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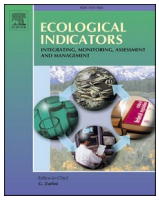



Honey volatile organic compounds as ecological indicators of floral diversity and ecosystem health across temperate and tropical agroecosystems of South Korea, Uganda, and Indonesia

Kenneth Happy [a,b], Kyeong-OK Choi [a], Yeongjun Ban [a,b], Joyce Adokorach [c], Hongmin Choi [d], Endang Rahmat [e], Joyce Mudondo [a,b], Islan Nor [f,g], Youngmin Kang [a,b,*]

[a] Korean Convergence Medical Science Major, University of Science and Technology (UST), Daejeon, 34113, South Korea
[b] Herbal Medicine Resources Research Center, Korea Institute of Oriental Medicine (KIOM), 111 Geonjae-Ro, Naju-Si, Jeollanam-Do, 58245, South Korea
[c] Uganda Martyrs University (UMU), Faculty of Agriculture, P.O.BOX 5498, Nkozi, Uganda
[d] Department of Agriculture Biology, National Institute of Agricultural Science, Rural Development Administration, Wanju 55365, Republic of Korea
[e] Bina Nusantara University, Biotechnology Department, Faculty of Engineering, Jakarta, 11480, Indonesia
[f] Universitas Muhammadiyah Banjarmasin (UMBjm), Faculty of Pharmacy, Barito, Kuala, Indonesia
[g] Bandung Institute of Technology, School of Pharmacy, Department of Pharmaceutical Biology, Bandung, Indonesia

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ABSTRACT

Honey volatile organic compounds (VOCs) serve as ecological indicators integrating floral resource diversity across pollinator foraging landscapes. Because honey reflects nectar collection over broad spatial and temporal scales, its VOC composition provides a biochemical archive of surrounding vegetation, climate, and ecosystem structure. In this study, multifloral honeys from Korea, Uganda, and Indonesia were analyzed using GC–MS and interpreted with multivariate statistical approaches to develop and evaluate VOC-based ecological indicators across the biodiverse countries. Rather than emphasizing aroma profiling alone, this work identifies diagnostic VOC patterns that capture ecosystem type, floral diversity, and land-use context. Distinct regional and ecological indicator signatures were detected across all study areas. Ugandan honeys exhibited pronounced intra-regional differentiation, with lowland Amuru and Wakiso samples enriched in (*Z*)-linalool oxide, reflecting linalool-producing flora typical of savanna and mixed agroecosystems, while highland Bushenyi honeys showed higher chemical complexity and were characterized by 2-methylheptan-3-ol, indicative of cooler, humid agroecological systems with diverse nectar sources. Indonesian honeys displayed island-specific indicator profiles, including 2-methyl-1-butanol in Java, 2-furfural in Borneo, and DL-menthol together with methyl salicylate in Sumbawa, corresponding to variation in forest structure, aromatic vegetation, and monsoon-influenced ecosystems. In contrast, Korean honeys were dominated by aldehydes and esters and exhibited reduced alcohol abundance, consistent with temperate climates, shorter flowering seasons, and comparatively limited floral diversity. Multivariate analyses revealed clear separation of honeys by ecological context, demonstrating strong climatic and ecosystem signals in VOC composition. Overall, this study establishes honey VOC profiling for ecological monitoring and biodiversity assessment across temperate and tropical landscapes.

1. Introduction

Honey is a widely produced apicultural product whose chemical composition reflects the ecological conditions under which it is generated. Its volatile and bioactive compounds are strongly shaped by environmental indicators such as regional flora, climate, altitude, and landscape structure (Oyedokun et al., 2025). Because honey bees forage across diverse plant communities, honey integrates chemical signals from surrounding vegetation, making it a natural indicator of ecosystem characteristics (Mohammed, 2022). Differences in ecological zones across South Korea, Uganda, and Indonesia therefore support distinct bee populations and floral assemblages, resulting in multifloral honeys with region-specific chemical fingerprints that reflect variations in ecosystems.

* Corresponding author at: Korean Convergence Medical Science Major, University of Science and Technology (UST), Daejeon, 34113, South Korea.
E-mail address: ymkang@kiom.re.kr (Y. Kang).

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The relationship between honey volatile organic compounds (VOCs) and ecosystems extends beyond floral diversity to reflect a network of interacting ecological process that provide insights into ecological indicators. These indicators encompasses soil health, floral and pollinator diversity, and habitat stability, all of which are linked to ecosystem health (Papa et al., 2022; Plutino et al., 2022). VOC variability serves as a biochemical archive that reflects these broader ecological factors, thereby providing a more comprehensive understanding of ecosystems (Oyedokun et al., 2025).

In South Korea, temperate climates and mountainous terrain influence nectar flow and seasonal floral availability (Na et al., 2024). The country produces approximately 25,000–30,000 tons of honey annually, reflecting a well-developed apicultural sector (Jung and Lee, 2018). Honey production relies heavily on nectar from *Robinia pseudoacacia* also known as black locust (Fig. 3G) and (Fig. 3H) and Salix spp., alongside other forage plants such as *Castanea crenata*, Euodia daniellii, *Brassica campestris*, *Fagopyrum esculentum*, *Astragalus sinicus*, *Malus pumila*, *Citrus unshiu*, *Tilia* sp., and *Lespedeza* spp. (Chan et al., 1988; Jung and Lee, 2018; Paek et al., 2024). Korean beekeeping involves both *Apis cerana* and the introduced *Apis mellifera* L., which now predominates (Frunze et al., 2020).

In Uganda, honey production occurs across tropical savannas, forest ecosystems, and mixed agroecosystems, where floral availability varies among agroecological zones (Otim et al., 2019). This ecological heterogeneity provides diverse nectar sources, enabling honey to function as a natural indicator of vegetation composition and landscape structure. Major bee forage plants include *Combretum* spp., *Lantana camara, Solanum incanum, Calliandra calothyrsus, Croton macrostachyus, Albizia* spp., *Bidens pilosa*, *Mangifera indica*, *Acacia* spp., *Eucalyptus* spp., *Syzygium guineense*, *Vitellaria paradoxa*, *Prunus africana*, and *Citrus* spp. (Ebuu et al., 2023). Cultivated crops such as Musa spp.(Banana), *Zea mays* (Maize), *Pisum sativum* (Peas), *Phaseolus vulgaris* (Beans), *Arachis hypogea* (Ground nuts), vegetables, and Coffee (*Coffae arabica* and *Coffae rubusta*) further contribute to nectar resources (Aciro et al., 2025; Nakabonge and Matovu, 2021; Otim et al., 2019). According to Statistics, U.B.o., 2021 Uganda produces approximately 4000–5000 metric tonnes of honey annually, with about 1.2 million people engaged in beekeeping. The country hosts diverse bee species, including *Apis mellifera scutellata*, *A. mellifera adansonii*, *A. mellifera monticola*, and stingless bees such as *Meliponula bocandei*; however, the dominant and native species is *Apis mellifera scutellate* (Oromokoma et al., 2023; Otim et al., 2019).

Indonesia represents one of the world's most biodiverse apicultural landscapes, hosting eight of the twelve recognized Apis species globally, including *Apis dorsata*, *Apis laboriosa*, *Apis cerana*, *Apis koschevnikovi*, *Apis nigrocincta*, and *Apis nuluensis*, in addition to more than forty stingless bee species (Harianja et al., 2023; Roubik, 2005). This exceptional bee diversity, closely linked to extensive forest and agroforestry ecosystems, underpins honey production across the archipelago, particularly among forest-dependent communities (Kahono et al., 2018). Indonesia produced 189,780 L of honey in 2021, increasing from 51,338.26 L the previous year (Buchori et al., 2022). Regionally, Java accounts for the highest production (41,614.26 L in 2020), followed by Sumatra (4010.00 L), Kalimantan (3007.00 L), and Sulawesi (500.00 L) (Juhari and Rachim, 2023). Managed beekeeping primarily involves native *Apis cerana* and Meliponini colonies (Schouten et al., 2019), while traditional honey hunting from wild *Apis dorsata* colonies remains common (Crane et al., 1993). The introduced *Apis mellifera*, brought to Java between 1967 and 1972, has since expanded widely, with managed *A. cerana* representing approximately 45–60% of colonies (Theisen-Jones and Bienefeld, 2016).Major forage plants that support bee keeping in Indonesia include *Cocos nucifera*, *Nephelium lappaceum*, *Mangifera indica*, *Durio zibethinus*, *Coffea arabica / C. canephora* (coffee), *Hevea brasiliensis*, *Acacia mangium*, *Calliandra calothyrsus*, Eucalyptus, *Dimocarpus longan*, crops like banana, sunflower, maize, beans, and various wild forest blossoms (Agussalim et al., 2018; Rosyidah et al., 2024). These plants provide abundant nectar and pollen, supporting Indonesia's diverse bee species.

Across South Korea, Uganda, and Indonesia, the dependence of apiculture on diverse floral resources underscores the value of honey as an integrative ecological matrix. Accordingly, honey VOC profiling presents a promising approach for ecological monitoring because honey integrates floral resources across spatial and temporal scales within bee foraging ranges, typically spanning a 2–5 km radius (Marcoccia et al., 2024). Unlike direct vegetation surveys, which are often labor-intensive, seasonal, and spatially constrained (Hao et al., 2020), honey-based indicators provide a cost-effective, non-destructive means of assessing key ecological attributes, including (1) floral diversity and plant community composition, (2) agroecosystem health and agricultural sustainability, (3) seasonal flowering dynamics and climate-driven impacts, (4) habitat quality for pollinators, and (5) environmental changes affecting vegetation communities (Ciulu et al., 2024). As honey reflects the cumulative foraging activity of bees across heterogeneous landscapes, its VOC composition serves as an integrative biochemical signal of surrounding ecosystems (Rahman et al., 2017).

The marked environmental and floral diversity across South Korea, Uganda, and Indonesia provides a strong basis for distinct honey volatile profiles shaped by geography, climate, and ecosystem structure. Variations in vegetation type, altitude, and climatic regime influence nectar composition and bee foraging patterns, thereby driving differences in VOCs that can function as indicators of botanical origin, authenticity, and product quality. Although the ecological relevance of honey VOCs is increasingly recognized, their systematic validation as indicators across contrasting climate zones and ecosystem types remains limited. Importantly, honeys from geographically distant regions may still share certain volatile compounds (Manyi-Loh et al., 2011). Such overlap can arise from the widespread distribution of plant families producing similar nectar metabolites, conserved biochemical pathways involved in nectar-to-honey transformation, and universal processes such as enzymatic activity and mild fermentation that generate common volatile groups, including aldehydes, alcohols, esters, and terpenes (Barberis et al., 2023). Consequently, while certain VOCs exhibit widespread occurrence across diverse botanical sources, others are more indicative of localized ecological conditions (Wang et al., 2022a). Accordingly, some VOCs may serve as exclusive floral markers for specific geographical and ecological regions, others act as contributory components within a broader VOC profile that can be detected across different geographical areas (Kaškonienė and Venskutonis, 2010). However, this duality underscores a critical knowledge gap in elucidating the extent of variation and similarity in VOC profiles across diverse and ecologically distinct regions, particularly in distinguishing ubiquitous compounds from those that reliably reflect localized environmental conditions. Addressing this gap is essential, as the ability to differentiate globally shared from region-specific VOCs directly influences their reliability and precision as ecological indicators, thereby determining their effectiveness in assessing ecosystem characteristics, environmental change, and geographical origin.

To address this knowledge gap, the present study comparatively examined multifloral honeys from South Korea (temperate Asia), Uganda (tropical Africa), and Indonesia (tropical Asia). These regions differ markedly in climate and ecosystem structure, with Uganda and Indonesia characterized predominantly by tropical systems, in contrast to the temperate environment of South Korea. Such differences are expected to shape floral resources, nectar chemistry, and honey maturation processes, thereby influencing volatile composition. This study distinguishes itself from prior region-specific VOC-based authentication studies by applying a cross-continental framework (Korea, Uganda, Indonesia), thereby capturing broader ecological variability. By integrating diverse ecological contexts, it demonstrates how ecosystem structure and environmental conditions shape VOC profiles, while advancing the field through combined chemometric classification, ecological interpretation, and the identification of regionally discriminant (tentative) marker compounds based on relative abundance and

statistical significance.

The objectives of this study were to: (1) characterize honey VOC patterns across contrasting ecosystem and climate types; (2) identify robust volatile compounds functioning as ecological indicator markers; (3) validate their discriminatory power for geographical and ecological origin; and (4) assess the suitability of honey VOCs as non-invasive tools for ecological monitoring and authenticity assessment. To achieve these aims, SPME-GC–MS was combined with multivariate analyses, including PCA and PLS-DA, enabling visualization of clustering patterns, enhanced discrimination by origin, and identification of key compounds considered as tentative marker compounds. Together, these approaches reveal shared and ecosystem-specific signatures shaped by botanical landscapes and environmental context.

1.1. Honey VOCs as ecological indicators

Honey serves as an integrative ecological matrix because its VOC profile reflects the combined influence of floral nectar chemistry, plant community composition, climate, and bee-mediated biochemical transformations (Jerković et al., 2019). As honey bees forage across diverse habitats, they consolidate metabolites from multiple taxa into a single matrix. Enzymatic activity and mild fermentation modify nectar while preserving botanical and environmental signatures, enabling VOCs to function as chemical proxies of ecosystem structure and function(Barberis et al., 2023). Because foraging spans broad landscapes and flowering periods, honey captures spatial and temporal ecological variability (Brosi et al., 2009), offering a non-destructive monitoring tool (Tsagkaris et al., 2021).

2. Materials and methods

2.1. Honey samples

Nine (9) organic multifloral honey samples were collected from three countries, with each selected location providing a representative snapshot of diverse ecological contexts. The distinct environmental conditions and floral assemblages of South Korea, Uganda, and Indonesia enhance the effectiveness of the sampling by capturing a broad range of ecosystem variability, thereby allowing for meaningful insights into broader ecological trends.

In South Korea, three samples originated from Andong (Gyeongsangbuk-do Province), Haman (Gyeongsangnam-do Province), and Cheorwon (Gangwon-do Province). These were collected by the Department of Agricultural Biology, National Institute of Agricultural Science, Rural Development Administration, Wanju 55,365, Republic of Korea, and donated to the Korea Institute of Oriental Medicine for research.

In Uganda, three samples were obtained from Amuru District (Northern Region), Wakiso District (Central Region), and Bushenyi District (Western Region). They were purchased from Guru Guru area (2°46′54″N) in Amuru, Namayumba Epicenter (0°31′41.56″S, 32°15′02″E) in Wakiso, and Ibaare area (0°37′27″S, 30°8′50″E) in Bushenyi through Uganda Martyrs University in collaboration with PELUM Uganda and The Hunger Project Uganda.

In Indonesia, three samples were sourced from Java, Borneo, and Sumbawa Islands, purchased from Global Honey, Jakarta, via Bina Nusantara University, Biotechnology Department. All nine samples (Fig. 1) were produced by *Apis mellifera* (Fig. 4 A-1), harvested between March and June 2024, and stored for less than four months at 20 ± 5 °C in sealed amber glass bottles protected from light until analysis.

To minimize post-harvest alterations and preserve the native volatile profiles, all honey samples were handled under standardized conditions immediately after collection. Samples were kept in airtight, food-grade containers to prevent contamination and loss of volatile compounds, and were transferred to sealed amber glass bottles to limit light-induced degradation following Ghazali et al. (2024). Storage temperature was carefully controlled at 20 ± 5 °C, in accordance with guidelines by da Silva et al. (2016), to prevent thermal fluctuations that could affect enzymatic activity and the stability of volatile compounds. In addition, prolonged exposure to air was minimized during handling to reduce

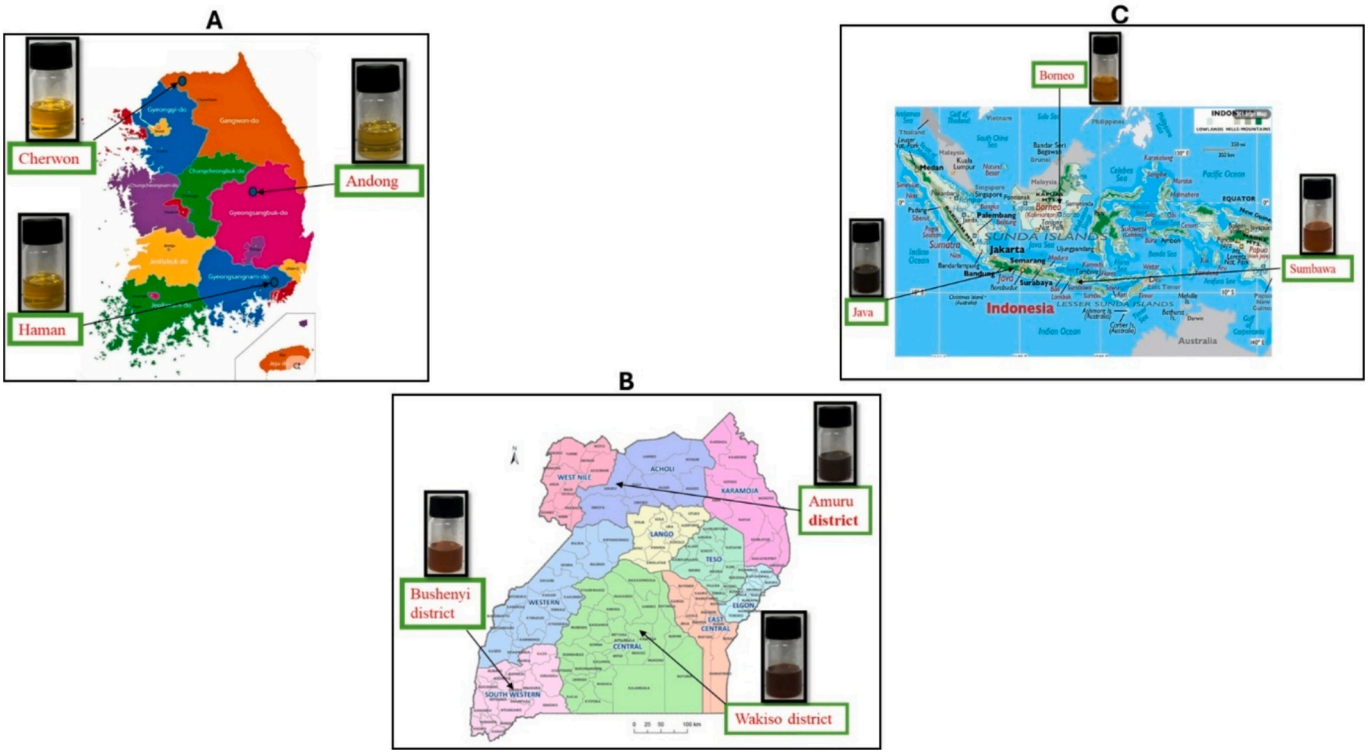

Fig. 1. Maps of the three countries showing the distinct geographical and ecological regions where the honey samples were collected.

oxidation. No heat treatment or processing was applied prior to analysis, ensuring that the VOC composition remained representative of the original ecological and floral conditions at the time of harvest.

2.2. SPME-GC–MS analysis

One gram (1 g) of honey was dissolved in 3.5 mL distilled water, mixed with 1.5 g NaCl, and placed in a 10 mL headspace vial, maintaining an approximate 1:1 headspace-to-sample ratio. Subsequently, 10 µL of fluorobenzene (50 ppm, internal standard) were added. The vial was incubated at 60 °C for 50 min, a condition selected based on previous studies, with slight modification, demonstrating optimal VOC extraction efficiency within this timeframe, while minimizing thermal degradation of sensitive compounds (Robotti et al., 2017). Volatiles were extracted by exposing the SPME fiber to the headspace for 25 min at 60 °C with constant agitation (500 rpm).

Analysis was performed using GC–MS equipped with a DB-624 capillary column (60 m × 0.25 mm i.d., 1.4 µm film thickness). The oven program was 40 °C (5 min), ramped to 250 °C at 5 °C min^{-1}, and held for 10 min. Helium served as the carrier gas. Raw data were processed using AMDIS (NIST) to deconvolute co-eluting peaks and obtain pure spectra. Compounds were tentatively identified by matching spectra with the NIST library and confirmed by comparing calculated retention indices (based on n-alkanes) with published RI values from PubChem and literature. Only compounds showing agreement in spectral similarity and RI were accepted. Quantification used fluorobenzene for internal standard normalization, with concentrations expressed as relative values (e.g., ng/g) based on peak area ratios. The workflow is presented in (Fig. 2), and identification relied on the nominal-resolution NIST library.

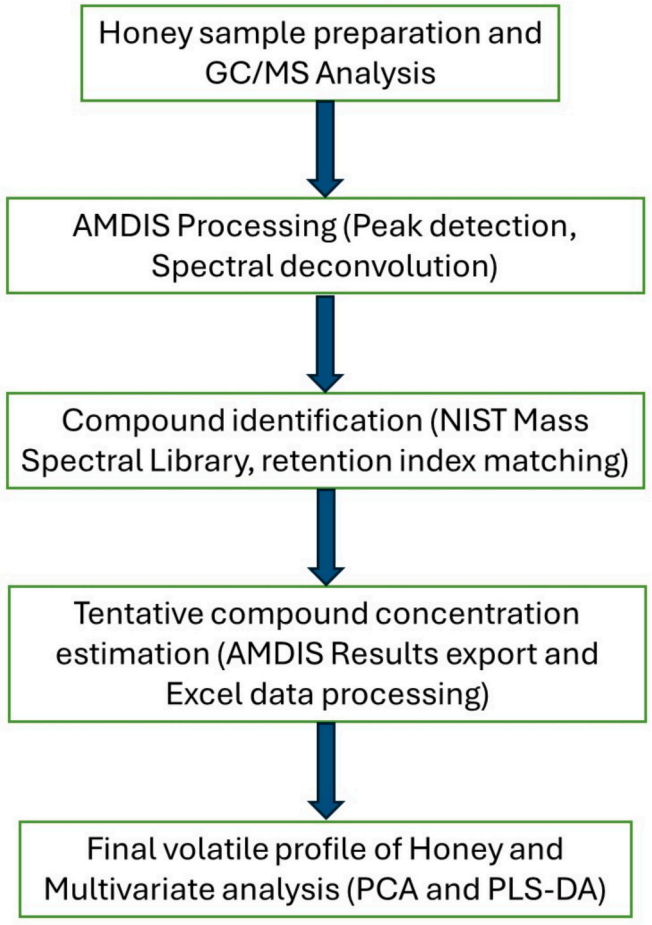

Fig. 2. Flow Chart of AMDIS-Excel-NIST Data Processing and multivariate analyses.

2.3. SPME-GC–MS-multivariate analysis

For multivariate analysis, quantified volatile data were organized into a matrix with honey samples as observations and compounds as variables. Data were normalized, mean-centered, and where appropriate autoscaled to reduce concentration bias. PCA was applied as an unsupervised approach to visualize clustering and major variance patterns. PLS-DA was then used to enhance geographical discrimination and identify key differentiating volatiles. Analyses were conducted using MetaboAnalyst 6.0 (https://www.metaboanalyst.ca/). Compounds with a VIP score greater that 1 on PLS-DA analysis were deemed to have a significant impact on differentiating the samples. The robustness and predictive performance of the PLS-DA model were evaluated using cross-validation and permutation testing.

3. Results and discussion

3.1. Qualitative results

Several studies have used solid-phase microextraction (SPME) combined with GC–MS to identify volatile compounds in honey (Manousi et al., 2023). This approach exploits the natural partitioning of aroma compounds into the headspace. SPME provides a solvent-free, selective, and sensitive extraction method that minimizes matrix interference from sugars, while GC–MS enables reliable separation and identification using retention indices and spectral matching (Eggermont et al., 2025).

Multivariate statistical tools are frequently employed to analyze honey VOC profiles and interpret complex GC–MS data. Methods such as principal component analysis (PCA) and partial least squares-discriminant analysis (PLS-DA) reduce dimensionality and highlight patterns linked to botanical and geographical origins. These techniques differentiate honey types, facilitate the identification of tentative marker compounds, and provide strong chemometric evidence for authentication and provenance determination (Akbari et al., 2020).

In this study, volatile compounds from nine honey samples collected in South Korea, Uganda, and Indonesia were analyzed using SPME–GC–MS, with three samples per country representing distinct ecological regions. A total of 146 compounds were identified. Fluorobenzene served as the internal standard and was consistently detected, confirming analytical stability. Multivariate analyses showed clear country-based clustering, with PCA and PLS-DA enhancing discrimination and identifying marker volatiles, demonstrating effective geographical differentiation.

3.2. Classification, concentration, and distribution of VOCs

The volatile constituents detected in the nine honey samples were classified into thirteen principal chemical groups, including esters, alcohols, monoterpenoids, aldehydes, furans, acids, ketones, indolic compounds, phenylpropanoids, phenolics, lactones, isoprenoids, and pyrazines, arranged according to their overall abundance. These classes were present at varying concentration levels among samples. Table 1 presents the detailed volatile composition of each honey, showing individual compound concentrations alongside the total contribution of each chemical group by geographical origin. The results demonstrate substantial variation in both composition and relative abundance, highlighting the chemical complexity of honey and its strong dependence on floral source, ecological setting, environmental conditions, and processing influences. Pronounced differences were observed among samples from Korea, Uganda, and Indonesia, reflecting regional botanical diversity and ecosystem characteristics. Furthermore, chromatograms (Fig. 5) and supplementary materials (SMs) illustrate dominant peaks corresponding to the most abundant volatiles identified across the

Table 1
Identified compounds in different honey samples in three countries.

Classification	Volatile compounds and Codes	CAS No	RI	Concentrations (ng/g Honey)								
				Andong	Haman	Cherwon	Amuru	Wakiso	Bushenyi	Java	Borneo	Sumbawa
Acids	Isobutyric acid (1)	79–31-2	836	0	0	0	0	115 ± 30.6	324 ± 46.67	0	0	0
Acids	Pentanoic acid (2)	109–52-4	865	0	0	0	0	0	0	0	0	1 ± 0.48
Acids	Butyric Acid (3)	107–92-6	866	0	0	0	0	0	0	0	9 ± 1.09	0
Acids	Isovaleric acid (4)	503–74-2	917	0	0	0	143 ± 17.42	79 ± 20.99	931 ± 19.22	0	0	0
Acids	2-Methylbutanoic Acid (5)	116–53-0	924	0	0	1 ± 0.1	0	145 ± 128.82	905 ± 400.96	0	0	0
Acids	Hexanoic acid (6)	142–62-1	1049	8 ± 0.79	0	0	146 ± 15.64	31 ± 13.9	4 ± 1.08	0	10 ± 5.26	14 ± 1.52
Acids	Heptanoic acid (7)	111–14-8	1050	0	0	0	0	0	6 ± 0.92	0	0	0
Acids	Octanoic acid (8)	124–07-2	1247	0	0	48 ± 55.16	59 ± 0.23	35 ± 3.06	407 ± 83.57	0	0	0
Acids	Nonanoic acid (9)	112–05-0	1346	4 ± 0.1	51 ± 3	0	0	0	277 ± 139.23	0	0	0
Total acids				12	51	49	348	405	2854	0	19	15
Alcohols	2-Methyl-1-butanol (10)	137–32-6	788	0	0	0	0	0	0	3 ± 4.34	0	0
Alcohols	Isoamyl alcohol (11)	123–51-3	789	0	0	0	0	0	333 ± 103.42	0	0	6200 ± 673.15
Alcohols	1-Pentanol (12)	71–41-0	789	0	2 ± 0.18	6 ± 1.03	9 ± 0.98	0	0	32 ± 7.76	0	284 ± 2.97
Alcohols	1,2-Butanediol (13)	584–03-2	875	0	0	0	0	0	68 ± 5.74	0	0	0
Alcohols	4-Methyl-1-pentanol (14)	626–89-1	889	0	0	0	0	0	2 ± 0.54	0	0	108 ± 15.61
Alcohols	3-Methyl-1-pentanol (15)	589–35-5	899	0	0	0	0	4 ± 0.07	0	0	0	0
Alcohols	3-Hexen-1-ol (16)	544–12-7	912	0	0	0	0	0	3 ± 0.35	0	0	0
Alcohols	(Z)-3-Hexenol (17)	928–96-1	912	0	0	0	0	0	11 ± 1.58	0	0	0
Alcohols	1-Hexanol (18)	111–27-3	919	0	0	0	21 ± 2.41	0	0	0	0	227 ± 27.26
Alcohols	4-Heptanol (19)	589–55-9	932	0	0	0	0	0	2066 ± 382.22	0	0	0
Alcohols	1-Heptanol (20)	111–70-6	939	0	0	0	0	0	5 ± 1.32	0	11 ± 2.75	0
Alcohols	2-Heptanol (21)	543–49-7	943	0	0	0	35 ± 4.88	80 ± 52.81	4 ± 0.79	0	0	0
Alcohols	3-Heptanol (22)	589–82-2	967	0	1 ± 0.4	0	0	0	7 ± 1.46	0	0	0
Alcohols	3-Methyl-3-heptanol (23)	5582-82-1	1002	0	0	0	0	0	30 ± 1.56	0	0	0
Alcohols	(Z)-3-Hepten-1-ol (24)	1708-81-2	1008	0	0	0	0	0	0	0	0	269 ± 22.62
Alcohols	1-Octen-3-ol (25)	3391–86-4	1021	6 ± 0.58	0	0	20 ± 3.66	0	0	0	0	0
Alcohols	2-Methylheptan-3-ol (26)	18,720–62-2	1023	0	0	0	0	352 ± 73.89	10,297 ± 115.58	0	0	0
Alcohols	(Z)-5-Octen-1-ol (27)	64,275–73-6	1037	0	0	0	0	0	0	0	0	16 ± 0.06
Alcohols	3-Methyl-1-heptanol (28)	1070-32-2	1087	0	0	6 ± 0.38	0	0	0	0	0	0
Alcohols	Benzyl Alcohol (29)	100–51-6	1109	0	0	0	0	0	0	0	0	0.11
Alcohols	1-Octanol (30)	111–87-5	1122	31 ± 0.04	0	0	56 ± 18.66	0	0	0	40 ± 11.99	0
Alcohols	1,2-Hexanediol (31)	6920–22–5	1125	0	0	0	0	0	533 ± 363.72	0	0	0
Alcohols	1-Nonen-4-ol (32)	35,192–73-5	1142	0	0	0	0	0	120 ± 7.51	0	0	0
Alcohols	2-Phenylethanol (33)	60–12-8	1212	0	0	113 ± 2.09	2075 ± 690.24	521 ± 441.91	1175 ± 504.66	1618 ± 117.68	407 ± 17.79	4272 ± 292.42
Alcohols	1-Decanol (34)	112–30-1	1223	0	0	0	46 ± 12.33	0	0	0	0	0
Alcohols	1-Nonanol (35)	143–08-8	1224	11 ± 0.7	0	30 ± 12.64	0	0	184 ± 19.28	0	47 ± 2.15	0
Alcohols	3,7-Dimethyl-1-octanol (36)	106–21–8	1237	0	0	0	0	0	0	0	8 ± 0.46	0
Alcohols	2-Butyl-1-octanol (37)	735,273	1266	0	0	0	576 ± 241.45	0	0	0	0	0
Alcohols	1-Dodecanol (38)	112–53-8	1530	0	0	0	1 ± 0.32	0	0	0	0	0
Total alcohols				48	3	155	2839	957	14,838	1653	513	11,376
Aldehydes	3-Methylbutanal (39)	590–86-3	699	0	0	0	0	0	0	10.02	0	0
Aldehydes	Hexanal (40)	66–25-1	845	0	0	0	0	0	1 ± 0.14	0	0	0
Aldehydes	3-Methyl-2-butenal (41)	107–86-8	850	0	0	1 ± 0.06	0	0	0	0	0	0
Aldehydes	(Z)-4-Heptenal (42)	6728-31-0	942	0	0	0	0	0	0	0	0	6 ± 0.08
Aldehydes	Heptanal (43)	111–71-7	946	55 ± 1.86	74 ± 4.02	0	15 ± 1.98	0	7 ± 5.09	5 ± 0.02	0	12 ± 3.92
Aldehydes	Benzaldehyde (44)	100–52-7	1034	255 ± 43.86	704 ± 136.09	339 ± 11.51	5796 ± 758.01	340 ± 308.65	769 ± 185.07	153 ± 17.03	181 ± 98.97	1296 ± 313.89
Aldehydes	Octanal (45)	124–13-0	1048	0	0	115 ± 5.41	0	0	0	0	0	0
Aldehydes	2,4-Heptadienal (46)	881,395	1068	0	0	0	0	0	0	0	0	22 ± 5.53
Aldehydes	Benzeneacetaldehyde (47)	122–78-1	1130	0	0	0	0	1383 ± 117.65	1572 ± 366.69	904 ± 96.27	0	0

(*continued on next page*)

Table 1 (*continued*)

Classification	Volatile compounds and Codes	CAS No	RI	Concentrations (ng/g Honey)								
				Andong	Haman	Cherwon	Amuru	Wakiso	Bushenyi	Java	Borneo	Sumbawa
Aldehydes	Undecanal (48)	112–44-7	1156	0	4187 ± 169.26	0	0	147 ± 9.4	0	0	0	0
Aldehydes	Nonanal (49)	124–19-6	1156	2954 ± 190.83	86 ± 1.47	1357 ± 118.25	463 ± 4.43	104 ± 21.22	1382 ± 21.46	232 ± 67.03	358 ± 288.73	352 ± 76.66
Aldehydes	Decanal (50)	112–31-2	1260	592 ± 19.43	522 ± 26.64	473 ± 28.66	118 ± 28.34	8 ± 4.3	0	0	274 ± 8.56	168 ± 20.22
Aldehydes	Tetradecanal (51)	124–25-4	1260	0	532 ± 61.66	0	0	0	0	0	0	0
Aldehydes	2,4-Decadienal (52)	2363-88-4	1406	5 ± 0.36	0	0	0	0	0	0	0	0
Aldehydes	Dodecanal (53)	112–54-9	1467	0	0	0	94 ± 44.49	55 ± 5.46	0	0	0	0
Total aldehydes				3861	6105	2285	6486	2037	3731	1304	813	1856
Esters	Ethyl Acetate (54)	141–78-6	649	0	0	0	0	0	0	36 ± 16.62	0	0
Esters	Methyl butyrate (55)	623–42-7	755	0	0	0	0	0	2 ± 0.67	0	3 ± 1.04	0
Esters	Ethyl butyrate (56)	105–54-4	829	0	0	0	0	0	0	6 ± 0.37	0	0
Esters	Ethyl 2-methylbutyrate (57)	7452-79-1	878	0	0	0	0	0	0	2 ± 0.19	0	0
Esters	2-Methyl-4-heptanone (58)	626–33-5	879	0	0	0	0	0	527 ± 34.72	0	0	0
Esters	Ethyl isovalerate (59)	108–64-5	881	0	0	0	0	0	0	18 ± 3.25	0	0
Esters	Isoamyl acetate (60)	123–92-2	906	0	0	0	0	0	44 ± 1.57	58 ± 6.81	0	40 ± 2.31
Esters	2-Methybutyl acetate (61)	624–41-9	909	0	0	0	0	0	0	6 ± 0.64	0	0
Esters	Ethyl valerate (62)	539–82-2	926	0	0	0	0	0	0	0	0	31 ± 3.42
Esters	Methyl hexanoate (63)	106–70-7	951	0	0	0	0	0	268 ± 4.76	0	0	0
Esters	Ethyl hexanoate (64)	123–66-0	1019	0	0	0	0	0	0	392 ± 24.69	0	217 ± 123.56
Esters	Isobutyl isovalerate (65)	589–59-3	1029	0	0	0	0	0	15 ± 3.24	0	0	0
Esters	Isoamyl isobutyrate (66)	0.2050-01-3	1040	0	0	0	0	0	22 ± 7.11	0	0	0
Esters	2-Hexenol acetate (67)	10,094–40-3	1048	0	0	0	0	0	16 ± 4.78	0	0	0
Esters	Ethyl Heptanoate (68)	106–30-9	1126	0	0	0	0	0	0	9 ± 4.64	0	0
Esters	Methyl Octanoate (69)	111–11-5	1155	0	0	0	188 ± 101.23	0	841 ± 419.41	0	0	0
Esters	Ethyl octanoate (70)	106–32-1	1226	0	0	0	0	0	0	162 ± 30.83	0	392 ± 89.3
Esters	Ethyl benzoate (71)	93–89-0	1239	0	0	0	0	0	0	39 ± 7.32	0	0
Esters	Methyl nonanoate (72)	1731–84-6	1257	169 ± 8.26	141 ± 28.69	0	0	33 ± 9.53	929 ± 631.24	0	0	112 ± 19.16
Esters	Methyl salicylate (73)	119–36-8	1279	5011 ± 302.64	4434 ± 1851.6	6194 ± 3341.58	2996 ± 3581.06	944 ± 279.68	1632 ± 976.96	2727 ± 128.14	2078 ± 614.24	3166 ± 2780.48
Esters	Ethyl phenylacetate (74)	101–97-3	1313	0	0	0	0	0	0	91 ± 5.2	0	0
Esters	2-Phenylethyl Acetate (75)	103–45-7	1329	0	0	0	0	0	0	85 ± 90.15	0	0
Esters	Menthyl acetate (76)	16,409–45-3	1350	0	0	0	0	0	0	0	0	1650 ± 15.87
Esters	Ethyl caprate (77)	110–38-3	1426	0	0	0	0	0	0	49 ± 2.39	0	0
Esters	Methyl Laurate (78)	111–82-0	1559	0	0	0	331 ± 263.2	0	0	0	0	0
Esters	Isopentyl phenylacetate (79)	102–19-2	1571	0	0	0	0	0	0	0	366 ± 1.44	0
Total esters				5180	4575	6194	3515	977	4296	3680	2447	5608
Furans	2,5-Dimethylfuran (80)	625–86-5	728	0	0	0	0	0	0	0	0	18 ± 2.97
Furans	3-Furfural (81)	498–60-2	880	0	0	0	0	0	83 ± 80.73	0	1 ± 0.24	0
Furans	2-Furfural (82)	98–01-1	908	86 ± 6.56	193 ± 1.61	12 ± 6.72	1322 ± 687.91	1204 ± 604.59	623 ± 11.62	600 ± 177.44	2714 ± 1254.01	86 ± 5.69
Furans	2-Furanmethanol (83)	4412-91-3	931	0	0	0	0	0	66 ± 21.61	0	0	0
Furans	2-Butylfuran (84)	4466-24-4	933	0	0	0	0	0	0	0	0	23 ± 3.97
Furans	2-Acetylfuran (85)	1192-62-7	979	0	7 ± 0.32	0	111 ± 9.96	0	0	113 ± 9.17	52 ± 2.63	1 ± 0.29
Furans	2-Pentylfuran (86)	3777-69-3	1008	0	0	0	0	0	10.17	0	0	0
Furans	2-Acetyl-5-Methylfuran (87)	1193-79-9	1041	0	0	0	0	0	405 ± 5.98	0	0	0
Furans	5-Methylfurfural (88)	620–02-0	1042	0	0	2 ± 0.23	0	0	0	466 ± 102.18	705 ± 55.04	22 ± 4.2
Furans	Ethyl 2-furoate (89)	614–99-3	1116	0	0	0	0	0	0	28 ± 11.61	0	0
Furans	2-Methylbenzofuran (90)	4265-25-2	1177	0	0	0	0	0	0	0	127 ± 12.71	0
Furans	3-Phenylfuran (91)	13,679–41-9	1303	0	0	0	0	0	162 ± 15.34	0	99 ± 5.84	0
Furans	5-Hydroxymethylfurfural (92)	67–47-0	1319	0	0	0	0	0	0	1067 ± 754.44	0	0
Total furans				86	200	14	1433	1204	1349	2274	3698	150
Indolics	Indole (3)	120–72-9	1257	0	0	0	1046 ± 320.61	36 ± 1.21	0	0	34 ± 3.44	0
Total indolics				0	0	0	1046	36	0	0	34	0
Isoprenoids	Sulcatone (94)	110–93-0	1034	23 ± 2.02	47 ± 2.16	0	0	0	0	0	0	0

(*continued on next page*)

Table 1 (*continued*)

Classification	Volatile compounds and Codes	CAS No	RI	Concentrations (ng/g Honey)								
				Andong	Haman	Cherwon	Amuru	Wakiso	Bushenyi	Java	Borneo	Sumbawa
Total isoprenoids				23	47	0	0	0	0	0	0	0
Ketones	3-Pentanone (95)	96–22-0	737	0	0	0	0	0	0	0	0	1 ± 0.15
Ketones	3-Hexen-2-one (96)	763–93-9	847	0	9 ± 0.77	0	0	0	8 ± 1.39	0	0	0
Ketones	3-Heptanone (97)	106–35-4	879	0	0	0	2 ± 0.3	0	0	0	0	0
Ketones	α-Methylbutyrolactone (98)	1679-47-6	918	0	0	0	10 ± 3.2	0	0	0	0	0
Ketones	4-Hydroxy-3-hexanone (99)	4984-85-4	919	0	0	0	0	0	1 ± 0.09	0	0	0
Ketones	2-Heptanone (100)	110–43-0	938	0	5 ± 0.07	0	0	17 ± 11.1	258 ± 15.42	0	0	2 ± 0.58
Ketones	2-Octanone (101)	6137-06-0	982	0	0	12 ± 4.8	0	0	0	0	0	0
Ketones	3-Hepten-2-one (102)	1119-44-4	990	0	0	0	9 ± 4.05	0	0	0	0	0
Ketones	3-Octanone (103)	106–68-3	1021	0	17 ± 6.42	0	0	0	0	0	0	23 ± 3.46
Ketones	2-Nonanone (104)	821–55-6	1145	0	0	0	0	0	290 ± 55.77	0	0	0
Ketones	Ketoisophorone (105)	1125-21-9	1243	0	0	0	0	0	1194 ± 60.91	0	0	0
Total ketones				0	31	12	21	17	1751	0	0	26
Lactones	α-Angelica lactone (106)	591–12-8	947	0	0	0	0	0	0	0	192 ± 3.26	0
Total lactones				0	0	0	0	0	0	0	192	0
Monoterpenoids	β-Pinene (107)	127–91-3	999	25 ± 0.23	0	0	0	0	0	0	0	0
Monoterpenoids	α-Phellandrene (108)	99–83-2	1028	0	0	0	11 ± 3.92	0	0	0	0	0
Monoterpenoids	Sulcatol (109)	1569-60-4	1037	0	0	0	0	0	45 ± 7.44	0	0	0
Monoterpenoids	ᴅ-Limonene (110)	138–86-3	1055	49 ± 9.12	53 ± 71.46	69 ± 21.66	166 ± 80.41	3 ± 0.19	18 ± 0.62	0	49 ± 3.31	0
Monoterpenoids	p-Cymene (111)	527–84-4	1059	0	77 ± 5.7	0	0	0	0	0	0	0
Monoterpenoids	α-Ocimene (112)	502–99-8	1064	1 ± 0.11	3 ± 0.02	0	0	0	0	0	0	0
Monoterpenoids	β-Phellandrene (113)	555–10-2	1064	0	0	0	13 ± 3.65	0	0	0	0	0
Monoterpenoids	Eucalyptol (114)	470–82-6	1072	0	67 ± 1.93	18 ± 0.55	44 ± 4.85	497 ± 388.36	9 ± 0.29	0	331 ± 55.14	0
Monoterpenoids	α-Pinene (115)	80–56-8	1084	0	13 ± 1.43	0	0	0	12 ± 1.35	0	0	0
Monoterpenoids	γ-Terpinene (116)	99–85-4	1084	0	0	0	15 ± 1.28	0	0	0	114 ± 19.54	0
Monoterpenoids	Terpinolene (117)	586–62-9	1118	0	0	6 ± 1.17	0	0	0	0	0	0
Monoterpenoids	(−)-Isopulegol (118)	89–79-2	1122	0	33 ± 1.54	0	0	0	0	0	0	0
Monoterpenoids	(Z)-Linalool oxide (119)	5989-33-3	1131	1459 ± 221.69	15 ± 2.56	40 ± 3.92	4198 ± 68.38	4018 ± 2316.58	5367 ± 1785.36	29 ± 1.86	0	0
Monoterpenoids	Linalool (120)	78–70-6	1151	0	272 ± 5.85	481 ± 41.53	389 ± 13.05	0	445 ± 14.12	0	0	0
Monoterpenoids	Hotrienol (121)	29,957–43-5	1163	856 ± 64.56	2187 ± 49.91	0	0	0	0	0	0	0
Monoterpenoids	Fenchone (122)	1195-79-5	1167	0	0	0	554 ± 76.1	0	0	0	0	0
Monoterpenoids	Nerol oxide (123)	1786-08-9	1197	0	267 ± 4.28	0	0	0	0	0	0	0
Monoterpenoids	Terpinen-4-ol (124)	562–74-3	1216	0	109 ± 11.87	0	123 ± 20.16	0	0	0	0	0
Monoterpenoids	Citronellal (125)	106–23-0	1229	0	215 ± 2.72	0	0	0	0	0	0	0
Monoterpenoids	Phellandral (126)	21,391–98-0	1237	0	16 ± 1.32	14 ± 3.28	0	0	0	0	0	0
Monoterpenoids	DL-Menthol (127)	89–78-1	1248	68 ± 3.67	12 ± 0.95	172 ± 66.03	0	81 ± 8.1	0	0	574 ± 3.5	5294 ± 567.42
Monoterpenoids	Linalool oxide (pyranoid) (128)	14,049–11-7	1253	0	0	117 ± 3.03	0	0	0	0	0	0
Monoterpenoids	1-p-Menthen-9-al (129)	29,548–14-9	1255	0	0	0	0	63 ± 21.98	0	0	0	0
Monoterpenoids	α-Terpineol (130)	98–55-5	1268	0	0	75 ± 4.46	109 ± 3.76	0	399 ± 95	0	796 ± 290.79	0
Monoterpenoids	Geraniol (131)	106–24-1	1275	0	0	0	0	0	107 ± 0.6	0	0	0
Monoterpenoids	Carvone (132)	99–49-0	1340	0	0	0	0	0	0	0	384 ± 147.72	0
Monoterpenoids	Thymol (133)	89–83-8	1391	0	0	0	52 ± 6.91	0	0	0	0	0
Monoterpenoids	Geranylacetone (134)	3796-70-1	1520	0	0	0	0	0	0	21 ± 3.48	0	40 ± 15.61
Total monoterpenoids				2458	3339	992	5674	4662	6402	50	2248	5334
Norisoprenoids	Cuminol (135)	536–60-7	1334	0	0	0	0	0	24 ± 32.92	0	0	0
Norisoprenoids	β-Damascenone (136)	23,726–93-4	1477	0	0	47 ± 27.5	0	0	0	0	0	0
Total norisoprenoids				0	0	47	0	0	24	0	0	0
Phenolics	Guaiacol (137)	90–05-1	1174	0	0	0	125 ± 59.78	0	68 ± 1.01	0	0	0
Phenolics	4-Methylcatechol (138)	452–86-8	1191	0	0	0	0	0	0	0	36 ± 3.98	0

(*continued on next page*)

Table 1 (*continued*)

Classification	Volatile compounds and Codes	CAS No	RI	Concentrations (ng/g Honey)								
				Andong	Haman	Cherwon	Amuru	Wakiso	Bushenyi	Java	Borneo	Sumbawa
Phenolics	p-Cresol (139)	106–44-5	1192	0	0	0	19 ± 7.63	0	18 ± 4.84	0	0	0
Phenolics	4-Ethylguaiacol (140)	2785-89-9	1373	0	0	0	0	0	0	0	0	228 ± 76.86
Total phenolics				0	0	0	144	0	86	0	36	228
Phenylpropanoids	Estragole (141)	140–67-0	1259	0	0	0	0	65 ± 6.48	0	827 ± 295.22	0	0
Total phenylpropanoids				0	0	0	0	65	0	827	0	0
Pyrazines	Tetramethylpyrazine (142)	1124-11-4	1128	0	0	0	0	0	33 ± 8.88	0	0	0
Total pyrazines				0	0	0	0	0	33	0	0	0

CAS No; Chemical Abstracts Service Registry Number, RI; Retention index, ng/g; Nanogram/g.

samples.

3.2.1. *Influence of floral diversity indices on VOC profiles of Korean honey*

In this study, Korean honey samples demonstrated clear regional differences in chemical diversity and dominant volatile constituents, closely indicating variations in local floral diversity indices, including species richness and Shannon diversity. Honey from Andong (Gyeongsangbuk-do Province) contained 20 volatile compounds and was strongly dominated by esters (5180 ng/g), particularly methyl salicylate (5011 ng/g) (Table 1, SM-1). Aldehydes were also abundant (3861 ng/g), with nonanal (2954 ng/g) as the principal component. The relatively low compound richness and pronounced dominance pattern correspond with lower floral diversity, indicating reliance on a limited number of prevailing nectar sources.

In contrast, Haman (Gyeongsangnam-do Province) honey exhibited greater chemical complexity, with 31 identified volatile compounds. Aldehydes predominated (6105 ng/g), led by undecanal (4187 ng/g), followed by benzaldehyde (704 ng/g) (Table 1, SM-2). This higher VOC richness aligns with elevated floral diversity indices, suggesting a more heterogeneous floral environment.

Cheorwon (Gangwon-do Province) honey contained 25 volatile compounds and was dominated by esters (6194 ng/g), largely methyl salicylate, while aldehydes (2285 ng/g), particularly nonanal (1357 ng/g), were secondary (Table 1, SM-3). Its intermediate VOC richness reflects moderate floral diversity and mixed nectar sources.

Overall, Korean honeys were characterized by a marked predominance of aldehydes and esters, underscoring their central role in shaping the volatile profiles of these samples. Aldehydes were particularly abundant in Haman and Andong honeys, consistent with their known origin from lipid oxidation, carbohydrate degradation, and plant-derived precursors, and their established contribution to honey aroma, especially in Korean acacia honeys (Manyi-Loh et al., 2011). Similarly, the high ester content, particularly methyl salicylate (73), reflects the influence of dominant floral sources such as acacia, *Cosmos bipinnatu* spp. (Fig. 3 C and D), chestnut, pear, and Salix spp., which are widespread in major honey-producing regions of Korea and are known to emit methyl salicylate (73) as a characteristic volatile marker (Bisrat, 2022; Dekebo et al., 2018; Jerković and Marijanović, 2010).

3.2.2. *Influence of floral diversity indices on VOC profiles of Ugandan honey*

Alcohols were the most abundant volatile class in Ugandan honeys, with particularly high levels observed in Bushenyi (14,838 ng/g), followed by Amuru (2839 ng/g), and Wakiso with (957 ng/g). This gradient in alcohol abundance parallels differences in floral species richness and Shannon diversity among the regions, with Bushenyi exhibiting the highest floral diversity and Wakiso the lowest. The abundant alcohol distribution across all honey samples in Uganda indicate strong floral inputs and/or microbial transformations during nectar ripening. Similar patterns have been reported by Kahwa et al. (2025), who identified alcohols as one of the prominent compound classes in Ugandan honey and propolis. In Bushenyi and Wakiso, the dominance of alcohols is consistent with the region's intensive cultivation of banana (*Musa* spp.) (Fig. 3F), a major nectar source whose fruits and flowers are known to contain alcohol-related volatiles, including isoamyl alcohol (11) (Beekwilder et al., 2004). In addition to banana, alcohol compounds detected in Ugandan honeys have been reported in nectar or plant tissues of eucalyptus, citrus, and *Bidens pilosa*, all of which are widely distributed across Amuru, Wakiso, and Bushenyi (Gindri et al., 2020; Lima Silva et al., 2011; Tao, 2000). The collective presence of these plant species provides a strong botanical explanation for the alcohol-rich volatile profiles characteristic of Ugandan honeys.

Ugandan honeys demonstrated clear regional differences in chemical diversity and dominant volatile constituents. Honey from Amuru (Northern Uganda) contained 39 volatile compounds and was primarily dominated by benzaldehyde (44) and (*Z*)-linalool oxide (119) (Table 1,

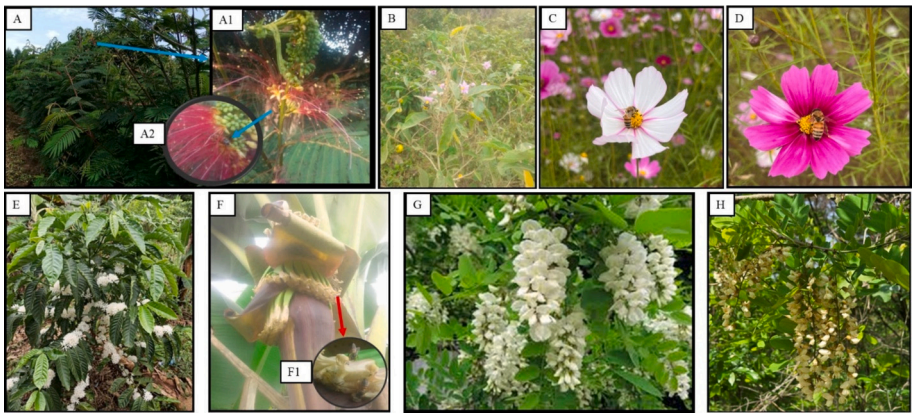

Fig. 3. Identified common multifloral diversitynectar sources; (A) *Callindra calothyrsus*, (A1) Flower of Calliandra calothyrsus, (A2) Bees on *Calliandra calothyrsus* flower, (B) *Solanun incanum*, (C) *Cosmos bipinnatu* (White cultivar) flower, (D) *Cosmos bipinnatu* (Mexican aster)n flower, (E) Coffee, (F) Banana inflorescence (flower), (F1) Bees on banana inflorescence, (G) two weeks old *Robinia pseudoacacia* flowers, three weeks old *Robinia pseudoacacia* flowers.



Fig. 4. Harvesting and preparation of honey samples for analysis; (A) Honey comb *Apis mellifera* L. Bees, (A-1) *Apis mellifera L.* Bee, (B), processed Bushenyi honey sample, (C) Honey sample preparation for analysis.

SM-4), consistent with moderate floral species richness and Shannon diversity typical of mixed savanna–agroecosystems. In contrast, Wakiso (Central Uganda) honey exhibited lower chemical complexity, with 26 identified compounds, and was strongly dominated by (*Z*)-linalool oxide (119) in both chromatographic intensity and concentration (Table 1, SM-5). This reduced VOC richness corresponds to lower floral diversity indices in this highly urbanized area, where nectar sources are relatively limited and homogenized. Bushenyi (Western Uganda) showed the highest chemical diversity, with 60 volatile compounds identified. It was characterized by 2-methylheptan-3-ol (26) as the principal compound, followed by (Z)-linalool oxide (119) and 4-heptanol (19) (Fig. 5). The recurrent prominence of (Z)-linalool oxide (119) reflects shared nectar sources, including Acacia spp., *Calliandra callothyrsus*, citrus, and *Eucalyptus* spp. (Castro-Vázquez et al., 2009; Juan-Borrás et al., 2014). The widespread natural occurrence of *Acacia* spp., *Solanum incanum* (Fig. 3B), extensive eucalyptus plantations, and community-level cultivation of citrus across Amuru, Wakiso, and Bushenyi provide a coherent botanical basis for this observation (Vesselly et al., 2022; Zivanayi et al., 2024).

Aldehydes represented another significant volatile class in Ugandan

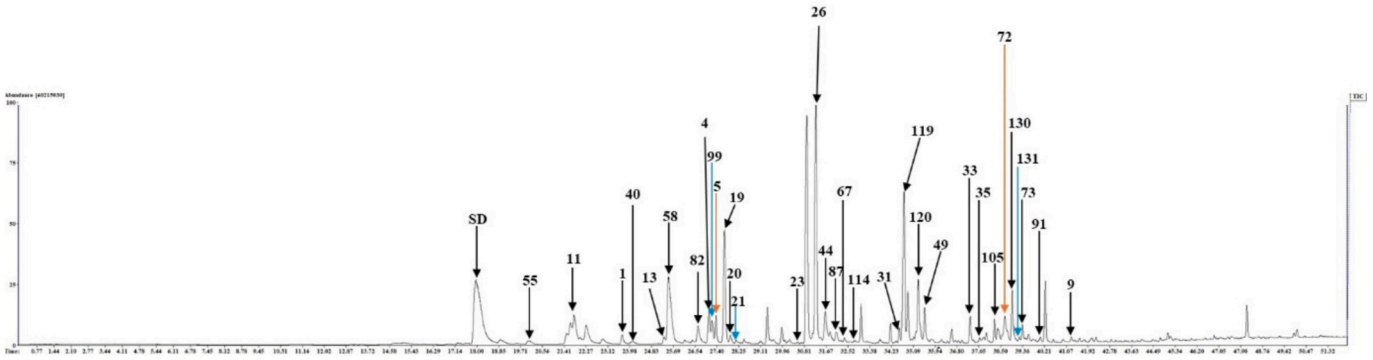

Fig. 5. Chromatographic profile of honey samples from Bushenyi, Uganda; Number of the volatile compounds refer to the Code No. given in Table 1.

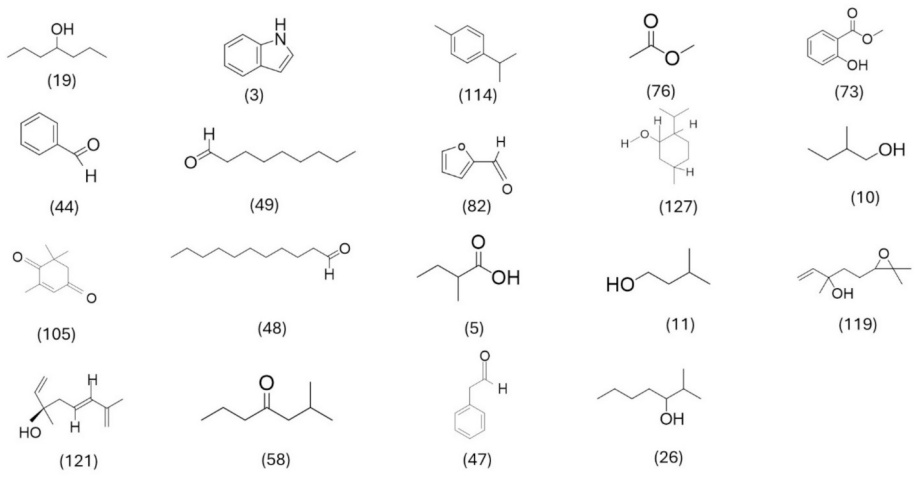

Fig. 6. Representative chemical structures of major compounds identified across honey samples from different origins; Number of the volatile compounds refer to the Code No. given in Table 1.

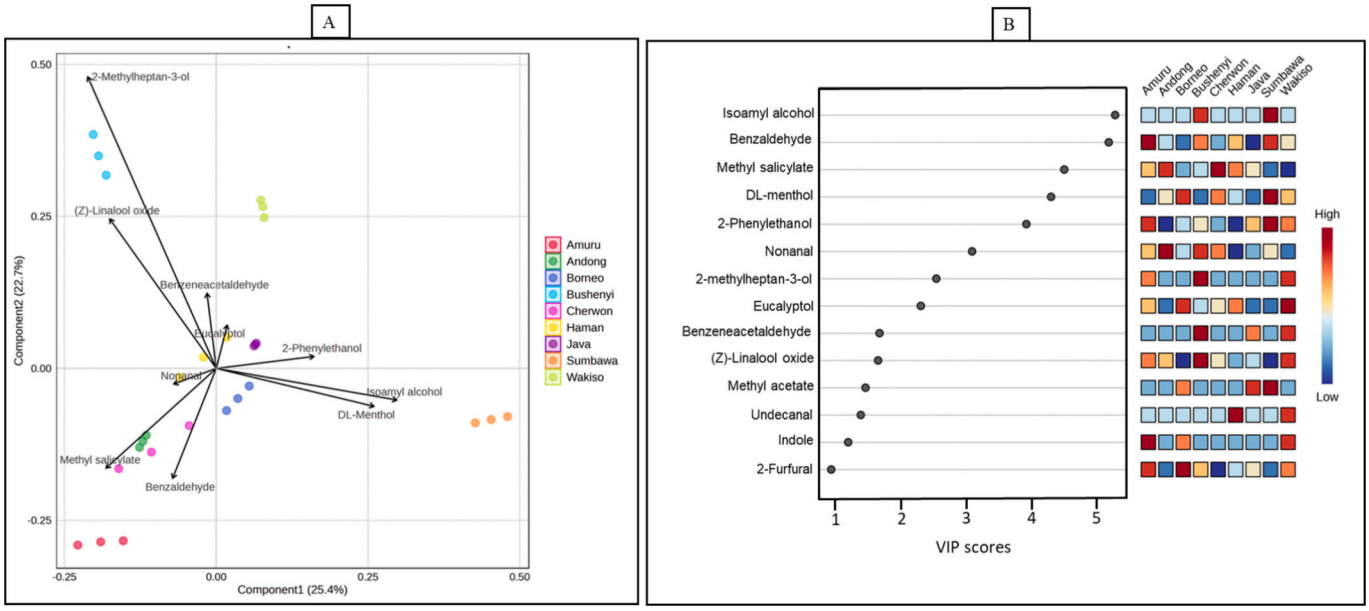

Fig. 7. Multivariate analysis; (7 A) PCA score plot, (7B), PLS-DA VIP heatmap analysis.

honeys. Amuru showed the highest aldehyde concentration (6486 ng/g), followed by Bushenyi (3731 ng/g), while Wakiso recorded lower levels (2037 ng/g). Aldehydes in honey commonly originate from lipid oxidation, carbohydrate degradation, and plant-derived precursors (Manyi-Loh et al., 2011). Although earlier studies detected aldehydes in Ugandan honeys and propolis without classifying them as dominant

(Kahwa et al., 2025), their regional variability here underscores differences in nectar sources and ecological conditions, alongside consistently high alcohol content (SM-9).

3.2.3. Influence of floral diversity indices on VOC profiles of Indonesian honey

Among the Indonesian honey samples, alcohols were the predominant volatile class, largely due to the exceptionally high alcohol concentration detected in Sumbawa honey (11,376 ng/g) (Table 1, SM-6). This profile was mainly driven by isoamyl alcohol (11) (6200 ng/g) and 2-phenylethanol (33) (4272 ng/g), indicating that these two compounds were the principal contributors to the volatile fraction. The pronounced enrichment of alcohols in Sumbawa honey (SM-9) likely reflects abundant floral precursors, active plant biosynthetic pathways, favorable tropical climatic conditions, and honey maturation processes that enhance alcohol formation and retention. Such alcohol-rich profiles are commonly linked to tropical nectar sources, including Eucalyptus, banana (Fig. 3F), citrus, coconut, and *Bidens pilosa,* which are widely distributed in Indonesian agroecosystems (Alissandrakis et al., 2011; Gindri et al., 2020). In addition to alcohols, Sumbawa honey exhibited high levels of esters (5608 mg/g) and monoterpenoids (5334 mg/g) dominated by methyl salicylate (73) (3166 mg/g) in the esters and DL-menthol (127) (5295 mg/g) in the monoterpenoids) Table 1, SM-8. The dominance of DL-menthol (127) suggests strong contributions from aromatic plant species, especially members of the Lamiaceae family such as *Mentha* spp., *Solanum lycopersicum, Solanum incanum* (Fig. 3B), *Ocimum* spp. (locally known as ruku-ruku), and *Hyptis suaveolens*, which are cultivated or naturally occurring in Sumbawa and have been reported these esters and monoterpenoids (Harismah et al., 2023; Salas-Marina et al., 2015; Singh, 2014).

In contrast, Java Island honey showed much lower total alcohol content (1653 ng/g) (Table 1, SM-6), almost entirely dominated by 2-phenylethanol (33) (1618 ng/g), while isoamyl alcohol (11) was not detected. This profile indicates a predominantly floral origin with minimal fermentation influence. The strong dominance of 2-phenylethanol (33), a common floral scent compound, reflects its widespread occurrence in nectar-producing taxa across diverse botanical families (Dötterl and Gershenzon, 2023). In Java, likely nectar contributors include fruit trees such as *Malus* spp., *Carica papaya*, and *Vitis* spp., as well as ornamental and tropical plants including *Magnolia* spp. and *Jasminum* spp., which are widely distributed across the island (Erbar and Leins, 2013; Waworuntu, 2024). The highest concentration in Java honey was recorded in esters (3680 mg/g), with methyl salicylate (73) dominating this class (2727 mg/g) (Table 1, SM-6). The presence of methyl salicylate (73) further suggests contributions from plants such as *Solanum lycopersicum*, *Capsicum* spp., and *Nicandra* spp., known producers of this ester and cultivated regionally (Frick et al., 2023; Salas-Marina et al., 2015).

Borneo Island honey exhibited a distinct volatile profile dominated by furans (3698 mg/g), particularly 2-furfural (82) (600 mg/g), with moderate 2-phenylethanol (33) (407 mg/g). Total alcohol content was low (513 ng/g) (Table 1, SM-7), supporting a mainly floral rather than fermentation-derived origin. The presence of 2-furfural (82) likely reflects ecological influences from forest, peatland, agroforestry, and mangrove ecosystems rather than a single botanical source (Ciotlaus et al., 2020). In Borneo, likely contributors include dominant tropical forest taxa such as *Shorea* spp., *Dipterocarpus* spp., and *Hopea* spp., as well as mangrove vegetation (*Sonneratia* spp.) and agroforestry crops including *Calliandra calothyrsus* (Fig. 3A), coffee (*Coffea canephora*) (Fig. 3E), coconut (*Cocos nucifera*), rubber (*Hevea brasiliensis*), and cocoa (*Theobroma cacao*) (Hayati et al., 2024; Paramita et al., 2024; Rosiak et al., 2021). These diverse sources reflect the ecological mosaic of Borneo, mirrored in the furan-rich volatile profile of its honey.

Compared with Ugandan and Indonesian honeys, Korean samples showed much lower alcohol contents (SM-9): Andong 48 ng/g, Haman 3 ng/g, and Cheorwon 155 ng/g (Table 1), values markedly below tropical levels. Alcohol concentrations are generally lower in temperate honeys, possibly due to reduced humidity, whereas higher tropical moisture can decrease sugar concentration and favor alcohol-related transformations (Hidayat et al., 2021), increasing susceptibility to spontaneous fermentation by yeasts and molds in raw materials. Fermentation produces ethanol and other volatile compounds (Li and Sun, 2019; Rosiak et al., 2021). According to Sharin et al. (2024), high relative humidity elevates moisture and water activity in honey due to its hygroscopic nature. Additional factors influencing the higher abundance of alcohol compounds in Ugandan and Indonesian honeys compared with Korean honey include differences in nectar chemistry between temperate and tropical flora and distinct tropical flowering cycles ((Machado et al., 2020). Overall, the higher alcohol abundance in Ugandan and Indonesian honey (SM-9) indicates similar chemical-ecological patterns across diverse tropical floral landscapes.

3.2.4. Influence of floral diversity indices on monoterpenoid VOC variation in honey samples

Monoterpenoids were another dominant class, particularly in Ugandan and Indonesian honeys. The highest concentrations were observed in Bushenyi (6402 ng/g), followed by Amuru (5674 ng/g), Sumbawa (5334 ng/g), and Wakiso (4662 ng/g). These compounds are typically associated with floral scent emissions and serve as important botanical markers. In Uganda, monoterpenids have been linked to nectar sources such as *Eucalyptus camaldulensis*, *Coffea canephora*, *Markhamia lutea*, *Calliandra calothyrsus*, *Bidens Pilosa*, *Vernomia sp,* Citrus*, Carapa grandifolia,* which are known to produce compounds including α-pinene, D-limonene (74), linalool (120), (*Z*)-linalool oxide (119), eucalyptol (114), α-Terpineol (130) of monoterpenoids class (Kahwa et al., 2025). Similarly, in Indonesia, monoterpenoids compounds have been associated with a wide range of plant species, reflecting the country's rich floral diversity. These include longan (*Euphorbia longan*), rubber tree (*Hevea brasiliensis*), Acacia (*Acacia mangium*, *Acacia crassicarpa), Eucalyptus spp, Koompassia excelsa, Pelawan Flower (Tristaniopsis merguensis), Bouea macrophylla Griffith, Lansium parasiticum, and several small plants such as Imperata cylindrica.* In addition, cultivated fruit crops such as Mango, *Durian (Durio zibethinus), Banana* (Fig. 3F), *coffee, oil palm (Elaeis guineensis), and longan (Euphorbia longan),* along with woody plants including *Hevea brasiliensis and Tectona grandis L.f.*, Acacia have also been reported as potential contributors (Suhandy and Yulia, 2021). Notably, Pattamayutanon et al. (2017), reported that linalool oxide derivatives occur in higher content being more in longan species than in many other plants, andAgussalim et al. (2018) indicates that logan trees are widely distributed across Indonesia. Whereas Korean honeys contained moderate monoterpenoid levels, with concentrations varying among regions, where Haman (3339 ng/g) and Andong (2458 ng/g) exhibited high levels than Cheorwon (992 ng/g). A key contributor of to this class of VOC was (*Z*)-linalool oxide (119), a monoterpenoid compound consistently detected across all three Korean samples. Previous studies by Dekebo et al. (2018) reported the presence of (*Z*)-linalool oxide (119) in Korean honeys and identified it as a characteristic volatile marker associated with acacia honey. Its consistent abundance in the present study aligns with earlier reports describing (Z)-linalool oxide (119) as a dominant and diagnostic component of Korean honey volatiles (Bisrat, 2022; Jerković et al., 2010). The high occurrence of this compound on the chromatograms in the three honey origins of Korea likely reflects the major nectar sources available in Korea, which include multifloral plants such as *Robinia pseudoacacia* (Acacia / Black locust) (Fig. 3G) and (Fig. 3H), *Castanea crenata / C. mollissima* (Chestnut), *Zelkova serrata*, *Tilia amurensis / Tilia mandshurica* (Linden) (Kim et al., 2020; Park et al., 2025). Together, these plant species are recognized sources of (Z)-linalool oxide (119), reinforcing the role of monoterpenoids as a reliable botanical and regional marker of Korean honey. Java honey exhibited markedly lower monoterpenoid content (50 ng/g) compared with honeys from other Indonesian islands and with samples from the same country. This

observation is consistent with previous studies reporting comparatively lower physicochemical and aromatic properties in Java honeys than in Kalimantan honeys (Waworuntu, 2024).

3.2.5. Influence of floral diversity indices on minor volatile constituents in honey

Minor volatile classes exhibited pronounced regional specificity, highlighting strong botanical and ecological influences across the studied honeys. Ketones were most abundant in Bushenyi honey (1751 ng/g), whereas only trace levels were detected in other regions, indicating localized nectar inputs or distinct biochemical transformations. Phenolic compounds were primarily detected in Sumbawa (228 ng/g), Amuru (144 ng/g), and Bushenyi (86 ng/g), suggesting contributions from aromatic and medicinal plant taxa. Phenylpropanoids were uniquely elevated in Java (827 ng/g), while indolic compounds were largely confined to Amuru (1046 ng/g), with only trace amounts in Wakiso and Borneo. Ketones have been reported in the flowers and leaves of *Bidens pilosa* (Paramasivam et al., 2024), a widespread weed in Ugandan and Indonesian agricultural systems that is frequently visited by honeybees for nectar collection (Rodríguez-Mesa et al., 2023; Wahjudi et al., 2023). Additional plant taxa known to produce ketone-containing nectar include *Eucalyptus* spp., *Coffea* spp., *Musa* spp. (banana fruits and flowers) (Fig. 3F), *Acacia* spp., and citrus plants (flowers, leaves, peels, and juice) (Alissandrakis et al., 2003; Aswathi et al., 2024), all widely distributed in Uganda and Indonesia (Kagezi et al., 2018; Suciati and Agusta, 2024).

The elevated indolic content in Amuru honey, compared with other regions, likely reflects specific nectar sources and climatic stress. Indole-related compounds have been reported in *Jasminum* species Venkatesha et al. (2025), with high indole (3) levels documented in jasmine from West Bengal Bera et al. (2015). Given the comparable tropical savanna climates of Northern Uganda and West Bengal (Halder et al., 2023; Omay et al., 2023), such conditions may enhance indolic volatile production. In contrast, Bushenyi's higher rainfall and humidity (Ojara et al., 2023) may reduce indole accumulation.

Lactones were detected exclusively in Borneo honey (192 ng/g), while pyrazines appeared only in Bushenyi (33 ng/g). The exclusive detection of α-angelica lactone in Borneo represents a novel finding. Although pyrazines are reported in coffee cultivated in Bushenyi (Li et al., 2014),they are generally associated with secondary formation processes (Adams et al., 2008). Given their detection in raw Bushenyi honey, further studies are required to elucidate the environmental, biochemical, or processing-related mechanisms contributing to their formation.

Korean honeys contained comparatively low levels of these minor classes, consistent with previous GC–MS analyses of acacia, chestnut, and jujube honeys (Dekebo et al., 2018), indicating more limited contributions from specialized aromatic flora under temperate conditions.

3.2.6. Reflection of ecosystem types in honey VOC profiles

The compositional patterns of honey VOCs observed in this study clearly differentiate tropical (Uganda and Indonesia) from temperate (Korea) ecosystems, as well as savanna-dominated from forested landscapes. Tropical honeys exhibited markedly higher chemical diversity and abundance across multiple compound classes, particularly alcohols, monoterpenoids, and minor specialized volatiles, compared with temperate Korean honeys. This aligns with greater plant species richness, prolonged flowering periods, and continuous nectar availability in tropical systems (Ndungu et al., 2024). In contrast, Korean honeys were dominated by fewer compound classes, mainly aldehydes and esters, reflecting shorter and more synchronized flowering seasons (Koyuncu, 2025). As illustrated in (Fig. 3G) two-week-old *Robinia pseudoacacia* flowers rapidly senesce by the third week (Fig. 3H), limiting nectar continuity. Within tropical regions, ecosystem structure further shaped VOC profiles. Ugandan honeys from savanna and mixed farming landscapes (Amuru, Wakiso) showed high alcohol content and frequent (*Z*)-linalool oxide, linked to *Acacia* and banana-dominated systems (Nuwategeka and Nyeko, 2019). Bushenyi displayed exceptionally high VOC richness, consistent with its heterogeneous highland agro-ecosystem (Ochungo et al., 2021).

In Indonesia, Borneo honey, derived from forest, wetland, and agroforestry systems, was dominated by furans and lactones, whereas Sumbawa favored DL-menthol (127) and methyl salicylate (73). Java showed lower diversity, reflecting intensive land management (Fathiarahmah et al., 2025). Collectively, VOC richness and Shannon diversity effectively captured gradients in floral diversity and ecosystem complexity.

3.3. Multivariate ecological analysis

The nine honey samples evaluated in this study reflected clear variation according to geographical origin and multifloral composition. Multivariate statistical modeling using principal component analysis PCA; (Fig. 7A) and partial least squares–discriminant analysis (PLS-DA; Fig. 7B) strengthened the differentiation of volatile chemical profiles among samples grouped by region. Application of these complementary approaches significantly improved geographical discrimination and revealed evident climatic structuring of honey volatile patterns. PCA based on SPME-GC–MS datasets demonstrated that each honey possessed a unique metabolite signature. However, samples from Cherwon and Haman clustered closely, as did those from Borneo and Java, indicating compositional similarity within comparable climatic and ecological contexts. In contrast, Sumbawa and Bushenyi honeys displayed markedly distinct metabolite compositions relative to other samples. The PCA model explained 64.4% of total dataset variability, with PC-1 accounting for 39.7% and PC-2 contributing 24.9% of the variance (Fig. 7A). Further discrimination was confirmed by PLS-DA, which identified a restricted subset of volatiles with strong regional discriminative capacity. Based on VIP values greater than 1, thirteen metabolites were recognized as key differentiating compounds (Fig. 7B). The VIP score represents the weighted contribution of each variable within the model, with values exceeding 1 considered significant for group separation (Wang et al., 2022b). Despite distinct clustering, several core volatiles were consistently detected across regions, suggesting a shared honey aroma matrix shaped by climate and floral availability rather than exclusive compound occurrence Akbari et al. (2020).

The VIP score plot (Fig. 7B) highlighted isoamyl alcohol (11), benzaldehyde (44), methyl salicylate (73), DL-menthol (127), 2-methylheptan-3-ol (26), and 2-phenylethanol (33) as the most influential variables contributing to regional differentiation. Isoamyl alcohol (11), which exhibited high relative abundance in tropical samples, particularly Indonesian and Ugandan honeys, was associated with fermentation-related processes promoted by warm hive temperatures and extended nectar flow typical of tropical climates (Li et al., 2026). Similarly, DL-menthol (127) and linalool derivatives, including (*Z*)-linalool oxide (119), significantly contributed to tropical honey separation and were consistently observed in Ugandan and Indonesian samples, indicating shared bioclimatic drivers.

In contrast, Korean honeys formed tighter clusters in both PCA and PLS-DA score plots and were more strongly associated with aromatic aldehydes and phenylpropanoid-related compounds such as benzaldehyde (44), ketoisophorone (105), methyl salicylate (73), nonanal (49), and eucalyptol (114), all showing moderate to high VIP values. These compounds are typically linked to temperate floral sources, cooler hive environments, and synchronized flowering periods (Koyuncu, 2025). The VIP heatmap further demonstrated that benzaldehyde (44), benzeneacetaldehyde (91), 2-phenylethanol (33), and nonanal (49) occurred across both tropical and temperate honeys at varying intensities, indicating universal markers rather than strictly region-exclusive compounds (Manyi-Loh et al., 2011).

Lower-VIP compounds, including indole (3), undecanal (48), and

menthyl acetate (116), supported finer-scale discrimination, particularly within tropical samples. Indole (3) was especially relevant for distinguishing specific Ugandan honeys, while furfural derivatives reflected environmental or processing influences beyond botanical origin alone. Regional structuring within tropical honeys was evident: Ugandan samples separated according to savanna (Amuru), (Nuwategeka and Nyeko, 2019), high-rainfall agro-forest (Bushenyi) (Jassogne et al., 2013), and peri-urban agricultural ecosystem (Wakiso) (Mugisa et al., 2017), while Indonesian honeys clustered by island-specific conditions including rainforest (Borneo) (Davis and Sutton, 1998), mixed agricultural landscapes (Java) (Fathiarahmah et al., 2025), and comparatively drier island conditions (Sumbawa) (Mahrup et al., 2021). The VIP heatmap (Fig. 7B) illustrates that these separations arise from shifts in the relative abundance of shared discriminant compounds-such as isoamyl alcohol (11), DL-menthol (127), methyl salicylate (73), and linalool derivatives-rather than from entirely region-exclusive volatiles. These separations arose primarily from shifts in the relative abundance of shared discriminant volatiles rather than the presence of unique regional compounds.

The robustness and predictive performance of the PLS-DA model were evaluated using cross-validation and permutation testing (supplementary materials 10, with model quality assessed based on R^2 and Q^2 metrics. Higher R^2 values indicate a better model fit, while Q^2 values greater than 0.5 are considered indicative of satisfactory predictive capability (Yang et al., 2022). Cross-validation results showed that model performance improved with an increasing number of components, with the three-component model providing the optimal performance ($R^2 = 0.83795$ and $Q^2 = 0.73296$). Although the classification accuracy was relatively low (0.25238), the strong Q^2 value suggests acceptable predictive ability, likely influenced by the limited sample size and the use of a stringent validation strategy. Furthermore, permutation testing ($n = 1000$), based on prediction accuracy during training, demonstrated that the original model significantly outperformed the permuted models ($p = 0.025$), with only a small proportion of permuted models achieving comparable performance. Collectively, these results confirm that the model is statistically robust, reliable for discriminant analysis, and not overfitted.

3.4. Ecological and authenticity insights derived from honey VOC profiles

The pronounced geographical and ecological separation among multifloral honeys from Korea, Uganda, and Indonesia (Table 1), (Fig. 6), (Fig. 7), (SMs 1–8) highlights the strong potential of honey VOCs as non-invasive ecological indicators, with this differentiation driven by distinct compounds identified as tentative marker compounds. Temperate Korean honeys were characterized by methyl salicylate (73) and hotrienol (121), reflecting cooler climates and synchronized flowering periods. Ugandan lowland samples were dominated Fby (*Z*)-linalool oxide (119), whereas highland Bushenyi honey was typified by 2-methylheptan-3-ol (26), indicating the influence of elevation, climatic gradients, and floral diversity. Indonesian honeys displayed island-specific markers, including DL-menthol (127), methyl salicylate (73), and aromatic esters, clearly distinguishing Java, Borneo, and Sumbawa and emphasizing localized vegetation structure and land-use patterns.

Collectively, these markers reflect localized floral assemblages and environmental conditions, demonstrating that honey VOCs integrate nectar chemistry, bee metabolic transformation, and broader ecosystem context into a unified chemical profile(Manyi-Loh et al., 2011). PCA and PLS-DA revealed a strong climatic gradient separating chemically complex tropical honeys from comparatively simpler temperate Korean samples. Because bees forage across large spatial ranges (Komasilova et al., 2021), honey VOCs capture landscape-level heterogeneity, offering cost-effective, non-destructive tools for ecological monitoring, authenticity verification, and detection of vegetation change across contrasting climate zones. Similarly, Radovic et al. (2001) demonstrated how honey VOC profiles obtained by GC–MS provide clear geographical and botanical discrimination, with specific aroma compounds reflecting local vegetation and climatic conditions.

3.5. Threats to floral resources inferred from honey VOC profiles

Honey VOC profiles reveal region-specific pressures on floral resources across Korea, Uganda, and Indonesia, reflecting land-use patterns, urbanization, and ecosystem modification. In Korean samples (Andong, Haman, Cheorwon), aldehydes and esters particularly methyl salicylate (73) and nonanal dominate, indicating reliance on limited nectar sources like acacia, chestnut, and jujube. This chemical uniformity reflects habitat simplification due to urban expansion, and shortened flowering periods, constraining floral diversity and nectar availability. These findings align with Dekebo et al. (2018) who documented the dominance of aldehydes and esters in Korean honeys primarily derived from acacia, chestnut, and jujube, further supporting the interpretation of a restricted floral base underpinning honey production in Korea.

In Uganda, contrasting patterns highlight differential land-use pressures. Amuru, characterized by woodland savanna and mixed rural landscapes (Nuwategeka and Nyeko, 2019), exhibited modorate chemical diversity. The VOC profile of Amuru honey reflects reduced floral abundance despite its woodland savanna, which naturally supports a diverse range of flowering plants (Cardoso et al., 2026). The lower diversity and altered composition of volatiles in Amuru is linked land conversion and habitat loss which limits nectar availability, signaling early ecological degradation in this savanna region. Laloyo and Tabitha (2022) reported that deforestation for charcoal production has reduced native vegetation, limiting nectar-producing plant availability and diversity. Bushenyi displayed the highest VOC richness and Shannon diversity, consistent with its heterogeneous highland agroecosystem comprising forest remnants, perennial crops, and mixed farming (Whitney et al., 2018). This chemical complexity serves as an ecological indicator of floral stability, highlighting sustained nectar availability and diverse plant resources that support resilient bee foraging and ecosystem health. In contrast, Wakiso, one of the most urbanized districts in Uganda (Kamukama et al., 2025), exhibited low chemical diversity with dominance of a few alcohols and monoterpenoids, reflecting floral homogenization from urbanization and small-scale monocropping. The prevalence of banana cultivation further restricts nectar sources, causing bees to forage repeatedly on chemically similar plants. Consequently, limited plant secondary metabolites produce simplified, repetitive honey VOC profiles with lower richness and Shannon diversity compared to less disturbed agroecosystems, highlighting the sensitivity of honey volatiles to land-use and ecological pressures.

In Indonesia, ecosystem-specific threats were also evident. Java, the most densely populated and intensively managed island, exhibited reduced VOC richness and evenness. This is inked to urbanization and agricultural intensification (Firman, 2017). Sumbawa, although situated within open tropical landscapes renowned for high floral diversity, exhibited relatively low VOC richness. This reduction in VOCs is associated with declining floral diversity, driven by ongoing land-use changes and climate variability, which threaten to simplify the region's previously diverse plant communities (Juliawati et al., 2025). Borneo, where honey VOC profiles exhibit relatively high levels, reflects the complexity of forest, wetland, and agroforestry ecosystems, indicating a moderately stable and diverse ecological environment. However, despite the well-recognized floral complexity of Borneo's forest, wetland, and agroforestry ecosystems, the current VOC levels in the honey do not fully reflect the expected abundance and compositional complexity. This reduced chemical expression may be associated with ongoing land-use changes, as multiple reports have documented extensive deforestation, plantation expansion, and habitat fragmentation across the region, potentially constraining nectar diversity and limiting the transfer of diverse secondary metabolites into honey (Gaveau et al.,

2016). The loss of these forested systems would likely eliminate specialized VOC markers associated with forest and wetland flora.

Collectively, these findings indicate that urbanization, agricultural intensification, and forest loss are key threats to floral resources across all sampled regions. However, it is important to note that in this study, direct vegetation surveys or quantitative floral diversity indices (e.g., Shannon index) were not measured at the sampling sites. Instead, references to "floral diversity" were inferred indirectly from the diversity and complexity of the detected VOC profiles, supported by existing literature linking honey volatile composition to botanical origin and surrounding vegetation heterogeneity.

3.6. Conservation and restoration priorities based on chemical diversity pattern

Honey VOC profiles not only identify conservation priorities but also guide ecological rehabilitation strategies aimed at increasing floral diversity (Ilić et al., 2024). The high chemical complexity and distinct VOC signatures observed in tropical honeys from Uganda and Indonesia indicate ecosystems with rich functional floral diversity that should be prioritized for protection. For example, areas such as Bushenyi, characterized by elevated VOC richness and the presence of compounds regarded as tentative marker compounds, represent biochemical hotspots where maintaining forest remnants, mixed farming systems, and diverse perennial crops is essential to sustain pollinator-driven ecosystem services.

At the same time, VOC patterns can signal where rehabilitation is urgently needed (Ilić et al., 2024). Regions showing reduced VOC richness or dominance of a few compound classes reflect floral simplification linked to land-use change, monoculture expansion, or urbanization. In such landscapes, restoration should prioritize re-establishing native flowering species, diversifying cropping systems, protecting forest edges, promoting pollinator-friendly land management, and incorporating social networking as a strategy to sustainably balance the needs of humans, the environment, and future generations (Wulandari et al., 2025). Lapinskienė et al. (2025) highlighted the importance of sustainable agricultural practices, this suitably strengthens the ecosystem stability and VOC diversification. Island ecosystems in Indonesia, where localized VOC markers are vulnerable to fragmentation, require targeted reforestation and agroforestry diversification to preserve unique biochemical signatures. Such reforestation not only enhances the availability of VOCs but also improves overall environmental quality (Siregar et al., 2025).

In temperate systems such as Korea, comparatively simpler VOC profiles highlight the need to enhance seasonal floral continuity through habitat restoration and the introduction of diverse native nectar plants. Overall, integrating VOC-based monitoring with conservation and rehabilitation planning provides a science-based framework for increasing floral diversity, strengthening ecological resilience, and sustaining honey authenticity and ecosystem integrity across climatic regions.

3.7. Future research directions

3.8.1. Seasonal and temporal variability of VOC profiles

Seasonal dynamics are likely to play a critical role in shaping honey VOC composition through shifts in floral availability and foraging behavior (Burkle and Runyon, 2019). As the present study reflects a specific flowering window, future research should incorporate multi-seasonal and multi-year sampling frameworks to capture temporal variability and improve the robustness of ecological interpretations. Integrating phenological data (e.g., flowering calendars, bloom intensity) would enable more precise linkage between VOC profiles and plant sources. Such approaches would also facilitate the identification of stable (core) versus seasonal (transient) VOC markers, thereby enhancing the generalizability and ecological relevance of VOC-based discrimination models.

3.7.1. Confirmation of tentative marker compounds

While this study identified several compounds as tentative marker compounds, their ecological assignment remains inferential. Future work should prioritize analytical confirmation using authentic standards to validate compound identities and improve chemical accuracy. In addition, coupling VOC profiling with melissopalynological analysis (pollen identification) and detailed vegetation surveys would allow direct quantification of floral diversity and strengthen the linkage between specific VOCs and their botanical origins. This integrative approach would enable more reliable differentiation between ubiquitous and region-specific markers, and provide a stronger ecological basis for interpreting VOC diversity in relation to floral diversity indices.

3.7.2. Strengthening ecological validation frameworks

To further advance the use of honey VOCs as ecological indicators, future studies should adopt multi-disciplinary validation strategies that combine chemometrics, field ecology, and botanical analysis. This includes correlating VOC richness with quantitative diversity indices (e.g., Shannon index derived from vegetation or pollen data), as well as incorporating land-use and environmental variables (e.g., degree of urbanization, agricultural intensity, forest cover). Such integrative datasets would improve model interpretability, reduce reliance on indirect inference, and support the development of standardized frameworks for ecological monitoring using honey VOCs.

4. Conclusion

This study demonstrates that honey VOC profiles systematically reflect ecosystem type, climate, and geographical context, confirming honey as an integrative reservoir of botanical and environmental information. Korean honeys exhibited aldehyde- and ester-dominated signatures consistent with cooler climates, shorter flowering periods, and dependence on a relatively limited range of temperate floral resources. In contrast, Ugandan and Indonesian honeys were enriched in alcohols and monoterpenoids, reflecting warmer climates, prolonged nectar flow, higher floral diversity, and more complex ecological interactions typical of tropical systems. Within tropical regions, additional differentiation was evident among savanna, highland agroecosystems, forest, and agroforestry mosaics, demonstrating the sensitivity of VOC composition to fine-scale ecological structure. The predominance of (*Z*)-linalool oxide (119) in Ugandan lowland honeys, 2-methylheptan-3-ol (26) in highland Bushenyi samples, and island-specific markers such as DL-menthol (127), methyl salicylate (73), and 2-furfural (82) in Indonesian honeys reflects localized floral assemblages and vegetation structure. Notably, Bushenyi exhibited high VOC richness and Shannon diversity, ecologically indicating floral complexity and relative landscape stability within its heterogeneous highland agroecosystem. Multivariate analyses (PCA and PLS-DA) robustly captured these patterns, clearly separating honeys by geographical and ecological origin through a limited set of high-impact VOCs. Because honey integrates nectar collection across wide foraging ranges and extended flowering periods, its VOC profile functions as a biochemical archive of surrounding ecosystems. Consequently, honey VOC profiling provides a scalable, non-invasive tool for ecological monitoring, authenticity verification, conservation planning, and sustainable land-use management across temperate and tropical landscapes.

CRediT authorship contribution statement

Kenneth Happy: Writing – review & editing, Writing – original draft, Visualization, Validation, Data curation, Conceptualization. **Kyeong-OK Choi:** Writing – review & editing, Validation, Methodology, Formal analysis, Data curation. **Yeongjun Ban:** Writing – review & editing, Visualization. **Joyce Adokorach:** Writing – review & editing,

Methodology, Data curation. **Hongmin Choi:** Writing – review & editing, Resources, Methodology, Data curation. **Endang Rahmat:** Writing – review & editing, Resources, Methodology, Formal analysis, Data curation. **Joyce Mudondo:** Writing – review & editing, Methodology, Data curation. **Islan Nor:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Youngmin Kang:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

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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.ecolind.2026.114910.

Data availability

Data will be made available on request.

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