

Urbanization and greenspace type as determinants of species and functional composition of collembolan communities

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ABSTRACT

Urban regions are rapidly expanding worldwide resulting in biotic homogenization and loss of ecological functions in urban ecosystems due to management practices targeting at satisfying aesthetic and health demands of urban residents. These practices also modify living conditions and food resources of soil invertebrates thereby affecting the structure and functional diversity of soil animal communities including collembolans. Here, we assessed the response of the community composition and functional diversity of collembolans as a major component of soil food webs to urbanization (suburban vs urban region) and greenspace types (including forest and four park-associated greenspaces: lawn, lawn with shrubs, lawn with trees, and lawn with shrubs and trees). Our results highlight that both urbanization and greenspace type significantly affect soil properties and community structure of collembolans. The negative effect of urbanization and park-associated greenspaces on species and functional composition of collembolan communities were likely due to both changes in soil abiotic conditions and bacterial community composition, whereas the reduction of collembolan functional traits likely resulted from changes in soil abiotic conditions and fungal community composition. In park-associated greenspaces richness and diversity of bacterial communities were highest in lawns with trees and lowest in forests. By contrast, species richness and diversity of fungal communities were highest in lawns with shrubs, but, similar to bacteria, lowest in forests. Community composition and functional traits of collembolans were more homogeneous in urban than suburban greenspaces pointing to reduced functioning of collembolan assemblages in urban areas. Overall, our results suggest that changes in soil properties and bacterial communities caused by urbanization and greenspace type are important factors contributing to taxonomic homogenization of collembolan communities, while the loss of functional traits of collembolan communities in urban greenspaces is likely caused by changes in soil properties and fungal community composition.

1. Introduction

Urban greenspaces, which comprise urban forests, parks, and grasslands, provide a wide variety of ecosystem services in urban regions, such as clean air, mitigating thermal radiation, and maintaining

biodiversity (Guilland et al., 2018; Matos et al., 2019; Perry et al., 2020). However, previous studies indicated that ecosystem services of urban greenspaces often fall short of expectations, for example, they can contribute to biodiversity homogenization due to urban expansion, ornamental plant cultivation, and greenspace management (Grimm

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et al., 2008; Groffman et al., 2017). In recent years, urban managers have increasingly emphasized the importance of conserving biodiversity in urban regions and implemented methods to increase vegetation diversity and the area of greenspaces, including forests, parks, and lawns in cities (Martin et al., 2021; Von Thaden et al., 2021). Nevertheless, ecological management of urban greenspaces still is in its infancy and urban managers mainly consider aboveground plant components of aesthetic value to urban residents, and to increase their ornamental value urban parks are split into smaller units such as lawns, shrub areas, and areas with trees. Although belowground biota in urban greenspaces, such as soil fauna and microorganisms, are known to function as key players in maintaining multiple ecological functions and ecosystem stability (Nilsson et al., 2019), they have been largely ignored in establishing and protecting urban greenspaces.

In urban ecosystems, soil conditions are strongly influenced by human-induced environmental changes, such as the formation of heat-islands, environmental pollution, and homogeneity in urban plant communities (Oleson et al., 2015; Stuhlmacher et al., 2022). These changes are particularly severe in the city centre, where the soils in greenspaces mainly originate from surrounding areas or are refilled with construction wastes, and plants are assembled based on aesthetic value by cultivating exotic ornamental plants or turfing lands with monoculture grass. Urban greenspace remodeling practices resulted in more compacted soils and lower plant species richness compared to suburban greenspaces and natural ecosystems (Kowarik, 2011; Wang et al., 2021). Further, urbanization-induced changes in soil physicochemical conditions, microclimatic conditions, and plant communities in urban ecosystems may shape soil microbial communities (Baruch et al., 2021; Miki, 2012), which may directly or indirectly regulate soil fauna communities in urban greenspace ecosystems via affecting their food resources (Chai et al., 2019; Chang et al., 2021; Oktaba et al., 2014).

Collembola, as one of the most abundant and diverse soil animal groups in terrestrial ecosystems, play important roles in biodiversity conservation, nutrient cycling, and transmission of energy, due to their high abundance, species richness, adaptability to a wide range of environmental conditions, and wide range of dietary sources (Hishi et al., 2007; Joimel et al., 2022; Luo et al., 2022; Rusek, 1998). Specific environmental conditions in urban ecosystems, including soil moisture, temperature, pH, nutrient content, and vegetation characteristics (Milano et al., 2017; Rzeszowski et al., 2017; Rzeszowski and Sterzyńska, 2016) are likely to select for specific collembolan communities thereby affecting their functioning. For example, *Mesaphorura macrochaeta* in the soil with higher values of soil pH that is optimal for progeny reproduction, whereas *Stenaphorura japygiformis* is reported to be tolerant of soils with low pH (Rzeszowski et al., 2017). Associated with the variety of habits they colonize, collembolan species occupy a range of trophic niches in soil food webs (Potapov et al., 2016a; Potapov et al., 2016b). Some of the collembolan species serve as primary decomposers which consume leaf litter, plant roots, and root exudates (Goncharov et al., 2016), but some also occupy higher trophic positions by feeding on soil microorganisms, particularly fungi, protozoa, and other smaller soil fauna (Chernova et al., 2007; Heidemann et al., 2014; Li et al., 2020; Pollierer and Scheu, 2021). Thus, they likely benefit from diverse fungal resources (Klironomos et al., 2002), but due to their wide food spectrum they colonize a wide range of habitats and ecosystems including urban greenspaces (Babenko, 2000; Basset et al., 2020). The sensitive response of collembolans to environmental changes and anthropogenic habitat modifications (Joimel et al., 2021) as well as pollutants, drought, and warming, make them ideal model organisms for evaluating consequences of urbanization processes (Luo et al., 2014).

Collembolans are highly differentiated in life-history, behaviour, and morphological characters (functional traits) to meet their diet and cope with environmental adversities (Parisi et al., 2005). Functional traits and respective functional groups are increasingly used as an effective tool to better understand the response of collembolan communities to environmental changes and their contribution to ecosystem functioning

(Malmström, 2012; Yin et al., 2020). For example, the removal of aboveground litter in urban greenspaces reduced epedaphic collembolans due to limited supply of aboveground litter resources. By contrast, hemiedaphic and euedaphic species were less influenced as they more heavily consume root-derived resources (Milano et al., 2017). To better represent functional differences among species, functional traits have been aggregated into functional diversity indices (Laliberté and Legendre, 2010; Pey et al., 2014), such as functional richness, functional evenness, and functional divergence, which quantify different aspects of functional diversity of species across the functional space of the community (Laliberté and Legendre, 2010). Functional richness indicates the functional hyperspace occupied by the species in the community, and functional evenness measures how evenly traits are distributed in trait space (Schleuter et al., 2012; Yin et al., 2020). Trait-based approaches provide a promising framework to better understand community responses to land-use changes and urbanization (Filser et al., 2002). Further, soil biological quality indices based on bacterial and fungal community structure allow linking the functional traits of soil fauna to soil functions (Yan et al., 2012). Soil biological quality indices considering soil fauna, such as collembolans, have been proposed as useful tools for the analysis of the capability of soil animal communities to adapt to changing environmental conditions and their vulnerability to changes in land use (Menta et al., 2018; Parisi et al., 2005).

Here, we investigated the consequences of urbanization and greenspace types for collembolan communities, as well as correlations between collembolan community structure (taxonomic composition and functional traits) and human activities (urbanization and greenspace types) mediated via changes in soil properties (physicochemical and microbial). We compared the taxonomic and functional composition of collembolan communities in different greenspace types in the suburban and urban regions of Xiamen city, China. We hypothesized that (1) urbanization and greenspace type influence soil properties, forming fundamental niche characteristics of collembolans and thereby structure their communities, and in addition to these changes in abiotic conditions that (2) environmental disturbances caused by urbanization and greenspace management influence soil microbial communities and thereby community composition and functional diversity of collembolans.

2. Materials and methods

2.1. Site description

The study was conducted at the city of Xiamen (117°53' – 118°26' E, 24°23'–24°54' N) located in the southern part of Fujian province, South China. The climate in Xiamen is subtropical with annual average temperature of about 21 °C and an annual average precipitation of 1,137 mm (Xu et al., 2014), with most rainy days occurring from May to August and the dominant northeast wind force. Soils in Xiamen city are relatively homogeneous, dominated by silt loam soil (Wang et al., 2017), but some areas have been backfilled with sandy loam from near mountains, deeper soils, or artificial residues (Technosols, Table 1, Fig. S1). The city is one of the most developed cities in Fujian province covering an area of 1700 ha and supporting a population of around 3.86 million inhabitants. As industry and tourism have grown in recent years, urban soil health and ecosystem functions became of increasing concern.

2.2. Experimental design and sampling

With the selected sites, we aimed at covering the interactive influence of urbanization and greenspace type in urban ecosystems on collembolan communities. Suburban areas are less populated (<4,000 inhabitants km⁻²), whereas population density in urban areas is more than three times higher (>13,000 inhabitants km⁻², Yearly Report of Xiamen 2021). In each suburban and urban region, we selected two greenspace types, forest (F) and park. Forests in both urban and

Table 1
Site descriptions. Geographic information, soil textures, and vegetation at each sampling site.

Greenspace	Site	Abbreviation	Construction year	Area (ha)	Longitude (°E)	Latitude (°N)	Elevation (m)	Soil Texture	Dominant trees
Forest	XianYueShan	U-F-X1	–	227	118.114	24.5022	58	Sandy loam	<i>Casuarina equisetifolia</i> , <i>Melia azedarach</i>
	XianYueShan	U-F-X2	–	227	118.086	24.4893	51	Sandy loam	
	HuWeiShan	U-F-HW	–	70.64	118.091	24.5033	41	Sandy loam	<i>Pinus massoniana</i> , <i>Schima superba</i>
Park	NanHu Park	U-P-NH	1990	16.10	118.100	24.4796	1	Silt loam	<i>Taxodium distichum</i> , <i>Delonix regia</i>
Park	Yat-Sen Park	U-P-YS	1927	16.00	118.084	24.4607	6	Silt loam	<i>Acacia confusa</i> , <i>Bombax ceiba</i>
Park	WuYuanwan Park	U-P-WY	2009	85.00	118.167	24.5152	5	Silt	<i>Acacia confusa</i> , <i>Rhizophora apiculata</i>
Park	ZhongLun Park	U-P-ZL	2004	64.90	118.141	24.4852	40	Silt, Technosols	<i>Eucalyptus citriodora</i> , <i>Acacia confusa</i>
Forest	TianZhuShan reserve	S-F-T1	–	3705	117.941	24.5962	197	Sandy loam	<i>Pinus massoniana</i> , <i>Schima superba</i>
	Forest	S-F-T2	–	3705	117.918	24.5928	345	Sandy loam	
	Forest	S-F-T3	–	3705	117.909	24.6124	352	Sandy loam	
Park	JingXian park	S–P–JX	2003	4.74	118.095	24.5801	9	Silt loam	<i>Ficus microcarpa</i> , <i>Delonix regia</i>
Park	Kah-Kee park	S–P–KK	1994	3.00	118.103	24.5717	5	Silt loam	<i>Bischofia javanica</i> , <i>Bauhinia purpurea</i>
Park	RiDong Park	S–P–RD	1995	11.98	118.032	24.5641	6	Silt loam	<i>Ficus microcarpa</i> , <i>Delonix regia</i>
Park	NingBao Park	S–P–NB	2016	2.01	118.048	24.5719	12	Silt loam	<i>Delonix regia</i> , <i>Bauhinia purpurea</i>

suburban areas are rather little disturbed, whereas parks are heavily managed, vary in vegetation characteristics and therefore were partitioned into four park-associated greenspaces, i.e., lawn (L), lawn with shrubs (LS), lawn with trees (LT), and lawn with shrubs and trees (LST). In November 2020, three forests and four parks were sampled in urban and suburban areas in Xiamen City. In each park, four park-associated greenspace types (plots) were identified, the plots were spaced at least 100 m to minimize autocorrelation. In each plot, three subplots of 5 × 5 m spaced by ca. 10 m were erected and from the centre of the subplot samples were taken using a steel corer (5 cm diameter, 10 cm depth). A total of 114 samples were taken [(2 urban regions × (3 forests + 4 parks × 4 park-associated greenspace types)) × 3 replicates] (Fig. 1). Prior to sampling we removed the litter layer from forest plots as park-associated greenspaces lacked a litter layer. Including the litter layer of forests would have biased comparison of greenspace types. Soil samples were placed in sterilized Ziplock bags and transported to the laboratory for soil fauna extraction and further analyses. Collembolans were extracted from soil cores of each subplot, whereas for analysing microorganisms the soil cores from the three replicate subplots were pooled and used for DNA extraction.

Both the suburban and urban forests were broadleaf evergreen forests with high canopy cover (>80 %). The forest plots in suburban regions were located at large remnant forests away from roads and buildings, urban forests were >20 ha also comprising remnant forests little disturbed by humans but surrounded by buildings and roads.

2.3. Soil physicochemical properties

Soil pH was measured using a pH meter (PHS-3C, Shanghai, China) in an aqueous suspension (soil: water = 1 W:5V). Soil moisture was determined gravimetrically using 10 g of fresh soil dried at 105 °C for 48 h. For measuring total carbon (TC), total nitrogen (TN), total phosphorus (TP), and total sulphur (TS), soil samples were ground to pass through a 0.16 mm mesh. TC and TN were determined by an elemental analyser (Elemental Analyzer System Vario Macro Cube, Langensfeld, Germany); soil TP and TS concentrations were measured using an inductively coupled plasma spectrometer (ICPS-7500, Kyoto, Japan) after digestion with H₂SO₄-HClO. Soil organic matter (SOM) concentration was measured using the potassium dichromate method.

2.4. Community and functional trait composition of collembolan

Soil samples were placed into Tullgren/Berlese funnels and left for one night at room temperature. Then, the temperature was gradually increased during the following day and kept at ~35°C for five days (Rousseau et al., 2019; Xie et al., 2022). Collembolans were preserved in 99.7 % alcohol and stored in the fridge prior to separation and identification. Collembolans were first picked under a stereomicroscope (Nikon SMZ745T, Tokyo, Japan), brightened with Nesbitt's fluid, and mounted individually on slides. Then, specimens were identified at genus or species level using the keys of Yin (1998), Weiner et al. (2019), Zhang et al. (2020), and the checklist of the collembolan website (<https://www.collembola.org/index.html>) and counted. Species richness (*S*) of collembolans was calculated as the total number of species per sample and the Shannon-Wiener index (*H'*) for diversity was calculated as.

$$H' = - \sum_{i=1} [P_i \times \log_e(P_i)] \quad (1)$$

with *P_i* the proportion of individuals belonging to the *i*th species (Pielou, 1969).

Based on primary literature, catalogues, and reference work (Gruss et al., 2019; Malmström, 2012; Moretti et al., 2017; Vandewalle et al., 2010), seven traits of collembolans were selected, which are likely to respond to variations in environmental conditions, and to provide complementary information to taxonomic information. The traits included life-history traits (life-form), behaviour trait (dispersal ability) and morphological traits (body size, length of furca, number of ocelli, pigmentation, and coverage by scales, Jagatap et al., 2019; Ponge et al., 2006; Saifutdinov et al., 2018). Life-history traits are among the most sensitive traits responding to environmental change, while morphological traits such as body size are likely to respond to both the abiotic and biotic environment (de Bello et al., 2010; Moretti et al., 2017; Rusek, 2002). For each (adult) individual body and furca length, as well as the number of ocelli were measured under the microscope (Nikon SMZ800). While behaviour and morphological traits, such as the dispersal ability, pigmentation, and cover by scales were assigned to each species assuming lack of intraspecific variation. Functional traits expect body length were scored from 0 to 4 (Gruss et al., 2019, see Table S1). Further, a soil biological quality index based on collembolan species (QBS-c) was

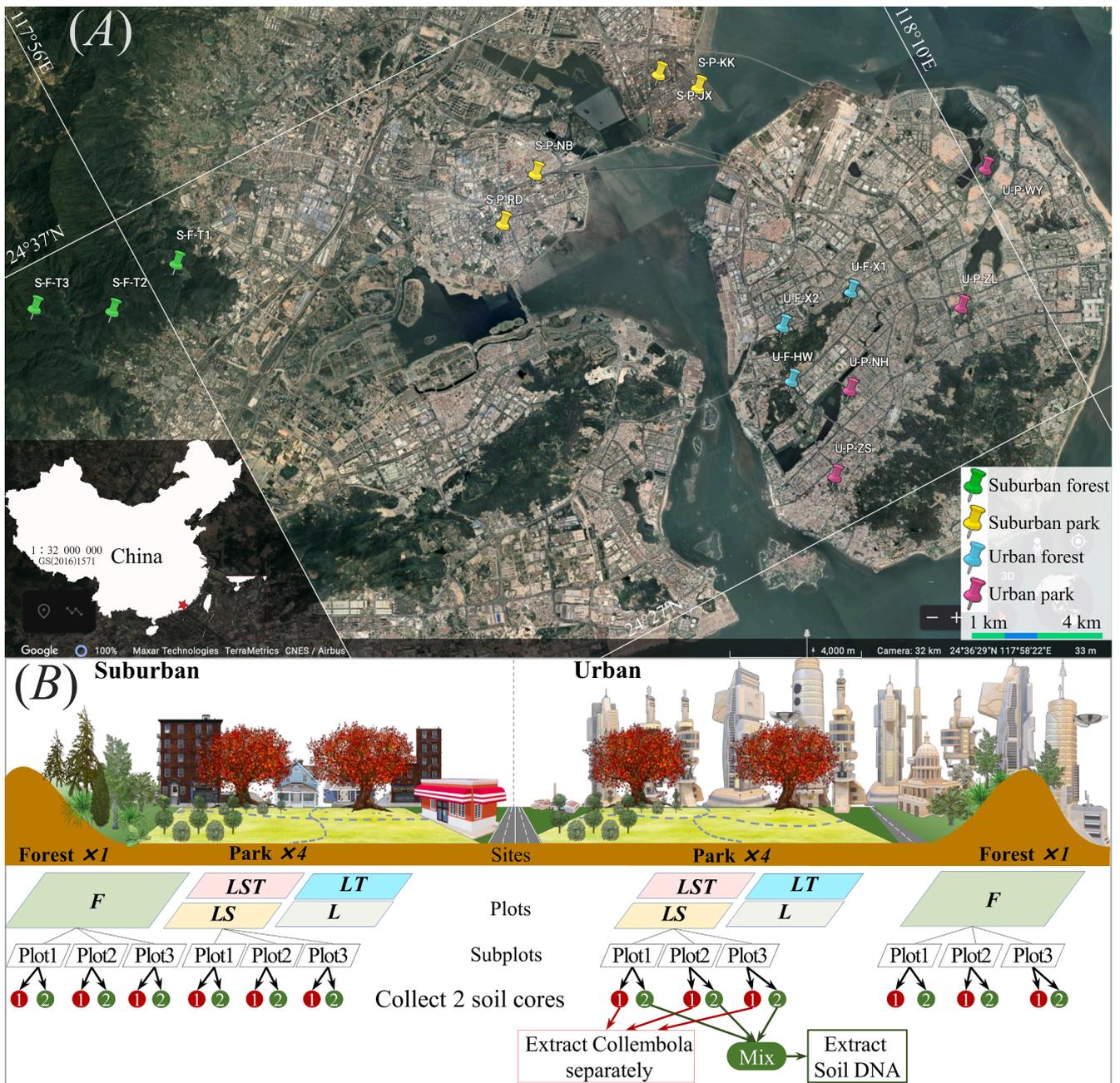


Fig. 1. Schematic overview of the site and plot location (A) and experimental set-up (B). Park-associated samples included four greenspace types, i.e. lawn (L), lawn with shrubs (LS), lawn with trees (LT) and lawn with shrubs and trees (LST). The map of China (NO. GS(2016)1571) was downloaded on <http://bzdt.ch.mnr.gov.cn/index.html>, the satellitic map of Xiamen city is a screen capture on Google Earth Pro (version 7.3.4.8248).

calculated as the sum of trait values of collembolan species in each sample (Gruss et al., 2019; Santorufo et al., 2014). High QBS-c values are representing high soil biological quality. Moreover, we calculated community-weighted mean (CWM) values of functional collembolan traits for each sampling site to account for differences in species abundance (Yin et al., 2020). CWM was calculated as.

$$CWM = \sum_{i=1}^n S_i \times X_i \quad (2)$$

with S_i the relative abundance of the i th species, X_i is the trait value of the i th species, and n the number of species in the community (Garnier et al., 2004). Functional richness, functional evenness, and divergence were calculated as described in Mason et al. (2005) and Villéger and Moullot (2008).

2.5. DNA extraction and high-throughput sequencing

Prior to DNA extraction, soil samples of the three replicate plots were thoroughly pooled (Fig. 1). Then, 10 g of soil was taken and homogenized. DNA was extracted from 0.5 g of the homogenized soil using the MP FastDNA spin kit for soil (MP Biomedicals, Solon, OH, USA) according to the manufacturer's instructions. Community composition and diversity of soil bacteria and fungi were analysed using high-throughput sequencing targeting the 16S rRNA gene for bacteria and the ITS1 region for fungi. The corresponding PCR amplification processes were performed using the 515F/907R and ITS1F/ITS2R primer pairs. The amplified products were purified and recovered by Qubit Fluorometer (version 3.0, Invitrogen, Carlsbad, CA, USA) for DNA concentration measurement and then sequenced on the Illumina NovaSeq PE250

platform (Illumina Inc., San Diego, CA, USA).

The obtained paired-end sequence data were processed with QIIME2 (version: 2018.11; <https://qiime2.org/>). The DADA2 pipeline was used for quality filtering, denoising, and chimera removal from the raw sequence data to obtain amplicon sequence variants (ASVs). The representative sequence and feature table files obtained after denoising were used for subsequent analysis. For taxon identification of bacterial and fungal representative sequences machine learning classifiers in QIIME2 were used to assign possible species annotations with the corresponding Greengene and Unite database.

2.6. Statistical analysis

All statistical analyses were performed using R statistical software version 4.0.4 (R Core Team, 2022). The diversity of collembolans, and read diversity of bacteria and fungi were calculated using the 'diversity' function (index = "shannon") in the 'vegan' package (Oksanen et al., 2022). The CWM of traits and functional diversity indices were calculated using the 'FD' package version 1.0–11 (Laliberté et al., 2022). The effect of urbanization (suburban and urban) and greenspace type (F, L, LS, LT, and LST) on soil physical (soil moisture content) and chemical parameters (pH, SOM, TC, TN C/N ratio, TP, and TS) as well as collembolan community structure (species abundance, richness, diversity), QBS-c, functional diversity indices (functional richness, evenness, divergence), and functional traits (life-form, dispersal ability, furca, body size, pigmentation, ocelli, and scale) were tested using linear mixed-effects models (LMM) with site and plot codes as the random effects; LMM analyses were conducted using the 'lmer' function in the 'lme4' package (Bates et al., 2022; Potapov et al., 2016a; Potapov et al., 2016b). Likelihood ratio tests ('lmerTest' package) were used to evaluate random effects by comparing the LMM with a linear model, which excluded random effects (Kuznetsova et al., 2020). The appropriate model was selected based on the lowest AIC (Akaike Information Criterion; (Remy et al., 2016; Riutta et al., 2012). Soil microbial communities were analysed by linear models as the soil samples of the three subplots were mixed prior to DNA extraction (for examples see Supporting information). For comparison of means, Tukey's honestly significant difference (HSD) tests at $p < 0.05$ were used as implemented in the 'multcomp' package (version 1.4–15).

Effects of greenspace type on collembolan community composition were analysed by non-metric multidimensional scaling (NMDS) using the 'vegan' package. Permutational multivariate analysis of variance (PERMANOVA) and 'betadisper' models (number of permutations = 1000) were further applied for testing differences in centroids and dispersion of collembolan communities between suburban and urban greenspaces (Anderson, 2005). Further, we used principal components analysis (PCA) to study the variation in soil physicochemical properties and functional traits of collembolan communities with urbanization and greenspace type using the 'prcomp' function in the 'factoextra' package (Kassambara and Mundt, 2020).

Structural equation modelling (SEM) was used for assessing relationships between urbanization, greenspace type, soil physicochemical properties, soil fungal and bacterial communities, and community and functional traits of collembolans as implemented in the 'psem' function in the 'piecewiseSEM' package (Lefcheck et al., 2020). The SEM included direct and indirect effects of urbanization, greenspace type (forest vs park-associated greenspaces), soil properties, and soil fungi and soil bacteria on the community structure (species richness) and functional traits of collembolans (Fig. S2). Five separate LMMs with study site and plot code as random terms (not included in models on the response of bacteria and fungi) were included into the stepwise structural equation model, where the response of the former model becomes a predictor in the next. Standardized indirect effects were calculated as the product of the standardized coefficients of the direct effects on the same effect chain. As the SEM coefficient requires trait independence, we transformed functional traits of collembolans and eight soil

physicochemical properties into two using PCA. Scores of principal components 1 and 2 (PC1 and PC2) were included in the SEM model to represent the response of functional traits of collembolans and soil physicochemical properties to urbanization and greenspace type, respectively (García-Palacios et al., 2016) in functional traits of collembolans PC1 represented most of the variation, whereas in physicochemical properties PC2 represented most of the variation between sites (Fig. S4A, Table S5).

3. Results

3.1. Soil properties

Soil physicochemical (moisture content, pH, and TP concentration) and soil biological properties (richness and read diversity of bacteria and richness of fungi) varied significantly with greenspace type, but not between urban and suburban areas (Table 2, 3 and S3). Soil moisture content was higher in LS and L than in LT, and soil TP concentrations were highest in LST (Table 2). Concentrations of TP was two times higher in park-associated greenspaces than in forest. Among soil biological properties, bacterial richness and read diversity also were higher in park-associated greenspaces than in forest, with these differences being more pronounced in suburban than in urban greenspaces (significant urbanization × greenspace type interaction; Table 3, S8). In contrast to bacterial richness and diversity, fungal richness and diversity were generally higher in LS and LT than in the other greenspace types.

3.2. Community structure of collembolan

A total of 2,066 collembolan individuals were extracted and identified belonging to 32 named species (including 3 new species) and 9 morphospecies identified at genus level from 10 families (Fig. S3, Table S6). Generally, the abundance of collembolans was two times higher in forests than in park-associated greenspace types (Fig. 2A), with the difference being particularly pronounced in Onychiuridae (Table S2). Further, the abundance of collembolans in the suburban region generally exceeded that in the urban region except for Isotomidae (Table S2). Across all sites, collembolan communities were dominated by *Coecobrya islandica* and *Folsomides parvulus*, which on average accounted for 21.3 % and 10.8 % of the total number of individuals, respectively. The abundance of *Cryptopygus thermophilus* and *Folsomides parvulus* were significantly lower in urban than in suburban greenspaces (Fig. S3A). Generally, the abundance of most collembolan species was lower in park-associated greenspaces than in the forest, with the decrease being most pronounced in *Folsomides parvulus*, *Rambusinella grinnelli*, and *Thalassaphorura* sp. n. (Fig. S3B).

Urbanization generally did not significantly affect the abundance, species richness, and diversity of collembolans (Table 4). However, collembolan community structure significantly differed among greenspace types, with abundance, richness, and diversity being significantly higher in forests than in most park-associated greenspaces. Richness and diversity of collembolans were highest in the suburban region, but the greenspace type × urbanization interaction was only marginally significant for collembolan diversity (Table 4, Fig. 2A-C).

Collembolan community composition also varied among greenspace types in both the urban and suburban region as indicated by differences in centroids and dispersion, but confidence ellipses overlapped in the NMDS space (Fig. 2D, E). Differences in community composition in the suburban region were more pronounced than in the urban region, with collembolan communities of forest and LST being significantly separated from those of the open greenspaces without trees (Table S3).

3.3. Functional traits of collembolans

Functional richness significantly varied with urbanization and greenspace type, but variations with greenspace type were much more

Table 2

Physicochemical and biological properties (means ± 1 SE) of soils from five vegetation types (F: forest, L: lawn, LS: lawn + shrub, LT: lawn + tree, and LST: lawn + shrub + tree) in suburban and urban regions of Xiamen city. Physicochemical properties: Soil moisture content, soil pH, total concentrations of soil organic matter (SOM), carbon (TC), nitrogen (TN), phosphorus (TP) and sulfur (TS); biological properties: Bacterial richness and diversity, and fungal richness and diversity. Values sharing the same letter do not differ significantly among greenspace types according to Tukey's HSD tests ($p < 0.05$).

Property	Indicators	Urbanization	F	L	LS	LT	LST	
Physical	Moisture (% dry weight)	Suburban	0.19 ± 0.01 ^{ab}	0.18 ± 0.01 ^{ab}	0.22 ± 0.02 ^a	0.13 ± 0.01 ^b	0.16 ± 0.02 ^{ab}	
		Urban	0.14 ± 0.02	0.22 ± 0.02	0.20 ± 0.03	0.16 ± 0.01	0.18 ± 0.02	
Chemical	pH	Suburban	4.53 ± 0.05 ^b	7.22 ± 0.10 ^a	7.15 ± 0.11 ^a	7.06 ± 0.21 ^a	7.16 ± 0.12 ^a	
		Urban	5.42 ± 0.35 ^b	7.05 ± 0.12 ^a	7.26 ± 0.13 ^a	7.27 ± 0.18 ^a	7.15 ± 0.17 ^a	
	SOM (g kg ⁻¹)	Suburban	30.77 ± 2.42	24.47 ± 3.67	17.69 ± 2.42	20.37 ± 2.78	29.34 ± 3.72	
		Urban	26.28 ± 2.91	27.14 ± 4.55	24.43 ± 2.05	28.03 ± 5.69	29.64 ± 3.46	
	TC (g kg ⁻¹)	Suburban	27.00 ± 1.83	22.35 ± 3.48	15.98 ± 2.43	18.45 ± 2.61	27.66 ± 3.49	
		Urban	22.42 ± 2.68	24.91 ± 4.33	22.74 ± 2.08	26.24 ± 5.62	27.54 ± 3.21	
	TN (g kg ⁻¹)	Suburban	2.00 ± 0.13 ^{ab}	1.87 ± 0.19 ^{ab}	1.48 ± 0.14 ^b	1.64 ± 0.15 ^{ab}	2.28 ± 0.21 ^a	
		Urban	2.17 ± 0.14	2.21 ± 0.33	2.05 ± 0.15	2.18 ± 0.35	2.31 ± 0.22	
	TP (mg kg ⁻¹)	Suburban	221.91 ± 14.58 ^c	622.43 ± 141.8 ^{ab}	492.45 ± 96.66 ^b	461.98 ± 73.15 ^b	912.79 ± 146.53 ^a	
		Urban	322.30 ± 61.03 ^b	904.56 ± 157.5 ^a	893.82 ± 59.30 ^a	897.09 ± 137.3 ^a	967.15 ± 93.35 ^a	
	TS (mg kg ⁻¹)	Suburban	33.73 ± 4.31 ^b	142.13 ± 17.82 ^a	150.12 ± 37.54 ^a	164.29 ± 15.82 ^a	161.30 ± 22.37 ^a	
		Urban	57.41 ± 6.42 ^b	222.48 ± 38.07 ^a	151.44 ± 14.98 ^a	183.47 ± 23.55 ^a	227.85 ± 52.73 ^a	
	Biological	Bacteria richness	Suburban	1276.33 ± 74.21 ^b	2096.50 ± 87.2 ^a	2167.50 ± 56.7 ^a	2308.50 ± 61.7 ^a	2348.25 ± 46.3 ^a
			Urban	1562.33 ± 123.4 ^b	2041.00 ± 12.5 ^a	1973.00 ± 54.5 ^a	2157.00 ± 25.1 ^a	1977.25 ± 12.8 ^a
Bacteria read diversity		Suburban	6.47 ± 0.06 ^c	7.01 ± 0.06 ^b	7.15 ± 0.04 ^{ab}	7.21 ± 0.03 ^a	7.23 ± 0.03 ^a	
		Urban	6.71 ± 0.10 ^b	7.12 ± 0.01 ^a	7.00 ± 0.04 ^a	7.13 ± 0.03 ^a	6.99 ± 0.01 ^a	
Fungi richness		Suburban	486.00 ± 20.66 ^b	329.50 ± 34.79 ^c	635.00 ± 30.11 ^a	501.50 ± 28.58 ^b	429.50 ± 31.31 ^{bc}	
		Urban	441.00 ± 36.09 ^b	420.25 ± 12.98 ^b	611.75 ± 19.23 ^a	553.50 ± 24.34 ^a	414.25 ± 16.63 ^b	
Fungi read diversity		Suburban	3.63 ± 0.17 ^b	3.26 ± 0.48 ^b	4.97 ± 0.12 ^a	4.22 ± 0.16 ^{ab}	3.81 ± 0.21 ^b	
		Urban	3.52 ± 0.33 ^c	3.91 ± 0.13 ^{bc}	4.46 ± 0.23 ^{ab}	4.79 ± 0.02 ^a	3.82 ± 0.29 ^{bc}	

Table 3

Linear mixed effects model table of F- and p-values on the effect of urbanization (S: suburban, U: urban) and greenspace type (F: forest, L: lawn, LS: lawn + shrub, LT: lawn + tree, and LST: lawn + shrub + tree) as well as their interaction on soil physicochemical [moisture content, total organic carbon (SOM), total carbon (TC), nitrogen (TN), phosphorus (TP), and sulfur (TS) concentration] and biological properties (bacteria richness, bacteria read diversity, fungi richness, and fungi read diversity). In case of a linear model, no random term is needed, in case of a linear mixed effect model (indicated with §) the study site and plot codes were used as random term. Significant effects ($p < 0.05$) are given in bold; DF, degrees of freedom. Greenspace types sharing the same letter do not differ significantly according to Tukey's HSD tests ($p < 0.05$).

Soil properties	Urbanization		Greenspace type		Interaction		
	DF=1		DF=4		DF=4		
	F	p	F	p	ANOVA (orders)	F	p
Moisture	0.56	0.45	3.66	0.01	LS ^a , L ^a , LST ^{ab} , F ^{ab} , LT ^b	1.90	0.12
pH [§]	0.78	0.41	13.11	<0.001	LS ^a , LST ^a , LT ^a , L ^a , F ^b	0.70	0.61
SOM [§]	0.17	0.69	2.28	0.12		0.62	0.66
TC [§]	0.17	0.69	2.56	0.09		0.83	0.53
TN [§]	0.69	0.44	2.64	0.08		0.82	0.54
N:C [§]	0.31	0.60	0.77	0.56		0.53	0.71
TP [§]	2.05	0.20	3.64	0.03	LST ^a , L ^a , LS ^a , LT ^a , F ^b	1.30	0.32
TS [§]	1.19	0.31	2.48	0.09		0.46	0.76
Bacteria richness [§]	0.94	0.37	8.54	0.001	LT ^a , LST ^a , LS ^a , L ^a , F ^b	1.55	0.24
Bacteria read diversity	0.51	0.48	12.99	<0.001	LT ^a , LST ^a , LS ^a , L ^a , F ^b	2.47	0.07
Fungi richness	0.21	0.65	7.60	<0.001	LS ^a , LT ^{ab} , F ^{bc} , LST ^{bc} , L ^c	0.62	0.65
Fungi read diversity	0.21	0.65	2.56	0.06		0.55	0.70

consistent and stronger than those with urbanization. In the urban region, functional richness was about 50 % lower than in the suburban region, further, it was much lower in park-associated greenspaces than

in forest (Fig. 3B). The other diversity indices, except functional evenness, varied significantly with greenspace type, however, the QBS-c, life form, and almost all morphological trait variations with greenspace type depended on urbanization (significant greenspace type × urbanization interaction; Table 4, Figs 3, S5). In suburban park-associated greenspaces, the QBS-c index and functional divergence of collembolan communities decreased in trend along with vegetation complexity, whereas functional richness and evenness increased. In the urban region, the QBS-c index and functional divergence of collembolan communities were similar among greenspace types being highest in L and lowest in F, but the greenspace type × urbanization interaction was only significant for the QBS-c index (Table 4, S8; Fig. 3A, D).

Confidence ellipses based on life-history, behaviour and morphological traits of collembolan communities separated the five greenspace types in the suburban region with the effect of greenspace type being significant in both the urban and suburban regions according to PERMANOVA (Fig. 3E, F). In the suburban region, collembolan communities in L, LS, and LT were characterized by long furca, fast dispersal, presence of scales as well as atmobiotic and epedaphic species separating the communities along PC1 from those in F and LST (Fig. 3E, S5). Further, collembolan communities in LS, LT, and LST were characterized by low number of ocelli, lack of pigmentation, and small body size separating them from those in F and L along PC2. Similarly, in the urban region, collembolan communities in L, LS, LT, and LST were characterized long furca, fast dispersal, presence of scales as well as atmobiotic and epedaphic species separating them from those in F along PC1 (Fig. 3F, S5). Further, collembolan communities in L were characterized by high number of ocelli and pigmentation separating them from those in F, LS, LT, and LST along PC2. Generally, the functional composition of collembolan communities in LS, LT, and LST were more homogeneous in the urban than in the suburban region (Fig. 3E, F, S5).

3.4. Structural equation models

Urbanization, greenspace type, physicochemical soil properties, and soil microbes accounted for c. 90 % of the variation in species richness and functional traits (PC1) of collembolans in the SEM (Fig. 4A). Urbanization ($r = -0.20$), greenspace type ($r = -0.32$), and the diversity of bacterial communities in soil ($r = -0.36$) showed significant direct negative effects on the species richness of collembolans ($p < 0.05$). By

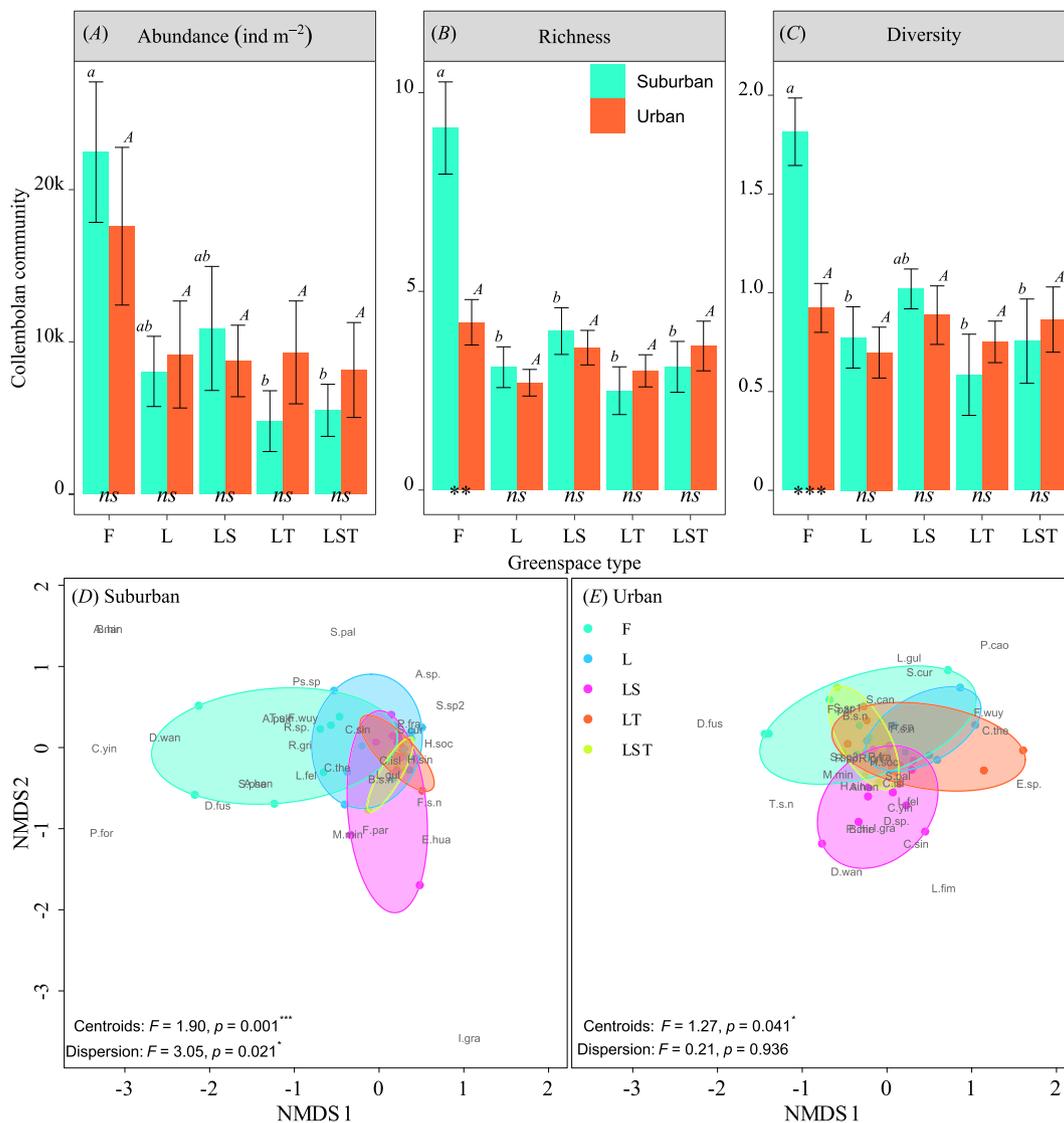


Fig. 2. Upper panel: Abundance (A), species richness (B) and species diversity (C) of collembolan in soil of five greenspace types (F: forest, L: lawn, LS: lawn + shrub, LT: lawn + tree, and LST: lawn + shrub + tree) in suburban and urban regions of the city of Xiamen. Asterisks at the bottom of the graphs (A-C) denote significant differences between the suburban and urban region, no significant effects are presented by *ns*. Letters (lowercase for suburban greenspaces and capital letters for urban greenspaces) above the boxplots indicate significant differences among the five types of greenspaces based on Tukey’s HSD tests ($p < 0.05$). Lower panel: Nonmetric multidimensional scaling (NMDS) ordination of collembolan community composition in five types of greenspace in the suburban (D) and urban region (E); ellipses represent 95 % confidence ranges; permutational multivariate analysis of variance (PERMANOVA) and Betadisper models are applied for testing differences in centroids and dispersion of collembolan communities among five greenspace types (see Table S3). For full species names see Table S6.

contrast, urbanization and greenspace type had non-significant direct effects on the functional traits of collembolans ($p > 0.05$). Urbanization ($r = 0.21$), but in particular greenspace type ($r = 0.76$), had positive direct effects on soil properties (PC2), with PC2 correlating positively with soil pH, and TP and TS concentrations, but negatively with SOM, and TC and TN concentrations (Table S5). Soil properties positively influenced the diversity of bacterial ($r = 0.26$) and fungal ($r = 0.38$) communities ($p < 0.05$). In addition, the diversity of fungal communities was the only factor significantly related to functional traits of collembolans ($r = -0.23$). Further, diversity of bacterial and fungal communities exerted negative indirect effects on the species richness and functional traits of collembolans, respectively. Greenspace type had the strongest indirect effect on collembolan species richness via bacterial diversity in soil (Fig. 4B). The indirect effect chain (from greenspace type to soil properties to bacterial diversity to species richness of collembolans) was the strongest chain of effects.

4. Discussion

We investigated the structure of collembolan communities in urban greenspaces and identified soil physicochemical and microbial properties driving the community and functional trait composition of collembolans in five greenspace types in urban and suburban regions. The results demonstrate significant direct effects of urbanization and greenspace types on soil properties and community structure of collembolans. Greenspace type was the main factor driving soil physicochemical properties and diversity of soil bacterial communities, and indirectly structured collembolan communities. However, the diversity of fungal communities was the main factor affecting the functional trait composition of collembolan communities.

Table 4

Linear mixed effects model table of F- and p-values on the effect of urbanization (suburban, urban) and greenspace type (F: forest, L: lawn, LS: lawn + shrub, LT: lawn + tree, and LST: lawn + shrub + tree) as well as their interaction on community structure (abundance, richness, diversity), QBS-c, functional diversity indices (functional richness, evenness, divergence), and functional traits (life-form, dispersal ability, furca, body size, pigmentation, ocelli, and scale) of collembolan. In case of a linear model, no random term is needed, in case of a linear mixed effect model (indicated with §) the study site and plot codes were used as random term. Bold values are significant ($p < 0.05$). Greenspace types sharing the same letter do not differ significantly according to Tukey's HSD tests ($p < 0.05$).

Parameters	Response	Urbanization		Greenspace types			Interaction	
		DF = 1		DF = 4		ANOVA (orders)	DF = 4	
		F	p	F	p			F
Community structure	Abundance [§]	0.01	0.98	3.39	0.04	F ^a , LS ^a , L ^{ab} , LST ^{ab} , LT ^b	0.76	0.57
	Richness [§]	0.39	0.55	4.33	0.02	F ^a , LS ^b , LST ^b , L ^b , LT ^b	1.01	0.44
	Diversity	2.25	0.14	7.99	<0.001	F ^a , LS ^{ab} , LST ^b , L ^b , LT ^b	3.06	0.02
QBS-c		2.41	0.12	6.71	<0.001	LS ^a , L ^{ab} , LT ^{bc} , LST ^c , F ^c	3.79	0.007
Functional diversity	Richness	8.52	0.01	4.46	0.01	F ^a , LST ^{ab} , LS ^{ab} , LT ^{ab} , L ^b	0.40	0.80
	Evenness	0.37	0.55	1.77	0.17		1.14	0.36
	Divergence	0.57	0.46	2.67	0.06		1.32	0.29
Functional traits	Life-form [§]	5.02	0.06	2.72	0.07		2.53	0.08
	Dispersal ability [§]	0	0.99	2.94	0.06		3.21	0.05
	Furca [§]	0.13	0.72	4.10	0.01	LS ^a , L ^{ab} , LT ^{ab} , LST ^b , F ^b	2.24	0.09
	Body size	0.08	0.77	0.92	0.46		3.82	0.006
	Pigmentation	3.53	0.06	3.19	0.02	L ^a , LS ^{ab} , LT ^{ab} , LST ^{ab} , F ^b	4.13	0.004
	Ocelli	0.1	0.76	3.75	0.01	L ^a , F ^a , LT ^{ab} , LS ^{ab} , LST ^b	0.27	0.90
	Scale	3.21	0.08	7.62	<0.001	LS ^a , LT ^{ab} , LST ^b , L ^b , F ^b	4.16	0.004

4.1. Changes in soil physicochemical properties and effects on collembolan

As indicated by our SEM, urbanization and greenspace type strongly affected physicochemical soil properties. Of the studied soil properties, soil pH best represented the differences in physicochemical properties between forest and park soils. In line with Mao et al. (Mao et al., 2014), we found that soils in park-associated greenspaces were alkaline ($pH > 7$), whereas those in forests were more acidic ($pH < 5.5$). Park management practices, such as the application of limed water for tree disease and pest control, or using Technosols, i.e., backfilled construction residues, excavated deep horizons or post-agricultural soils with or without topsoil addition, might explain the changes in soil pH (Vergnes et al., 2017). The difference in soil pH between forests and park-associated greenspaces may directly affect the community structure of collembolans since different species have different pH preferences (da Silva et al., 2016). For example, on average the abundance of *Coecobrya islandica*, *Cryptopygus thermophilus*, and *Folsomia* sp. n., preferring high pH soils, were two times higher in park-associated greenspaces than in forests, while species preferring low pH soils, such as *Brachystomellides* sp. n., *Rambusinella grinnellia*, and *Thalassaphorura* sp. n. were rare in park-associated greenspaces. Consequently, the sensitivity of collembolan species to acidic and alkaline soil conditions likely contributed to the observed differences in collembolan community composition between forests and park-associated greenspaces. This is in line with earlier studies highlighting soil pH as a significant driver of collembolan community composition (Ponge, 2000; Rzeszowski et al., 2017). However, soil pH may also indirectly influence collembolan communities by altering the structure and composition of soil microbial communities. Soil pH has been shown to be the most important environmental predictor of fungal richness on a global scale (Tedersoo et al., 2014). The increase in fungal diversity with soil pH presumably is associated with more diverse fungal food resources for collembolans in park-associated greenspaces. Supporting this conclusion, we found the relative abundance of Ascomycota and Basidiomycota, major food resources of many collembolan species (Endlweber and Scheu, 2007), to be increased in alkaline soils of park-associated greenspaces compared to those in forests. However, unexpectedly, the high fungal diversity in park-associated greenspaces did not significantly contribute to species richness of collembolans, but correlated negatively with collembolan functional traits, suggesting that higher diversity of fungi reduces trait diversity of collembolans, presumably by favouring fungivore species characterized by narrow trait spectrum.

Besides soil pH, soil TP concentrations were increased two to five times in park-associated greenspaces compared to forest soils. The increase in TP concentrations in park soils presumably was due to the application of fertilizers to urban greenspaces (Salomon et al., 2020). TP concentration in greenspace soils was one of the significant predictors of collembolan community structure, which is consistent with results of Rzeszowski et al. (Rzeszowski et al., 2017) investigating collembolan communities in urban lawns in Warsaw city, Poland. High concentrations of TP in park soils favoured particular generalist species, such as *Cryptopygus thermophilus*. The lack of response of collembolan communities to SOM, TC, and TN concentrations also is consistent with results (Rzeszowski et al., 2017). Concentrations of SOM, TC, and TN in Xiamen city are high and therefore carbon and nitrogen may not function as limiting factors for collembolans (Xu et al., 2009), suggesting that other factors such as TP are more important in structuring collembolan communities.

4.2. Effects of urbanization and greenspace type on collembolan community structure

Collembolan communities in park-associated greenspaces were more homogeneous than in forests and characterized by lower abundance, species richness and diversity. Seven collembolan species only occurred in forests but not in park-associated greenspaces including *Arrhopalites nanjingensis*, *Arrhopalites* sp., *Dicyrtomidae fusca*, *Paleonura formosana*, *Pseudosinella* sp., *Sminthurinus* sp.1., and *Sminthurinus* sp.3. On the other hand, nine species only occurred in park-associated greenspaces including *Homidia sinensis*, *Homidia socia*, and *Isotoma gracillisetia*, species known to be native and widespread in the study region (Shi and Pan, 2012). The other six species were only present at single or few greenspace sites, for example, *Lepidocyrtus fimetarius*, *Entomobrya huangi*, *Pseudachorutes cheni*, and *Drepanura* sp only occurred in few LS plots (with a total of 14, 4, 2, and 1 individual, respectively), and *Entomobrya* sp. and *Sminthurinus* sp.2 each occurred in a single LT plot (with 1 individual each). Some of these species have been reported previously from countries outside China, e.g., *Lepidocyrtus fimetarius* (Raghuraman and Singh, 2015), and therefore likely have been introduced with ornamental plants or exotic soil during park establishment.

Further, species richness and abundance of collembolans were highest in forests indicating that forests maintain higher diversity of collembolans than park-associated greenspaces. Similarly, da Silva et al. (da Silva et al., 2016) also found species and functional diversity of collembolans in forests to exceed that in other land-use types such as

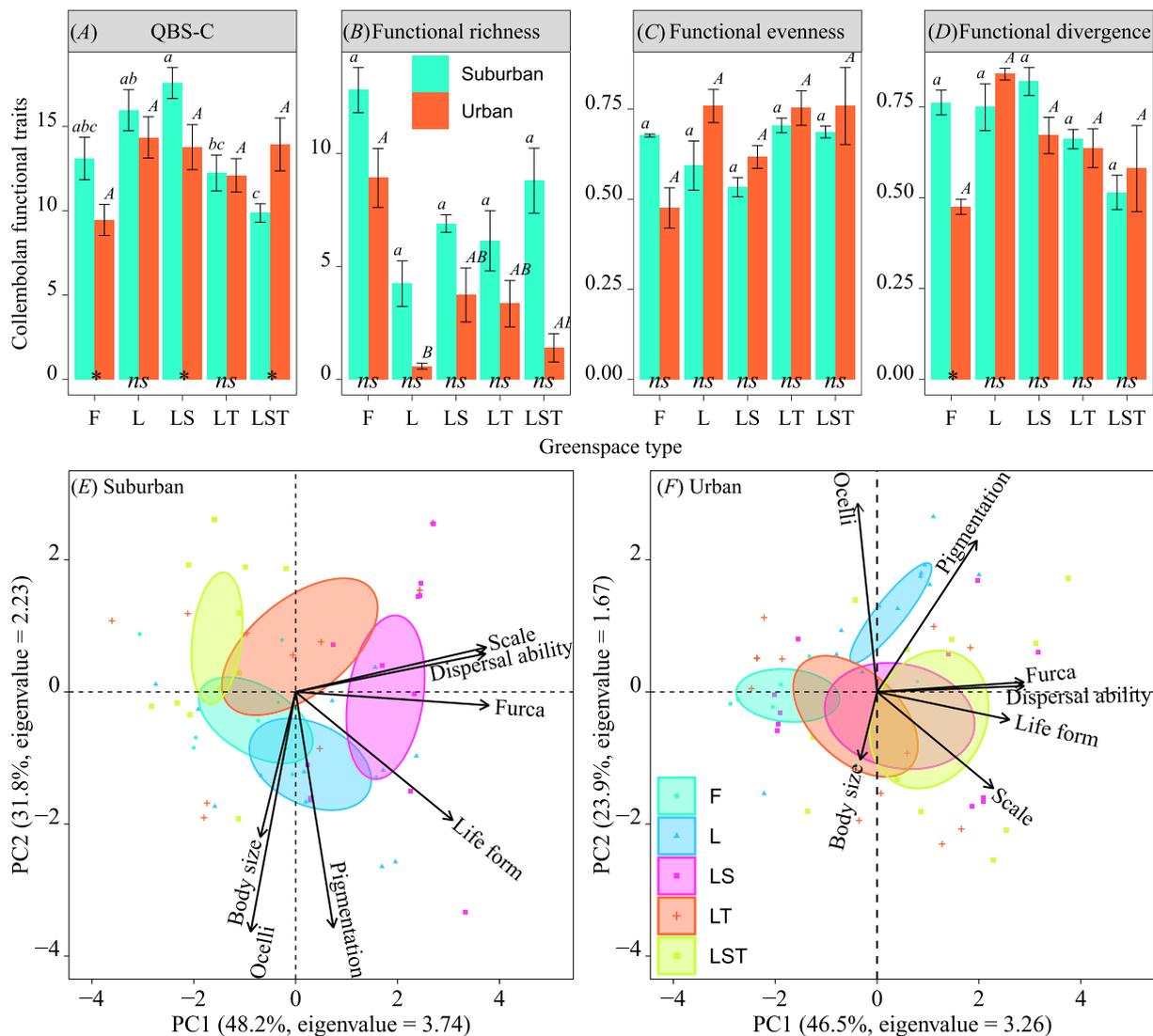


Fig. 3. Upper panel: Effects of urbanization and greenspace type on QBS-c index (soil biological quality index based on collembolan species) (A), and collembolan functional richness (B), functional evenness (C) and functional divergence (D). Asterisks on bottom of the graphs (A-D) denote significant differences between the suburban and urban region, no significant effects are presented by *ns*. Letters (lowercase for suburban greenspaces and capital letters for urban greenspaces) above the boxplots indicate significant differences among the five types of greenspaces based on Tukey’s HSD tests. Lower panel: Principal components analysis of collembolan functional traits in the suburban (E) and urban (F) region. Contribution of individual traits to the separation are indicated by arrows. Effects of greenspace type on functional traits was tested by PERMANOVA.

grassland and arable land. Despite the parks in Xiamen city are managed to increase vegetation diversity, and to increase the structural diversity of plants by planting turfgrass with shrubs and trees, our results suggest that the belowground animal community still is impoverished compared to forests. At least in part, this may be attributed to the lower diversity of plants in park-associated greenspaces compared to forests since plant diversity may improve the diversity and quality of litter, the main habitat and food resource of collembolan species (Hopkin, 1997). However, park management practices such as regular litter removal, and pesticide and fertilizer application likely also affect *Collembola* diversity in urban greenspaces (Heiniger et al., 2015).

Bacteria are important for collembolans, at least for most leaf litter consumers, as they are the main producers of enzymes for lignocellulose degradation in the collembolan gut and provide energy and nutrients for collembolans (Buse et al., 2014). Thus, bacterial communities might be another driving factor for the composition of collembolan communities. In our study bacterial communities (which positively correlated with greenspace type) had a negative direct effect on the collembolan communities. Our data also showed that the relative abundance of

Actinobacteria, Bacteroidetes, and Firmicutes were higher in park-associated greenspaces than in forests. These bacterial groups have previously been shown to possess lignocellulose-degrading activities (Okeke and Lu, 2011; Rossmassler et al., 2015). Associated with the increase in these bacterial communities in park-associated greenspaces, the abundance and diversity of epedaphic collembolan species, most of them detritivores, in urban parks were also increased including *Coecobrya islandica*, *Lepidocyrtus fimetarius*, and *Homidia sinensis*, whereas the diversity of the other collembolan species were all decreased.

4.3. Effects of urbanization and greenspace type on collembolan functional traits

Functional traits of collembolans are closely related to morphological, physiological, and phenological characteristics of species, and a promising tool for exploring the effect of environmental change on collembolan communities (da Silva et al., 2016; de Bello et al., 2010; Pey et al., 2014). Environmental filtering and biotic interactions are likely to result in the assembly of communities characterized by similar

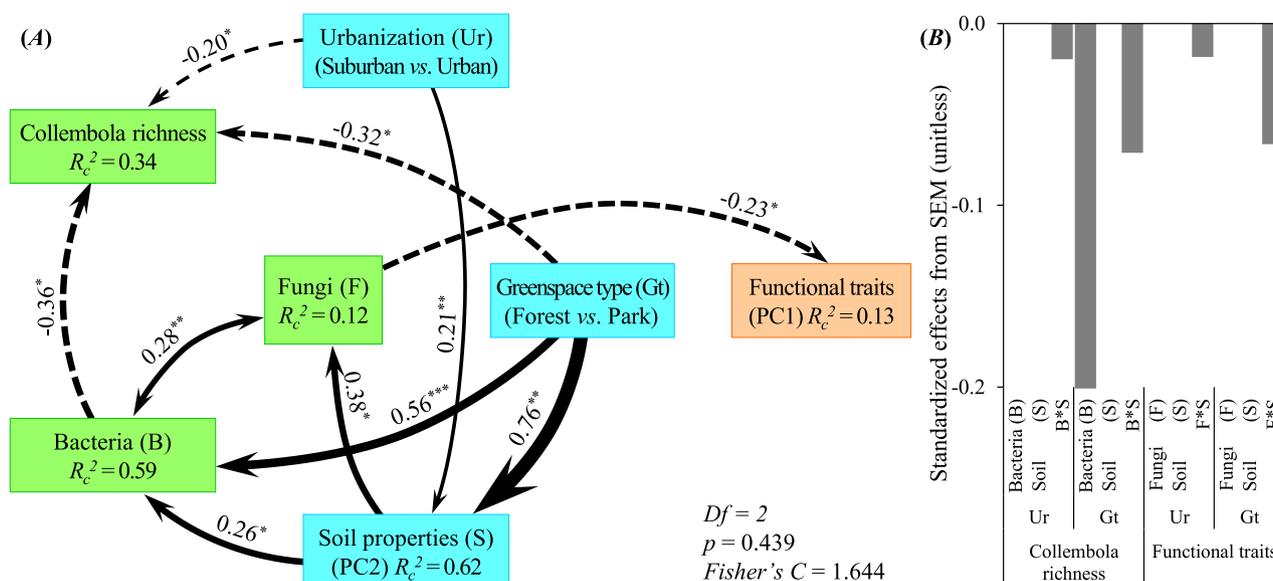


Fig. 4. (A) Structural equation model on the role of urbanization (Ur) and greenspace type (Gt), as driving factors of soil collembolan richness, soil properties, bacterial and fungal read diversity, as well as functional traits of collembolan. “Soil properties” and “Functional traits” are the PC2 and PC1 from two different PCAs (Fig. S4). Solid arrows denote positive and dashed arrows negative relationships. Arrows for non-significant paths ($p > 0.05$) have been omitted for clarity, but included in the model (see Fig. 2 for more details). The thickness of the paths is scaled based on the magnitude of the standardized regression coefficient given above the arrows; overall variance explained (conditional R^2) of response variables are given in the respective boxes. (B) Standardized indirect effects via bacteria (B), fungi (F), soil (S), B*S, and F*S as indicated by the SEMs. Note that some columns are omitted as any path with $p > 0.05$ was removed from the model.

functional traits (Pillar et al., 2009; Van den Brink et al., 2013). Previous studies on the response of collembolans to land-use intensification and urbanization showed that their response was related to shifts in functional traits related to both life-history, behaviour and morphology (de Bello, 2012; Potapov et al., 2022; Santorufo et al., 2015). In our study, epedaphic species with patterned pigmentation, well-developed furca, large number of ocelli, and fast dispersal increased in open greenspace habitats, and this is consistent with findings of (da Silva et al., 2016, 2012; Salmon and Ponge, 2012). By contrast, soil-dwelling euedaphic species with white pigmentation, absent furca and ocelli, and slow dispersal ability were more abundant in forest soils pointing towards feeding on resources deeper in the soil such as those associated with roots and indicating a more porous soil allowing to access these resources (Heiniger et al., 2015; Santorufo et al., 2014).

Functional diversity indices revealed that collembolan functional richness was reduced in the urban region and higher in forests than in park-associated greenspaces. As stressed above for collembolan diversity and abundance, low functional richness in the urban region is likely related to the more pronounced disturbance (leaf litter removal) and use of pesticides and other chemicals than in the suburban region. High functional richness in forests, on the other hand, again indicates that high diversity and heterogeneity of the soil and litter in forests improves habitat quality and food resources for collembolan (Krab et al., 2013). The QBS-c index, which reflects the environmental adaptability of collembolans (Gruss et al., 2019), differed between urban and suburban regions. Specifically, QBS-c decreased with vegetation complexity in suburban park-associated greenspaces, whereas it did not differ between urban park-associated greenspaces. A similar pattern was observed in functional divergence of collembolans. These findings suggest that human interference, such as urbanization and vegetation management, detrimentally affects habitat quality for collembolans (Salmon et al., 2019). According to our SEM findings, greenspace type did not directly affect functional traits of collembolans, but indirectly influenced functional traits via soil properties and fungal community composition. As discussed above, the high diversity of fungal communities in alkaline park-associated soils was associated with collembolans with lower functional trait values, reflecting that the dominating fungivore

euedaphic and hemiedaphic species are characterized by a narrow spectrum of traits (Berg and Bengtsson, 2007). Moreover, low amounts of plant residues in park-associated greenspaces caused by tree litter removal, mowing, or evergreen plants might inhibit the population growth of epedaphic species, resulting in a negative correlation between greenspace type and functional traits of collembolans (Youngsteadt et al., 2015). These results suggest that the high diversity of fungal communities selects for euedaphic and hemiedaphic species of narrow trait spectrum, such as species without pigmentation, ocelli, furca, and scales.

5. Conclusions

Both greenspace type and urbanization strongly affected the taxonomic and functional composition of collembolan communities. Changes in taxonomic composition were due to changes in soil properties and bacteria diversity resulting in taxonomic homogenization of collembolan communities in urban greenspaces. By contrast, changes in functional composition of collembolan communities were due to changes in soil properties and fungal community composition, with functional richness being particularly low in urban greenspaces. Generally, species and functional diversity of collembolans were much lower in park-associated greenspaces than in forests, indicating that the diversity and functioning of soil invertebrates may benefit from greenspace management targeting at establishing greenspace types resembling forests. The results highlight that both species and functional composition of soil invertebrates need to be considered for advancing greenspace management of urban regions towards increasing their role in biodiversity conservation and ensuring the provisioning of ecosystem services in the long-term.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2022.116175>. These data include Google maps of the most important areas described in this article.

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