



# Exchange of volatile organic compounds between the atmosphere and the soil

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## Abstract

**Background** Volatile organic compounds (VOCs) play a crucial role in understanding soil ecology and the atmospheric environment. However, the biochemical cycles of VOCs in soil systems and their relationship to atmospheric VOC exchange remain unclear. The soil system serves as a primary site for the generation, emission, and uptake of VOCs, yet these processes lack sufficient understanding.

**Scope** This review aims to provide a comprehensive overview of the exchange of VOCs between the soil and the atmosphere. We explore the mechanisms governing the generation, emission, and uptake of VOCs in soils, quantitatively summarizing available data

on emission and uptake. Additionally, we highlight common and specific VOCs emitted by various soil sources (litter, roots, bare soil, and soil microbes) and examine their interactions.

**Conclusions** The composition and emission rates of VOCs display significant variability across different soils, attributed in part to variations in the contributions of different VOC sources within the soils. Litter and roots predominantly release terpenes, benzenoids, and alcohols, while bare soil and microbes emit higher proportions of alkanes, esters, and alcohols. Despite often being overlooked, soils serve as essential sinks for VOCs, and global environmental changes may reshape patterns of soil VOC sources and sinks.

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## Introduction

Volatile organic compounds (VOCs) play vital roles in governing atmospheric chemistry and climate, such as being involved in producing secondary organic aerosols and photochemical ozone (Andreae and Crutzen 1997; Atkinson 2000; Williams 2004; Tunved et al. 2006; Lelieveld et al. 2008). VOCs are also crucial in multiple interactions, such as plant-animal, plant-microbe, and microbe-microbe communication (Insam and Seewald 2010; Peñuelas et al. 2014; Honeker et al. 2021; Meredith and Tfaily 2022). Terrestrial vegetation and anthropogenic activities are the main sources of VOCs (Guenther et al. 1993), but soil may be an overlooked contributor (Peñuelas et al. 2014; Bourtsoukidis et al. 2018; Llusà et al. 2022). Accurately estimating soil VOCs is crucial for predicting global VOC emissions, however, these emissions from soils have not been assessed (Guenther et al. 2012; Sindelarova et al. 2014).

Soils are widely recognized as a source of VOCs due to the continuous production and release of VOCs from various contributors, including litter (Leff and Fierer 2008; Gray et al. 2010; Viros et al. 2020; Isidorov and Zaitsev 2022), roots (Lin et al. 2007; Mäki et al. 2017; Tsuruta et al. 2018), microorganisms (Bäck et al. 2010; Veres et al. 2014; Isidorov et al. 2016; Bourtsoukidis et al. 2018; Honeker et al. 2023) and soil organic matter (SOM) (Leff and Fierer 2008; Insam and Seewald 2010; Monard et al. 2021). Generally, the concentration of atmospheric VOCs is higher than that of soil VOCs. Although VOCs emission from soils have typically been reported to be 1–2 orders of magnitude lower than those from plant canopies (Peñuelas et al. 2014), soil emissions can indeed be significant, depending on factors such as the habitat type (Bourtsoukidis et al. 2018; Llusà et al. 2022) and season (Aaltonen et al. 2011; Mäki et al. 2017). Different ecosystems vary significantly in the characteristics and magnitudes of plant VOCs released due to variations in vegetation composition and climate (Guenther et al. 2012), which directly affect the concentration of the surrounding atmospheric VOCs. The concentration of atmospheric VOCs is significantly negatively correlated with soil VOCs emission rate (Llusà et al. 2022; Yang et al. 2024), indicating that aboveground vegetation VOCs may strongly contribute to the VOCs that enter the soils (Mu et al. 2023). The high concentration gradient between the

atmosphere and the soil likely enhances the soil's capacity to act as a sink for VOCs through physicochemical uptake (Li et al. 2019) or microbial biodegradation (Pegoraro et al. 2006).

Soil VOC emissions are bidirectional; these processes are related to multiple factors (Asensio et al. 2007c; Bachy et al. 2018; Trowbridge et al. 2020; Pugliese et al. 2023). Firstly, soil microorganisms can utilize VOCs as a carbon source for growth and reproduction (Chaignaud et al. 2018; Shrestha et al. 2019; Abis et al. 2020; Carrión et al. 2020). Accumulating evidence suggests that soils have the potential to act as a net VOC sink and are also essential in controlling net fluxes (Isidorov et al. 1999; Spielmann et al. 2017; Albers et al. 2018; Trowbridge et al. 2020), though the magnitude of this sink capability remains uncertain (Cleveland and Yavitt 1997; McGenity et al. 2018; Rinnan and Albers 2020; Honeker et al. 2023). Moreover, different ecosystems vary significantly in the characteristics and magnitudes of plant VOCs released due to variations in vegetation composition and climate (Guenther et al. 2012), which directly affect the concentration of the surrounding atmospheric VOCs. The concentration of atmospheric VOCs is significantly negatively correlated with soil VOCs emission rate (Llusà et al. 2022; Yang et al. 2024), indicating that aboveground vegetation VOCs may strongly contribute to the VOCs that enter the soil (Mu et al. 2023). In the context of increasing global atmospheric concentration of VOCs induced by vegetations (Peñuelas and Staudt 2010), it has also become imperative to understand the balance of source-sink functions of soil VOCs. However, the absence of VOCs uptake data, however, can lead to potentially incorrect calculations of net VOCs emission (Rinnan and Albers 2020; Jiao et al. 2023; Pugliese et al. 2023).

Most studies focused on soil VOCs have not sampled directly from soils but from soils plus short plant cover (Aaltonen et al. 2013; Tang et al. 2018; Zhang-Turpeinen et al. 2020). The measurement of VOC fluxes from soils covered with surface vegetation does not truly represent VOCs from soil sources, as this also contains contributions from green leaves (Isidorov and Zaitsev 2022), which may mask or lead to underestimations in the soil function of VOC uptake (Ramirez et al. 2010), resulting in a significant bias for modeling global VOCs when integrated with the soil ecosystem. So, distinguishing the VOCs from

floor and soil is essential for understanding the balance of VOCs between the soil and the atmosphere.

Global models currently exclude soil VOC fluxes due to insufficient data (Guenther et al. 2012). With the increase in soil-related VOC studies in recent decades, the variations of soil VOC exchange among ecosystems due to differences in climate (Kramshøj et al. 2016; Mäki et al. 2019b; Huang et al. 2021; Llusà et al. 2022; Romero-Olivares et al. 2022; Yang et al. 2024), vegetation composition (Kivimäenpää et al. 2018; Mäki et al. 2019c; Ghirardo et al. 2020) and soil organisms (Bourtsoukidis et al. 2018; Trowbridge et al. 2020) have been uncovered. However, even more field data are needed across various ecosystems, especially in soils with high microbial activity in subtropical and tropical regions (Llusà et al. 2022; Mu et al. 2023; Pugliese et al. 2023).

VOC fluxes between the soil and the atmosphere are predominantly influenced by isoprenoids, as indicated by studies such as Asensio et al. (2007a) and Mäki et al. (2019a). In this review, we classify isoprenoids into four main classes: isoprene, monoterpenes, sesquiterpenes, and other VOCs, aligning with categories commonly utilized in previous studies (Kramshøj et al. 2016; Mäki et al. 2017). Our discussion encompasses recent developments in soil VOC research, offering insights into potential soil VOC emissions and uptake. Additionally, we present an analysis of soil VOC characteristics across diverse ecosystems, examine the sources of VOCs in soil ecosystems, outline the primary mechanisms governing the return of atmospheric VOCs to soils.

## Materials and methods

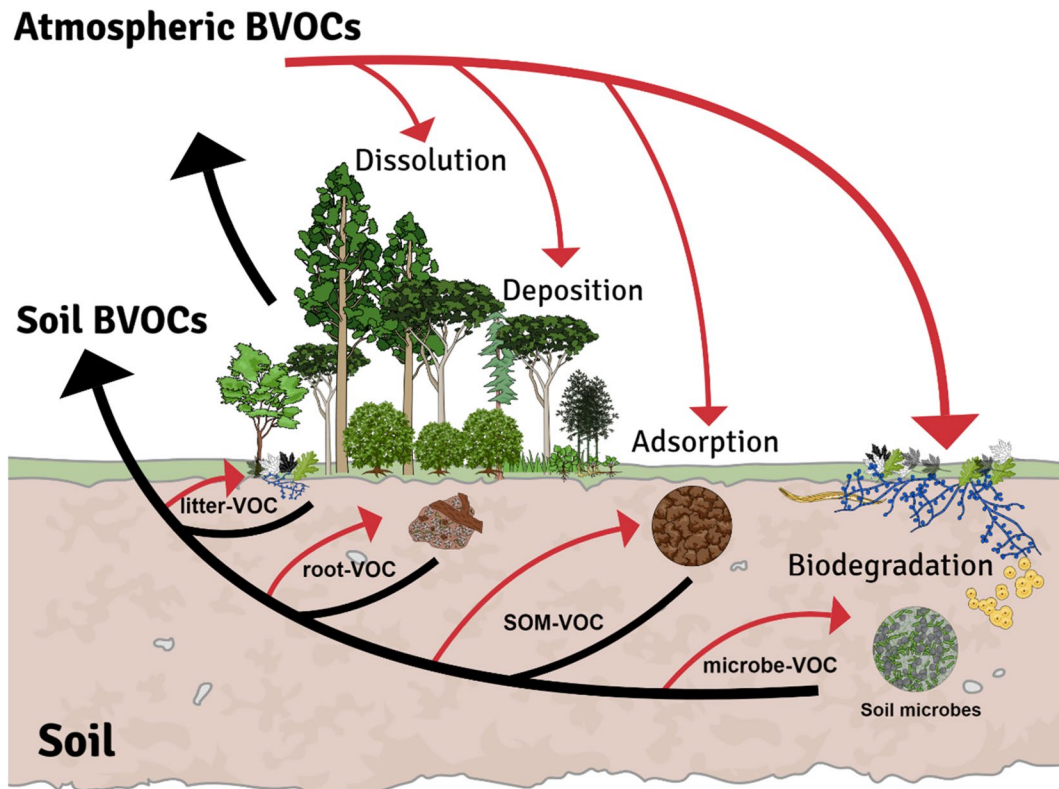
### Data collation

In the paper, we are focused on the VOCs released from soils with litter cover. Hence, the soil is defined as comprising decomposing organic matter (mainly consisting of leaf litter), roots, bare soil, and soil microbes (Fig. 1). We collected data related to VOCs from soil-related sources by searching the Web of Science and Google Scholar for peer-reviewed journal articles published until the end of 2021. The search terms were (volatile organic compound\* OR VOC OR isoprenoids OR monoterpene OR sesquiterpene) AND (soil OR plant litter OR plant root)

contained in the title, keyword, or abstract. The VOC data are divided into two subsets: quantitative and qualitative. For the quantitative analysis of VOCs, we included field experiments of soil VOCs flux and concentration and studies of VOC release rates from decaying plant litter in the laboratory. In contrast, for the qualitative data on VOCs, we focused on VOCs release species from different soil sources under laboratory conditions. Therefore, different collection strategies were used for the two datasets. The quantitative data collected compounds that appeared in each article and had a corresponding rate. The qualitative data recorded every compound released from the different sources reported in each article.

Quantitative data of VOCs from soil-related sources article was cross-checked to determine whether the studies met the following criteria: (1) the flux and concentration of VOCs in soils or soil profiles were studied in field conditions; (2) the flux of VOC was directly sampled from soil sources (including soil with litter, without litter, without root, without understory); (3) the rate value of litter VOCs was available or could be extracted from figures; (4) the VOC flux could be extracted directly from the text, table, figure or published supplementary material. The Engauge Digitizer version 12.1 (<http://markumitchell.github.io/engauge-digitizer>) was assisted to digitally estimate from the figures in the published literature when the results were graphically reported. After the aforementioned criteria, these studies could be used for data analysis (for more details, see Table S1 in the Appendix), representing three ecosystems (forest, tundra, and cropland). For the forest ecosystem, six different vegetation types are included (boreal forest, subalpine forest, Mediterranean forest, temperate forest, subtropical forest and tropical forest). Additionally, six papers are shown for comparison of litter VOC rates in Table 3.

For the qualitative analysis, each article was cross-checked to determine whether the studies met the following criteria: (1) plant litter material, either from falling leaves or decomposing litter on the floor; (2) root samples must be living roots; (3) microbes are extracted from within the soil or in the litter habitat; (4) the bare soil source VOCs could be from (sterile) cultured soil, which removed roots and litter; (5) the VOC data was able to be extracted directly from the text, table, figure and/or published supplementary material. Following the aforementioned criteria,



**Fig. 1** Schematic of the main flows and processes that determine levels of biogenetic volatile organic compounds (BVOCs) between the atmosphere and the soil ecosystem. The black arrow represents soil BVOCs emitted by related soil sources (litter, root, SOM, and microbes), and the red arrows represents

atmospheric VOCs that are absorbed by soil by related (biotic and abiotic) mechanisms. Abbreviations: litter-VOC, VOCs derived from litter; root-VOC, VOCs derived from roots; SOM-VOC, VOCs derived from SOM; microbe-VOC, VOCs derived from microbes

these studies could be used for the qualitative analysis (for more details, see Table S2), representing four soil sources (plant litter, roots, bare soil, and soil microbes).

#### Data analysis

Before the statistical analysis, conversions were made of all necessary data so they were fully comparable. In the literature, VOC exchange rates reported with other units (e.g.,  $\text{pmol m}^{-2} \text{s}^{-1}$  and  $\text{nmol m}^{-2} \text{h}^{-1}$ ) were converted to  $\text{ug m}^{-2} \text{h}^{-1}$ . To compare soil VOC exchange in various ecosystems, the range of rates for the main VOC classes (isoprene, monoterpenes, sesquiterpenes, other VOCs) was summarized. PubChem (<https://pubchem.ncbi.nlm.nih.gov/>) was used to verify molecular formulas and chemical classes for these VOCs

not classified in the original paper. Additionally, to highlight the uptake capacity of soils, studies that found uptake rates are shown separately.

To explore the correlations of VOCs among different soil sources, all components underwent certification by Pubchem and mVOCs 3.0 (<https://bioinformatics.charite.de/mvoc/>), with verification of the molecular formula, PubChem ID and chemical classification. Those compounds that could not be certified were rejected in the following analysis. The relative abundance of VOCs from the different soil sources, such as decomposing litter, roots, bare soil and soil microbe, were summarized in pie charts as the ratio between the number of VOCs in that chemical class and the total number of VOCs in all classes. An additional graphical representation was made (Cytoscape 3.9.1) to highlight the associations between groups of VOCs and their sources. The Venn diagrams were

generated using EVenN (<http://www.ehbio.com/test/venn>) (Chen et al. 2021).

## Results

### Main detectable VOCs emitted from soils

The global VOC emissions from terrestrial vegetation are estimated to be 500, 89 and 36 Tg C y<sup>-1</sup> for isoprene, monoterpenes and sesquiterpenes, respectively (Guenther et al. 2012; Acosta Navarro et al. 2014), based on the Model of Emissions of Gases and Aerosols from Nature (MEGAN). Their emissions from soil sources, however, have received considerably less attention and are rarely estimated at a global scale (Tang et al. 2019).

### Isoprene

Isoprene is the most globally abundant VOC emitted from aboveground sources (Guenther et al. 1993), but its flux rate in soil systems needs to be clarified (McGenity et al. 2018). Plant litter and soil microbes serve as the primary sources of isoprene in soils (Guenther et al. 1993; Insam and Seewald 2010; Gray et al. 2010; Mancuso et al. 2015; Svendsen et al. 2018), which have higher concentrations in topsoil (Table 1). In contrast, plant roots seem to produce less isoprene, as shown by a laboratory study in which isoprene emissions below the limits of quantification from the bare roots of 15 different tree species (Tsuruta et al. 2018). Isoprene emissions from litter occur mainly during the initial phase of decomposition (Gray et al. 2010; Svendsen et al. 2018). This can be attributed to the ability of some cells in fresh leaf litter to maintain isoprene synthesis.

Compared to aboveground sources, isoprene emissions from soils have been reported to be relatively low (Gray et al. 2014; Mäki et al. 2019b), with the highest rate observed in cropland being 5.7 µg m<sup>-2</sup> h<sup>-1</sup> (Fig. 2; Table 2). Other ecosystems, such as forests in the boreal and Mediterranean, have shown low emission rates and low concentrations in the soil horizon (Tables 1 and 2) (Asensio et al. 2007b; Mäki et al. 2017, 2019b). Moreover, isoprene emission is not always detectable in soil samples because it depends heavily on the litter plant species and microbes present (Veres et al. 2014).

Although generally in low concentrations, isoprene appears in a wide variety of soil ecosystems, generated by bacteria, fungi, protists, algae and animals (Scholler et al. 2002; Murrell et al. 2020). Some bacteria and fungi, such as *Bacillus* sp., *Burkholderia* sp. and *Tuber borchii* have been found to release isoprene as a means of defense and communication (Lemfack et al. 2018). However, the role of soil microbes in isoprene emission may be insignificant, possibly due to the consumption of soil isoprene-degrading bacteria that can exceed its production in soil ecosystems (Cleveland and Yavitt 1998; Carrión et al. 2020; Trowbridge et al. 2020; Mu et al. 2023). This phenomenon will be discussed further in a subsequent section.

### Monoterpenes

Globally, monoterpenes make up the second largest class of atmospheric VOCs (Guenther et al. 2012). In soils, monoterpene concentrations were highest in the litter layer and O-horizon compared to others (Table 1), due to the high levels of organic matter that accelerates microbial decomposition and typically releases α-pinene (Asensio et al. 2012; Svendsen et al. 2018). Monoterpenes tend to have relatively high emissions from soils and constitute a substantial proportion of soil VOCs, particularly in forest soils, except for subalpine forests (Table 2). Extensive research has been conducted on the emissions of monoterpenes in boreal forest floors (Hellén et al. 2006; Aaltonen et al. 2011; Wang et al. 2018; Mäki et al. 2019b), but there is less research for other soil types (Mäki et al. 2017). Boreal forest soils reveal considerable emissions of monoterpenes with rates ranging from 38.4 to 49.5 µg m<sup>-2</sup> h<sup>-1</sup>, with the variability influenced by seasons, soil characteristics and litter cover characteristics (Mäki et al. 2017).

For temperate forests, Staudt et al. (2019) measured significantly higher monoterpene emissions (from 558.3 to 4548.1 µg m<sup>-2</sup> h<sup>-1</sup>) from soils with litter during summer in a *Pinus pinaster* forest in France. There was high heterogeneity in the emission of monoterpenes among different plots, which was partially caused by variations in the quantity and traits of litter present (Leff and Fierer 2008; Viros et al. 2020). Litter is a strong emitter of monoterpenes, and the amount of litter biomass strongly affects the emission rate of monoterpenes. This also helps to

**Table 1** Concentrations and emission rates of VOC in soil profiles

Reference	Technique	Vegetation	Soil source	Unit	Iso-prene	Monoterpenes	Sesquiterpenes	Other VOCs
Asensio et al. 2008a	TD-GC-MS	<i>Pinus halepensis</i>	Litter	mg/m <sup>2</sup>	/	701.4 ( $\alpha$ -pinene:59%; sabinene:22%; $\beta$ -pinene:19%)	2795.4 ( $\beta$ -caryophyllene: 75%; $\alpha$ -humulene:25%)	/
			Root <sup>a</sup>	mg/m <sup>2</sup>	/	22.0 ( $\alpha$ -pinene:93%; sabinene:0.8%; $\beta$ -pinene:6%)	1.6 ( $\beta$ -caryophyllene:79%; $\alpha$ -humulene:21%)	/
			Mineral <sup>b</sup>	ug/g	/	4.2 ( $\alpha$ -pinene:89%; sabinene:4%; $\beta$ -pinene:7%)	2.4 ( $\beta$ -caryophyllene:69%; $\alpha$ -humulene: 31%)	/
Mäki et al. 2019b <sup>c</sup>	TD-GC-MS	<i>Pinus sylvestris</i>	O-horizon	ug/m <sup>3</sup>	0.017	443.4 ( $\alpha$ -pinene:72%; $\Delta$ 3-carene:13%; limonene:4%)	5.1 ( $\alpha$ -gurjunene: 67%; iso-longifolene: 6%)	13.9 (1-butanol:20%; cis-3-hexenyl acetate:8%)
			A-horizon	ug/m <sup>3</sup>	0.042	99.4 ( $\alpha$ -pinene:71%; $\Delta$ 3-carene:17%; limonene:4%)	31.6 ( $\alpha$ -gurjunene:81%; iso-longifolene: 0.1%)	34.5 (1-butanol:26%; cis-3-hexenyl acetate:3.4%)
			B-horizon	ug/m <sup>3</sup>	0.016	145.8 ( $\alpha$ -pinene:75%; $\Delta$ 3-carene:21%; limonene:2%)	11.8 ( $\alpha$ -gurjunene:26%; iso-longifolene: 0.4%)	9.6 (1-butanol:24%; cis-3-hexenyl acetate: 10%)
			C-horizon	ug/m <sup>3</sup>	0.020	13.6 ( $\alpha$ -pinene:49%; $\Delta$ 3-carene:21%; limonene:14%)	5.5 ( $\alpha$ -gurjunene:56%; iso-longifolene: 1%)	7.2 (1-butanol:23%; cis-3-hexenyl acetate:22%)
Wester-Larsen et al. 2020 <sup>d</sup>	TD-GC-MS	Transect	0–15 cm	ng/L	0.23	1.94 ( $\alpha$ -pinene:52.3%, eucalyptol:11.1%)	0.99 (2,6,11-Trimethyl-dodecane:36.2%, Farnesane:17.6%)	40.7 (Cyclopentane:13.7%)
			0–15 cm	ng/L	0.43	3.44 ( $\alpha$ -pinene:34%)	2.45 (2,6,11-Trimethyl-dodecane:24.1%)	130.6 (Cyclopentane:6.8%)
			0–15 cm	ng/L	0.40	4.46 ( $\alpha$ -pinene:28.5%)	2.94 (2,6,11-Trimethyl-dodecane:10.2%)	210.6 (Cyclopentane:7.6%)
			0–15 cm	ng/L	0.24	0.30 ( $\alpha$ -pinene:23%)	1.07 (2,6,11-Trimethyl-dodecane:13.1%)	82.16 (Cyclopentane:1.6%)
			0–15 cm	ng/L	0.21	2.81 ( $\alpha$ -pinene:14.6%)	2.90 (2,6,11-Trimethyl-dodecane:11.7%)	259.8 (Cyclopentane:4.3%)
Mu et al. 2022	PTR-MS	Shrubland	0–25 cm	ppb	0.014	0.845	0.083	2.2 (methanol:23%)
			0–25 cm	ppb	0.013	0.041	0.089	2.1 (methanol:39%)
Bourtsoukidis et al. 2018 <sup>e</sup>	PTR-MS	Tropical forest	O-horizon	ug m <sup>-2</sup> h <sup>-1</sup>	/	/	48.09 ( $\alpha$ -himachalene:35%, $\alpha$ -gurjunene:16.6%)	/
			A-horizon	ug m <sup>-2</sup> h <sup>-1</sup>	/	/	5.65 ( $\alpha$ -himachalene:28.8%, $\alpha$ -gurjunene: 40%)	/
			B-horizon	ug m <sup>-2</sup> h <sup>-1</sup>	/	/	1.12	/

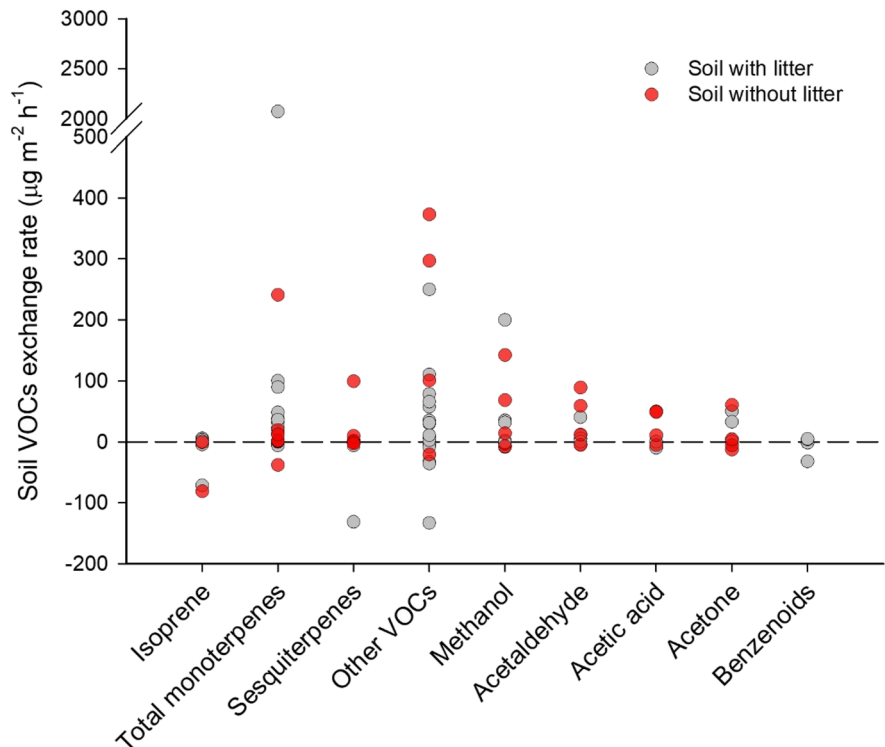
**Table 1** (continued)

Reference	Technique	Vegetation	Soil source	Unit	Iso-prene	Monoterpenes	Sesquiterpenes	Other VOCs
Mäki et al. 2019b <sup>c</sup>	TD-GC-MS	<i>Pinus sylvestris</i>	O-horizon	$\mu\text{g m}^{-2} \text{h}^{-1}$	/	333	2	/
			A-horizon	$\mu\text{g m}^{-2} \text{h}^{-1}$	/	87	13	/
			B-horizon	$\mu\text{g m}^{-2} \text{h}^{-1}$	/	133	4	/
			C-horizon	$\mu\text{g m}^{-2} \text{h}^{-1}$	/	11	2	/
Yang et al. 2024	SPME-GC-MS	<i>Quercus ilex</i>	Top soil	$\text{ng h}^{-1}$	0.16 <sup>f</sup>	0.7–1.86 <sup>g</sup>	0.12–5.43 <sup>g</sup>	/

Where,

- <sup>a</sup> is the mean value from root top and root low,
- <sup>b</sup> is the mean value of mineral top and mineral low,
- <sup>c</sup> is the data of the year 2016 only,
- <sup>d</sup> is average value of the year 2016 only,
- <sup>e</sup> is the data from mean values of TF1, TF2 and TF3 only,
- <sup>f</sup> is the data of autumn,
- <sup>g</sup> is the range value of four seasons,
- “/” is data not available

**Fig. 2** Soil VOC exchange rates reported in all ecosystems. Data includes measurements in soil with litter (grey points) and without litter (red points). Treatments (e.g., warming and N addition) and zero value are not included. Data are extracted form Table S1 in the Appendix



**Table 2** Ranges of soil VOC exchange rates ( $\mu\text{g m}^{-2} \text{h}^{-1}$ ) in different ecosystems based on the available data. Data are extracted from Table S1 in the Appendix

Ecosystem	Isoprene	Monoterpenes	Sesquiterpenes	Other VOCs	Methanol
Tundra	0.4–3.0	0.2–2.1	0.1 <sup>a</sup>	30.7–113.2	/
Boreal forest	1.0–4.1 <sup>a</sup>	38.4–49.5	0.4–0.7 <sup>a</sup>	/	/
Mediterranean forest	–4.4–0.4	–8.1–6.2	–0.98–2.4	–32.9–373.2	–6.9–142.7
Subalpine forest	–0.1 <sup>b</sup>	0.1–0.7 <sup>b</sup>	0.3 <sup>c</sup>	1.6–4.0	1.7
Temperate forest	–0.04–3.5	0.04–2073.6	–0.1–0.7	31.3–110.4	–0.04–31.8
Subtropical forest	–80.9–0.7	–21.9–89.9	–4.2 <sup>a</sup>	–133.2–65.6	/
Tropical forest	/	–2.4–23.3	–66–48.9	/	/
Cropland	5.7 <sup>a</sup>	0.5 <sup>a</sup>	/	/	–9–200

This summary includes VOCs from field studies on soil (with and without litter), but data from soils with plant cover and treatment manipulation (e.g., warming, nutrient addition) were not considered. The range of soil VOCs were calculated from mean value the mean values of every individual forest site and soil source in each included article. Positive and negative values are emissions and uptakes, respectively

<sup>a</sup>, data from only one study

<sup>b</sup>, mean cited from original study

<sup>c</sup>, mean value extracted from paper

“/” indicates data not available

explain the difference in emission rates of monoterpenes reported by Staudt et al. (2019) and Mäki et al. (2017), as litter biomass in the former study (740 g dry weight  $\text{m}^{-2}$ ) was around 60 times higher than that in the latter study (12 g dry weight  $\text{m}^{-2}$ ). However, the soil in the study by Staudt et al. (2019) still maintained a high rate of monoterpene emission (245  $\mu\text{g m}^{-2} \text{h}^{-1}$ ) after litter removal, indicating that other soil characteristics (e.g., SOM and soil microbes), as well as litter, are also essential sources of monoterpenes (Llusià et al. 2022).

Compared to boreal and temperate forests, the emission rates of soil monoterpenes are relatively low in tundra, subalpine and Mediterranean forests (Table 2). According to a study by Kramshøj et al. (2016), the mean emission rate of monoterpenes in tundra soil during the growing season was 1.73  $\mu\text{g m}^{-2} \text{h}^{-1}$ , and  $\alpha$ -terpineol was found to be the primary compound. The low emission of monoterpenes in tundra soil may be attributed to the absence of litter cover in combination with the low temperature, which can reduce microbial decomposition. Similarly, subalpine forest soils are also weak emitters of monoterpenes with emission rates ranging from 0.05 to 0.7  $\mu\text{g m}^{-2} \text{h}^{-1}$  due to low temperatures and slow microbial activity (Greenberg et al. 2012; Gray et al. 2014; Trowbridge et al. 2020). However, in Mediterranean soils, the low monoterpene emissions seem to

be limited by soil water content (Asensio et al. 2007b, c) strong uptake by soil was observed in a recent study (Yang et al. 2024).

Lastly, tropical forest soils are generally predicted to be considerable sources of monoterpenes due to their abundant litter cover, high root density and relatively high temperature. But their fluxes of monoterpene much lower than those in boreal and temperate forest soils, which range from –2.4 to 23.3  $\mu\text{g m}^{-2} \text{h}^{-1}$  (Table 2). Bourtsoukidis et al. (2018) revealed that monoterpenes in tropical forest soils were weakly emitted under high water conditions and moderately consumed in the low-moisture range, which was also confirmed by Llusià et al. (2022), who found a significant shift from source to sink of terpenoids in the wet and the dry season. The low emission of monoterpenes in tropical forest soils can be attributed to high consumption by soil microbes, which utilize VOCs as a carbon source and energy supply (Albers et al. 2018; Bourtsoukidis et al. 2018; Pugliese et al. 2023).

#### Sesquiterpenes

The concentration of sesquiterpenes has been shown to be higher in the A-horizon compared to the O- and B-horizons Mäki et al. (2019) (Table 1). This is due to the fact that sesquiterpene production in soils is strongly associated with high emissions from plant



roots (Mäki et al. 2017; Tsuruta et al. 2018) and soil fungi (Asensio et al. 2008a; Horváth et al. 2011; Bourtsoukidis et al. 2018). In Amazonian soils, sesquiterpene production of soil microbes is also higher in the O- and A-horizons than in the B-horizon (Bourtsoukidis et al. 2018). The high concentration of sesquiterpenes in the litter layer in the *Pinus halepensis* tree (Table 1) can be attributed to the high amount of fungal hyphae growing on the litter (Asensio et al. 2008a).

A wide variety of sesquiterpenes is generated in the soil horizons of the boreal forest, such as  $\alpha$ -gurjunene,  $\alpha$ -humulene and  $\beta$ -farnesene. However, due to their low volatility, their emission rates to the atmosphere are typically low, ranging from 0.4 to 17.5  $\mu\text{g m}^{-2} \text{h}^{-1}$  (Mäki et al. 2017, 2019b). Table 2 shows that other ecosystems, such as tundra and Mediterranean forests, also exhibit low emissions of sesquiterpenes. For instance, a study on tundra soils detected only one sesquiterpene during the growing season, with an emission rate of 0.14  $\mu\text{g m}^{-2} \text{h}^{-1}$  (Kramshøj et al. 2016). Similarly, an experiment in Mediterranean forest soils found the highest rate of soil sesquiterpenes to be 2.40  $\mu\text{g m}^{-2} \text{h}^{-1}$  (Asensio et al. 2007b). Compared with those low emissions of sesquiterpenes, tropical forest soils were found to have high sesquiterpene emissions (a maximum of 210  $\mu\text{g m}^{-2} \text{h}^{-1}$ ) in recent studies (Bourtsoukidis et al. 2018; Llusà et al. 2022), which highlights the potential source of sesquiterpenes inherent in this soil type. The substantial variation in sesquiterpene emissions among different ecosystem soils may be attributed, in part, to differences in soil microorganism communities, which are the primary contributors of sesquiterpenes in soils (Horváth et al. 2011, 2012; Weigl et al. 2016). Additionally, some studies have suggested that high microbial biomass in soils may result in higher emissions of sesquiterpenes (Weigl et al. 2016; Bourtsoukidis et al. 2018; Kramshøj et al. 2018).

#### Other VOCs

Most of the research on soil VOC exchanges has focused on terpenoids. Notably, other VOCs seem to have a stronger emission than isoprenoids (Table 2). Other VOCs, such as methanol (Asensio et al. 2007b; Mu et al. 2022), carbonyl compounds (e.g., acetone, acetaldehyde and acetic acid) (Asensio et al. 2008a;

Gray et al. 2014; Mielnik et al. 2018), benzenoids (Zheng et al. 2015), sulphurous compounds (e.g., dimethyl sulphide, carbon disulphide and dimethyl disulphide) (Yi et al. 2010) and formaldehyde (Gray et al. 2014; Li et al. 2016) have also been reported as being emitted from soils, but are rarely studied.

The annual global emissions of methanol, acetone, formic and acetic acids from terrestrial ecosystems are estimated to be 187 Tg  $\text{y}^{-1}$  (Stavrou et al. 2011), 95 Tg  $\text{y}^{-1}$  (Jacob et al. 2002), 57 Tg  $\text{y}^{-1}$  and 85 Tg  $\text{y}^{-1}$  (Paulot et al. 2011), respectively. Some of these compounds have high emission rates in a specific type of soil (Kramshøj et al. 2016; Bourtsoukidis et al. 2018; Mäki et al. 2019b). For example, aldehydes (octanal, nonanal, and hexanal) are found in tundra soils and account for about 75% of the total VOC emissions in that ecosystem (78.4  $\mu\text{g m}^{-2} \text{h}^{-1}$ ) (Kramshøj et al. 2016), and methanol is predominant in cropland soils (Bachy et al. 2018).

Methanol is mainly emitted by soil bacteria and the decomposition of residual organic matter, so methanol synthesis is likely driven by temperature-dependent enzymatic activity and microbial community structure. In fact, methanol emission is generally positively correlated with temperature (Schade and Goldstein 2001), but recent experiments have suggested that this relationship could also be affected by soil water content. In one study, methanol emissions under dry conditions were strongly positively correlated with soil temperature, but methanol was taken up under wet conditions in the same cropland, and the amount taken up increased with temperature (Bachy et al. 2018). Similarly, in Mediterranean forest soils, methanol emission was high during a dry summer, and uptake was strong in a wet autumn (Asensio et al. 2008b).

#### Sources of VOCs in soils

The profiles of VOCs from the same soil sources are vary widely due to different species. Therefore, the focus of this section is to examine the diversity of VOCs originating from soil compartments and compare them among different sources to determine if distinct characteristics exist in the VOC profiles that can be helpful in understanding the belowground information network formed by various soil sources through VOCs.

## VOC emissions from decomposing litter

Comparisons of sterile and non-sterile litters could give an insight into the VOCs derived from plant litter and or microbes (Gray et al. 2010). Litter produces abundant VOCs during its decomposition process, and the emission rate and diversity of these VOCs vary with changes in the environment (Schade and Goldstein 2001; Gray et al. 2010; Isidorov et al. 2016; Svendsen et al. 2018; Viros et al. 2021). While early field studies suggested that litter may be a minor source of VOCs compared to aboveground plant emitters (Schade and Goldstein 2001; Faubert et al. 2010; Greenberg et al. 2012), a recent study emphasized that a thick litter layer above the soil may be a large potential source, with the removal of that litter layer substantially reducing (by 81%) total soil VOC emissions in that system (Staudt et al. 2019). Results from laboratory litter incubation experiments show that litter emission rates range from 0.1 to 265.5  $\mu\text{g g (dw)}^{-1} \text{h}^{-1}$  (Table 3), depending on litter types, degree of decomposition and incubation conditions (Leff and Fierer 2008; Gray et al. 2010; Isidorov et al. 2016; Svendsen et al. 2018). It is worth mentioning that decomposing litters seem to be a particularly important source of methanol (Warneke et al. 1999), which, in one study with litter from 12 different plant species, accounted for the majority litter emissions (Gray et al. 2010).

In general, the decomposition of broadleaf litter is faster than other types of litter; thus, the emission rate of VOCs may be higher in broadleaf forest soils than in others. For instance, the VOC emission rates of broadleaf litters (e.g., *Eucalyptus sp.*, *Fraxinus sp.* and *Populus sp.*) are shown to be higher than from litters of conifer (e.g., *Pinus contorta*), grasses (e.g., *Miscanthus sp.*) and shrubs (e.g., *Cassiope sp.*) (Table 3), and that is partly attributed to litter quality. On the other hand, conifer litters strongly correlate with terpenoids, while for deciduous tree trends are much weaker (Table 3). One possible reason is that conifer leaf litter contains structures for storing terpenoids, which benefits terpenoid emissions (Viros et al. 2020).

Incubation experiments have shown that the VOC emission rates in the early stage of decomposition are positively related to the amount of labile C in the litter and the presence of terpene storage structures (Leff and Fierer 2008; Ramirez et al. 2010; Gray et al.

2010; Svendsen et al. 2018; Viros et al. 2020). However, there is a burst of VOC emissions in the litter during the early decomposition stage, possibly due to the contribution of green leaf volatile compounds, which can constitute more than 75% of the emissions from *Betula pendula* litter (Holopainen et al. 2010). Overall, the VOC emission rate of litter decreases with the time of decomposition (Ramirez et al. 2010; Isidorov et al. 2010; Viros et al. 2021; Isidorov and Zaitsev 2022). Increased temperature can stimulate emission rates, especially for alkenes and terpenoids (Svendsen et al. 2018). The profiles of litter VOCs are also highly associated with the community structure of microbes in the litter (Isidorov et al. 2016; Svendsen et al. 2018), with litter in different decomposition stages being dominated by different fungi, accounting for some of the differences in emitted VOCs that are found (Isidorov et al. 2016).

The full range of VOCs emitted by litter is still unclear. Here, we collected references of VOCs emitted from litter from 40 plant species, encompassing 285 different VOCs belonging to twelve chemical groups (Fig. 3a). These VOCs included 106 terpenes (37% of those described), 46 benzenoids (16%), 25 alkanes (9%), 19 alcohols (7%), 16 aldehydes (6%), 16 esters (6%), 13 ketones (4%), 13 alkenes (4%), nine halogenated compounds (3%), eight furans (3%), seven ethers (2%), six sulphur (S) compounds (2%), four acids (1%) and one nitrogen (N) compound (0.4%). The first four classes, which comprise 68% of the measured VOCs, represented the major classes of litter VOCs. After comparing VOCs from litter with VOCs emitted from other sources (root, bare soil and microbes), our Venn diagram revealed that litter emitted 147 unique VOCs not shared by any other sources (Fig. 4), with most belonging to terpenes (60) and benzenoids (21) and alkanes (10 VOCs) (Table 4).

## VOC emissions from active roots

Plants allocate 40–73% of the photosynthesized C for root metabolism, root growth and to root-associated microbes in the rhizosphere (Grayston et al. 1997). Roots are known to produce VOCs for defence and communication (Schenkel et al. 2015), but little is known about the production and emission rates (Lin et al. 2007; Asensio et al. 2008a; Tsuruta et al. 2018). Furthermore, evidence has suggested that the rate of production of root VOCs

**Table 3** Average VOC emission rates from various litter sources measured in laboratory studies

Species	Functional Type	Condition	Main VOCs and their compositions	Overall rate <sup>1</sup>	Reference
<i>Centaurea maculosa</i>	Grass	22 °C/20d	Isoprene, 0.05%; monoterpenes, 0.01%; other VOCs, 99.94%; methanol, 96.69%	19.7	Gray et al. 2010
<i>Centaurea maculosa</i> *	Grass	22 °C/20d	Isoprene, 3.53%; monoterpenes, 0.29%; other VOCs, 96.19%; methanol, 43.40%	10.8	Gray et al. 2010
<i>Eucalyptus</i> sp.	Broadleaf	22 °C/20d	Isoprene, 0.16%; monoterpenes, 22.16%; other VOCs, 77.96%; methanol, 70.83%	265.5	Gray et al. 2010
<i>Eucalyptus</i> sp.*	Broadleaf	22 °C/20d	Isoprene, 0.35%; monoterpenes, 85.72%; other VOCs, 14.72%; methanol, 7.56%	58.4	Gray et al. 2010
<i>Fraxinus pennsylvanica</i>	Broadleaf	22 °C/20d	Isoprene, 0.07%; monoterpenes, 0.01%; other VOCs, 99.92%; methanol, 98.71%	142.9	Gray et al. 2010
<i>Fraxinus pennsylvanica</i> *	Broadleaf	22 °C/20d	Isoprene, 1.9%; monoterpenes, 0.32%; other VOCs, 97.79%; methanol, 65.80%	14.3	Gray et al. 2010
<i>Miscanthus</i> sp.*	Grass	22 °C/20d	Isoprene, 1.16%; monoterpenes, 0.34%; other VOCs, 98.49%; methanol, 35.29%	5.0	Gray et al. 2010
<i>Miscanthus</i> sp.	Grass	22 °C/20d	Isoprene, 0.06%; monoterpenes, 0.05%; other VOCs, 99.36%; methanol, 85.35%	4.3	Gray et al. 2010
<i>Pinus contorta</i>	Conifer	22 °C/20d	Isoprene, 0.15%; monoterpenes, 9.74%; other VOCs, 90.19%; methanol, 85.15%	23.0	Gray et al. 2010
<i>Pinus contorta</i> *	Conifer	22 °C/20d	Isoprene, 1.50%; monoterpenes, 16.04%; other VOCs, 82.56%; methanol, 40%	14.4	Gray et al. 2010
<i>Pinus ponderosa</i>	Conifer	22 °C/20d	Isoprene, 0.23%; monoterpenes, 4.65%; other VOCs, 95.24%; methanol, 90.41%	89.9	Gray et al. 2010
<i>Pinus ponderosa</i> *	Conifer	22 °C/20d	Isoprene, 1.14%; monoterpenes, 33%; other VOCs, 66.22%; methanol, 32.51%	13.6	Gray et al. 2010
<i>Populus deltoides</i>	Broadleaf	22 °C/20d	Isoprene, 0.04%; monoterpenes, 0.04%; other VOCs, 99.92%; methanol, 98.30%	226.8	Gray et al. 2010
<i>Populus deltoides</i> *	Broadleaf	22 °C/20d	Isoprene, 0.66%; monoterpenes, 0.41%; other VOCs, 90.94%; methanol, 60.1%	10.5	Gray et al. 2010
<i>Populus tremuloides</i>	Broadleaf	22 °C/20d	Isoprene, 0.09%; monoterpenes, 0.02%; other VOCs, 99.89%; methanol, 97.86%	78.5	Gray et al. 2010
<i>Populus tremuloides</i> *	Broadleaf	22 °C/20d	Isoprene, 0.67%; monoterpenes, 0.40%; other VOCs, 98.95%; methanol, 60.86%	7.5	Gray et al. 2010
<i>Quercus macrocarpa</i>	Broadleaf	22 °C/20d	Isoprene, 0.62%; monoterpenes, 0.77%; other VOCs, 98.64%; methanol, 70.72%	4.7	Gray et al. 2010
<i>Quercus macrocarpa</i> *	Broadleaf	22 °C/20d	Isoprene, 0.71%; monoterpenes, 0.88%; other VOCs, 98.42%; methanol, 58.13%	5.4	Gray et al. 2010
<i>Quercus rubra</i>	Broadleaf	22 °C/20d	Isoprene, 0.5%; monoterpenes, 0.31%; other VOCs, 99.21%; methanol, 85.11%	7.4	Gray et al. 2010
<i>Quercus rubra</i> *	Broadleaf	22 °C/20d	Isoprene, 0.83%; monoterpenes, 0.86%; other VOCs, 98.32%; methanol, 35.63%	9.2	Gray et al. 2010
<i>Rhododendron maximum</i>	Shrub	22 °C/20d	Isoprene, 0.05%; monoterpenes, 0.03%; other VOCs, 99.92%; methanol, 97.53%	52.2	Gray et al. 2010
<i>Rhododendron maximum</i> *	Shrub	22 °C/20d	Isoprene, 0.35%; monoterpenes, 0.06%; other VOCs, 99.59%; methanol, 71.77%	7.1	Gray et al. 2010
<i>Thinopyrum intermedia</i>	Grass	22 °C/20d	Isoprene, 0.20%; monoterpenes, 0.03%; other VOCs, 99.78%; methanol, 89.33%	5.8	Gray et al. 2010
<i>Thinopyrum intermedia</i> *	Grass	22 °C/20d	Isoprene, 0.94%; monoterpenes, 0.61%; other VOCs, 98.44%; methanol, 46.90%	4.3	Gray et al. 2010

**Table 3** (continued)

Species	Functional Type	Condition	Main VOCs and their compositions	Overall rate <sup>1</sup>	Reference
<i>Pinus sylvestris</i>	Conifer	20 °C/0d	Monoterpenes	2.0	Isidorov et al. 2010
<i>Pinus sylvestris</i>	Conifer	20 °C/77d	Monoterpenes	7.5	Isidorov et al. 2010
<i>Pinus sylvestris</i>	Conifer	20 °C/165d	Monoterpenes	1.6	Isidorov et al. 2010
<i>Pinus sylvestris</i>	Conifer	20 °C/282d	Monoterpenes	0.3	Isidorov et al. 2010
<i>Pinus sylvestris</i>	Conifer	20 °C/490d	Monoterpenes	0.2	Isidorov et al. 2010
<i>Norway spruce</i>	Conifer	20 °C/0d	Monoterpenes	0.2	Isidorov et al. 2010
<i>Norway spruce</i>	Conifer	20 °C/77d	Monoterpenes	1.5	Isidorov et al. 2010
<i>Norway spruce</i>	Conifer	20 °C/165d	Monoterpenes	1.3	Isidorov et al. 2010
<i>Norway spruce</i>	Conifer	20 °C/282d	Monoterpenes	0.5	Isidorov et al. 2010
<i>Norway spruce</i>	Conifer	20 °C/490d	Monoterpenes	0.2	Isidorov et al. 2010
<i>Acer rubrum</i>	Broadleaf	21 °C/73d	Monoterpenes, 0.19%; other VOCs, 95.55%; methanol, 89.40%	0.6	Ramirez et al. 2010
<i>Pinus taeda</i>	Conifer	21 °C/73d	Monoterpenes, 34.90%; other VOCs, 54.58%; methanol, 31.50%	0.3	Ramirez et al. 2010
<i>Cassiope tetragona</i>	Shrub	5 °C/14d	Monoterpenes, 53.1%; sesquiterpenes, 2.6%; other VOCs, 44.3%	0.2	Svendsen et al. 2018
<i>Cassiope tetragona</i>	Shrub	12 °C/14d	Isoprene, 1.0%; monoterpenes, 62.4%; sesquiterpenes, 6.7%; other VOCs, 29.9%	0.3	Svendsen et al. 2018
<i>Cassiope tetragona</i>	Shrub	16 °C/14d	Isoprene, 0.1%; monoterpenes, 58.2%; sesquiterpenes, 24.3%; other VOCs, 17.5%	0.4	Svendsen et al. 2018
<i>Cassiope tetragona</i>	Shrub	19 °C/14d	Isoprene, 0.2%; monoterpenes, 76.4%; sesquiterpenes, 9.7%; other VOCs, 13.8%	0.7	Svendsen et al. 2018
<i>Salix glauca</i>	Shrub	5 °C/14d	Isoprene, 0%; monoterpenes, 24.18%; other VOCs, 75.82%	0.4	Svendsen et al. 2018
<i>Salix glauca</i>	Shrub	12 °C/14d	Isoprene, 0%; monoterpenes, 32.6%; sesquiterpenes, 1.1%; other VOCs, 66.35%	0.1	Svendsen et al. 2018
<i>Salix glauca</i>	Shrub	16 °C/14d	Isoprene, 0%; monoterpenes, 8.92%; sesquiterpenes, 27.46%; other VOCs, 63.62%	0.1	Svendsen et al. 2018
<i>Salix glauca</i>	Shrub	19 °C/14d	Isoprene, 0%; monoterpenes, 10.78%; sesquiterpenes, 14.56%; other VOCs, 74.66%	0.1	Svendsen et al. 2018
<i>Cistus albidus</i>	Shrub	30 °C/fresh litter	monoterpenes, 50.0%; sesquiterpenes, 13.3%; other VOCs, 36.7%	0.3	Viros et al. 2020
<i>Cistus salvifolius</i>	Shrub	30 °C/fresh litter	monoterpenes, 14.3%; sesquiterpenes, 71.4%; other VOCs, 14.3%	0.21	Viros et al. 2020
<i>Cotinus coggygria</i>	Shrub	30 °C/fresh litter	monoterpenes, 91.1%; sesquiterpenes, 2.1%; other VOCs, 6.8%	3.37	Viros et al. 2020
<i>Eucalyptus globulus</i>	Broadleaf	30 °C/fresh litter	monoterpenes, 70%; sesquiterpenes, 20%; other VOCs, 5%	0.2	Viros et al. 2020
<i>Juniperus oxycedrus</i>	Broadleaf	30 °C/fresh litter	monoterpenes, 33.3%; sesquiterpenes, 57.1%; other VOCs, 9.5%	0.21	Viros et al. 2020
<i>Pinus halepensis</i>	Conifer	30 °C/fresh litter	monoterpenes, 29.6%; sesquiterpenes, 60.5%; other VOCs, 10.5%	1.52	Viros et al. 2020

**Table 3** (continued)

Species	Functional Type	Condition	Main VOCs and their compositions	Overall rate <sup>1</sup>	Reference
<i>Pinus pinea</i>	Conifer	30 °C/fresh litter	monoterpenes, 59.3%; sesquiterpenes, 33.3%; other VOCs, 7.4%	0.54	Viros et al. 2020
<i>Rosmarinus officinalis</i>	Shrub	30 °C/fresh litter	monoterpenes, 93%; sesquiterpenes, 7%; other VOCs, 0%	0.71	Viros et al. 2020
<i>Thymus vulgaris</i>	Shrub	30 °C/fresh litter	monoterpenes, 97.5%; sesquiterpenes, 2.1%; other VOCs, 0.2%	4.74	Viros et al. 2020
<i>Acer monspessulanum</i>	Broadleaf	30 °C/fresh litter	other VOCs, 100%	0.01	Viros et al. 2020
<i>Erica arborea</i>	Shrub	30 °C/fresh litter	other VOCs, 100%	0.04	Viros et al. 2020
<i>Quercus coccifera</i>	Shrub	30 °C/fresh litter	other VOCs, 100%	0.32	Viros et al. 2020
<i>Quercus ilex</i>	Broadleaf	30 °C/fresh litter	other VOCs, 100%	0.01	Viros et al. 2020
<i>Quercus pubescens</i>	Broadleaf	30 °C/fresh litter	other VOCs, 100%	0.61	Viros et al. 2020
<i>Quercus suber</i>	Broadleaf	30 °C/fresh litter	other VOCs, 100%	0.02	Viros et al. 2020
<i>Ulex parviflorus</i>	Shrub	30 °C/fresh litter	other VOCs, 100%	0.01	Viros et al. 2020
<i>Pinus halepensis</i>	Conifer	30 °C/fresh litter	monoterpenes, 14.5%; sesquiterpenes, 16.6%; other VOCs, 4.4%	3.38	Viros et al. 2021
<i>Pinus halepensis</i>	Conifer	30 °C/90d	monoterpenes, 50.4%; sesquiterpenes, 36.8%; other VOCs, 5.8%	9.18	Viros et al. 2021
<i>Pinus halepensis</i>	Conifer	30 °C/180d	monoterpenes, 12.4%; sesquiterpenes, 63.2%; other VOCs, 6.8%	3.52	Viros et al. 2021
<i>Pinus halepensis</i>	Conifer	30 °C/270d	monoterpenes, 9.6%; sesquiterpenes, 38.6%; other VOCs, 8.6%	1.56	Viros et al. 2021
<i>Pinus halepensis</i>	Conifer	30 °C/360d	monoterpenes, 11.3%; sesquiterpenes, 28.2%; other VOCs, 22.8%	0.57	Viros et al. 2021
<i>Pinus halepensis</i>	Conifer	30 °C/450d	monoterpenes, 18.6%; sesquiterpenes, 47.6%; other VOCs, 11.6%	1.60	Viros et al. 2021

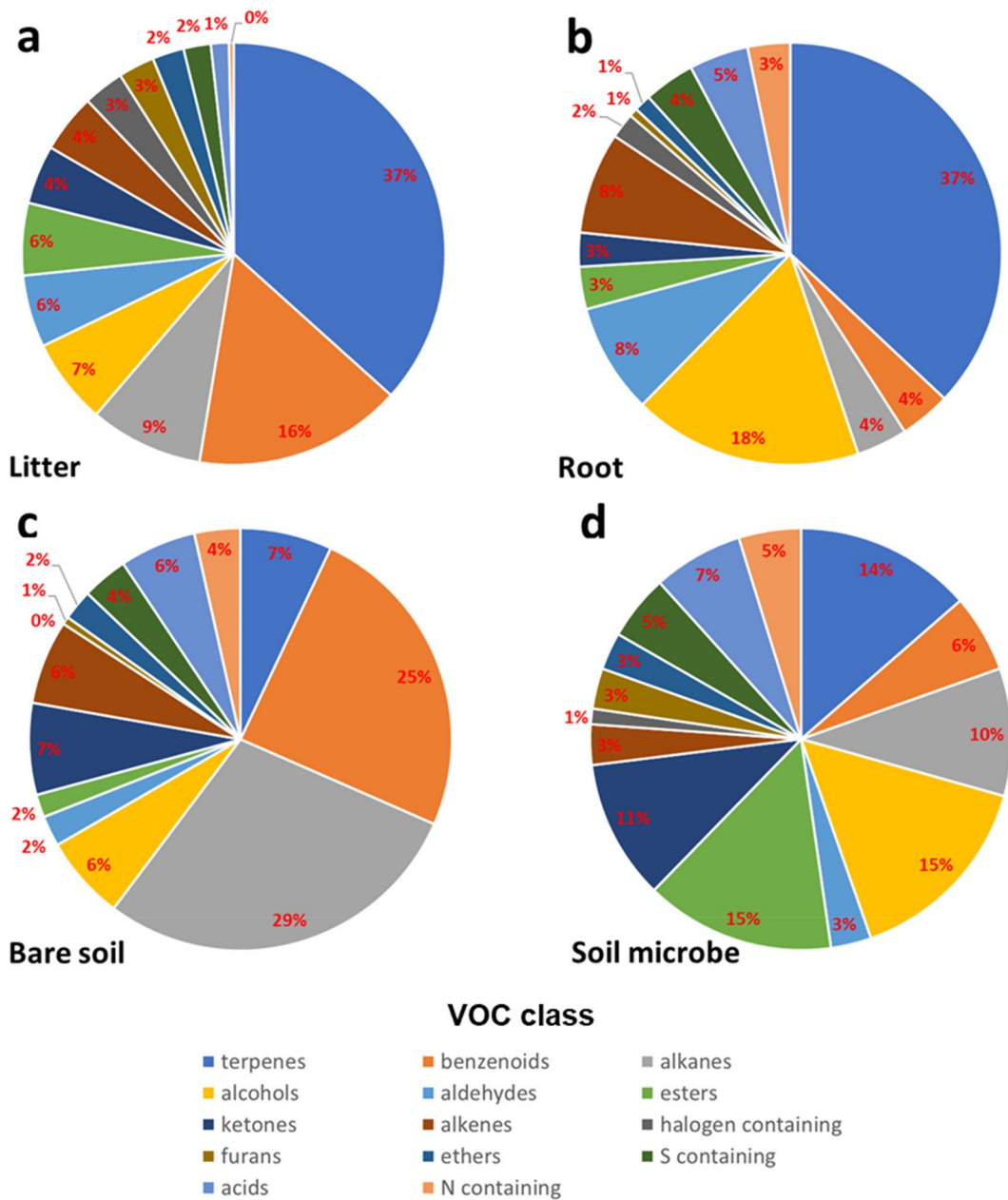
\*Litter samples were sterilized in the study. <sup>1</sup>Rates were converted to  $\mu\text{g g}^{-1} \text{h}^{-1}$  where necessary

might correlate with morpho-anatomical traits of roots, such as root taxonomy and mycorrhizal type (Tsuruta et al. 2018). Otherwise, the presence of roots in soils have an inconsistent effect on soil VOC emissions (Rinnan et al. 2013; Gray et al. 2014), with positive, negative and no impacts, which are related to individual VOCs (Asensio et al. 2007a; Mäki et al. 2017).

The low number of papers published on root VOCs is likely due to the technical difficulties in sampling VOCs in soil matrices (Peñuelas et al. 2014; Tsuruta et al. 2018). We collected six papers focused on root VOCs and found a total of 153 different compounds produced by the roots of 24 plant species (Table S1). The majority (71%) of the identified VOCs were terpenes (57 VOCs), alcohols (27 VOCs), aldehydes (13 VOCs) and alkenes (12 VOCs) (Fig. 3b), and the remaining 29% was composed of ten groups (Fig. 3b). Moreover, most

VOCs from roots are shared with VOCs measured from soil microbes (74 VOCs, Fig. 4), with the remaining 57 unique VOCs including 23 terpenes (most belong to sesquiterpenes), 13 alcohols and seven alkanes (Table 4).

In the few that studies have tried to quantify the rate of VOC emission by roots, a mean emission rate of  $24.3 \mu\text{g g}^{-1} \text{h}^{-1}$  for eight monoterpenes (mainly  $\alpha$ -pinene,  $\beta$ -pinene, and limonene) was found for the washed roots of *Pinus spp.* growing in pots (Lin et al. 2007), and another study using a similar method with *Pinus densiflora* roots found the same monoterpenes but a higher emission rate ( $122.6 \mu\text{g g}^{-1} \text{h}^{-1}$ ) (Tsuruta et al. 2018). This difference may be associated with root traits such as oleoresin content and stored terpenoid pools (Tsuruta et al. 2018). Oleoresin consists of a mixture of terpenoids and is produced by specialized secretory tissues of coniferous tree roots (Lewinsohn et al.



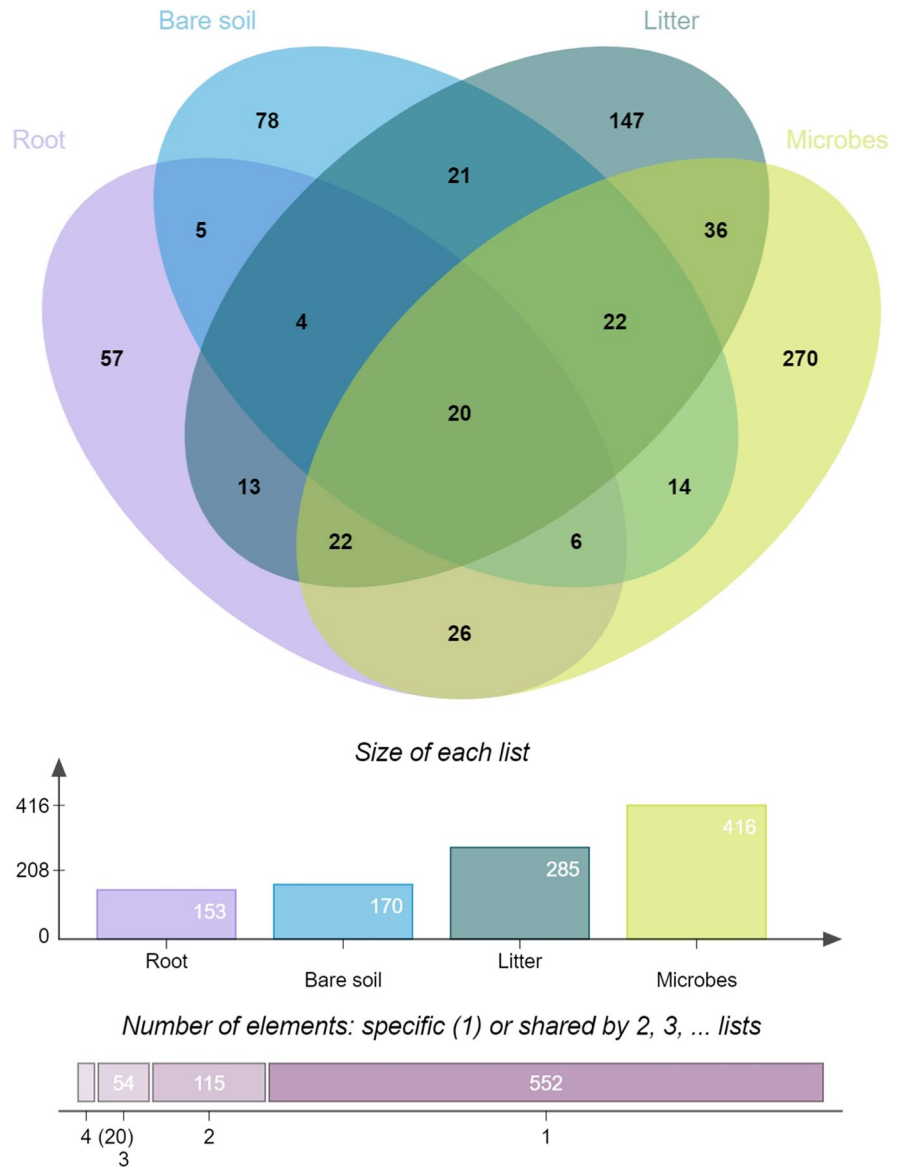
**Fig. 3** Classes and diversity of VOCs emitted by soil sources based on lab studies (litter, root, bare soil, and soil microbes). **a** Relative abundance of litter VOC chemical classes, given by the ratio between the number of VOCs in a chemical class and the number of VOCs in all classes (total 285 compounds);

**b** Relative abundance of plant root VOC chemical classes (total 153 compounds); **c** Relative abundance of bare soil VOC chemical classes (total 170 compounds). **d** Relative abundance of soil microbial VOC chemical classes (total 416 compounds). Data are extracted from Table S2 in the Appendix

1991). Large differences were also found amongst the emission rates of monoterpenes and sesquiterpenes from the roots of 15 tree species, with the roots of gymnosperms associated with ectomycorrhiza

having a strong potential for releasing monoterpenes. In contrast, angiosperm roots emitted low amounts of monoterpenes regardless of mycorrhizal type (Tsuruta et al. 2018).

**Fig. 4** Number of VOC specific and common to bare soil, plant root, plant litter, and soil microbes. A total of 675 VOCs emitted by soil was grouped based on their sources (litter, root, bare soil and soil microbe) in the four categories and were displayed in a Venn diagram. The numbers of VOCs specific and shared among categories were displayed below. Data are extracted from Table S2 in the Appendix and more detail information is available in the [Appendix excel](#)



A field trenching experiment in a forest dominated by *Pinus contorta* estimated that roots contributed to 53% of total soil VOC emissions. However, the removal of roots did not affect the rate of emission of soil monoterpenes (Gray et al. 2014), which could indicate that the roots of the study species are a minor emitter of monoterpenes. Currently, assessing the contribution of root emissions in situ to overall soil VOC fluxes is difficult because of their linkages with soil organisms, which inevitably impact the potential soil sink and source of VOCs (Trowbridge et al. 2020).

VOC emissions from soil organic matter

Although soil organic matter (SOM) could emit a series of VOCs naturally, given that the strengths and composition of VOC emissions are always associated with microbial activities, it is a challenge for researchers to verify the source of VOCs derived from SOM or soil microbes (Veres et al. 2014; Monard et al. 2021). SOM-derived VOCs are emitted during the SOM breakdown and decomposition processes, which are dominated by different pathways of microbial metabolism, such as aerobic decomposition,

**Table 4** Number of unique VOCs from different soil sources

Unique VOCs	Litter	Root	Bare soil	Soil microbes
Acids	1	1	2	15
Alcohols	6	13	1	30
Aldehydes	5	4	1	2
Alkanes	10	7	30	11
Alkenes	10	0	5	3
Benzenoids	21	1	19	10
Esters	9	2	2	31
Ethers	5	3	0	2
Furans	3	1	0	4
Halogenated containing	8	0	1	13
Ketones	4	0	5	33
Nitrogen containing	0	2	4	13
Sulfur containing	5	0	5	10
Terpenes	60	23	3	4

More information is available in the [Appendix excel](#)

fermentation, and terpenoid biosynthesis (Tang et al. 2019). Therefore, the community and function of microbes in soils play a vital role in determining the production and emission of SOM-derived VOCs (Leff and Fierer 2008; Mancuso et al. 2015). Additionally, soil microbes are an essential contributor to the diversity of VOCs, summarized in the mVOC 3.0 database, which has documented about 2000 microbial VOCs emitted by almost 1000 microbial species (Lemfack et al. 2018).

Use of experimental methods combining litter removal and root trenching could potentially estimate the contribution of SOM to VOC emissions from field soils, although it appears that the emission rates of VOCs derived from SOM only are small compared to the rates from litter and roots (Lin et al. 2007; Leff and Fierer 2008). For example, one study detected an obvious emission of formic acid from sterilized soil with an average rate of  $\sim 6 \times 10^{-3}$  nmol m<sup>-2</sup> s<sup>-1</sup> (Li et al. 2019). Rossabi et al. (2018) incubated three distinct ecosystem soils (agricultural soil, grassland soil and subalpine soil) at room temperature and measured the rates of VOCs emission ranging from 25 to 190 ng g<sup>-1</sup> dry soil h<sup>-1</sup>. These rates are lower than the emission of litter in the same region, which varied from 81 to 960 ng g<sup>-1</sup> dry soil h<sup>-1</sup>, which is caused by the litter decomposition periods and incubation temperature (Svendsen et al. 2018). The amount of

VOC production from bare soils was 10–100 folds lower than from litter emitters (Leff and Fierer 2008).

The profiles of VOCs from bare soils were also dramatically changed by incubation temperature and soil water content. One incubation study suggested that higher temperature can increase the emission of soil VOCs emission, but soil water had the opposite effect (Raza et al. 2017). Incubated permafrost soils with different water conditions (drained and non-drained) under two temperature levels (10 °C and 20 °C) resulted in total VOC measurements ranging from 2.5 to 42.7 ng g<sup>-1</sup> dry soil h<sup>-1</sup>, also demonstrating that higher temperature and drained soils produced more VOCs (Kramshøj et al. 2019). Besides soil temperature and water, the quantity of VOCs emitted from bare soils positively correlates with SOC and microbial biomass (Mancuso et al. 2015). For example, ethanol and methanol are strongly emitted from soils with high SOM content and active microbes (Kramshøj et al. 2018).

In this review, a total of 170 VOCs were found emitted from bare soils, with the main chemical classes comprising alkanes (49), benzenoids (42), terpenes (12), ketones (12), alcohols (11), alkenes (11), acids (10), totaling 86% of the sum of VOCs (Fig. 3c). The VOC profile of bare soils in chemical classes differs from that of litter and roots, which are dominated by terpenes (Fig. 3a-c). Compared with other sources, bare soils have 78 unique volatiles not shared by other sources (Fig. 4), and these VOCs include alkanes (30 VOCs), benzenoids (19 VOCs), ketones (five VOCs), but no ethers and furans were found (Table 4).

#### VOC emissions from soil microorganisms

Microbial VOCs (mVOCs) are produced by various microorganisms ranging from bacteria to fungi. VOC profiles emitted by microorganisms are usually consistent, relating to microbial traits, culture conditions, and environments (Bäck et al. 2010). The measurement of species-specific mVOC emissions, even when grown on the same cultivation media, indicates that soil microbes differ in the qualitative and quantitative composition of their volatiles produced (Isidorov and Zaitsev 2022). Nutrient availability may have an impact on emissions, with a laboratory experiment finding parallel changes in soil VOC emissions and the composition of fungal communities after the application of different fertilizers (Insam and Seewald



2010). Moreover, the emission of sesquiterpenes by fungi (e.g., *Alternaria alternata*) was strongly related to fungal growth phases rather than its biomass, with fungi in the early stages of growth being able to emit much higher amounts of sesquiterpenes than in their mature stages, with higher biomass (Weigl et al. 2016). Another study noted that bacteria may be as important as fungi in releasing sesquiterpenes in Amazonian soils (Bourtsoukidis et al. 2018).

The mVOC 3.0 database has summarized 2061 VOCs emitted by microbes, including human pathogens, plant pathogens and soil microorganisms (Lemfack et al. 2014, 2018), identifying more than 841 VOCs that are known to be produced by soil microbes from different soil habitats (e.g., rhizosphere, bulk soil) (Schenkel et al. 2015). High amounts of VOCs are released from microbes as end and intermediate products of primary metabolism, and some are emitted as secondary metabolites (Insam and Seewald 2010). From the recently updated database of mVOC 3.0, the profiles of bacterial VOCs are dominated by (in descending order) alkenes, alcohols, ketones, terpenes, benzenoids, pyrazines, acids and esters. The profiles of fungal VOCs are dominated by alcohols, benzenoids, aldehydes, alkenes, acids, esters, and ketones. We summarised 22 papers related to soil microbe-only incubations and found a total of 416 VOCs produced by 36 microbial species. Our data show that soil microbes have higher production of alcohols (64 VOCs), esters (61 VOCs), terpenes (57 VOCs), ketones (45 VOCs) and alkanes (41 VOCs), which comprised 64% of total VOCs (Fig. 3d). Moreover, there are 270 unique VOCs, shared with neither litter, roots or bare soils (Fig. 4), with most of them belonging to esters (31 VOCs), alcohols (30 VOCs) and ketones (33 VOCs) (Table 4).

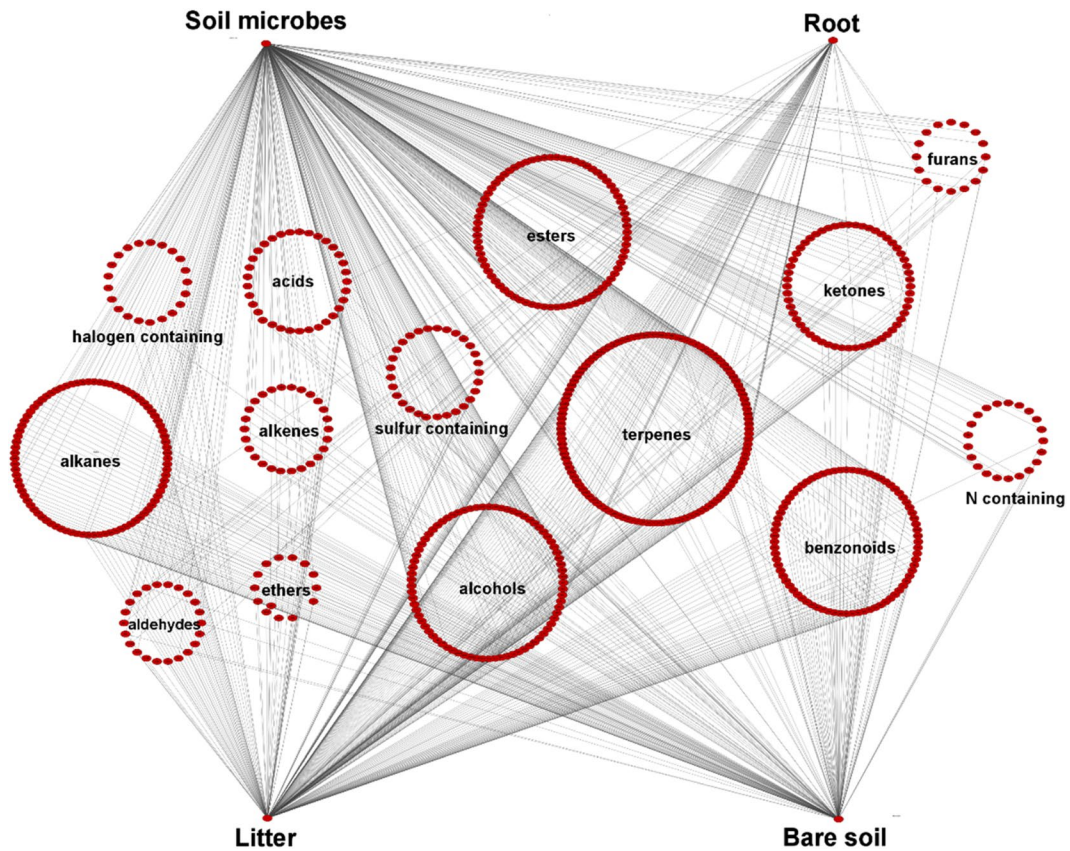
In soil ecosystems, VOCs are important for information communication among organisms, and they are “ambassadors” linking understory root-microorganism-SOM cycle and carbon flow, which are of great ecological significance (Honeker et al. 2021; Minerdi et al. 2021; Meredith and Tfaily 2022). Soil sources share general VOCs while retaining their unique components, forming a complex network (Fig. 5), which themselves vary between different ecosystems. This diversity of soil-derived VOCs, as

well as their specific functions in soils, are potential mechanisms for shedding light on the counter-intuitive nature of certain soil processes (Honeker et al. 2021; Meredith and Tfaily 2022). For example, the home-field advantage of decomposition of litter may be attributed to the changes in decomposers dominated by the characteristics of VOCs released from decomposing litter (Austin et al. 2014; Isidorov et al. 2016).

### Soil's capacity to uptake VOCs

Field chamber and continuous-flow studies have demonstrated that soils are a potential biological sink for VOCs at environmentally relevant concentrations (Table 5) (McGenity et al. 2018; Trowbridge et al. 2020; Abis et al. 2020; Jiao et al. 2023). VOCs can also be taken up by soils and subjected to biotic and abiotic processes, including microbial degradation (Cleveland and Yavitt 1997; Gray et al. 2015), chemical oxidation (Insam and Seewald 2010), and physical desorption (Ruiz et al. 1998). Recent studies have highlighted that the capacity of soils to act as a sink for VOCs is affected by the diversity, community structure, biomass and growth phases of soil microbes (Trowbridge et al. 2020; Abis et al. 2020). Microorganisms can metabolize and utilize VOCs as carbon and energy sources (Cleveland and Yavitt 1998; Owen et al. 2007; Albers et al. 2018), and soil microbes have been shown to consume the majority of VOCs released by other sources (Ramirez et al. 2010; Bachy et al. 2018). Moreover, soils containing high SOC may have a stronger potential ability to take up VOCs than mineral soils (Kramshøj et al. 2018). A recent study demonstrated that VOC metabolism (e.g., of methanol and acetone) in soils may be a previously unrecognized carbon sequestration pathway by contributing to the accumulation of soil labile C and increasing the immobilization of N (McBride et al. 2019).

An initial attempt to quantify the rate of isoprene uptake in a laboratory setting soils led to an estimate of  $-97.3 \mu\text{g m}^{-2} \text{h}^{-1}$  and global isoprene sink strength was calculated as  $20.4 \text{ Tg C y}^{-1}$  under a given isoprene concentration (385 ppb), which is higher than the current atmospheric concentration (Cleveland



**Fig. 5** Classes and diversity of VOCs emitted by soil sources (litter, root, bare soil, and microbes). Graphical representation of VOC associations described in the literature (Cytoscape 3.9.1). Each line represents one hit for a given VOC associa-

tion; the diameters of the circles that represent each chemical class are proportional to the number of different VOCs within that class. More detail information is available in the Appendix S2

and Yavitt 1997). Much higher estimates of rates of isoprene uptake have since been calculated (from  $-4168.9$  to  $-987.7 \mu\text{g m}^{-2} \text{h}^{-1}$ ) using higher concentrations of isoprene under mesocosm conditions (up to 1000 ppb) (Pegoraro et al. 2005). The isoprene concentrations used in that study, however, greatly exceeded those in the atmosphere, which is generally lower than ten ppb. The clear positive correlation between air isoprene concentration and the rate of isoprene deposition suggests that an increasing isoprene gradient can increase the rate of deposition of isoprene in soils (Pegoraro et al. 2005; Spielmann et al. 2017). Although such a high atmospheric concentration of isoprene is not realistic, a recent study conducted in a subtropical *Eucalyptus urophylla* plantation reported a high rate of isoprene uptake ( $-80.88 \mu\text{g m}^{-2} \text{h}^{-1}$ ) measured under ambient conditions (Mu et al. 2023),

which was close to the estimates by Cleveland and Yavitt (1997). This high uptake rate can be attributed to the high ambient concentrations of isoprene ( $17.5 \text{ ng L}^{-1}$ ) and high soil microbial consumption following long-term adaptation of soil microbes to the *Eucalyptus urophylla* plantation, which is a high emitter of isoprene. Overall, the capacity of soils to take up isoprene has likely been overestimated (Table 5).

The highest reported uptake rate of monoterpenes was  $37.55 \mu\text{g m}^{-2} \text{h}^{-1}$  in subtropical forest soils (without litter) (Mu et al. 2023). Similarly, net uptake of monoterpenes by soils has been demonstrated in Mediterranean forest soil, where the rate of uptake was highest ( $27.96 \mu\text{g m}^{-2} \text{h}^{-1}$ ) in summer (Yang et al. 2024), and a simulated drought generally enhanced the capability of sinking monoterpenes (Asensio et al. 2007c; Yang et al. 2024).

**Table 5** Mean uptake rates of soil VOC ( $\mu\text{g m}^{-2} \text{h}^{-1}$ ) across various ecosystems

Reference	Ecosystem	Source	Sampling season	Isoprene	Monoterpenes	Sesquiterpenes	Other VOCs	Methanol
Asensio et al. 2007b	Mediterranean forest	Soil with litter	Autumn	4.4	/	/	32.9	/
	Mediterranean forest	Soil with litter	Summer	2.8	2.5	/	/	/
Asensio et al. 2008b	Mediterranean shrub	Soil without litter	Autumn	/	/	0.4 <sup>a</sup>	20.6	6.9
Gray et al. 2014	Subalpine forest	Soil with litter	summer	0.1	/	/	/	/
Zhang et al. 2017	Subtropical forest	Soil with litter	spring	0.8	32.8	/	133.2	/
Bachy et al. 2016	Cropland	Soil with litter	spring	/	/	/	/	35.1
Bachy et al. 2018	Cropland	Soil with litter	spring	/	/	/	/	9
Trowbridge et al. 2020	Temperate forest-AM	Soil with litter	September-October	0.1	/	0.22 <sup>b</sup>	/	1.9
	Temperate forest-ECM	Soil with litter	May-June	0.07	/	0.15	/	3.8
Huang et al. 2021	Subtropical-PF	Soil with litter	spring	/	8.89	/	/	/
Huang et al. 2021	Subtropical-BF	Soil with litter	spring	/	4.51	/	/	/
Llusià et al. 2022	Tropical forest	Soil with litter	wet	/	/	131.6	/	/
	Tropical forest	Soil with litter	dry	/	2.4	0.37	/	/
Mu et al. 2023	Subtropical forest	Soil with litter	summer	71.84	6.2	6.19	/	/
	Subtropical forest	Soil without litter	summer	80.88	37.55	2.28	/	/
Yang et al. 2024	Mediterranean forest <sup>c</sup>	Soil with litter	spring	0.11	/	0.02	/	/
	Mediterranean forest <sup>c</sup>	Soil with litter	summer	0.01	24.88	1.0	/	/
	Mediterranean forest <sup>c</sup>	Soil with litter	autumn	/	/	1.52	/	/
	Mediterranean forest <sup>c</sup>	Soil with litter	winter	0.09	2.64	0.03	/	/
	Mediterranean forest <sup>c</sup>	Soil without litter	spring	0.09	/	/	/	/
	Mediterranean forest <sup>c</sup>	Soil without litter	summer	0.24	27.96	0.57	/	/
	Mediterranean forest <sup>c</sup>	Soil without litter	autumn	0.3	2.04	1.95	/	/
	Mediterranean forest <sup>c</sup>	Soil without litter	winter	0.09	1.57	0.02	/	/

Rates reported with other units (e.g.,  $\text{pmol m}^{-2} \text{s}^{-1}$  and  $\text{nmol m}^{-2} \text{h}^{-1}$ ) in the literature were converted to  $\mu\text{g m}^{-2} \text{h}^{-1}$ . AM is arbuscular mycorrhizal; ECM is ectomycorrhizal; PF is masson pine forest; BF is monsoon evergreen broadleaved forest

<sup>a</sup> is summer and winter

<sup>b</sup> is value at the May-June (period II)

<sup>c</sup> is average data from all treatments

The uptake of sesquiterpenes and whether microbes can directly consume them is unclear, as they are quickly oxidized into other compounds (Tang et al. 2019). However, an increasing number of field experiments have shown that soils are also weak sinks for sesquiterpenes (Table 5). It is interesting to point out that tropical rainforest soils were previously reported to be a significant source of sesquiterpenes (Bourtsoukidis et al. 2018); subsequent reports, however, have also demonstrated that tropical forest soils can uptake a large amount of sesquiterpenes (Llusà et al. 2022). Such variability in tropical forests is partly related to season, elevation and topography (Llusà et al. 2022).

Other VOCs, such as acetaldehyde and methanol, are readily taken up by soils (Asensio et al. 2007b; Bachy et al. 2018; Albers et al. 2018; Jiao et al. 2023). Field studies showed that cropland soils take up methanol at high rates and that the net uptake is high in summer ( $306.0 \mu\text{g m}^{-2} \text{h}^{-1}$ ) and autumn ( $243.0 \mu\text{g m}^{-2} \text{h}^{-1}$ ) (Bachy et al. 2018). The differences in uptake ability between seasons may be due to environmental factors, especially soil water content. For example, soils can switch between releasing methanol when dry and taking up methanol when wet (Bachy et al. 2018; Bourtsoukidis et al. 2018). Regarding other compounds, a study in a subtropical pine forest detected high uptakes of undecane ( $-66.2 \mu\text{g m}^{-2} \text{h}^{-1}$ ) and dodecane ( $-36.2 \mu\text{g m}^{-2} \text{h}^{-1}$ ) by soils during sampling in spring (Zhang et al. 2017). Additionally, 2-hexenal was taken up in the highest amounts in a Mediterranean forest in autumn ( $-26.0 \mu\text{g m}^{-2} \text{h}^{-1}$ ), even under drought conditions, but was not stored in soils in other seasons (Asensio et al. 2007b, c).

### Main pathways of atmospheric VOCs into the soils

The main pathways of how the soils can act as a sink can be divided into abiotic processes (e.g., adsorption and deposition) and biotic processes (e.g., microbial consumption and mineralization). The mechanisms of the uptake of VOCs into soils likely differ between compounds due to their high heterogeneity and specificity (Cleveland and Yavitt 1997; Ruiz et al. 1998; Asensio et al. 2007a; Albers et al. 2018; Li et al. 2019). The abiotic processes are primarily driven by concentration gradients and soil properties, which generally do not change the VOCs, and balance is

established with the surrounding air concentrations over time (Rinnan and Albers 2020). The biotic processes, however, are mostly the result of microbial activity and VOCs are ultimately degraded to  $\text{CO}_2$  (Albers et al. 2018; Carrión et al. 2020).

### VOC deposition

An estimated  $130\text{--}270 \text{ Tg C y}^{-1}$  of atmospheric VOCs are deposited on vegetation and soil surfaces (Goldstein and Galbally 2007), which accounts for 17–36% of annual terrestrial vegetation emissions of VOCs ( $760 \text{ Tg C y}^{-1}$ ) (Sindelarova et al. 2014). The deposition of VOCs to vegetation is ubiquitous, but it has become clear that deposition onto soils also plays a more important role than previously thought (Goldstein and Galbally 2007; Hallquist et al. 2009; Laffineur et al. 2012; Park et al. 2013; Spielmann et al. 2017). Atmospheric VOC deposition includes wet deposition (hydrophilic VOCs dissolved in precipitation) and dry deposition (VOCs deposited onto the soil surface) (Nguyen et al. 2015; Rinnan and Albers 2020). It has been suggested that the process of wet deposition of VOCs is dependent on the physico-chemical properties of atmospheric water and surrounding air temperatures (Šoštarić et al. 2017; Stojčić et al. 2019), whereas dry deposition of VOCs is affected by the aboveground plant species, surrounding VOC concentrations and light (Spielmann et al. 2017; Staudt et al. 2019). There are reports of several chemical classes of VOC, including aldehydes, ketones, aromatic hydrocarbons and isoprenoids, being deposited on various soil types (Asensio et al. 2008a; Gray et al. 2014).

### Adsorption and dissolution

VOCs can be adsorbed to SOM or dissolved in the vapor and water phases of soils (English and Loehr 1991; Tang et al. 2019). They can be adsorbed by soils directly, or indirectly by first reacting with ozone and hydroxyl radicals on the soils surface (Li et al. 2016). The soil surface area and other properties regulate the capacity of soils to adsorb VOCs (Petersen et al. 1994; Ruiz et al. 1998). A soil surface that is completely covered with water molecules can increase VOC adsorption and dissolution, and characteristic hydrophilic VOCs such as methanol, ethanol, formaldehyde, and acetone can be adsorbed onto the soils at high levels

and can then diffuse into the soil water (Li et al. 2016; Bachy et al. 2018). Under dry conditions, however, soil properties such as aggregate structure and SOC content are important for affecting the strength of VOC adsorption (Ruiz et al. 1998; Hamamoto et al. 2009). For example, in dry soil, soil macroaggregates and a high SOC content can increase the adsorption of VOCs (e.g., isohexane) (Van Roon et al. 2005; Hamamoto et al. 2009). Also, the capacity of VOCs to be adsorbed can be an order of magnitude higher for clay than for sand and two orders of magnitude higher than for limestone (Ruiz et al. 1998).

### Biodegradation of VOCs by soil microbes

The microbial sink of VOCs in soils is potentially highly important to both carbon cycling and the atmospheric concentrations of these gases (Owen et al. 2007; Albers et al. 2018). Several isoprene-degrading bacteria have been detected in various ecosystems (Cleveland and Yavitt 1997, 1998; El Khawand et al. 2016; Carrión et al. 2020). For example, the following genera have been linked to isoprene degradation: *Rhodococcus*, *Nocardia*, *Arthrobacter*, *Gordonia*, *Mycobacterium*, *Leifsonia*, *Alcaligenes*, *Alcanivorax*, *Pseudomonas*, *Alcaligenes*, and *Klebsiella* (Gray et al. 2015; El Khawand et al. 2016; Carrión et al. 2020). However, there seem to be no anaerobes, archaea or fungi that have been isolated from soils that can grow on isoprene as a C source (McGenity et al. 2018).

Soil microorganisms seem to be more in favour of the biodegradation of small compounds with lower reactivity in the atmosphere, such as methanol and methane (Jacob et al. 2005). Methylophs are microorganisms that can consume these small compounds as their sole source of C (Kolb 2009), and soil methylophic communities can vary with ecosystem type and soil pH (Stacheter et al. 2013). Methanol uptake in a Mediterranean forest was higher in rhizosphere soils than in bare soils, indicating that rhizosphere microorganisms can consume methanol (Asensio et al. 2007a). Moreover, Trowbridge et al. (2020) have uncovered that soil parameters related to different mycorrhizal communities are important for affecting exchanges of VOC, and ectomycorrhizal (EMC) soils exhibited greater uptake of methanol than arbuscular mycorrhiza (AM) dominated soils due to high methylophic taxa in EMC soil. Although the microbial degradation of VOCs in soils is widely recognized to occur (Albers et al. 2018), it is challenging to estimate

the degradation rate due to the variability of rates based on compound specificity and various soil types.

### Measurements of soil VOCs

Experimental studies typically employ three primary approaches to investigate the composition and flux of VOCs in soil: direct thermal desorption gas chromatography-mass spectrometry (TD-GC-MS), proton transfer reaction mass spectrometry (PTR-MS) and solid-phase microextraction (SPME).

TD-GC-MS can identify various compounds, but it cannot be continuously monitored in real-time (Mäki et al. 2019a, b; Ghirardo et al. 2020; Llusà et al. 2022). PTR-MS can perform real-time measurements of VOC rate but is limited to discerning compounds with the same mass, isomers, and isobaric compounds, such as monoterpenes and furans with a molecular weight of 136 amu (Veres et al. 2014; Mancuso et al. 2015; Isidorov and Zaitsev 2022). SPME is similar to TD-GC-MS; using it alone cannot quantify the flux of VOCs, although it can analyze all targeted and non-targeted compounds. Moreover, based on the targeted VOCs, fibres made from different polymers can be chosen for different research purposes (James and Stack 1996; Brown et al. 2021a, b). Therefore, the PTR-MS method can be combined with TD-GC-MS or SPME, which are beneficial to the complementarity of a single method, and ensure simultaneous qualitative and quantitative analysis. This combination method has been effectively applied in laboratory and field soil experiments in recent studies (Faiola et al. 2014; Bourtsoukidis et al. 2018; Ghirardo et al. 2020; Viros et al. 2021; Rezaie et al. 2023).

It can be difficult to measure VOC uptake capacity in soil, as oxidants (e.g., ozone and hydroxyl radicals) rapidly degrade VOCs, and the chamber-based method of removing VOCs from the air of the sampling tube using active materials typically cannot reveal soil sink activity (Aaltonen et al. 2011, 2013; Mäki et al. 2019a). Thus, it is important to adopt a suitable sampling method to characterize the uptake capacity of soil VOCs and their emission rates. The method of concentration difference is, so far, an effective method to study the exchange flux of soils and atmospheric VOCs (Asensio et al. 2007b; Trowbridge et al. 2020; Mu et al. 2020; Huang et al. 2021; Yang

et al. 2024). This method separately obtains the air VOC concentration during the measurement period and the soil source VOC concentration after mixing the air VOCs. The concentration resulting from the difference between the former and the latter shows whether the soil is a source or a sink for compounds.

The sampling method and sampling date also significantly affect the source-sink pattern of soil VOCs. To better uncover the source-sink function of soil VOCs, we first recommend avoiding the inclusion of green plants in the chamber when measuring soil VOCs. The presence of plants leads to overestimates of the VOC emission from soil sources and may also cover up the potential sink function of soils (Mäki et al. 2017). We therefore recommend removing the surface plants at least one day in advance before sampling soil VOCs. Second, the dynamic chamber method is generally used for studying soil VOCs exchange rate; that is, the VOCs in the inlet and outlet are collected, or the blank sample of the chamber on the film is collected while collecting soil VOCs. So, a purified inlet air by an activated charcoal filter is not recommended as it can mask the sink function of soil VOCs (Aaltonen et al. 2011, 2013; Mäki et al. 2019a). Third, the source-sink function of soil VOCs has obvious seasonal characteristics (Asensio et al. 2007c; Llusà et al. 2022), so long-term or across-season samplings should be performed in field soil VOC studies, and extreme weather (e.g., rainy) should also be avoided as it may significantly affect VOC emissions (Staudt et al. 2019). Lastly, there is high heterogeneity in soil VOC characteristics in the field, as the litter traits and surface roots affect not only the release of VOCs but also the micro-habitat (e.g., rhizosphere) they form, which is an active place for microorganisms producing and consuming VOCs. Therefore, it is recommended to try to avoid excessive heterogeneity between VOC sampling points, especially in studies where the effects of climate factors are simulated.

## Conclusions and prospects

The exchange rate between the soil and the atmosphere is a dynamic process. Changes in aboveground VOC concentrations due to global change can directly impact the potential for soil sinks, as highlighted by studies such as Llusà et al. (2022) and Yang et al. (2024). However, given the current limitations in

research on soil VOC exchange, quantifying the magnitude of soil VOC sources and sinks remains challenging. Thus, there is a need for more field studies on soil VOCs.

Ecosystems, vegetation types, and rhizobacterial types may significantly influence soil VOC source-sink characteristics (Wester-Larsen et al. 2020; Llusà et al. 2022) given the substantial differences in VOC release from various soil sources (Gray et al. 2014; Mäki et al. 2017; Staudt et al. 2019; Mu et al. 2023) and the potential of the soil microbial community to consume VOCs (Ramirez et al. 2010; Albers et al. 2018). Therefore, we recommend simultaneous investigation of both soil biotic factors (e.g., microbial characteristics) and abiotic factors (e.g., soil water content) to unveil soil VOC patterns.

Furthermore, soil VOCs exhibit temporal dynamics with alternating source-sink processes (Asensio et al. 2007b; Mäki et al. 2019b). Thus, cross-seasonal and long-term monitoring prove more informative than a single observation date for understanding soil VOC source-sink function.

VOCs in soils impact biogeochemical cycling processes (Smolander et al. 2006) and microbial community structure and function (Asensio et al. 2012; McBride et al. 2023), coordinating various ecological interactions between species and organism groups (Meredith LK and Tfaily MM. 2022). Our results reveal shared and specific VOCs among soil sources, indicating that linkages through VOC within soils are complex and overlapping (Schenkel et al. 2015). Overall, a better understanding of the mechanisms underlying VOC exchange between soils and the atmosphere is crucial for elucidating global biogeochemical cycles and ecosystem function.

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**Data availability** The datasets generated during the current study are available from the corresponding author on reasonable request.

## Declarations

**Conflict of interest** All authors declare that there are no conflicts of interest relevant to this work.

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