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Research

Microbial diversity and cover plants in de-sealed urban soil as strategies for mitigating anthropogenic volatile organic compounds

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Abstract
Urbanization exacerbates soil degradation, compromising global soil health and biodiversity. To reduce this, strategies for soil de-sealing and bioremediation are necessary. In a mesocosm experiment using a de-sealed soil from an urban site as substrate, an inoculum of arbuscular mycorrhizal fungi (AMF) and two cover plants, *Cynara cardunculus* L. and *Trifolium repens* L., were utilized to assess their effects on volatile organic compound (VOC) emissions and soil microbial community dynamics. The soil status was investigated employing soil VOC and metabarcoding analyses. Our results showed that the soil VOC emission was mainly composed by anthropogenic derived VOCs, especially arene and furan classes. These two classes were shown to be less concentrated in *C. cardunculus* soils, with and without AM fungal inoculation, suggesting a positive impact of these conditions on soil health restoration. Additionally, AM fungal inoculation of *C. cardunculus* resulted in increased bacterial alpha diversity, with enhanced Proteobacteria/Acidobacteria, Cyanobacteria/Chloroflexi, and Fungi/Bacteria ratios, suggesting an improvement in soil quality conditions. In our experimental conditions, order Chloroflexales and specific bacterial genera, including *Ralstonia*, *Delftia*, *Ramlibacter*, were identified as contributors to VOC degradation, highlighting their adaptability in contaminated environments. Overall, this study provided evidence on the importance of integrating AM fungal inoculation and specific flowerbed/ornamental plants in urban soil management after de-sealing processes.

Keywords AMF · Beneficial microbes · Bioremediation · Urbanization · Pollutant breakdown · Soil degradation · Soil microbiome

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1 Introduction

Global urbanization exacerbates climate change [1, 2], causing extreme ecosystem alterations that impact soil health [3–5]. By 2050, it is predicted that half of the world's population will live in urban areas [6], leading to land degradation [7] and a decline in soil ecosystem services [6, 8, 9]. Soil sealing, which involves covering soil with waterproof materials due to urban development [10], is considered a form of land degradation that negatively impacts soil health [11]. This process can have a negative impact on soil health, by reducing its fertility, biodiversity, water infiltration, increasing surface runoff and pollution, and intensifying greenhouse gas emissions [12–14]. To mitigate these effects, there is an urgent need to increase green spaces in urban areas. The primary recommended actions include soil de-sealing, to reinstate the optimal soil physicochemical properties [15, 16]. However, the use of de-sealed soils in urban green spaces is still challenging, since these soils can be potentially contaminated by anthropogenic compounds, as well as they may have issues with soil compaction and drainage [15]. Additionally, the potential fertility of soils that have been de-sealed remains largely unknown [15].

In this scenario, a promising approach to restore the health status of de-sealed soils can be represented by bioremediation [17]. Bioremediation is an eco-friendly method that involves the use of soil microbes and plants (i.e., phytoremediation), suitable to restore soil health in urban areas [17, 18]. This approach has deemed to reduce soil pollutants also coming from urban activities such as traffic and industries [19, 20]. The use of arbuscular mycorrhizal fungi (AMF) is considered an important tool for improving soil health and facilitating ecological restoration [21, 22]. Particularly, AMF form symbiotic associations with approximately 80% of land plants, enhancing soil fertility by increasing plant nutrient uptake and promoting their growth [23, 24]. They are crucial for plant survival, especially in polluted environments, as they can enhance plant tolerance through improved mineral nutrition [25]. AM fungal mycelium may help to compensate for reduced root growth caused by pollutants, and some fungi are well-adapted to harsh soil conditions [26]. The Mycorrhizal Assisted Remediation (MAR) effectively remediated soils contaminated with organic and inorganic pollutants, such as heavy metals and poly-aromatic hydrocarbons (PHAs) [27–31]. Additionally, the use of both AM fungal and bacterial inocula (e.g., *Bacillus*, *Sphingomonas*, *Acinetobacter* sp.), or of inocula based on *Trichoderma* sp., has allowed to reduce soil contamination. [32–36]. However, to the best of our knowledge, the potential of AM fungal inoculation in restoring desealed soils has not yet been explored. Although colonization can still begin from resting spores, hyphae, or root fragments containing fungal structures, even in highly hydrocarbon-polluted sites [25], no information is available regarding the survival and functionality of native AMF inhabiting degraded de-sealed soils. Concerning phytoremediation, cardoon (*Cynara cardunculus* L.; [37–39]) and white clover (*Trifolium repens* L.; [40, 41]) are promising plant species in Mediterranean and temperate areas, respectively. They are considered for their ability to thrive in stressful, polluted environments and can absorb and accumulate contaminants, contributing to sustainable soil remediation and ecosystem restoration [42, 43].

Soil microbial communities are intrinsically linked to its physicochemical properties, and are adapted to its various environmental conditions [44–48]. In addition, the microorganisms are also able to degrade toxic compounds [49–55], playing a crucial role in restoring soil health by enhancing pollutant breakdown [48]. Changes regarding the improvement of soil health status may be predictable based on several indicators [56–59] and volatile organic compound (VOC) profiling is still a pioneer method [60, 61]. Soils represent both a sink and a source of VOCs [62–64]. Along with the presence of biogenic VOC (BVOC) imprint (e.g., alcohols, ketones, and terpenes) the de-sealed soils may have a strong anthropogenic VOC (AVOC) signature given by BTEX (benzene, toluene, xylene, and related chemicals) and polycyclic aromatic hydrocarbons (PAHs) with negative effects on human health [65, 66]. Nevertheless, reusing the soil after de-sealing may promote a fast breakdown of these VOCs from both biological and chemical point of view [67, 68]. Hence, the VOC profile could mirror the soil health status and could enhance our knowledge regarding the microbial community activity in soils subjected to different managements and bioremediation methods.

The aim of this study was to investigate the status of an urban soil after de-sealing using VOC emission and microbial communities as markers for soil health and fertility in a mesocosm experiment with soil collected from a recently de-sealed area. Particularly, a bioremediation approach based on the use of *Cynara cardunculus* and *Trifolium repens* as flowerbed/ornamental, due to the important role of these species in phytoremediation and their utilization in urban greenspaces was exploited. In addition, *C. cardunculus* pots were also inoculated with a commercial AM fungal inoculum, to assess the combined effect mediated by both plants and beneficial fungi. The rationale behind this study was connected to three questions:

1. can an AM fungal inoculum successfully colonize plants in a reused soil after de-sealing?
2. can an AM fungal inoculum and cover plants be effective in restoring the health status of a de-sealed soil through the improvement of pollutant (i.e., AVOC) breakdown?
3. can native AMF survive, recover and colonize plant roots after soil de-sealing, further contributing to the soil health status restoration?

2 Materials and methods

2.1 Site and soil sample collection

The soil sampled in 2023 has originated from a sealed urban site in Prato, Tuscany (43° 52′ 09.1″ N 11° 03′ 54.6″ E), in the frame of the project Prato Urban Jungle (https://www.uia-initiative.eu/en/uia-cities/prato). The project aimed to re-naturalize areas of the Prato Municipality by improving the soil through de-sealing and further developing "*Urban Jungles*", i.e., regions with a high density of green. After de-sealing intervention, approximately 40 kg of soil was collected from different 18 random points at approximately 60 cm depth below the road surface, and stored at 4 °C. The sampled site showed a complex subsurface composition, which included the following layers: the uppermost layer made up of asphalt at a depth of 10–15 cm, and beneath the asphalt layer at a depth ranging from 30 to 50 cm, the original gravel subbase was present. The de-sealed soil averaged a sandy loam texture (80% sand, 12% silt, 8% clay), very low organic matter (0.5%) and total nitrogen (0.4%) content, and moderately alkaline pH (7.8). The physical and chemical characteristics of the soil immediately after de-sealing (T0) are reported in Table 1.

2.2 Experimental design and sampling

A mesocosm experiment was carried out using the sampled de-sealed soil. The experiment was performed in 5 L capacity pots, filled with 66% of sampled soil and 33% of sterile sand. The experimental design included three conditions with three replicates each, as follows: *Trifolium*—pots where seeds of *Trifolium repens* were sown, *Cynara*—pots sown with *C. cardunculus*, *Cynara* MYC—pots sown with *C. cardunculus* in which, prior sowing, the soil was mixed with a mixture of two commercial AM fungal inocula (INOQ, Germany), composed by *Funneliformis mosseae* and *Rhizophagus irregularis* (1:1). In addition to these three conditions, a Ctrl—control soil neither inoculated nor sown—was also considered. Pots were prepared at the end of March 2023, watered with 1 L of tap water for each pot every two days, and maintained in an open space under natural climatic conditions [average temperature between 17–35 °C, average precipitation between 53 and 155 mm (https://www.arpa.piemonte.it/ and https://www.weatherworld.com/yearly-climate/it/turin.html)] for six months, until the end of September 2023. At this date (T1), a visual inspection of spontaneous flora grown during the experimental time course was performed (supplementary information SI). Immediately after plants removal, the soil sampling has been performed for all the pots. After homogenization, one part of the soil samples was air—dried, 0.2 mm sieved and used for the physical and chemical characterization according to standardized protocols by an analytical laboratory (Demetra, Pescia, Italy). Two additional parts of the sampled soil were kept at – 20 °C for metabarcoding or at 4 °C for VOC measurements, carried out within a week from collection.

2.3 Assessment of arbuscular mycorrhizal (AM) fungal colonization

Arbuscular mycorrhizal fungal colonization was assessed on all plant roots from both inoculated and non-inoculated (i.e., control) pots, including *C. cardunculus*, *T. repens* and all spontaneous grown plant species, considering each pot as a biological replicate ($n = 3$). Roots were cleared with a KOH (10%) solution in a water bath at 80 °C for 30 min, then stained at room temperature overnight with 0.1% Cotton Blue in lactic acid. The next day, the roots were washed several times with lactic acid and the percentage of arbuscules, vesicles and hyphae was estimated under a dissecting microscope using the grid line intersection method [69].

2.4 Assessment of soil microbial biodiversity through metabarcoding

Total genomic DNA was extracted from approximately 400 mg of each soil sample using the DNeasy PowerSoil Pro Kit (Qiagen GmbH, Hilden, Germany), following the manual instructions, for a total of 12 samples. Prior sequencing

Table 1 Soil physical–chemical parameters at T0 and T1 in all three considered conditions: *Cynara*, *Trifolium* and *Cynara* MYC as well as in Ctrl soil samples

Conditions	pH	CE	Salinity	Nt	Pass	K	Ca	Mg	Fe	Mn	Cu	Zn	B	SOM	C/N
		mS/cm	‰	N g/Kg	P_2O_5 mg/Kg	K_2O mg/Kg	Ca mg/Kg	Mg mg/Kg	Fe mg/Kg	Mn mg/Kg	Cu mg/Kg	Zn mg/Kg	B mg/Kg	%	
T0	7.7	0.15	0.2	0.4	29	43	1169	55	14	6	1.9	0.2	0.12	0.39	5.2
T1-Ctrl	7.8	0.19	0.2	0.3	25	28	772	30	14	3	1.0	0.4	0.10	0.27	5.2
T1-*Cynara*	8.1	0.16	0.2	0.2	17	16	624	23	9	6	0.8	0.6	0.06	0.21	5.5
T1-*Trifolium*	8	0.17	0.2	0.3	15	24	541	28	8	4	0.8	1	0.07	0.29	5.8
T1-*Cynara* MYC	8.2	0.14	0.2	0.2	18	26	543	25	8	3	0.8	0.6	0.04	0.2	5.5

**CE* electrical conductivity, *Nt* total nitrogen, *Pass* assimilable phosphorus, *K* potassium, *Ca* calcium, *Fe* iron, *Mn* manganese, *Cu* copper, *Zn* zinc, *B* boron, *SOM* soil organic matter, *C/N* carbon/nitrogen ratio

(Novogene), DNA quantity and purity were measured using a Nanodrop 2000 (Thermo Scientific, Wilmington, U.S.A.). The bacterial 16S rRNA gene V3-V4 hypervariable regions and the fungal nuclear ribosomal ITS2-5.8S regions were sequenced. Sequencing libraries were generated using TruSeq® DNA PCR-Free Sample Preparation Kit (Illumina, USA) following manufacturer's recommendations and index codes were added. Library quantity and quality was assessed using the Qubit® 2.0 Fluorometer (Thermo Scientific) and the Agilent Bioanalyzer 2100 system. Libraries were sequenced on an Illumina NovaSeq platform and 250 bp paired-end reads were generated. Raw sequence files were submitted to the NCBI Sequence Read Archive (SRA) under the Bioproject ID PRJNA1133247.

The 16S and ITS sequences were clustered into amplicon sequence variants—ASVs [70] using QIIME 2 v2022.8 [71]. The taxonomic annotation was performed using the Silva database version 138 [72] and the UNITE database [73] for 16S and ITS data, respectively. Additionally, the MaarjAM database [74] was used for the AMF to pre-train the Naive Bayes classifier sequences (99% identity) for AM fungal taxonomic assignment of ITS sequences. The ASV tables were used as inputs for Microbiome Analyst 2.0 (https://www.microbiomeanalyst.ca/; Chong et al. [75]) for data visualization and statistical assessment. Data were filtered to remove low quality and not informative features by setting the minimum count of the low counter filter at two and the prevalence in samples at 10%. Data were then rarefied to the minimum library size, scaled with the total sum scaling method.

2.5 Volatile organic compound (VOC) analysis

Within a week after soil sampling, emitted VOCs have been determined as described in Neri et al. [60] and in Sillo et al. [61], for all the three conditions (*Trifolium*, *Cynara*, and *Cynara* MYC) and the Ctrl soil samples. In detail, before VOC analysis, 12 soil samples were homogenized and stabilized at ambient temperature. Volatile emission was measured from 300 g soil using a dynamic headspace (DHS) technique continuously flushing VOC-free air obtained through a custom-made catalytic converter (ZAG) to purify air from undesired VOC and contaminant, collecting the soil enriched air exiting the DHS in specific traps filled with 200 mg of Tenax and Carbograph at a flow rate of 200 ml min^{-1}. Traps were desorbed using a thermal desorber (Markes International, Series 2 Unity) and analyzed with a 7890A gas chromatograph coupled with a 5975C mass detector (GC–MS, Agilent Technologies), following the method of Baraldi et al. [76]. Identification was carried out by comparing retention times and fragmentation patterns with the NIST 11 database and external reference compounds. The identified compounds, after correcting for VOC deriving from sampling system, were quantified using external standard calibration. VOC emissions were expressed as ng kg^{-1} h^{-1}.

2.6 Statistical analysis

Statistical assessment of diversity at microbial level was performed through the estimation of different ecological indices.

Concerning microbial diversity in soil, both communities, total bacteria and fungi, and AMF were characterized according to alpha-diversity indices (Chao1 and Shannon indices) within samples. Additionally, beta-diversity among conditions was assessed by PERMANOVA using the Bray–Curtis dissimilarity index and Principal Coordinate Analysis (PCoA) for result visualization. Statistical differences among bacterial and fungal communities were assessed using univariate test in Microbiome Analyst 2.0. Furthermore, based on the prokaryotic diversity results, the annotation tool FAPROTAX [77] has been used to ascribe the functional ecological role to the identified bacteria.

For bacteria, the ratios between Proteobacteria (copiotrophs) and Acidobacteria (oligotrophs) (P/A) that is indicative of the trophic level of the soil [78], was calculated. In addition, Cyanobacteria/Chloroflexi (C/C) ratio, which was proposed as an early warning tool of soil degradation [79], was estimated. The Fungi/Bacteria (F/B) ratio was also considered, since higher abundance ratio of fungi to bacteria may suggest higher degree of ecosystems sustainability [80, 81]. Differences in the calculated ratios were statistically assessed by Student's t test ($p < 0.05$), using Ctrl as reference.

To assess the presence of putative positive/negative correlations between specific microbial taxa and VOC class amounts, a Spearman rank correlation co-occurrence network analysis at the order level was conducted with a p-value cutoff of 0.05 and a correlation threshold of 0.5 using R version 4.2.1. To test the influence of soil chemical properties and VOCs in all considered conditions, including Ctrl, a Principal Component Analysis (PCA) was performed using the "made4" package of R. For positive correlations, the database mVOC 3.0 [82] was used to investigate the reported putative association between detected microbial taxa and emitted VOCs. Differences in emission rates of VOC categories and classes of each conditions (*Trifolium*, *Cynara*, and *Cynara* MYC) with respect to the Ctrl were assessed by one-way ANOVA followed by Tukey's HSD post hoc test (by using the software JMP v. 7) and by Student's t test ($p < 0.05$).

3 Results

3.1 Soil physical–chemical parameters at T1

The physical–chemical characteristics of soil samples at the end of experimental time (T1) are reported in Table 1. Overall, with respect to the T0 samples, a slightly increase of pH, C/N ratio and Zn content, along with a decrease in total N, soil organic matter (SOM), assimilable P, K, Ca, Mg, Fe, Cu and B content have been observed in the three tested conditions, i.e., *Trifolium*, *Cynara*, and *Cynara* MYC. Conversely, the pH was similar and the Fe content did not change in Ctrl soil samples at T1 with respect to T0 (Table 1). The PCA based on physical–chemical soil parameters evidenced a clear separation of all three conditions from Ctrl, especially guided by pH and C/N ratio (Fig. S1a).

3.2 Arbuscular mycorrhizal (AM) fungal colonization

The grid method allowed to evaluate the AM fungal colonization assessment. Accordingly, a mean colonization level of 53% (range 19–72%) was observed in roots of all *C. cardunculus* plants collected from pots of *Cynara* MYC condition. Details about colonization percentage of all plants from pots of all considered experimental conditions were presented in Table 2. Typical AM fungal structures (i.e., intraradical hyphae, arbuscules, and vesicles)were observed within the root tissues of *C. cardunculus* plants from *Cynara* MYC pots (Fig. 1), while no typical structures associated to AMF were observed neither in roots from both *Cynara* and *Trifolium* conditions nor in those of Ctrl.

3.3 Composition and structure of soil microbial communities

In profiling the microbial sequencing data, the high-quality sequences, obtained after quality filtering, were accurately mapped into bacterial and fungal ASVs, with a total of 387,698 total reads—35,254 average counts *per* sample for 16S, and 636,856 total reads—45,489 average counts *per* sample for ITS, respectively.

Table 2 Percentage* of mycorrhizal colonization in roots of grown plants in *Trifolium*, *Cynara*, and in *Cynara* MYC conditions

Condition	Plant species	Mycorrhizal colonization (%)
Ctrl	*Populus × canadensis*	–
	Euphorbia maculata	–
	Salix aurita	–
	Ambrosia sp.	–
	Hypochaeris sp.	–
Trifolium	*Trifolium repens*	–
	Hypochaeris sp.	–
	Euphorbia maculata	–
Cynara	*Cynara cardunculus*	–
	Euphorbia maculata	–
	Populus × canadensis	–
	Salix aurita	–
	Salix triandra	–
Cynara MYC	*Cynara cardunculus*	19–72
	Populus × canescens	11
	Salix triandra	0–47
	Euphorbia maculata	60
	Ambrosia sp.	67
	Populus × canadensis	48–72

A control soil neither inoculated nor sown (Ctrl) was also considered

*Results are presented as range of percentage within plant species of each experimental condition

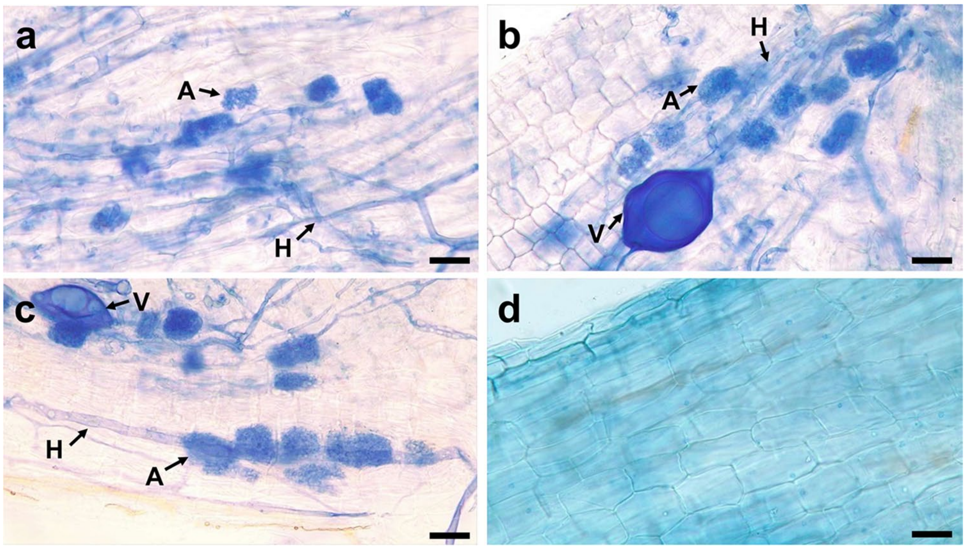


Fig. 1 Evaluation of mycorrhizal colonization by staining with cotton blue of *Cynara cardunculus* roots sown in pots inoculated with AMF (*Cynara* MYC), showing typical AM fungal structures, such as intraradical hyphae (H), arbuscules (A) and vesicles (V) within the root tissues (**a**–**c**); roots of *Cynara cardunculus* sown in the absence of AM fungal inoculum (*Cynara*) did not show typical AM fungal structures (**d**). Bar = 30 µm

Regarding the prokaryotic community, at Phylum level all soils were dominated by Proteobacteria with the highest percentage in *Cynara* soils (47%), followed by Ctrl (45%), *Cynara* MYC (37%) and *Trifolium* (33%); Acidobacteria with an average of 10% among theses and 20% in the Ctrl; Actinobacteria in a percentage of 19% in *Trifolium* soil samples, followed by 15% in *Cynara* MYC soil samples and 12% in Ctrl and *Cynara* soil samples. Bacteroidota was among the dominant phyla in all conditions (5%) but not in the Ctrl. Chloroflexi phylum was dominant in *Trifolium* and *Cynara* MYC soil samples and Firmicutes was among the dominant phyla only in Ctrl soil samples. Cyanobacteria phylum was more abundant in *Cynara* MYC soil samples (3.7%), followed by *Cynara* (1.4%) and *Trifolium* (0.45%), whereas no representatives of this phylum were detected in Ctrl soil samples (Fig. 2a–d).

The most relevant Orders within Phylum/Class of each considered conditions were as follows: in Ctrl soil samples: Burkholderiales (Betaprotebacteria) (35%), Pseudomonadales (Proteobacteria) (7%), Gaiellales (Actinobacteria) (4%), Propionibacteriales (Actinobacteria) (3%); in *Cynara* MYC soil samples: Burkholderiales (Betaprotebacteria) (16%), Rhizobiales (Proteobacteria) (5%), Sphingomonadales (Alphaproteobacteria) (5%), Rhodobacterales (Alphaproteobacteria) (4%), Gemmatimonadales (Gemmatimonadota) (3%), Gaiellaes (Actinobacteria) (3%); in *Cynara* soil samples: Burkholderiales (Betaprotebacteria) (27%), Vicinamibacterales (Acidobacteria) (4%), Rhizobiales (Alphaproteobacteria) (4%); in *Trifolium*: Burkholderiales (Betaproteobacteria) (12%), Rhizobiales (Alphaproteobacteria) (7%), Vicinamibacteriales (Acidobacteria) (5%), Sphingomonales (Pseudomonadota) (4%) and Gaiellales (Actinobacteria) (3%) (Fig. 3).

The univariate test allowed the discrimination of several orders more abundant in soil samples of the three conditions compared to Ctrl (Table S1). In addition, the following genera were found more abundant with respect to the Ctrl: *Nocardioides* (Actinobacteria) (*p*-value 0.004, FDR 0.045) and *Sphingobium* (Proteobacteria) (*p*-value 0.005, FDR 0.05702) in *Cynara* soil samples, *Ramlibacter* (Pseudomonadota) (*p*-value 2.50E-04, FDR 0.034) in *Cynara* MYC soil samples and *Ralstonia* (Proteobacteria) (*p*-value 2.99E-05, FDR 0.006) in *Trifolium* soil samples.

In general, several genera/families were identified as core microbiome in all tested conditions as well as in the Ctrl, and they are reported in Table S2. Particularly, common genera included *Ralstonia, Sphingomonas*, *Gaiella*, *Rubellimicrobium*, *Haliangium*, *Ramlibacter*, *Pseudarthrobacter*, *Nocardioides*, *Latescibacter*, *Bacillus*, *Streptomyces*, *Bryobacter*, *Noviherbaspirillum*, *Novosphingobium*, *Nitrospira*, *Nocardia*, and *Pseudomonas*, and families included Vicinamibacteraceae and Vermiphilaceae. On the other hand, exclusive genera in Ctrl were *Caulobacter, Cupriavidus*, *Acinetobacter*, *Acidovorax*, *Massilia*, *Rhodococcus* (prevalence = 0.33); in *Trifolium* soil samples: *Terrimonas*, *Microbacterium* (prevalence = 0.33); in *Cynara* MYC soil samples: *Polycyclovorans*; *Paenibacillus* (prevalence = 0.5); in *Cynara* soil samples: *Kapabacteriales* (prevalence = 0.33).

Alpha-diversity of bacterial communities showed significant differences among samples (Chao 1 index, *p*-value 0.014). Accordingly, a higher diversity in *Trifolium* soil samples was found when compared with Ctrl (*p*-value 0.017362, FDR 0.104; Fig. 4a), followed by *Cynara* MYC and *Cynara* soil samples. The result was also confirmed by the Shannon index, which takes into account both richness and evenness (*p*-value $1.1055e^{-05}$, FDR 74.845; Fig. 4b). Based on the beta-diversity, a clear separation of all three conditions from the Ctrl was shown (Fig. S2). The prokaryotic communities were more similar in *Cynara* MYC and *Trifolium* soil samples than those from Ctrl and *Cynara* soil samples (R 0.666, *p*-value < 0.003).

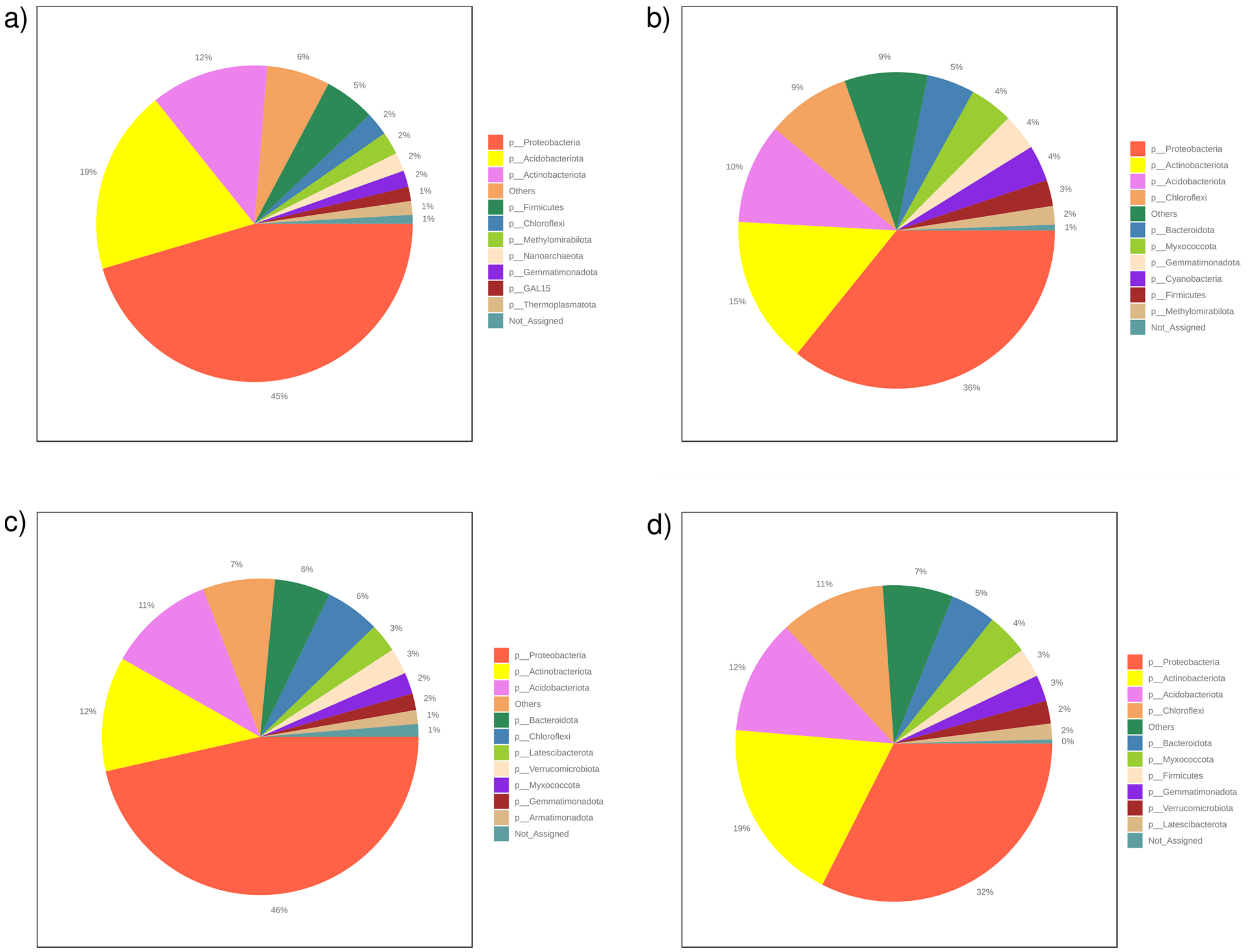
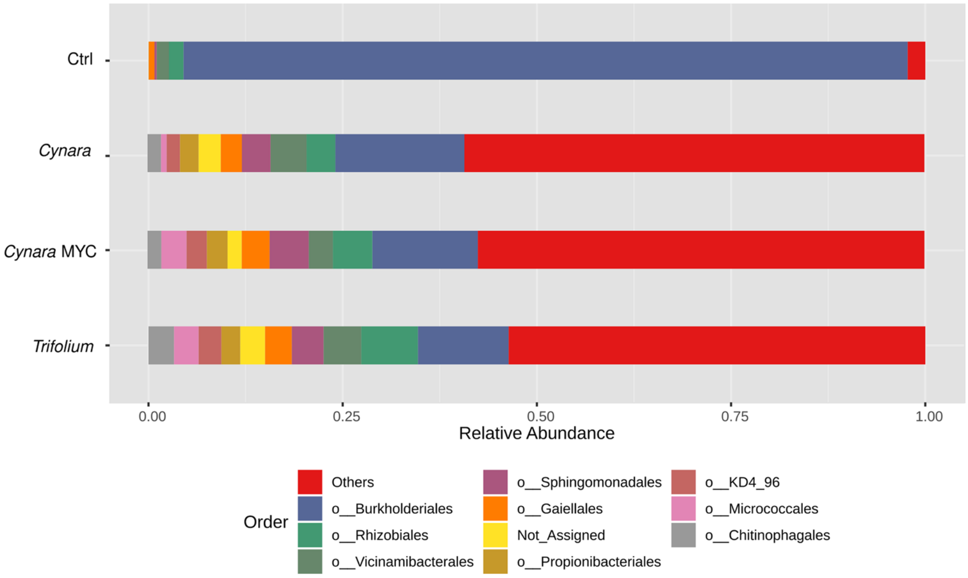


Fig. 2 Pie charts of main bacterial community composition at Phylum level in **a** Ctrl; **b** *Cynara* MYC; **c** *Cynara*; **d** *Trifolium* soil samples

Fig. 3 Stacked barplots of bacterial relative abundance of community composition at Order level in Ctrl, *Cynara* MYC, *Cynara* and *Trifolium* soils samples



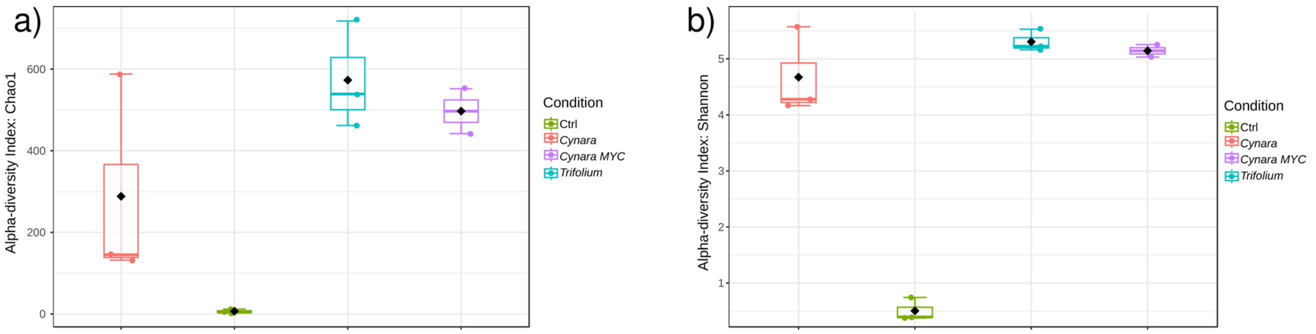


Fig. 4 Alpha diversity of bacterial communities in all three considered conditions: *Cynara*, *Trifolium* and *Cynara* MYC as well as in Ctrl soil samples: **a** Chao 1 index and **b** Shannon index

Concerning the fungal community, at Phylum level the soils were dominated by Mucoromycota (average 50%) and Ascomycota as follows: 23% in Ctrl, 19% in *Trifolium*, 16% in *Cynara* MYC inoculated soils and 5% in *Cynara* soil samples. However, an average percentage of 70% of reads was not assigned. At class level, Glomeromycetes was the most dominant one as follows: 49% in Ctrl soil samples, 43% in *Cynara* MYC soil samples, 31% in *Trifolium* soil samples and 11% in *Cynara* soil samples. The fungal orders were displayed in abundance pie charts, excluding the unclassified and unassigned ones (Fig. 5). From the assigned taxa, the most dominant fungal orders were identified as Sordariales (18%), Glomerales (16%), Capnodiales (14%) and Hypocreales (12%) in Ctrl (Fig. 5a); Hypocreales (57%), Pleosporales,

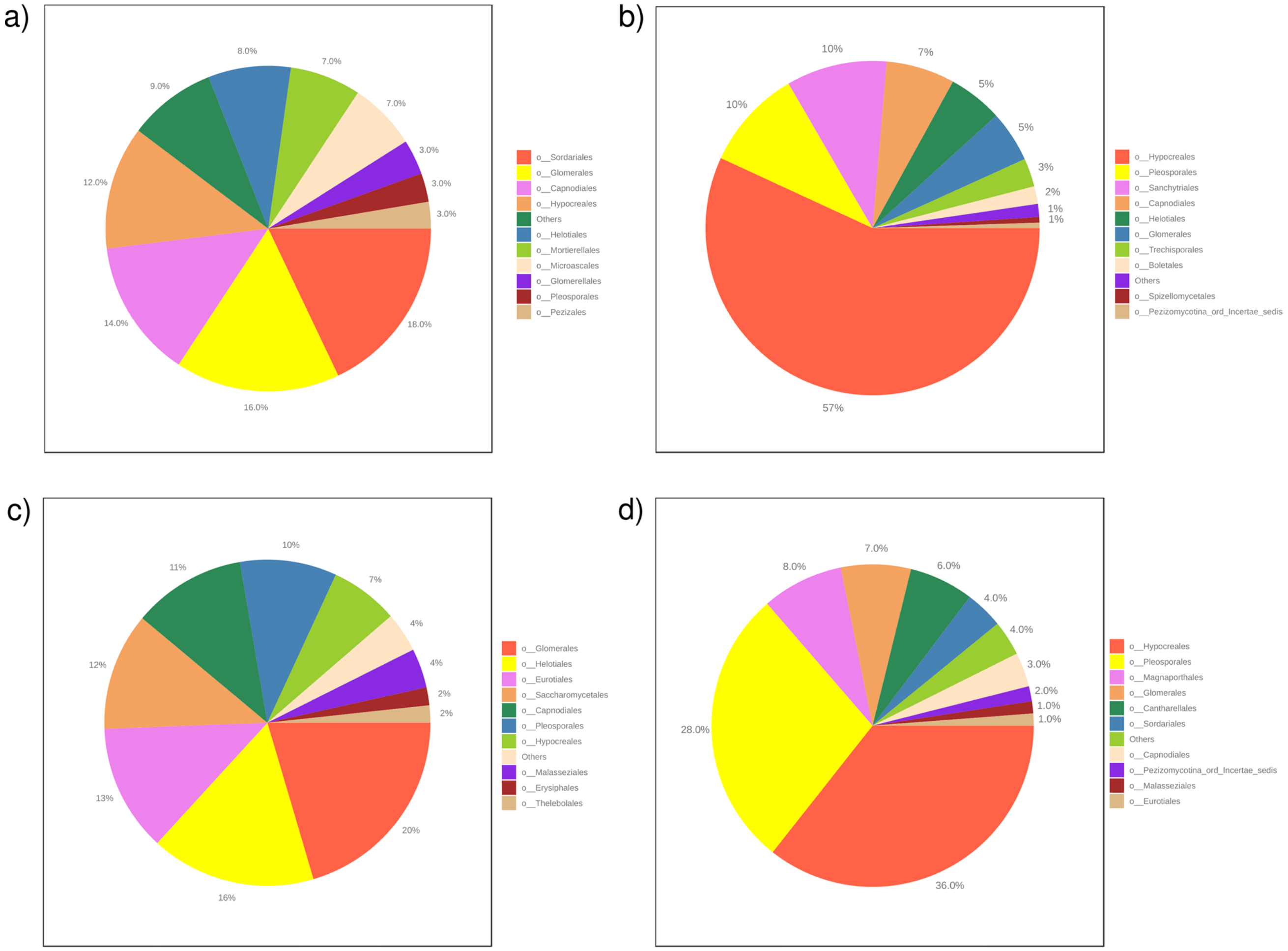


Fig. 5 Pie charts of main fungal community composition at Order level in **a** Ctrl; **b** *Cynara* MYC; **c** *Cynara*; **d** *Trifolium* soil samples

Sanchytriales (10%), Capnodiales, Helotiales and Glomerales (7%) in *Cynara* MYC soil samples (Fig. 5b); Glomerales (20%) and Helotiales (16%), Eurotiales (15%), Saccharomycetales (12%), Capnodiales (11%) in *Cynara* soil samples (Fig. 5c). The dominant fungi at order level in *Trifolium* soil samples were *Hypocreales* (36%), Pleosporales (28%), Magnaporthales (8%) and Glomerales (7%) (Fig. 5d).

Regarding the fungal core microbiome, the following genera were common to all conditions: *Glomus*, *Hyalocypha*, *Cladosporium*, *Penicillium*, *Fusarium*. Based on univariate test, no significant differences in fungal taxa abundances were detected ($p > 0.05$).

Regarding the total fungal and AM fungal communities, no significative differences have been found on both alpha (Chao 1 index, *p*-value 0.522, FDR 0.811 and Shannon index, *p*-value 0.741, FDR 0.423) (Fig. 6a–d) and beta diversity (R^2 0.263, *p*-value 0.58). However, although not significant, a slight increase in alpha diversity of both total fungi and AM fungal communities has been observed in MYC soil samples (Fig. 6a–d).

Both Proteobacteria/Acidobacteria (P/A) and Cyanobacteria/Chloroflexi (C/C) ratios showed similar results, with significant higher values in *Cynara* (P/A = 4.3; C/C = 4) and *Cynara* MYC (P/A = 3.5; C/C = 4) soil samples, with respect to *Trifolium* (P/A = 2.7; C/C = 0.004) and Ctrl (P/A = 2.4; C/C = 0) (Student's t-test, $p < 0.05$) (Fig. 7a). The Fungi/Bacteria (F/B) ratio showed a significant increase in *Cynara* MYC soil samples with respect to all other conditions ($p < 0.05$) (Fig. 7b).

Functional annotation of bacterial communities by FAPROTAX allowed to identify several categories reported in Fig. S3. There was a prominent occurrence of sequences of bacteria associated with putative aerobic chemoheterotrophy, with a higher abundance in *Trifolium* soil samples and a lower abundance in *Cynara* MYC soil samples. Aromatic hydrocarbon and aliphatic degradation showed higher abundances in *Trifolium* and Ctrl conditions. Denitrifies seemed to be more abundant in the *Cynara* soil samples, while methane processes were more prevalent in Ctrl soil samples. In addition, a high abundance of photoautotrophs was observed in *Cynara* MYC and *Cynara* soil samples with respect to the Ctrl soil samples.

3.4 Soil VOC signature

A total of 62 VOCs were identified in the soils samples from all the three experimental conditions (*Cynara*, *Trifolium* and *Cynara* MYC) and the Ctrl; the majority belonged to 14 chemical classes (acid, alcohol, aldehyde, alkane, alkene,

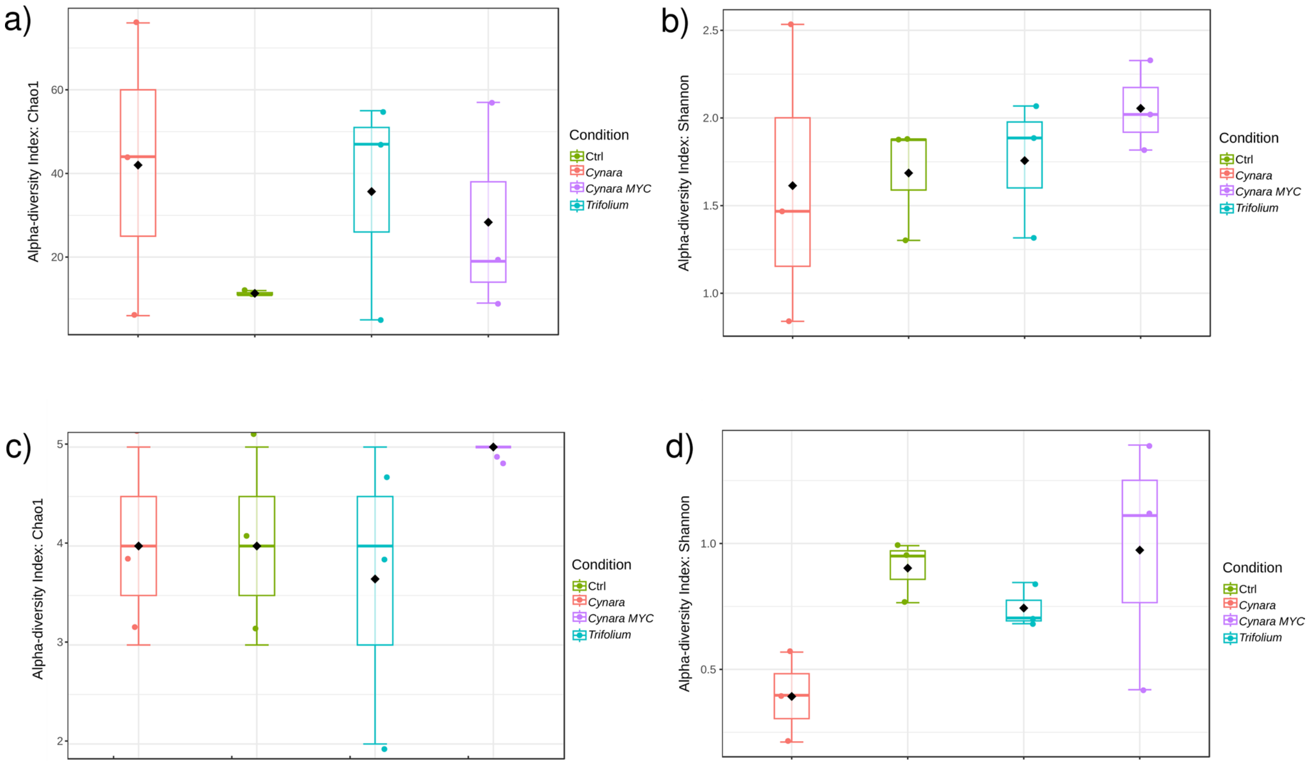


Fig. 6 Alpha diversity of total fungal communities **a** Chao 1 index and **b** Shannon index, as well as alpha diversity of AMF **c** Chao 1 index and **d** Shannon index, in all three considered conditions: *Cynara*, *Trifolium* and *Cynara* MYC as well as in Ctrl soil samples

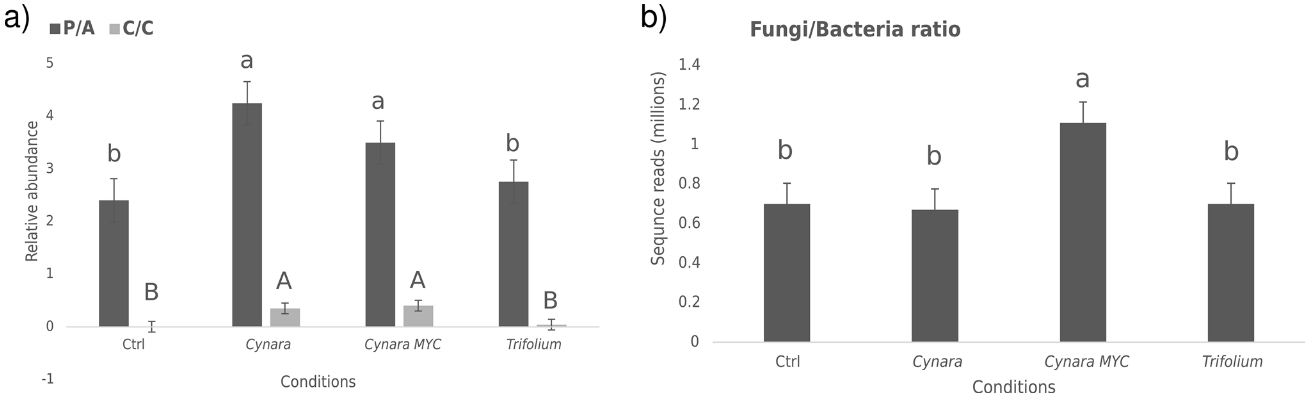


Fig. 7 Proteobacteria/Acidobacteria (P/A) and Cyanobacteria/Chloroflexi (C/C) ratios (**a**) and Fungi/Bacteria (F/B) ratio (**b**), in all three considered conditions: *Cynara*, *Trifolium* and *Cynara* MYC as well as in Ctrl soil samples (letters indicate significant differences at $p < 0.05$, based on Student's t test between the conditions and the control soil samples)

arene, ester, ether, furan, ketone, phenol, terpene, terpenoid, chloromethane), except for only two compounds belonging to other classes and one compound (putative n-C9) that could not be identified using the NIST 11 library (Table S3). Some significant differences in VOC emission among the experimental conditions were observed: the arene toluene was more abundant in Ctrl soil samples; the arene ethyl-benzene and p- and o-xylene were more abundant in *Trifolium* samples; the chloromethane dichloromethane was higher in Ctrl soil samples, the furan tetrahydrofuran and the organic disulfide dimethyl disulfide were more abundant in *Trifolium* soil samples (Table S3). Generally, the emitted VOC were mostly anthropogenic belonging mainly to furan and arene classes, which were significantly higher in the *Trifolium* soil samples (Fig. 8a). Considering VOC emission without the furan and arene classes, some significant differences were detected: the higher emission values have been observed for ester class, with significant differences among conditions and control as follows *Trifolium* = *Cynara* > *Cynara* MYC > Ctrl. No ether or very low concentration were observed in Ctrl and *Cynara* soil samples, respectively, while higher concentrations were detected in *Trifolium* and *Cynara* MYC soils. Low amounts of chloromethanes were detected in all of the treatments compared with the Ctrl. High emissions of acid compounds (acetic acid) were detected only in *Cynara* MYC soil samples and relatively high emissions, although not significant, of alcohols were observed in *Cynara* MYC and *Trifolium* soil samples (Fig. 8b).

As for soil chemical parameters, the PCA performed on all VOC classes showed distinct separation between the tested conditions and the Ctrl, driven mainly by terpene and ester classes (Fig. S1b).

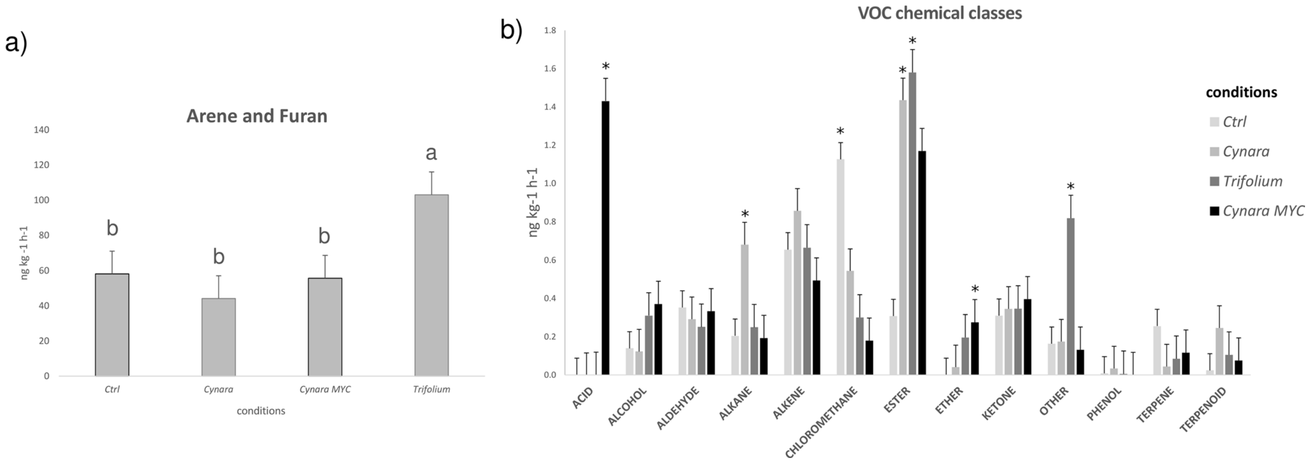


Fig. 8 Arene and Furan classes (**a**) and VOC chemical classes (**b**), in all three considered conditions: *Cynara*, *Trifolium* and *Cynara* MYC as well as in Ctrl soil samples (different letters and asterisks indicate significant differences at $p < 0.05$, based on Student's t test between the conditions and control soil samples)

3.5 Correlation between VOC emissions and microbial communities

Correlation between identified VOCs and microbial communities allowed to detect in general multiple bacterial and fungal taxa negatively associated to specific VOC classes, especially with those with anthropogenic origin. Outcomes from correlation between detected microbial orders and genus were reported in Tables S4–11. In *Cynara* MYC soil samples Chloroflexales as well as genera *Delftia*, *Ralstonia* and *Ramlibacter* were negatively correlated with arenes class. Ten orders have been found negatively correlated with esters class (Acidobacteriales, Chitinophagales, Kapabacteriales, Micromonosporales, Myxococcales, Pyrinomonadales, Reyranellales, Thermoactinomycetales, Vicinamibacterales, Xanthomonadales), ten orders were found negatively correlated with alkenes class (Haliangiales, Kapabacteriales, Micromonosporales, Myxococcales, Opitutales, Paenibacillales, Pyrinomonadales, Reyranellales, Thermoactinomycetales, Xanthomonadales). In *Cynara* MYC soil samples, also some positive correlations were detected: fifteen bacterial orders have been found positively correlated with acid class (i.e., acetic acid), with some important genera as *Lysinibacillus*, *Brevibacillus*, *Pseudomonas*, *Psedoxanthomonas*; seven orders were found positively correlated with alcohol class (Acetobacterales, Azospirillales, Chloroflexales, Cytophagales, Propionibacteriales, Sphingobacteriales, Sumerlaeales); four orders were found positively correlated with terpenoids class (Micrococcales, Microtrichales Sphingomonadales, Streptosporangiales). Additionally, positive correlations were observed with dimethyl sulfide at order (Kapabacteriales) and genus level (*Aeromicrobium*, *Ahniella*, *Haliangium*, *Luteobacter*, *Nitrospira*). In *Cynara* soil samples negative correlations dominated with phenol (Gaiellales, Holosporales, Methanomassiliicoccales), ketone (Myxococcota), furan (Coxiellales, Gemmatales, Pyrinomonadales, and *Coxiella*, *Flavobacterium*, *Paenibacillus* at genera level), ester (*Ramlibacter*), alkene (Methylomirabilota, Thermoplasmatota, Micrococcales, Rokubacteriales), alkans (Desulfobacterota, Planctomycetota, Coxiellales, Gemmatales, Microtrichales, Pyrinomonadales), alcohol (Nitrospirota, Gemmatimonadales, Nitrospirales, Polyangiales, Thermoactinomycetales) and acid classes (*Ramlibacter*). Some positive correlations have been found for terpenoids (Microtrichales, Pedosphaerales, Solibacterales) and terpene (i.e., limonene) (*Bauldia*) classes. In addition *Lacunisphaera*, *Sphingobium* genera were positively correlated with dimethyl disulfide. Negative correlations dominating the *Trifolium* soil samples have been found with 11 VOC classes, the predominant ones with furans: Nitrospirales, Polyangiales, Salinisphaerales, Sphingomonadales, Woesearchaeales at order level and *Acinetobacter*, *Ammoniphilus*, *Brevibacillus*, *Coxiella*, *Dongia* at genus level. In *Trifolium* soil samples *Ammoniphilus* genus was positively correlated with dimethyl disulfide. In Ctrl soil samples, general negative correlations at phylum level were observed with furan class (Proteobacteria) and terpenes at order level (Vicinamibacterales). Vicinamibacteraceae was also negatively correlated with dichloromethane compound. Positive correlation were found with terpenoids class (Vicinamibacterales), and genus level with terpenes (*Nocardioides, Cupriavidus*), phenol (*Actinoplanes*, *Devosia*, *Gaiella*, *Nocardia*, *Sphingomonas*), ester (*Caulobacter*, *Stenotrophomonas*) and alkene (*Actinoplanes*, *Devosia*, *Gaiella*, *Nocardia*, *Sphingomonas*) classes.

Regarding the fungal communities, negative correlations dominated in all conditions, with Trechisporales, Eurotiales—*Penicillium* sp., Capnodilaes and *Glomus* negatively correlated with furan, arene, alkene and alkane classes, respectively, in *Cynara* MYC soil samples; Pleosporales, Hypocreales, Eurotiales, Glomerales, Helotiales negatively correlated with terpenoid, furan, ester, arene and alcohol classes in *Trifolium* soil samples; Hyaloscypha, Capnodiales, Glomerales, Sordariales, Hypocreales negatively correlated with phenol, ketone and arene classes (Tables S8–S11).

Concerning the positive correlations, the mVOC3.0 database confirmed the microbial origin of acetic acid: *Bacillus* sp. [83], and *Pseudomonas* sp. [84, 85].

4 Discussion

Rapid urbanization is transforming our cities, reducing green spaces, which are essential for mitigating the effects of global warming and for enhancing urban biodiversity [19, 86, 87]. Soil de-sealing and further bioremediation management are crucial for renovating soil health, which is mainly defined by the stability and resilience of the soil microbiome [88].

4.1 Application of AM fungal inoculum might enhance microbial diversity and soil health status

Our results showed that a de-sealed soil could restore its health and fertility when specific cover plants (e.g., *C. cardunculus*), both alone or inoculated with AMF have been used. Renella [89] demonstrated "in situ" the recovery of soil fertility after de-sealing of urban soils that underwent colonization by spontaneous plants. To the best of our knowledge this was the first study, which evidenced a successful AM fungal colonization of plant roots from a de-sealed, degraded and reused soil, by a commercial AM fungal inoculum. On the other hand, no colonization was observed where the inoculum was not added, thus suggesting that despite the relative high abundance of Glomeromycetes in control soils, the native AMF lost their colonization potential, probably due to the contaminants and harsh conditions induced by soil sealing. Previous studies suggested that AM fungal spores can still colonized host roots effectively in degraded polluted soils (e.g., heavy metals), despite low counts [90, 91] Cabello et al. [25] pointed out that native AM fungal propagules from extremely hydrocarbon polluted soils had a high colonization capacity. On the other hand, our findings aligned with broader observations indicating that soil degradation generally resulted in decreased diversity and colonization capacity of native AMF [92]. Further studies on how different materials used for soil sealing (e.g., semipervious pavements) as well as sealing duration may affect functionality of native AMF should be considered.

Both *C. cardunculus* with and without inoculum played a crucial role in enhancing soil bacterial diversity, confirming the "*Microbiome Rewilding Hypothesis*" [88]. The beneficial effects on soil fertility of *C. cardunculus* as cover plant, as well as the symbiotic relationships formed by AMF with plant roots, created favorable conditions for the establishment of diverse bacterial communities. This increased bacterial diversity may further have contributed to the overall soil status resilience and improvement. The importance of symbiotic interactions in promoting soil health and vegetation growth efficiency was emphasized, as shown by the estimation of the detected spontaneous plant species richness, when mycorrhizal inoculum and *C. cardunculus* were used (Fig. S4). The presence of *C. cardunculus* alone, as well as AMF and *C. cardunculus* consociation, positively influenced the soil health status, as indicated by shifts in key microbial community ratios. The diverse array of bacterial species was also underlined by the pH change, widely recognized indicator of functional microbial patterns [93, 94]. The increase in Proteobacteria/Acidobacteria ratio, along with the enhanced Cyanobacteria/Chloroflexi, suggested a favorable shift within copiotroph communities, as *r*-strategists, towards increased nutrient availability. These changes aligned with findings by Smit et al. [78], indicating a potential restoration of soil fertility and improvement in nutrient cycling processes. Moreover, Chloroflexi and Cyanobacteria could be used as tool of soil degradation status, as members of Chloroflexi phylum may have a competitive advantage over Cyanobacteria in nutrient-limiting environments [96] as observed in control soils and in pots where *Trifolium* was sown.

Noteworthy, the observed shift from bacterial to fungal dominance, as showed by the Fungi/Bacteria ratio, in soils of *C. cardunculus* plants colonized by AMF suggested a potential role of mycorrhizal fungi in the improvement of the health soil status [95]. This was further evidenced also by the higher diversity of total fungi as *K*-strategists in inoculated soils, and by lower Ascomycota abundance in *C. cardunculus* pots with inoculum, which may represent an indicator of ecosystem health recovery [96].

4.2 The interaction between *C. cardunculus* and AMF contributed to AVOC biodegradation and restoration of soil health status

In our study multiple negative correlations between microbial communities and the identified compounds have been observed, supporting a clear VOC signature, which indicated an overall degradation/consumption pattern. This underlined the fact that soil uptake based on anthropogenic compound degradation may have exceeded the overall VOC production, as they were readily available, as inferred by Jiao et al. [97]. In our experiment, the degradation process was sustained by the soil core microbiome identified as an unique consortium containing genera able to degrade AVOCs (i.e., BTEX -benzene, toluene, ethylbenzene, xylene- and chlorinated methane) under aerobic conditions. This soil core microbiome included taxa reported to be degraders of anthropogenic based VOC, such as *Pseudomonas*, *Cupriavidus* [98], *Streptomyces* [99], *Acinetobacter* [100], *Bacillus* [101], *Microbacterium* [102], *Massilia* [103], and *Rhodococcus* [104]. Particularly, bacterial strains such as *Acinetobacter* sp., *Pseudomonas* sp., and *Rhodococcus* sp. are well known to secrete biosurfactants to degrade oil-based contaminants [105].

Our FAPROTAX-based analysis highlighted the functional roles of chemoheterotrophs as *r*-strategists, in nutrient cycling within de-sealed and reused soils. The relevant presence of chemoheterotrophic bacteria in the de-sealed soil can be linked to its high mineralization degree, as evidenced by the observed low C/N ratio. These microorganisms, deriving energy from the oxidation of organic compounds, revealed the degradation of complex AVOCs as preferential metabolic pathway. Therefore, our data suggested the breakdown of various organic pollutants in a de-sealed and reused soil. The co-occurrence of multiple AVOCs in our soil samples made difficult to define a clear pattern of BVOC production. In the specified soil conditions, diverse interactions among AVOCs led to different degradation pathways, influenced by the types of microorganisms and enzymes present. Microbes may have broken down and transformed certain compounds, while using a specific AVOC as their primary substrate for energy and growth [106, 107]. Hence, the high concentration of AVOCs in soils sown with *Trifolium* might have been caused by a continuous organic C turnover, which further inhibited the VOC degradation [108, 109]. Interestingly, tetrahydrofuran, an AVOC previously detected in urban flowerbeds [61] and known as a potential groundwater contaminant, predominantly dominated the AVOC emissions from *Trifolium* soil samples. This compound is very susceptible to chemical and biological reactions and only a limited number of microbes capable of degrading tetrahydrofuran has been documented [110, 111]. Additionally, dimethyl disulfide was significantly higher in *Trifolium* samples as well. This sulfur-containing compound, known for its well-documented antifungal activity, has been isolated from soil inhabitants such as *Pseudomonas chloraphis* and *Stenotrophomonas rhizophila* [112, 113], which exhibited biocontrol activity against phytopathogenic fungi. Here it was positively correlated with *Ammoniphilus* genus (Firmicutes, Bacillales, Paenibacillaceae), a chemo-organotroph producing hydrogen sulfide taxon harboring ammonium-dependent bacteria [114–116]. The dimethyl disulfide production was previously documented in *Bacillus* sp., as a plant growth promotion mechanism [117].

Conversely, our results showed lower concentrations of anthropogenic VOC classes in *C. cardunculus* associated soils, both with and without AMF, and in control samples compared to soils sown with *Trifolium*. This suggested the presence of a more efficient microbial consortium capable of aerobic degradation of these compounds, as reported by Yoshikawa et al. [107] and Wu et al. [118]. Indeed, Rhodobacterales and Gemmatimonadales associated to *Cynara*/AMF conditions were less abundant in *Trifolium* soils. Rhodobacterales is well known to include many members that have the ability to degrade a wide range of hydrocarbons [119], while Gemmatimonadales order was found to have a high efficiency of C utilization [120, 121]. A negative correlation between the arene class and *Ralstonia* genera indicated its potential role in VOC degradation as inferred by Ryan et al. [122]. Additionally, *Delftia*, *Ramlibacter*, and Chloroflexales were identified as key degraders of organic pollutants in AM fungi-colonized soils [65, 123–128] and here they were negatively correlated with VOCs. The VOC content in AM fungal inoculated soils showed a high absorption of VOCs by the soil microbial communities, likely due to improved pollutant breakdown, suggesting that the presence of AMF might enhance the soil capacity to degrade AVOCs, as proposed by Volante et al. [129]. This observed positive effect of inoculation may be attributed not only to the applied AM fungal species but also to their associated microbiota containing genes encoding catabolic enzymes [129, 130] or to the AMF-mediated changes observed in soil native microbial communities [97]. In addition, the phototroph-heterotroph partnership detected in inoculated soils may have significantly contributed to the overall degradation of AVOCs [131]. The association of AMF and *C. cardunculus* favored an initial rapid pollutant degradation by *r*-strategists, which created a favorable environment for *K*-strategists that then took over for sustained degradation once primary contaminants were reduced [132]. On the other hand, the low arene and furan concentrations from the soils of non-inoculated *C. cardunculus* might be explained by the presence of *Nocardioides*, a very versatile genus with an interesting potential in the degradation of various organic pollutants and bioremediation [133]. Additionally, the emissions of dichloromethane, quantitatively the most important chlorinated solvent industrially produced [134], were lower in all treatments compared to the control. Our metabarcoding results highlighted several genera known to degrade dichloromethane, including *Ralstonia, Mycobacterium*, *Rhodococcus*, *Bacillus*, *Burkholderia*, *Micrococcus*, *Pseudomonas* [134]. In addition, a negative correlation was found in control soil samples between this AVOC and Vicinamibactereaceae family, part of the control soil core microbiome, and known for chemo-organoheterotroph metabolism and its ability to thrive in nutrient-poor, neutral, and heavy metal-tolerant environments [135]. The overall observed decrease in VOC concentration in our experimental conditions can serve as "*proxy*" for the efficiency of VOC degradation process, occurring in contaminated soils, as recently proposed [61].

Notably, in our study, the *Caulobacter* presence was observed exclusively in the core microbiome of control soils, revealing physiological adaptations to low nutrient conditions [136]. The ability of this bacterium, to outlive other bacterial organoheterotrophs in nutrient depleted, long-term incubations, has been already documented [137]. It was worth noting that this bacterium may be involved alone or in consortia (i.e., with *Pseudomonas*, *Burkholderia*, *Mycobacterium*) in biodegradation of hydrocarbons or other organic pollutants [124, 138, 139] and these genera belong to highly abundant orders in our control conditions. The presence of *Caulobacter* only in the core microbiome of control soils underscored that a degraded soil may function as a reservoir of microbes involved in decontamination processes, which could be potentially exploited for the restoration of soil ecological functions [136].

Positive correlations have been found between several bacterial taxa and terpene/terpenoid classes especially in *C. cardunculus* inoculated soil. It is widely considered that terpenes are plant or fungal metabolites [140], but predicted terpene synthases were also found in bacteria belonging orders like Myxococcales, Burkholderiales, Rhizobiales, Sphingobacteriales, Pseudomonadales [141] detected in our experimental conditions. The identified microbial consortium may have utilized terpenes/terpenoids as C source and energy for the subsequent soil contaminants degradation [142–144]. However, further studies on *bacterial terpenome* [145] and its role in bioremediation are required.

4.3 Synergistic effects within the mycorrhizosphere of AMF-inoculated plants contributed to soil nutrient availability

Interestingly, a high content of acetic acid was observed in the presence of AMF and several positive correlations between bacteria and this VOC class were identified. Various soil/rhizosphere-inhabiting microorganisms release different amounts of organic acids in the soil [146–148]. The presence of some of them, such as *Bacillus* sp., *Lysinibacillus* sp., and *Pseudomonas* sp., strongly correlating with acetic acid, suggested that the production of this organic acid was occurring in the soil. Acetic acid production by microbes has been linked to an improved availability of phosphorus [149, 150]. In this line, *Bacillus*, *Lysinibacillus* and *Pseudomonas* taxa correlating with high level of acetic acid in soil of AMF-inoculated plants may be indicative of the presence of the so-called *mycorrhizosphere*, which is composed by different microbial communities supposed to have a synergistic effect with AMF on different processes, including phosphorus solubilization [151].

5 Conclusions

This study demonstrated the colonization of plant roots by AMF in a de-sealed and degraded soil inoculated with an AMF-based inoculum. No native AM fungal colonization was observed in non-inoculated pots. Inoculating a de-sealed and degraded soil with a commercial AM fungal inoculum and using cover plants like *Cynara cardunculus* restored soil health status, also by improving soil bacterial diversity. The presence of complex microbial consortia facilitated AVOC degradation, highlighting the bioremediation potential of this approach in urban soils. Chemoheterotrophic microorganisms were key players in pollutant breakdown. The findings supported the "*Microbiome Rewilding Hypothesis*" showing that reintroducing beneficial microorganisms and plants can create a dynamic, enriched soil ecosystem that fosters microbial diversity and resilience against urban degradation**.**

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Data availability Sequence data that support the findings of this study have been deposited with the primary accession code PRJNA1133247.

Code availability Not applicable.

Declarations

Competing interests The authors declare no competing interests.

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