties

The total soil microbial biomass was positively correlated with soil pH ($R^2 = 0.257$, $P < 0.001$), SOM ($R^2 = 0.173$, $P = 0.004$), TN ($R^2 = 0.081$, $P = 0.041$), and heavy metal comprehensive pollution index (*CPI*) ($R^2 = 0.136$, $P = 0.009$) (Figs. 5 and S1). Only SOM ($R^2 = 0.173$, $P = 0.004$) had a significant relationship with soil bacterial biomass (Figs. 5 and S1); however, soil pH ($R^2 = 0.322$, $P < 0.001$), SOM ($R^2 = 0.241$, $P < 0.001$), TN ($R^2 = 0.099$, $P = 0.025$), and heavy metal CPI ($R^2 = 0.174$, $P = 0.003$) were also positively correlated with soil Actinobacterial biomass (Figs. 5 and S1), while Soil pH ($R^2 = 0.213$, $P = 0.001$) and heavy metal CPI ($R^2 = 0.127$, $P = 0.012$) were positively correlated with soil fungal biomass (Figs. 5 and S1).

Discussion

Urbanization significantly affected soil microbial community

Urban soils are often manipulated by construction practices or human management, which may alter soil microbial communities. Previous studies have shown that GPB and Actinobacterial biomarker proportions were nearly 2.5 times higher in urban soils with longer management time since initial urbanization than in urban soils with shorter management times (Sapkota et al. 2021). Here, we found that the biomass of bacteria in urban greenspaces was higher than that

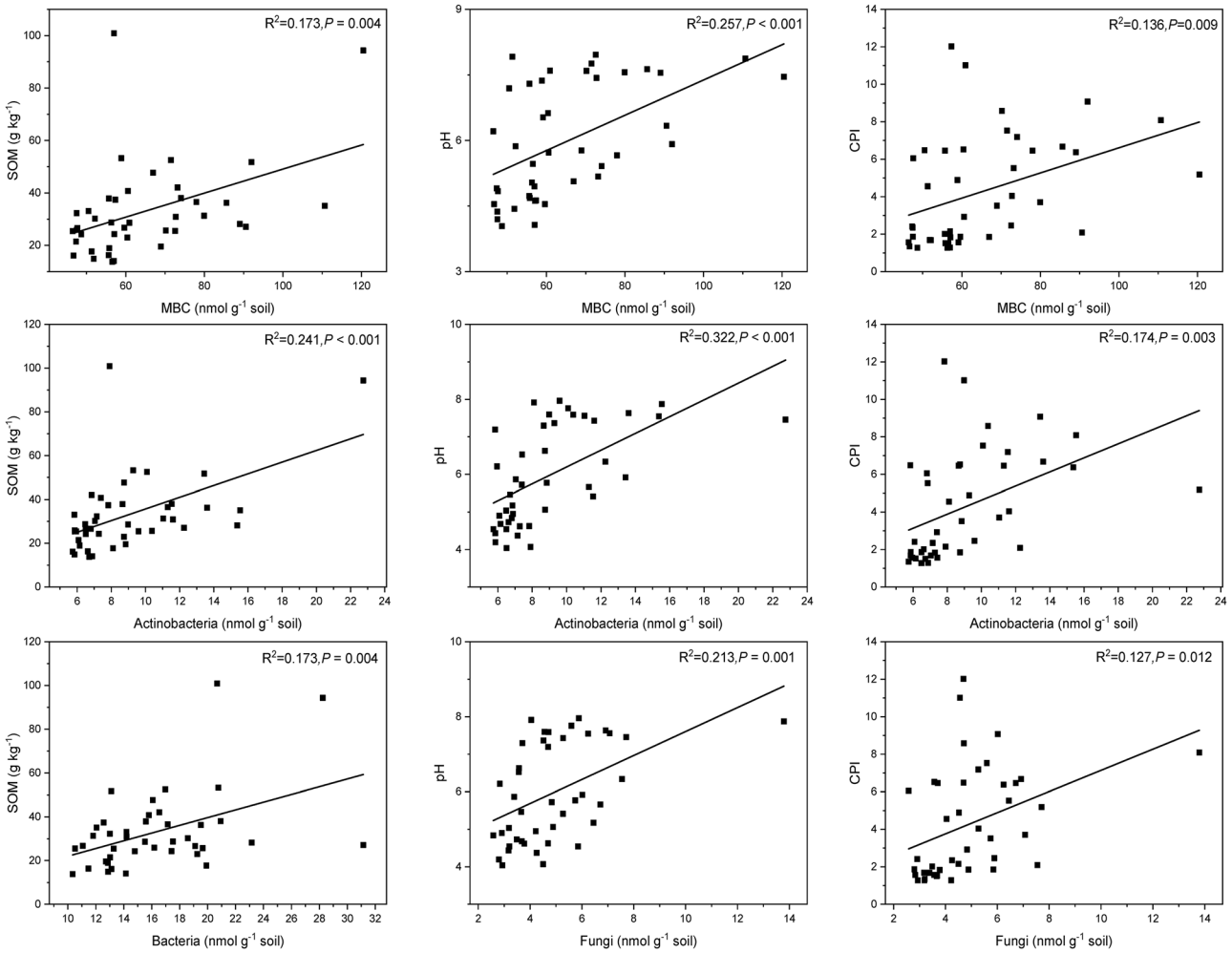

Fig. 5 Relationships between total soil microbial, Actinobacterial, bacterial, fungal biomass, physical–chemical properties, and CPI, R^2 and *P* represent the fitness and significance of the linear regression models. CPI is the comprehensive pollution index of soil heavy metal

in adjacent natural ecosystems (Delgado-Baquerizo et al. 2021), further indicating that bacterial biomass increased with urbanization. Conversely, the biomass of fungi did not change significantly with respect to degree of urbanization, which could be due to special transporter proteins and stress enzymes in fungi creating more resilience and stress tolerance than that of bacteria (Hildebrandt et al. 2007).

The soil microbial community composition reflected by PLFAs was significantly different between rural and urban low-impacted forest fragments of lower urbanization intensity and urban parks and urban high-impacted forest fragments of higher urbanization intensity in our results (Fig. 3). With increasing urbanization, the abundance of Actinobacteria and bacteria and the ratio of GPB to GNB increased, likely owing to the higher soil pH seen in urban parks (Table S2), which was more suitable for the growth of bacteria, like Actinobacteria (Rai et al. 2018b). This finding agrees with previous research showing that soil disturbance or manipulation from anthropogenic activities in urban soils is expected to affect FAs (Mummey et al. 2002). Similar shifts in microbial community structure have been documented in urban greenspace soil microbiomes, which are distinct from adjacent natural ecosystems (Delgado-Baquerizo et al. 2021; Tan et al. 2019). These results further demonstrate that degree of urbanization significantly altered the composition of the soil microbial community. Changes in the microbial community structure indicated that, at the level of the PLFA profiles, the abundance of Actinobacteria and GPB was positively affected by human activities (Tischer et al. 2015).

Soil microbial biomass and composition are two important biological indicators of soil health (Sapkota et al. 2021). For example, increased fungal biomass, reflected by a higher ratio of fungi to bacteria is often interpreted as an indicator of healthier soil (Ananyeva et al. 2015). We found that the biomass of bacteria increased with urbanization, possibly due to overall lower soil health in urban areas from pollution (Sapkota et al. 2021); thus urbanization might have persistent negative effects on soil microbial communities.

Soil properties and heavy metal content regulated soil microbial community

Altered soil properties caused by compaction, construction, mixing, and landfilling can reduce soil moisture and pore space. The reduction of soil moisture and porosity will reduce the ability of soil to fic nutrients, leading to the reduction of SOM in urban soils (Rai et al. 2018b). The measure of SOM is a vital factor that affects the microbial biomass content and structure of the microbial community in the soils (Degens et al. 2000). Our results also confirmed that the total biomass of MBC, Actinobacteria, and bacteria were significantly correlated with SOM. Fungal biomass, however, was not corelated with SOM contents because fungi generally degrade recalcitrant compounds present in SOM using a wide range of enzymes (Boberg et al. 2011). Our results showed that the soil pH in urban high-impacted forest fragments and urban parks were higher than that in rural forests and urban low-impacted forest fragments (Table S2). Previous studies have confirmed that higher soil pH could have affected the nitrogen mineralization and nitrification process, resulting in the depletion of nitrogen content in urban soil, thus, affecting soil microbial biomass and community (Baxter et al. 2002). This is consistent with our finding that soil pH was significantly correlated with soil MBC, Actinobacterial and fungal biomass, which indicates that the increase in pH caused by urbanization may positively affect soil microbial biomass. Previous studies have also demonstrated that SOC, pH, soil available nitrogen, soil exchangeable calcium, and magnesium were the primary soil factors influencing soil bacterial and fungal composition (Tischer et al. 2014; Yan et al. 2016).Therefore, the above results suggest that soil pH and nutrients have the greatest effects on soil microbial biomass. The biomarker method used to measure the microbial community in our study might show different results. Therefore, rigorous molecular methods (such as DNA sequencing) should be considered in future studies.

To understand how heavy metal contamination affects the microbial community, we studied the relationship between the microbial biomass and CPI. We observed a significant positive relationship between CPI and the total amount of MBC, Actinobacterial and fungal biomass, but there was no significant correlation between CPI and soil bacterial biomass. These findings were inconsistent with many assumptions regarding the effects of pollution on organisms. Although the heavy metal content in urban parks was higher than that in rural forests (Table S2), urban parks are highly managed ecosystems in which vegetation is often trimmed, watered, and fertilized, which can provide nutrients for the soil microbial community. Ultimately, the soil microbial biomass did not decrease with the increase in heavy metal. Previous studies have also demonstrated that Cu, Pb and Zn shape the soil microbial communities through metabolic regulation of soil carbon and nitrogen cycling (Dai et al. 2004; Kou et al. 2018; Li et al. 2015). However, a recent study showed that bacterial communities are sensitive to heavy metals, and their composition is significantly affected by Cu, Zn, and Pb, while, fungal communities did not vary significantly by heavy metals contamination (Singh et al. 2019). This indicates that fungi are more tolerant to heavy metals (Gadd 2007).

Conclusion

Urbanization has a significant effect on soil microbial communities. Compared to the rural forest ecosystems, the biomass of Actinobacteria and GPB in urban high-impacted forest fragments were 53.8% and 31.23% greater, respectively, and the biomass of Actinobacteria and GPB in urban park ecosystems were 67.8% and 37.45% greater, respectively. The microbial communities of rural forests and urban low-impacted forest fragments with lower urbanization intensity were dominated by Actinobacteria and bacteria, whereas those of urban parks and urban high-impacted forest fragments with higher urbanization intensity were dominated by GNB and fungi. Soil pH, SOM, and CPI were the main factors affecting the soil microbial biomass and community. Our results showed that urbanization affects urban soil microbial biomass and composition by altering soil properties, which can in turn affect the ecological functions of urban soil. Therefore, it is essential to better understand the effects of the urbanization on soil microbial community composition and function. Specifically, we need to learn more about how urbanization may affect the ecosystem services provided by soil microbes, and how these services and mechanisms impact human and environmental health. A deeper understanding of urban ecosystems, beginning with foundational elements like soil, is required for successful sustainability of urban development.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11252-022-01279-8.

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Authors' contributions Conceptualization, data collection, data analysis and writing—original draft were performed by Min Wang. Material preparation was performed by ShiqinYu, Xiaohua Chen, Xiaodong Liu, Huixian Zeng, Wenkun Wu, Mengyun Liu and Chenhui Su. Supervision and writing—review & editing were performed by Guoliang Xu. All authors read and approved the final manuscript.

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Availability of data and material Not applicable.

Code availability Not applicable.

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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

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