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Original article

Bacterial communities are poorer at urban park entrances in Finland than Russian Tatarstan – Testing the core presumption of the biodiversity hypothesis

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ABSTRACT

Urban green spaces are known to host diverse microbiota and provide beneficial ecosystem services for humans. Several studies have shown that exposure to environmental microbiota is lower among urbanites in Western lifestyle countries than in the former Eastern bloc, which has been linked to differences in lifestyle and urban environmental factors. Surprisingly, no studies have yet investigated whether urban green spaces host similar microbiota between countries which have different socio-economical backgrounds. To fill this gap, we sampled surface soil microbiota at urban park entrances in four cities with similar climates in Finland and Russian Tatarstan. We hypothesized to find richer and more diverse microbiota, core microbiome, and indicator species assemblage in Russian Tatarstan. We also hypothesized that park maintenance practices are different between the two countries, which is connected to soil microbiota. The results confirmed all the hypotheses and since we evaluated park characteristics, we were able to connect the observed differences to park management practices. Switching from intensively manicured green surfaces to non-manicured and benign neglect may favor richer microbiota, including those connected to human health.

1. Introduction

Soils are recognized as one of the largest reservoirs of microbial diversity (von Hertzen & Haahtela, 2006). In highly urbanized environments, green spaces—such as parks and community gardens—host significantly richer and more abundant microbiota than surrounding grey infrastructure dominated by impervious surfaces like concrete and asphalt (Potter et al., 2023). The composition of microbial communities in urban green spaces is shaped by various factors, including vegetation type, soil characteristics, and environmental conditions (Fierer & Jackson, 2006; Baruch et al., 2020; Gill et al., 2020; Fritze et al., 2025). In contrast, grey spaces typically exhibit lower microbial diversity and abundance due to the lack of plant cover and organic matter that support microbial growth (Parajuli et al., 2018; Manninen et al., 2025). These differences in microbial diversity have important implications for urban ecosystem functioning such as nutrient cycling, decomposition, and maintaining soil health (Sun et al., 2023).

Microbial diversity within green spaces also varies depending on the design and management of green infrastructure (Gill et al., 2020). Over time, microbial communities have adapted to both past and present human disturbances (Liddicoat et al., 2019; Sinkkonen, 2022). In particular, the maintenance of urban grasslands—especially in parks—can influence soil organic matter dynamics and the structure of microbial communities (Thompson and Kao-Kniffin, 2019). Management practices vary across countries, often reflecting differences in socio-economic conditions, cultural values, and land-use traditions. For example, urban areas shaped by socialist urban planning in Eastern Europe the second half of the 20th century was designed with generously sized green open spaces integrated into the residential environment, aiming to fulfill the collective needs of the socialist society

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(Kristiánová, 2016). However, many of these areas experienced inconsistent maintenance, limited oversight, and varying social use (Kristiánová, 2016)—practices that still persist today and influence current ecological functioning, including the composition of microbial communities, and may contribute to differences compared to more managed green spaces in Western countries.

In addition to ecological functions, variations in urban microbiomes may have significant health implications, as different urban environments host distinct microbial communities that influence environmental microbiota exposure—an important determinant of human microbiome and immune regulation (Parajuli et al., 2020; Selway et al., 2020; Roslund et al., 2020, 2022). According to the Hygiene, the Old Friends, and the Biodiversity hypotheses, exposure to rich and diverse environmental microbiota is essential for health and a balanced development of immune regulation (Strachan, 1989; Rook et al., 2003; von Hertzen et al., 2011). In highly urbanized countries like Finland, immune-mediated diseases (IMDs) such as asthma, atopy, and allergies have increased for several decades, while their incidence has remained low in Russia and other Eastern Europe countries with different socio-economic and cultural backgrounds (Björksten et al., 1998; Kondrashova et al. 2012; Urban et al., 2020, Vartiainen et al., 2002; Kramer et al., 2009; Laatikainen et al., 2011). One of the most studied comparisons is the Finnish-Russian border, where populations share a similar genetic background but differ in disease prevalence (Haahtela et al., 2015). It has been suggested that greater exposure to environmental microbes play a key role in the lower incidence of IMDs in these areas (Seiskari et al., 2007; Kondrashova et al. 2012; Hanski et al., 2012, Haahtela et al., 2021). However, no studies have yet investigated whether urban green spaces host similar microbiota between countries which have different socio-economical backgrounds with different prevalence of IMDs. Especially environmental bacteria from phylum Proteobacteria have been recognized to be beneficial for immune regulation and has connected to e.g. lower prevalence of allergies (Debarry et al., 2007; Hanski et al., 2012; Fyhrquist et al., 2014; Roslund et al. 2022). In addition, exposure to soil microbial communities might be an important source of butyrate producing microbes, like Firmicutes, which are known to be beneficial for human gut (Parajuli et al., 2020; Brame et al., 2021). Both bacteria groups are widely present in different kinds of soil environments as they are involved in organic matter decomposing.

Since urban green spaces play a crucial role in maintaining soil health and providing health-beneficial exposure to environmental microbes and, given the lack of studies comparing microbial communities in urban green areas between these two regions, we focused on surface soil at urban park entrances—locations where most citizens pass through and are likely to pick up these microbes. We hypothesized that park management practices differ between countries, and as a result, we expected to find richer and more diverse environmental bacterial communities, characterized by a more abundant core microbiota and a higher number of indicator species specifically in Russian Tatarstan samples. We also hypothesized that the characteristics of the Finnish microbial communities reflect more challenging environmental conditions, likely due to differences in park management practices. Finally, we assumed that taxa associated with health are more numerous and richer in Russian Tatarstan than Finnish park entrances.

2. Methods

2.1. Soil sampling

Surface soil was collected at park entrances in the summer of 2021 (late June–early July) in Finland and Russian Tatarstan, two regions

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Fig. 1. Map of the study areas in Finland and Western Russia.

within a continental climate zone characterized by warm summers, cold winters, and equal precipitation (Fig. 1, SI1). While all cities share broadly similar climatic conditions, according to the Köppen classification Lahti, Kazan, and Zelenodolsk are categorized as Dfb (warm-summer humid continental climate), whereas Joensuu falls under Dfc (subarctic climate). Samples from Finland were collected from the cities of Lahti (~120 000 habitants) and Joensuu (~78 000 habitants) and from the Russian Republic of Tatarstan, from the cities of Kazan (~1 300 000 habitants) and Zelenodolsk (~101 000 habitants). For park selection, parks in the city centers were haphazardly divided into two groups and it was randomized which group was sampled in each city. In Zelenodolsk, all city center parks were sampled due to the low number of parks. Each soil sample (10–50 g) consisted of three subsamples of equal size collected from the main entrance of each park. If there were more than one main entrance, the southernmost entrance was sampled. Sampling spots were inside the park in the immediate vicinity of green space. At each entrance, the left and right corners and the middle spot (10 cm^2, depth 0–3 mm) were sampled. Stones, wood sticks and leaves were left aside or removed using sterile polyethene gloves, and the three subsamples were mixed before immediate freezing in dry ice and storing at −75 °C on the same day. Dirt was collected using a single-packed brand-new toothbrush and a sterilized teaspoon that was used to transfer dirt into a polyethene bag. The sampling consisted of a total of 49 park entrance samples (49 ×3 subsamples), 29 from Finland and 20 from Russian Tatarstan (SI2).

2.2. Plant diversity and park characteristics

Plant inventory was done in a 100-square-meter area in each park. The nearest green area at the main entrance was chosen and measured as the inventory area. If there were multiple main entrances, the area was measured from the southernmost entrance. The name of each plant found in the inventory area was recorded on the inventory form. If the plant could not be identified at the species level, it was recorded at the genus level. The abundance of each plant taxa was estimated at a scale from 1 to 5, where 1 =very rare (less than five individual plants), 2 =quite rare (more than five individual plants), 3 =two to three established plant populations/clones/patches, each of which contained at least five individuals/stems, 4 =more than three established plant populations/clones/patches, and 5 =very abundant (dominates the growing area). Dominating species are presented in SI3.

The background information for the whole park included the country, city, address, park name, whole park area (m^2), park age (<5, 5–10, 11–25, 25–50, 50–100, >100 years), sampling date, park description and park state (non-manicured and manicured %) (SI2). Land cover estimations for the whole park and the inventory area were recorded on the inventory form separately. These included the estimated frequency of gravel/sand, paved surface (tiles, concrete, asphalt), mowed lawn, moss coverage, dry meadow, meadow, tree canopy, ditch, flowers or other perennials, ornamental shrubs, berry bushes, rock, fruit trees, shoreline or wetland, forest stand, idle land and bare organic ground.

2.3. Soil properties analyses

Water content of the soil samples was determined by drying samples overnight in 105 °C and calculated by subtracting the weight of the dry soil from the weight of the moist soil and then dividing by the weight of the dry soil and transformed to percentages. Soil organic matter was determined from dried samples by burning in an oven at 550 °C for 4 h and then calculated by subtracting the weight of the burnt soil from the weight of the dried soil, then dividing by the weight of the burnt soil and transformed to percentages. Soil texture of all samples was categorized by particle diameter size (USDA) to mixture of fine and coarse sand with one exception which was classified as gravel with coarse sand.

2.4. Sample preparation for MiSeq sequencing

Bacterial communities in the soil samples were analyzed using Illumina MiSeq 16S rRNA gene metabarcoding with a read length of 2 × 300 bp using a V3 reagent kit. To extract the DNA, the PowerSoil® DNA Isolation Kit from Qiagen (Hilden, Germany) was utilized, following the manufacturer's standard protocol. The quality of the extracted DNA was assessed by agarose gel electrophoresis (1.5 %) and quantified using the Quant-iT™ PicoGreen® dsDNA reagent kit from Thermo Scientific (MA, USA). The DNA concentration for each sample was adjusted to 0.4 ng/µl. The V4 region within the 16S rRNA gene was amplified in PCR (three replicates from each sample) using 505 F and 806 R primers (Caporaso et al., 2012). Negative and positive controls were included during the sampling process. Sterile water was used as negative control and a mock community (ZymoBIOMICS) as positive control. The PCR products were purified using Agencourt AMPure XP solution (Beckman) (Greenwald et al., 2019).

2.5. Bioinformatics

The sequencing data obtained from the soil samples were processed and analyzed using Mothur (version 1.48.0), following the protocol described by Schloss et al. (2009). The sequence processing protocol mainly followed the Miseq standard operating procedure as suggested by Kozich et al. (2013). To ensure data quality, the sequences were trimmed and screened to remove any mismatches to the primers, ambiguous bases, and homopolymers longer than 8 bp. Bacterial sequences were aligned against the SILVA reference (version 132) (Quast et al., 2013). To minimize sequencing errors, preclustering was implemented and similar sequences were grouped into amplicon sequence variants (ASV) (Huse et al., 2010). Chimeric sequences were identified and removed using the VSEARCH algorithm (Rognes et al., 2016). Sequences classified as Chloroplast, Mitochondria, unknown, Archaea, and Eukaryota were excluded from further analysis. ASVs with low abundance (≤10) were removed from the sequence data.

2.6. Statistics

Statistical tests were done with the R version 4.3.1 using RStudio IDE ('R Core Team, 2023; RStudio Team, 2020). Differences of park characteristics between countries were tested by Student's *t*-test or Wilcoxon rank-sum test depending on normality of the data. Normality of the data was determined using the Shapiro-Wilk test (Shapiro and Wilk, 1965). Correlations between characteristics were calculated using Spearman's rank correlation with function *cor*. Whittaker's beta diversity index was calculated to describe beta diversity of plant communities for each sampling site.

For the bacterial data, the *phyloseq* package (McMurdie and Holmes, 2013) was used. The Shannon and Simpson diversity indices and observed richness were determined using the function *estimate_richness* for phyla, class, order, family and genus taxa. Data was normalized and transformed by using the centered log ratio (clr) method (Aitchison, 1982). The urban park surface soil bacterial communities were studied with the permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2017) with function *adonis2* (McArdle and Anderson, 2001) in the *vegan* package (Oksanen et al., 2022), where countries, cities, soil moisture content, soil organic matter content, plant beta diversity, plant species richness and Shannon diversity, tree canopy cover, park age and unmanicured share of park were used as predictors. In addition to PERMANOVA, the analysis of multivariate homogeneity of groups dispersions (PERMDISP, function *betadisper*) followed by a permutation test with function *permutest* (Zhu et al., 2007) and Tukey's honestly significant difference (HSD) test were used to determine differences between cities. Principal coordinate analysis (PCoA) with the Euclidean distance was used to visualize the differences in the bacterial community composition. Differences in ASV-level alpha diversity between cities within each country were tested using Student's *t*-test or Wilcoxon rank-sum test.

Linear mixed models or generalized linear mixed models (LMM/GLMM) were constructed to analyze the differences in the bacterial communities in urban park soils between countries using function *lmer* in the *lme4* package (Bates et al. 2015). Bacterial alpha diversity and relative abundance were used as dependent variables, country (Finland/Russia) as a repeated measure factor, and the cities as a random factor. To test the effects of soil organic matter, soil moisture content, the proportion of unmanicured park areas, plant richness, park age, and tree canopy coverage on bacterial alpha diversity and relative abundances, linear models and generalized linear models with negative binomial (for count data) and Tweedie (for continuous data) distributions using the *MASS* and *statmod* packages (Venables and Ripley, 2002; Giner and Smyth, 2016) were used. In GLM's, the McFadden pseudo R^2 was used as a measure of model fit (McFadden, 1974). To control the false discovery rate (FDR), the Benjamini–Hochberg correction (q-value) was performed for the statistical tests in which multiple comparisons were used (Benjamini and Hochberg, 1995). To exclude the potential influence of geographic distance, we repeated the regression models using only the Russian Tatarstan samples.

Indicator species analysis was done to at the ASV level using the R package *indicspecies* (De Cáceres and Legendre, 2009), and the core microbiome was determined with a 75 % prevalence threshold and a detection rate of 0.001 % using the R package *microbiome* (Lahti and Shetty, 2023). Co-occurrence networks were constructed at the genus level for both groups, Finland and Russia, using the *cooccur* package (Griffith et al., 2016) and visualized using package *visNetwork* (Almende, 2019). The co-occurrence network analysis calculates the observed and expected frequencies of co-occurrence between each pair of taxa. It examines the relationships and interactions between different genera within the samples. The analysis provides information on the number of edges, which represent the connections between bacterial genera, and the number of nodes, which represent individual genera within the network. These metrics help to understand the complexity and patterns of microbial interactions within the studied ecosystems.

3. Results

3.1. Park characteristics differed between countries

In Russian Tatarstan, there was higher percentage of unmanicured urban green spaces ($p = 0.026$). Also, soil organic matter (SOM) content was higher in Tatarstan urban green parks entrances compared to Finnish ones ($p = 0.0098$) and it was positively correlated with unmanicured share of urban green spaces ($p = 0.017$). Plant richness ($p = 0.338$), plant Shannon diversity ($p = 0.48$) soil moisture content ($p = 0.95$) and tree canopy coverage ($p = 0.1$) did not significantly differ between countries. In Finland, the parks were generally older than those in Russian Tatarstan.

3.2. Beta diversity of soil microbial communities differs between Finnish and Russian park entrances

Bacterial community compositions differed at the amplicon sequence variant (ASV) level and all other taxonomic rank levels in urban park surface soil between Finland and Russian Tatarstan (Table 1A). When both countries (Finland/Russia) were plotted together using the principal coordinate analysis (PCoA), the bacterial community compositions at park entrances differed from each other (Fig. 2A). PERMANOVA also revealed that the city, unmanicured share of the parks and soil organic matter content (SOM) affected the bacterial community composition at the ASV level (Table 1B, Fig. 2B). Analysis of multivariate homogeneity of groups dispersions (PERMDISP) showed no differences, which indicates that differences observed in PERMANOVA are likely due to true shifts in bacterial composition rather than disparities in the variability of the communities within each city. While PERMANOVA detected an overall effect of city, Tukey's HSD tests for pairwise city comparisons were not significant (SI4).

Table 1
Differences in the bacterial community composition in the surface soil bacteriota of urban park entrances A) at all taxonomic levels using country (Finland/Russia) as the predictor, and B) with other predictors at ASV level. Method: PERMANOVA. R^2=coefficient of determination, F=dispersion, p = significance, q=Benjamini–Hochberg critical value.

	F	R^2	p-value	q-value
A) Taxonomic level				
Phylum	5.480	0.10	**0.001**	**0.002**
Class	5.275	0.10	**0.001**	**0.002**
Order	7.193	0.13	**0.001**	**0.002**
Family	7.573	0.14	**0.001**	**0.002**
Genus	5.985	0.11	**0.001**	**0.002**
ASV	5.755	0.11	**0.001**	**0.002**
B) Predictor				
City	2.807	0.16	**0.001**	**0.002**
Unmanicured (%)	3.539	0.07	**0.001**	**0.002**
Soil organic matter (%)	1.115	0.05	**0.0002**	**0.002**
Soil water content (%)	1.524	0.03	**0.018**	**0.031**
Plant richness	1.341	0.03	0.068	0.096
Plant Shannon index	0.873	0.03	0.092	0.111
Plant Beta diversity (βw)	1.295	0.03	0.083	0.109
Paved surface (%)	1.359	0.03	0.066	0.096
Gravel/sand (%)	0.855	0.02	0.763	0.763
Tree canopy cover (%)	1.024	0.02	0.384	0.408
Park age	1.083	0.04	0.234	0.265

3.3. Soil bacterial richness and diversity are higher in Russian park entrances than in Finnish

The average richness of ASVs (mean ± standard deviation) was higher in Russian Tatarstan cities' dirt samples (Kazan 2249 ± 510, Zelenodolsk 2332 ± 301) as compared with Finnish ones (Joensuu 1903 ±417, Lahti 1944±209). No significant differences in bacterial alpha diversity, measured by observed species richness, Shannon, and Simpson diversity indices, were observed in the intra-country comparisons between Lahti and Joensuu in Finland, or between Kazan and Zelenodolsk in Tatarstan (SI4B). Bacterial richness was higher in Russian Tatarstan urban park entrances at the order, family, genus, and ASV levels. The Shannon diversity of the surface soil bacteriota in urban parks in Tatarstan was higher at the family level. Before the Benjamini–Hochberg correction (q value), the difference in the Shannon diversity was significant also at the order and genus levels (Fig. 3, SI5A). After the p-value adjustment, there were no differences in the Simpson diversity between Finland and Russian Tatarstan.

The Shannon diversity of the soil bacteriota were higher in the Russian Tatarstan urban parks than in the Finnish parks for the phyla Proteobacteria, Firmicutes, Verrucomicrobia and Planctomycetes. Only Cyanobacteria had a higher Shannon diversity in Finnish urban park surface soil when compared to Russian Tatarstan urban parks (Fig. 4A, SI5B). At the class level, Shannon diversity was higher in Russia for Blastocatellia subgroup 4, Deltaproteobacteria, Thermoleophilia, Bacilli, Verrucomicrobiae, Gammaproteobacteria, and Acidobacteria subgroup 6. Only for the class Oxyphotobacteria, which belongs to the phylum Cyanobacteria, the Shannon diversity was higher in Finland (Fig. 4B, SI5B).

In Russia, the observed bacterial richness was higher at the phylum level for Actinobacteria, Chloroflexi, Verrucomicrobia, and Planctomycetes (Fig. 4C, SI5C). As with the Shannon diversity, only the phylum Cyanobacteria was richer at the Finnish urban park entrances than in the Russian ones. At the class level, richer bacterial classes in Russia were Deltaproteobacteria, Theremoleophilia, Chloroflexia, Verrucomicrobiae, and Acidobacteria subgroup 6. In accordance with the diversity results, only the class Oxyphotobacteria had a higher bacterial richness

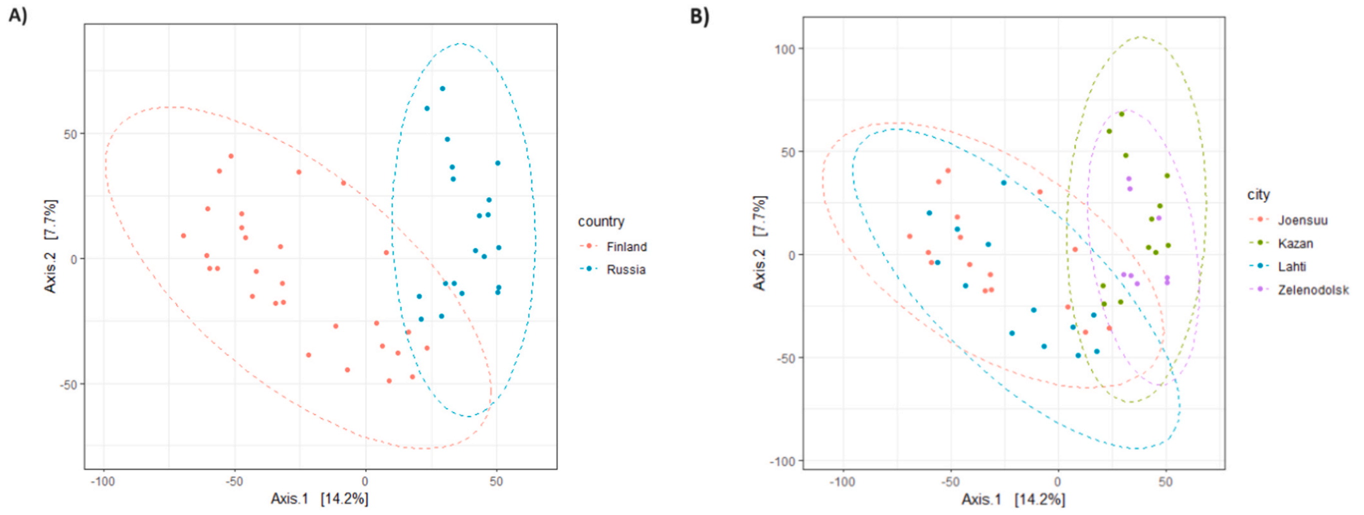

Fig. 2. Principal coordinate analysis (PCoA) plots representing differences in the composition of bacterial communities in urban park dirt (A) between Finland and Russia and (B) between cities at amplicon sequence variant (ASV) level. Significance was determined by PERMANOVA (Table 1).

at the class level in Finland (Fig. 4D, SI5C).

When alpha diversity was observed at family level between countries, bacterial taxa *Xanthomonadaceae* (phylum Proteobacteria), *Acetobacteraceae* (phylum Proteobacteria), *Sphingobacteriaceae* (phylum Bacteroidetes), *Blastocatellaceae* (phylum Acidobacteria), *Sphingomonadaceae* (phylum Proteobacteria) and *Nocardioidaceae* (phylum Actinobacteria) had higher Shannon diversity in Russian Tatarstan urban park entrances. In Finland only the family *Microbacteriaceae* (Actinobacteria) had higher Shannon diversity. The Simpson diversity between countries gave similar results excluding the family *Nocardioidaceae.* Also, *Sphingobacteriaceae* and *Xanthomonadaceae* had higher observed richness in Russian urban parks surface soil (Fig. 5). At genus level, unclassified *Burkholderiaceae* genus (phylum Proteobacteria) had higher observed richness ($p < 0.0001$, $q=0.0001$), Shannon ($p = 0.001$, $q=0.01$) and Simpson diversity ($p = 0.007$, $q=0.07$) and unclassified Intrasporangiaceae (phylum Actinobacteria) higher observed richness ($p = 0.007$, $q=0.02$) in Russian urban parks surface soil.

3.4. *Soil bacterial relative abundances vary between Finland and Russian Tatarstan*

Multiple bacterial taxa's relative abundances significantly differed between countries. For example, at higher taxonomic levels, patterns in relative abundance were consistent with those observed for alpha diversity: Verrucomicrobiae, Thermoleophilia, and Acidobacteria subgroup 6 were more abundant in Russian Tatarstan (Fig. 6A), whereas Cyanobacteria and Oxyphotobacteria were more abundant in Finland (Fig. 6B). Also, Gemmatimonadetes had higher relative abundance in Finland. Similar trends were observed at lower taxonomic levels. At genus level, the clearest difference between these relative abundances is that genera of group Cyanobacteria have high presence in those bacterial taxa which were higher in Finland than in Russia. Instead in those genera which had higher relative abundances in Russia, Cyanobacteria genera were absent which is consistent with our alpha diversity results.

3.5. *Park characteristics shape bacterial alpha diversity and relative abundances in surface soil of the urban parks*

Based on regression models the amount of unmanicured share of green spaces affected negatively to observed species richness and Shannon diversity of phylum Cyanobacteria and class Oxyphotobacteria which had higher diversity in Finnish parks, while on the contrary manicured share affected positively to alpha diversity of these bacterial taxa. Instead, the unmanicured share positively affected alpha diversity of class Thermophilia, class Acidobacteria subgroup 6, and the total Shannon and Simpson diversity at the order and family levels, all of which were significantly higher at the entrances of Russian Tatarstan urban green parks. Additionally, the unmanicured share seemed to increase the relative abundances of several taxa more abundant in Russian Tatarstan and decrease Cyanobacteria and Oxyphotobacteria, which were more abundant in Finland, although these effects were not significant after p-value adjustment.

Soil organic matter (SOM) content had positive effect to observed species richness of class Thermoleophilia and Acidobacteria subgroup 6 and also to the Shannon and Simpson diversity of family *Xanthomonadaceae* and unclassified *Burkholderiaceae* genus which all were higher in Russian Tatarstan (Table 2, Figs. 4 and 5). Instead, SOM content had negative effects to observed species richness of phylum Cyanobacteria and class Oxyphotobacteria. SOM content also had negative effect to relative abundance of multiple taxa belonging to phylum Gemmatimonadetes, which were more abundant in Finnish parks.

Plant diversity had positive effect on Simpson diversity of genus Methylobacterium, which is known to have role in plant growth promotion (Jinal et al., 2020). Instead, plant richness had negative effect on alpha diversity of family Beijerinckiaceae and genus Sphingomonas (Table 2C). Soil moisture content, park age or tree canopy coverage had no effect on soil bacterial alpha diversities or relative abundances. Models analyzed with the Russian sample set alone, to exclude geographic influence, showed similar trends to the full dataset (SI9).

3.6. *Indicator species and core microbiome are twice as rich at Russian Tatarstan urban park entrances*

The indicator species analysis revealed that 2202 ASVs were indicators of Russian park entrances and 1147 ASVs were indicators of Finnish park entrances (SI6). Differences were also evident in the number of indicative ASVs when observed at the phylum level. The number of indicative ASVs was clearly higher in urban park dirt in Russian Tatarstan than in Finland for the phyla Proteobacteria, Actinobacteria, Bacteroidetes, Acidobacteria, Chloroflexi, Verrucomicrobia, Planctomycetes, and Firmicutes. In Finland, there were more indicative ASVs in the phyla Cyanobacteria, Armatimonadetes, and Deinococcus-Thermus. Although the total number of these indicative ASVs were rather low, the difference between the countries was still considerable (Table 3).

When the core microbiome was determined with a 75 % prevalence

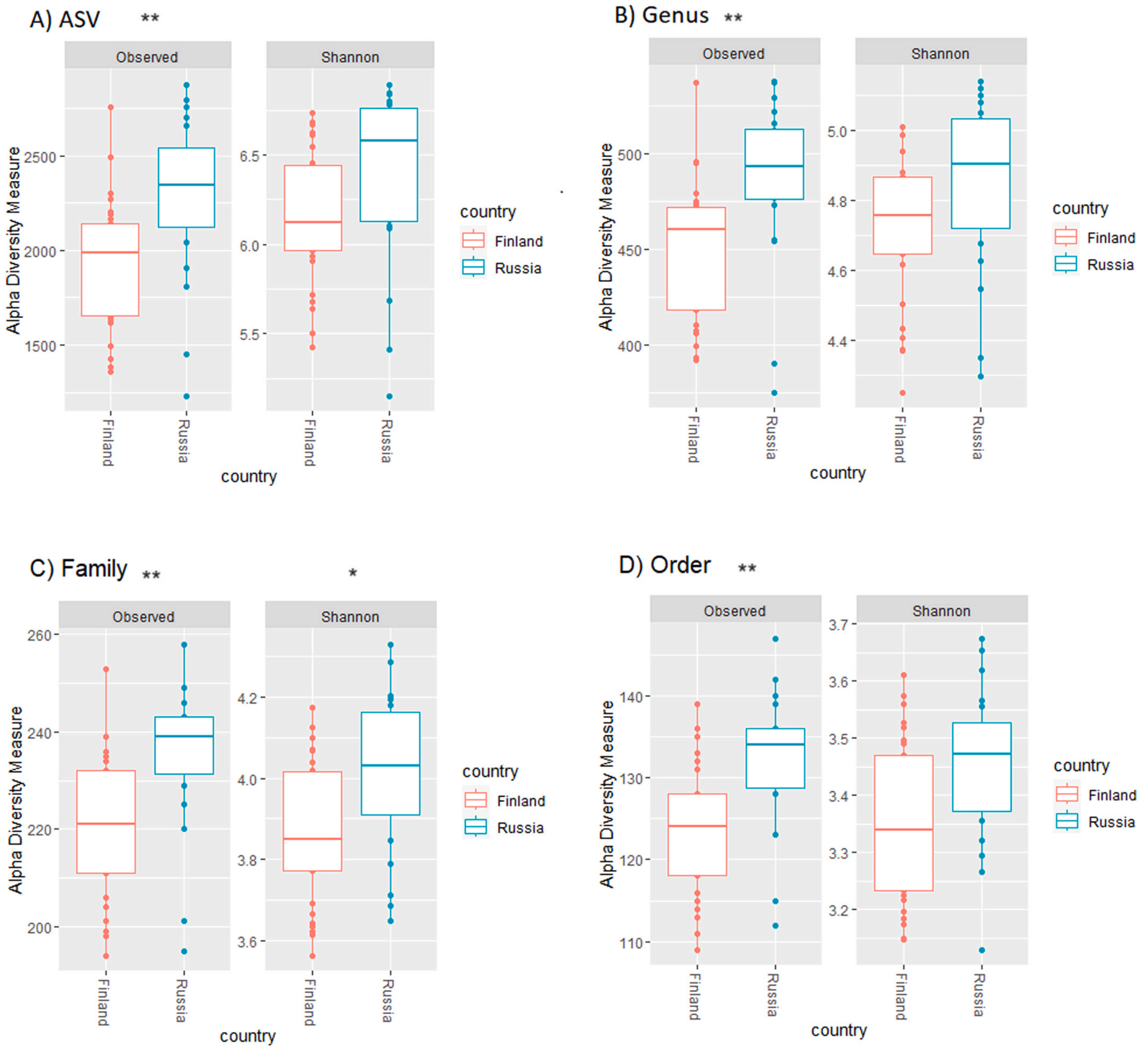

Fig. 3. Observed richness and the Shannon diversity of soil bacteriota were higher in the Russian urban park entrances (turquoise) than in the Finnish urban park entrances (red) at the (A) ASV, (B) genus, (C) family, and (D) order levels. Significance codes after Benjamini-Hochberg correction: *q< 0.05, **q< 0.01 and ***q< 0.001.

threshold and a 0.001 % detection rate, the core microbiome of the park entrance dirt in Russia was richer than in Finland. Russian core microbiome consisted of 294 ASVs, of which 206 occurred only in the Russian core microbiome, while in Finland these numbers were 179 and 91 ASVs, respectively. Based on this, the core soil microbiome that occurred in Russia only (206 ASVs) was twice as rich as in Finland (91 ASVs). In the surface soil core microbiome in Russia, there were over 30 % more Proteobacteria than in Finland and the number of Actinobacteria was up to 60 % higher in Russia than in Finland. At the class level, the difference was especially visible in Alphaproteobacteria, which were present 40 % more in the Russian than in the Finnish core microbiome. The number of core Gammaproteobacteria ASVs was also more than 20 % higher in Russian Tatarstan than in Finland (SI7).

The Russian core microbiome consisted of a total of 15 phyla while the Finnish core microbiome covered 11 phyla. There were five phyla that occurred only in the Russian soil core microbiome: Verrucomicrobia, Armatimonadetes, Nitrospirae, BRC1, and FBP candidatus. Correspondingly, phylum Deinococcus-Thermus was only present in the soil core microbiome of Finnish parks. At the class level, the core microbiome in Russia consisted of 30 classes and in Finland 19 classes. There were 11 classes which were only present in the core microbiome of Russian park dirt, which were Armatimonadia, Bacilli, Ignavibacteria, Nitrospira, Planctomycetacia, Rubrobacteria, Thermoanaerobaculia, TK10, Verrucomicrobiae, and two unclassified classes that belonged to the phyla BRC1 and FBP. There was only one class, Deinococci, which was present in the Finnish core microbiome only (SI7).

3.7. Soil bacterial communities in Finnish urban park entrances form more complex networks

Co-occurrence network analysis revealed that the dirt microbiome of Finnish parks had 6324 edges formed by 500 bacterial genera nodes;

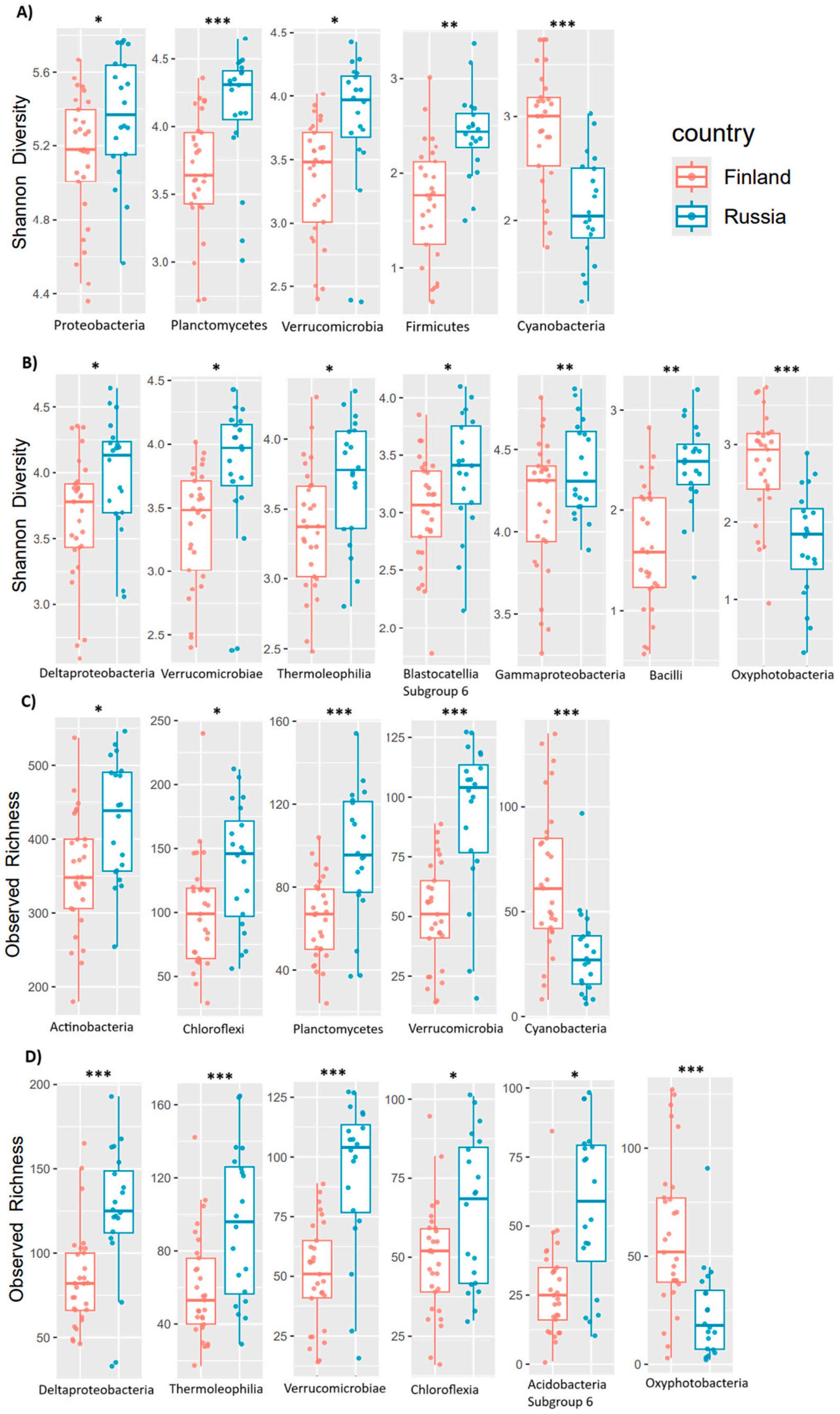

Fig. 4. Differences in the Shannon diversity (A=phylym & B=class) and the observed richness (C=phylum & D=class) between Russian (blue) and Finnish (red) urban green space surface soil bacteriota. Significance codes after Benjamini-Hochberg correction: *q< 0.05, **q< 0.01 and ***q< 0.001. Boxplots show medians (thick line), upper and lower hinges (box), values 1.5 times the interquartile range (whiskers).

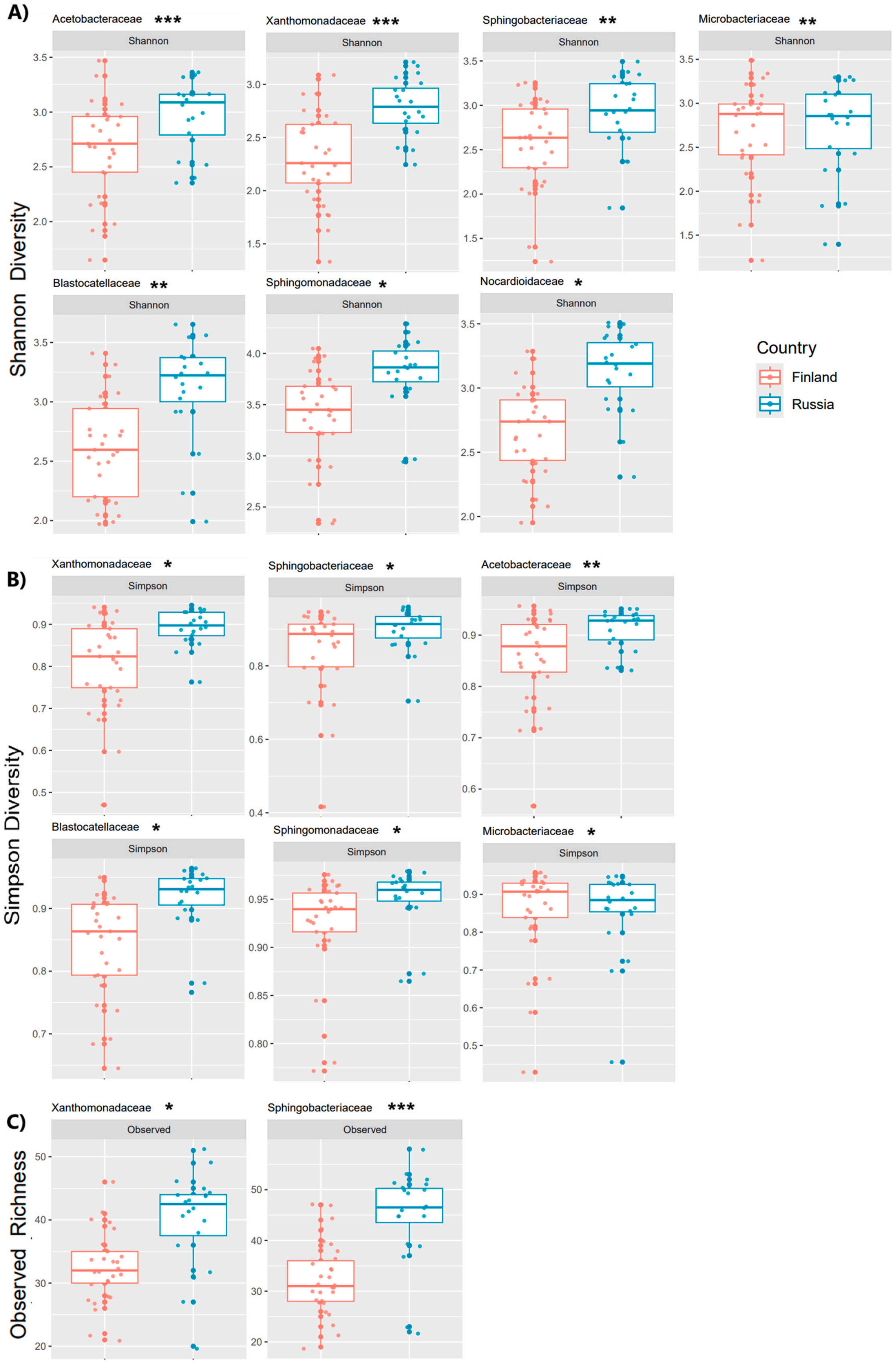

Fig. 5. Differences in A) the Shannon diversity, B) the Simpson diversity and C) the observed richness at family level between Russian (blue) and Finnish (red) urban green space surface soil bacteriota. Significance codes after Benjamini-Hochberg correction: *q< 0.05, **q< 0.01 and ***q< 0.001. Boxplots show medians (thick line), upper and lower hinges (box), values 1.5 times the interquartile range (whiskers).

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Fig. 6. Relative abundances (clr) of soil bacterial taxa which were A) higher in Russian (blue) and B) higher in Finnish (red) urban green space entrances. Results with q< 0.05 are presented.

61 % of the edges were positive and 39 % negative. In Russian Tatarstan park dirt, bacterial genera formed a network containing 4032 edges between 481 bacterial genera nodes; 68 % of the edges were positive and 32 % negative. Based on this, the bacteria in the dirt of Finnish parks form 57 % more connections with each other compared to the dirt bacteria of Russian Tatarstan parks (SI8). In addition to one large network, the bacteria in Russian Tatarstan urban park dirt form more small, independent networks than bacteria in the dirt at Finnish park entrances (Fig. 7).

Table 2

Regression model (LM & GLM) results of A) unmanicured share (%) of urban green spaces and B) soil organic content C) plant richness on bacteriota of urban green space surface soil bacteria. R^2=coefficient of determination (LM) or McFadden's pseudo R^2 as measure of model fit (GLM), p = significance, q=Benjamini–Hochberg critical value. Results with $p < 0.05$ and $q < 0.10$ are presented.

A) Unamnicured share (%)	**Metric**	**Estimate**	**p-value**	**q-value**	**R^2**
Phylum Cyanobacteria	richness	−0.007	< **0.0001**	< **0.0001**	0.10
Class Acidobacteria subgroup 6	richness	0.004	< **0.0001**	< **0.0001**	0.04
Class Oxyphotobacteria	richness	−0.007	< **0.0001**	< **0.0001**	0.12
Class Thermoleophilia	richness	0.003	< **0.0001**	< **0.0001**	0.03
Phylum Cyanobacteria	shannon	−0.007	**0.003**	**0.018**	0.15
Class Oxyphotobacteria	shannon	−0.008	**0.004**	**0.032**	0.14
Genus Nocardioides	shannon	0.005	**0.013**	**0.048**	0.07
Genus Enterobacteriaceae unclassified	shannon	−0.002	**0.021**	0.051	0.08
Family total diversity	shannon	0.002	**0.016**	**0.048**	0.10
Order total diversity	shannon	0.001	**0.044**	0.066	0.06
Class Oxyphotobacteria	simpson	−0.002	**0.014**	0.070	0.10
Family total diversity	simpson	0.0001	**0.026**	0.053	0.12
Order total diversity	simpson	0.0001	**0.009**	**0.036**	0.08
Phylum Cyanobacteria	relative	−0.01	**0.047**	0.071	0.06
Phylum Verrucomicrobia	relative	0.007	**0.019**	0.058	0.09
Class Oxyphotobacteria	relative	−0.02	**0.024**	0.061	0.08
Class Thermoleophilia	relative	0.006	**0.011**	0.056	0.11
Class Verrucomicrobiae	relative	0.006	**0.047**	0.074	0.09
Order Chthoniobacterales	relative	0.008	**0.007**	0.069	0.13
Family Chthoniobacteraceae	relative	0.008	**0.009**	0.087	0.12
B) Soil organic matter content (%)					
Phylum Cyanobacteria	richness	−1.71	**0.047**	0.091	0.07
Class Oxyphotobacteria	richness	−0.05	< **0.0001**	< **0.0001**	0.17
Class Thermoleophilia	richness	0.01	< **0.0001**	**0.0001**	0.06
Class Acidobacteria subgroup 6	richness	0.02	< **0.0001**	< **0.0001**	0.10
Genus Burkholderiaceae unclassified	shannon	0.02	**0.007**	**0.036**	0.14
Family Xanthomonadaceae	shannon	0.02	**0.004**	**0.030**	0.15
Family Xanthomonadaceae	simpson	0.01	**0.014**	0.084	0.11
Phylum Acidobacteria	relative	0.02	**0.025**	0.098	0.09
Phylum Gemmatimonadetes	relative	−0.04	**0.003**	**0.010**	0.16
Class Gemmatimonadetes	relative	−0.05	**0.002**	**0.008**	0.16
Order Gemmatimonadales	relative	−0.05	**0.002**	**0.020**	0.16
Family Gemmatimonadaceae	relative	−0.05	**0.008**	**0.077**	0.13
Genus Gemmatirosa	relative	−0.11	**0.0002**	**0.014**	0.13
Genus Skermanella	relative	0.08	**0.002**	**0.074**	0.19
C) Plant richness					
Family Beijerinckiaceae	shannon	−0.76	**0.0009**	**0.015**	0.73
Family Beijerinckiaceae	simpson	−0.56	**0.0003**	**0.005**	0.75
Genus Methylobacterium	simpson	0.70	**0.0007**	**0.003**	0.51
Genus Sphingomonas	simpson	−1.80	**0.0002**	**0.002**	0.66

Table 3

Number of ASVs at the phylum level from indicator species analysis.

Phylum	Russia	Finland
Proteobacteria	628	382
Actinobacteria	423	207
Bacteroidetes	334	221
Acidobacteria	222	73
Chloroflexia	189	55
Verrucomicrobia	115	17
Planctomycetes	105	34
Gemmatimonadetes	69	53
Firmicutes	60	2
Cyanobacteria	9	37
Armatimonadetes	5	32
Deinococcus-Thermus	3	14

4. Discussion

This study examined differences in bacterial communities in surface soil from urban park entrances in Finland and Russian Tatarstan, with a particular focus on aspects of planetary health, the Biodiversity hypothesis, and the potential influence of park management practices. As we hypothesized, bacterial communities differed between the sampled regions and the surface soil bacteriota of urban park entrances in Russian Tatarstan had higher alpha diversity, which were associated especially with less manicured park conditions and higher soil organic matter content. Additionally, park entrances in Russian Tatarstan had different bacterial community composition, twice the number of indicator species, two times richer core microbiome, and a more stable bacterial community network structure compared to those in Finland. All these findings support the core assumption of the Biodiversity hypotheses that less artificial and unmanicured environments provide more possibilities for contact with environmental microbiota which might be beneficial for the health of citizens (Ege et al., 2012; Valkonen et al., 2015; Roslund et al., 2020, 2022).

The fact that our hypotheses were consistently supported across all analyses—including PERMANOVA, regression models, core microbiome analysis, indicator species analysis, and co-occurrence network analysis—indicates a fundamental difference in urban environmental bacterial communities between the two study areas with differing park management practices. While most of the analyses provide insights into the diversity and uniqueness of the studied communities, the fact that co-occurrence network analysis revealed Finnish urban park entrances to have almost 60 % more connections between genera than the Russian Tatarstan study sites might refer to more challenging environment as aspect of bacteria. Indeed, several previous investigations found that bacteria occur together and possibly interact with each other more often to survive in challenging environmental conditions (Paerl and Pinckney, 1996; de Vries et al., 2018; Dong et al., 2022; Manninen et al., 2025). In light of this, the results indicate that the surface soil at the Russian

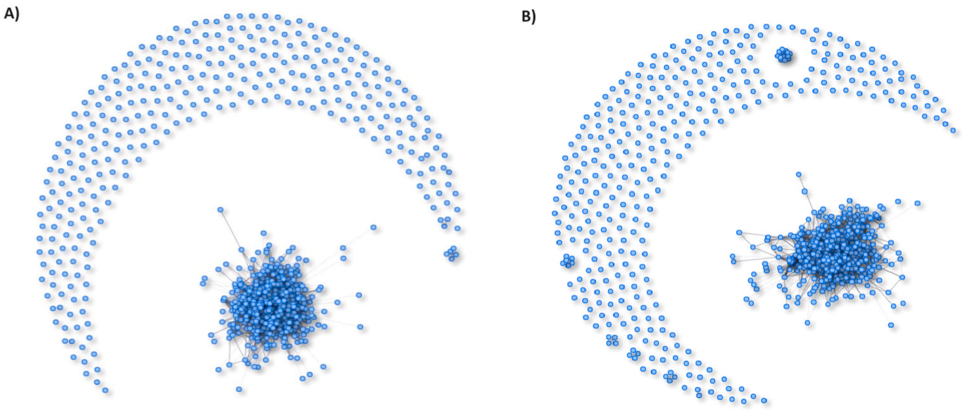

Fig. 7. Co-occurrence networks formed by bacterial genera in urban parks in (A) Finland and (B) Russian Tatarstan. Statistics are shown in SI8.

Tatarstan urban park entrances offer bacteria more stable conditions, which also enable more diverse bacterial communities.

In the context of the Biodiversity hypothesis, differences in the bacteriota were also found taxa which are commonly found in both soil and human commensal microbiota – particularly Proteobacteria, Verrucomicrobia, and Firmicutes (Grice and Segre, 2011; Fujio-Vejar et al., 2017; Brame et al., 2021; Roslund et al., 2022)—which were more diverse in Russian Tatarstan urban green space entrances than in Finnish ones. Since previous studies have highlighted the role of diverse environmental microbiota in the development of microbiome and immune modulation (Debarry et al., 2007; Fyhrquist et al., 2014; Hanski et al., 2012; Roslund et al., 2020 ,2022; Saarenpää et al., 2024), urbanites in Russian Tatarstan could unintentionally pick more species with them for exposure while passing by. Interestingly, previous studies have also found that bacterial groups such as Nocardioides and Burkholderiaceae, more diverse in Russian Tatarstan and associated with higher unmanicured share and SOM content in the current study, were transferred from the environment to the human body following exposure to green spaces (Selway et al., 2020). However, variation in soil bacterial diversity on its own is not enough to substantiate claims of improved human health outcomes, particularly within urban settings. Delgado-Baquerizo et al. (Delgado-Baquerizo et al., 2021) demonstrated that although urban green spaces may harbor greater bacterial diversity than natural areas, they also tend to be enriched with fast-growing bacterial groups, some of which can include potential pathogens. This presents a paradox: while such microbes may pose risks to human health, the Hygiene and Old Friends hypothesis suggests that controlled exposure to potential or opportunistic pathogens is nonetheless critical for the development of a resilient immune system (Strachan, 1989; Rook et al., 2003). Reflecting this tension, the evidence is contradictory: whereas some evidence indicates that urban green spaces with high soil biodiversity may harbor higher levels of potential pathogens than natural areas (Delgado-Baquerizo et al., 2021), other studies argue the opposite, showing that biodiverse and microbially rich environments are actually less susceptible to invasion by pathogenic species (van Elsas et al., 2012; Civitello et al., 2015).

Based on our results, unmanicured share of urban green spaces and soil organic matter content were key factors which had positive effects on bacterial diversity. Since certain health-associated bacteria—such as Proteobacteria—have been found to be more abundant in areas where plant litter is not mechanically removed (Yan et al., 2020), and since they are known as primary degraders in organic matter (Tláskal et al., 2016; Bani et al., 2018), the unmanicured green spaces in Russian Tatarstan may simply offer more niches to microbial communities. Instead, these factors affected negatively to group Cyanobacteria, which had a higher observed species richness, Shannon diversity, relative abundance and number of indicative species in Finland. In Finnish parks frequent maintenance—like mowing and removing weeds— may keep organic inputs low. These conditions create nutrient-poor and low organic matter conditions, where nitrogen-fixing Cyanobacteria often thrive (Sukenik et al. 2019; Chamizo et al., 2019) and strengthen the view that Finnish park entrances are more challenging living environments for some bacteria.

Because the unmanicured share of green spaces positively influenced the amount of soil organic matter, it can be concluded that unkempt maintenance practices may affect positively bacterial diversity through changes in soil organic matter. Russian Tatarstan urban parks clearly had a larger share of unkempt green space, while Finnish parks, had bigger share of manicured green spaces, mowed lawn and gravel. Hence, leaving the green areas in as natural state as possible might be an important factor in higher bacterial diversity. Leaving parks completely in their natural state can be challenging from a recreational point of view, but benign neglect would also offer a more cost-effective option for urban planners and gardeners, potentially increasing the attractiveness of this option.

While this study provides valuable insights into urban microbial communities, certain limitations must be acknowledged. First, in the year of the sampling, the vegetation period was longer than average (~170 days) (Vladimirovna Demina et al., 2020) in Russian Tatarstan, which might influence the vegetation and microbial communities. Second, the original plan to conduct sampling over two consecutive summers in multiple cities across both countries was disrupted by the COVID-19 pandemic and the subsequent Russian invasion of Ukraine. As a result, issues such as spatial autocorrelation and pseudo-replication are present in our study design, particularly in the sampling conducted in the Tatarstan region. These factors should be considered when interpreting the results, and future studies with broader spatial replication would help address these limitations more effectively. Third, the use of 16S rRNA amplicon sequencing limits the resolution to genus level, preventing the detection of species-level or functional differences that are critical for a comprehensive understanding of bacterial communities, particularly from a health perspective. Use of shotgun sequencing could address these gaps by providing more detailed functional and taxonomic information.

Despite the lack of second-year sampling and the limited spatial scope, this comparison provides a meaningful first step for understanding how socio-environmental factors may shape urban microbial communities. Integrating these ecological considerations into the design and maintenance of urban green spaces may contribute to health relevant microbial exposures and support planetary health. Overall, future research including a broader range of countries with diverse economic, geographic, and park management contexts, alongside more comprehensive metagenomic methods, is necessary to more robustly test hypotheses related to microbial exposure, biodiversity, and public health

5. Conclusions

We sampled park entrances in two regions, Finland and Russian Tatarstan, aiming to test whether differences in urban soil surface bacteriota exist in the context of the Biodiversity hypothesis, while also considering how varying park management practices may influence microbial communities. The differences found in bacterial communities support the view that Russian Tatarstan urban green spaces offer better opportunities for health-beneficial microbial exposure than the Finnish ones. It also seems that the dirt at Finnish urban park entrances, which are surrounded mostly by manicured lawns, might offer bacteria more challenging conditions than the green areas in Russian Tatarstan, where larger areas in parks are in unmanicured state. The current paper underlines the connections between health-relevant environmental microbiota and urban green space and emphasizes the dependence of well-being on well-functioning natural ecosystems as described by the planetary health paradigm. Finally, the results offer solutions for the development of urban green space: Benign neglect and unkempt patches in urban parks deserve to be studied for potential health and ecosystem benefits.

CRediT authorship contribution statement

Polina Galitskaya: Writing – review & editing, Supervision, Resources, Investigation. **Olli Laitinen:** Writing – review & editing. **Mika Saarenpää:** Writing – review & editing. **Juulia Manninen:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Anna Luukkonen:** Investigation, Writing – review & editing. **Marja Roslund:** Writing – review & editing, Supervision, Investigation, Data curation, Conceptualization. **Aki Sinkkonen:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Aki Sinkkonen reports equipment, drugs, or supplies was provided by University of Helsinki Institute for Molecular Medicine Finland. Aki Sinkkonen reports financial support was provided by Kone Fundation. Aki Sinkkonen reports financial support was provided by The Strategic Research Council of Finland. Olli Laitinen reports financial support was provided by The Strategic Research Council of Finland. Aki Sinkkonen reports equipment, drugs, or supplies was provided by CSC IT Center for Science Ltd. Aki Sinkkonen reports financial support was provided by Horizon Europe. Aki Sinkkonen reports a relationship with Uute Scientific Ltd that includes: board membership. Olli Laitinen reports a relationship with Uute Scientific Ltd that includes: board membership. Aki Sinkkonen has patent #EP3551196 issued to EPO. Olli Laitinen has patent #EP3551196 issued to EPO. Aki Sinkkonen has patent #US-11786564-B2 issued to USPTO. Olli Laitinen has patent #US-11786564-B2 issued to USPTO. Aki Sinkkonen has patent #US-11318173-B2 issued to USPTO. Olli Laitinen has patent #US-11318173-B2 issued to USPTO. Aki Sinkkonen has patent #EP3589300 issued to EPO. Marja Roslund has patent #EP3589300 issued to EPO. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ufug.2025.129060.

Data availability

All bacterial sequence data were accessioned into the Sequence Read Archive (BioProject ID: PRJNA1063546). All other data needed to support the conclusions of this manuscript are included in the main text and supplementary appendix.

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