

# Impact of pepper varieties on microbial succession and correlation with physicochemical properties and volatile compounds during pickled pepper fermentation

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## ABSTRACT

This study investigates the microbial succession dynamics and volatile compound formation during pickled pepper fermentation using two pepper varieties. Between *Xiaomola* (XML) and *Zhuzijiao* (ZZJ) fermentation process, salinity reduction from 9 % to 4.12 %, pH stabilization at 3.3 after 66 days. As the fermentation proceeds, XML exhibited 55.70 % shared bacterial Operational Taxonomic Units, 2.4-fold higher than ZZJ, with fungal communities shifting to *Starmerella* and *Candida*, whereas ZZJ transitioned to 93.42 % *Wickerhamomyces* dominance. Ethyl acetate, linalool, isoamyl acetate, ethyl hexanoate, acetic acid, and 2-methyl-1-propanol were potential as markers for tracking the fermentation processes. *Lactobacillus*, *Enterobacter*, *Starmerella*, *Debaromyces*, and *Wickerhamomyces* are key in regulating the flavor quality of pickled peppers. These findings propose strategies to standardize flavor profiles through microbial and volatile compound markers monitoring, offering actionable insights to optimize industrial fermentation processes and enhance product consistency in pickled pepper production using different pepper varieties.

## 1. Introduction

Peppers (*Capsicum* spp.) are native to South America and are now among the most widely cultivated vegetables worldwide because of their high nutritional value. According to the 2023 data from the United Nations Food and Agriculture Organization, Asia accounts for 65.5 % of the global pepper production, with China being the leading producer (FAOSTAT, 2023). Fermentation using acid-producing microorganisms is commonly employed to extend the shelf life and enhance the flavor of pepper products, leading to the development of spicy and sour condiments that are integral to many cuisines worldwide. The flavor profiles of fermented peppers exhibit distinct regional variations, with pickled peppers (*Paojiao*) serving as a representative fermented product in western China (Liu et al., 2023). In Yunnan Province, *Xiaomila* (*Capsicum frutescens*, XML) serves as the primary variety for pickled

pepper production due to its stable yield, high pungency, and thick pericarp. In contrast, *Zhuzijiao* (*Capsicum annuum*, ZZJ) is predominantly utilized in Sichuan Province, characterized by moderate pungency intensity, thin epidermis, and juicy mesocarp, which collectively contribute to its unique fermented flavor profile. As dominant pepper materials in the pickled pepper industry, XML and ZZJ collectively accounting for over 80 % of China's pickled pepper market share. Typically, fresh whole peppers of XML and ZZJ are fermented as pickled peppers through brine fermentation for approximately 3 months at 25–30 °C in sealed containers (Ye et al., 2020; Ye et al., 2022). Physicochemical properties, microbial succession, and volatile compounds formed during fermentation significantly influence the quality of the final fermented pepper product (Liu et al., 2023). These factors vary widely depending on the pepper variety used, as different varieties exhibit distinct physicochemical characteristics and volatile profiles (Ye

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et al., 2022).

Common pepper varieties include *Capsicum annuum*, *C. frutescens*, *C. chinense*, *C. baccatum* and *C. pubescens*. These varieties significantly influence the microbial communities during fermentation, which in turn affects their physicochemical properties and volatile compound production (Zhang et al., 2024). Thus, different varieties substantially affect the quality of the final pepper processed product (Taiti et al., 2024), which is further accentuated during the fermentation process (Ye et al., 2022). For instance, *Xiaomijiao* produces higher total volatile compounds, while *Huanggongjiao* generates more floral and fruity aromas in fermented minced pepper preparation (Liu et al., 2024). Notably, the two predominant commercial cultivars XML and ZZJ exhibit distinct sensory profiles in pickled pepper products. However, their differential impacts on fermentation dynamics, particularly regarding microbial succession patterns and metabolite evolution trajectories, remain systematically uncharacterized. This gap presents an opportunity to gain a deeper understanding of the microbial communities and changes in volatile compounds that influence the quality of the final product.

Alterations in physicochemical properties and volatile compounds during pepper fermentation are largely driven by the succession of microbial communities (Tang et al., 2024), which predominantly involved microorganisms from the phyla Firmicutes, Proteobacteria, and Ascomycota, with significant variation in genus composition and abundance. Dominant fungal genera include *Hanseniaspora*, *Wickerhamomyces*, and *Zygosaccharomyces* (Li et al., 2023; Liu et al., 2024; Tang et al., 2024; Xiao et al., 2024), while key bacterial genera include Lactic acid bacteria (LAB, e.g., *Lactobacillus*, *Weissella*), *Pantoea*, *Lactococcus*, and *Erwinia* in fermented peppers. The high-salt tolerance (Nguyen, Nguyen-Thi, Nguyen, Pham, & Nguyen, 2024) and antimicrobial activity against pathogens (Rao et al., 2019) of *Lactobacillus* have made it a subject of significant interest in fermented pepper fermentation. *Erwinia* exhibits notable extracellular pectinase and cellulase activities, facilitating the degradation of the pepper cell wall during fermentation (Zhao et al., 2024). Inoculation with the *Pediococcus ethanolidurans* has been shown to significantly reduce the relative abundance of *Erwinia* in fermented peppers, thereby mitigating the detrimental effects of pectinase and enhancing both the texture and fracturability of the final product (Li et al., 2023). Existing studies have extensively explored microbial succession dynamics and their interactions with physicochemical and volatile compound profiles in fermented foods such as kimchi, sauerkraut, and soy products. Additionally, *Hyphopichia*, *Lactiplantibacillus*, *Clostridium*, *Zygosaccharomyces*, *Kazachstania*, and *Clavispora* in fermented peppers are significantly correlated with the volatile compounds production, such as 4-ethyl-2-methoxyphenol, acetoin, ethyl propanoate, 2-octanone, and linalool oxide (Xu et al., 2021; Li et al., 2023). However, studies on fermented peppers have predominantly focused on single variety, systematic investigations into how pepper variety-specific traits modulate these dynamics remain limited. Therefore, exploring the impact of different pepper varieties on microbial succession dynamics and the production of volatile compounds during fermentation holds substantial theoretical and practical significance for enhancing the flavor quality of fermented pepper products.

This study investigated the relationship between the changes in physicochemical indices, microbial communities, and volatile compounds during the fermentation of two commercially pepper varieties (XML and ZZJ). Physicochemical indices, including salinity, pH, total acidity (TA), reducing sugars, soluble solids, and nitrite content, were monitored throughout the fermentation process for both pepper varieties. High-throughput sequencing was used to examine the composition and structural succession of the microbial communities. Additionally, dynamic differences in volatile compounds between the two pepper varieties were investigated using headspace-solid phase microextraction-gas chromatography-mass spectrometry (HS-SPME-GC-MS). Finally, by correlating physicochemical indicators with microbial community dynamics and analyzing microbial diversity and the key volatile compounds, we aimed to identify the critical factors

influencing the quality of pickled pepper products of different pepper varieties. These findings establish a varietal-specific fermentation framework by elucidating the distinct roles of core microorganisms in flavor compound formation, to optimize industrial pickle production through targeted pepper varieties.

## 2. Materials and methods

### 2.1. Pickled pepper fermentation and chemicals

Fresh and ripe XML and ZZJ peppers were purchased in August 2024 from Tongzhiyuan Agricultural Products Co., Ltd. in Zunyi City, Guizhou Province, China. Ginger (*Zingiber officinale*), garlic (*Allium sativum*), Chinese liquor, sugar, and edible salt were purchased from a local Walmart supermarket (Guiyang, Guizhou Province, China). Pepper samples were thoroughly washed with distilled water, air-dried at 25 °C, and fermented in sterilized fermentation vessels with the brine solution (9 % edible salt, 2.5 % sugar, 1 % Chinese liquor, 1 % minced ginger and, 1 % garlic). To minimize environmental interference, pickled pepper fermentation was in a dedicated fermentation chamber maintained at 25 °C and 70 % relative humidity. A multi-vessel parallel fermentation strategy was implemented to prevent cross-contamination from repeated sampling. From designated fermentation vessels, samples were collected at day(D) 0, D7, D14, D21, D49, D63, and D77, 100 g samples were collected for physicochemical analysis. Microbial communities and volatile compounds were analyzed in samples spanning D0 to D63.

Dipotassium hydrogen phosphate, potassium dihydrogen phosphate, and 3,5-dinitrosalicylic acid (DNS) were obtained from the Fuchen Chemical Reagent Co., Ltd. (Tianjin, China). Sodium hydroxide was obtained from Chengdu Jinshan Chemical Reagent Co., Ltd. (Chengdu, China). C7-C30 n-alkane mixture, toluene-*d*<sub>8</sub> (purity ≥ 99 %, CAS 203726-5), and ethyl-*d*<sub>5</sub> acetate-*d*<sub>3</sub> (purity ≥ 99 %, CAS 117121-81-0) were obtained from Sigma-Aldrich Co., Ltd. (Shanghai, China). Sodium chloride (NaCl) was purchased from the China National Pharmaceutical Group Co., Ltd. (Shanghai, China).

### 2.2. Physicochemical analysis of pickled pepper

#### 2.2.1. Salinity, pH and TA

A total of 20 g of pickled pepper samples and 20 g of brine were separately weighed and homogenized for 40 s using a laboratory homogenizer (GT300; Beijing Grinder Instrument Co., Ltd., China). The resulting homogenate was subsequently filtered and the filtrate is collected. The salinity was determined using a digital salinity meter calibrated with standard NaCl solution. Furthermore, using a calibrated pH meter (pH -25; Shanghai Yueping Scientific Instrument Co., LTD., China) determined the pH value of the sample. All measurements should be in triplicate to ensure accuracy. TA was determined according to the method (Hu et al., 2025) with modifications. In brief, approximately 5 g of pickled pepper sample was homogenized to 50 mL with ultra-pure water and boiled in a water bath for 30 min. After cooling to room temperature, the mixture was diluted with 250 mL ultra-pure water and filtered. The diluted pickled pepper samples were titrated with 0.1 mol/L NaOH to reach pH  $8.2 \pm 0.2$ , and the TA content was calculated based on the volume of NaOH consumed. A blank control was prepared using ultra-pure water, and all measurements were performed in triplicate.

#### 2.2.2. Soluble solids content (SSC), reducing sugars and nitrite concentration

The pickled pepper supernatant was taken for SSC using a handheld refractometer (Beijing Jinkelida Electronic Technology Co., Ltd., China). The reducing sugar content was determined according to the DNS method described in the Chinese National Standard GB 5009.7-2016 (Han et al., 2025). Briefly, 5 g of homogenized pickled pepper sample was mixed with 25 mL ultra-pure water and heated in a water bath at 80 °C for 30 min. After cooling to room temperature, the mixture was

filtered and diluted to 100 mL with ultra-pure water. Subsequently, 2 mL of the filtrate was mixed with 1.5 mL DNS reagent and reacted in a constant-temperature water bath at 100 °C for 5 min. The reaction mixture was then diluted to 25 mL with ultra-pure water, and the absorbance was measured at 540 nm using a UV-Vis spectrophotometer (Shanghai Yidian Scientific Instrument Co., Ltd., China). The reducing sugar content was calculated based on a glucose standard curve ( $y = 0.723x + 0.0059$ ,  $R^2 = 0.9996$ ). Nitrite content was assessed using a Food Nitrite Content Assay Kit (Sangon Biotech, Shanghai, China), which is based on a colorimetric method. Nitrite reacts with N-(1-naphthyl)-ethylenediamine hydrochloride to form a stable purple-red azo dye with a characteristic absorption peak at 540 nm. The nitrite concentration was quantified by measuring the absorbance and comparing it with a standard curve.

### 2.3. Analysis of bacterial and fungal diversity

Approximately 10 g of solid-liquid mixed pickled pepper samples were filtered through a 50 mm × 0.22 µm aqueous membrane. The microbial biomass retained on the membrane was subsequently sent to Shanghai Personalbio Technology Co., Ltd. (Shanghai, China) for high-throughput sequencing (Li et al., 2022). Microbial DNA was extracted using the Mag-Bind® Soil DNA Kit M5635-02 (Omega Bio-Tek, Norcross, GA, USA) according to the manufacturer's instructions. Bacterial DNA was amplified using the primers 338F (5'-ACTCTACGGGAGG-CAGCA-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3'), targeting the V3-V4 hypervariable region of the 16S rRNA gene (Chen et al., 2021). For fungal DNA, primers ITS1F (5'-CTTGGTCATTTA-GAGGAAGTAA-3') and ITS2R (5'-GCTGCGTCTTCATCGATGC-3') were employed. Raw sequencing data were subjected to quality filtering using the PacBio SMRT Link portal (v5.0.1.9585) (Xiong et al., 2024). Sequence clustering was performed using Usearch (v11.0) software, with a 97 % similarity threshold to define Operational Taxonomic Unit (OTU). OTU sequences were compared against the Silva database (for bacteria) and the Unite database (for fungi) for taxonomic classification, with a comparison threshold of 75 %. Finally, chimeric sequences were identified and removed using QIIME2 2022.11, resulting in the final, high-quality dataset for subsequent analysis.

### 2.4. Analysis of volatile compounds

The analysis of the pickled pepper at different fermentation stages was conducted using headspace solid-phase microextraction coupled with HS-SPME-GC-MS. To ensure the representativeness of the analyzed samples, four randomly selected pickled pepper from the same fermentation stage were placed in a ball mill (Type GT300, Beijing Grinder Instrument Co., Ltd., China) for grinding. A homogeneous 1 g sample was accurately weighed and placed in a 20 mL headspace vial. Then, 5 mL of saturated NaCl solution was added, followed by 25 µL of internal standards (toluene- $d_8$ , 0.5 mg/L; ethyl- $d_5$  acetate- $d_3$ , 9.85 mg/L). The sample in the headspace vial was equilibrated at 45 °C for 10 min. Afterward, a SPME fiber (50/30 µm DVB/CAR/PDMS, 2 cm) was used to extract the volatile compounds at 45 °C for 30 min (Li et al., 2024).

After the volatile compounds in pickled peppers were enriched using an HS-SPME fiber, they were desorbed at the injection port of the GC under conditions of 250 °C for 5 min in splitless mode. The volatile compounds were analyzed on a DB-WAX capillary column (60 m × 0.25 mm i.d., 0.25 µm film thickness). The oven temperature program started at 40 °C (held for 1 min), then increased at a rate of 6 °C/min to 230 °C, where it was held for 15 min. Helium was used as the carrier gas at a flow rate of 2 mL/min. The mass spectra were obtained using electron ionization with an ionization energy of 70 eV. The ion source temperature was set to 230 °C, and the mass range was scanned from 35 to 350 amu.

Volatile compounds were identified by comparing their spectra with

those in the NIST database (matching rate > 70 %). The retention index (RI) of each compound was calculated using an alkanes mixture (C7-C30). The experimental RI values were compared to those reported in the literature, with the difference maintained within ≤15 units. The relative concentrations of volatile compounds were quantified with internal standards. For compounds containing benzene rings or heterocyclic structures, toluene- $d_8$  was employed as the internal standard, whereas ethyl- $d_5$  acetate- $d_3$  was used for the remaining compounds. A semi-quantitative approach, based on the referenced method (Qian et al., 2024), was applied. All measurements were performed in triplicate, and the average concentrations were used for further analysis.

### 2.5. Statistical analysis

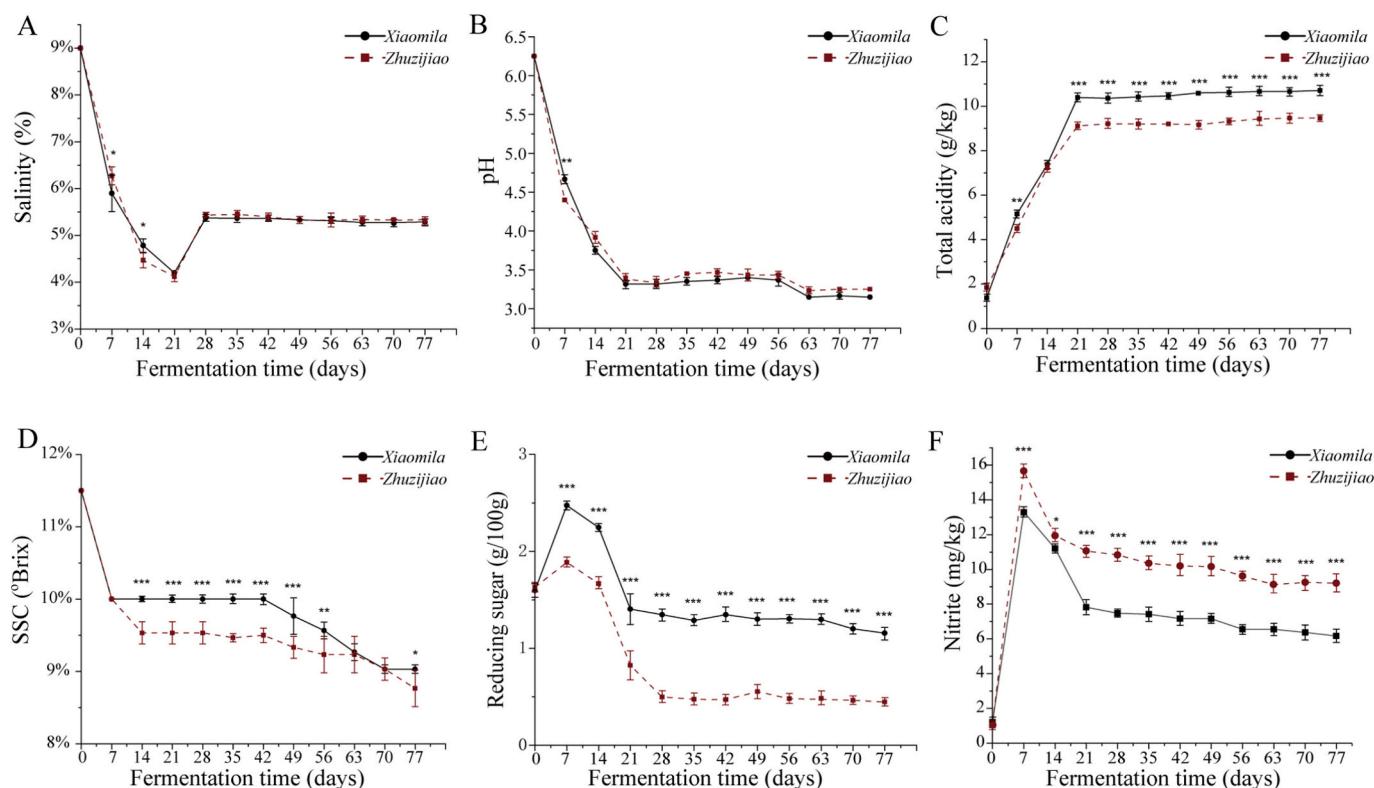
Statistical analysis of all data was conducted using IBM SPSS Statistics version 26, with results expressed as means ± standard deviation. Statistical significance was determined at a  $p$  value threshold of <0.05. All experiments were performed in triplicate. Principal component analysis (PCA) and partial least squares discriminant analysis (PLS-DA) were carried out using SIMCA 14.1 software to identify the main patterns and discriminating factors between fermentation stages. Mantel tests were performed with R software (v4.2.2) to assess relationships between microbiota structure and environmental variables. Redundancy analysis (RDA) was implemented in Canoco 5.0 to elucidate the associations between keystone microbial taxa and environmental physico-chemical variables. The correlation between the dominant microbial community and the significantly volatile compounds was established according to Spearman correlation coefficient combined with the  $P$  value of ANOVA. Cytoscape v3.10.3 software was used to visualize the correlation network.

## 3. Results and discussion

### 3.1. Physicochemical indexes of pickled pepper

The two pepper varieties used for pickled pepper production exhibited identical initial salt concentrations and followed a similar trend of salt reduction throughout fermentation, with the lowest salinity (approximately 4.12 %) observed on D21, which decreased from the initial level of 9 % (Fig. 1A). In an initially high-salinity environment, it is conducive to promoting the rapid growth of halotolerant bacteria (Nguyen et al., 2024). This rapid decline in salt content can be attributed to osmotic water loss from vegetable tissues, acid production by LAB, and concurrent microbial metabolic activities, which collectively contribute to a reduction in salinity (Zhou et al., 2023). The pH and TA trends during XML and ZZJ fermentation were similar (Fig. 1B, C). Both varieties showed minimal changes in pH and TA from D21 to D77, with final pH values stabilizing at 3.31 and 3.38, respectively, aligned with the established maturity criteria (Chen et al., 2022). XML accumulated more acids than ZZJ, with a 7.53- and 4.95-fold increase in TA, respectively, compared to the beginning of fermentation levels (Fig. 1C). LAB, which dominate the later stages of fermentation, produce organic acids, contributing to pH reduction and acidification (Wang et al., 2019). The low pH will inhibit the pathogenic bacteria (e.g., *Rothia*) and spoilage organisms (e.g., *Pseudomonas*) growth in the fermentation product (Li & Liu, 2022).

SSC exhibited a general declining trend (Fig. 1D), with a more pronounced reduction during ZZJ fermentation. Compared with XML, ZZJ exhibited a lower solid content and softer texture after fermentation. During the fermentation of pickled pepper, *Erwinia* and other microorganisms hydrolyze pepper peel by cellulase to release reducing sugar (Zhao et al., 2024), the reducing sugar showed an increase and follow decrease in the XML and ZZJ fermentations (Fig. 1E), the trends also observed in pepper paste fermentation (Liang et al., 2022). As *Weissella* and abundance increase during fermentation, reducing sugar is consumed to form differences. Finally, the reducing sugars of XML and



**Fig. 1.** Changes in salinity (A), pH value (B), total acidity (C), soluble solids content (D); reducing sugar (E), and nitrite level (F) of pickled peppers during fermentation. The solid dark line indicates *Xiaomila*, and the dashed red line indicates *Zhuzijiao*. \* means  $p < 0.05$ , \*\* means  $p < 0.01$ , \*\*\* means  $p < 0.001$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ZZJ fermentations with a reduction of 27.55 % and 72.39 %, respectively. The fluctuations in reducing sugar content caused via microbial metabolism and utilization of carbon sources during pepper fermentation (Rodríguez et al., 2021), which is consistent with that observed in other fermented vegetables (Zhou et al., 2023). Given nitrite's potential health risks in traditional pickled vegetable fermentation (Ren, Kamangar, Forman, & Islami, 2012), this process necessitates dynamic monitoring throughout the fermentation process to ensure food safety compliance. The nitrite content in both pepper varieties initially increased and then decreased during fermentation, showing a trend consistent with that observed in fermented peppers (Cai et al., 2023). The peak nitrite concentrations were 13.31 and 15.67 mg/kg for XML and ZZJ varieties, respectively, both of which occurred on D7. Throughout fermentation, the nitrite levels in both varieties remained below the maximum permissible limit for fermented vegetables (Shang et al., 2022). At the end of fermentation, the nitrite concentration in ZZJ was 49.3 % higher than that in XML (Fig. 1F). This difference may be due to the low pH and high TA of the XML fermentation environment, which inhibits nitrate reductase activity (Zhao et al., 2021).

### 3.2. Microbial community succession during pickled pepper fermentation

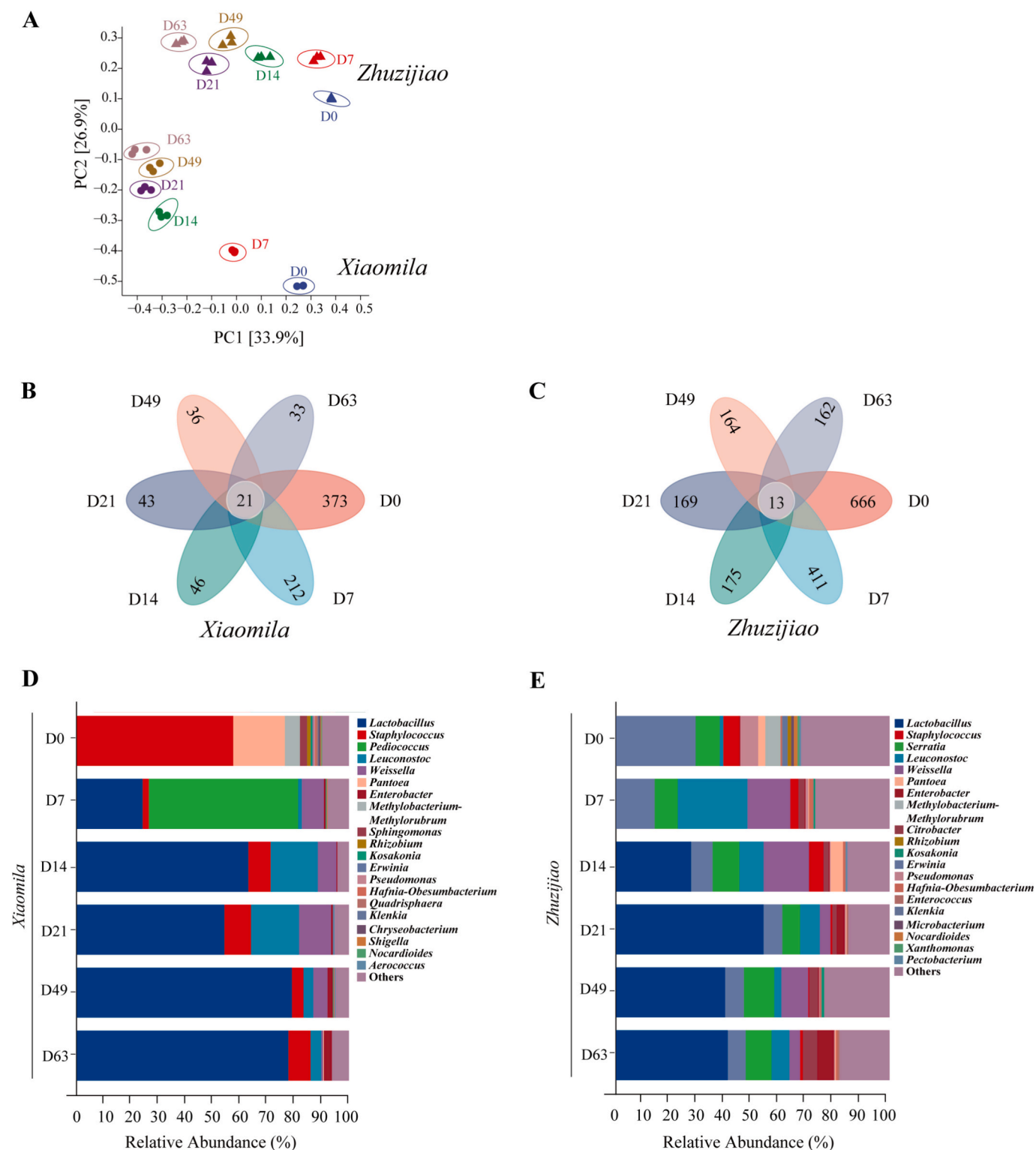
#### 3.2.1. Bacterial community

OTUs clustered using a 97 % similarity threshold provide an approximation of the microbial taxa and serve as an essential tool for studying community composition and diversity. OTU distribution and abundance can indicate the variety of microorganisms present in a sample and their relative proportions. A total of 723 and 1127 bacterial OTUs were identified in XML and ZZJ fermentations, respectively. PCA based on bacterial genus level OTUs showed that the contribution rates of PC1 and PC2 were 33.9 % and 26.9 % for XML and ZZJ (Fig. 2A). The proximity between the samples in the PCA plots indicates a similarity in their microbial community structures (Li et al., 2022). Over the course of

a fermentation, the bacterial communities within each sample tended to become more similar, as both fermentation time and environmental changes influenced the microbial composition.

Venn diagrams illustrating the distribution of shared and unique bacterial OTUs in the samples during fermentation revealed a gradual reduction in bacterial abundance with increasing fermentation time (Fig. 2B, C), whereas the proportion of shared bacterial species increased (Fig. S1A). Notably, there was a significant difference in the bacterial composition between the two pepper varieties at the start of fermentation. 44 shared bacterial OTUs were shared on D63, accounting for 55.70 % and 23.16 % of the total bacterial OTUs in XML and ZZJ, respectively (Table S1). Fermentation time had a more pronounced effect on bacterial community succession in XML, consistent with results from other fermented pepper studies (Li et al., 2024), while in ZZJ, which exhibited higher bacterial abundance, unique bacterial species predominated during fermentation.

To analyze the dominant microorganisms during fermentation, a threshold of an average relative abundance  $>1$  % was applied. The bacterial community compositions at the phylum and genus levels during fermentation are shown in Fig. S2A, 2D, and 2E. The dominant bacterial phyla in both XML and ZZJ fermentations were Firmicutes and Proteobacteria, with Firmicutes serving as an active indicator during the fermentation of peppers (Liu et al., 2024). At the beginning of fermentation, the major bacteria in XML were *Staphylococcus* (57.63 %), *Pantoea* (18.67 %), others (9.18 %), and *Methylobacterium-Methylorubrum* (5.43 %), while in ZZJ the dominant bacteria were others (32.26 %), *Erwinia* (29.21 %), *Serratia* (8.78 %), and *Staphylococcus* (5.90 %). Over the course of fermentation, the relative abundance of *Lactobacillus* gradually increased in both pepper varieties. On D63 of fermentation, *Lactobacillus* reached its highest abundance, comprising 77.76 % of bacteria in XML and 42.76 % in ZZJ. During the later stages of fermentation, the abundance of *Weissella* was suppressed by *Lactobacillus* in the two pepper varieties (Wang et al., 2019). On D7 of



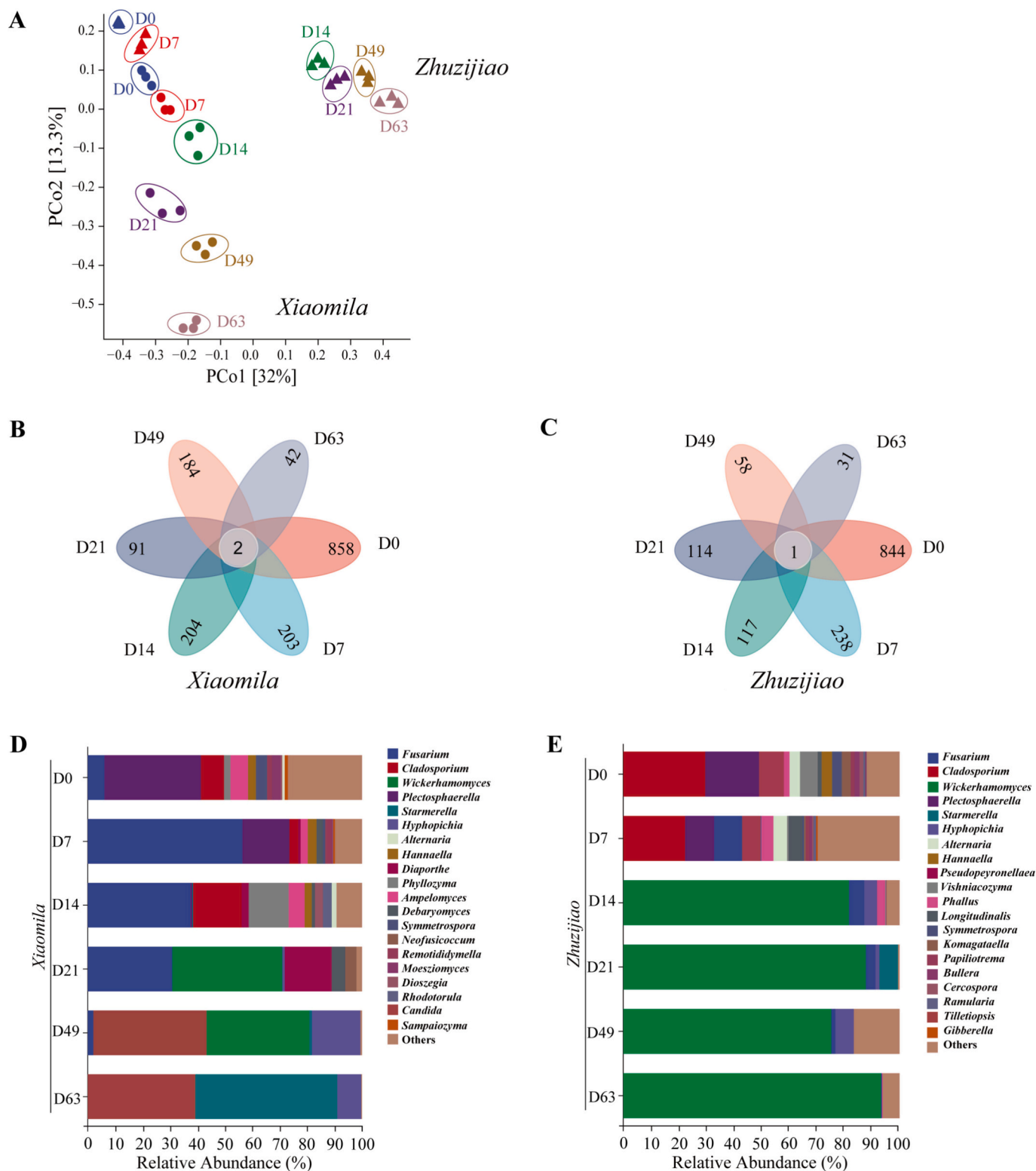
**Fig. 2.** Changes of bacterial community during pickled peppers fermentation. Principal component analysis of Operational Taxonomic Units (OTUs) at bacterial genus level (A); venn diagrams of bacterial OTUs (B, C); histogram of the relative abundance of bacteria at the phylum level (D) and the genus level (E). D0, D7, D14, D21, D49, and D63 means fermentation for day 0, day 7, day 14, day 21, day 49 and day 63, respectively.

fermentation, the relative abundance of *Weissella* was 8.31 % in XML and 15.54 % in ZZJ. By D63, these values had decreased to 0.57 % and 3.75 %, respectively. *Erwinia* and *Serratia* were identified as core microorganisms during ZZJ fermentation. The abundance of *Erwinia* decreased over time, with relative abundances of 14.82 %, 8.31 %, and 6.79 % on D7, D14, and D63, respectively. In contrast, *Serratia* showed

minimal variation in abundance, maintaining levels between 8.67 % and 9.78 % throughout fermentation.

### 3.2.2. Fungal community

The succession of fungal communities in XML and ZZJ during fermentation is illustrated in Fig. S2B and Fig. 3. PCA of the fungal



**Fig. 3.** Changes of fungal community during pickled peppers fermentation. Principal component analysis (PCA) of Operational Taxonomic Units (OTUs) at fungal genus level (A); venn diagrams of fungal OTUs (B, C); histogram of the relative abundance of fungi at the phylum level (D) and the genus level (E). D0, D7, D14, D21, D49, and D63 means fermentation for day 0, day 7, day 14, day 21, day 49 and day 63, respectively.

genera in XML and ZZJ showed that the first and second principal components contributed 32 % and 13.3 %. Notably, the trends in fungal community succession differed between XML and ZZJ fermentation. In XML fermentation, the fungal composition was similar on D0, D7, and D14, followed by a distinct separation in the subsequent fermentation

stages (Fig. 3A). However, in ZZJ, there was greater compositional variation during the early fermentation stages (D0-D7), whereas the fungal composition was more similar during the later stages (D14-D63) (Fig. 3A). A total of 1584 and 1403 fungal genera OTUs were identified in XML and ZZJ fermentations, respectively. Fungal abundance

significantly decreased over time in both varieties. During XML fermentation, two common fungi were identified, belonging to *Cladosporium* and *Fusarium*, while only one common fungus was identified in ZZJ fermentation process (Fig. 3C, D). The presence of shared fungi remained relatively low in the two pepper varieties during fermentation (Fig. S1B, Table S2), indicating that pepper variety had a substantial influence on fungal community dynamics during fermentation. These findings are consistent with those of previous studies on fermented pepper (Li et al., 2024).

The annotations of the fungal community composition at the phylum and genus levels during fermentation are presented in Fig. S2, Fig. 3D, and Fig. 3E. During the fermentation of XML and ZZJ, the average abundance of the Ascomycota was 89.02 % and 87.55 %, respectively, which is consistent with findings from other fermented pepper studies (Shi et al., 2022). At the onset of fermentation, the dominant fungi in XML included *Plectosphaerella* (34.99 %), others (27.11 %), *Cladosporium* (8.54 %), and *Fusarium* (6.15 %). Whereas in ZZJ, the dominant fungi at the start of fermentation were *Cladosporium* (29.59 %), *Plectosphaerella* (19.38 %), others (11.79 %), and *Pseudopeyronella* (8.21 %). During XML fermentation, the changes in the dominant fungi were significant, with the relative abundance of *Fusarium* initially increasing and then decreasing. By D63, the dominant fungi in the XML had shifted to *Starmerella* (51.59 %), *Candida* (39.13 %), and *Hyphopichia* (8.76 %). During ZZJ fermentation, the dominant fungi were relatively stable during the early stages (D0 and D7), *Fusarium*, *Hyphopichia*, *Starmerella*, and other genera exhibited some fluctuations in abundance. *Wickerhamomyces* is a non-*Saccharomyces* yeast widely distributed in fruits, vegetables, flowers, and fermented foods (Yoo et al., 2024). In the fermentation of XML and ZZJ peppers, the initial relative abundance of *Wickerhamomyces* was 0.02 % and 0.003 % on D0, respectively. The high-salinity environment during the initial fermentation stage inhibited the growth of *Wickerhamomyces*. As salinity decreased, its abundance in XML fermentation reached 40.14 % on D21 and 37.49 % on D49. In contrast, *Wickerhamomyces* dominated ZZJ fermentation from D14 to D63, maintaining a high relative abundance of 75.19–93.42 %, consistent with observations in other fermented pepper studies (Chen et al., 2022). *Wickerhamomyces* exhibits strong proteolytic enzyme activity, hydrolyzing proteins into small peptides and amino acids, which serve as flavor precursors. This process directly contributes to umami taste and enhances the sensory characteristics of fermented foods.

### 3.3. Correlations between microbial community and physicochemical indexes

Mantel tests were conducted to analyze the correlations between the six physicochemical indices and bacterial and fungal communities during the fermentation of pickled peppers. In Fig. 4A, B, the solid lines indicate positive correlations between these parameters. During fermentation of the two pepper varieties, physicochemical parameters were positively correlated with microbial communities, particularly in XML fermentation ( $p < 0.01$ ), suggesting that these parameters have a potential influence on the microbial community composition during XML fermentation (Louw, Lele, Ye, Edwards, & Wolfe, 2023). In contrast, during ZZJ fermentation, no significant correlations were observed between bacteria and reducing sugars, or between fungi and SSC, salinity, and nitrites. The differences in changes in reducing sugars and SSC between XML and ZZJ could be attributed to variations in the bacterial and fungal communities, respectively.

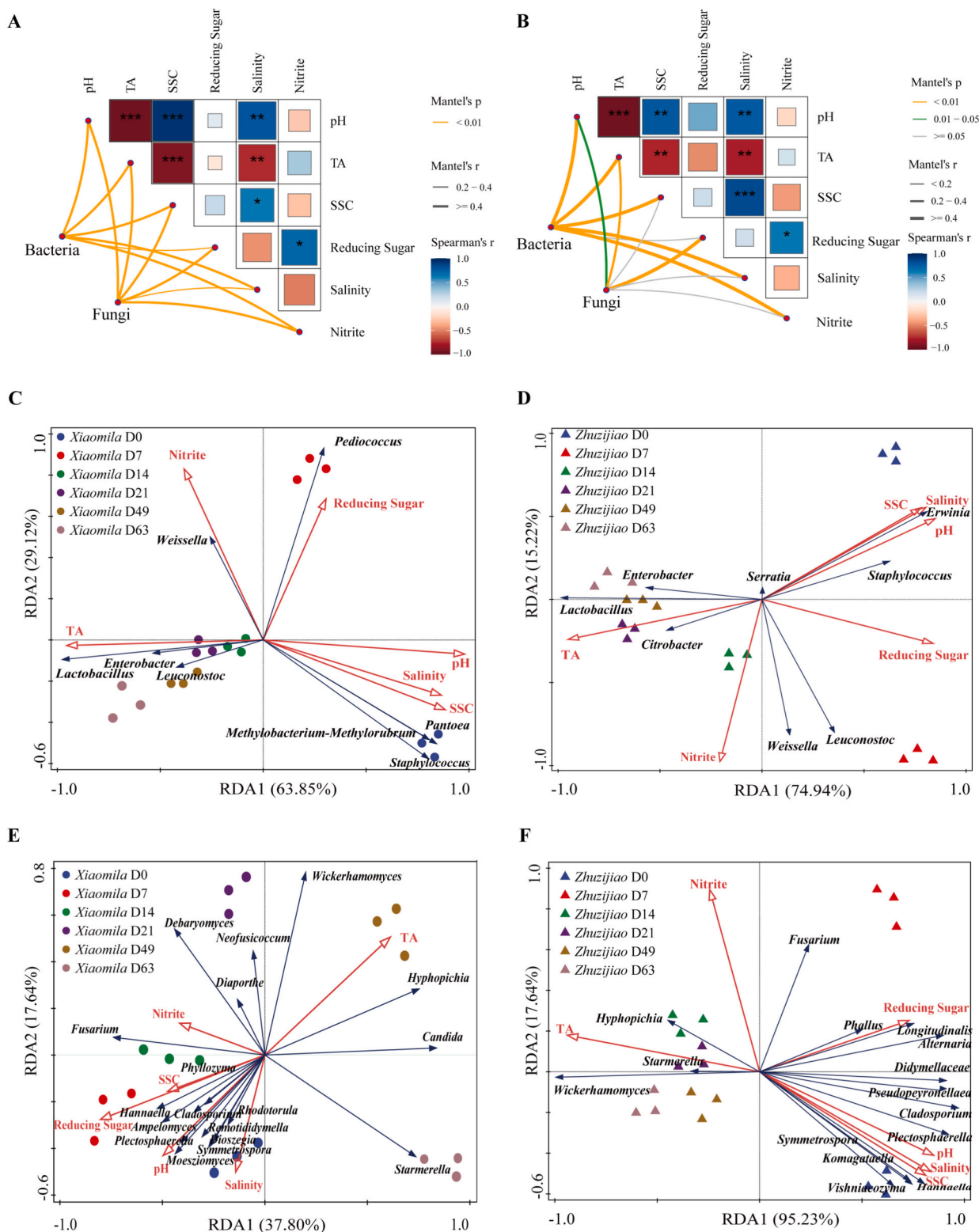
The RDA method was employed to explore the potential correlations between microbial communities with relative abundances greater than 1 % and physicochemical parameters, which could provide insights into the underlying mechanisms the formation of the quality of pickled pepper (Wang et al., 2024). The correlation between bacteria and physicochemical parameters during the XML fermentation was 97.10 %, whereas fungi showed a correlation of 55.44 % (Fig. 4C, E). In the ZZJ fermentation, the corresponding correlations were 93.14 % for bacteria

and 96.66 % for fungi (Fig. 4D, F). Salinity, pH, SSC, and reducing sugars were primarily positively correlated with the dominant microbes during the early fermentation stages (D0–D14), indicating that microorganisms rapidly adapted to the fermentation conditions, altering the environment through biochemical reactions and leading to noticeable changes in microbial composition in the early fermentation phase. Salinity primarily influenced fungal genera of pickled pepper during early stage (D0–D7). As shown in Fig. 3B, C, both XML and ZZJ pepper fermentation samples initially exhibited higher fungal OTUs at the early stage, when the salinity of the brine remained high (6 %–9 % NaCl). During this period, fungal OTUs sharply decreased by 76.17 % and 71.72 % in XML and ZZJ samples, respectively, indicating significant inhibition of fungal growth under high salinity. Salinity during the early fermentation stages is closely associated with *Staphylococcus*, *Erwinia*, and *Serratia* (Fig. 4C, D). Although high salt concentrations in the early fermentation stages reduce the abundance of these genera (Fig. 2D, E), certain pathogenic bacteria in fermented foods exhibit strong tolerance to 10 % NaCl concentrations (Ming et al., 2019). Therefore, suppressing pathogenic bacteria during industrial production requires stringent quality control of raw materials and consistent maintenance of salinity levels throughout the fermentation process. The required salinity maintenance can be operationalized through cold fill pickling, a process employing brine (5 % acetic acid, 5 % NaCl) that establishes critical food safety control via acidification-salinity synergy (Gaydos, Cutter, & Campbell, 2016). TA and pH showed an inverse relationship and correlation to the dominant microbes after D14. In the first week of ZZJ fermentation, *Erwinia* and *Staphylococcus* were the dominant bacteria and exhibited a highly significant positive correlation with the SSC.

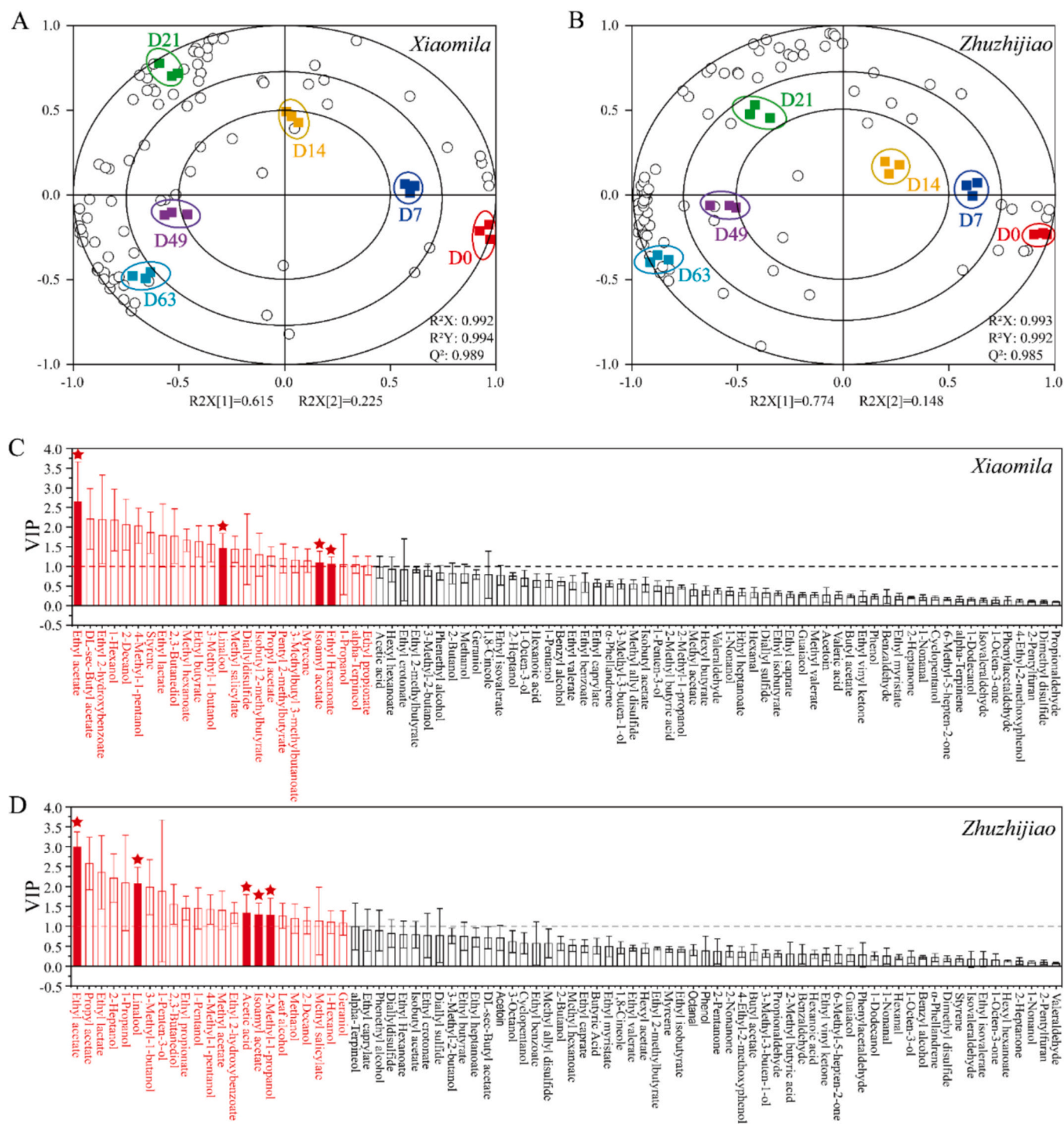
### 3.4. Volatile compounds during fermentation

Aroma profiling of the fermented peppers was conducted using HS-SPME-GC-MS. During the fermentation of XML and ZZJ, 82 volatile compounds were detected. Significant changes were observed in the types and concentrations of the volatile compounds during fermentation. PLS-DA is a method for identifying patterns in data and expressing the data in such a way as to highlight their similarities and differences (Li et al., 2024). Based on the PLS-DA model, a biplot was constructed with the volatile compounds as the X variable and fermentation time as the Y variable (Fig. 5A, B). The high model parameters obtained using this procedure (XML:  $R^2X = 0.992$ ,  $R^2Y = 0.994$ , and  $Q^2 = 0.989$ ; ZZJ:  $R^2X = 0.993$ ,  $R^2Y = 0.992$ , and  $Q^2 = 0.985$ ) demonstrated strong confidence and predictive abilities with no signs of overfitting (Huang et al., 2024). The regions of variation in volatile compounds in the two pepper varieties were consistent. Fermentation began in the fourth quadrant of the PLS-DA plot, gradually transitioned to the first and second quadrants, and finally reached the third quadrant. According to the variable importance of projection values ( $VIP > 1.0$ ) from the PLS-DA model, 25 and 23 volatile compounds were considered key differential flavor compounds in the XML and ZZJ fermentations, respectively (Fig. 5C, D). These compounds were selected because of their significant impact on the overall aroma profile and their correlation with the fermentation time. The results indicate that peppers at different fermentation time points contain characteristic volatile compounds and that identifying markers during the production process is important for quality monitoring.

Further analysis of the compounds with VIP values  $> 1.0$  showed that four compounds in XML and five compounds in ZZJ exhibited gradual increases in their content during fermentation. Ethyl acetate, characterized by its fruity aroma and a threshold of 1.0  $\mu\text{g/kg}$  (Li et al., 2023), exhibits the highest VIP values in both XML (VIP = 2.6) and ZZJ (VIP = 3.0). Following fermentation, the concentration of ethyl acetate increased 6.8- and 8.9-fold relative to the raw materials, reaching 2726.5  $\mu\text{g/kg}$  and 5375.4  $\mu\text{g/kg}$ , respectively (Fig. 6A, B). Besides ethyl acetate, other compounds showing an increasing trend in both varieties include linalool (Fig. 6C, D) and isoamyl acetate (Fig. 6E, F). Linalool,



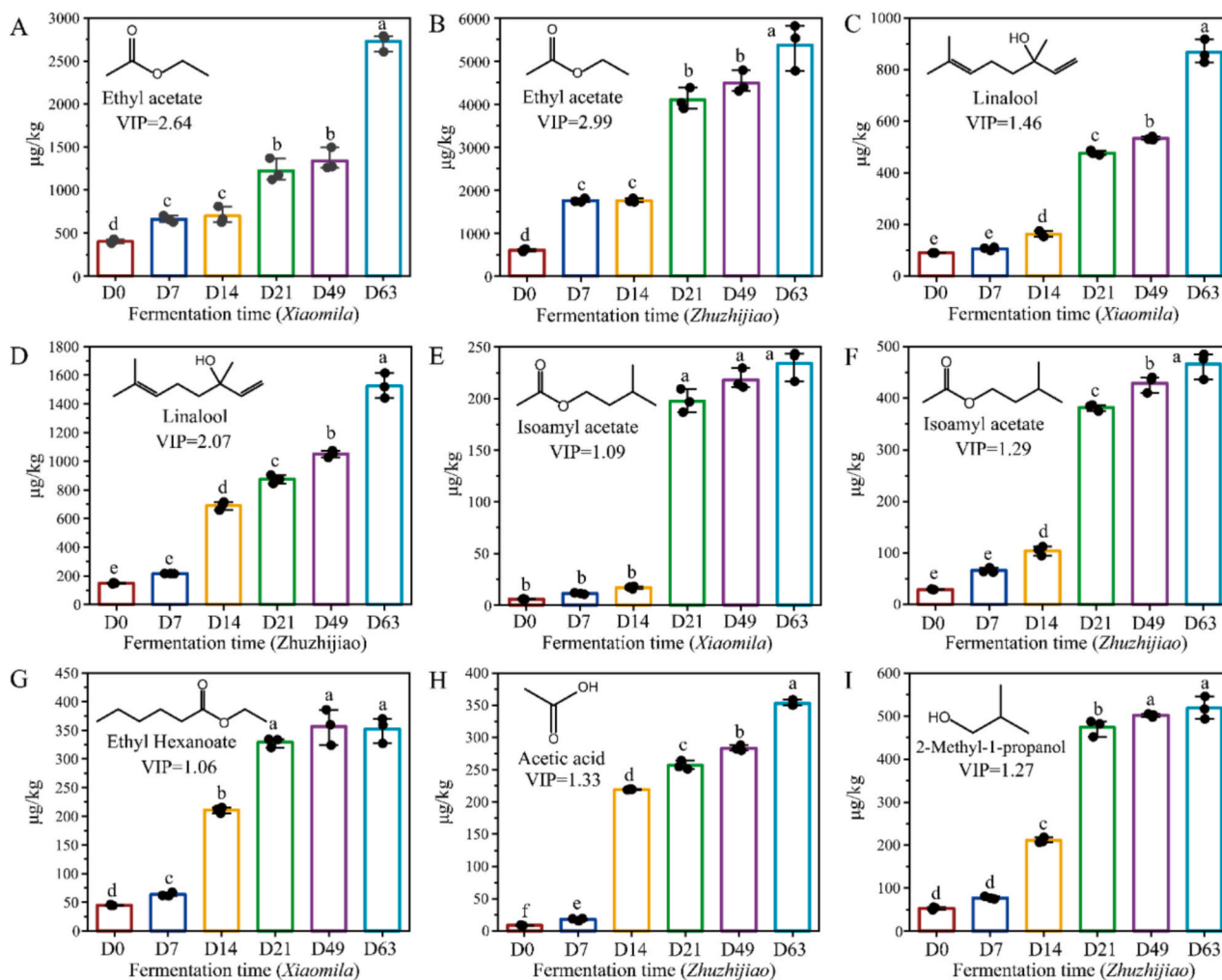
**Fig. 4.** Correlation analysis between physicochemical indexes and microbial community. The relationship analysis between the microbial communities and physicochemical indexes of *Xiaomila* (XML) using the Mantel test (A); the relationship analysis between the microbial communities and physicochemical indexes of *Zhuzijiao* (ZZJ) using the Mantel test (B); Redundancy analysis (RDA) of dominant bacterial genus and physicochemical indexes in XML fermentation (C) and ZZJ fermentation (D); RDA of dominant fungal genus and physicochemical indexes in XML fermentation (E) and ZZJ fermentation (F). TA and SSC indicated total acidity and soluble solids content, respectively. D0, D7, D14, D21, D49, and D63 means fermentation for day 0, day 7, day 14, day 21, day 49 and day 63, respectively. The width of the connecting line corresponds to the r-value derived from Mantel test, the colour of the connecting line corresponds to the p-value. In RDA, red lines with arrows indicate physicochemical properties, black lines with arrows represent major microbial genus. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 5.** PLS-DA model plots illustrating the fermentation time of two pepper varieties and their volatile compounds (A, B), with colored boxes indicating the peppers at various fermentation stages and hollow circles denoting the volatile compounds. The VIP values were derived from the PLS-DA model (C, D). The bar chart, marked with asterisks, highlights compounds exhibiting increasing trends, which are further analyzed in Fig. 6. D0, D7, D14, D21, D49, and D63 means fermentation for day 0, day 7, day 14, day 21, day 49 and day 63, respectively.

known for its floral aroma and a threshold of 8.32  $\mu\text{g/kg}$ , has been reported to significantly contribute to the aroma of fermented peppers and is the aroma compound with the highest OAV value (Xiao et al., 2024). After fermentation, its concentration increased 9.7- and 10.3-fold in XML and ZZJ, respectively. Ethyl hexanoate, acetic acid, and 2-methyl-1-propanol content increased gradually, but this trend was observed only in specific pepper varieties. In XML, the concentration of ethyl hexanoate increased with fermentation time, however, after D21, the

increase was no longer significant (Fig. 6G). In ZZJ, the acetic acid concentration gradually increased, reaching a 41-fold increase at the end of fermentation (Fig. 6H). Among all the analyzed compounds, acetic acid was the only compound measured that showed significant changes in concentration at each fermentation stage. Acetic acid has a sour aroma and studies on fermented pepper aromas have indicated that it is the only volatile acid with an OAV greater than 1.0 (Xiao et al., 2024). The compound 2-Methyl-1-propanol, which has a fruity aroma,



**Fig. 6.** The relative concentrations of volatile compound in pepper samples under different fermentation times. Different letters represent significant differences ( $p < 0.05$ ). D0, D7, D14, D21, D49, and D63 means fermentation for day 0, day 7, day 14, day 21, day 49 and day 63, respectively.

increased 9.8-fold by the end of fermentation (Fig. 6I).

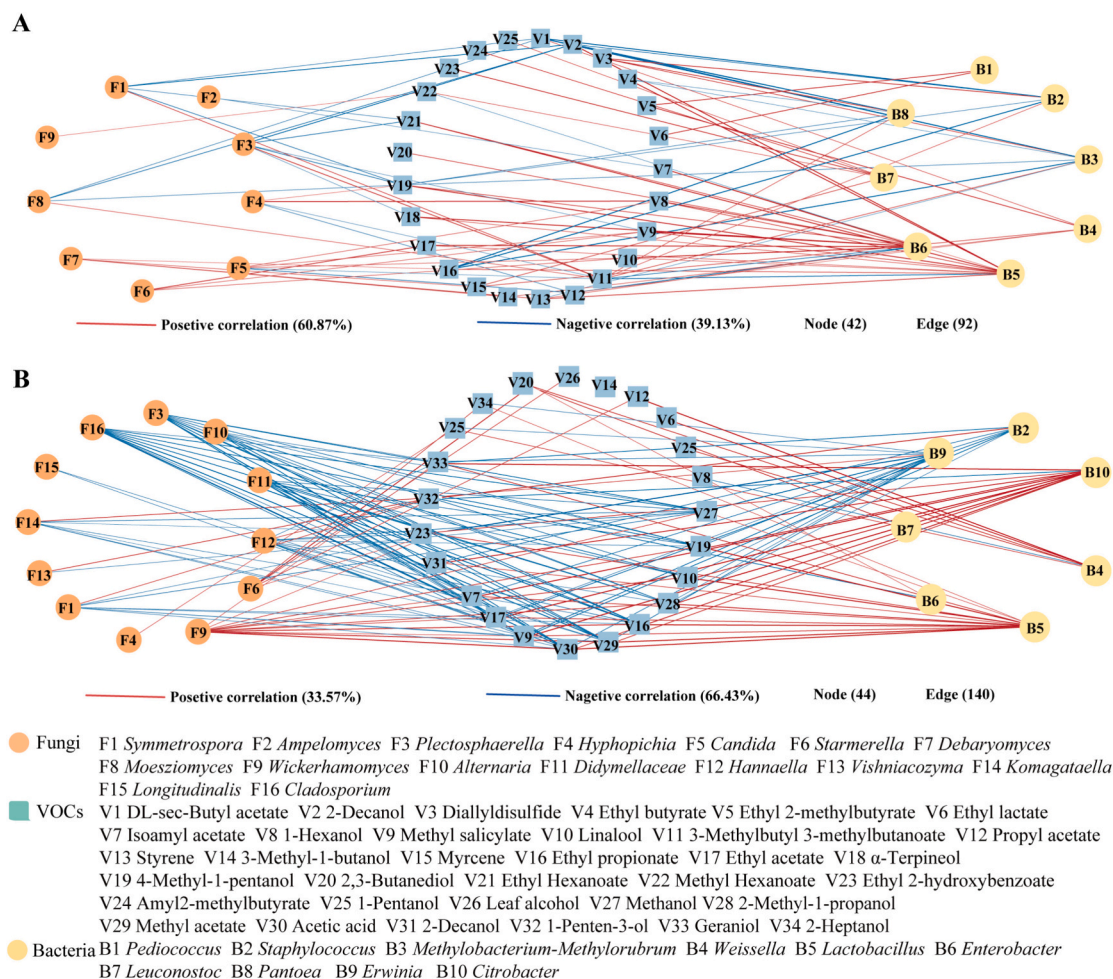
### 3.5. Correlation analysis between core microorganisms and flavor components

As fermentation relies on microbial metabolism, microorganisms play a crucial role in generating typical fermentative flavors (Ampemohotti et al., 2025). Microbial metabolism underpins fermentation and is essential for the development of characteristic fermentative flavors (Zhang et al., 2023). To clarify the associations between microbial taxa and volatile metabolite production, correlation analyses were performed between key volatiles (VIP > 1.0; Fig. 5) and dominant microbial communities (Fig. 2D, E, 3D, and E). Only strong ( $|r| > 0.70$ ) and significant ( $p < 0.05$ ) correlations were considered. In total, 92 and 140 significant metabolite-microbe association pairs were identified in the XML and ZZJ pepper varieties, respectively (Fig. 7A, B), suggesting key contributors to flavor development during fermentation.

In XML, fungi were positively correlated with flavor compounds, including *Debaryomyces* (F7), *Candida* (F5), and *Starmerella* (F6). Among these, *Debaryomyces* was associated with the highest number of flavor compounds, exhibiting positive correlations with 3-methyl-1-butanol (V14, fruity), ethyl propionate (V16, fruity), myrcene (V15, herb), and styrene (V13, balsamic). *Debaryomyces* is a key functional fungus in traditional dry sausages and is significantly correlated with volatile compounds, such as ethyl acetate and methyl hexanoate (Wen, Sun, Li, Chen, & Kong, 2021). Our study also showed that *Debaryomyces*

positively correlated with ethyl propionate formation. In XML, fungi including *Plectosphaerella* (F3), *Symmetrospora* (F1), and *Moesziomyces* (F8) negatively correlated with flavor compounds. *Lactobacillus* (B5) and *Enterobacter* (B6) are the two primary bacterial species that play crucial roles in flavor formation. Both species positively correlated with nine volatile compounds, primarily esters, alcohols, and terpenes. *Lactobacillus* and *Enterobacter* are critical microorganisms that influence the quality of fermented foods and, play key roles in the development of aroma and taste (Cui et al., 2019; Li et al., 2024). Since certain species within the genus *Enterobacter* may act as opportunistic pathogens, species-level identification of this genus is critical. Therefore, further culturing and species- and strain-level identification of *Enterobacter* during pickled pepper fermentation are warranted.

The interactions between microorganisms and flavor compounds in ZZJ were more complex (Fig. 7B). Similar to XML, *Starmerella* is a key fungus that is positively correlated with flavor compounds and is involved in the formation of five distinct flavor compounds. Compared to XML, *Wickerhamomyces* (F9) played a more significant role in ZZJ flavor, being positively correlated with 12 flavor compounds, including 6 esters, 3 alcohols, 2 terpenes, and 1 acid. It is the primary fungus in ZZJ that promotes the formation of flavor compounds. *Wickerhamomyces* metabolizes carbohydrates and proteins to produce volatile aldehydes, esters, and alcohols, thereby enhancing the flavor of fermented products. It is a crucial microorganism in fermented foods like pepper paste (Chen et al., 2022), wine (Wang et al., 2023), and kiwi wine (Li et al., 2022). Notably, 3 fungi, *Plectosphaerella*, *Cladosporium* (F16), and



**Fig. 7.** Correlation network diagram of dominant microorganisms and flavor compounds during pickled pepper fermentation. *Xiaomila* fermentation (A); *Zhuzijiao* fermentation (B).

*Alternaria* (F10) were significantly negatively correlated with several flavor compounds in ZZJ. Inhibiting the growth of these fungi during fermentation or utilizing them to regulate pepper flavor may be novel approaches. In addition to *Lactobacillus* and *Enterobacter*, which are also present in ZZJ, *Citrobacter* (B10) and *Weissella* (B4) also promote the formation of flavor compounds. *Lactobacillus* was the bacterium most strongly associated with volatile compounds and exhibited the highest correlation with acetic acid (V30, vinegar), a finding consistent with results from rice wine fermentation analyses (Qian et al., 2024). *Citrobacter* was correlated with eleven compounds, with the strongest positive correlation observed for geraniol (V33, floral).

#### 4. Conclusion

This study reveals that pepper varieties significantly influence microbial succession and volatile compound formation during pickled pepper fermentation. Key physicochemical indices, including salinity, pH, TA, and nitrite levels, directly influenced microbial succession and volatile compound production. XML exhibited higher shared bacterial OTUs and divergent fungal succession patterns, while ZZJ showed *Wickerhamomyces* dominance. *Lactobacillus* was the dominant microorganism during the later stages of fermentation in both pepper varieties. Ethyl acetate, linalool, and acetic acid, as critical flavor markers, strongly correlated with *Lactobacillus*, *Enterobacter*, and fungi (*Debaryomyces* in XML, *Wickerhamomyces* in ZZJ). These findings propose actionable industrial strategies, such as designing targeted starter cultures through the inoculation of *Lactobacillus* and *Wickerhamomyces* to

standardize flavor profiles, with concurrent implementation of nitrite and mycotoxin monitoring protocols to mitigate potential health risks associated with traditional fermentation practices. Additionally, alongside implementing quality control protocols through microbial marker monitoring and volatile compound tracking of fermentation progress while maintaining food safety standards. This study was conducted under controlled lab-scale conditions, temperature fluctuations, brine homogeneity, and raw material variability should be control in industrial-scale production. Future research should validate these findings in industrial settings and explore engineering microbial consortia to optimize flavor profiles. Collectively, this work establishes a theoretical foundation for refining fermentation processes and advancing product quality in the pickled pepper industry.

#### CRediT authorship contribution statement

**Qi Huang:** Writing – original draft, Visualization, Software, Formal analysis, Data curation, Conceptualization. **Cen Li:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Yongjun Wu:** Writing – review & editing, Supervision, Project administration, Investigation. **Shuoqiu Tong:** Writing – review & editing, Investigation. **Lincheng Zhang:** Writing – review & editing, Investigation. **Jing Jin:** Writing – review & editing, Investigation. **Qiyang Zhu:** Writing – original draft, Data curation. **Yan Yan:** Writing – review & editing, Formal analysis, Data curation.

## 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.fochx.2025.102551>.

## Data availability

Data will be made available on request.

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