







# Floral volatiles of Maldivian mangroves: Insights into unexplored chemotypes and pollinator interactions

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## ABSTRACT

Volatile organic compounds (VOC) emitted by flowers are key drivers of pollinator attraction and plant reproductive success. Despite the ecological importance of mangroves, their floral VOCs are still largely unexplored. Here, we report the floral VOC profiles of eight mangrove species from the Maldivian archipelago, where the related ecosystems are critically endangered. Specifically, we analyzed *Ceriops tagal*, *Bruguiera cylindrica*, and *Rhizophora mucronata*, for which no previous floral scent reports are available worldwide, together with *Avicennia marina*, *Lumnitzera racemosa*, *Pemphis acidula*, *Bruguiera gymnorrhiza*, and *Rhizophora apiculata*. A total of 949 distinct molecular features were individuated by untargeted GC-MS analysis. 27 were confidently annotated on the basis of NIST library match score (>90%). Multivariate statistical analysis revealed a species-dependent organization of floral scent bouquets, with mangrove taxa differing both in the degree of olfactory distinctiveness and in intra-species chemical variability. *C. tagal* was characterized by 2-phenylethanol and other volatiles commonly associated with moth attraction, whereas *B. cylindrica* emitted linalool, phenylacetaldehyde, and (E)-4,8-dimethyl-1,3,7-nonatriene, compounds typically linked to a broader range of insect visitors. *R. mucronata*, traditionally regarded as wind-pollinated, unexpectedly released several VOCs known to attract bees, moths, flies, and beetles. Overall, by providing a first chemical baseline, this work aims to improve the understanding of mangrove reproductive ecology and to support sustainable management of Maldivian mangrove ecosystems.

## 1. Introduction

Floral volatile organic compounds (VOCs) play a central role in mediating plant–pollinator interactions by acting as long-distance chemical signals that guide pollinators toward floral resources (Knudsen et al., 2006; Dudareva et al., 2013). Floral scents are emitted as complex blends whose composition, rather than the presence of single compounds, determines their ecological function (Bruce et al., 2005; Klatt et al., 2013). These bouquets must simultaneously attract effective pollinators and limit exploitation by florivores, nectar thieves, and microbial colonizers, resulting in highly structured and species-specific chemical signatures (Muhlemann et al., 2014; Dötterl and Gershenzon, 2023). Accordingly, suites of floral traits, including scent, have been conceptualized within the framework of pollination syndromes, linking floral chemistry to different pollinator groups (Fenster et al., 2004).

Mangroves are woody angiosperm plants capable of tolerating saline conditions and grow in the intertidal region at tropical and subtropical latitudes. They provide essential ecosystem services, including shoreline stabilization, carbon sequestration, nutrient cycling, and habitat provision for a wide range of marine and terrestrial organisms (Eong, 1993; Das and Vincent, 2009). Despite their ecological importance, mangroves are increasingly threatened worldwide by coastal development, habitat fragmentation, and climate change, making their conservation a global priority. Currently, 65 mangrove species are reported worldwide (Kathiresan and Bingham, 2001).

Considering their floral morphology, phenology, and reproductive strategies, mangroves display considerable diversity (Tomlinson et al., 1979). While pollination is a key process in mangrove reproduction, plant–pollinator interactions remain poorly understood for many mangrove species. A detailed understanding of their reproductive

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ecology is fundamental since successful reproduction underpins population maintenance, genetic diversity, and long-term ecosystem stability (Vinaya and Binoy, 2024). Under this light, improving knowledge of the mechanisms governing pollinator attraction and reproductive success must be considered therefore critical for informing mangrove conservation and restoration strategies. Till now mangrove floral VOC composition has been associated with diverse pollination strategies. Bat-pollinated taxa were found to emit sulfur-containing compounds, moth-pollinated species oxygenated terpenoids and benzenoids. Other insect-pollinated mangroves displayed blends rich in carotenoid derivatives, whereas bird-pollinated species resulted generally weakly scented or scentless (Azuma et al., 2002). Beyond pollinator attraction, mangrove floral VOCs may also serve protective or defensive roles. In *Bruguiera gymnorrhiza*, isoprenoid emissions from open flowers have been inferred to deter opportunistic herbivores or pathogens rather than attract pollinators, reflecting a balance between stress-responsive and reproductive functions in floral scent composition (Paul et al., 2024). Such defensive roles of volatile isoprenoids in floral tissues are consistent with their broader involvement as herbivore deterrents, anti-feedants, and toxins, as well as their capacity to limit microbial growth in these vulnerable reproductive organs, which lack physical barriers (Loreto et al., 2014; Muhlemann et al., 2014).

Since the floral scent chemistry of mangroves remains characterized for only a limited number of species and geographic regions, it is not possible to generalize patterns and assess their ecological relevance. This knowledge gap is particularly relevant for the Maldivian archipelago, where mangroves have historically received limited scientific attention even though they have recently been classified as critically endangered (IUCN, 2024; Cerri et al., 2024, 2025). In fact, no data are currently available regarding the Maldivian mangroves' floral volatile emissions, hindering the efforts to integrate chemical ecological information into conservation planning.

To address this gap and provide a first chemical baseline, we characterized the Floral VOCs profiles of eight mangrove species collected in three different atolls of the Maldivian archipelago. Specifically, our objectives were (i) to describe the floral scent composition of previously uncharacterized mangrove species (*Ceriops tagal*, *Bruguiera cylindrica*, and *Rhizophora mucronata*), and (ii) to compare whole-bouquet VOC profiles across taxa, including other mangrove species (*Avicennia marina*, *Lumnitzera racemosa*, *Pemphis acidula*, *Bruguiera gymnorrhiza*, and *Rhizophora apiculata*), using an untargeted volatilomic approach to identify species-dependent patterns in overall VOC composition.

## 2. Materials and methods

### 2.1. Collection of study material

Mangrove flowers were collected during a field campaign carried out in the Maldives in 2024 using our research center in the area as the research station (Marhe center, <https://marhe.unimib.it>). Specifically, sampling was conducted at three distinct locations: Huraa Island (Kaafu Atoll), Fuvalmulah Island (Gnaviyan atoll) and Hulhumeedhoo Island (Seenu Atoll). Species identification was performed visually using the identification guide of Primavera et al. (2004) and available literature (Sheue et al., 2005; Tomlinson et al., 1979; Selvam, 2007). Fig. 1 shows representative pictures of the species analyzed.

Samples were collected at peak anthesis, specifically fully open flowers with intact reproductive structures and no visible signs of senescence, following the protocol previously published by Azuma et al. (2002), which is suitable for field conditions and minimizes stress-induced volatile emission. For each species, flowers were sampled from at least ten individual plants. Briefly, flowers were excised using sterilized scissors and immediately placed in glass containers partially filled with sterile distilled water. After that, they were stored at 4 °C and



**Fig. 1.** Flowers of *Bruguiera cylindrica* (a, b), *Ceriops tagal* (c), and *Rhizophora mucronata* (d). The basic unit of the inflorescence of *B. cylindrica* is a regular dichasium, generally consisting of three-flowered cymes in axillary position with about 1 cm long peduncle. Flowers are relatively small (0.8-1 cm long, 1-1.2 cm diameter), white in colour with eight white petals and a light green calyx with six-eight sepals. The inflorescence of *C. tagal* is composed of five to ten flowers in an axillary position. The flowers are small (0.6-0.9 cm long and 0.6-0.9 cm diameter) with 4-6 white petals and deeply sunken calyxes with 4-6 light green sepals. The inflorescence of *R. mucronata* is a pedunculate dichotomized cyme in leaf axils generally consisting of 4-6 flowers per cluster. Flowers are pendulous (3-5 cm long peduncle), cup-shaped (1.2-2 cm long, 1-1.5 cm wide), with a hard, creamy-white calyx bearing four persistent sepals and four hairy, white petals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

transported to the laboratory within a few hours. Upon arrival at the laboratory, they were gently dried with sterile paper to remove excess surface moisture. After that samples were transferred into 20 mL sealed glass headspace vials, designed to withstand the pressure generated during headspace gas chromatography analysis. Samples were transferred into 20 mL sealed glass headspace vials designed to withstand the pressure generated during headspace gas chromatography analysis. Specifically, we used 20 mL headspace vials (22.75 × 75 mm) with silver aluminum crimp caps and molded PTFE/silicone septa, purchased from Agilent Technologies (Santa Clara, CA, USA).

## 2.2. Headspace solid-phase microextraction-gas chromatography-mass spectrometry (HS-SPME-GC/MS) analysis

For the analysis of VOCs we applied headspace solid-phase microextraction coupled to gas chromatography–mass spectrometry (HS-SPME-GC–MS), a solvent-free technique widely used for the extraction and characterization of volatile and semi-volatile compounds, which offers high sensitivity and easy manipulation of the sample. Specifically, VOCs were sampled from the vial headspace using a triphasic Divinylbenzene/Carboxen/Polydimethylsiloxane (DVB/CAR/PDMS) fiber (10 mm length, 100 µm coating thickness; Agilent Technologies, Santa Clara, CA, USA). This extraction phase was chosen because it suitable for a broad range of volatile compounds, from apolar to polar. Before VOC collection, vials were equilibrated at room temperature for 15 min. Solid-Phase Microextraction (SPME) fiber exposure time was set to 10 min. Analyses were then carried out using an Agilent 8860 gas chromatograph (GC) coupled to an Agilent 5977B mass spectrometer (MS). Fiber desorption was carried out for 3 min at 230 °C. Gas chromatographic separation was obtained by using a 5% Phenyl Methyl Siloxane column (DB5, Agilent, 30 m × 250 µm × 0.25 µm). Oven temperature was held at 40 °C for 3 min, then raised to 180 °C at a rate of 7.5 °C/min and finally increased to 280 °C at a rate of 15 °C/min. The flow of helium in the column during the analyses was 1.2 mL/min. Mass detector was run in Full scan mode, at 45–400 m/z range using a scan speed (u/s) of 1.562 (N = 2), a frequency of 4.0 (scans/sec), a cycle time of 249.84 ms and a step size of 0.1 m/z. Compound identification was performed by comparison of mass spectra with the National Institute of Standards and Technology library (NIST 23), using a minimum match score of 90%. Identification was also supported by reference retention index comparison when available.

## 2.3. Multivariate statistical analysis

The collected floral VOC profiles were analyzed using multivariate statistical approaches to investigate similarities and differences among mangrove scent bouquets. To account for the full emission profiles, including non-annotated compounds, Gas chromatography-mass spectrometry (GC–MS) raw data were at first subjected to peak deconvolution and feature extraction using the tools available on the Global Natural Products Social Molecular networking (GNPS)–MSHub platform (<https://gnps.ucsd.edu>; Wang et al., 2016). The resulting feature table was then processed using the open-access software MetaboAnalyst 6.0 (<https://www.metaboanalyst.ca>). Principal component analysis (PCA) was applied as an unsupervised method to explore the organization of samples in a multivariate odour space, while hierarchical cluster analysis (HCA) coupled with heatmap visualization was used to identify species-dependent combinations of largely shared VOCs. Partial least squares discriminant analysis (PLS-DA) was additionally employed as a complementary supervised approach to evaluate the potential separability of mangrove species based on their volatilomic profiles. Before multivariate analysis, data were normalized by total sum normalization, log<sub>10</sub>-transformed, and autoscaled. For HCA, the top 50 most significant features, selected based on analysis of variance (ANOVA) p-values, were used to generate the heatmap. Clustering was performed using Euclidean distance and Ward's linkage method. Additional details on

data processing and statistical parameters are provided in the Supplementary Information.

## 2.4. Literature survey on flower visitors, pollinators, and VOC functions

Information on flower visitors and pollinators for the studied mangrove species was obtained from the literature through targeted searches in Google Scholar. Keywords included the scientific name of each plant species combined with terms such as “pollinators” “flower visitors”, and “insects”. The potential role of the tentatively identified VOCs in pollinator attraction was similarly investigated using Google Scholar, with searches combining the specific compound name with terms like “pollinators” “pollinator attraction”, and “flower visitors”. Additionally, Scifinder<sup>n</sup> was used to examine each molecule, and relevant references were screened using keywords such as “flower” and “pollinators” to assess documented ecological roles.

## 3. Results and discussion

### 3.1. Characterization of the floral scent of *Ceriops tagal*, *Bruguiera cylindrica*, *Rhizophora mucronata*

Ecological interpretation of floral volatile organic compounds in this study is based on a literature-guided, trait-based approach that links chemical features to potential pollination functions. Individual VOCs are discussed in relation to documented behavioral or physiological responses of pollinators, and interpretation is subsequently extended to the level of the complete floral scent profile emitted by each species. Under this framework, the potential ecological role of a floral scent is inferred from the relative prevalence and co-occurrence of compounds associated with specific pollinator groups, allowing assessment of whether overall chemical profiles are consistent with more specialized or generalist attraction strategies.

Table 1 reports the list of the compounds identified with a National Institute of Standards and Technology (NIST) library match score higher than 90% in the floral scent of *Ceriops tagal*, *Bruguiera cylindrica*, *Rhizophora mucronata* for which the current study also represents the first report worldwide of their VOCs emission (Azuma et al., 2002; Paul et al., 2024). The related chemical structures are provided in Fig. 2. As can be seen, a total of 27 compounds mostly belong to the chemical classes of benzenoids, monoterpenoids, sesquiterpenoids, and aliphatic esters.

To support the interpretation of the floral scent profiles in a pollination context, the documented association between the volatile organic compounds identified in this study (Table 1) and pollinator groups reported in the literature are summarized in Table S1. Specifically, the floral scent of *C. tagal* was dominated by 2-phenylethanol (21), a benzenoid widely emitted by angiosperms (Knudsen et al., 1993) and primary associated with moth pollinators (Jacobson et al., 1976; Dobson, 2006; Svensson et al., 2010; Dötterl and Gershenson, 2023). This compound is also known to attract diurnal butterflies, bees, flies and beetles (Zhu et al., 1999; Dobson, 2006; Dötterl and Vereecken, 2010; Primante and Dötterl, 2010). Noteworthy, the additional volatiles retrieved further support the potential for multi-taxon attraction, including 3-methyl-1-butanol (1), a bisexual lure for noctuid moths (Szanyi et al., 2022); 3-hexen-1-ol (5), associated with attraction of noctuid moths, hawkmoths, and other insects (Levin et al., 2001; Raguso et al., 2003; James, 2005); styrene (7), involved in pollination mutualism with the sphinx moth *Manduca sexta* (Reisenman et al., 2013); α-pinene (8) and β-pinene (11), monoterpenes linked to attraction of noctuid moths and bees, respectively (Landolt and Smithhisler, 2003; Dobson, 2006; Dötterl and Gershenson, 2023); limonene (14), eliciting physiological responses in several pollinators, including moths, beetles, and bees (Dobson, 2006; Byers et al., 2014; Dötterl and Gershenson, 2023); 2-methoxyphenol (17), common in moth-pollinated flowers (Knudsen et al., 1993) and known to elicit antennal responses in flies (Heiduk et al., 2019); and β-caryophyllene (27), a widespread floral

**Table 1**

Volatile organic compounds identified in the floral scent of *Ceriops tagal* (CT), *Bruguiera cylindrica* (BC), and *Rhizophora mucronata* (RC), listed according to retention order. For each species, the presence of a compound is indicated together with a letter denoting its chemical class: F = fatty acid derivatives; B = benzenoids; M = monoterpenoids; A = aliphatic esters; S = sesquiterpenoids. The final column reports the occurrence of each compound in the floral scent of other mangrove species (NF = *Nypa fruticans*; RS = *Rhizophora stylosa*; LR = *Lumnitzera racemosa*; AM = *Avicennia marina*; HF = *Heritiera fomes*; BG = *Bruguiera gymnorrhiza*; SA = *Sonneratia alba*; PA = *Pemphis acidula*), together with the corresponding references.

No	RT	Name	Formula	CT	BC	RM	Mangrove occurrence
1	3.81	3-Methyl-1-butanol (isoamyl alcohol)	C <sub>5</sub> H <sub>12</sub> O	F			NF (Azuma et al., 2002)
2	4.83	2-Ethylbutanal	C <sub>6</sub> H <sub>12</sub> O		F	F	
3	5.35	Hexanal	C <sub>6</sub> H <sub>12</sub> O		F	F	RS (Azuma et al., 2002)
4	6.24	3-Hexenal	C <sub>6</sub> H <sub>10</sub> O		F	F	
5	6.53	3-Hexen-1-ol	C <sub>6</sub> H <sub>12</sub> O	F			LR, AM (Azuma et al., 2002)
6	6.58	2-Hexenal	C <sub>6</sub> H <sub>10</sub> O		F	F	BG (Paul et al., 2024)
7	7.41	Styrene	C <sub>8</sub> H <sub>8</sub>	B			
8	8.51	α-Pinene	C <sub>10</sub> H <sub>16</sub>	M	M	M	HF (Paul et al., 2024)
9	8.85	Camphene	C <sub>10</sub> H <sub>16</sub>	M			
10	9.42	Sabinene	C <sub>10</sub> H <sub>16</sub>	M			HF (Paul et al., 2024)
11	9.53	β-pinene	C <sub>10</sub> H <sub>16</sub>	M		M	HF, BG (Paul et al., 2024)
12	10.16	Octanal	C <sub>8</sub> H <sub>16</sub> O		F		HF (Paul et al., 2024)
13	10.62	p-Cymene	C <sub>10</sub> H <sub>14</sub>	M			HF (Paul et al., 2024)
14	10.73	Limonene	C <sub>10</sub> H <sub>16</sub>	M			HF, BG (Paul et al., 2024)
15	11.08	Benzeneacetaldehyde (phenylacetaldehyde)	C <sub>8</sub> H <sub>8</sub> O		B		PA, HF (Azuma et al., 2002; Paul et al., 2024)
16	11.66	Octyl formate	C <sub>9</sub> H <sub>18</sub> O <sub>2</sub>		A		
17	11.94	2-Methoxyphenol (guaiacol)	C <sub>7</sub> H <sub>8</sub> O <sub>2</sub>	B			RA (Azuma et al., 2002)
18	12.19	Methyl benzoate	C <sub>8</sub> H <sub>8</sub> O <sub>2</sub>			B	BG, SA, NF (Azuma et al., 2002)
19	12.30	Linalool	C <sub>10</sub> H <sub>18</sub> O		M		BG, RS, NF, LR (Azuma et al., 2002; Paul et al., 2024)
20	12.40	Nonanal	C <sub>9</sub> H <sub>18</sub> O			F	BG, HF (Paul et al., 2024)
21	12.56	Phenylethyl alcohol (2-Phenylethanol)	C <sub>8</sub> H <sub>10</sub> O	B			NF, AM, PA, HF, BG (Azuma et al., 2002; Paul et al., 2024)
22	12.57	(E)-4,8-Dimethyl-1,3,7-nonatriene	C <sub>11</sub> H <sub>18</sub>		S	S	BG, RS, LR, PA (Azuma et al., 2002)
23	13.84	Borneol	C <sub>10</sub> H <sub>18</sub> O	M			
24	14.26	Methyl salicylate	C <sub>8</sub> H <sub>8</sub> O <sub>3</sub>			B	BG, LR (Azuma et al., 2002)
25	17.72	α-copaene	C <sub>15</sub> H <sub>24</sub>	S			BG (Paul et al., 2024)
26	17.25	Eugenol	C <sub>10</sub> H <sub>12</sub> O <sub>2</sub>			B	AR, RS, BG (Azuma et al., 2002; Paul et al., 2024)
27	18.51	β-Caryophyllene	C <sub>15</sub> H <sub>24</sub>	S			NF, HF (Paul et al., 2024)

VOC (Knudsen et al., 2006), primarily involved in attraction of moths and hawkmoths (Levin et al., 2001; Raguso et al., 2003; Dobson, 2006), and also reported to attract flies, bees, and fig wasps (Ibanez et al., 2010; Soler et al., 2012). Taken together, the chemical profile of *C. tagal* is consistent with moth attraction but remains sufficiently generalist to appeal to a broad range of floral visitors. This aligns with classical descriptions of the species, in which crepuscular anthesis, the small size, the white petals visible at night, the delicate explosive pollen release mechanism, and the floral scent at night were interpreted as adaptations for nocturnal moth pollination (Tomlinson et al., 1979). The VOC blend may also explain occasional evening visits by honeybees and flies previously documented in India (Raju and Karyamsetty, 2008; Karyamsetty and Raju, 2009).

The floral scent of *B. cylindrica* was dominated by (E)-4,8-dimethyl-1,3,7-nonatriene (22), a sesquiterpene commonly produced by night-blooming white flowers (Dötterl and Gershenzon, 2023) and a key volatile in moth- and hawkmoth-pollinated species (Levin et al., 2001; Raguso et al., 2003). Additional compounds included octanal (12), associated with moth-pollinated flowers (Waelti et al., 2009); phenylacetaldehyde (15), a widespread moth attractant (Fraser et al., 2003; Huber et al., 2005; Dobson, 2006; Waelti et al., 2009; Dötterl and Gershenzon, 2023), also eliciting responses in flies and beetles (Primante and Dötterl, 2010; Dötterl and Vereecken, 2010); and linalool (19), a ubiquitous floral volatile attracting moths, bees, butterflies, beetles, and flies (Fraser et al., 2003; Dobson, 2006; Ibanez et al., 2010; Blažytė-Čereškienė et al., 2019; Zhang et al., 2023). In contrast, octyl formate (16), currently has no documented role in pollinators attraction. Morphology traits of *B. cylindrica*, including small and open flowers, have been interpreted as adaptations for butterfly pollination (Tomlinson et al., 1979). However, the predominance of moth-associated VOCs suggests that nocturnal visitors may also play a role. Field studies from other regions documented a diverse assemblage of flower visitors, including thrips, solitary bees, wasps, and occasional Lepidoptera (Nagarajan et al., 2008; Sophia et al., 2013; Aluri and Karyamsetty, 2018; Vinaya and Binoy, 2024).

Species of *Rhizophora* have long been considered primarily wind-pollinated based on morphological and phenological traits, including abundant light and powdery pollen, anthesis in bud, lack of nectar, short-lived stamens, and pendulous flowers that open below the foliage (Tomlinson et al., 1979). However, the analysis of *R. mucronata* displayed several VOCs with known roles in insect attraction, including α-pinene (8) and β-pinene (11), monoterpenes associated with attraction of moths, bees, and beetles in the former (Williams and Whitten, 1983; Landolt and Smithhisler, 2003; Vuts et al., 2018) and primary bees in the latter (Dobson, 2006; Dötterl and Gershenzon, 2023); methyl benzoate (18), important in hawkmoths and bees attraction (Dudareva et al., 2000; Yue et al., 2021); Nonanal (20), attracting beetles, bees and, mosquito pollinators (Klatt et al., 2013; Blažytė-Čereškienė et al., 2019; Jermakowicz et al., 2025); (E)-4,8-dimethyl-1,3,7-nonatriene (22); methyl salicylate (24), a linalool oxide well known to attract noctuid moths and hawkmoths, bees, and flies (Williams and Whitten, 1983; Levin et al., 2001; Raguso et al., 2003; Fraser et al., 2003; Dötterl and Vereecken, 2010; Primante and Dötterl, 2010; Ibanez et al., 2010); and eugenol (26), known to attract nocturnal Lepidoptera and bees (Schiestl and Roubik, 2003; Huber et al., 2005). These findings are consistent with reports of opportunistic insect visitors to *Rhizophora* flowers in other regions, including Hymenoptera, Coleoptera and Diptera (Remadevi et al., 2019; Panda et al., 2019). While abiotic pollen transfer likely remains dominant, the presence of biologically active VOCs suggests that biotic interactions may be more important than previously assumed.

Finally, both *R. mucronata* and *B. cylindrica* emitted four fatty acid aldehydes, 2-ethylbutanal (2), hexanal (3), 3-hexenal (4), and 2-hexenal (6), which do not play a role in pollination mechanisms. Compounds 3, 4, and 6 are green leaf volatiles (GLVs) (Ibanez et al., 2010), which serve important functions in plant defense and signaling (Kishimoto et al., 2008; Engelberth and Engelberth, 2020). As these compounds are typically released from leaf tissue following mechanical damage (Scala et al., 2013), their detection likely reflects sampling artifacts, appearing in floral headspace due to handling or cutting that occurred during

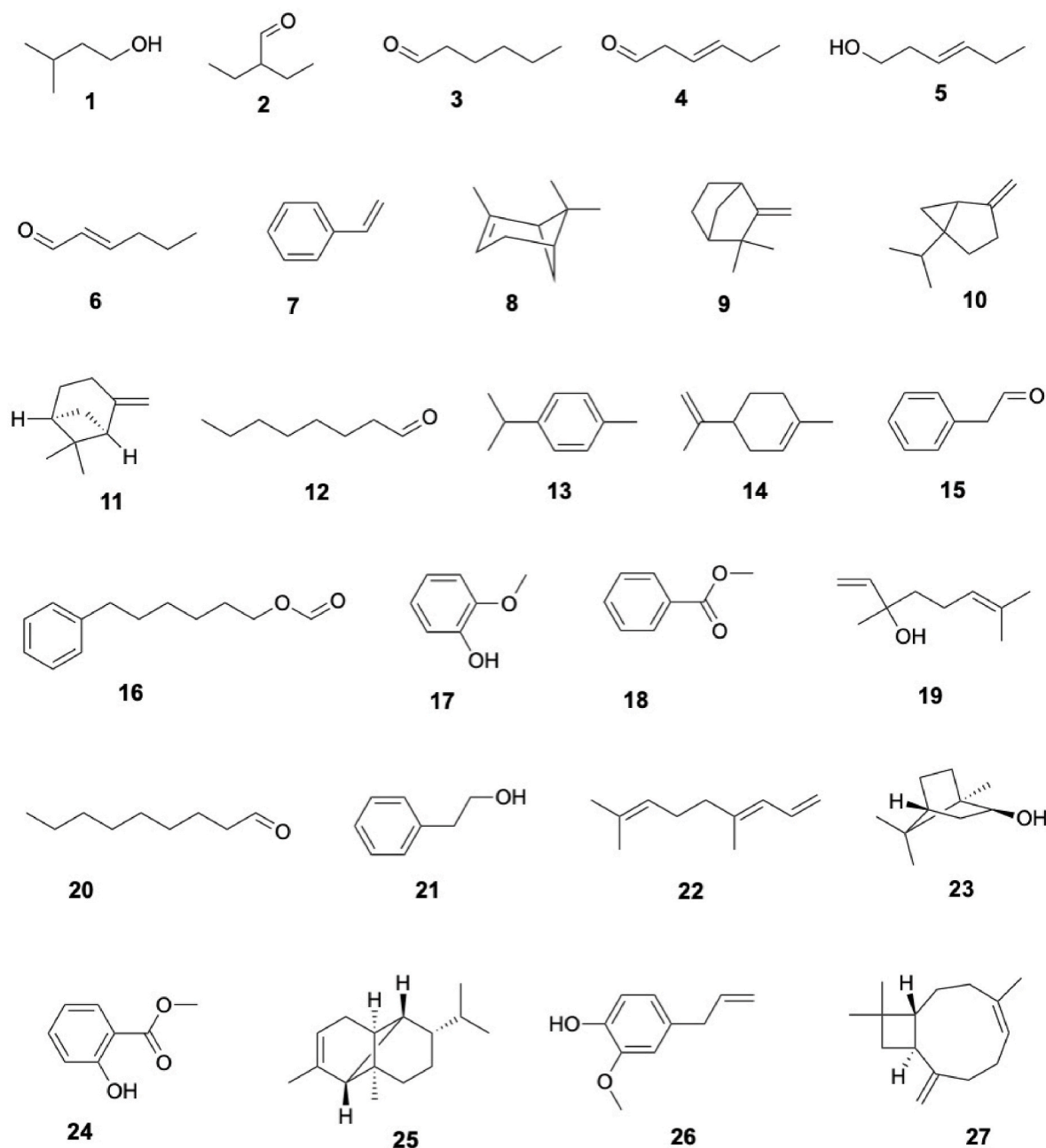


Fig. 2. Main VOCs detected the floral scent of the Mangroves object of the present study. Structures are numbered according to Table 1.

sample preparation (Azuma et al., 2002).

### 3.2. Untargeted analysis

The present study was initially conceived to characterize the floral VOCs emitted by three mangrove species whose scent chemistry has not been previously reported worldwide, namely *Ceriops tagal*, *Bruguiera cylindrica*, and *Rhizophora mucronata*. However, inspection of the corresponding GC-MS chromatograms (Supplementary Fig. S2-S4) revealed a high level of chemical complexity, with a substantial proportion of chromatographic peaks remaining unresolved or poorly annotated due to a low number of spectral matches with the NIST reference library at a match score >90%. From a chemical ecology perspective, this observation highlighted the need to apply an analytical framework capable of capturing the full structure of floral scent bouquets, beyond the subset of confidently annotated compounds. Consequently, we

adopted an untargeted volatilomic approach that accounts for both annotated and non-annotated features, allowing a comprehensive comparison of the entire VOC emission profiles. Moreover, the dataset was expanded to include more mangrove species, even if their floral scent data are already available in the literature. The aim was to provide a broader interpretative context and enable a better assessment of interspecific similarities and differences. Under this view, all the consistent molecular features were extracted from the raw chromatograms of the eight species surveyed and submitted to multivariate statistical analysis.

Specifically, the chromatogram deconvolution led to the identification of a total of 949 molecular features. Only 81 were confidently annotated based on an acceptable library matching with a reference in the MassIVE open access library provided on the GNPS platform (in this case we applied a larger match score >85% in order to have around to 10% rate of annotation for the statistically significant features). Application

of principal component analysis (PCA) to the extracted features revealed the occurrence of clear and biologically meaningful organization of floral VOCs profiles (Fig. 3). In particular, the PCA model explained 59.2% of the total variance on PC1, PC2, and PC3, respectively. Samples from *R. mucronata*, *B. gymnorrhiza*, *B. cylindrica* and *P. acidula* each formed well-defined clusters in the principal component space (PC1–PC3), suggesting that these species emit distinct and internally consistent scent bouquets. The other species displayed broader loadings dispersion and partial overlap. Examination of the loading structure revealed that species separation along PC1 was primarily driven by high positive contributions from features 409, 923, 848, 359, and 502, whereas negative PC1 loadings were mainly associated with features 516, 517, 356, 330, and 657. These compounds contributed to the horizontal separation observed between *Rhizophora* spp. and *Avicennia marina* from the remaining species. PC2 discrimination was influenced by features 426 and 528 (positive loadings), contrasted with features 185 and 533 contributing in the opposite direction. These variables were mainly responsible for the vertical differentiation observed between *Ceriops tagal* and *Bruguiera cylindrica* relative to other taxa. The third component (PC3), as visualized in the 3D representation, further refined species segregation by emphasizing the contribution of features such as 44 and 380, which showed directional influence in the multivariate space. Hierarchical cluster analysis (HCA) highlighted that the separation among clusters was driven primarily by differences in the relative abundance and combination of shared volatile features, rather than by the presence of species-exclusive compounds (see the related heatmaps in the supplementary, S11). Finally, partial least squares discriminant analysis (PLS-DA) (supplementary, S12) confirmed the occurrence of species-specific patterns and marked differences in intra-species variability, suggesting that the floral odours of the different mangrove species are chemically structured and potentially recognizable as distinct olfactory signals, despite substantial overlap in individual volatile components. In fact, the PLS-DA model confirmed the clear segregation among mangrove species observed in PCA and provided improved separation across the first latent components. Also in this case, the two *Rhizophora* species formed a distinct but closely related cluster, clearly separated from *Bruguiera* species and, in turn, sharply distinguished from *Pemphis* and the other taxa surveyed, which display a greater intra-species chemical variability. Variable importance in projection (VIP) scores highlighted several key discriminant compounds, e. g. feature 588 (Fiehn VocBinbase Bin #1190), 467 (Fiehn VocBinbase

Bin #757), and 661 (Fiehn VocBinbase Bin #1408), as well as identified volatiles including terpinen-4-ol (feature 458), (E)-3,7-dimethyl-2,6-octadien-1-ol (feature 427), 1-nonene (feature 563), 2-methylcyclohexanol (feature 420), and 2-methoxyethanol (feature 560). These compounds showed the highest discriminative power among species and largely contributed to interspecific differentiation of floral scent blends. Notably, several of the volatiles contributing to the discrimination resulted to belong to monoterpene and aliphatic hydrocarbon classes, highlighting the potential role of these classes in structuring species-specific chemical signals.

In summary, the multivariate approach allowed us to evaluate whether species-specific patterns and clustering could still be resolved despite the large proportion of unknown features, and to establish a baseline framework suitable for future investigations addressing local-scale variability and environmentally driven modulation of floral scent emissions. In fact, it is very common that in untargeted GC–MS analyses, annotation rates often remain limited due to incomplete spectral libraries (Wang et al., 2016) and the intrinsic ambiguity of similarity-based matching. Established mass spectrometry frameworks emphasize that compound identification confidence should not rely solely on spectral similarity scores, but rather integrate orthogonal evidence, including retention indices, comparison with authentic standards, and biosynthetic plausibility (Schymanski et al., 2014). In ecological metabolomics, recent perspectives have further suggested that annotation can benefit from contextual constraints, such as known biosynthetic pathways and documented chemical repertoires of the investigated taxa, thereby reducing the likelihood of environmentally implausible assignments (Wang et al., 2016; Lao et al., 2025). In this study, mass spectral matching was therefore interpreted in light of retention index agreement, known volatile biosynthetic pathways in mangrove species, and ecological plausibility, aiming to enhance annotation reliability in complex floral emission datasets. Notably, although a large fraction of the VOC features detected remained unannotated, the consistent species-specific bouquets strongly suggest ecological relevance. Pollinators respond to a bouquet of compounds, and low abundance or unresolved compounds can play specific roles in attracting pollinator groups (Dobson, 2006; Wang et al., 2016). Despite substantial overlap in individual VOCs, the distinct olfactory signatures of mangrove species indicate that these unknown components may contribute to species recognition and bouquet-level properties. While their precise behavioral functions cannot be inferred from the current

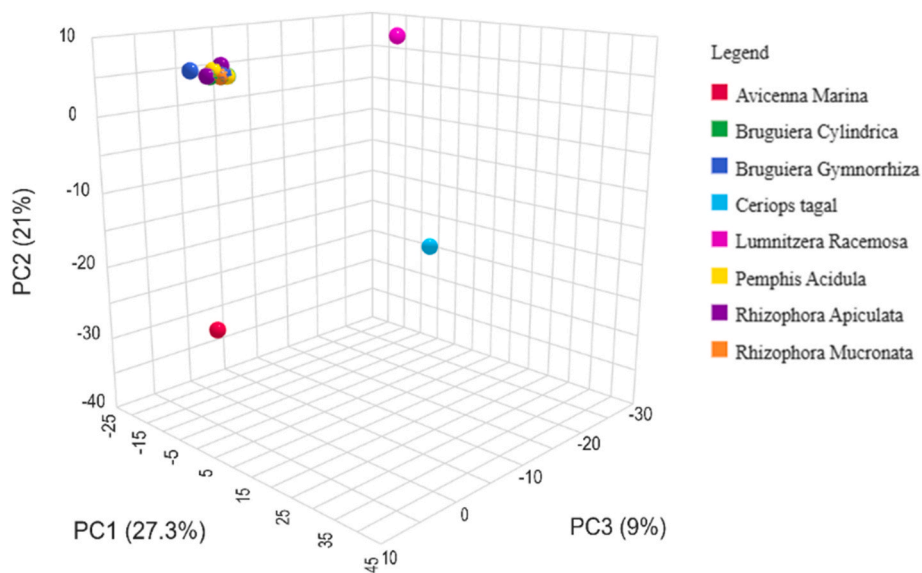


Fig. 3. 3D-Plot obtained from the PCA applied to the VOCs profiles of eight Maldivian mangroves object of the present study. Axes represent the main three principal component (PC1, PC2 and PC3) with the respective contribution to total variance. Point represent the samples (scores), colored according to species.

database, their presence underscores the value of untargeted approaches for capturing the full complexity of floral scents and highlights the need for future studies combining their chemical identification with behavioral assays to clarify their ecological role.

### 3.3. Context-dependent variation in mangrove floral volatile profiles within the Maldivian archipelago

Considering the whole dataset explored in this study, 94 features were found to be specific to one of the surveyed mangrove species (supplementary S8). Among these features, six were positively annotated, seven resulted in not being previously reported in mangrove floral scents, namely octyl formate, borneol, camphene, methyl propionate pentyl acetate 4-methyl-1-phenyl-2-pentanol and styrene although all are known plant-emitted VOCs. Since most of the features were found to be shared among the different species surveyed, and 21 of the 27 VOCs positively identified by high NIST library match have been already reported in mangroves from different geographic regions (Azuma et al., 2002; Paul et al., 2024), a shared chemical repertoire across mangrove taxa can be hypothesized. However, it must be taken in account that the occurrence of similar compounds does not necessarily translate into similar floral scent profiles, as demonstrated by the results we obtained from the multivariate analysis carried out on the complete floral scent bouquets (including not annotated VOCs). Overall, the results suggest that mangrove, rather than relying on species-exclusive compounds, can shape their floral odours by differential combinations and relative abundances of a largely shared set of volatiles. Moreover, it is likely that such bouquet-level variation may encode species-specific olfactory signals modulated by local environmental conditions and biotic interactions. Floral VOC composition is in fact recognized as context dependent and strongly influenced by environmental factors such as climate, seasonality, soil characteristics, and the composition of local pollinator communities (Farré-Armengol et al., 2020; De Agostini et al., 2022). In this respect, the Maldivian archipelago represents a particularly relevant environmental setting, characterized by small, isolated islands and limited terrestrial habitats. These conditions are likely to impose specific ecological and physiological constraints on mangrove species, potentially shaping their floral volatile emissions at both quantitative and qualitative levels. From an environmental perspective, the distinct floral scent bouquets described here provide a first chemical framework for exploring how insular and coastal conditions may modulate mangrove reproductive traits. Although 21 pollinator species have been documented in the Maldives, including bees, wasps, hoverflies, and several Lepidoptera (Meyrick, 1902; Eitschberger and Fischer, 2009; Nuppenon and Saldaitis, 2013; Biella et al., 2022), no studies have yet investigated mangrove–pollinator interactions in this region. The present findings therefore establish a baseline for future research aimed at linking floral scent variability to environmental drivers, biotic interactions, and ecosystem functioning in vulnerable coastal systems.

## 4. Conclusion

A first chemical framework for understanding floral scent diversity in Maldivian mangroves and highlights the presence of species-specific volatile signatures was established. The identification of distinct chemical blends across co-occurring mangrove species suggests that floral VOCs may contribute to ecological partitioning and potentially reflect divergent pollination strategies in this largely unexplored biogeographic context. The observed interspecific variability in volatile composition raises important ecological questions regarding pollinator selectivity, reproductive isolation, and adaptive chemical communication. To elucidate further the functional role of mangrove flowers VOCs, future studies should integrate chemical analysis with ecological and behavioral validation, for instance by combining headspace profiling with controlled olfactometer bioassays, and by performing field-based attraction experiments using synthetic blends to determine which

compounds actively mediate pollinator responses. Additionally, long-term monitoring of flower visitor assemblages will be fundamental to clarify how chemical diversity influences reproductive success and community dynamics, further supporting conservation strategies in these vulnerable tropical coastal ecosystems.

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## CRedit authorship contribution statement

**Federico Cerri:** Investigation, Writing – original draft. **Alessandro Becchi:** Investigation, Software. **Francesco Saliu:** Supervision, Writing – original draft. **Paolo Biella:** Investigation. **Shazla Mohamed:** Investigation. **Paolo Galli:** Funding acquisition, Supervision.

## Declaration of competing interest

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

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2026.109859>.

## Data availability

Data will be made available on request.

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