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Analytical Methods

Phage succession and putative mechanisms of microbial community regulation in Sichuan radish paocai (traditional Chinese fermented vegetable)

Yuli Huang [a,b], Menglu Yang [b], Jiaqi Liu [b,c], Min Zhang [b,c], Petri Penttinen [a,d], Lingzi Zhang [a], Lihong Ge [c], Xiaoping Zhang [a,*], Nan Zhao [b,*]

[a] College of Resources, Sichuan Agricultural University, Chengdu, China
[b] Institute of Agro-products Processing Science and Technology (Institute of Food Nutritional and Health), Sichuan Academy of Agricultural Sciences, Chengdu, China
[c] College of Life Science, Sichuan Normal University, Chengdu, China
[d] Faculty of Agriculture and Forestry, University of Helsinki, Helsinki, Finland

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ABSTRACT

Spontaneous fermentation of Sichuan paocai is shaped by complex microbial and environmental factors, yet phage communities remain understudied. This study presents integrated viromic and metagenomic analysis of radish paocai combined with metabolite profiling to elucidate phage diversity, dynamics, ecological roles, and sources. Time-series metagenomics revealed *Lactiplantibacillus* increasing from 11% to 71%, while viromics showed phages comprising 78% of viral contigs, with Uroviricota reaching 88% by day 5. Host prediction indicated that 89% of phages targeted *Lactiplantibacillus*, mainly *L. plantarum*. Correlation analysis suggested that core phages were associated with fermentation-related metabolites, including volatile compounds (e.g., decanal), implicating that phages might influence metabolism by modulating host activity. Functional annotation showed phage encoded amino acid and carbohydrate metabolism genes, suggesting auxiliary metabolic roles. Source analysis suggested that most phages in radish paocai may be derived from bacterial prophages. This work advances understanding of phage diversity and ecological function in fermented vegetable ecosystems.

1. Introduction

Sichuan paocai, a traditional Chinese fermented vegetable with a history of over 3500 years, is widely appreciated for its unique probiotic and nutritional properties shaped by microbial communities during fermentation (Zhao et al., 2024). Although modern paocai production has largely shifted from traditional spontaneous fermentation toward starter inoculation to ensure product consistency, fermentation with a synthetic keystone microbiota starter did not reproduce the unique quality flavour of spontaneously fermented paocai (Zhao et al., 2023). The unique quality of paocai is mainly attributed to bacterial genera *Lactiplantibacillus*, *Pediococcus*, *Levilactobacillus*, and *Secundilactobacillus*, as well as fungal genera *Kazachstania* and *Debaryomyces* (Huang et al., 2022; Kang et al., 2024; Xu et al., 2024; Yang et al., 2025). Such microbial community complexity is the cornerstone of industrial brine fermentation. Previous studies have primarily focused on bacteria, fungi, and their associations with flavour compounds (Hao et al., 2025; Zhao et al., 2025), whereas the viral component of the fermentation system—particularly phages—has received limited attention.

Phages are among the most abundant and diverse regulators of microbial communities in natural ecosystems, where they shape host population dynamics, metabolic processes, as well as microbial evolution (Jansson & Wu, 2023; Shkoporov & Hill, 2019). Additionally, phages exert species specific control that can alter fermentation outcomes in food production (Du et al., 2023; Kang et al., 2022; Ma et al., 2024). For instance, phages modulate *Clostridium* metabolism in cheese (Ávila et al., 2023), delay rind discolouration by targeting *Brevibacterium* (Melo de et al., 2023), and inhibit spoilage bacteria in wine fermentation (Du et al., 2023). While phages have been extensively studied in various food fermentation systems, their specific roles in Sichuan paocai are yet to be fully understood.

Previous studies have revealed phages present in Sichuan paocai, including a large number of lactic acid bacteria (LAB) infecting phages. These phages coexist with their host strains through strain-level

* Corresponding authors.
E-mail addresses: zhangxiaopingphd@126.com (X. Zhang), demonzn1115@163.com (N. Zhao).

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selection and play an important role in maintaining the stability of the fermentation ecosystem (Yang et al., 2025). In vegetable fermentation, phage communities display higher sensitivity to geographic origin than bacterial communities, which further highlights their ecological importance (Kang et al., 2022; Ma et al., 2024). However, it remains unclear how phages interact with dominant LAB populations during Sichuan paocai fermentation and whether such interactions contribute to microbial succession and fermentation-related metabolites.

Therefore, this study aimed to elucidate the diversity, dynamics, and ecological roles of phages in Sichuan paocai fermentation, with a particular focus on their interactions with bacterial communities and their potential contributions to fermentation performance. To achieve this, viromic and metagenomic approaches were employed to characterize both phage and bacterial communities during radish fermentation. By integrating virome and microbiome datasets, we identified phage hosts, lifestyles, and temporal dynamics, and explored their relationships with microbial composition and fermentation-related metabolites. In addition, potential sources of microbes and phages (fresh vegetables, rhizosphere soil, and induced prophages) were comparatively analysed. The results improve our understanding of the potential ecological roles of phages in the Sichuan paocai fermentation and provide a foundation for future studies aimed at managing fermentation microecosystems and exploring raw material associated microbial inputs.

2. Materials and methods

2.1. Sample collection

2.1.1. Preparation of fermented radish

To improve the representativeness of the experimental system, the fermentation conditions were established with reference to industrial low-salt Sichuan paocai production and previous reports (Yang et al., 2025; Zhao et al., 2023). Fresh radishes (*Raphanus sativus*) were washed, dried, and cut into 1 × 1 × 4 cm strips. Brine containing 4% salt was prepared using boiled water, and the radish and brine were fermented at a ratio of 1:1 (w: v) in 500 mL sealed glass bottles. A total of 15 bottles were prepared and fermented in a constant temperature incubator at 25 °C for 5 days. Three bottles were taken as three parallel samples on days 0, 1, 2, 3, and 5 for analysis. Microbial growth in the brine was determined immediately. Radish samples used for the analysis of physicochemical properties and distribution of organic acids were stored at −20 °C, whereas the brine samples used for the analysis of the metagenome and viral metagenome were stored at −80 °C.

2.1.2. Collection of fresh radishes and rhizosphere soil

Fresh radishes were collected following a three-point sampling method in a radish planting base (30°17′N, 104°4′E) in Chengdu, Sichuan, China, in February 2024. As described Sugihara et al. (2021) and Eze and Amuji (2024), the soil around the radish was pried loose with a shovel, and the radish was gently pulled out of the soil. Thereafter, the soil loosely attached to the root system was first shaken off, leaving rhizosphere soil strongly adhering to the root surface. The rhizosphere soil was brushed gently from the surface (≤3 mm from the root of radish) of the radish using a sterilised brush and collected in a sterilised container. Samples were gathered in pre-sterilised containers and transported to the laboratory on ice. The fresh radishes and rhizosphere soil were stored at −80 °C for metagenomic and viral metagenomic analysis, each containing three parallel samples.

2.2. Microbial counts and fermentation-related metabolites

To determine the microbial counts in fermented radish, fresh radish, and rhizosphere soil, the samples were diluted with sterile physiological saline under sterile conditions (Zhao et al., 2024) The diluted samples were inoculated onto Plate Count Agar (PCA), MRS agar, and Bengal Red agar, and the total number of bacteria, LAB, as well as yeast colonies were counted separately (Huang et al., 2022). The PCA and MRS agar plates were incubated at 37 °C for 3 days, whereas the Bengal Red agar plates were incubated at 30 °C for 3 days. The microbial counts were documented as log colony-forming units (CFU)/g.

pH, titratable acidity (TA), and contents of reducing sugar, nitrite, and organic acids (lactic, acetic, citric, malic, and succinic) were determined following established protocols (Huang et al., 2022; Zhao et al., 2024). For pH measurement, 5 g of vegetable samples were homogenised with 45 mL of distilled water, and pH was determined using a pH meter (FiveEasy Plus™, Mettler Toledo, Switzerland). TA and reducing sugar content were measured after lyophilising 2 g of samples, homogenising with ultrapure water, and applying ultrasound-assisted extraction. TA was determined via titration with 0.1 M NaOH to pH 8.5 and expressed as g/kg, with lactic acid as a standard. The reducing sugar was quantified by the 3,5-dinitrosalicylic acid method, with absorbance measured at 540 nm and results expressed as g/100 g. Nitrite content was determined using the diazotisation method. Briefly, 5 g of fermented radish was homogenised with saturated borax solution and treated with potassium ferrocyanide and zinc acetate to precipitate the proteins, followed by color development with sulphanilic acid and N-(1-naphthyl) ethylenediamine dihydrochloride. Absorbance was measured at 538 nm, and concentrations were calculated using a standard curve.

For organic acid analysis, 2 g of vegetables were extracted with 0 0.004 M H_2SO_4 via ultrasonication, followed by centrifugation and filtration (0.22 μm). The brine samples (1 mL) were filtered directly. Organic acids were quantified at 35 °C using a high-performance liquid chromatography (HPLC) machine (Agilent 1260, Agilent Technologies, USA) equipped with a UV detector and Aminex HPX–87H column (300 × 7.8 mm, Bio-Rad, USA). The mobile phase consisted of 0.004 M H_2SO_4 supplied at 0.6 mL/min. Each measurement was performed in triplicate, and the results were expressed as g/kg.

Volatile compounds were extracted, identified, and quantified by SPME Arrow (120 μm DVB/CWR/PDMS) coupled with Agilent 8890 GC system equipped with a 5977B MS detector (Agilent Technologies, USA), following the methods of Mei et al. (2023) and Zhao et al. (2023) with minor modifications. Briefly, 5 g of homogenised sample was mixed with 3 g NaCl and 10 μL methyl octanoate (73 μg/mL) as an internal standard in a 20 mL headspace vial. After equilibration at 50 °C for 15 min, the SPME Arrow fiber was exposed to the headspace for 45 min at the same temperature, then thermally desorbed in the GC injector at 270 °C for 5 min in splitless mode. Separation was performed on a DB-WAX (30 m × 0.25 mm × 0.25 μm, Agilent Technologies, USA) capillary column with helium (>99.99%) as carrier gas at 1.0 mL/min. The oven temperature program was as follows: 40 °C for 5 min, ramped at 4 °C/min to 100 °C, then at 6 °C/min to 230 °C, and 230 °C for 10 min. MS parameters were set as follows: electron ionization (EI) mode at 70 eV; Transfer line, 250 °C; Ion source, 230–250 °C; Mass scan range, *m/z* 30–450; Solvent delay, 3 min. Volatile compounds were identified by comparing mass spectra with the NIST 2020 library (similarity >800), along with retention indices (RIs, C4–C30 n-alkanes) and retention times. Quantification was performed based on the internal standard method. All measurements were performed in triplicate.

2.3. Microbial metagenomics

2.3.1. DNA extraction, library construction, and metagenomic sequencing

Based on the physicochemical properties of the fermented radish, samples were collected on days 0, 2, and 5 of fermentation, along with brine, fresh radish, and rhizosphere soil, for comparative analysis. A 40 mL aliquot of fermentation brine was collected and centrifuged at 10,000 ×*g* for 10 min to obtain a precipitate. In addition, 5 g of rhizosphere soil and 5 g of fresh radish were collected for analysis. 100 mg of the samples that passed the quality control assessment were subjected to DNA extraction using an ALFA-SEQ Plant DNA Kit (Findrop Biosafety Technology Co., Ltd., Guangzhou, China). Samples were analysed on a

Qsep400 High-Throughput Nucleic Acid-Protein Analysis System (Houze Biotech, Hangzhou, China) to determine fragment size, and library concentration was measured using Qubit4.0 (Thermo Fisher Scientific, Waltham, MA, USA). Paired-end sequencing was performed on an Illumina NovaSeq 6000 PE150 platform (Illumina Inc., CA, US) at the Magigene Company (Guangzhou, China) according to the manufacturer's protocol.

2.3.2. Bioinformatics analysis

Raw sequencing reads were subjected to quality control using Trimmomatic (parameters: LEADING:3, TRAILING:3, SLIDINGWINDOW:5:20, and MINLEN:50) to remove sequencing adapters and low-quality bases. Reads derived from the host were filtered out by mapping against the *Raphanus sativus* reference genome with Burrows-Wheeler Aligner (BWA) (http://bio-bwa.sourceforge.net) and Bowtie2 (http://bowtie-bio.sourceforge.net/bowtie2/index.shtml). The quality of the remaining sequences was assessed using FastQC (http://www.bioinformatics.babraham.ac.uk/projects/fastqc/). De novo assembly of quality-controlled reads was performed with MEGAHIT (https://github.com/voutcn/megahit), using k-mers ranging from 35 to 95 with a step of 20 to produce contigs. Contigs containing ambiguous bases (N) were split at consecutive Ns to generate N-free fragments (scaftigs). Scaftigs shorter than 500 bp were discarded. Open reading frames (ORFs) were predicted using Prodigal (https://github.com/hyattpd/Prodigal), and ORFs shorter than 90 bp were excluded. To reduce redundancy, predicted genes were clustered using Linclust (default parameters: -e 0.001, −-min-seq-id 0.9, −c 0.80), and the longest sequence within each cluster was retained as the representative sequence, ultimately yielding a non-redundant gene catalogue (Unigenes). Thereafter, the Unigene sequences were annotated by homology search against the NCBI-NR database using BLASTP (version 2.2.31+, http://blast.ncbi.nlm.nih.gov/Blast.cgi) with a significance threshold e-value $\leq$1e−4.

2.4. Viral metagenomics

2.4.1. Virome extraction and sequencing

Virus-Like Particle (VLP) enrichment and subsequent nucleic acid extraction was performed by Magigene Company (Guangzhou, China) as described in Yang et al. (2025). The samples were initially subjected to tissue fragmentation and homogenisation, followed by low-speed centrifugation to remove tissue and cellular debris. Finally, VLP purification and concentration were achieved via reduced ultracentrifugation at 4 °C and 160,000 ×g for 2 h. DNA was extracted from the viral fractions, and a shotgun metagenomic library was constructed by multiple displacement amplification. Paired-end sequencing with 150-bp read lengths was performed on an Illumina HiSeq platform, attaining approximately 10 Gb sequencing depth.

2.4.2. Quality control, assembly, and viral identification

Adapter-containing reads, low-quality bases and sequences, duplicated reads potentially derived from PCR amplification, and PolyX-containing reads were removed using Fastp (v0.23.2). Host-derived sequences were removed by aligning the quality-controlled reads to the *Raphanus sativus* reference genome using BWA-MEM (v0.7.17, parameter: -k 30). Reads with alignment coverage $\geq$80% of their length were considered host-derived and discarded. De novo assembly of the remaining reads was performed using MEGAHIT v1.1.2 (−-presets meta-large –min-contig-len 300). The resulting contigs (hereafter referred to as viral contigs after host filtering) were annotated with CheckV to assess completeness. Viral sequences were identified using both the Magigene viral database (v4) and VirSorter2 (high-confidence category), with results combined to maximise sensitivity. Redundant sequences were clustered with CD-HIT (PSI-CD-HIT script) at 95% sequence identity and 90% coverage. Taxonomic classification of viral contigs was further refined using PhaGCN2. The quality-controlled reads were mapped back to the identified viral contigs, and viral abundance was quantified as reads per kilobase per million mapped reads (RPKM).

2.4.3. Host prediction, lifestyle prediction, and function annotation

Viral host prediction was performed using CHERRY, a deep learning framework combining graph-convolutional encoding and link-prediction decoding to infer virus–host interactions. Predictions were filtered based on a score threshold >0.9 to ensure high confidence, and manual curation to exclude eukaryotic viral entries. Viral lifestyle (lytic vs. temperate) was predicted using VIBRANT (https://github.com/AnantharamanLab/VIBRANT). For functional annotation, predicted viral genes were mapped against the KEGG database (v2023.1, https://www.kegg.jp/) using DIAMOND (v2.1.8, e-value $\leq$1e−3). To avoid redundancy, sequences were clustered into non-redundant gene sets, and for each gene, only the hit with lowest e-value was retained for downstream analyses.

2.5. Statistical analysis

Statistical analyses were conducted using one-way analysis of variance (ANOVA), and post hoc comparisons among group means were performed with Duncan's multiple range test at a significance level of $P < 0.05$. Figures were generated in GraphPad Prism 9.0. Mantel test was utilised to assess the strength and significance of associations between microbial community composition and environmental variables, using Euclidean distance matrices and Pearson's correlation coefficient with 999 permutations. Orthogonal partial least squares discriminant analysis (OPLS-DA) and variable importance in projection (VIP) scores were calculated using SIMCA-P software (v14.0, Umetrics, Umeå, Sweden). Correlations were analysed by calculating pairwise Spearman's correlations among phage contigs with relative abundance >1%. Correlation structures were further visualized as heatmaps constructed with the corr plot package in R. Bray-Curtis dissimilarity was visualized using non-metric multidimensional scaling in R packages vegan and ggplot2 in R v.4.5.1.

3. Results and discussion

3.1. Microbial counts and fermentation-related metabolites of radish paocai

Overall, microbial counts changed over the course of fermentation. At the beginning of the fermentation process, fungi and total bacteria counts were low, possibly attributed to their infrequent presence on fresh radish (Fig. 1A). Total bacteria and LAB counts increased in a similar manner over fermentation time, reaching maximum values at day 5, implying that radish fermentation was primarily performed by the LAB. Furthermore, fungi (mainly yeasts) were also reported to participate in fermentation based on a complementary action pattern and generated flavoured compounds throughout the process (Zhao et al., 2025). In our study, fungi initially increased till day 2, and subsequently decreased.

Previous research on fermented vegetables has already established the impact of abiotic factors on microbial counts and communities (Zhao et al., 2024). In our study, pH decreased from approximately pH 6 to pH 4.3 and titratable acidity increased over fermentation time (Fig. 1B), possibly due to the increased LAB population. During days 3–5 of fermentation, reducing sugars were undetectable, suggesting rapid microbial consumption of sugars as a carbon source (Ge et al., 2024). Nitrite is a predominant nitrogen compound in fermented vegetables and may potentially compromise the safety and quality of pickles (Wang, Huang, et al., 2025). Nitrite concentration peaked on fermentation day 2 and subsequently decreased close to detection level, indicating the safety of the fermented radish.

Organic acids reflected the microbial metabolic shifts in vegetable fermentation (Wang, Liu, et al., 2025). Consistent with previous findings (Zhao et al., 2022), succinic acid, malic acid, citric acid, and acetic acid

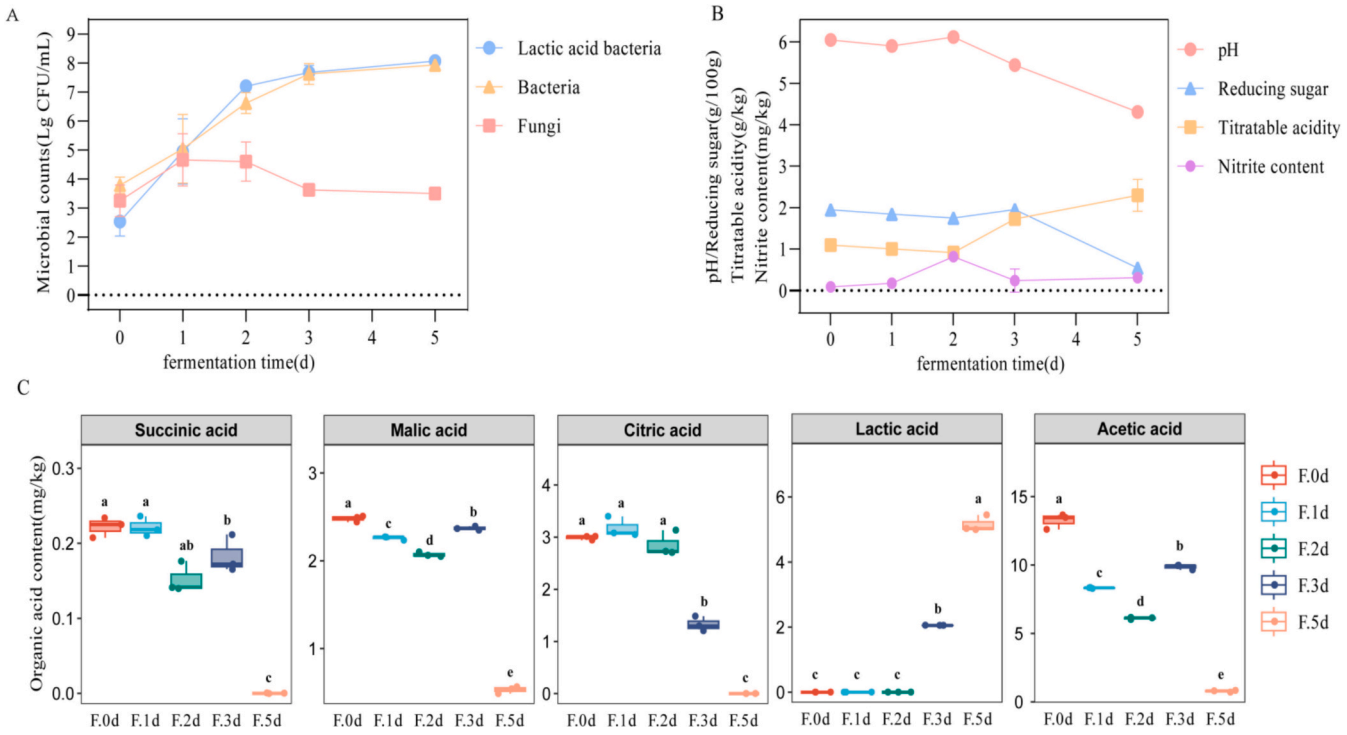

Fig. 1. Dynamics of microbial and physicochemical parameters during fermentation. (A) Microbial counts. (B) Physicochemical properties. (C) Organic acid profiles. Different lowercase letters above bars indicate statistically significant differences among time points ($P < 0.05$, one-way ANOVA with Tukey's test).

were all detected in large quantities during the initial fermentation stage (Fig. 1C). Their levels then gradually diminished as fermentation proceeded, implying that these organic acids originated from the fresh radish. In contrast, lactic acid was undetectable in the first 2 days of fermentation, but its concentration increased steadily after this period. By day 5, lactic acid reached 5.2 ± 0.25 g/kg, indicating fermentation completion (Ge et al., 2024). Based on the results, day 0, the start of the fermentation, day 2, the turning point in fermentation, and day 5, the end of the fermentation, were selected for subsequent metagenomic and viromic analyses.

To characterize volatile compound distribution during fermentation, OPLS-DA combined with VIP score analysis (threshold = 1.0) was applied. The model ($R^2Y = 0.978$, $Q^2 = 0.883$) effectively discriminated volatile profiles across fermentation stages, and 200 permutation tests ($R^2 = 0.644$, $Q^2 = -0.673$) confirmed the absence of overfitting (Fig. 2A-B) (Biancamaria et al., 2023). A total of 51 key differential compounds (VIP ≥ 1.0) were identified (Fig. 2C), spanning isothiocyanates, sulfur compounds, acids, alcohols, aldehydes, ketones, esters, and aromatics. Sulfur compounds and isothiocyanates ($n = 10$) and esters ($n = 8$) were the two most abundant classes. Notably, isothiocyanates and dimethyl trisulfide, responsible for the pungent aroma of fresh radish, were abundant early but declined markedly by day 5, reflecting glucosinolate depletion. Conversely, fermentation-derived compounds including organic acids, esters, alcohols, and aromatic compounds accumulated progressively, with several of them (e.g., phenylethyl alcohol, 2,4-butanediol) absent at day 0 but emerging during fermentation. Overall, these results indicate a transition from a pungent, sulfur-dominated aroma toward a complex, mild flavour profile characterised by fruity, floral, and fermented notes, consistent with flavour evolution reported in other cruciferous vegetable fermentations (Mei et al., 2023; Zhao et al., 2023).

3.2. Microbial diversity and composition during fermentation

After filtering out radish DNA reads, over 842,000 and 42,000 ORFs were identified in the radish rhizosphere and inside the radish, respectively; over 218,000, 77,000, and 26,000 ORFs were identified in radish paocai on days 0, 2, and 5, with GC contents of 59% 51%, and 46%, respectively (Table S1). Similar with Xie et al. (2025), Chao1 and Shannon indices gradually decreased over the course of fermentation (Fig. S1), likely due to the increased dominance of LAB in the communities.

On the average, 83% of the sequences were assigned to bacteria, whereas less than 1% to eukaryota, archaea, or viruses. The microbial community composition was complex and diverse on day 0, containing Proteobacteria, Firmicutes, Actinobacteria, and Acidobacteria (Fig. 3). While Proteobacteria and Actinobacteria are typically thought to be endophytic and periphytic microbes in vegetables (Wei et al., 2023), Actinobacteria, Proteobacteria, and Acidobacteria are common in soil (Hua et al., 2024). In line with the cell counts, Firmicutes dominated on days 2 and 5, aligning with established vegetable fermentation patterns, whereby salty, acidic, and anoxic environment favours Firmicutes over phyla sensitive to the extreme conditions (Louw et al., 2023; Van der Loos et al., 2023).

From day 0 to day 5, the relative abundance of *Lactiplantibacillus* increased gradually, and that of *Leuconostoc* initially increased and then decreased, suggesting that radish fermentation began as heterolactic and subsequently progressed to homolactic fermentation. Zhou et al. (2023) also identified *Lactobacillus* and *Leuconostoc* as core bacterial genera in the radish paocai during spontaneous fermentation and found that LAB produced lactic acid via homolactic fermentation in the late fermentation period. L. *pentosus* and *L. plantarum*, the major species identified on fermentation day 5, are considered probiotics and found naturally in the human body and fermented foods (Nguyen & Nguyen, 2024).

The species level taxonomic composition of fresh radish, rhizosphere soil and paocai at day 0 were similar (Fig. S2), implying that the initial microbial load originated from epiphytic/endophytic or soil organisms. In the Bray-Curtis dissimilarity based NMDS, fresh radish and fermentation day 0 samples clustered together, slightly supporting a conclusion that the paocai communities were mostly from the fresh radish (Fig. S4A). The results aligned with previous findings, indicating that

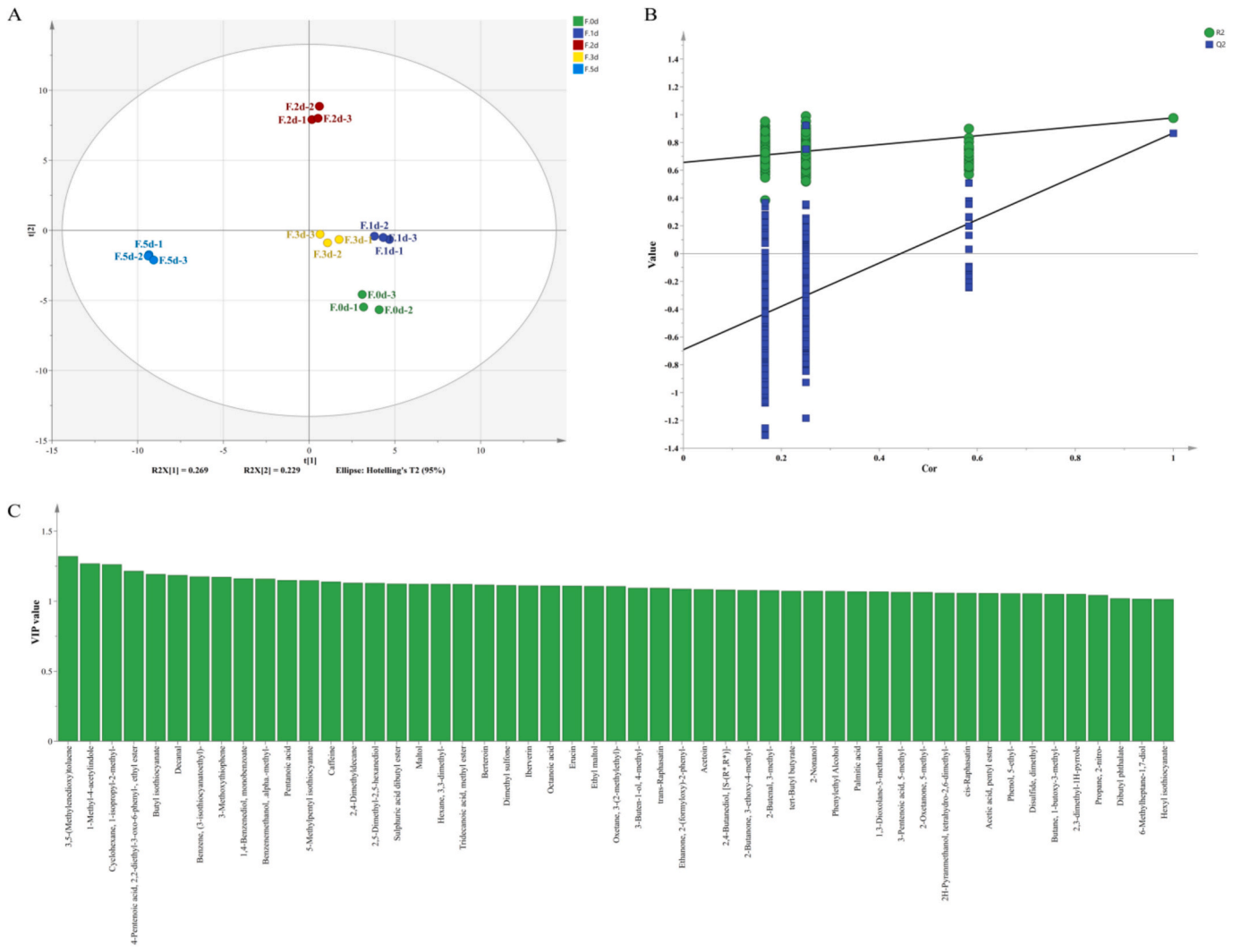

Fig. 2. OPLS-DA analysis of volatile compounds during fermentation. (A) OPLS-DA score plot of samples at different fermentation stages. (B) Statistical validation of the OPLS-DA model by permutation test (200 times). (C) Variable Importance in Projection (VIP) values of differential metabolites.

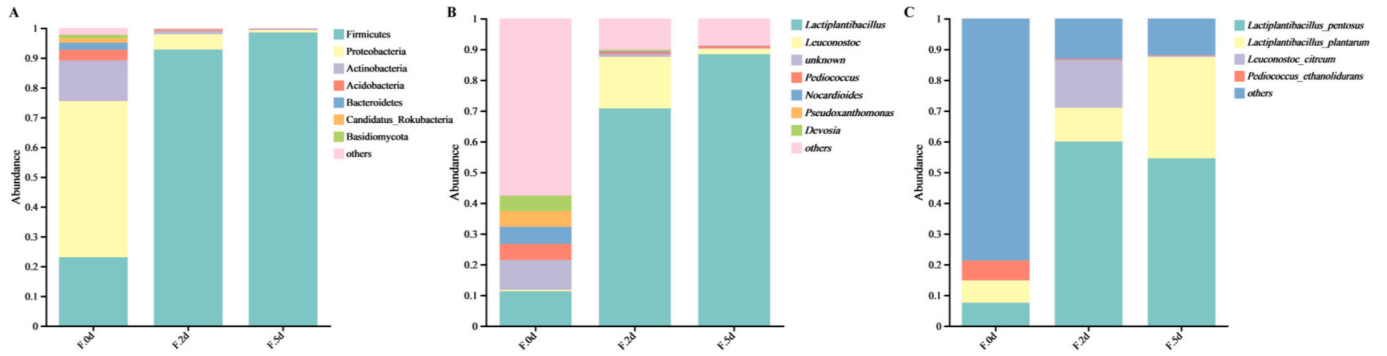

Fig. 3. Temporal changes in microbial community composition during fermentation. (A) Phylum-level composition. (B) Genus-level composition. (C) Species-level composition. Relative abundance is shown as percentage of total sequences.

fermented foods provide a stable, resource-rich, relatively simple, and less competitive ecosystem. This ecological niche often harbours higher microbial density, but its diversity is notably lower than in other microbial habitats (Du et al., 2023).

3.3. Phage composition and diversity during fermentation

After filtering out radish DNA reads, 78% and 4.2% of the reads were assigned to phages and other viruses, respectively. Although viral metagenomics captures a broad spectrum of viruses, bacteriophages dominated the viral community in this study; therefore, the term "phage" is used where appropriate to reflect host-specific interactions. Overall, the

alpha diversity exhibited different trends in the virome than in the microbiome, consistent with the results on other fermented foods (Zhang, Zhang, Du, Yu, & Xu, 2025); in the radish paocai, Both Chao1 and Shannon indices were slightly higher on fermentation day 2 than in the beginning or on day 5.

A total of 14,065 contigs were divided into 35 families using the traditional taxonomic classification system (ICTV 2021) (Zhang, Zhang, Du, Zhang, et al., 2025). On fermentation day 0, the relative abundances of phylum Uroviricota and Phixviricota were 55% and 23%, respectively (Table S2), whereas on days 2 and 5, the relative abundances of Uroviricota were over 85% and that of Phixviricota below 1%. At the family level, most of the reads remained unidentified (Table S2), which indicated a large number of new, unannotated viruses in the paocai fermentation process. This occurrence of unmatched viral sequences in sequence reference databases is termed "viral dark matter" in viral metagenomics research. It is primarily caused by the paucity of entire viral genome sequences from various samples in reference databases and the rapid rate of viral evolution (Santiago-Rodriguez & Hollister, 2022).

To identify core phages in the fermentation system, an integrated strategy combining occurrence frequency, relative abundance, and co-occurrence network analysis was employed. Phage contigs detected in more than 80% of all samples were first selected as high-frequency members of the phage community. Meanwhile, contigs with a relative abundance greater than 1% were subjected to co-occurrence network analysis, and highly connected contig nodes were further screened (Fig. 4A). Co-occurrence network analysis provided the information on the cooccurrence pattern of phage contigs which might play crucial roles in stabilizing the virome structure. Network analysis showed that these contigs exhibited degree values ≥5, indicating strong associations within the phage community. Ten phage contigs simultaneously meeting the criteria of occurrence frequency > 80%, relative abundance >5%, and network degree ≥5 (Fig. 4B) were defined as core phages (Zhao et al., 2023; Guo et al., 2022; Lin et al., 2023).

Out of all phage contigs, 1699 were identified as lytic and 73 as lysogenic. Lytic phages may directly impact both the structure and diversity of the fermentation microbiota, whereas lysogenic phages could contribute to fermentation processes by transitioning to the lytic cycle during unfavourable bacterial growth periods (Du et al., 2023). Three of the core phage contigs were lytic, whereas the lifestyle of seven core phages remained unknown (Fig. 4C). As viruses lack independent metabolic capacity, they require compatible hosts for replication. The predicted host of four core phage contigs was L. *plantarum*, aligning with the other results showing *Lactiplantibacillus* as the dominant microbial genus in the radish paocai. Both lytic and lysogenic phages are capable of infecting *Lactiplantibacillus*. Previous studies have shown that L. *plantarum* strains isolated from pickles harbour at least one complete prophage (Park et al., 2022). Furthermore, fermentation could induce these prophages to transition into the lytic cycle (Thierry et al., 2023).

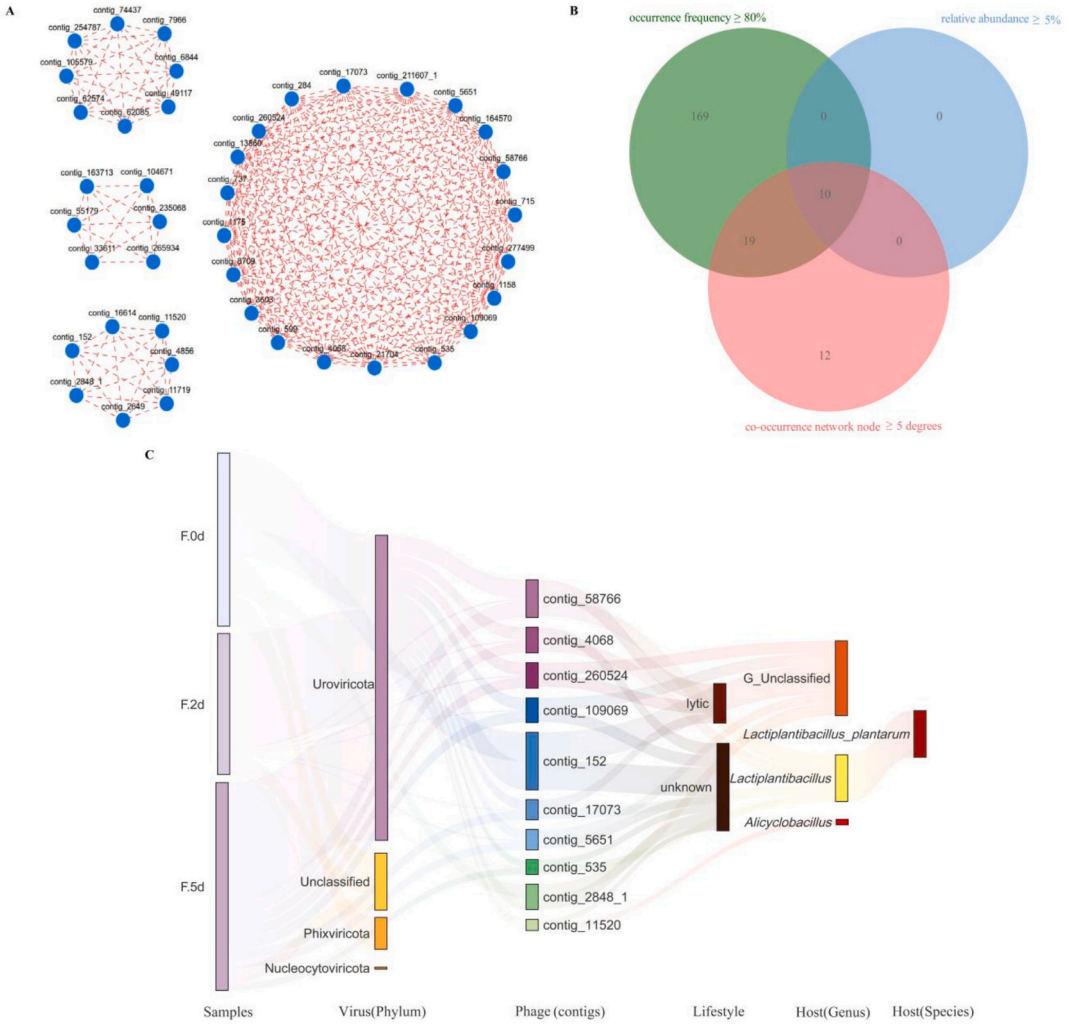

Fig. 4. Core phages and phage host and lifestyle in fermented radish. (A) Co-occurrence networks of contigs with relative abundance > 1%. (B) Venn diagram of dominant phage contigs, co-occurring phage contigs and occurrence frequency phage contigs in radish paocai. (C) Predicted associations between core phage contigs and bacterial hosts (genus/species level). Connection line colors represent bacterial phyla, while line thickness corresponds to the number of predicted host linkages.

Lactobacillus rhamnosus Pen was previously shown to spontaneously release phage BH1. This strategy conferred resistance to other phages, thereby enhancing bacterial colonisation and survival within its ecological niche (Jarocki et al., 2019). Consequently, the dominant microorganism in radish paocai, *L. plantarum*, might employ a similar colonisation strategy.

3.4. KEGG analysis of potential phage regulation

In total, phage genes were assigned to KEGG pathways mainly in five major functional categories, including metabolism, genetic information processing, cellular processes, environmental information processing, and organismal systems (Fig. 5A). A total of 680 genes were mapped to metabolic pathways, indicating a substantial repertoire of phage-encoded genes potentially associated with metabolic functions. Among these, 165 phage genes were annotated to amino acid metabolism and 223 to carbohydrate metabolism, suggesting that these metabolic activities may represent the most common or active phage related functions in radish paocai. The results showed that multiple metabolic pathways, including carbohydrate metabolism, amino acid metabolism, and fatty acid metabolism, as well as environmental adaptation pathways such as carbon fixation and benzoate degradation, were significantly enriched (Fig.5B). In the carbohydrate metabolism category, there were 29 gene entries in the pathway of starch and sucrose metabolism. For example, the gene encoding fructokinase (*scrK*, K00847) was involved in fructose utilisation, and loss of this gene has been reported to markedly impair the ability of bacterial strains to metabolise fructose (Wu et al., 2025). These results suggested that phages may harbour auxiliary metabolic genes (AMGs), such as *UGP2*, *galU*, and *scrK*, which encoded carbohydrate related enzymes and may assist host microorganisms in degrading and utilising complex sugars, potentially conferring a competitive advantage in polysaccharide rich environments. The butanoate metabolism pathway (ko00650) was also enriched, with a total of 48 gene entries. This pathway was central to the transformation of various short-chain fatty acids (SCFAs). For instance, the *paah* gene (K00074) encoded a 3-hydroxybutyryl-CoA dehydrogenase (EC 1.1.1.157), which participated in specific metabolic routes associated with adipate biosynthesis (Yuan et al., 2025). Within amino acid metabolism, the valine, leucine and isoleucine degradation pathway was enriched with 38 genes entries. Among these, genes encoding aspartate kinase (*lysC*, K00928), serine hydroxymethyltransferase (*glyA*, K00600), and aromatic L-amino acid decarboxylase (*ddc*, K13745) were abundant on fermentation day 2. These enzymes were involved in key steps of lysine biosynthesis, glycine and serine metabolism, and biogenic amine formation, respectively. Collectively, these observations indicated that phage-associated genes may be linked to metabolic processes related to flavour development during fermentation (Du et al., 2023). To sum up, phages may contribute to host metabolic modulation by introducing auxiliary metabolic genes (AMGs) into host genomes via horizontal gene transfer (HGT) and lysogenic conversion, thereby potentially influencing host metabolic capacity, environmental adaptability, and ecological niche differentiation (Sousa De et al., 2023; Huang et al., 2024; Tan et al., 2023).

3.5. Relationships between phages, bacteriome, and fermentation-related metabolites

Based on Pearson correlation analysis ($|r| > 0.6$, $p < 0.05$), *Lactiplantibacillus* showed positive correlations with nearly 70% of the phages, while exhibiting a negative correlation with phage contig_152 (Fig. 6A). Similarly, phage contig_2848_1 and contig_11520 were correlated negatively with *Leuconosto* but positively with *Pedicoccus*. The results revealed that both *Lactiplantibacillus* and the phages it hosted increased during fermentation, which suggested a symbiotic relationship between them, as opposed to host killing by phages in an unstable fermentation environment. In environments characterised by high microbial density, for example solid-liquid fermentation, and physicochemical changes, phage-host relationships tend to exhibit fluctuating-

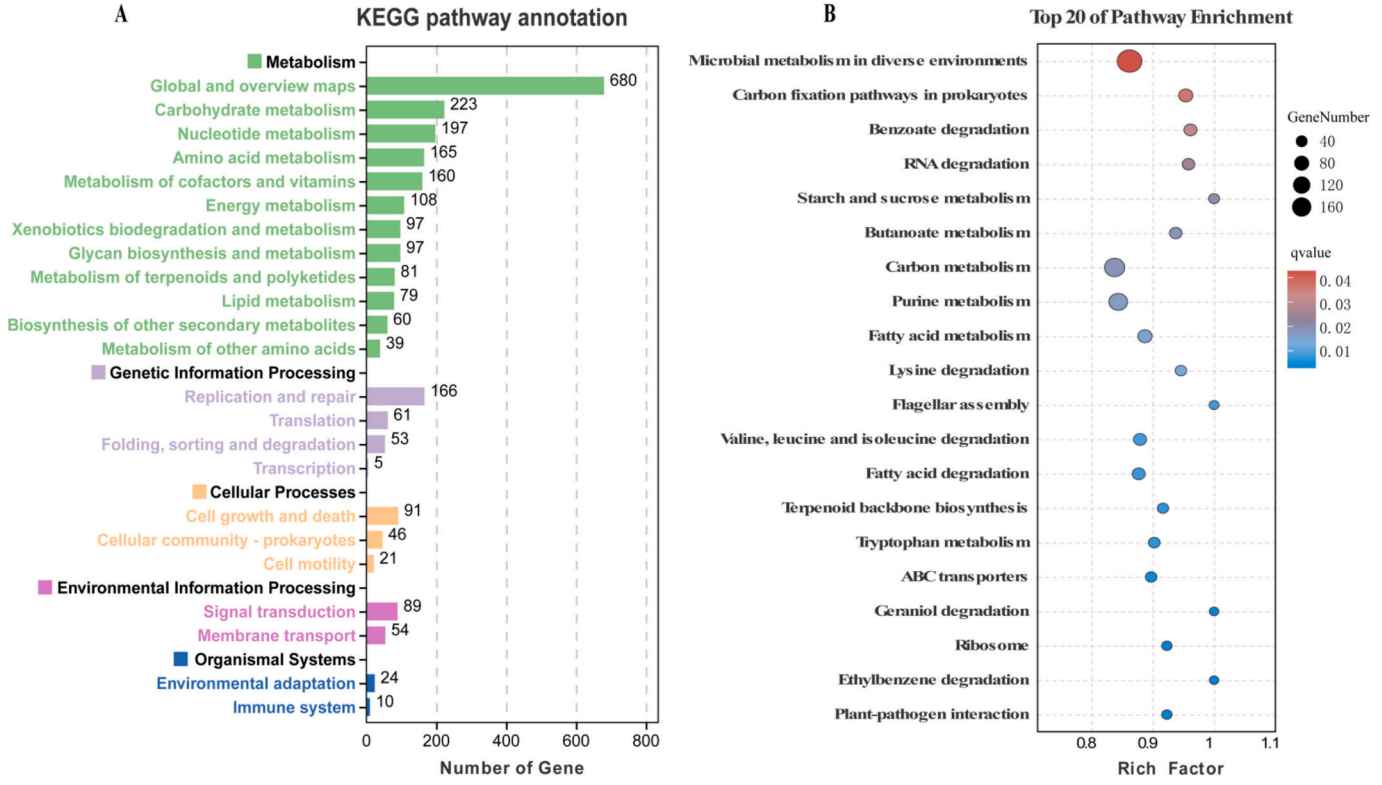

Fig. 5. KEGG pathway enrichment analysis of differentially expressed genes. Dot size represents the number of differentially expressed genes per pathway. Color intensity indicates the significance level (*P* value).

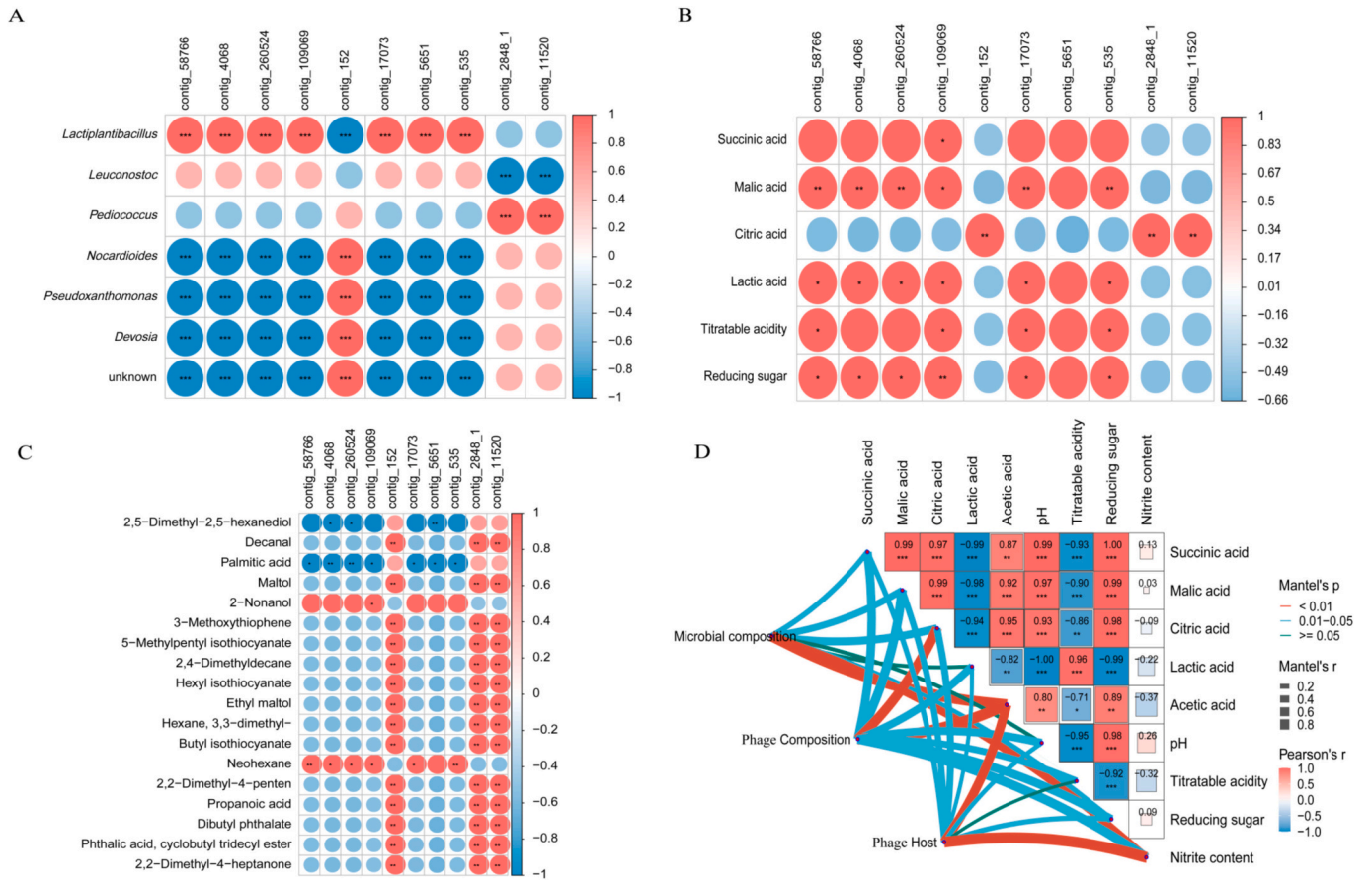

Fig. 6. Correlations among microbial communities, phage populations, and physicochemical factors. (A) Pearson correlations between dominant microbial genera and core phage contigs. (B). Pearson correlations between core phage contigs and key physicochemical parameters. (C). Pearson correlations between core phage contigs and volatile flavour compounds. (D) Mantel test results. Microbial composition was determined based on the genera making more than 5% of total relative abundance; Phage composition was determined based on the core contigs; Phage host was determined based on the predicted numbers of host of the *Lactiplantibacillus* and L. *plantarum*.

selection dynamics. This property allows phages to co-exist with their hosts under various circumstances, both in laboratory and natural conditions (Chen et al., 2024).

Most core phages correlated positively with most of the organic acids, titratable acidity, and reducing sugars, while negatively correlated with pH and citric acid (Fig. 6B). These observations suggested a potential correlation between the fluctuation of core phage abundance and the physicochemical changes related to fermentation. Therefore, phages may reshape the metabolic potential of the host by HGT and indirectly affect the biochemical processes related to fermentation.

In the Pearson correlation analysis, 18 of the 51 key differential volatile compounds correlated with core contigs ($|r| > 0.6$, $p < 0.05$) (Fig. 6C). Two distinct correlation patterns were observed between phages and volatile compounds. Contig_152, contig_2848_1, and contig_11520 correlated positively correlations ($p < 0.01$) with the majority of key volatile compounds, including isothiocyanates, alcohols, and organic acids compounds known to contribute to the characteristic flavour profile of radish paocai (Mei et al., 2023). In contrast, the remaining core phage contigs correlate with only a few compounds, suggesting potential functional divergence among phage groups. These contrasting patterns imply that phages may be indirectly associated with flavour development by modulating bacterial community composition and metabolic activity, potentially through mechanisms such as lysogenic conversion or horizontal gene transfer (Sousa De et al., 2023; Tan et al., 2023).

Microbial composition was associated with succinic acid, malic acid, citric acid, acetic acid, reducing sugar, and nitrite levels in radish paocai (Fig. 6D), further emphasizing the major role of bacteria, especially LAB, during paocai fermentation. Phage composition correlated with all physicochemical parameters. Lactic acid correlated negatively with the other measured organic acids, but positively with total acid content. This suggests that the increase in total acid content observed during radish fermentation was mainly driven by lactic acid accumulation. This finding also aligned with the established acid metabolism pattern in fermented vegetables, characterised by the consumption of citric, malic, acetic, and succinic acids alongside lactic acid generation (Huang et al., 2022). In summary, these results indicated that as fermentation progresses, LAB phages became dominant within the phage community and may modulate lactic acid dynamics by influencing the growth and metabolism of LAB.

3.6. Potential sources of phages in radish paocai

Although phage abundance fluctuated during fermentation and exhibited a correlation with bacterial and physicochemical dynamics, the source of phages in the fermentation system remained unclear. Notably, only 11 phage contigs were shared across all sample types, indicating that the phage population was highly variable in different environments (Fig. 7A). The number of unique contigs was highest on fermentation day 2, exceeding those detected in rhizosphere soil. This suggested that prophages may escape from host microorganisms to the fermentation environment due to variations in acid, salt, and oxygen contents during fermentation. In the fresh radish, Nucleocytoviricota and Uroviricota were the most abundant viral phyla, similar to most

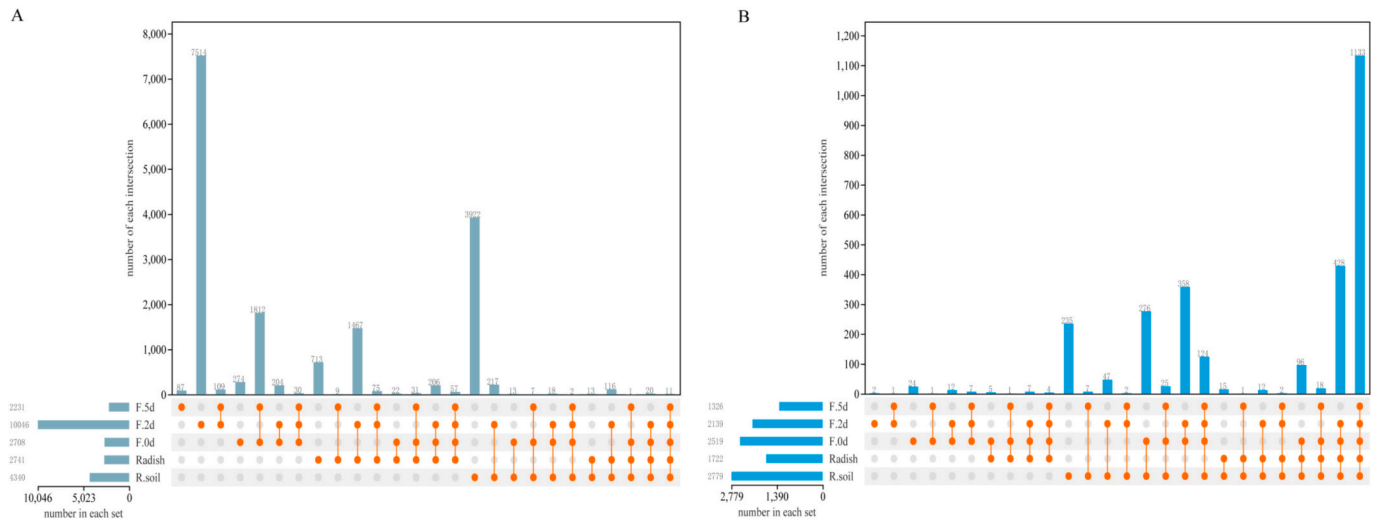

Fig. 7. Upset plots analysis of phage and microbial communities. (A) Phage contigs distribution. (B) Microbial genus distribution. Bottom-left bar plots (Set Size) show total elements per group. Right-side bar plots (Intersection Size) display shared elements across groups. Connected dots represent unique elements specific to group combinations.

characterised viromes in rhizosphere soil (Fig. S5). However, the microbial genus level exhibited a completely different commonality with phage contigs in the Upset plots (Fig. 7B). Notably, the soil, fresh radish, and fermented radish system contained 1133 genera. Moreover, fresh radish did not have any unique genera, indicating that both endophytic and surface bacteria or fungi could be found in the rhizosphere soil of radishes. These findings and the highest number of genera in the soil were consistent with previous observations on the universal origin of all microorganisms in soils (Banerjee & Van Der Heijden, 2023). Terrestrial ecosystems maintain the planet's most phylogenetically diverse microbial reservoir, with soil serving as the predominant origin of plant endophytic communities. Through rhizosphere-plant continuum transmission, these edaphic-originated microbiota ultimately translocate into human and animal gut systems via food chain transfer (Banerjee & Van Der Heijden, 2023). Therefore, the highly unique phage community and highly shared microbial community in the rhizosphere soil—fresh radish—fermented radish system indicated that during physicochemical shifts and prophage induction, phages in fermentation may originate from resident microbial prophages. This finding aligns with the observations of Yang et al. (2025). In the NMDS based on Bray–Curtis dissimilarity, the day 0 fermentation sample was closer to fresh radish than to rhizosphere soil, whereas the day 2 and day 5 samples clustered together (Fig. S4), suggesting that the phages entered paocai mostly via bacteria prophage or radish. The analysis of phage origins was based on a single location and batch; therefore, future studies should conduct replicated fermentation experiments across different regions and independent batches to further validate and generalize these findings.

4. Conclusions

We characterised the temporal dynamics of viral (predominantly phage) and microbial communities, and fermentation-related metabolites during radish fermentation for Sichuan paocai. Our findings revealed that *Lactiplantibacillus* and *Uroviricota* became gradually dominant in the bacteria and phage communities, respectively, as fermentation progressed. A subset of phage-associated genes was assigned to amino acid and carbohydrate metabolism pathways, suggesting that these genes could represent auxiliary metabolic genes (AMGs) with potential relevance to host metabolism during fermentation. Core phages exhibited correlations with bacteria and fermentation-related metabolites, including volatile compounds, indicating that phages may indirectly influence lactic acid accumulation by modulating host growth and metabolic activity via lysogenic conversion or horizontal gene transfer (HGT). Source analysis indicated that microorganisms within the fermentation system originated primarily from the soil and the phages were mainly derived from activated prophages. Overall, these results indicate that phages represented an integral component of the Sichuan paocai fermentation ecosystem and were closely associated with microbial succession and fermentation characteristics, providing a basis for further exploration of phage and bacteria interactions in fermented vegetable systems.

CRediT authorship contribution statement

Yuli Huang: Writing – review & editing, Writing – original draft, Visualization, Software, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Menglu Yang:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Formal analysis, Conceptualization. **Jiaqi Liu:** Writing – original draft, Visualization, Investigation, Data curation. **Min Zhang:** Writing – original draft, Visualization, Investigation, Data curation. **Petri Penttinen:** Supervision, Software, Methodology, Formal analysis, Conceptualization. **Lingzi Zhang:** Supervision, Investigation, Formal analysis, Conceptualization. **Lihong Ge:** Validation, Supervision, Software, Methodology, Investigation, Formal analysis. **Xiaoping Zhang:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Nan Zhao:** Writing – review & editing, Visualization, Supervision, Software, Resources, Project administration, Funding acquisition, Conceptualization.

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.2026.103997.

Data availability

Data will be made available on request.

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