Urban land uses shape soil microbial abundance and diversity

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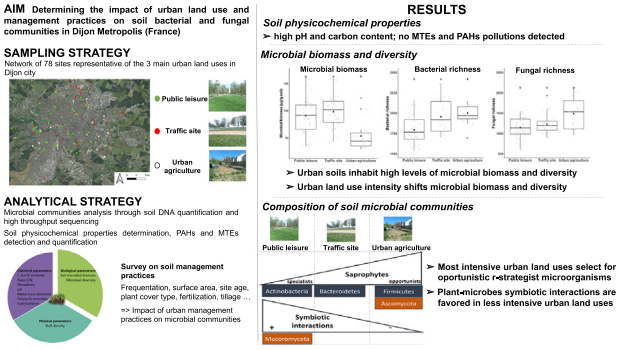
HIGHLIGHTS

- 78 urban sites were sampled to characterize urban soil microbial communities.
- Urban soils harbored high levels of microbial biomass and diversity.
- Microbial biomass and diversity were influenced by urban land use intensity.

GRAPHICAL ABSTRACT



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ABSTRACT

Soil microbial biodiversity provides many useful services in cities. However, the ecology of microbial communities in urban soils remains poorly documented, and studies are required to better predict the impact of urban land use. We characterized microbial communities (archea/bacteria and fungi) in urban soils in Dijon (Burgundy, France). Three main land uses were considered – public leisure, traffic, and urban agriculture – sub-categorized in sub-land uses according to urban indexes and management practices. Microbial biomass and diversity were determined by quantifying and high-throughput sequencing of soil DNA. Variation partitioning analysis was used to rank soil physicochemical characteristics and land uses according to their relative contribution to the variation of soil microbial communities. Urban soils in Dijon harbored high levels of microbial biomass and diversity that varied according to land uses. Microbial biomass was 1.8 times higher in public leisure and traffic sites than in urban agriculture sites. Fungal richness increased by 25 % in urban agriculture soils, and bacterial richness was lower (by 20 %) in public leisure soils. Partitioning models explained 25.7 %, 46.2 % and 75.6 % of the variance of fungal richness, bacterial richness and microbial biomass, respectively. The organic carbon content and the C/N ratio were the best predictors of microbial biomass, whereas soil bacterial diversity was mainly explained by soil texture and land use. Neither metal trace elements nor polycyclic aromatic hydrocarbons contents explained variations of microbial communities, probably due to their very low concentration in the soils. The microbial composition results highlighted that leisure sites represented a stabilized habitat favoring specialized microbial groups and microbial plant symbionts, as opposed to urban agriculture

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sites that stimulated opportunistic populations able to face the impact of agricultural practices. Altogether, our results provide evidence that there is scope for urban planners to drive soil microbial diversity through sustainable urban land use and associated management practices.

1. Introduction

Today, >50 % of the world's population is urban, and this proportion is expected to increase up to 70 % by 2050 (United Nations, 2018). This leads to negative externalities like pollution, declining biodiversity, or/and artificialization that affect environmental resources and compromise the quality of urban environments (Morel et al., 1999; Schwartz et al. 2001; McKinney, 2006; Alberti, 2015; Fenoglio et al., 2020). Recognition of these threats evidenced the need to move toward new models of urban development based on the "return of nature to cities" (Pollak, 2006; Mata et al., 2020). Improving our knowledge of urban ecosystems is required to achieve this transition, with special attention to be paid to soil ecosystem. Long considered only as support for urban constructions and activities, soil fullfills many other functions and provides services useful for the well-being of urban populations and more widely urban sustainability, such as water regulation, support for plant production, urban heat islands mitigation (Morel et al., 2015; Mata et al., 2020). Most of these services rely on the diversity and activity of the biological organisms they host (Bardgett and van der Putten, 2015). Soil biodiversity covers a huge range of organisms, from microorganisms to macrofauna, and represents 1/3 of biodiversity on Earth (FAOSTAT, 2021). With several thousands of species *per* gram of soil, microoorganisms account for a large part of this biodiversity. They are key participants to soil functioning through the regulation of important soil functions such as organic matter decomposition and nutrient cycling (Van Der Heijden et al., 2008; Maron et al., 2018; Pandey et al., 2018) and the building up of the soil structure. They also interact with each other and contribute to regulate pathogens (Vivant et al., 2013).

To date, most of the research on soil microbial ecology has focused on rural areas (Guilland et al., 2018) . The main drivers of soil microbial abundance and diversity have been identified (Dequiedt et al., 2011; Martiny et al., 2011; Zhalnina et al., 2015) together with the most influencing agricultural practices (Constancias et al., 2015; Le Guillou et al., 2019; Karimi et al., 2020; Dunn et al., 2021). Collected data also led to identifying sustainable farming systems in terms of soil biodiversity preservation (Christel et al., 2021; Dunn et al., 2021; Matteoli et al., 2022). Contrastingly, the ecology of microbial communities in urban soils still remains poorly documented (Hahs and Evans, 2015; Guilland et al., 2018), and direct transposition of knowledge acquired on rural soils is not trivial due to the strongly distinctive features of urban soils. In urban areas, soils are created during the urbanization process, and human action represents the main determinant of their genesis and evolution, which is much faster compared to rural soils (Morel et al., 2015). Moreover, soils in urban ecosystems are highly spatially fragmented, so that they offer a mosaic of conditions for microbial development. They are exposed to high levels of atmospheric nitrogen deposits and to heat island effects. They also often suffer from accumulation of industrial or traffic pollutants due to present or historic activities (Yang et al., 2006; Chen et al., 2013) and to compaction caused by trampling and traffic density (Pouyat et al., 2010). Altogether, this suggests that urban soils may offer particular habitats for soil organisms and be associated to a particular microbial ecology which still needs to be deciphered to drive urban land management toward greater sustainability.

Available literature data shows that despite the stressing conditions evoked above, urban soils host abundant and diverse bacterial and fungal communities (Enloe et al., 2015; Reese et al., 2016; Guilland et al., 2018). However, urban land uses have an impact on soil microbial communities. For example, higher microbial biomass levels were observed in tree pits compared to street-side infiltration swales and vegetation swales (Deeb Collet et al., 2018). The homogeneity of microbial community composition can increase with urbanization (Liu et al., 2021). Soil bacterial interaction networks were found more complex in green park spaces than in adjacent green spaces (Feng et al., 2020). The frequency of potentially pathogenic populations was found higher in the soil of Central Park, probably as a result of the very large numbers of visitors (Ramirez et al., 2014). Altogether, these studies provide valuable information about the ecology of microbial communities in urban soils. However, most papers were focused on parks or specific green infrastructures without considering the diversity of greenspaces and associated habitats for microoganisms or the soil management practices possibly impacting microbial communities. In addition, although bacteria were taken into account in most of the works, fungal communities were rarely characterized (Reese et al., 2016; Hui et al., 2017). This makes it difficult to get an overview of microbial diversity and abundance at the city scale and identify land uses and management practices suitable for soil microbial communities. To our knowledge, no study has considered the diversity of both bacterial and fungal communities in the green spaces that characterize urban ecosystems. Gill et al. (2020) recently illustrated the high potential of simultaneously studying multiple green infrastructure types. They showed that soil microbial community diversity in New-York city differed between engineered and non-engineered green infrastructures. They also concluded that the diversity and composition of microbial community are driven by environmental filters in engineered habitats, *versus* stochastic processes in non-engineered soils (Gill et al., 2020). However, they did not take management practices into account despite their potential strong influence as drivers of soil microbial diversity (Karimi et al., 2020; Turley et al., 2020; Christel et al., 2021).

In this context, the aim of this study was to characterize soil microbial communities in Dijon city, a medium-sized French city hosting 155,000 citizens on a 40 km^2 area. We hypothesized that (i) the abundance and diversity of the soil microbial communities depend on urban land use and soil management practices, and (ii) soil microbial abundance and diversity are improved in less intensively managed spaces. To test these hypotheses, we investigated the mosaic of urban land uses by sampling 78 soils distributed across the city and representative of the main types of spaces occurring in the city: leisure sites, traffic sites, and urban agriculture sites. We determined molecular microbial biomass and diversity by quantifying and high-throughput sequencing of soil DNA. We also computed site history and collected the management practices applied at each site (mowing, watering, crop protection, tillage, and fertilization). As a result, we were able to explore the effects of urban land uses and associated practices on soil properties and microbial communities.

2. Materials and methods

2.1. Study area

The study was conducted in the city of Dijon, located in east-central France in the Burgundy region (47°19′N, 5° 01′E), at an altitude of 220 to 350 m. It is a medium-sized French city hosting 155,000 citizens and representing a 40 km^2 area. The percentage of sealed soils is around 14 % (Dijon city, 2022). The continental climate of Dijon city is marked by cold temperatures in winter and fairly hot summers. The average annual temperature is around 11 °C and total annual rainfall is around 982 mm (Climate data, 2022).

2.2. Sampling design

The sampling design covered Dijon city together with 3 municipalities of the conurbation (Fig. 1). A partnership with the "Jardin de l'Arquebuse"

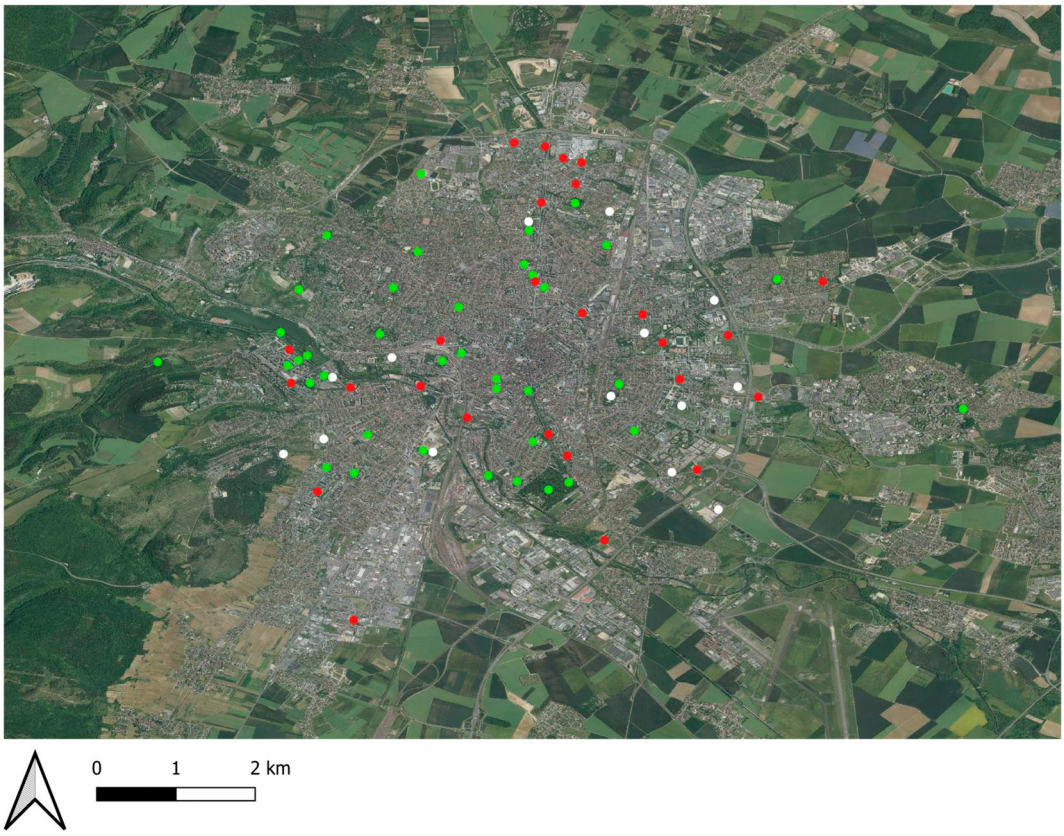

Fig. 1. Localization of the sampled sites in Dijon city. Green points, leisure sites; red points, traffic sites; white points, urban agriculture sites.

– the Science Museum of Dijon – allowed selecting 78 green spaces covering the whole urban territory and the diversity of land uses in Dijon city. The selected green spaces were located outside private spaces, had an area > 100 m^2, and were easily accessible.

The sites were grouped into three main land uses, namely (i) leisure sites, including four sub-land uses (public green areas, public parks, public squares, school areas); (ii) traffic sites, including three sub-land uses (road sides, roundabouts, tramway railway); and (iii) urban agriculture, including two sub-land uses (allotment gardens and community gardens). Land use history and management practices were surveyed for each site to describe the green space types (Table 1, Supplementary material Tables 1 and 2). The level of urbanization was evaluated according to the following criteria: frequentation, surface area, and site age. Management practices were described in terms of vegetation cover (type and time), watering, fertilization (organic and mineral inputs), weeding, mulching, tillage, and mowing.

Table 1
Descriptive characteristics of the three main urban land uses in Dijon.

		Public leisure (n = 38)	Traffic site (n = 26)	Urban agriculture (n = 14)
Description		Public parks, schools and public areas used as recreational spaces	Road sides, roundabouts and tramway rail road used as traffic accessory	Allotment gardens and community gardens used for vegetable production
Plant cover type		Herbaceous vegetation Permanent cover	Herbaceous vegetation Permanent cover	Cultivated vegetation Non permanent cover
Mean Size (m^2)		4181.16	1716.28	424.00
Number of sites as a function of user visits (number of users *per* day)	≤10	3	13	5
	10 to 50	18	13	9
	50 to 100	7	0	0
	>100	10	0	0
Number of sites as a function of site age	≤10 years	6	10	6
	10 < age ≤ 50	7	12	3
	>50 years	25	4	5
Watering		4	9	14
Organic fertilization		0	8	3
Mineral fertilization		0	8	3
Manual weeding		28	15	14
Mulching		11	2	12
Tillage		0	0	14
Frequency of mowing(number of passages *per* year)	No mowing	3	1	14
	≤3	6	6	0
	4 to 6	13	8	0
	>6	16	11	0
Export of mowing residues		14	12	–

2.3. Soil sampling

Sampling was carried out in spring 2021. Soil samples for bulk density analysis corresponded to triplicate undisturbed soil cores taken at 0–20 cm depth using a bulk density sampling kit (Manual corer, diam. 53 mm, SDEC, France). The soil samples for physico-chemical and microbial analyses were composite samples made of 9 soil cores collected over a 100-m^2 area (0–20 cm depth, 5 cm diam.). Part of these composite samples was sieved through a 4-mm mesh, freeze-dried and stored at −40 °C in the soil conservatory of the GenoSol platform (Dijon, France) until subsequent microbial analysis. The other part was air-dried and stored at room temperature for subsequent physico-chemical analysis.

2.4. Soil physicochemical analysis

The physicochemical properties of each soil sample were determined at the Laboratory of Soil Analysis of the National Research Institute of Agronomy of Arras (France) (https://www6.hautsdefrance.inrae.fr/las). The measured parameters were soil pH (NF ISO 10390), the total organic carbon content (SOC, $g.kg^{-1}$, NF ISO 10694), the total nitrogen content (TN, $g.kg^{-1}$, NF ISO 13878), and the clay, silt and sand percentages (NF ISO 11277). Bulk density was measured by weighing soil cores after drying at 105 °C for 5 days. For each site, the three cores were weighed before and after oven-drying at 105 °C. The concentrations of the following 16 polycyclic aromatic hydrocarbons (PAHs) were measured (XP X33–012): naphthalene (Naph), acenaphtylene (Acy), acenaphthene (Ace), fluorene (Flu), phenanthrene (Phe), anthracene (Ant), fluoranthene (Flh), pyrene (Pyr), benzo(*a*)anthracene (BaA), chrysene (Chry), benzo(*b*)fluoranthene (BbF), benzo(*k*)fluoranthene (BkF), benzo(*a*)pyrene (BaP), dibenzo(*ah*)anthracene (DahA), indeno(123,*cd*)pyrene (IndP), and benzo(*ghi*)perylene (BghiP). The concentrations of cadmium (Cd), nickel (Ni) and lead (Pb) were determined (NF ISO 11885). All pollutant analyses were conducted at the Aurea AgroSciences Laboratory (https://www.aurea.eu).

2.5. Molecular analyses of soil microbial communities

DNA was extracted from each soil sample and quantified from 1 g of soil using a single procedure standardized by the GenoSol platform (INRAe, Dijon, France; Terrat et al., 2012). Briefly, this protocol is based on three specific steps: (i) microbial cell lysis by chemical and physical action; (ii) deproteination; and (iii) alcohol precipitation and washing of the extracted nucleic acids. Crude DNA extracts were quantified by electrophoresis in a 1 % agarose gel and ethidium bromide staining, using calf thymus DNA as a standard curve. Quantified crude DNA was used as an estimate of soil microbial biomass (Dequiedt et al., 2011). Then, crude DNA was purified using a Nucleospin Soil PCR purification kit (Macherey Nagel, illkirch, France). The purified DNA extracts were quantified using a Quantifluor staining kit (Promega, Madison, Wisconsin, USA).

Archaeal/bacterial diversity was estimated in all 78 soil samples by metabarcoding of the 16S rRNA gene following the method described by Terrat et al. (2015). A gene fragment targeting the V3 to V4 regions was first amplified using primers F479 (5′CAG CMG CYG CNG TAA NAC3′) and R888 (5′CCG YCA ATT CMT TTR AGT3′). The PCR products were purified with a Pronex purification kit (Promega, USA). A second PCR was run on the purified PCR products using 10-base-pair multiplex identifiers (MID) added at the 5′ and 3′ ends of the primers for subsequent sample identification. For all libraries, equal amounts from the 78 samples were pooled and purified to remove excess nucleotides, salts and enzymes using a Pronex purification kit (Promega, USA). Finally, sequencing was carried out with an Illumina MiSeq instrument (Illumina Inc., San Diego, CA, USA) operating with V3 chemistry and producing 300-bp paired-end reads. Fungal diversity was similarly estimated by metabarcoding of the 18S rRNA gene. A gene fragment targeting the V7 to V8 regions was first amplified using primers FR1 (5′ ANC CAT TCA ATC GGT ANT3′) and FF390 (5′CGA TAA CGA ACG AGA CCT3′) (Chemidlin Prévost-Bouré et al., 2011). The subsequent sequencing steps were similar to those of the 16S analysis described above.

2.6. Bioinformatic analyses

Bioinformatic analyses of the generated DNA sequences were performed using BIOCOM-PIPE pipeline (Djemiel et al., 2020). First, 16S and 18S raw reads were trimmed and merged using FLASH and PRINSEQ, demultiplexed, and filtered based on their length, number of ambiguities, and primers sequences. The reads were dereplicated to simplify the subsequent steps of the pipeline (*i.e.*, clustering of strictly identical sequences). The dereplicated reads were aligned using infernal alignment (Nawrocki and Eddy, 2013) and clustered at 95 % similarity into operational taxonomic units (OTUs). A filtering step was carried out to check all single singletons (reads detected only once and not clustered (possible artifacts, *e.g.*, PCR chimeras)) based on the quality of their taxonomic assignments (Djemiel et al., 2020).

Finally, to compare the datasets efficiently and avoid biased community comparisons, the retained reads were homogenized by random selection of 10,000 reads. The retained reads were used for (i) defining global OTU matrices using ReClustOR (Terrat et al., 2020) – a post-clustering tool that improves the reliability of OTU-based results and analyses, based on French RMQS biological reference databases of archaeal/bacterial communities (Terrat et al., 2017) and fungal communities; (ii) taxonomy-independent analyses to determine richness indexes, using the OTU dataset; (iii) taxonomy-based analyses, using similarity approaches against curated reference databases from SILVA r132 (Quast et al., 2012). The raw datasets are available in the EBI database system under project accession number PRJEB50819.

2.7. Statistical analyses

All statistical analyses were performed in R environment (v4.0.) (R Core Team, 2021) using the vegan package (Oksanen et al., 2011). The overall effects of land uses on the physicochemical parameters and characteristics of microbial communities were evaluated using Student test or analysis of variance (ANOVA, multiple pairwise comparisons), and significant differences between land uses were identified using a least significant difference test ($P < 0.1$) with Bonferroni correction. When ANOVA conditions were not satisfied, the effect of land uses was evaluated using the non-parametric Kruskal-Wallis test (Kruskal function, agricolae package).

The relative contributions of soil physicochemical properties and farming practices to shaping the microbial community characteristics were evaluated by variance partitioning. In total, three land uses and eleven soil physicochemical properties were selected as explanatory variables of microbial biomass and bacterial and fungal diversity indexes (explained variables). The selected physicochemical properties were bulk density, pH, clay, silt, $CaCO_3$, organic carbon, the C/N ratio, available phosphorus, cadmium, lead, and PAHs. These explanatory variables were selected based on the exclusion of collinear variables ($r < 0.7$), maximum representativeness, and homogenous distribution of values across the 78 samples. These selection steps are necessary criteria for accurate model prediction (Ramette, 2007). Data were standardized to approximate a Gaussian and homoscedastic residual distribution. This approach involved using the regsubsets function in the leaps package in R (Moore, 1995). The selection criteria were the Bayesian information criterion (BIC) and the adjusted coefficient of determination (R^2 adj), and involved minimizing the first and maximizing the second. The respective amounts of variance (marginal and shared) were determined by canonical variation partitioning, and R^2 adj was determined by RDA (Ramette, 2007). The statistical significance of the marginal effects was assessed from 1000 permutations of the reduced model.

We used linear discriminant analysis effect size (LEfSe) to detect taxa with significant differential abundances whatever their taxonomic rank, for each soil with a different land use and land cover history (Segata et al., 2011). The LEfSe method is based on (i) a non-parametric Kruskal-Wallis rank sum test to search for statistically different microbial groups, followed by (ii) linear discriminant analysis (LDA scores >3 for 16S and for 18S) to assess the effect size of each differentially abundant group.

3. Results

3.1. Soil physicochemical properties

The soils of the 78 sites samples had quite similar physicochemical properties, as indicated in Supplementary material Table 3. They all had a silty clay texture and a bulk density ranging from 0.4 g/m^3 in traffic sites to 1.6 g/m^3 in public leisure sites (mean 1.0 g/m^3). The trend was different for chemical components: the organic carbon and total nitrogen contents were overall high and ranged from 16.1 to 74.9 g/kg soil and 1.5 to 6.2 g/kg soil, respectively. The soil organic carbon content was similar for all three main land uses, whereas the total nitrogen content was significantly lower and the C/N ratio higher in urban agriculture soils (Supplementary material Table 3). Available P ranged from 0.008 to 0.15 g/kg soil. The significantly lowest values were recorded in public leisure sites compared to traffic and urban agriculture sites. Within the range of alkaline pH values, urban agriculture soils had a significantly higher pH than public leisure and traffic site soils (Supplementary material Table 3). Based on metal trace elements (MTEs) and PAHs, urban soils in Dijon city were not polluted. Only three public leisure sites showed values that exceeded the contamination thresholds. The MTE concentration did not significantly differ between the three main land uses; only Pb was significantly higher in public leisure sites than in traffic sites (Supplementary material Table 3). The same trend was observed for PAHs. The analysis of sub-land use types revealed that tramway sites stood out among traffic sites with a higher organic carbon content and lower Pb and PAH contents, and a particurlarly lower pH than in roundabout soils (Supplementary material Table 5). In urban agriculture soils, community gardens significantly differed from allotment gardens, with a higher organic carbon content, a lower pH and also lower MTE contents (Supplementary material Table 6).

3.2. Effects of urban land uses on soil molecular microbial biomass

Soil molecular microbial biomass ranged from 29.0 to 163.1 μg DNA/g soil (Supplementary material Table 3). The variability of microbial biomass was quite large within each urban land use type (Fig. 2). The mean microbial biomass in public leisure and traffic sites was 1.8 times significantly higher than the mean microbial biomass in agriculture sites.

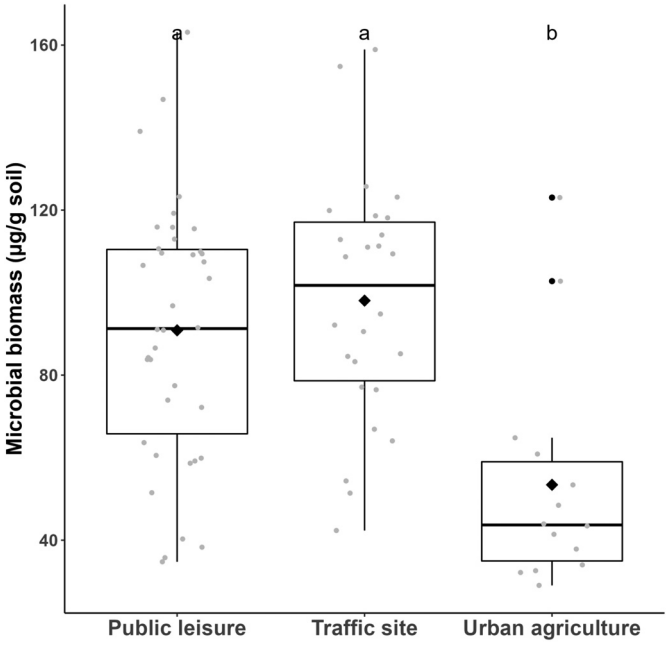

Fig. 2. Soil molecular microbial biomass according to the main urban land uses: public leisure, traffic, and urban agriculture sites. Letters indicate significant differences between land use types ($P < 0.1$).

The analysis of sub-land use types evidenced different soil properties. Despite a slight upward trend (school < square < park < urban meadow), the four types of public leisure sites did not show significant differences ($P < 0.1$) in microbial biomass (Fig. 3.A). Among the traffic sites, microbial biomass was significantly higher in the soils of tramway railroads, with a mean value 33 and 34 % higher than in roundabouts and roadsides, respectively (Fig. 3.B). Among the urban agriculture sites, allotment gardens harbored around 40 % less mean microbial biomass than community gardens (Fig. 3.C).

3.3. Effects of urban land uses on microbial diversity

Archeal/bacterial and fungal richness ranged from 1540 to 2365 OTUs and from 598 to 2133 OTUs, respectively (Supplementary material Table 3). Both bacterial and fungal richness differed significantly among the three main urban land uses (Fig. 4.A & B). Fungal richness was significantly higher in the urban agriculture sites than in the public leisure sites. Bacterial and fungal richness were significantly higher in the urban agriculture sites than in the public leisure sites. Traffic sites had a significantly higher bacterial richness ($P < 0.1$) but similar fungal richness to public leisure sites.

Regarding sub-land use types within each main land use, bacterial and fungal diversity were similar among the four types of public leisure land use (Fig. 5.A & D), but significantly different within traffic sites and urban agriculture sites. In traffic sites, lower bacterial richness and fungal richness were observed in roundabout soils compared to the other two sub-land uses. Bacterial richness was significantly higher in the soils of tramway railroad compared to roundabouts and roadsides (Fig. 5.B, $P < 0.1$). Such a stimulation in the tramway rail-road sites was not observed for fungal richness for which highest values were measured in roadside soils (Fig. 5.E). Bacterial richness did not significantly differ between the two types of garden, but fungal richness was 1.5-fold higher in allotment gardens than in community gardens (Fig. 5.C & F, $P < 0.1$).

3.4. Ranking of the influence of soil physicochemical properties and land use on soil molecular microbial biomass and diversity

Variance partitioning was used to rank the relative contributions of the main physicochemical soil properties and the three main urban land uses (leisure site, traffic site and urban agriculture) influencing the microbial community parameters.

The total amount of explained variance was relatively high for the three microbial indicators. It ranged from 25.7 % for fungal richness to 46.2 % for bacterial richness and 75.6 % for soil molecular microbial biomass (Fig. 6). Soil physicochemical parameters were the main drivers of soil microbial biomass (38.8 % of the observed variance, $P < 0.01$) and bacterial richness (21.5 % of the observed variance, $P < 0.01$). However, the identity and/or rank of the most predictive soil parameters differed between these two indicators. SOC (21.5 % of the observed variance, positive correlation, $P < 0.01$), the C/N ratio (10.3 % of the observed variance, negative correlation, $P < 0.01$), and to a lesser extent available P (4.2 % of the observed variance, $P < 0.01$) and the pH (2.8 % of the observed variance, negative correlation, $P < 0.01$) were the main predictors of microbial biomass. On the other hand, bacterial richness was mainly explained by clay (18.2 % of the observed variance, $P < 0.01$) and the soil $CaCO_3$ content (3.3 % of the observed variance, $P < 0.05$), both through a significant negative correlation. Soil physicochemical parameters also significantly explained fungal richness, but to a lesser extent, mainly through the soil P content that accounted for 5.56 % of the variance ($P < 0.05$) with a negative effect. Urban land use only had a significant effect on bacterial richness (13.7 %, $P < 0.01$), with lower richness in public leisure and traffic sites (Supplementary material Table 7). Interactions between soil physicochemical properties and urban land uses accounted for a relatively small amount of the variance of bacterial richness (11.0 %). Inversely, they explained the biggest amount of the variance of soil fungal richness (20.1 %) and almost

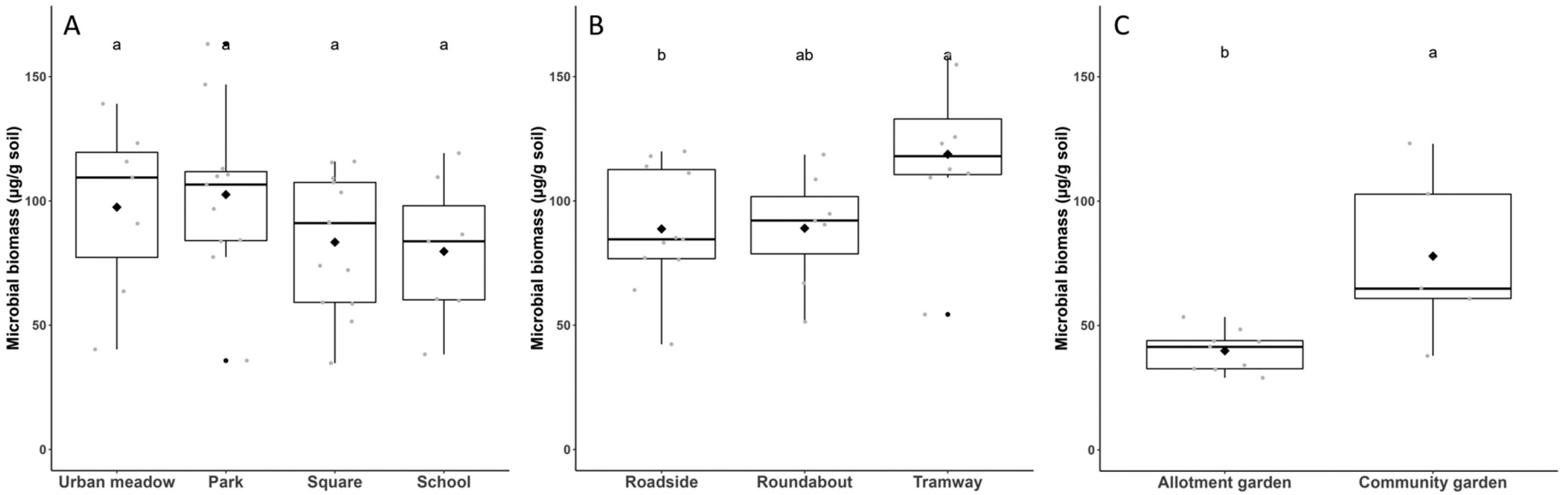

Fig. 3. Soil molecular microbial biomass according to sub-land uses: (A), four public leisure land uses; (B) three traffic land uses; (C) two urban agriculture land uses. Letters indicate significant differences between land use types ($P < 0.1$).

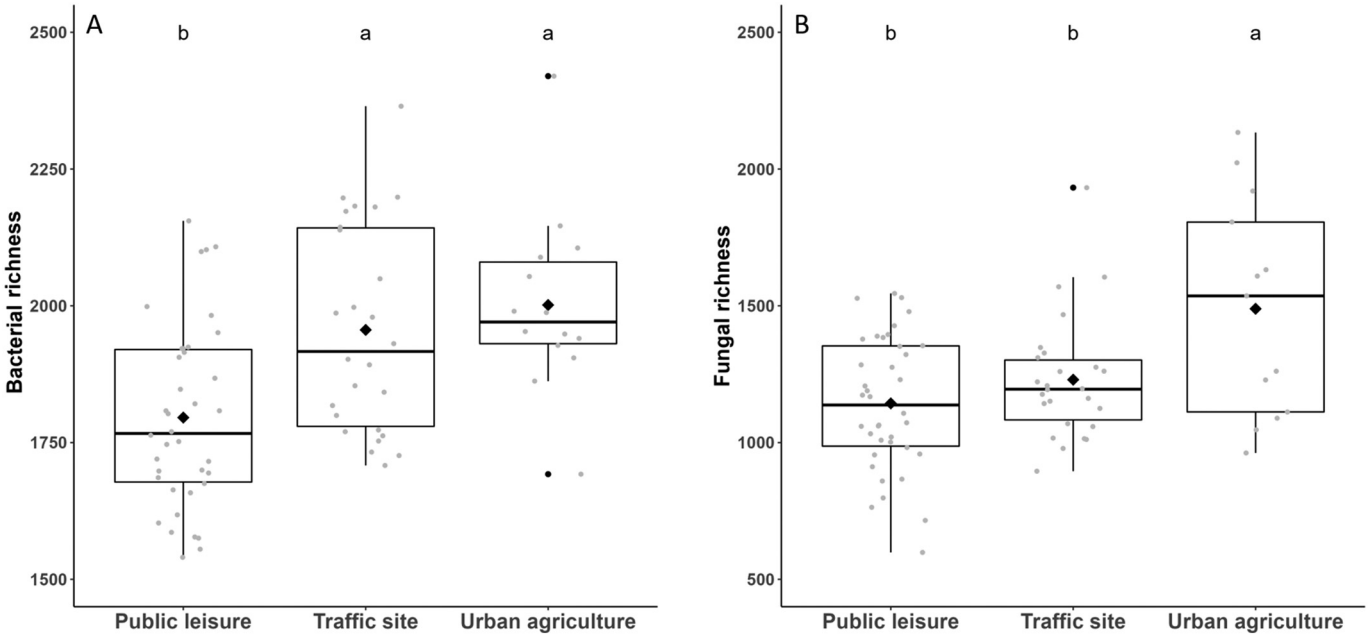

Fig. 4. Bacterial richness (A) and fungal richness (B) in the soils of the three main land use sites: public leisure, traffic, and urban agriculture. Letters indicate significant differences between land use types ($P < 0.1$).

the same part as these of physicochemical properties for soil microbial biomass (36.8 %).

3.5. Archaeal/bacterial and fungal taxonomic composition of soils according to urban land uses

The same dominant archaeal/bacterial and fungal phyla were detected in all soils, but the relative distribution of the groups varied according to the land use (Supplementary material Fig. 1). Most discriminating groups were identified based on LEfSe analysis. Groups with LDA scores above 3.9 or 4 for 16S and 18S, respectively, were identified as significantly stimulated in each of the three land use types (Fig. 7). With 27 microbial genera identified, urban agriculture was the land use with the highest number of specifically stimulated microbial groups compared to public leisure (15 genera) and traffic sites (14 genera). Such stimulation was mainly ascribed to an increase of the diversity of the fungal discriminating genera, from 5 in public leisure and traffic sites to 17 in urban agriculture sites. More precisely, urban agriculture sites were mainly discriminated from the other sites by a specific stimulation of a diversity of fungal genera belonging to Ascomycota and Cryptomycota phyla. Contrastingly, Mucoromycota phylum was specifically stimulated in public leisure sites through an increase of the diversity of genera including mycorrhizal *Glomus*, *Funneliformis*, *Claroideoglomus*, *Diversispora* and *Rhizophagus*. Basidiomycota were stimulated in all land uses but genera differed. *Catathelama* was found in the public leisure sites, *Marasmius* in the traffic sites, and *Vanrija* and *Ruinenia* in the urban agriculture sites.

At the phylum taxonomic level, Proteobacteria and Basidiomycota representatives were stimulated whatever the land use. At a higher taxonomic level, symbiotic Proteobacteria genera such as *Mesorhizobium*, *Bradyrhizobium* were stimulated in public leisure sites but not in traffic and urban agriculture sites. Chloroflexi, Firmicutes, Gemmatimonadetes and Nitrospirae phyla were specifically stimulated in the urban argriculture sites. Public leisure sites were discriminated from the other two land uses by a specific stimulation of a diversity of genera belonging to Actinobacteria and Entotheonellaeota phyla. Traffic sites were discriminated from the other two land uses through the stimulation of different genera belonging to Bacteroidetes phylum, and of the *Scytonema* genus belonging to the Cyanobacteria phylum.

Archaea were mainly stimulated in public leisure sites, with an increase of representatives of the Thaumarchaeota phylum and the *Candidatus Nitrososphaera* genus. Archaea were also stimulated in the urban agriculture sites, mainly through the increase of the *Candidatus Nitrocosmicus* genus. Contrastingly, no particular archae group was stimulated in the traffic sites.

4. Discussion

Dijon is a medium-sized French city covering a 40 km^2 area. We focused our soil sampling on the three main land uses represented in the city and providing different services to citizens: a recreational value for leisure sites, transport support for traffic sites, and food production for urban agriculture. As evidenced by our survey, these three land uses differed according to the site history and the management practices. Leisure sites were established first, had a permanent grass cover and were managed through minimal practices (no tillage, no fertilization, no watering, only mowing). Traffic sites were mainly more recent than leisure sites but similarly managed. Only tramway sites differed because they were watered and fertilized to maintain a green grass cover all year long. Urban agriculture was under more intensive practices than leisure and traffic sites through fertilizer inputs, soil tillage and watering.

4.1. Physicochemical characteristics of Dijon soils

The soil physicochemical characteristics revealed that the different soils were probably indigenous or originated from the close rural areas. Dijon city is located in a limestone area, which explains the high soil pH values. In addition, high values of total C and N may also reflect the origin of Dijon soils as rural topsoils initially rich in organic matter. They may also result from the accumulation of carbon over time through the development of a permanent plant cover and management practices such as mineral fertilizer inputs (Vasenev and Kuzyakov, 2018) and organic matter inputs (compost, green waste, mowing products). Several authors reported similar higher C and N contents in urban soils compared to rural soils (Kaye et al., 2005; Edmondson et al., 2014; Joimel et al., 2016). As opposed to other studies reporting high levels of pollution and compaction in urban soils (Morel et al., 2015; Foti et al., 2017), we observed very low concentrations of MTEs and PAHs compounds.The low historical industrial activity, less traffic and a lower population density in Dijon may have preserved soils

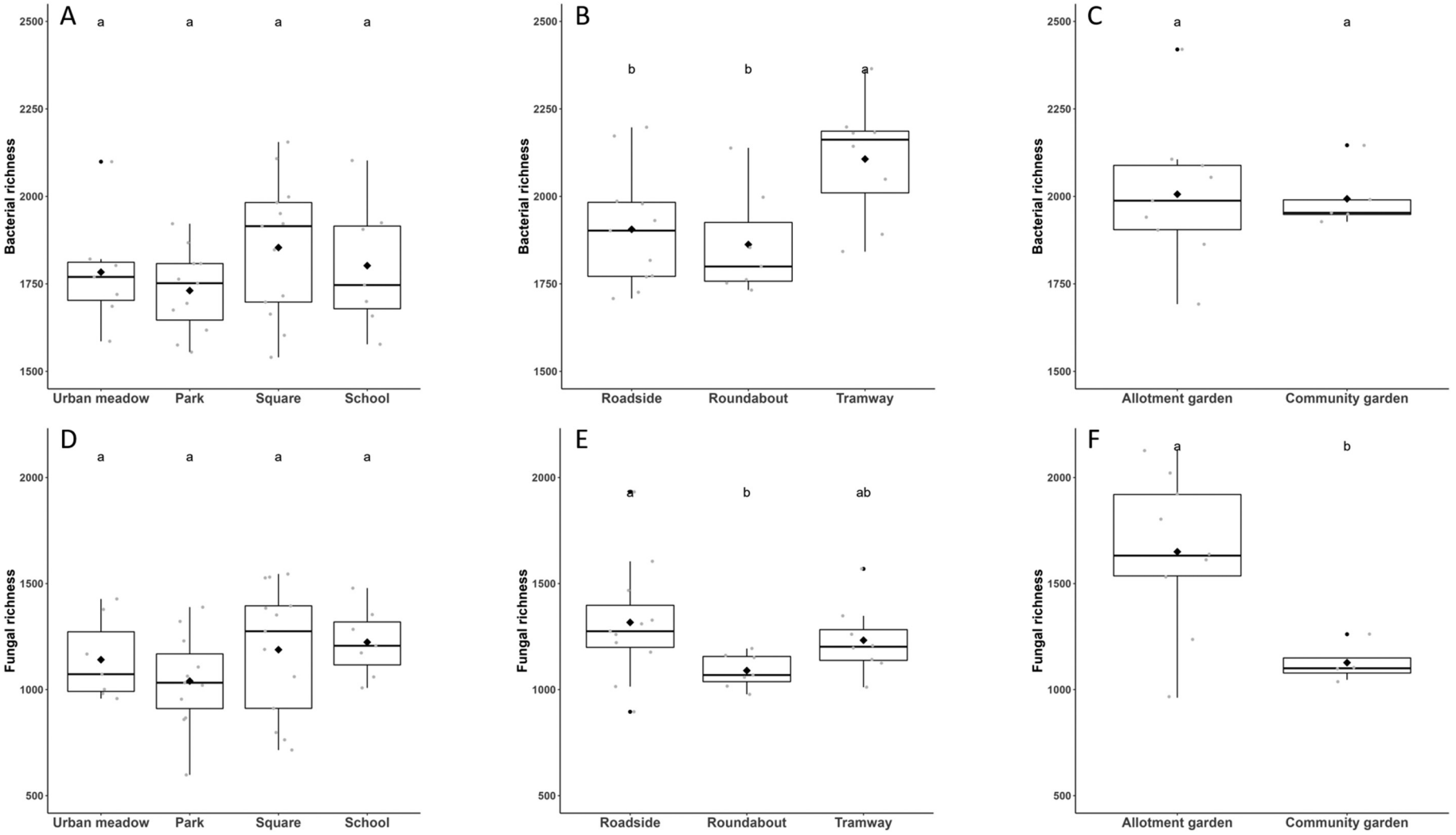

Fig. 5. Soil bacterial richness in all sub-land uses (A), in four public leisure land uses (B), in three traffic land uses (C), and in two urban agriculture land uses. Distribution of the mean value of fungal richness in all sub-land uses (D), in four public leisure land uses (E), in three traffic land uses (F), and in two urban agriculture land uses. Letters indicate significant differences between land use types ($P < 0.1$).

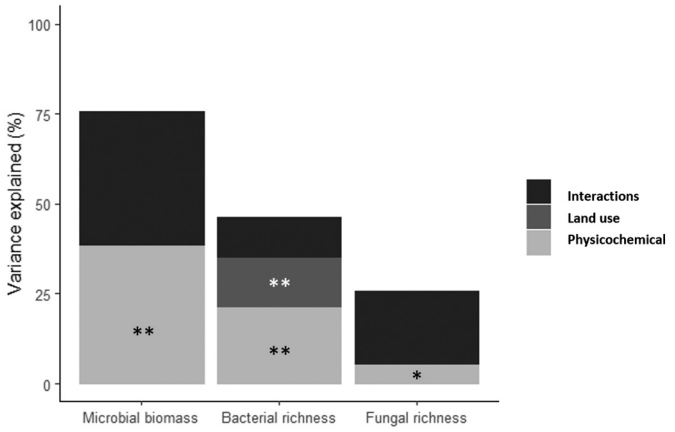

Fig. 6. Variance partitioning of the molecular microbial biomass, and bacterial and fungal diversity variables as a function of soil physicochemical and land use factors (and their interactions).

from the impact of urbanization. Altogether, the high pH, high C and N contents, low compaction and pollutant contents that characterize Dijon soils may offer better conditions for microbial development than observed in other cities where a decrease of microbial parameters was observed (Zhao et al., 2013; Rai et al., 2018; Shen et al., 2022; Yang et al., 2006; Chen et al. 201; Abdu et al., 2017).

4.2. General characteristics of microbial biomass and diversity in Dijon urban soils

With a mean value of 81 μg DNA/g soil, Dijon soils harbored higher levels of microbial biomass than soils at the national scale (61 μg DNA/g soil, Dequiedt et al., 2011), and at the scale of an agricultural landscape near Dijon (64 μg DNA/g soil, Dunn et al., 2021). Such high levels of microbial biomass in urban soils have been observed previously and reveal that urban soils represent favorable environments for microbial development (Kaye et al., 2005; Enloe et al., 2015; Stoma et al., 2020; Santorufo et al., 2021). Variance partitioning analysis highlighted that these high levels of microbial biomass were mainly related to the high soil C content, and to a lower extent to the low *C/N* ratio and high pH characterizing Dijon urban soils. Altogether, these three parameters explained almost 40 % of the variance, which is highly significant. The positive effect of soil organic carbon on microbial biomass is well documented for rural soils (Constancias et al., 2015; Horrigue et al., 2016; Dunn et al., 2021) and it has also been observed in urban soils (Zhao et al., 2013; Deeb Collet et al., 2018). Since most of the soil microorganisms are heterotrophs, microbial communities highly depend on C resources for their growth and activity (Drenovsky et al., 2010; Maron et al., 2018). A negative influence of an increase of the C/N ratio on microbial biomass has been observed in an urban context (Zhao et al., 2013) as it represents an increase of the recalcitrance of the soil organic matter to decomposition by microbial communities. Interestingly, contrastingly to other reports (Chen et al., 2013), in our study MTEs and PAHs compounds were not predictors of microbial biomass probably because they were present at very low concentrations in Dijon soils.

As observed for microbial biomass, microbial diversity was high in Dijon soils, with mean values of 1918 OTUs and 1287 OTUs for bacterial and fungal richness, respectively. Bacterial richness was within the range recently reported at the scale of an agricultural landscape near Dijon (Dunn et al., 2021), but lower than the mean value of 2079 OTUs measured at the national scale (Terrat et al., 2017). In comparison with other cities, bacterial diversity was lower than previously reported in Beijing (Hu et al., 2018) or in New-York (Joyner et al., 2019), but similar to diversity levels reported in Tucson city, USA (Chen et al., 2021). Fungal diversity was higher than previously reported in Tucson city (Chen et al., 2021). Contrasted soil physicochemical properties are likely to largely account for differences observed between cities since they were demonstrated to be the main drivers of the soil microbial diversity (Fierer and Jackson, 2006; Dequiedt et al., 2011; de Vries et al., 2012; Kuramae et al., 2012). Variance partitioning analysis highlighted that the high levels of bacterial diversity observed in Dijon were mainly ascribed to the low clay content of the soil (24 % of the variance), in agreement with previous reports (Wang et al., 2018). It may reflect the decreasing diversity of soil habitats with increasing soil clay (Chau et al., 2011). As observed for microbial biomass, MTEs and PAHs were not identified as predictors of the microbial diversity.

The dominant microbial phyla observed in the soils of Dijon were similar to those classically reported in rural soils (Karimi et al., 2018; Behnke et al., 2021; Romdhane et al., 2022) or in other cities (Hu et al., 2018; Tan et al., 2019; Gill et al., 2020; Chen et al., 2021; Delgado-Baquerizo et al., 2021). This highlights that the core soil microbial diversity does not differ between urban and rural environments. Proteobacteria and Bacteroidetes – previously described as copiotrophic bacterial groups (Pascault et al., 2013; Tardy et al., 2015; Hu et al., 2018) – dominated bacterial phyla in the three main land uses, in agreement with the global high carbon content and the related C substrate availability observed in Dijon soils. Ascomycota also dominated fungal phyla, in agreement with a recent study on five urban land uses in Adelaide city (Australia) (Baruch et al., 2020).

4.3. Microbial biomass and diversity across urban land uses

Despite general high levels of molecular microbial biomass and diversity observed at the scale of Dijon city, our study shows significant variations according to urban land uses and associated practices. Together with the identification of the microbial groups discriminating the three land uses, our results provide indications about the drivers (*i.e.,* management practices, physicochemical characteristics, plant cover) of microbial communities in urban soils.

The 'public leisure' land use overall exhibited the lowest diversity values while supporting the highest levels of molecular microbial biomass. Two characteristics of public leisure sites could explain these seemingly contradictory results. First, leisure sites have a permanent plant cover. On the one hand, this practice favors soil microbial biomass (Wang et al., 2011; Tresch et al. 2018; Wang et al., 2018) due to an increase in soil moisture and nutrient contents through massive inputs of roots exudates (Steinauer et al., 2016; Romdhane et al., 2022). On the other hand, plants select specific populations in the rhizosphere, hence a decrease of microbial diversity (García-Salamanca et al., 2013). Discrimination of public leisure sites based on a specific stimulation of fungal symbiotic microorganisms belonging to the Mucoromycota phylum (the *Glomus*, *Funneliformis*, *Claroideoglomus* and *Diversispora* genera) and to rhizobial bacterial genera (*Bradyrhizobium* and *Mesorhizobium*) illustrates selection by the plant cover. In addition to a permanent plant cover, the longer history and soil management practices of leisure sites involving no tillage, no fertilization, no watering and a permanent grass cover may confer leisure sites the status of "less perturbed and more stabilized habitats". Therefore, our results are in agreement with previous observations of a decrease of soil microbial diversity with decreasing perturbation intensity (Tardy et al., 2015; Terrat et al., 2017; Le Guillou et al., 2019; Quiquerez et al., 2022). This relationship between biodiversity and the perturbation level is described by the hump back model (Giller et al., 1997) that predicts a decrease in diversity in unstressed stable environments as a result of the selection of particular species through competitive exclusion. Microbial diversity was similar among the leisure sub-land use types, possibly as a result of similar grass covers in the meadows, parks, squares or schools where soils were sampled. An influence of vegetation on microbial diversity has been found under contrasting vegetation types (Hui et al., 2017; Tan et al., 2019; Buil et al., 2021). In leisure sites, it is likely that the diversity of discriminating symbiotic microorganisms was favored by the absence of soil tillage, the permanent plant cover and the longer history of the sites (Bonfante and Venice, 2020). Buil et al. (2021) also found that the Glomeraceae family was more dominant in less pertubed habitats. In the same way, stimulation of

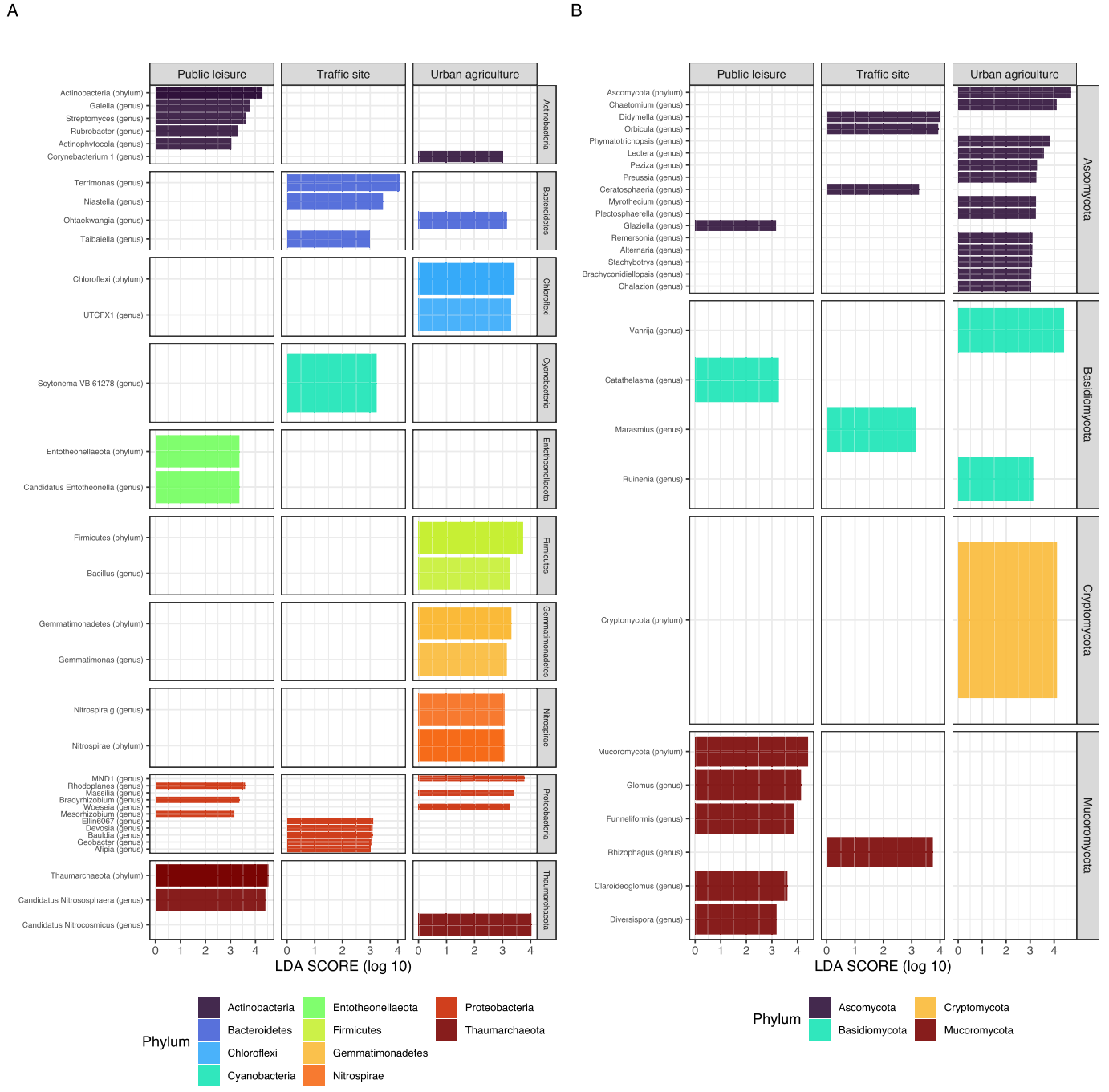

Fig. 7. Results of LEfSe for (A) archaeal/bacterial taxonomic composition and (B) fungal taxonomic composition.

several genera belonging to Actinobacteria may also reflect the stability of soil microbial habitats in public leisure sites. These groups are recognized as k-strategist copiotrophs favored in stable environments such as forest and natural grassland (Acosta-Martinez et al., 2008; Lienhard et al., 2013; Tardy et al., 2015; Stoma et al., 2020). They can also decompose recalcitrant C substrates known to be more represented in stabilized plant-covered environments (Tardy et al., 2015).

Traffic sites harbored similar levels of molecular microbial biomass than leisure sites. This is consistent with the common characteristics noted for these two urban land uses, and more particularly the permanent grass cover demonstrated to favor soil microbial biomass (see discussion above). Interestingly, microbial biomass was even higher in tramway soils compared to roadside and roundabout soils, suggesting that they may offer the best conditions for microbial development despite their very low soil depth and high artificiality. This is not in agreement with works in Stuttgart city (Lorenz and Kandeler, 2005). In Dijon, the particular care provided to tramway sites that are under a permanent grass cover maintained green all year long through regular fertilization and watering may explain the high values of soil carbon and associated microbial biomass (Naylor and Coleman-Derr, 2018). Interestingly, bacterial diversity was significantly higher in traffic site soils than in leisure site soils, but fungal diversity was not. In agreement with the hump back model (Giller et al., 1997), traffic sites may represent more perturbed and/or less stable environments for bacterial communities despite overall similar management practices. We assume that the more recent history of traffic sites may partly explain these results. On the one hand, organic matter may still not have evolved as much as in leisure sites. Consequently, easily decomposable soil organic matter may represent an important source of C substrate preferentially

stimulating fast-growing bacterial populations (Maron et al., 2018). This hypothesis may explain why bacterial diversity increased compared with leisure sites while fungal diversity did not, and why the difference was even greater in tramway site soils where the grass cover was particularly active. This is also in agreement with the stimulation of Bacteroidetes observed in traffic sites, whereas Actinobacteria dominated among the discriminating bacterial groups in leisure sites. Representatives of the Bacteroidetes phylum have been showed to be copiotrophic groups less favored in stable environments and less able to decompose complexe C substrates compared to Actinobacteria (Pascault et al., 2013; Tardy et al., 2015). The *Rhizophagus* genus was the only discriminating fungal symbiotic population in traffic sites. The presence of this mycorrhizal fungus may reflect the establishment of stable microbial habitats and increased interactions between plants and soil microbial communities in traffic sites. However, we assume that such interactions may still remain less developed than in public leisure sites because of the shorter history of these sites.

Urban agriculture represented the most perturbed of the three land uses due to the various agricultural practices applied yearly such as fertilizer inputs, soil tillage, and watering. In addition, urban agriculture differed from the other land uses because soils were devoid of a plant cover most of the year. Our results show that all these characteristics resulted in a particular ecology of the soil microbial community. The absence of a grass cover probably contributed to the low levels of microbial biomass observed compared to the other two land uses. Constrastingly, in agreement with the hump back model (Giller et al., 1997), the increased perturbation intensity in agricultural sites may explain the increase of microbial diversity compared to leisure and traffic sites. The model suggests that agricultural management practices represent a moderate stress that increases microbial diversity through decreased competitive exclusion and selection mechanisms, as reported in rural (Tardy et al., 2015; Terrat et al., 2017) and urban (Baruch et al., 2020) agrosystems. In addition to the overall depletion of microbial biomass and promotion of microbial diversity, urban agriculture sites were discriminated from the other land uses by the selection of a much higher number of specific microbial genera. This selection appeared particularly high for fungi: 17 genera were specifically detected in the urban agriculture sites, *versus* 5 in the public leisure and traffic sites. Many of these genera belonged to the Ascomycota phylum, in line with other studies performed in cultivated soils (De Castro et al., 2008; Klaubauf et al., 2010; Tardy et al., 2015) because their cellulolytic, hemicellulolytic and lignolytic abilities confer them a strong ability for plant debris decomposition (Tardy et al., 2015; Marczylo et al., 2021). The Firmicutes phylum was also stimulated. It is favored in C-rich environments or as a response to fresh, easily decomposable organic matter inputs (Pascault et al., 2013; Karimi et al., 2018). We assume that regular soil tillage and organic inputs applied by gardeners to increase soil fertility accounted for the stimulation of these copiotrophic r-strategist, fast-growing populations. Interestingly, none of the microbial groups discriminating urban agriculture sites was symbiotic, evidencing the impact of the absence of a plant cover and of the recurrence of soil tillage and mineral fertilization (Bonfante and Venice, 2020; Buil et al., 2021). The absence of a plant cover resulting from intensive soil tillage may also have contributed to select *Bacillus* genera because they can produce endospores. Spore forming may confer advantages over other phyla to survive stressful climatic conditions such as warming and desiccation, more likely to occur in bare soils (Hayden et al., 2012; Sharmin et al., 2013). The stimulation of Chloroflexi – photosynthetic oligotrophic bacteria that can thrive following strong soil exposure to sunlight in bare soils (Lan et al., 2022) – may also have resulted from the absence of a plant cover. Nitrogen inputs may also contribute to select microbial populations in urban agriculture sites, as evidenced by the stimulation of Nitrospirae (Vijayan et al., 2021) or *C. Nitrocosmicus* (Jung et al. 2016), both involved in the nitrification process.

5. Conclusion

Our study illustrates the value of city-scale sampling of different land uses to further our knowledge of urban soil ecology. Urban soils form a suitable matrix for the development of soil microbial communities, but microbial biomass, diversity and composition are shaped by land use and management practices. Public leisure and traffic sites represent a more stable microbial habitat promoting specialized k-strategist microbial populations and symbiotic interactions, while urban agriculture sites select rather generalist r-strategist copiotrophic populations. Altogether, these results highlight that it is possible to improve microbial biomass and diversity in urban soils through suitable management practices and also improve their variation at the city scale to promote various associated ecological services necessary for a sustainable urban development. Our work provides first evidence about the most suitable practices such as a permanent plant cover, regular organic matter inputs and reduced soil tillage. Further investigations including vegetation type or other urban land uses such as urban wasteland could also be relevant to refine our understanding of the influence of site history and practices on soil microbial communities.

CRediT authorship contribution statement

PAM, NCPB and LR designed the study, AC, FM, JT, GC, LB, EM, AF, JBMP performed the research, AC, SD and CD performed bioinformatic and statistical analysis, AC and PAM wrote the first draft of the manuscript and all authors contributed substantially to revision.

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Ethics approval

Not applicable.

Consent to participate

All the authors mentioned in the manuscript have agreed for authorship, read and approved the manuscript.

Consent for publication

All the authors mentioned in the manuscript have given consent for submission and subsequent publication of the manuscript.

Code availability

Not applicable.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that there is no conflict of interest.

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Appendix A. Supplementary data

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References

Abdu, N., Abdullahi, A.A., Abdulkadir, A., 2017. Heavy metals and soil microbes. Environ. Chem. Lett. 15, 65–84. https://doi.org/10.1007/s10311-016-0587-x.

Acosta-Martinez, V., Dowd, S., Sun, Y., Allen, V., 2008. Tag-encoded pyrosequencing analysis of bacterial diversity in a single soil type as affected by management and land use. Soil Biol. Biochem. 40, 2762–2770.

Alberti, M., 2015. Eco-evolutionary dynamics in an urbanizing planet. Trends Ecol. Evol. 30, 114–126. https://doi.org/10.1016/j.%20tree.2014.11.007.

Bardgett, R., van der Putten, W., 2015. Belowground biodiversity and ecosystem functioning. Nature 515, 505–511. https://doi.org/10.1038/nature13855.

Baruch, Z., Liddicoat, C., Laws, M., Marker, L., Morelli, H., Yan, D., Young, J., Breed, M., 2020. Characterising the soil fungal microbiome in metropolitan green spaces across a vegetation biodiversity gradient. Fungal Ecol. 47. https://doi.org/10.1016/j.funeco.2020.100939.

Behnke, G., Kim, N., Zabaloy, M., Riggins, C., Rodriguez-Zas, S., Villamil, M., 2021. Soil microbial indicators within rotations and tillage systems. Microorganisms 9, 1244. https://doi.org/10.3390/microorganisms9061244.

Bonfante, P., Venice, F., 2020. Mucoromycota: going to the roots of plant-interacting fungi. Fungal Biol. Rev. 34, 100–113. https://doi.org/10.1016/j.fbr.2019.12.003.

Buil, P., Renison, D., Becerra, A.G., 2021. Soil infectivity and arbuscular mycorrhizal fungi communities in four urban green sites in Central Argentina. Urban For. Urban Green. 64, 127285. https://doi.org/10.1016/j.ufug.2021.127285.

Chau, J.F., Bagtzoglou, A.C., Willig, M.R., 2011. The effect of soil texture on richness and diversity of bacterial communities. Environ. Forensic 12, 333–341.

Chemidlin Prévost-Bouré, N., Christen, R., Dequiedt, S., Mougel, C., Lelièvre, M., Jolivet, C., Shahbazkia, H.R., Guillou, L., Arrouays, D., Ranjard, L., 2011. Validation and application of a PCR primer set to quantify fungal communities in the soil environment by real-time quantitative PCR. PLoS One. 6 (9), e24166. https://doi.org/10.1371/journal.pone.0024166.

Chen, J., He, F., Sun, X., Zhang, X., Zheng, J., Zheng, J., Li, L., Yu, X., Wang, J., 2013. Heavy metal pollution decreases microbial abundance, diversity and activity within particle-size fractions of a paddy soil. FEMS Microbiol. Ecol. 87. https://doi.org/10.1111/1574-6941.12212.

Chen, Y., Martinez, A., Cleavenger, S., Rudolph, J., Barberán, A., 2021. Changes in soil microbial communities across an urbanization gradient: a local-scale temporal study in the arid southwestern USA. Microorganisms 9 (7), 1470. https://doi.org/10.3390/microorganisms9071470.

Christel, A., Maron, P.A., Ranjard, L., 2021. Impact of farming systems on soil ecological quality: a meta-analysis. Environ. Chem. Lett. 19. https://doi.org/10.1007/s10311-021-01302-y.

Climate data, 2022. Consulted the 5th september 2022. Available on https://fr.climate-data.org/europe/france/bourgogne/dijon-338/.

Constancias, F., Terrat, S., Saby, N., Horrigue, W., Villerd, J., Guillemin, J.P., Luc, Biju-Duval, Nowak, V., Dequiedt, S., Ranjard, L., Chemidlin Prevost-Boure, N., 2015. Mapping and determinism of soil microbial community distribution across an agricultural landscape. Microbiol.Open 4. https://doi.org/10.1002/mbo3.255.

De Castro, A.P., Quirino, B.F., Pappas, G., Kurokawa, A.S., Neto, E.L., Krüger, R.H., 2008. Diversity of soil fungal communities of cerrado and its closely surrounding agriculture fields. Arch. Microbiol. 190, 129–139. https://doi.org/10.1007/s00203-008-0374-6 PMID: 18458875.

Deeb Collet, M., Groffman, P., Joyner, J., Lozefski, G., Paltseva, A., Lin, B., Mania, K., Cao, D., McLaughlin, J., Prithiviraj, B., Kerwin, J., Cheng, Z., 2018. Soil and microbial properties of green infrastructure stormwater management systems. Ecol. Eng. 125, 68–75. https://doi.org/10.1016/j.ecoleng.2018.10.017.

Delgado-Baquerizo, M., Eldridge, D.J., Liu, Y.R., Sokoya, B., Wang, J.T., Hu, H.W., et al., 2021. Global homogenization of the structure and function in the soil microbiome of urban greenspaces. Sci. Adv. 7 (28), eabg5809. https://doi.org/10.1126/sciadv.abg5809 PMID: 34244148; PMCID: PMC8270485.

Dequiedt, S., Saby, N.P.A., Lelievre, M., Jolivet, C., Thioulouse, J., Toutain, B., Arrouays, D., Bispo, A., Lemanceau, P., Ranjard, L., 2011. Biogeographical patterns of soil molecular microbial biomass as influenced by soil characteristics and management. Glob. Ecol. Biogeogr. 20, 641–652. https://doi.org/10.1111/j.1466-8238.2010.00628.x.

Dijon city, 2022. Personnal Communication.

Djemiel, C., Dequiedt, S., Karimi, B., Cottin, A., Girier, T., Djoudi, Y., Wincker, P., Lelièvre, M., Mondy, S., Chemidlin Prevost-Boure, N., Maron, P.A., Ranjard, L., Terrat, S., 2020. BIOCOM-PIPE: a new user-friendly metabarcoding pipeline for the characterization of microbial diversity from 16S, 18S and 23S rRNA gene amplicons. BMC Bioinformatics 21. https://doi.org/10.1186/s12859-020-03829-3.

Drenovsky, R.E., Steenwerth, K.K.L., Jackson, L.E., Scow, K.M., 2010. Land use and climatic factors structure regional patterns in soil microbial communities. Glob. Ecol. Biogeogr. 19, 27–39. https://doi.org/10.1111/j.1466-8238.2009.00486.x.

Dunn, L., Lang, C., Marilleau, N., Terrat, S., Biju-Duval, L., Lelièvre, M., Perrin, S., Chemidlin Prévost-Bouré, N., 2021. Soil microbial communities in the face of changing farming practices: a case study in an agricultural landscape in France. PLoS One 16 (6), e0252216.

Edmondson, J., Davies, Z., Gaston, K., Leake, J., 2014. Urban cultivation in allotments maintains soil qualities adversely affected by conventional agriculture. J. Appl. Ecol. 51. https://doi.org/10.1111/1365-2664.12254.

Enloe, H., Lockaby, B.G., Zipperer, W.C., Somers, G.L., 2015. Urbanization effects on soil nitrogen transformations and microbial biomass in the subtropics. Urban Ecosyst. 18 (3), 963–976. https://doi.org/10.1007/s1125 2-015-0462-8.

FAOSTAT, 2021. Food and Agriculture Organization of the United Nations (FAO). Available at: https://www.fao.org/fasotat/en/#home.

Feng, X., Sun, X., Li, S., Zhang, J., Hu, N., 2020. Relationship study among soils physicochemical properties and bacterial communities in urban green space and promotion of its composition and network analysis. Agron. J. 113. https://doi.org/10.1002/agj2.20460.

Fenoglio, M.S., Rossetti, M.R., Videla, M., 2020. Negative effects of urbanization on terrestrial arthropod communitiesA meta-analysis. Global Ecol. Biogeogr. 29, 1412–1429. https://doi.org/10.1111/geb.13107.

Fierer, N., Jackson, R.B., 2006. The diversity and biogeography of soil bacterial communities. Proc. Natl. Acad. Sci. U. S. A. 103, 626–631. https://doi.org/10.1073/pnas.0507535103.

Foti, L., Dubs, F., Gignoux, J., Lata, J.C., Lerch, T., Mathieu, J., Nold, F., Nunan, N., Raynaud, X., Abbadie, L., Barot, S., 2017. Trace element concentrations along a gradient of urban pressure in forest and lawn soils of the Paris region (France). Sci. Total Environ. 598, 938–948. https://doi.org/10.1016/j.scitotenv.2017.04.111.

García-Salamanca, A., Molina-Henares, M.A., van Dillewijn, P., Solano, J., Pizarro-Tobías, P., Roca, A., Duque, E., Ramos, J.L., 2013. Bacterial diversity in the rhizosphere of maize and the surrounding carbonate-rich bulk soil. Microb. Biotechnol. 6, 36–44.

Gill, A., Purnell, K., Palmer, M., Stein, J., Mcguire, K., 2020. Microbial composition and functional diversity differ across urban green infrastructure types. Front. Microbiol. 11. https://doi.org/10.3389/fmicb.2020.00912.

Giller, K.E., Beare, M.H., Lavelle, P., Izac, A.M.N., Swift, M.J., 1997. Agricultural intensification, soil biodiversity and agroecosystem function. Appl. Soil Ecol. 6, 3–16. https://doi.org/10.1016/S0929-1393(96)00149-7.

Guilland, C., Maron, P.A., Damas, O., Ranjard, L., 2018. Biodiversity of urban soils for sustainable cities. Environ. Chem. Lett. 16, 1267–1282. https://doi.org/10.1007/s10311-018-0751-6 hal-02620873.

Hahs, A., Evans, K., 2015. Expanding fundamental ecological knowledge by studying urban ecosystems. Funct. Ecol. 29. https://doi.org/10.1111/1365-2435.12488.

Hayden, H.L., Mele, P.M., Bougoure, D.S., Allan, C.Y., Norng, S., Piceno, Y.M., Brodie, E.L., Desantis, T.Z., Andersen, G.L., Williams, A.L., Hovenden, M.J., 2012. Changes in the microbial community structure of bacteria, archaea and fungi in response to elevated CO (2) and warming in an Australian native grassland soil. Environ. Microbiol. 12, 3081–3096. https://doi.org/10.1111/j.1462-2920.2012.02855.x Epub 2012 Oct 8 PMID: 23039205.

Horrigue, W., Dequiedt, S., Chemidlin Prévost-Bouré, N., Jolivet, C., Saby, N.P.A., Arrouays, D., Bispo, A., Maron, P.A., Ranjard, L., 2016. Predictive model of soil molecular microbial biomass. Ecol. Indic. 64, 203–211. https://doi.org/10.1016/j.ecolind.2015.12.004.

Hui, N., Jumpponen, A., Francini, G., Kotze, D.J., Liu, X., Romantschuk, M., Strömmer, R., Setälä, H., 2017. Soil microbial communities are shaped by vegetation type and park age in cities under cold climate. Environ. Microbiol. 19, 1281–1295.

Hu, Y., Dou, X., Li, J., Li, F., 2018. Impervious surfaces alter soil bacterial communities in urban areas: a case study in Beijing, China. Front Microbiol. 27 (9), 226. https://doi.org/10.3389/fmicb.2018.00226 PMID: 29545776; PMCID: PMC5839015.

Joimel, S., Cortet, J., Jolivet, C.C., Saby, N., Chenot, E.D., Branchu, P., Consalès, J.N., Lefort, C., Morel, J.L., Schwartz, C., 2016. Physicochemical characteristics of topsoil for contrasted forest, agricultural, urban and industrial land uses in France. Sci. Total Environ. 545. https://doi.org/10.1016/j.scitotenv.2015.12.035.

Joyner, J.L., Kerwin, J., Deeb, M., Lozefski, G., Prithiviraj, B., Paltseva, A., McLaughlin, J., Groffman, P., Cheng, Z., Muth, T.R., 2019. Green infrastructure design influences communities of urban soil bacteria. Front. Microbiol. 16 (10), 982. https://doi.org/10.3389/fmicb.2019.00982 PMID: 31156569; PMCID: PMC6531853.

Jung, M.Y., Kim, J.G., Sinninghe Damsté, J.S., Rijpstra, W.I., Madsen, E.L., Kim, S.J., Hong, H., Si, O.J., Kerou, M., Schleper, C., Rhee, S.K., 2016. A hydrophobic ammonia-oxidizing archaeon of the Nitrosocosmicus clade isolated from coal tar-contaminated sediment. Environ. Microbiol. Rep. 8 (6), 983–992. https://doi.org/10.1111/1758-2229.12477.

Karimi, B., Terrat, S., Dequiedt, S., Saby, N.P.A., Horrigue, W., Lelievre, M., Nowak, V., Jolivet, C., Arrouays, D., Wincker, P., Cruaud, C., Bispo, A., Maron, P.A., Chemidlin Prévost-Bouré, N., Ranjard, L., 2018. Biogeography of soil bacteria and archaea across France. Sci. Adv. 4, eaat1808.

Karimi, B., Cahurel, J.Y., Gontier, L., Charlier, L., Chovelon, M., Mahé, H., Ranjard, L., 2020. A meta-analysis of the ecotoxicological impact of viticultural practices on soil biodiversity. Environ. Chem. Lett. 18. https://doi.org/10.1007/s10311-020-01050-5.

Kaye, J., Mcculley, R., Burke, I., 2005. Carbon fluxes, nitrogen cycling, and soil microbial communities in adjacent urban, native and agricultural ecosystems. Glob. Change Biol. 11, 575–587. https://doi.org/10.1111/j.1365-2486.2005.00921.x.

Klaubauf, S., Inselsbacher, E., Zechmeister-Boltenstern, S., Wanek, W., Gottsberger, R., Strauss, J., Gorfer, M., 2010. Molecular diversity of fungal communities in agricultural soils from Lower Austria. Fungal Divers. 44, 65–75 PMID: 23794962.

Kuramae, E.E., Yergeau, E., Wong, L.C., Pijl, A.S., van Veen, J.A., Kowalchuk, G., 2012. Soil characteristics more strongly influence soil bacterial communities than land-use type. FEMS Microbiol. Ecol. 79, 12–24. https://doi.org/10.1111/j.1574-6941.2011.01192.x.

Lan, J., Wang, S., Wang, J., Qi, X., Long, Q., Huang, M., 2022. The shift of soil bacterial community after afforestation influence soil organic carbon and aggregate stability in karst region. Front. Microbiol. 13, 901126. https://doi.org/10.3389/fmicb.2022.901126.

Le Guillou, C., Chemidlin Prévost-Bouré, N., Karimi, B., Akkal-Corfini, N., Dequiedt, S., Nowak, V., Terrat, S., Menasseri-Aubry, S., Viaud, V., Maron, P.A., Ranjard, L., 2019. Tillage intensity and pasture in rotation effectively shape soil microbial communities at a landscape scale. Microbiol. Open 8 (4), e00676.

Lienhard, P., Terrat, S., Prévost-Bouré, N.C., Nowak, V., Régnier, T., Sayphoummie, S., Panyasiri, K., Tivet, F., Mathieu, O., Levêque, J., Maron, P.A., Ranjard, L., 2013.

Pyrosequencing evidences the impact of cropping on soil bacterial and fungal diversity in Laos tropical grassland. Agron. Sustain. Dev. https://doi.org/10.1007/s13593-013-0162-9.

Liu, L., Barberán, A., Gao, C., Zhaochen, Z., Wang, M., Wurzburger, N., Wang, X., Zhang, R., Li, J., Zhang, J., 2021. Impact of urbanization on soil microbial diversity and composition in the megacity of Shanghai. Land Degrad. Dev. 33. https://doi.org/10.1002/ldr.4145.

Lorenz, K., Kandeler, E., 2005. Biochemical characterization of urban soil profiles from Stuttgart, Germany. Soil Biol. Biochem. 37, 1373–1385. https://doi.org/10.1016/j.soilbio.2004.12.009.

Marczylo, E., Macchiarulo, S., Gant, T., 2021. Metabarcoding of soil fungi from different urban greenspaces around Bournemouth in the UK. EcoHealth 18. https://doi.org/10.1007/s10393-021-01523-1.

Maron, P.A., Sarr, A., Kaisermann, A., Lévêque, J., Mathieu, O., Guigue, J., Karimi, B., Bernard, L., Dequiedt, S., Terrat, S., Chabbi, A., Ranjard, L., 2018. High microbial diversity promotes soil ecosystem functioning. 16Appl. Environ. Microbiol. 84 (9), e02738-17. https://doi.org/10.1128/AEM.02738-17 PMID: 29453268; PMCID: PMC5930326.

Martiny, J.B., Eisen, J.A., Penn, K., Allison, S.D., Horner-Devine, M.C., 2011. Drivers of bacterial beta-diversity depend on spatial scale. Proc. Natl. Acad. Sci. U. S. A. 108 (19), 7850–7854. https://doi.org/10.1073/pnas.1016308108 Epub 2011 Apr 25. PMID: 21518859; PMCID: PMC3093525.

Mata, L., Ramalho, C., Kennedy, J., Parris, K., Valentine, L., Miller, M., Bekessy, S., Hurley, S., Cumpston, Z., 2020. Bringing nature back into cities. People Nat. 2. https://doi.org/10.1002/pan3.10088.

Matteoli, F., Silva, A., Feiler, H., Araújo, V., Cardoso, E., 2022. Predicting soil farming system and attributes based on soil bacterial community. Appl. Soil Ecol. 171, 104335. https://doi.org/10.1016/j.apsoil.2021.104335.

McKinney, L.M., 2006. Urbanization as a major cause of biotic homogenization. Biol. Conserv. 127 (3), 247–260. https://doi.org/10.1016/j.biocon.2005.09.005.

Moore, D., 1995. The Basic Practice of Statistics. Freeman.

Morel, J.L., Florentin, L., Scwartz, C., 1999. Définition, diversité et fonctions des sols urbains. Comptes rendus des séances de l'Académie d'Agriculture de France. 85, pp. 141–152.

Morel, J.L., Chenu, C., Lorenz, K., 2015. Ecosystem services provided by soils of urban, industrial, trafc, mining, and military areas (SUITMAs). J. Soils Sediments 15 (8), 1659–1666. https://doi.org/10.1007/s11368-014-0926-0.

Nawrocki, E.P., Eddy, S.R., 2013. Infernal 1.1: 100-fold faster RNA homology searches. Bioinformatics 29 (22), 2933–2935. https://doi.org/10.1093/bioinformatics/btt509 15.

Naylor, D., Coleman-Derr, D., 2018. Drought stress and root-associated bacterial communities. Front. Plant Sci. 9 (8), 2223. https://doi.org/10.3389/fpls.2017.02223 PMID: 29375600; PMCID: PMC5767233.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Wagner, H., 2011. Vegan: Community Ecology Package. R Package Version 2.2-1.

Pandey, S., Abid, M., Khan, M.M., 2018. Diversity, Functions, and Stress Responses of Soil Microorganisms. https://doi.org/10.1007/978-981-10-5514-0_1.

Pascault, N., Ranjard, L., Kaisermann, A., Bachar, D., Christen, R., Terrat, S., Mathieu, O., Lévêque, J., Mougel, C., Henault, C., Lemanceau, P., Péan, M., Boiry, S., Fontaine, S., Maron, P.A., 2013. Stimulation of different functional groups of bacteria by various plant residues as a driver of soil priming effect. Ecosystems 16, 810–822. https://doi.org/10.1007/s10021-013-9650-7.

Pollak, L., 2006. The landscape for urban reclamation-infrastructures for the every days pace that includes nature. Lotus Int. 128, 32–45.

Pouyat, R.V., Szlavecz, K., Yesilonis, I.D., Groffman, P.M., Schwarz, K., 2010. Chemical, physical, and biological characteristics of urban soils. In: Aitkenhead-Peterson, J., Volder, A. (Eds.), Urban Ecosyst. Ecol https://doi.org/10.2134/agronmonogr55.c7.

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Glöckner, F., 2012. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic Acids Res. 41. https://doi.org/10.1093/nar/gks1219.

Quiquerez, A., Garcia, J.P., Dequiedt, S., Djemiel, C., Terrat, S., Mathieu, O., Sassi, A., Ranjard, L., 2022. Legacy of land-cover changes on soil microbiology in Burgundy vineyards (Pernand-Vergelesses, France). OENO One 56, 223. https://doi.org/10.20870/oeno-one.2022.56.2.5432.

Rai, P., Rai, A., Singh, S., 2018. Change in Soil Microbial Biomass Along a Rural-Urban Gradient in Varanasi (U.P., India). 2, pp. 15–21. https://doi.org/10.1080/24749508.2018.1438743.

Ramette, A., 2007. Multivariate analyses in microbial ecology. FEMS Microbiol. Ecol. 62, 142–160. https://doi.org/10.1111/j.1574-6941.2007.00375.x.

Ramirez, K.S., Leff, J.W., Barberán, A., Bates, S.T., Betley, J., Crowther, T.W., Kelly, E.F., Oldfield, E.E., Shaw, E.A., Steenbock, C., Bradford, M.A., Wall, D.H., Fierer, N., 2014. Biogeographic patterns in belowground diversity in New York City's Central Park are similar to those observed globally. Proc. Biol. Sci. https://doi.org/10.1098/rspb.2014.1988.

Reese, A.T., Savage, A., Youngsteadt, E., McGuire, K.L., Koling, A., Watkins, O., Frank, S.D., Dunn, R.R., 2016. Urban stress is associated with variation in microbial species composition-but not richness-in Manhattan. ISME J 10 (3), 751–760. https://doi.org/10.1038/ismej.2015.152.

Romdhane, S., Spor, A., Banerjee, S., Breuil, M.C., Bru, D., Chabbi, A., Hallin, S., Van der Heijden, M.G.A., Saghai, A., Philippot, L., 2022. Land-use intensification differentially affects bacterial, fungal and protist communities and decreases microbiome network complexity. Environ. Microbiome 17, 1.

Santorufo, L., Memoli, V., Panico, S.C., Esposito, F., Vitale, L., Di Natale, G., Trifuoggi, M., Barile, R., De Marco, A., Maisto, G., 2021. Impact of anthropic activities on soil quality under different land uses. Int. J. Environ. Res. Public Health 18 (16), 8423. https://doi.org/10.3390/ijerph18168423.

Schwartz, C., Florentin, L., Charpentier, D., Muzika, S., 2001. Le pédologue en milieux industriels et urbains. Etude et Gestion Des Sols 8, 135–148.

Segata, N., Izard, J., Waldron, L., Gevers, D., Miropolsky, L., Garrett, W.S., Huttenhower, C., 2011. Metagenomic biomarker discovery and explanation. Genome Biol. 12 (6), R60 24.

Sharmin, F., Wakelin, S., Huygens, F., Hargreaves, M., 2013. Firmicutes dominate the bacterial taxa within sugar-cane processing plants. Sci. Rep. 3, 3107. https://doi.org/10.1038/srep03107 PMID: 24177592; PMCID: PMC3814580.

Shen, H., Yang, B., Wang, H., Sun, W., Jiao, K., Qin, G., 2022. Changes in soil ectomycorrhizal fungi Community in oak Forests along the urban-rural gradient. Forests 13 (5), 675. https://doi.org/10.3390/f13050675.

Steinauer, K., Chatzinotas, A., Eisenhauer, N., 2016. Root exudate coktails : the link between plant diversity and soil microorganisms? Ecol. Evol. 6. https://doi.org/10.1002/ece3.2454.

Stoma, G., Manucharova, N., Belokopytova, N., 2020. Biological activity of microbial communities in soils of some Russian cities. Eurasian Soil Sci. 53, 760–771. https://doi.org/10.1134/S1064229320060125.

Tan, K., Su, C., Liu, Z., Yiyi, 2019. The composition and diversity of soil bacterial and fungal communities along an urban-to-rural gradient in South China. Forests 10, 797. https://doi.org/10.3390/f10090797.

Tardy, V., Spor, A., Mathieu, O., Leveque, J., Terrat, S., Plassart, P., Maron, P.A., 2015. Shifts in microbial diversity through land use intensity as drivers of carbon mineralization in soil. Soil Biol. Biochem. 90, 204–213. https://doi.org/10.1016/j.soilbio.2015.08.010.

Terrat, S., Christen, R., Dequiedt, S., Lelievre, M., Nowak, V., Regnier, T., Ranjard, L., 2012. Molecular biomass and MetaTaxogenomic assessment of soil microbial communities as influenced by soil DNA extraction procedure. Microb. Biotechnol. 5, 135–141. https://doi.org/10.1111/j.1751-7915.2011.00307.x.

Terrat, S., Plassart, P., Bourgeois, E., Ferreira, S., Dequiedt, S., Adele-Dit-De-Renseville, N., Lemanceau, P., Bispo, A., Chabbi, A., Maron, P.A., Ranjard, L., 2015. Meta-barcoded evaluation of the ISO standard 11063 DNA extraction procedure to characterize soil bacterial and fungal community diversity and composition. Microb. Biotechnol. 8 (1), 131–142. https://doi.org/10.1111/1751-7915.12162.

Terrat, S., Horrigue, W., Dequietd, S., Saby, N.P.A., Lelièvre, M., Nowak, V., Tripied, J., Régnier, T., Jolivet, C., Arrouays, D., Wincker, P., Cruaud, C., Karimi, B., Bispo, A., Maron, P.A., Chemidlin Prévost-Bouré, N., Ranjard, L., 2017. Mapping and predictive variations of soil bacterial richness across France. PLoS ONE 12 (10), e0186766. https://doi.org/10.1371/journal.pone.0186766.

Terrat, S., Djemiel, C., Journay, C., Karimi, B., Dequiedt, S., Horrigue, W., Maron, P.A., Chemidlin Prévost-Bouré, N., Ranjard, L., 2020. ReClustOR: a re-clustering tool using an open-reference method that improves operational taxonomic unit definition. Methods Ecol. Evol. 11 (1), 168–180 .

Tresch, S., Moretti, M., Le Bayon, R.C., Mäder, P., Frey, D., Zanetta, A., Fliessbach, A., 2018. A Gardener's Influence on Urban Soil Quality. Front. Environ. Sci. 6. https://doi.org/10.3389/fenvs.2018.00025.

Turley, N., Bell-Dereske, L., Evans, S., Brudvig, L., 2020. Agricultural land-use history and restoration impact soil microbial biodiversity. J. App. Ecol. 57. https://doi.org/10.1111/1365-2664.13591.

United Nations, 2018. World Urbanization Prospects 2018. Department of Economic and Social Affairs, Population Dynamics.

Vasenev, V., Kuzyakov, Y., 2018. Urban soils as hotspots of anthropogenic carbon accumulation: review of stocks, mechanisms and driving factors. Land Degrad. Dev. 29. https://doi.org/10.1002/ldr.2944.

Van Der Heijden, M.G.A., Bardgett, R.D., Van Straalen, N.M., 2008. The unseen majority : soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol. Lett. 11, 296–310. https://doi.org/10.1111/j.1461-0248.2007.01139.x.

Vijayan, A., Rejish, K., VJ, Pillai, D., Geetha, P., Joseph, V., Sarojini, B., 2021. Nitrospira as versatile nitrifiers: taxonomy, ecophysiology, genome characteristics, growth, and metabolic diversity. J. Basic Microbiol. 61. https://doi.org/10.1002/jobm.202000485.

Vivant, A.L., Garmyn, D., Maron, P.A., Nowak, V., Piveteau, P., 2013. Microbial diversity and structure are drivers of the biological barrier effect against listeria monocytogenes in soil. PLoS ONE 8 (10), e76991. https://doi.org/10.1371/journal.pone.0076991.

de Vries, T.F., Manning, P., Tallowin, R.B.J., Mortimer, R.S., Pilgrim, S.E., Harrison, A.K., Hobbs, J.P., Quirk, H., Shipley, B., Cornelissen, H.C.J., Attge, J., Bardgett, D.R., 2012. Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. Ecol. Lett. 15, 1230–1239. https://doi.org/10.1111/j.1461-0248.2012.01844.x.

Wang, M.E., Markert, B., Shen, W., Chen, W., Peng, C., Ouyang, Z., 2011. Microbial biomass carbon and enzyme activities of urban soils in Beijing. Environ. Sci. Pollut. Res. Int. 18, 958–967. https://doi.org/10.1007/s11356-011-0445-0.

Wang, H., Cheng, M., Dsouza, M., Weisenhorn, P., Zheng, T., Jack, G., 2018. Soil bacterial diversity is associated with human population density in urban greenspaces. Environ. Sci. Technol. 52. https://doi.org/10.1021/acs.est.7b06417.

Yang, Y., Campbell, C.D., Clark, L., Cameron, C.M., Paterson, E., 2006. Microbial indicators of heavy metal contamination in urban and rural soils. Chemosphere 63 (11), 1942–1952. https://doi.org/10.1016/j.chemosphere.2005.10.009.

Zhao, D., Li, F., Yang, Q., Wang, R., Song, Y., Tao, Y., 2013. The influence of different types of urban land use on soil microbial biomass and functional diversity in BeijingChina. Soil Use Manag. 29. https://doi.org/10.1111/sum.12034.

Zhalnina, K., Dias, R., de Quadros, P.D., Davis-Richardson, A., Camargo, F.A., Clark, I.M., McGrath, S.P., Hirsch, P.R., Triplett, E.W., 2015. Soil pH determines microbial diversity and composition in the park grass experiment. Microb. Ecol. 69 (2), 395–406. https://doi.org/10.1007/s00248-014-0530-2.