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A multi-omics strategy to reveal the effect of raw meat differences on volatile organic compounds and microbial communities of fermented sour meat

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ABSTRACT

This study elucidates the physicochemical, volatile, and microbial characteristics of sour meats fermented from beef (BSM), goose (GSM), pork (PSM), and yak (YSM). The results showed all samples reached a similar pH (approximately 3.9), though color and texture varied notably. E-nose analyses of the four sour meat revealed significant differences. GC-MS, and GC-IMS analyses identified 104 and 41 volatile compounds, including 42 and 11 differential VOCs (VIP >1, $p < 0.05$). Fermentation markedly reshaped the microbiota, with *Firmicutes* dominating and *Lactobacillus* emerging as the principal genus alongside group-specific co-dominants. Spearman analysis revealed positive correlations between *Lactobacillus* and key flavor compounds. PICRUSt2 indicated microbial activities influence the metabolites of sour meat products through amino sugar and nucleotide sugar metabolism, glycolysis/gluconeogenesis, pyruvate metabolism, and starch and sucrose metabolism. These findings provide an evidence-based foundation for optimizing the production process and improving the quality of the product.

1. Introduction

Sour meat, a delicacy traditional in the Southwest China, is appreciated for its nutritional attributes and, most of all, for its peculiar flavor (Y. Zhang, Hu, Xie, & Wang, 2020). Typically, sour meat preparation requires mixing raw meat with salt, rice, and various seasonings, followed by natural fermentation under anaerobic conditions leading to its characteristic flavor. Lactic acid bacteria (LAB) and yeasts that naturally occur in the raw ingredients drive a spontaneous fermentation. These microbes are essential for developing fermented meat's defining sensory properties, including firm texture, balanced acidity, and complex ester-rich aroma profile (Lv et al., 2021). To present, researches on fermented meat products have largely focused on pork-based systems, reflecting their dominance in both traditional and industrial production. Existing literature on sour meat have primarily focused on the optimization of fermentation parameters, such as temperature, salt concentration, and processing conditions, as well as their effects on microbial succession and flavor formation (He et al., 2020; Lv et al., 2019; Wang et al., 2022a). However, the consequences of different raw meat sources on the flavor profile and microbial communities remains underexplored, underscoring a key knowledge gap in sour meat research.

The type of raw meat is a critical factor in fermented meat products because its nutrient composition, muscle structure, and fat content create distinct ecological niches that shape the associated microbial communities (Song et al., 2020). As a nutrient-rich substrate with high water activity and near-neutral pH, raw meat supports the growth of diverse food-associated microorganisms, whose metabolic activity ultimately influences the nutritional, sensory, quality, and safety attributes

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of the final product (Patra et al., 2016; Tamang et al., 2016).

With respect to sensory attributes, the role of the raw meat is particularly evident in flavor formation. The complex flavor profile of sour meat results from microbial and enzymatic metabolism, which generates compounds such as organic acids, alcohols, esters, and free amino acids. These compounds arise from processes including autoxidation, proteolysis, lipid hydrolysis, and the metabolism of carbohydrates and amino acids (Guo et al., 2024). The impact of raw meat on the flavor profile of the final product has been evidenced in a previous study of ours that compared pork and goose (Zhao et al., 2023). This study expands those observations to beef and yak meats (Li et al., 2023; Zhang, Lu, & Chen, 2023), recognized as low in fat and rich in proteins and essential nutrients. Including meats perceived as alternatives to pork and goose as raw materials for sour meat production is particularly appealing, as such comparisons can provide valuable insights into the impact of quality differences on consumer preferences.

To comprehensively grab how different raw meats affect the flavor profile of fermented products, this study employed E-nose, along with GC-IMS and GC-MS. In addition, 16S ribosomal RNA gene analysis was used to examine the impact of different raw meats on the microbial communities characterizing the final products. By relating meat-specific characteristics to microbial dynamics and sensory outcomes, the results help identify key factors underlying quality differences and provide a scientific basis for improving traditional processing practices and developing sour meat products with enhanced nutritional and sensory properties.

2. Materials and methods

2.1. Preparation of the samples

The samples were prepared by slightly modifying the method of Zhao et al. (Zhao et al., 2023). Fresh pork (*Sus scrofa domesticus*), goose (*Anser cygnoides domesticus*), beef (*Bos taurus*), and yak (*Bos grunniens*) were purchased in local markets in Chengdu, Sichuan (China). For each meat type, three independent batches of raw meat were obtained and processed as biological replicates. Visible fat, connective tissue, and skin were trimmed before use. Lean portions of pork, goose, beef, and yak meat were prepared by trimming and cutting into uniform pieces (0.6 cm × 5 cm × 3 cm, with a weight around 200 g). The meat was salted and marinated at 4 °C for 2 h, after which pepper, fried crushed glutinous rice, and steamed glutinous rice were incorporated. The mixture was transferred to airtight jars and subjected to natural fermentation at room temperature (approximately 20–25 °C) for 45 days. The proportion of added ingredients was adjusted to each sample's mass. Each biological replicate was subjected to independent natural fermentation under identical controlled conditions. Before any further analysis the samples were stored at −80 °C. The four types of sour meat were prepared in triplicate to ensure reproducibility. For each biological replicate, three technical measurements were performed, and the averaged values were used for subsequent statistical analyses.

2.2. Physical and chemical analyses

2.2.1. pH and color analysis

For the analysis of pH, 2 g of minced sour meat were put into a 50 mL beaker together with 20 mL of distilled water, and mixed thoroughly at 7000 rpm for 2 min with a digital T25 (ULTRA-TURRAX®, IKA, Germany) homogenizer. The homogenate's pH was measured using a Five Easy Plus FE28 pH meter (Mettler Toledo, China). The color parameters (L^*, a^*, and b^*) of sour meat samples from pork, goose, beef, and yak were measured using a CR-400 colorimeter from Konica Minolta (Tokyo, Japan). Measurements were taken at three distinct points on the cross-sectional surface after exposing the samples to air at 4 °C for 30 min.

2.2.2. Textural analysis

The texture properties of the four types of meat were analyzed using a TA-XT Plus texture analyzer from Stable Micro Systems (UK) according to the method suggested by Lv et al. (Lv et al., 2019), partially modified as follows: the speed during the test and during the pre and post-test was 2.0 mm/s; first and second compressions were 5 s apart; and the threshold of the applied force was set to 10 g. The type of probe used was P/50, and the compression ratio was set at 30 %. The texture characteristics of the sour meat were expressed in terms of chewiness, cohesiveness, hardness and springiness. Moisture content was not normalized prior to texture measurements. All samples were analyzed in their fermented state under identical processing conditions to reflect realistic product characteristics.

2.3. Analysis by E-nose

A FOX 3000 E-nose from Alpha MOS (Toulouse, France) allowed assessing the sour meat's odor profile, according to the method by Zhao et al. (Zhao et al., 2023). The E-nose system consists primarily of three chambers equipped with metal oxide sensors and a total of 18 gas sensors (Table S1).

Each analysis required 0.25 g samples, placed into 10 mL headspace vials. The samples were then incubated at a constant temperature of 70 °C for 5 min to fully release their VOCs. Subsequently, the sample was manually injected into the system for E-nose analysis. The measurement process was strictly controlled to be completed within 120 s. After each measurement, the rinsing phase lasted 240 s and was designed to effectively clean and reset the sensor array to avoid cross contamination between samples. Five replicate observations were performed for each sour meat sample. Considering the stabilization characteristics of metal oxide sensors, the initial responses may exhibit minor fluctuations. Therefore, three measurements with consistent signal intensity and response profiles were selected from the five replicates, and used for subsequent analyses.

2.4. Analysis by GC-MS

The analysis of the VOCs in the samples of fermented meat was conducted by HS-SPME (microextraction by headspace solid-phase), in agreement with the method by Zhong et al., partially modified (Zhong et al., 2022). In brief, 5 g of minced sour meat were placed in 20 mL headspace vials for volatile compound analysis. The HS-SPME procedure involved using a 50/30 μm DVB/CAR/PDMS extraction fiber, pre-equilibrated at 80 °C for 10 min, extracted for 30 min at 80 °C, and then transferred at 230 °C for 2 min to the injection port. A TG-WAXMSB chromatographic column (0.25 μm, 30 m × 0.25 mm) was employed in non-split mode, with 230 °C of inlet temperature. The temperature of the column was kept for 3 min at 40 °C, then brought to 210 °C at 5 °C/min and then kept constant for 5 min. The carrier gas was helium (purity >99.999 %), at a rate of flow of 1.0 mL/min. The energy of the source for electron ionization was set to 70 eV, with temperatures of the ion source and of the transmission line of 250 °C and 230 °C, respectively. The masses were scanned between 40 and 500 m/z, with a scan time of 2 s, operating in full scan mode. The retention indices of the compounds were calculated relative to standard alkanes (C8-C26), and compounds were identified when the match score exceeded 90 % in the NIST 11 library.

2.5. Analysis of GC-IMS

By following the methodology of Zhao et al. (Zhao et al., 2023), samples of 0.25 g were incubated at 50 °C for 10 min in a vial with a 20 mL headspace. With a heated syringe, a headspace sample of 100 μL was introduced into the injector (splitless mode), set at 65 °C. The chromatographic column was kept at 60 °C, while the drift tube was maintained at 45 °C, with a flow rate of the drift gas at 150 mL/min. Nitrogen

with a purity higher than 99.999 % was employed as the carrier gas. The flow rate program of the gas chromatography (GC) column was set as follows: 5 min at 2 mL/min, 10 min at 10 mL/min, then 5 min at 15 mL/min, 10 min at 50 mL/min, and finally 10 min at 100 mL/min. N-ketones (C4-C9) were used as references for the calculation of retention indices (RI) of VOCs, following established methods (Liu et al., 2023; Q. Wang et al., 2022b). VOCs' accurate identification was achieved by comparison of the ion drift time and RI with the corresponding values of the GC-IMS library's standards. The relevant formulae were obtained from Guo et al. (Guo et al., 2022). Quantitative analysis was conducted based on peak signal intensities, with each sample analyzed once.

2.6. 16S rRNA analysis

By using the method described by Zhang et al.(Q. Zhang, Zeng, Tang, Jiang, & Zhu, 2024b) as a reference, slightly modified. 0.25 g of sour meat from pork, goose, beef, and yak was collected under aseptic conditions, immediately placed into sterile cryovials, rapidly frozen in liquid N_2, and kept at −80 °C. The extraction of total DNA from genome was obtained with the E.Z.N.A.® Soil DNA Kit (Omega Bio-tek, Norcross, GA, USA), by relying on the protocol of the manufacturer. The bacterial 16S rRNA gene was targeted at the V3-V4 hypervariable region using primers 338F (5′-ACTCCTACGGGAGGCAGCAG-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′). PCR amplification was performed with an AT100 Thermal Cycler (Bio-Rad, USA). The obtained amplicons were purified, quantified, and combined in equimolar amounts prior to paired-end sequencing on the Illumina MiSeq platform (PE300/PE250; Illumina, San Diego, USA) following the manufacturer's standard procedures provided by Majorbio Bio-Pharm Technology Co., Ltd. (Shanghai, China).

The raw reads were demultiplexed and quality-filtered using *fastp* (v0.20.0), and overlapping reads were merged with *FLASH* (v1.2.7). After quality optimization, sequence variants were inferred with the DADA2 pipeline to correct for sequencing and amplification errors, generating high-resolution Amplicon Sequence Variants (ASVs). The microbiological data was analyzed by online tool (https://cloud.majorbio.com). Non-metric multidimensional scaling (NMDS) analysis was employed to test the β-diversity of microbial communities. Linear discriminant analysis Effect Size (LEfSe) analysis (LDA>2, $p < 0.05$) was used to spot taxa significantly different in microbial concentration at the phylum and at the genus levels. PICRUSt2 (version 2.2.0) software was used for 16S functional prediction analysis.

2.7. Statistical analysis

All statistical analyses were conducted using the R language (version 4.4.1). Prior to univariate statistical analysis, data were normalized using the Box-Cox transformation (Box & Cox, 1964). Differences among groups were evaluated by one-way analysis of variance (ANOVA), with statistical significance set at $p < 0.05$. Multivariate statistical analyses involving GC-MS and GC-IMS datasets were performed using Principal component analysis (PCA) and Partial Least Squares Discriminant Analysis (PLS-DA) through the online platform MetaboAnalyst 6.0. These datasets were normalized and appropriately scaled before modeling. Important features were extracted based on Variable Importance in Projection (VIP) scores, in combination with univariate statistical significance, to minimize confounding effects arising from highly redundant information. Data visualization and integrative analyses, including Venn diagrams, radial column charts, heatmap and correlation network analyses, were conducted using online tools (https://www.omicstudio.cn). Multiple Factor Analysis (MFA) was employed R language (version 4.4.1) to integrate and compare datasets derived from GC-MS and GC-IMS by projecting them into a common multidimensional space, thereby enabling the exploration of relationships among variables across datasets.

3. Results

3.1. Physicochemical analysis

Fig. 1 presents the color, pH, and textural properties (hardness, springiness, cohesiveness, chewiness) of sour meat fermented from different raw meats. Among the four groups, no significant differences were identified in pH values. The L* values of PSM did not differ significantly ($p > 0.05$) from those of GSM, whereas they were significantly higher ($p < 0.05$) than those recorded for BSM and YSM. The a^* values registered on BSM samples were higher ($p < 0.05$) than the a^* values of the other three groups. BSM showed the highest b^* values, followed by PSM and GSM, while YSM showed the lowest b^* values. Regarding texture, PSM had the greatest hardness and chewiness, whereas BSM exhibited the lowest hardness and chewiness. In contrast, BSM and YSM showed greater springiness and cohesiveness than PSM and GSM.

3.2. Analysis of sensory differences in sour meat fermented from different raw meats by E-nose

ANOVA showed that the responses of 10 E-nose sensors were significantly ($p < 0.05$) different. The sensors were P10/2, T30/1, PA/2, T70/2, P40/2, P30/1, P30/2, T40/2, TA/2, and T40/1. The response data from these sensors are presented in Table S1. These sensors are mainly sensitive to alcohols, aldehydes, hydrocarbons, aromatic compounds, and general air-quality-related volatiles, indicating substantial differences in overall odor composition among sour meats fermented from different raw meats. The results from these 10 sensors were used as the database for the rPCA model. Fig. 2 reports the results. In the rPCA score plot (Fig. 2(a)), the first PC represented the 91.7 % of the total variability, distinguishing with effectiveness the four experimental groups. PSM appeared at negative scores along PC1, while GSM, BSM, and YSM showed positive scores. Besides, GSM, BSM, and YSM were separated along PC2. The loadings plot (Fig. 2(b)) showed PSM had higher response values of P30/2, T70/2, PA/2, P30/1, and T30/1 but lower response values of TA/2. T40/1, T40/2, and P10/2 compared with the other groups.

3.3. Analysis of variations in the flavor characteristics of sour meat produced from different raw meat types

3.3.1. Comprehensive characterization of VOCs profiles by GC-MS and GC-IMS

Among the 104 volatile organic compounds (VOCs) identified by GC-MS, it was possible to identify 4 acids, 11 alcohols, 10 aldehydes, 52 esters, 9 hydrocarbons, 6 ketones, and 16 compounds belonging to other classes (Table S2). Among the 41 VOCs characterized by GC-IMS, there were 1 acid, 10 alcohols, 3 aldehydes, 14 esters, 4 ketones, and 9 others (see Table S3). The variations in the VOCs characterized with GC-MS and GC-IMS are shown in Fig. 3. Together, the two methods identified a total of 140 VOCs, but only five VOCs (1-hexanol, 1-pentanol, limonene, hexanal, and acetic acid) were detected by both (Fig. 3(b)).

The proportion of VOC categories in the four types of sour meats, identified with GC-MS (Fig. 3(c)) and GC-IMS (Fig. 3(d)), illustrates the characteristics of each technique. Esters, aldehydes, and alcohols were the predominant VOCs across all sour meat types in both analyses. In GC-MS analysis, GSM had the highest levels of esters (86.79 %) and aldehydes (10.71 %), while PSM had the highest levels of alcohols (12.01 %) compared with the other groups. YSM contained esters (85.64 %) and alcohols (6.46 %) at levels second only to GSM and PSM, respectively (Fig. 3(c)). In GC-IMS analysis, GSM showed the highest levels of esters (39.89 %) and aldehydes (4.20 %), whereas PSM had the lowest. BSM exhibited the highest alcohol content (32.55 %), while PSM had the lowest.

The heatmaps illustrate the differences in VOCs levels identified with

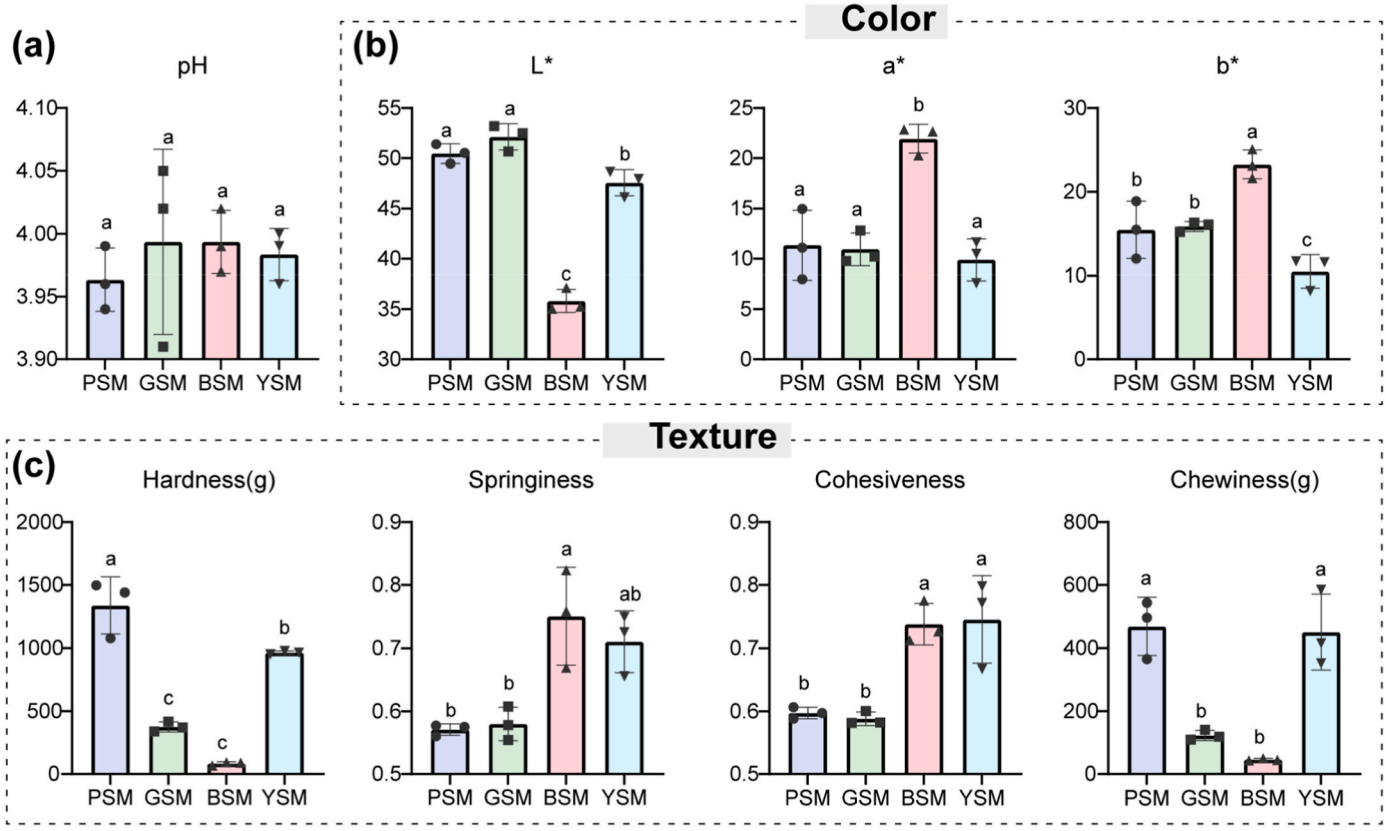

Fig. 1. pH (a), color (b), and texture (c) of fermented meat from pork (PSM), goose (GSM), beef (BSM), and yak (YSM).

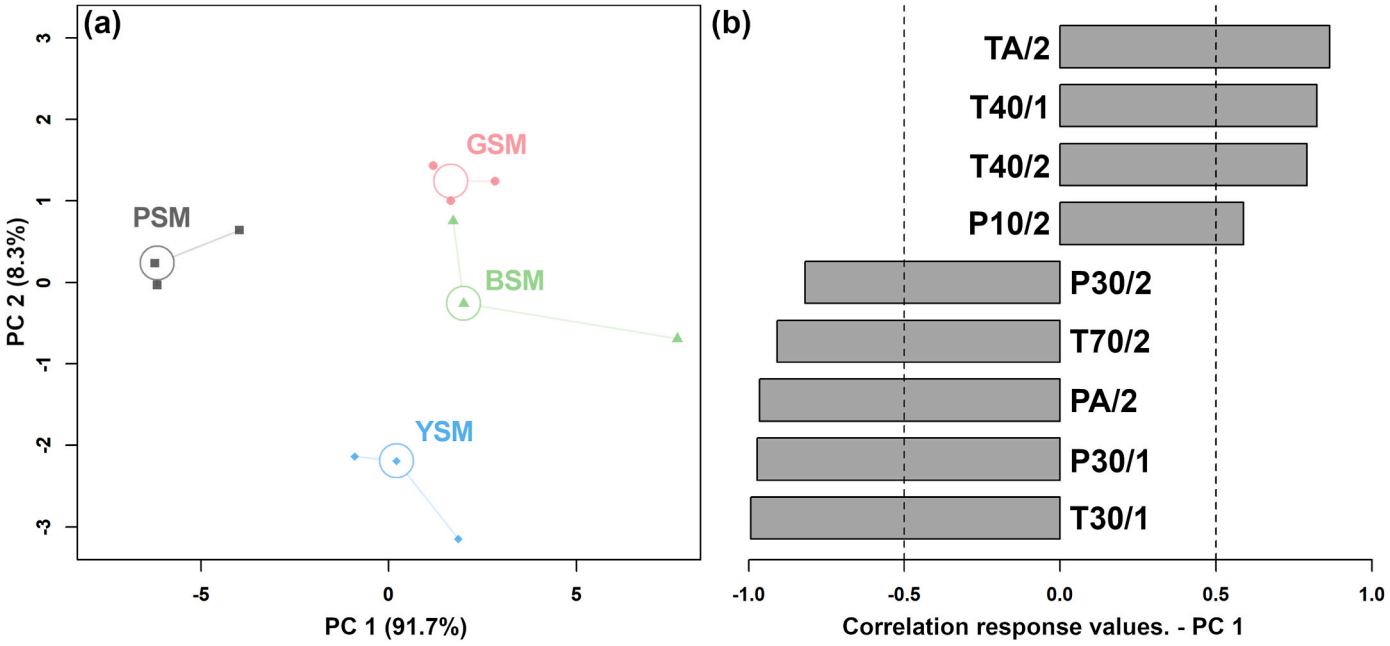

Fig. 2. Model rPCA (a) calculated on E−nose responses. How the responses are correlated to their significance in determining PC 1 is reported in loading plots (b). Bars shown in gray represent statistically significant correlations ($p < 0.05$).

GC-MS and GC-IMS, as depicted in Fig. 3(e) and (f), respectively. The colors in the heatmap are a representation of peaks' intensities after normalization, where red is used for high values while blue for low values. Overall, VOC levels in sour meats fermented from different raw meats were clearly distinct according to both analyses.

3.3.2. Screening of characteristic flavor metabolites of sour meat fermented from different raw meats based on GC-MS and GC-IMS

To differentiate the compounds in the four types of sour meat detected by GC-MS and GC-IMS, PCA models were calculated using compounds showing significant differences in pairwise comparisons between PSM, GSM, BSM, and YSM. As depicted in Fig. 4 (a) and 4(d),

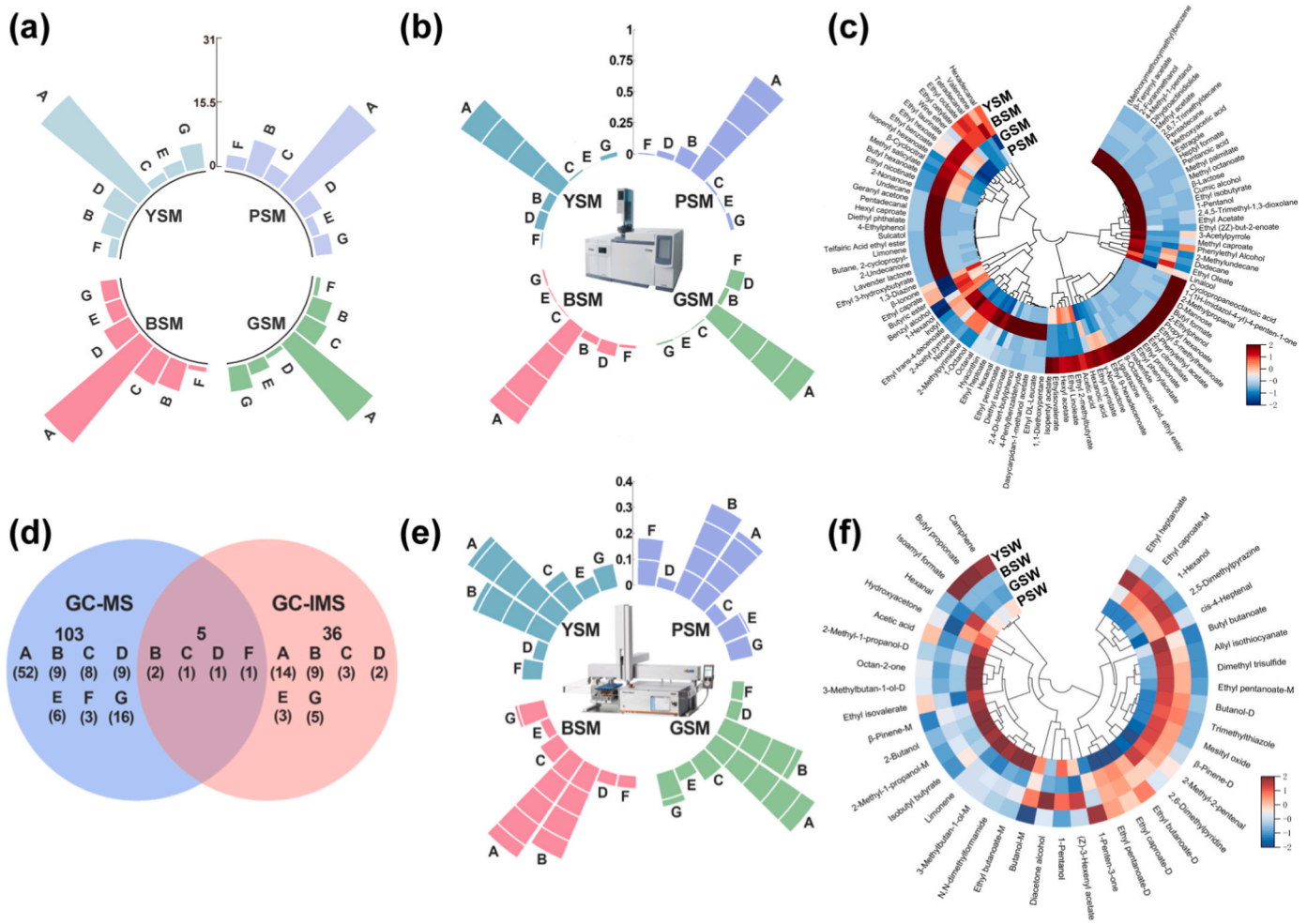

Fig. 3. Number (a) of VOCs pertaining to the different molecular classes identified by GC-MS in the samples from beef (BSM), goose (GSM), pork (PSM), and Yak (YSM) meat. Number of VOCs identified by GC-IMS and GC-MS represented as Venn diagram (b). Radial column chart shows the percentage of each VOCs type detected in the four types of sour meats relying on GC-MS (c) and on GC-IMS (d). Here, esters (A), alcohols (B), hydrocarbons (C), aldehydes (D), ketones (E), acids (F), and others (G), are reported. Heatmap of VOCs' relative content in the four types of sour meats using GC-MS (e) and GC-IMS (f).

The PCA model constructed from the GC-MS data revealed a distinct separation among the sour meat samples produced from different raw meats, while the PCA model based on GC-IMS showed partial overlap among samples.

Models based on PLS-DA, with a higher capability of prediction, allowed to obtain variable importance in projection (VIP) values for in-depth analysis. As shown in Fig. 4(b) and (e), the fermented samples obtained from the different sources showed clear differences in the PLS-DA model calculated from GC-MS and GC-IMS data. The PLS-DA 's VIP plots were allowed assessing how each individual variable contributed to the groupings. Typically, compounds having VIP values above 1 are considered key contributors to distinguishing among groups (Wang et al., 2022a). As Fig. 4 (c) shows, 42 differential VOCs characterized by a VIP>1 were identified. Most of these VOCs were present in the highest concentrations in BSM, with 21 VOCs exhibiting the greatest levels, while most were at the lowest levels in PSM. As illustrated in Figs. 4(f), 11 differential VOCs with VIP>1 were detected by GC-IMS, including 1-hexanol, ethyl hexanoate-M, ethyl heptanoate, mesityl oxide, butanol-D, acetic acid, dimethyl trisulfide, allyl isothiocyanate, β-pinene-D, cis-4-heptenal, and butyl butanoate. Most of these differential VOCs were present in the highest levels in GSM, particularly ethyl hexanoate-M, mesityl oxide, butanol-D, dimethyl trisulfide, allyl isothiocyanate, β-pinene-D, and butyl butanoate. In contrast, the lowest concentrations of most differential VOCs were found in PSM, including 1-hexanol, ethyl hexanoate-M, ethyl heptanoate, mesityl oxide, butanol-D, β-pinene-D, cis-4-heptenal exhibiting the lowest concentration based on GC-IMS data.

3.3.3. *Assessment of the discriminative power of various detection methods using MFA*

An examination of the previous sections suggested that combining GC-MS and GC-IM datasets might lead to a more comprehensive approach for the characterization of the volatile profiles of different sour meat samples. To verify this, MFA was used to compare the above described four methods E-nose, GC-MS, GC-IMS, and GC-MS and GC-IMS combined, in terms of ability to distinguish the volatile profiles of the meat fermented from the different raw meats selected for the present work. Extending PCA, MFA is particularly effective for analyzing the relationships among diverse analytical methods applied to the same dataset, thus providing insight into the discriminating ability of various detection methods.

As Fig. 4 (g) shows, the resulting MFA's coordinates are represented by the centroid. The projections of variable contributions are represented by the points connected to the centroid so that projections closer to the centroid highlight similarities between the descriptions. The GC-MS and GC-IMS combination was the closest to the centroid for most samples, suggesting a more comprehensive representation of volatile characteristics. Notably, for all samples the discriminating ability of GC-IMS was higher, or at least close to, the one of GC-MS. Projections of all variables from the four analytical methods on the first dimension (Dim1)

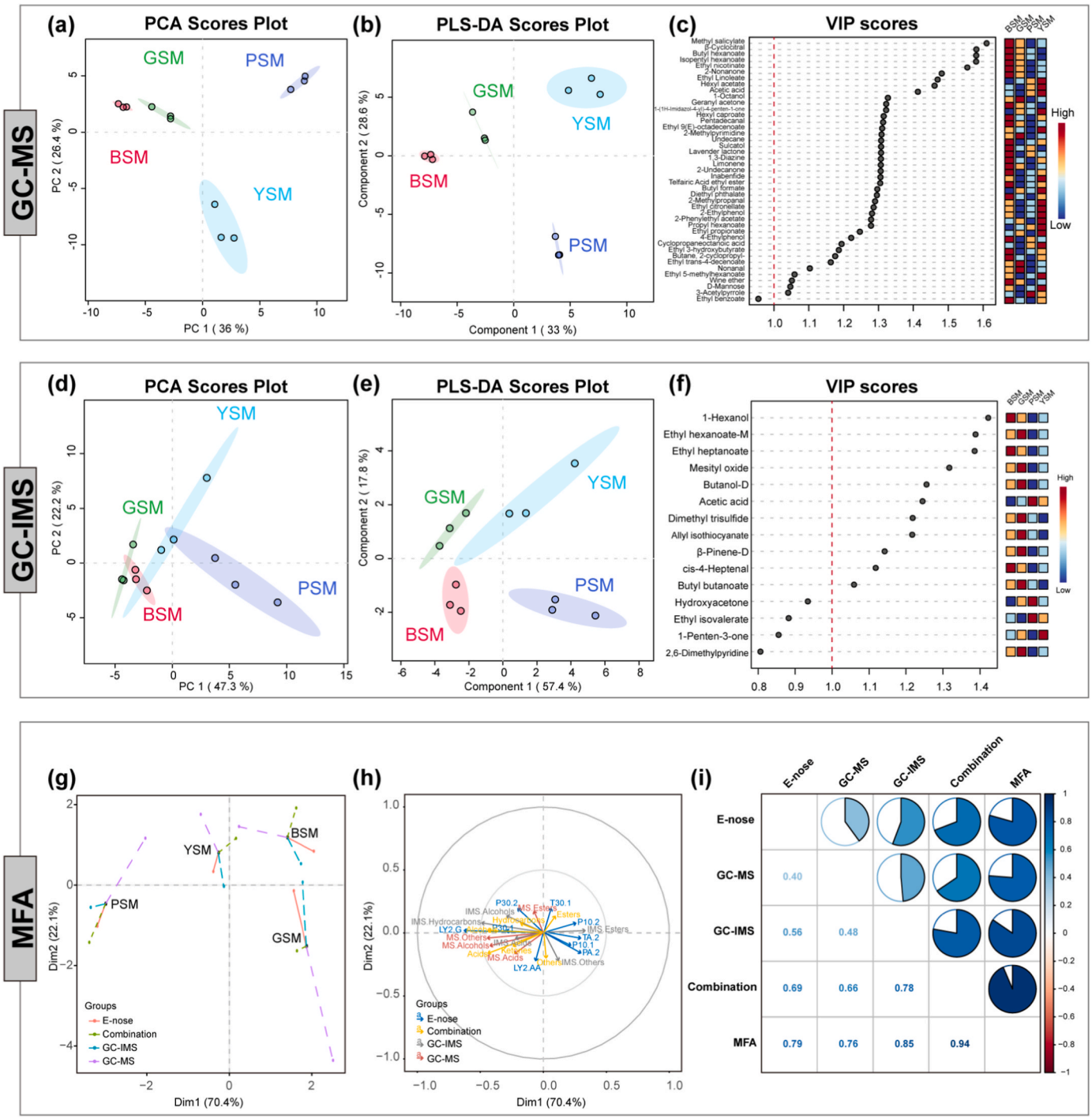

Fig. 4. Plots showing the PCA (a), the PLS-DA (b), and the VIP (c) scores of the all samples based on GC-MS. PCA (d), PLS-DA (e), and VIP (f) scores of the all samples based on GC-IMS. Positions of the projected points representing the MFA variations (g). Projections of all variables in MFA (h). RV coefficients between variable sets of detection methods (i). GC/MS and GC-IMS combined. Here, X include VOCs pertaining to the classes of esters, alcohols, hydrocarbons, aldehydes, ketones, acids, and others detected GC-MS. Conversely, Y include VOCs pertaining to the classes of esters, alcohols, hydrocarbons, aldehydes, ketones, acids, and others detected by GC-IMS.

and the second dimension (Dim2) are shown in Fig. 4 (h). The Dim1 (70.4 %) was strongly correlated with LY2/G, IMS-hydrocarbons, and Combination-acids, whereas the Dim2 (22.1 %) was strongly correlated with P30/2 and LY2/AA. Fig. 4 (i) represents the RV coefficients between variables from the different detection methods. Established literature suggests that RV coefficients higher than 0.7 highlight good levels of differentiation. The RV coefficient of the datasets combined was 0.94, remarkably higher than the coefficients obtained with GC-MS (0.76), E-nose (0.79), and GC-IMS (0.85), confirming the suitability of combining GC-MS and GC-IMS to discriminate sour meat samples.

3.4. Microbiological differences

3.4.1. Microbial diversity analysis and compositional differences of microbial community in the samples analyzed

The distribution of ASVs (Amplicon Sequence Variant) among the

four groups of sour meat samples before and after fermentation was shown in Venn diagrams (Fig. 5(a) and (b)). ASVs' number shared by all samples decreased from 73 before fermentation to 27 after fermentation. Among the four groups, before fermentation PSM had the greatest number of unique ASVs, whereas after fermentation the greatest number was shown by ASVs.

The changes in the microbial community abundance in the four groups of sour meat samples were further investigated. The community structures at the phylum level as well as at the genus level are presented in Fig. 5(c-f). At the phylum level, as much as 95 % of the microbiota

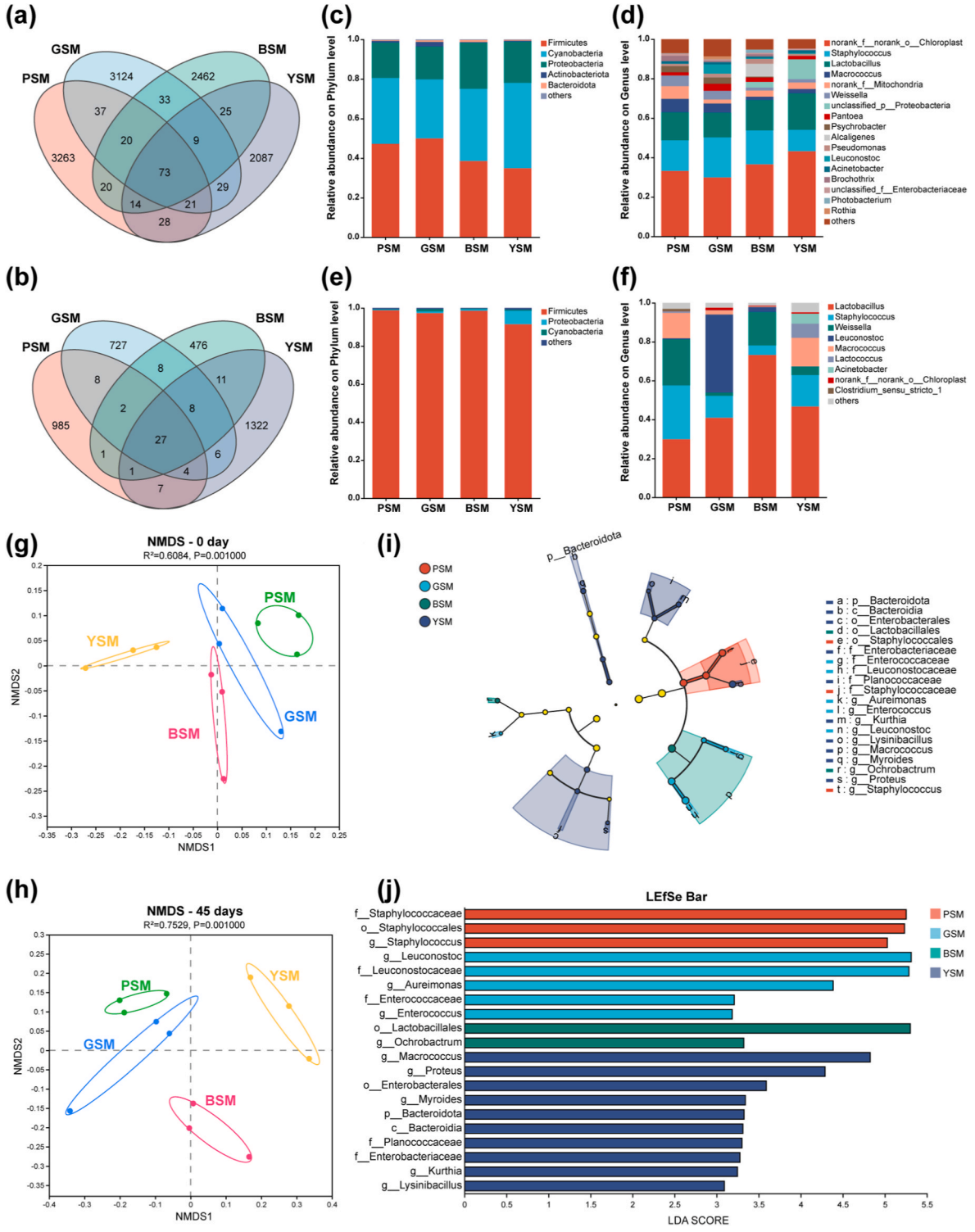

Fig. 5. Changes in microbial community in fermented sour meat produced with the four types of raw meats. microbial community's venn diagram at the ASV level on day 0 (a) and day 45 (b). The relative abundance (%) of microbial communities at the phylum level (c) and genus level (d) before fermentation and relative abundance (%) of microbial communities at the phylum (e) and genus (f) levels at the end of fermentation for four types of raw meats-fermented sour meats. NMDS of the bacteria community based on the ASV level of four sour meat on day 0 (g) and day 45 (h). Cladogram (i) and bar (j) plots of LEfSe analysis with LDA score threshold >2.0.

across all samples before fermentation was represented by *Firmicutes*, *Proteobacteria*, and *Cyanobacteria*. After fermentation, *Firmicutes* markedly increased, rising from 47.30 % (PSM), 49.97 % (GSM), 38.53 % (BSM), and 34.95 % (YSM) to 98.83 %, 97.35 %, 98.52 %, and 91.45 %, respectively. Concurrently, *Proteobacteria* and *Cyanobacteria* declined in all groups. At the genus level, notable shifts were observed between the pre- and post-fermentation stages (Fig. 5(e) and f). Before fermentation, 17 genera exhibited relative abundances greater than 1 %, with *norank_f_norank_o_Chloroplast*, *Lactobacillus*, and *Staphylococcus* mostly represented genera in all raw meats. After fermentation, the number of genera exceeding 1 % abundance declined to 11, with clear differences emerging among the four groups. PSM was dominated by *Lactobacillus*, *Staphylococcus*, and *Weissella*; GSM by *Lactobacillus*, *Leuconostoc*, and *Staphylococcus*; BSM by *Lactobacillus*, *Weissella*, and *Staphylococcus*; and YSM by *Lactobacillus*, *Staphylococcus*, and *Macrococcus*.

β-diversity describes the structure of the microbiota between the sour meats fermented from the four different raw meats. β-diversity was analyzed by NMDS based on the abundance of ASVs (Fig. 5(g) and (h)). NMDS analyses showed that all four types of sour meats could be effectively separated ($p < 0.01$) before and after fermentation, confirming distinct microbial community structures associated with different raw meat sources.

We applied LEfSe for the identification of bacterial taxa that mainly contributed to the differences among four groups (Fig. 5(i)). A total of 20 microbial clades were significantly different, when setting a threshold for LDA of 2.0, as shown in Fig. 5(j). At the level of genus, *Staphylococcus* appeared as the major bacteria of the PSM. In GSM, *Leuconostoc*, *Aureimonas*, and *Enterococcus* showed significant differences compared to the other three sour meats. *Ochrobactrum* was the principal genus of BSM. In contrast, YSM was characterized by significantly higher abundances of *Macrococcus*, *Proteus*, *Myroides*, *Kurthia*, and *Lysinibacillus* relative to the other sour meat samples.

3.4.2. Prediction of microbial function in sour meat

PICRUSt2 allowed the comparison of the predicted metabolic functions of microbial communities in sour meats fermented from different raw meats (Fig. 6). Six primary metabolic pathways were identified across all groups, as illustrated in Fig. 6(a), where metabolism is the dominant process. Within this overarching metabolic category, 12 secondary metabolic pathways were detected, among which carbohydrate metabolism was the principal pathway, excluding the global and overview maps, as shown in Fig. 6(b). Comparative analysis revealed that 14 tertiary metabolic pathways related to carbohydrate metabolism differed significantly among the four sour meat types (Fig. 6(c)). Key pathways included glycolysis/gluconeogenesis, the metabolism of amino sugars and nucleotide sugars, the metabolism of pyruvate, and starch and sucrose metabolism. Specifically, these pathways appeared to be significantly higher in PSM compared to the other three groups.

3.5. Correlation analysis

To explore how microbial activity influenced sour meat's flavor profile, the volatile compounds with VIP >1 and $p < 0.05$ detected by GC-MS and GC-IMS were correlated with the responses from E-nose sensor. The 30 most abundant microbial genera across samples fermented from different raw meats, showed in Fig. 7. Spearman correlation coefficients ($|r| > 0.6$) with significance at $p < 0.05$ were considered indicative of strong associations within the network. The line's thickness is proportional to the correlation's strength. To improve clarity, the correlations between key volatile compounds identified by GC-MS and microbial genera were additionally visualized using a correlation heatmap, which is provided in Fig. S1.

Lactobacillus showed a strong positive correlation with most volatile compounds of key importance detected by both GC-IMS and GC-MS, while showing negative correlations with butanol-D and ethyl-

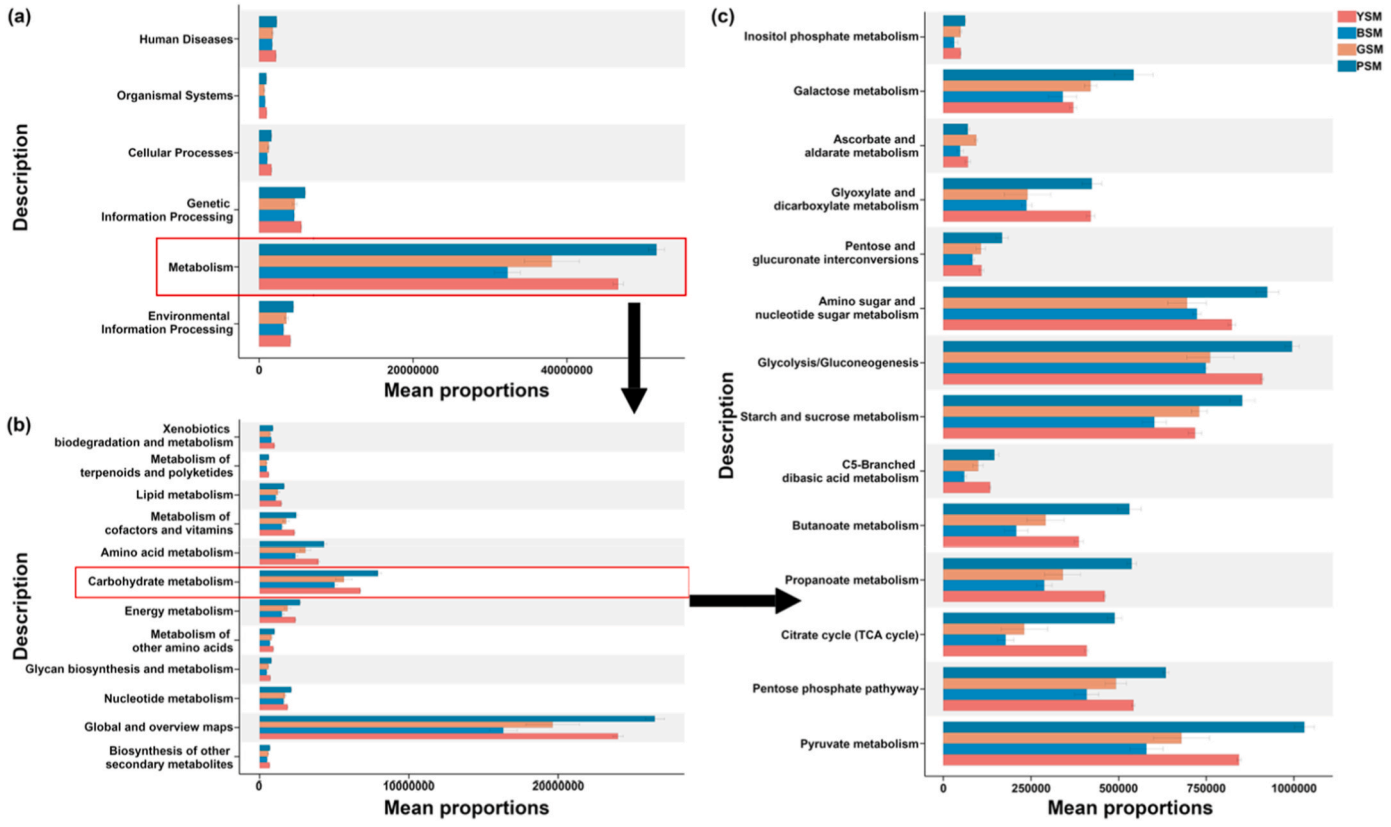

Fig. 6. Predicting the microbiological function of sour meat fermented from different raw meats. (a) metabolic pathways of primary, (b) of secondary, and of (c) the tertiary importance.

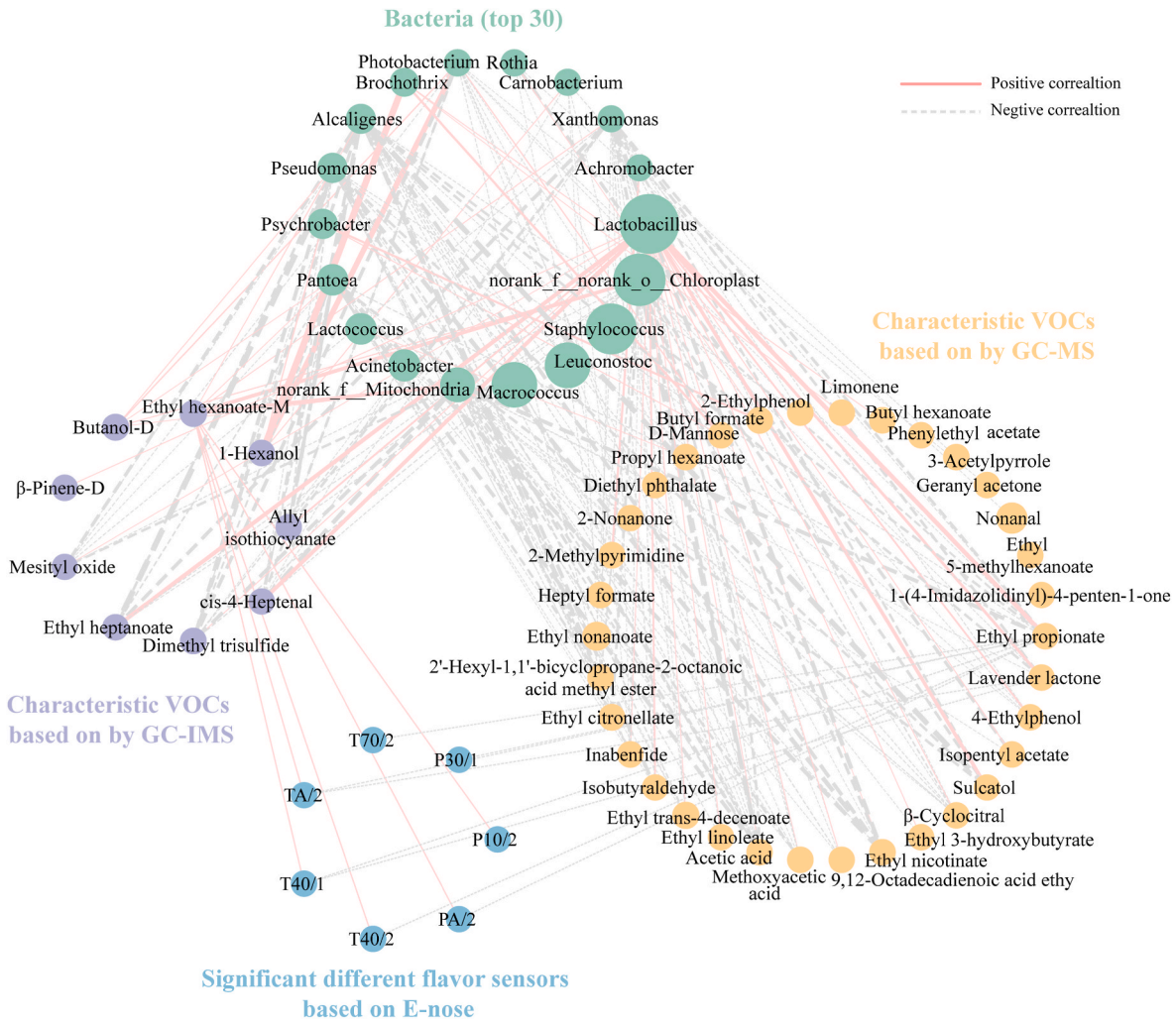

Fig. 7. Correlation network model showing the correlations between key flavor compounds characterized by GC-MS and GC-IMS with microbial genera and sensors values based on E-nose in four sour meats.

hexanoate-M. In contrast, genera like norank_f_norank_o_Chloroplast, *Pantoea*, and *Psychrobacter* showed positive correlations with butanol-D and ethyl-hexanoate-M but negative correlations with other important volatile compounds. Among the volatile compounds, ethyl-hexanoate-M exhibited a positive correlation with E-nose sensors, including P10/2, T70/2, PA/2, T40/1, and T40/2. Ethyl propionate was found to be negatively correlated to TA/1, P30/1, PA/2, T40/1, T40/2, and T70/2.

4. Discussion

Sour meat, consumed throughout Southwest China, has been popular and well known for hundreds of years because of its unique flavor and nutritional values. The highly complex flavor profile of sour meat is deeply influenced by the type of raw meat, alongside fermentation parameters and environmental factors. In fact, the raw meat shapes the composition of the food-associated microbial communities (Song et al., 2020), determining, in turn, the nutritional content, flavor compounds, overall quality, and physicochemical properties of the end product (Patra et al., 2016; Zhong et al., 2021). Currently, most of the research is focused on microbial communities (Corbo et al., 2017; Lv et al., 2019), proteins' and fat's degradation (de Almeida et al., 2018; Flores, 2018) and volatile molecules contributing to the flavor (Bis-Souza et al., 2019). This work seeks to investigate, for the first time, the microbial communities and flavor profiles in sour meats fermented from four types of raw meats combining 16S rRNA sequencing, E-nose, GC-MS and GC-IMS. From an industrial production perspective, a deep understanding of the raw meat sources is critical because such knowledge allows manufacturers to rationally select raw materials, standardize fermentation outcomes, improve product consistency, and develop differentiated fermented meat products with predictable quality and flavor profiles.

All four types of sour meat reached a pH of approximately 3.9, with no significant differences among the groups. The type of raw meat played a role in determining the color, in terms of L^*, a^*, and b^*. The product obtained from beef exhibited the most intense red color. This may be attributed to the reduction of nitrite, derived either directly or from nitrate, during fermentation to nitric oxide, which subsequently binds to myoglobin in beef to form nitroso myoglobin, the pigment responsible for the characteristic red color (Huang et al., 2020; Zhang, Lu, & Chen, 2023). Indeed, previous studies have shown that this series of reactions is promoted by the low pH conditions (Hu et al., 2021). The yellowness (b* value) was also affected by fermentation, with beef-fermented sour meat appearing more yellow, possibly as a result of lipid oxidation (P. Liu, Wang, Zhang, Wang, & Kong, 2019). Variations in texture, in particular in hardness, were likely influenced by differences in muscle fiber thickness among the raw meats (Żochowska-Kujawska et al., 2022).

Ten of the 18 E-nose sensors showed significantly different responses across the four types of fermented sour meats, demonstrating the tool's high sensitivity to the complex flavor profiles of these foods. However, it

provides only holistic fingerprints and does not provide compound-level information. GC-MS enables reliable identification of diverse volatile compounds, but may show limited sensitivity toward low-molecular-weight or trace microbial metabolites in complex matrices. In contrast, GC-IMS offers high sensitivity to small and low-abundance volatiles closely associated with microbial metabolism, although its compound identification capability is relatively constrained. The integration of GC-MS and GC-IMS combines the strengths of both techniques while compensating for their individual limitations. As demonstrated by the MFA and RV coefficient analysis (Fig. 4(g-i)), the combined dataset exhibited the highest discriminative power (RV = 0.94), highlighting the advantage of a multi-platform strategy for comprehensively characterizing microbial-derived VOCs and elucidating the role of lactic acid bacteria in sour meat fermentation. Consistent with published literature (Lv et al., 2021), alcohols, aldehydes, and esters were found to be the key flavor components of sour meat. Esters, produced from carboxylic acids and alcohols, give sweet, fruity, and fatty notes to meat-based foods (Carrapiso et al., 2015). Additionally, this class of compounds is, in fermented foods, a key indicator of the degree of maturity of the final product (Sánchez-Peña et al., 2005). Characteristic ethyl esters were identified in different meat types, including ethyl nicotinate, ethyl linoleate, telfairic acid ethyl ester, and ethyl heptanoate in BSM; ethyl 9 (E)-octadecenoate and ethyl propionate in YSM; ethyl isovalerate in PSM; and ethyl hexanoate in GSM. These ethyl esters not only enhance flavor but also inhibit rancidity and impart fruity, floral, creamy, and sweet notes (Wang, Su, Mu, & Zhao, 2021a). Sour meats fermented from beef and yak contained higher levels of key ethyl esters compared to both pork and goose, resulting in more complex and desirable flavor profiles. This difference might be attributed to the higher abundance of *Lactococcus* in BSM and YSM samples, a genus widely used in fermented foods to increase ester production (Juárez-Castelán et al., 2019). Among the various esters, butyl hexanoate and isopentyl hexanoate found especially in BSM contributed walnut-skin and raw-grape aromas, respectively, alongside intense fruity flavors (Forero et al., 2009; Huang et al., 2023).

Alcohol formation can occur from the reduction of aldehydes and ketones, generated by the peroxidation of lipids (Bassam et al., 2022). Alcohols, with a low odor threshold, strongly influence aroma, contributing herbal, woody, fatty, sweet, fruity, onion-like, or mushroom-like notes. 1-Hexanol, derived from oleic and palmitic acids, is the principal volatile compound present in meat (Y. Yang, Sun, Pan, Wang, & Cao, 2018). During later stages of fermentation, continuous oxidation of alcohols leads to the formation of aldehydes, esters, and acids. Additionally, aldehydes can also be produced, especially by the genera *Lactobacillus* and *Enterococcus*, through microbial oxidation of polyunsaturated fatty acids (Du et al., 2019). Hexanal, a reliable indicator of lipid oxidation (Bak et al., 2020), was detected at varying levels among the four sour meat types, likely due to differences in residual enzyme activity (Xu et al., 2022). β-cyclocitral imparted floral and fruity flavors to beef fermented sour meats (L. Yang, Li, Wu, Liu, & He, 2024).

Ketones are primarily generated through breakdown of lipids or amino acids by microorganisms' enzymes (Zhong et al., 2022). In fermented meats, high concentrations of ketones produce floral and spicy flavors (Wang et al., 2021b). This work highlighted 2-nonanone, 2-undecanone, and geranyl acetone as key VOCs, especially in BSM samples. This peculiarity might be due to the high abundance of *staphylococci*, that can generate ketones through oxidation of free fatty acids (Wang et al., 2021b). 2-Nonanone, a methyl ketone with a characteristic cheese-like aroma, can arise from amino acid catabolism or β-oxidation of fatty acids during heat treatments (Yin et al., 2021; Zhou et al., 2021). This molecule can be formed also during subsequent cooking of sour meat. Another ketone that we found as a product of fermentation was geranyl acetone. Although detected below its quantification threshold, geranyl acetone still contributed subtle floral note (Chen et al., 2022; Wang et al., 2021a). Notably, elevated ketone levels have been associated with reduced quality in dry-cured ham (Tian et al., 2022). Terpenes, such as camphene, may originate from added spices like pepper (Kasaiyan et al., 2023). Interestingly, camphene concentrations were significantly higher in YSM, compared to the other groups, as a probable consequence of the more efficient absorption of pepper-derived components by yak meat.

Fermentation significantly reshapes the microbial communities of sour meats, leading a reduction in microbial diversity. This reduction in dominant microbial species during sour meat fermentation can be attributed to the fermentation environment's effect, specifically the low pH, which inhibits some microorganisms during the fermentation process (Hu et al., 2020). At the phylum level, *Firmicutes*, *Proteobacteria*, and *Cyanobacteria* dominated all sour meat groups, consistently with previous findings (Lv et al., 2021). At the genus level, *Lactobacillus* emerged as the major genus in all samples, likely due to its superior tolerance to acidic conditions compared to *Lactococcus* and *Weissella* (H. Li, Li, Qu, & Wang, 2017; Minervini et al., 2015). In this study, aside from *Lactobacillus*, different dominant genera were identified in fermented sour meats, including *Staphylococcus* and *Weissella* in PSM and BSM, *Leuconostoc* and *Staphylococcus* in GSM, and *Macrococcus* and *Staphylococcus* in YSM. *Leuconostoc*, as a heterotypic LAB, has been found to correlate significantly with VOCs in a variety of fermented foods and is a major contributor to flavor (He et al., 2020; Tian et al., 2023). In fermented meat, its bacteriocins play a protective role, acting synergistically with other fermentative agents (Shin & Han, 2015). This can improve the safety of sour meat fermented from goose meat. The presence of *Staphylococcus* and *Macrococcus* in fermented meat products contributes to the safety of the meat and adds a distinctive flavor to the final product. Moreover, the type of raw meat influences not only the final product's microbial communities but also their metabolic activities, particularly in carbohydrate-related pathways, which may further affect the flavor and nutritional profiles.

The microbiota plays a complex role in determining the flavor profiles of various products based on fermented meat. In this study, *Lactobacillus* showed a positive correlation with major VOCs, highlighting the key contribution to flavor development exerted by its metabolic activities. *Lactobacillus* and other lactic acid bacteria (LAB) contribute to flavor formation through the release of endo- and exopeptidases, increasing the concentration of free amino acid (Flores & Toldrá, 2011), and through the production of organic acids and aroma compounds via carbohydrate fermentation. LAB also enhance food safety by producing antimicrobial molecules such as ethanol, bacteriocins, and hydrogen peroxide (Reis et al., 2012). Therefore, the dominance of LAB under acidic conditions not only promoted flavor formation but also improved the safety, quality, and shelf life of sour meat. These mechanisms are likely applicable to other naturally fermented meats with similar fermentation conditions, although variations in processing and microbial ecology may limit direct generalization.

However, it should be emphasized that correlation analysis reveals statistical associations rather than direct metabolic causality. The dominance of a bacterial genus within the microbial community does not necessarily imply a greater capacity to produce a wider diversity or higher concentrations of volatile metabolites. In some cases, microorganisms present at relatively low abundance may exert a substantial influence on flavor due to the production of compounds with low odor thresholds or high metabolic efficiency. Accordingly, the microbial-VOC relationships identified in this study should be interpreted as indicative of potential functional links under the specific fermentation conditions rather than definitive evidence of causation. Nevertheless, the consistency of the observed correlations with established metabolic pathways of lactic acid bacteria (Lan et al., 2025), together with the complementary information provided by multiple VOC analytical methods, supports the relevance of these associations in shaping the overall flavor profile of sour meat. Future studies involving controlled inoculation or functional validation approaches would be required to further elucidate causal relationships between specific microorganisms and flavor compounds.

Importantly, the present study highlights the advantages of applying multiple complementary analytical platforms to improve the interpretation of microbial VOCs. As demonstrated by the MFA results (Fig. 4(g-i)), the combined GC-MS-GC-IMS dataset showed the highest RV coefficient (0.94), indicating a markedly enhanced discriminative capability compared with GC-MS or GC-IMS alone. GC-MS enables the reliable identification of structurally diverse volatile metabolites, whereas GC-IMS provides superior sensitivity toward low-molecular-weight and trace compounds that are often closely associated with LAB metabolism. The integration of these two techniques therefore allows a more comprehensive characterization of microbial-driven volatile signatures, reducing the risk of biased interpretation arising from a single analytical method. Future studies employing controlled inoculation experiments or functional validation approaches will be required to further elucidate causal relationships between specific microorganisms and flavor compounds. PICRUSt2 indicated microbial activities influence the metabolites of sour meat products through amino sugar and nucleotide sugar metabolism, glycolysis/gluconeogenesis, pyruvate metabolism, and starch and sucrose metabolism. These pathways are directly involved in the generation of key volatile precursors, as carbohydrate metabolism supplies pyruvate and other intermediates that are subsequently converted into organic acids, alcohols, aldehydes, and esters, while associated metabolic fluxes also promote amino acid catabolism and esterification reactions. This mechanistic linkage supports the role of microbial functional potential in shaping the volatile profiles of sour meat.

5. Conclusion

This study investigated the differences in physical properties, sensory, VOCs and microbial communities in four different raw meat fermented sour meats. The key flavor components of the four sour meats were analyzed, and potential relationships between microbes and key flavors were explored. After fermentation, E-nose highlighted significant differences in the sensory profile of the products from different raw meat types. Although there is a marked difference between the VOCs of the four sour meats, esters, aldehydes, and alcohols still predominate. After fermentation, the number of dominant microbial species in sour meat decreases. The microbial composition of sour meat from yak was found to be the richest. Significant differences in microbial community composition were observed among the four types of sour meat, attributable to differences in raw meat. Functional prediction and correlation analyses of microbiota and key VOCs were conducted to preliminarily investigate flavor formation mechanisms in sour meat. However, further studies are needed to determine whether microorganisms associated with key volatiles in sour meats from different raw meat fermentations are involved in specific flavor formation mechanisms. In conclusion, this study offers a practical approach to optimize the raw meat source of sour meat and serves as a valuable reference for quality control in foods and other fermented meat products.

CRediT authorship contribution statement

Qiuyu Lan: Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Yankai Hou:** Writing – review & editing, Formal analysis. **Xin Zhao:** Writing – review & editing, Methodology, Data curation. **Zijian Cai:** Writing – review & editing. **Junni Tang:** Writing – review & editing. **Rui Zeng:** Writing – review & editing. **Chenglin Zhu:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Luca Laghi:** Writing – review & editing, Writing – original draft, Methodology.

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.lwt.2026.119112.

Data availability

Data will be made available on request.

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