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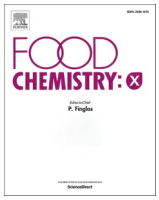

Improving the bacterial community, flavor, and safety properties of northeastern sauerkraut by inoculating autochthonous *Levilactobacillus brevis*

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ABSTRACT

The effect of *Levilactobacillus brevis* as a starter in northeastern sauerkraut fermentation is still unknown, and further evaluation is worthwhile. Hence, this study aimed to evaluate the effect of autochthonous *L. brevis* inoculation on the bacterial community succession and formation of flavor and harmful substances in sauerkrauts. Inoculation with *L. brevis* lowered the pH and increased the total acid content of sauerkrauts ($P < 0.05$). The nitrite content of the inoculated sauerkraut was significantly lower than that of control ($P < 0.05$). Moreover, the spoilage bacteria of the inoculated sauerkraut were decreased and nitrogen metabolism was improved. The contents of aldehydes, alcohols, esters, acids, and alkanes increased significantly ($P < 0.05$), and the sensory attributes such as aroma, sourness, and gloss were also improved. *L. brevis* was positively and negatively correlated with flavor metabolites and nitrite, respectively, which proved to be a potential starter culture to manufacture sauerkraut.

1. Introduction

Northeastern sauerkraut is a representative fermented vegetable product in Northeast China, and its unique flavor and rich nutrition are favored by consumers. The cabbages are pre-treated, sealed in a fermenter with brine, and fermented naturally at an appropriate temperature (Zhao et al., 2023). Lactic acid bacteria (LAB) are the predominant bacteria in sauerkraut and contribute to giving sauerkraut its unique sensory attributes (Liu et al., 2023). Nitrite is produced by nitrate-reducing bacteria during sauerkraut fermentation, and human ingestion of 0.3 g of nitrite can cause poisoning (Song, Zhao, Wang, Han, & Zhou, 2021). Consumption of fermented vegetable may have a risk of harm to human health caused by excessive nitrite. Therefore, spontaneous fermentation is highly dependent on native microorganisms, making it challenging to control the flavor and safety of sauerkraut. In order to standardize the flavor and quality of sauerkraut, it has become popular to inoculate the predominant bacteria (Li, Han, Wu, Li, & Zhang, 2023).

As reported, *Leuconostoc mesenteroides*, *Lactiplantibacillus plantarum*, and *Levilactobacillus brevis* were the predominant bacteria during sauerkraut fermentation (Thierry et al., 2023). *Leu. mesenteroides* grows quickly in the early stage of fermentation, which can rapidly improve physicochemical properties of sauerkraut (Zhao et al., 2023). *L. plantarum* and *L. brevis* are the dominant bacteria in the latter stage of fermentation. In particular, *L. plantarum* is widely used as a starter culture in sauerkraut production as it enhances the formation of flavor metabolites (Song et al., 2021). In addition, some LAB such as *Lacticaseibacillus paracasei*, *Latilactobacillus curvatus*, and *Weissella cibaria* shorten the fermentation time and reduce the nitrite content of sauerkraut (Yang et al., 2020). Although *L. brevis* has been identified as the predominant bacterium in sauerkraut, the effect of *L. brevis* as a starter in northeastern sauerkraut fermentation is still unknown, and further evaluation is worthwhile.

L. brevis is an important LAB strain, which has good fermentation characteristics such as acid resistance, antibacterial activity, nitrite degradation, and low temperature growth ability (Alfano et al., 2020; Rodrigues, Garcia, & De Souza, 2021), so it gradually began to be applied to manufacture fermented vegetables. Zhang et al. (2023) found that inoculation with *L. brevis* PL6–1 shortened the fermentation time of radish paocai and improved its texture and color. *L. brevis* AR123 was used as a starter for Chinese pickles to reduce the nitrite content, improve sensory attributes, and shorten the fermentation time (Xia

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et al., 2017). In addition, *L. brevis* possesses probiotic properties, including antioxidant, hypoglycemic, and improving liver and kidney function (Fan, Xue, Bai, Bo, & Zhang, 2022). Therefore, *L. brevis* has a good application prospect in manufacturing fermented vegetables.

To sum up, in this study, to evaluate the effects of *L. brevis* on the formation of flavor and harmful substances in northeastern sauerkraut, organic acids and volatile compounds were determined by high performance liquid chromatography (HPLC) and headspace solid-phase microextraction-gas chromatography-mass spectrometry (HS-SPME-GC-MS), respectively, and the nitrite content and sensory attribute were also determined. In addition, bacterial communities were determined by high-throughput sequencing (HTS) and their relationship to flavor metabolite formation were investigated by Spearman's correlation analysis. This study will provide a valuable reference for the application of *L. brevis* to fermented vegetables.

2. Materials and methods

2.1. Preparation of starter cultures

L. brevis was isolated from spontaneously fermented northeastern sauerkrauts, which has potential good fermentation characteristics at low temperature (Wang et al., 2023). The strain was identified using primers 27F (5'-AGAGTTTGATCCTGGCTCAG-3') and 1492R (5'-GGTTACCTTGTTACGACTT-3') for 16S rRNA gene sequencing, and it is currently maintained in the China General Microbiological Culture Collection Center (CGMCC No. 28114). *L. brevis* was inoculated into fresh sterile de Man, Rogosa, and Sharpe (MRS) broth (Hopebio, Qingdao, China) and cultured at 30 °C for 16 h. The cultures were collected and centrifuged at 10,000 *g* for 10 min. The precipitates were washed three times with sterile water to remove impurities and ensure that no contaminants were introduced before use.

2.2. Preparation of sauerkraut

Three distinct batches of northeastern sauerkrauts (replicates) were prepared on different days followed the method of Yang et al. (2020), with some modifications. Fresh cabbages (*Brassica rapa* ssp. *pekinensis*) were obtained from Xiangfang Market (Xiangfang District, Harbin, Heilongjiang Province, China). The cabbages (approximately 1.5 kg each) were washed, dried, and soaked for 5 s in boiling water. Then, the cabbages (approximately 15 kg) were put into a 60 L of sterile fermenter (Dingsheng, Guangzhou, China) and soaked in sterile brine (2% NaCl, *w*/w) to which 10^7 CFU/g cabbage of starter culture was inoculated. The strain was cultured in MRS broth (Hopebio, Qingdao, China) at 30 °C for 24 h, the optical density (OD) of the strain at 600 nm was adjusted with sterile brine and measured by UV-vis spectrophotometry (721G, Jingke, Shanghai, China) to ensure that the cell density reached the expected level (Dong, Dai, Ma, & Hu, 2014). Fermentation was conducted with the sealed container at 15 °C for 30 days and one control (spontaneous fermentation, CS) and one inoculated sauerkraut (inoculation of *L. brevis*, LB) were prepared. The brines and sauerkrauts were collected on days 0, 5, 10, 15, 20, 25, and 30. The sauerkraut was measured for pH, total acid, nitrite content, flavor metabolites, and sensory attributes and the brine was measured for bacterial communities. The brines (approximately 500 mL) were collected from a mixture of the upper, middle, and lower sections of the fermenters. The sauerkrauts (approximately 1.5 kg) were collected from the same sections.

2.3. Determination of pH, total acid, and nitrite content

The pH was determined in accordance with ISO 1842 (ISO, 1991), with slight modifications. The sauerkraut was ground into a pulp using a grinder (HX-J3063, AUX, Ningbo, China), and 50 mL of filtrate was determined using a pH meter (PB-30, Sartorius, Shanghai, China). The total acid was determined in accordance with ISO 750 (ISO, 1998), with slight modifications. The sauerkraut (10 g) was added with distilled water to 100 mL and homogenized using a homogenizer (Seward Medical, London, UK). After filtration, the sample was titrated with 0.1 M NaOH (Hengxing, Tianjin, China) until it was slightly red (phenolphthalein as an indicator), and the volume of NaOH was recorded. A detection kit (BC1490, Solarbio, Beijing, China) was used to determine the content of nitrite in the sauerkrauts.

2.4. Determination of bacterial counts

A total of 1.0 mL of brines were gradient diluted with sterile normal saline (0.9% *w*/w NaCl) and then poured into the corresponding agar medium to determine the bacterial counts (ISO 4833-1, 2013). LAB counts were determined on MRS (Hopebio, Qingdao, China) after incubation at 37 °C for 48 h. Aerobic bacteria counts were determined on plate count agar (Hopebio, Qingdao, China) after incubation at 37 °C for 48 h. Enterobacteriaceae counts were determined on violet red bile agar (Hopebio, Qingdao, China) after incubation at 37 °C for 48 h.

2.5. Determination of bacterial community

Genomic DNA extraction kits (D3146, Magen, Guangzhou, China) were used to extract total genomic DNA (Wang et al., 2023). The quality of the DNA was determined using a microspectrophotometer (Nanodrop 2000, Thermo Fisher Scientific, Waltham, USA). The V3 and V4 regions on the 16S rRNA gene were amplified using primers 341F (CCTACGGGNGGCWGCAG) and 806R (GGACTACHVGGGTATCTAAT) following the manufacturer's protocols. The amplified products were retrieved with the Gel Extraction Kit (K0692, Thermo Fisher Scientific, Waltham, USA). DNA library sequencing was performed on NovaSeq 6000 sequencing platform (Illumina, San Diego, USA). After sequencing, the sample reads were spliced to obtain raw tags, and the quality control of the raw tags was carried out to obtain clean tags. The chimeras were detected and removed, effective tags were obtained, and annotated using the SILVA bacterial 16S rRNA database (http://www.arb-silva.de/). The composition and differences of bacterial communities were analyzed using QIIME2 software. The Functional Annotation of Prokaryotic Taxa (FAPROTAX) was used to predict the ecological function of the bacterial community.

2.6. Determination of flavor metabolites

2.6.1. Determination of organic acids

The HPLC instrument (Agilent, Santa clara, USA) was used to determine the contents of lactic acid, tartaric acid, malic acid, and succinic acid following the method by Zhao et al. (2023), with slight modifications. The sauerkraut (5 g) was ground into a pulp using a grinder (HX-J3063, AUX, Ningbo, China) and centrifuged at 12,000 *g* for 5 min. The supernatant was filtered through 0.22 μm membrane filters (Jinteng, Tianjin, China) for analysis. The HPLC with a diode array detector (Agilent, Santa clara, USA) equipped with a C18 column (4.6 × 250 mm; Agilent, Santa clara, USA). A mixed solution (97.5:2.5, *v*/v) of 0.1% phosphoric acid (P112025, Aladdin, Shanghai, China) and methanol (M116118, Aladdin, Shanghai, China) was used as the mobile phase.

2.6.2. Determination of volatile compounds

Volatile compounds were determined followed the method of He et al. (2020), with slight modifications. The sauerkraut (5 g) was ground into a pulp using a grinder (HX-J3063, AUX, Ningbo, China) and put into a headspace vial (CNW Technologies, Duesseldorf, Germany). Then, 5 μL of 1,2-dichlorobenzene (CDGG-020043-04, o2si, Charleston, USA) was added as an internal standard. The headspace vial was sealed and volatile compounds were extracted at 60 °C using a divinylbenzene/carboxen/polydimethylsiloxane (DVB/CAR/PDMS) SPME fiber (57328-U, Supelco, Missouri, USA) for 40 min. A gas chromatograph-mass

spectrometer (QP2020 NX, Shimadzu Co., Kyoto, Japan) with a 30 m × 0.25 mm × 0.25 μm Rxi-5Sil MS column (Restek, Bellefonte, PA, USA) was used to analyze the compounds. The oven was maintained at 35 °C for 5 min, then increased by 3 ° C/min to 50 °C, 5 °C/min to 150 °C, and 20 °C/min to 250 °C. Volatile compounds were identified by mass spectra and comparison of retention times in the NIST mass spectra library or the retention indexes of a homologous series of n-alkanes (C8–C26).

2.7. Sensory evaluation

The sensory attributes of sauerkrauts were evaluated based on quantitative descriptive at the conclusion of fermentation on day 30. It is not customary to obtain approval from the Research Ethics Committee

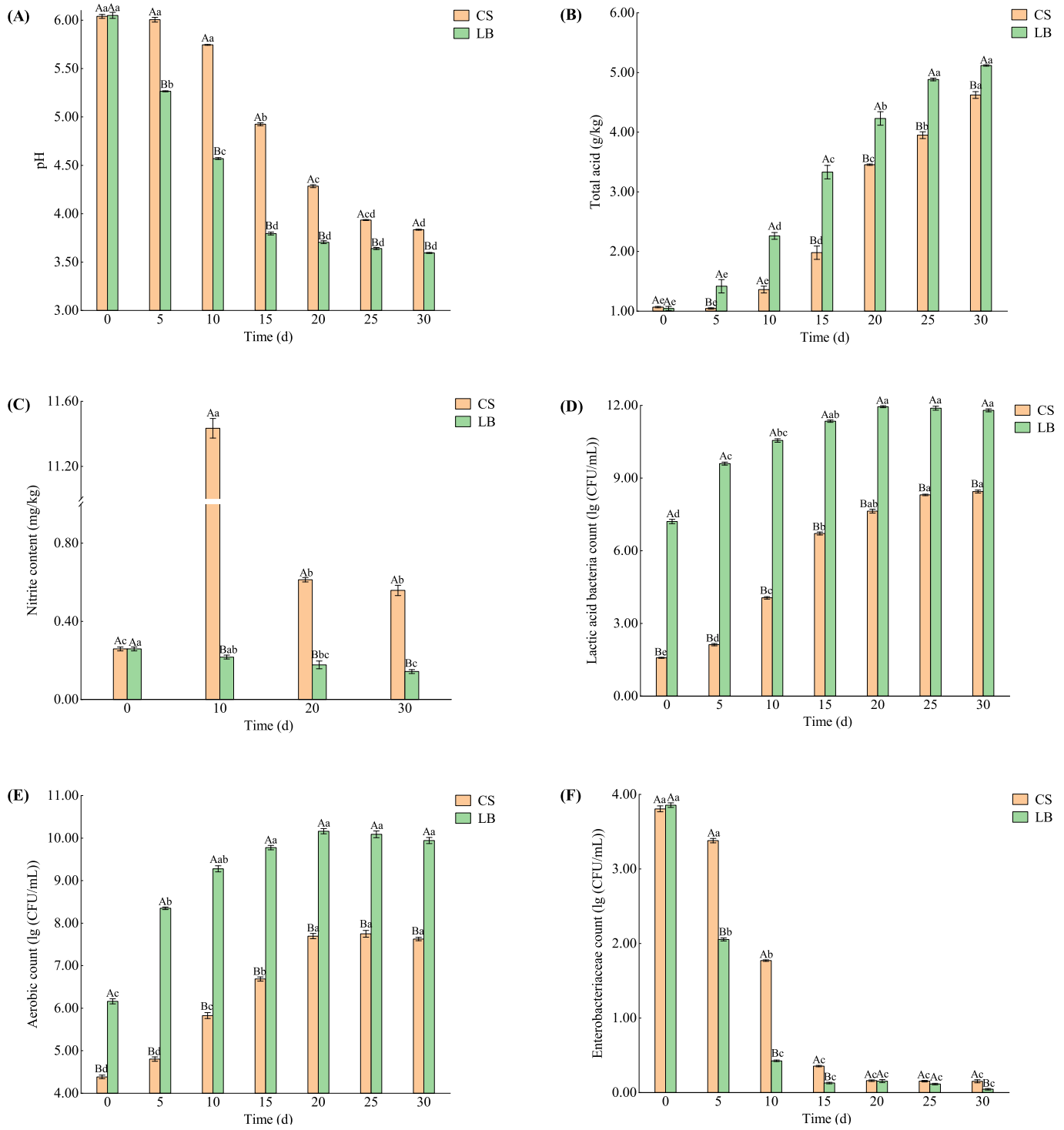

Fig. 1. The pH (**A**), total acid (**B**), nitrite content (**C**), lactic acid bacteria (**D**), aerobic bacteria (**E**), and Enterobacteriaceae counts (**F**) in northeastern sauerkrauts during fermentation. Different uppercase letters (A-B) indicate significant differences between the different treatments for the same fermentation time, and different lowercase letters (a-e) indicate significant differences between the different fermentation times for the same treatment ($P < 0.05$). CS: control with spontaneous fermentation; LB: sauerkraut inoculated with *Levilactobacillus brevis*.

to conduct sensory evaluations in our institution. All panelists agree to participate in the experiment and use their data/answers, while using appropriate protocols to protect their rights and privacy. This study does not involve any human or animal experiments. The sensory panelists with experience in judging sauerkrauts (10 males and 10 females) were selected, trained, and supervised in a specific room according to ISO 8589-1 (ISO, 2007) and ISO 8586 (ISO, 2012). Three training sessions (2 h each session) were conducted over two weeks to help panelists familiarize themselves with sauerkrauts. The first two sessions were dedicated to establishing descriptive terms to evaluate the saltiness, aroma, sourness, off-odor, astringency, fresh cabbage odor, gloss, and fracturability. The panelists were introduced to reference samples associated with debated descriptors to achieve a consensus in third session. The panelists were well trained in each session. Sauerkrauts were randomly placed on white sterile plates and labeled (3-digit random numbers). All attributes ranged from 1 ("weak") to 7 ("strong"). After evaluating one sample, pure water and crackers were provided for the panelists to rinse their mouths.

2.8. Statistical analysis

Three independent sauerkraut batches (replicates) were prepared on different days, and each batch was measured in triplicate (triplicate observations). Nine technical replicates (3 triplicates × 3 batches [replicates]) were measured for each sample. The data were analyzed using Statistix 8.1 (Analytical Software, St. Paul, MN, USA) and were expressed as mean ± standard error (SE). Tukey's multiple comparison analysis of variance (ANOVA) was used to evaluate the significance between groups ($P < 0.05$). Spearman's rank correlation coefficients were calculated using Origin 2023 (OriginLab Corporation, MA, USA).

3. Results and discussion

3.1. Analysis of pH, total acid, and nitrite content

As shown in Fig. 1A, the pH of CS and LB showed a gradually decreasing trend, and the pH of LB was lower than that of CS during the fermentation. At the early stage of fermentation (day 5), the pH of CS did not significantly ($P > 0.05$) change, but the pH of LB was significantly decreased ($P < 0.05$). At the end of the fermentation (day 30), the pH of CS and LB was decreased to below 4.0. The fermented vegetable maturation can be assessed by pH, and when pH is less than 4.0, it is generally considered fermented ripeness (Zhang, Zhang, & Liu, 2021). Therefore, it showed that sauerkrauts on day 30 of fermentation were ripe for consumption in this study. The pH in this study were lower than that in sauerkraut inoculated with *L. curvatus* and *Leu. mesenteroides*, which may be related to the good fermentation characteristics of *L. brevis* at low temperature (Yang et al., 2020). The total acid of CS and LB showed a gradually increasing trend, and the total acid of LB was higher than that of CS during the fermentation (Fig. 1B). At the early stage of fermentation (day 5), the total acid of CS did not significantly ($P > 0.05$) change, but the total acid of LB was significantly increased ($P < 0.05$). At the end of the fermentation (day 30), the total acid of LB reached 5.12 g/kg. These results show that inoculation with *L. brevis* accelerated the fermentation process and promoted sauerkraut maturity. The changes of pH and total acid were related to the organic acids produced by LAB metabolizing carbohydrates during fermentation (Chen et al., 2024). As shown in Fig. 1C, the content of nitrite in CS peaked (11.43 mg/kg) on day 10, and then gradually decreased to 0.56 mg/kg on day 30. The content of nitrite in LB decreased gradually with fermentation and reached 0.14 mg/kg on day 30. It also showed good results compared to similar studies, for example, *L. brevis* AR123 reduced nitrite content to 0.83 mg/kg in pickles (Xia et al., 2017). The content of nitrite in LB was always lower than that in CS, indicating that inoculation with *L. brevis* could effectively degrade nitrite. On the one hand, *L. brevis* can produce a large amount of nitrite reductase and denitrifying enzymes to reduce nitrite; on the other hand, *L. brevis* also produces a large amount of acid, and both factors together accelerate the degradation of nitrite (Song, Zhao, Wang, Han, & Zhou, 2021).

3.2. Analysis of bacterial counts

As shown in Fig. 1D, the LAB count of LB was higher than that of CS during fermentation. The LAB count of LB reached the maximum on day 20, then decreased slightly and reached 11.80 lg (CFU/mL) on day 30. The LAB count of CS gradually increased and stabilized on day 25, and was significantly lower than that of LB on day 30 ($P < 0.05$). The aerobic bacteria count of LB was higher than that of CS during the fermentation (Fig. 1E). The aerobic bacteria count of LB reached the maximum on day 20, then decreased slightly, and reached 9.94 lg (CFU/mL) on day 30. The aerobic bacteria of CS gradually increased and reached the maximum on day 25. The Enterobacteriaceae counts of CS and LB showed a gradually decreasing trend, and the Enterobacteriaceae count of LB was lower than that of CS during the fermentation (Fig. 1F). On day 5, the Enterobacteriaceae count of CS did not significantly ($P > 0.05$) change, but that of LB significantly decreased ($P < 0.05$). On day 30, the Enterobacteriaceae counts of LB and CS were below 1.0 lg (CFU/mL) ($P < 0.05$). These above results show that inoculation with *L. brevis* significantly inhibited the growth of Enterobacteriaceae in sauerkrauts, which may be related to the decrease of pH and the production of antibacterial substances (Alfano et al., 2020).

3.3. Analysis of bacterial community

3.3.1. Composition and functional prediction of bacterial community

At the phylum level, the top 10 in relative abundance were *Proteobacteria*, *Firmicutes*, *Bacteroidota*, *Cyanobacteria*, *Campilobacterota*, *Actinobacteriota*, *Desulfobacterota*, *Fusobacteriota*, *Bdellovibrionota*, and *Chloroflexi* (Fig. 2A). On day 0, the relative abundances of *Bacteroidota* and *Proteobacteria* in CS and LB were significantly ($P < 0.05$) higher than those of other phyla; thus, they were considered to be the dominant phyla at the beginning of fermentation. With the progress of fermentation, the relative abundance of *Firmicutes* in CS and LB increased. The relative abundance of *Proteobacteria* in CS was always higher than that in LB, whereas the relative abundance of *Firmicutes* in LB was always higher than that in CS. *L. brevis* belongs to *Firmicutes* and inhibits the growth of other bacteria such as *Bacteroidota* and *Proteobacteria*, which may explain this result. *Firmicutes* are the dominant phyla in vegetable fermentation, which can produce acids, improve flavor, and shorten fermentation time (Liu et al., 2023).

At the genus level, the top 10 in relative abundance were *Lactobacillus* (*Levilactobacillus*), *Pseudomonas*, *Acinetobacter*, *Chryseobacterium*, *Serratia*, *Erwinia*, *Pantoea*, *Rhizobium*, *Stenotrophomonas*, and *Sphingobacterium* (Fig. 2B). On day 0, *Pseudomonas* and *Chryseobacterium* were the dominant genus in CS and LB. *Pseudomonas* and *Chryseobacterium* may originate from fresh cabbage and the fermentation environment, and they are common spoilage bacteria in sauerkraut (Thierry et al., 2023). As the fermentation progressed, *Lactobacillus* (*Levilactobacillus*) was the dominant genus in LB, which is related to the rapid growth of *L. brevis*. In CS, *Pseudomonas* was the dominant genus on days 10 and 20, but *Lactobacillus* gradually became the dominant genus on day 30. Additionally, the abundance of spoilage bacteria (such as *Pseudomonas* and *Acinetobacter*) in LB was lower than that in CS during the fermentation, indicating that *L. brevis* had strong antibacterial activity and could inhibit spoilage bacteria in the sauerkraut fermentation system.

The FAPROTAX function prediction was performed, which was especially suitable for analyzing the ecological function of the bacterial community (Fig. 2C). Inoculation with *L. brevis* can enhance functions such as nitrate ammonification, reduction, and respiration, nitrite ammonification and respiration, nitrogen respiration, and improve the progress of fermentation. The obtained results show that inoculation with *L. brevis* enhanced the conversion of nitrogen compounds, such as

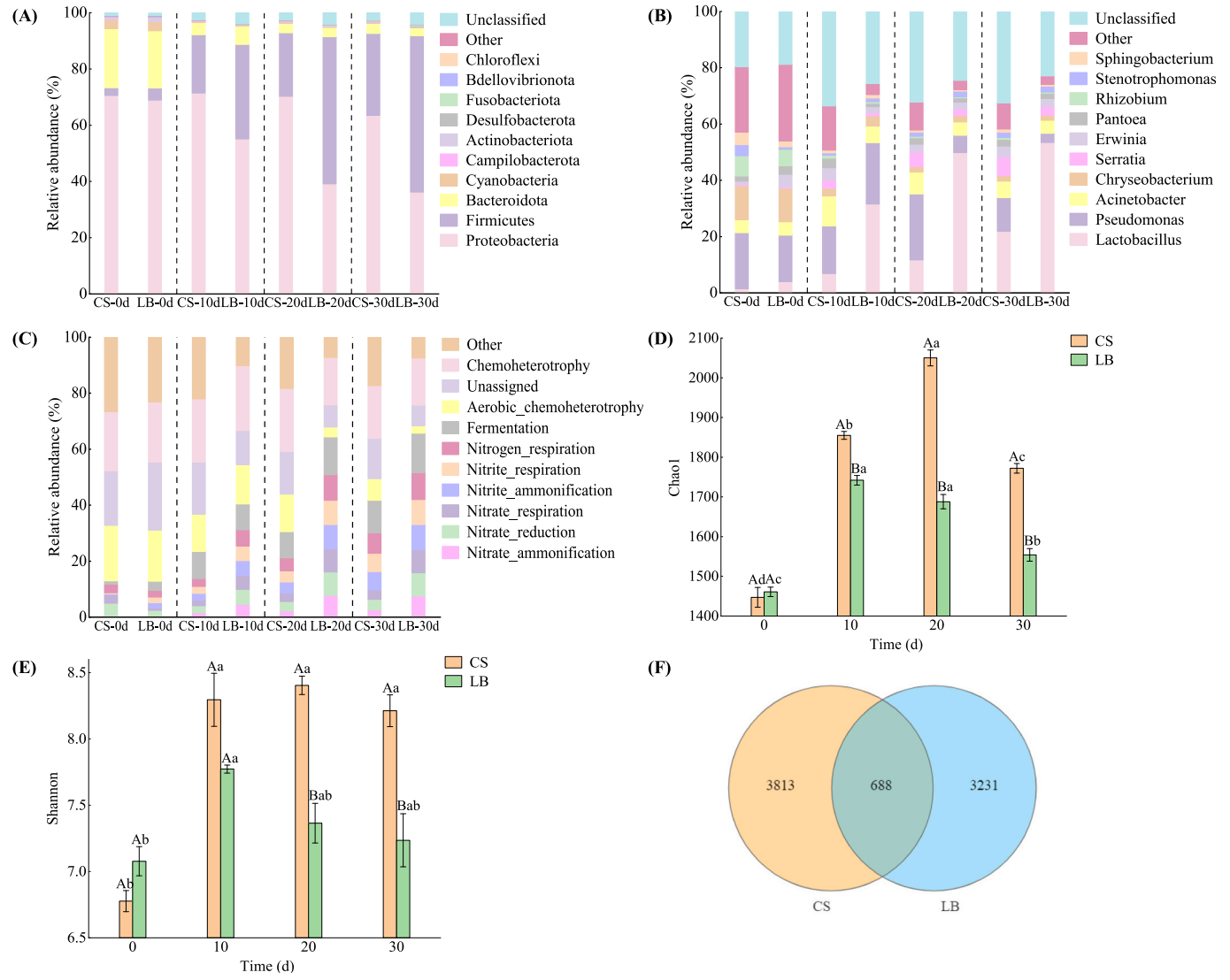

Fig. 2. Relative abundance at the phylum level (**A**), genus level (**B**), FAPROTAX function prediction (**C**), α-diversity indices (**D** and **E**), and Venn diagram (**F**) of bacterial communities in northeastern sauerkrauts during fermentation. Different uppercase letters (A-B) indicate significant differences between the different treatments for the same fermentation time, and different lowercase letters (a-c) indicate significant differences between the different fermentation times for the same treatment ($P < 0.05$). CS: control with spontaneous fermentation; LB: sauerkraut inoculated with *Levilactobacillus brevis*.

the conversion of nitrite to ammonia by dissimilar reduction as well as the reduction of nitrate to nitric oxide, nitrogen dioxide, and nitrate, which as the final hydrogen acceptor of the respiratory chain was reduced to nitric oxide, nitrogen dioxide, and nitrogen. Therefore, the functional prediction results may explain the significant decrease in the nitrite content caused by inoculation with *L. brevis*, which enhanced metabolic pathways related to nitrite decomposition (such as nitrite reduction and denitrification), leading to the rapid decomposition of nitrite in sauerkraut.

3.3.2. *Differences of bacterial community*

During the fermentation, the Chao1 of CS was greater than that of LB. CS and LB reached the maximum Chao1 on days 20 and 10, respectively, and then gradually decreased (Fig. 2D). The Shannon of CS and LB showed the same trend as Chao1 (Fig. 2E). The richness and diversity of the bacterial community increased first and then decreased, which was likely due to the lack of nutrients and bacteriostasis at the end of the fermentation (Liu et al., 2017). In Fig. 2F, 688 operational taxonomic units (OTUs) were shared by CS and LB, whereas 3813 and 3231 unique OTUs were identified in CS and LB, respectively. The number of OTUs significantly ($P < 0.05$) decreased by inoculation with *L. brevis*. The diversity and richness of the bacterial community in the sauerkraut fermentation system decreased by inoculation with *L. brevis*, which was probably due to the high antibacterial activity of *L. brevis*, which inhibited the growth of other bacteria, and could be explained by the results of bacterial composition (Hakim, Jang, Lee, & Paik, 2022).

Fig. 3A shows an evolutionary branching map of differential bacteria by linear discriminant analysis (LDA). There were 39 and 9 bacteria with significant abundance differences ($P < 0.05$) in CS and LB, respectively, which were identified by mapping the differential bacteria to a taxonomic tree with a known hierarchy. Fig. 3B shows 41 and 10 bacteria with significant abundance differences ($P < 0.05$) in CS and LB, respectively, which were identified by LDA scores above 2. These results demonstrate that inoculation with *L. brevis* reduced the bacterial diversity, which was related to the strong antibacterial ability of the strain (Hakim et al., 2022). The abundance differences of *Pseudomonas psychrophila*, *Acinetobacter sp.* ADP1, *Sphingobacterium siyangense*, and *Alcaligenaceae* were significantly higher than those of other bacteria in CS (LDA scores above 3). The abundance differences of *Fusobacteriaceae*, *Fusobacteriota*, *Cetobacterium*, *Fusobacteriales*, and *Fusobacteriia* were significantly higher than those of other bacteria in LB (LDA scores above 3), indicating that these bacteria are more likely to be biomarkers.

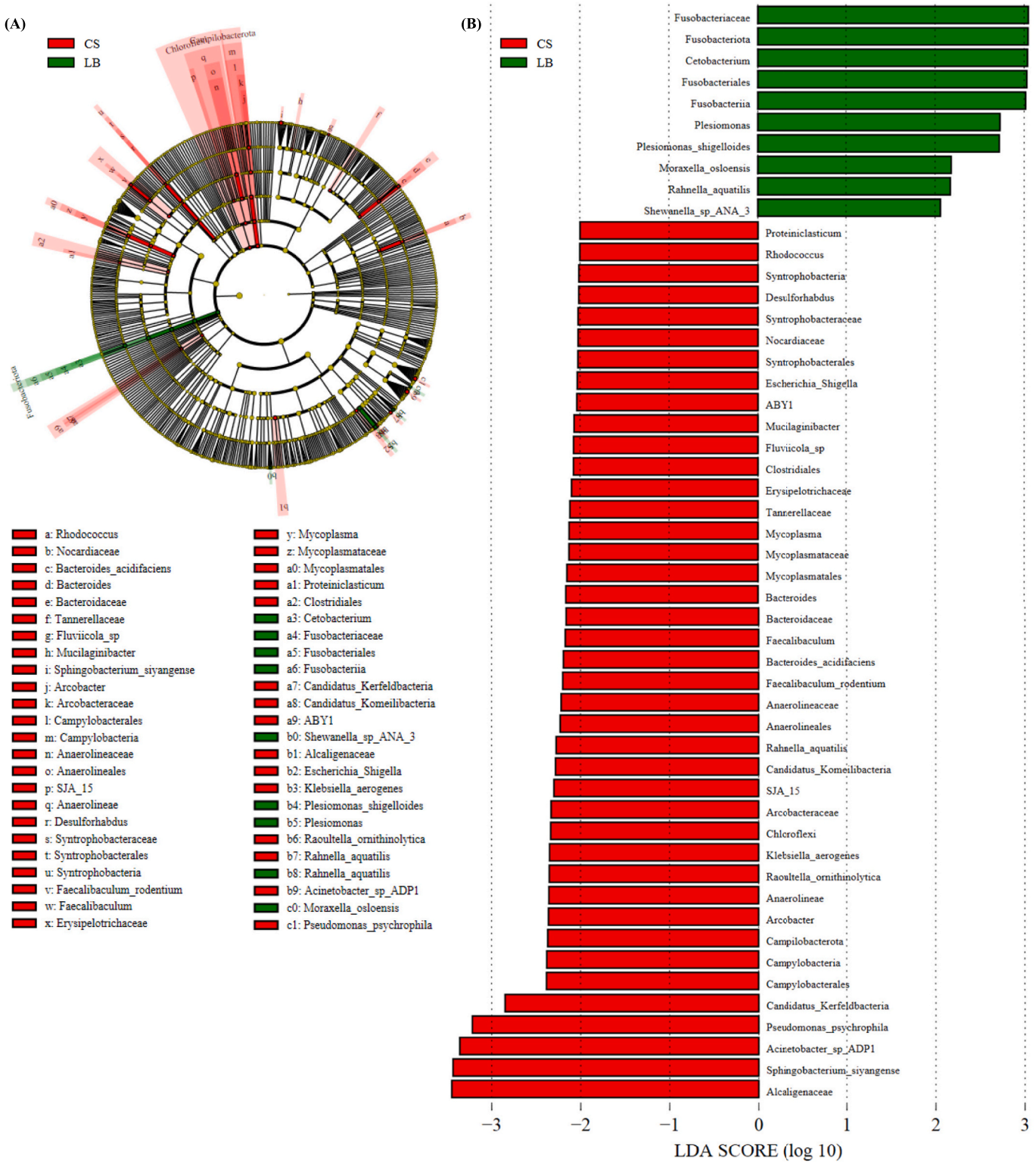

Fig. 3. Evolutionary branching diagram (**A**) and linear discriminant analysis effect size (**B**) of bacterial communities in northeastern sauerkrauts during fermentation. CS: control with spontaneous fermentation; LB: sauerkraut inoculated with *Levilactobacillus brevis*.

However, the specific role of most bacteria has not been reported in sauerkraut, and further studies are needed.

3.4. Analysis of organic acid contents

Organic acids are the main metabolites in sauerkraut and the main contributors to sourness. For example, lactic acid has a mild sourness, malic acid has a pleasant sourness, and succinic acid has a shell-like umami (Gerardi et al., 2019; Picariello et al., 2019). The interaction of organic acids with ketones, alcohols, and aldehydes produces flavor compounds, enhancing the richness of flavor (Liu et al., 2023). Additionally, organic acids can be used as an energy source for bacterial

growth (Yao et al., 2015). During the fermentation, there was no difference between the contents of tartaric acid and malic acid in LB and CS. Compared with CS, the lactic acid content in LB was significantly increased ($P < 0.05$) (Table 1). At the end of the fermentation, the lactic acid contents in LB and CS were 13.56 and 10.61 mg/g, respectively ($P < 0.05$). Lactic acid is produced mainly by LAB and the main contributor to forming the unique flavor of sauerkraut; thus, lactic acid is considered to be an irreplaceable organic acid during sauerkraut fermentation, and it is also considered to be the main factor affecting the reduction of pH and the increase of total acid (Hu, Yang, Ji, & Guan, 2021; Yang et al., 2020). The succinic acid contents in LB and CS were 0.63 and 0.52 mg/g, respectively ($P < 0.05$). Succinic acid is the main metabolite of the tricarboxylic acid (TCA) cycle; thus, the observed increase in the succinic acid content indicates that inoculation with *L. brevis* may promote the metabolic activities of microorganisms, in turn improving the flavor of sauerkraut, which also indicates that *L. brevis* may have a strong ability to grow and metabolize at low temperature (Liu et al., 2017).

3.5. Analysis of volatile compounds

In Fig. 4A, a total of 161 volatile compounds were obtained in CS and LB, which included 35 alcohols, 32 esters, 25 aldehydes, 22 alkanes, 13 acids, 9 ketones, 5 olefins, 4 phenols, 3 isothiocyanates, 2 ethers, and 11 other compounds. The numbers of aldehydes, alcohols, esters, and alkanes were substantially higher than those of other compounds. The number of volatile compounds in LB was higher than that in CS during sauerkraut fermentation (Fig. 4B). The numbers of volatile compounds in LB and CS were 82 and 66 on day 30, respectively. Inoculation with *L. brevis* can promote the interaction of organic acids and other metabolites to produce a variety of volatile compounds, which explains the substantially greater numbers of aldehydes, alcohols, esters, and alkanes in LB compared to CS (Liu et al., 2023). The growth and metabolism of *L. brevis* in the sauerkraut fermentation system promoted the production of metabolites. Moreover, the interactions between volatile compounds such as alcohols, aldehydes, and ketones produce numerous compounds (Yao et al., 2015).

In Fig. 4C, the contents of isothiocyanates, esters, acids, and aldehydes were 38.15, 30.71, 181.52, and 84.04 μg/kg, respectively, and were significantly ($P < 0.05$) higher than those of other compounds on day 0. Subsequently, the contents of aldehydes, acids, and isothiocyanates in both the control and inoculated sauerkrauts decreased, while the contents of esters increased during the fermentation. The contents of aldehydes, esters, acids, and isothiocyanates in CS were 11.25, 37.61, 64.09, and 4.32 μg/kg on day 30, respectively. The contents of aldehydes, esters, acids, and isothiocyanates in LB were 30.14, 39.04, 66.96, and 1.57 μg/kg, respectively. The above results demonstrate that inoculation with *L. brevis* increased the contents of aldehydes, esters, and acids, which was due to the high metabolic activity of *L. brevis* at low temperature and interactions among the metabolites (Liu et al., 2017; Yao et al., 2015). Moreover, Yang et al. (2020) found that *L. plantarum* could increase the contents of esters, *L. paracasei* could increase the contents of lactones, and *W. cibaria* could increase the contents of ketones during sauerkraut fermentation. Therefore, this study also shows a good effect compared to the existing studies.

Table 1
The organic acid contents (mg/g) in northeastern sauerkrauts during fermentation.

Organic acid		Day 0	Day 10	Day 20	Day 30
Lactic acid	CS	n.d.	3.20 ± 0.04^{Bc}	7.34 ± 0.12^{Bb}	10.61 ± 1.40^{Ba}
	LB	n.d.	6.15 ± 0.20^{Ac}	9.02 ± 0.82^{Ab}	13.56 ± 1.44^{Aa}
Succinic acid	CS	n.d.	0.08 ± 0.01^{Ac}	0.22 ± 0.01^{Bb}	0.52 ± 0.03^{Ba}
	LB	n.d.	0.10 ± 0.01^{Ab}	0.57 ± 0.03^{Aa}	0.63 ± 0.02^{Aa}
Tartaric acid	CS	n.d.	0.02 ± 0.01^{Aa}	0.06 ± 0.01^{Aa}	0.07 ± 0.01^{Aa}
	LB	n.d.	0.04 ± 0.01^{Ab}	0.10 ± 0.02^{Aa}	0.10 ± 0.02^{Aa}
Malic acid	CS	n.d.	0.01 ± 0.00^{Aa}	0.01 ± 0.00^{Aa}	0.02 ± 0.01^{Aa}
	LB	n.d.	0.02 ± 0.01^{Aa}	0.04 ± 0.02^{Aa}	0.04 ± 0.01^{Aa}

Different uppercase letters (A-B) indicate significant differences between the different treatments for the same fermentation time, and different lowercase letters (a-c) indicate significant differences between the different fermentation times for the same treatment ($P < 0.05$).
n.d.: not detected.
CS: control with spontaneous fermentation; LB: sauerkraut inoculated with *Levilactobacillus brevis*.

Aldehydes are an important class of volatile compounds and are mainly produced by fatty acid oxidation. Inoculation with *L. brevis* promoted lipid oxidation and degradation (Hu et al., 2021), which was reflected in the decrease in the contents of 2,3-eepoxypropyl oleate, elaidic acid, and stearic acid during the fermentation (Table S1). Aldehydes generally have grassy and fruity odors and have a significant effect on the flavor formation of food (Shen et al., 2021). Esters are volatile compounds that are widely present in fermented foods, they are generally produced by esterification of alcohols and acids and are key contributors to flavor (e.g, ethyl lactate and ethyl 3-phenylpropionate) (Brendel, Hofmann, & Granvogl, 2020). Ethyl lactate has fruity and buttery odors and can be formed by the reaction of lactic acid with ethanol. Ethyl 3-phenylpropionate has fruity, floral, and sweet odors and can be used to prepare food flavoring agents (Hu et al., 2021). The contents of both ethyl lactate and ethyl 3-phenylpropionate increased by inoculation with *L. brevis*. Isothiocyanates are representative volatile compounds in cabbage; they contribute to the formation of characteristic flavors and have beneficial effects on human health (Ciska, Honke, & Drabinska, 2021). The cabbage tissue was loosened after pretreatment and brine soaking, which promoted the reaction between glucoside and myrosinase to generate isothiocyanates; thus, the contents of isothiocyanates were high on day 0. The contents of isothiocyanates in LB were significantly higher than those in CS on day 10. As the fermentation progressed, the contents of isothiocyanates in LB decreased compared to those in CS, which may be ascribed to the decreased pH. A similar finding was reported by Gil and Macleod (1980) during the preparation of a glucoside hydrolysate from mustard powder, and the effect of pH on the formation and transformation of isothiocyanates was explored. When the pH was in the range of 4–5, it was conducive to the formation of isothiocyanates but the opposite occurred when the pH was lower than 4. At the end of the fermentation, the contents of alcohols in CS and LB were 172.24 and 175.92 μg/kg, respectively, which were much higher than the 6.80 μg/kg on day 0 ($P < 0.05$). Alcohols such as 2-ethylhexanol are generally produced by lipid oxidation and have unique sweet and floral odors. The content of 2-ethylhexanol was significantly higher than those of other alcohols, but its odor threshold was high and thus contributed little to flavor development. The contents of alkanes in CS and LB on day 30 were 52.82 and 55.38 μg/kg, respectively, which were much higher than the 2.09 μg/kg on day 0 ($P < 0.05$). These results show that the inoculation with *L. brevis* also increased the contents of alcohols and alkanes. Similarly, *L. brevis* can increase the contents of alcohols, acids, and phenols in radish paocai, giving floral and sour odors (Zhang et al., 2023).

Principal component analysis (PCA) based on the volatile compound content is shown in Fig. 4D. The interpretation of the first component (PC1) and second component (PC2) was 65.6% and 21.1%, respectively, and the total variance was 86.7%. PC1 was the most important principal component for comparing the differences between sauerkrauts. Phenols, ethers, olefins, alkanes, ketones, alcohols, esters, and acids were distributed on the positive axis of PC1. Aldehydes, isothiocyanates, and other compounds were located on the negative axis of PC1. In addition, LB on days 20 and 30 and CS on day 30 were distributed on the positive axis of PC1, whereas LB on day 10, and CS on days 10, 20, and 0 were distributed on the negative axis of PC1. LB on days 10 and 0 was closely related to aldehydes, isothiocyanates, and other compounds in the third quadrant. LB on day 20 was closely related to phenols, ethers, alkanes, and olefins in the first quadrant. LB and CS on day 30 were closely related to ketones, alcohols, esters, and acids in the fourth quadrant. On

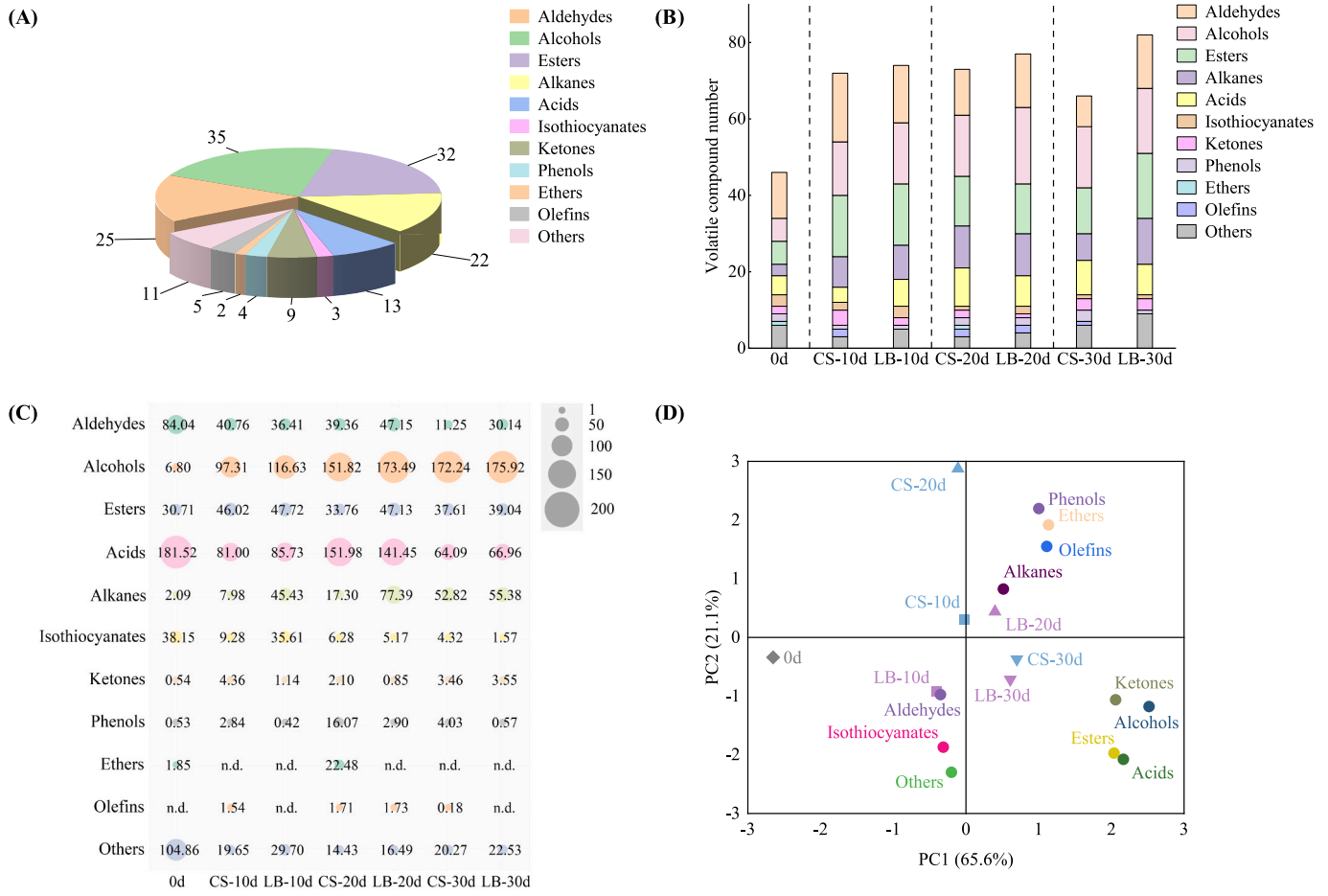

Fig. 4. Classification (**A**), number (**B**), content (**C**), and principal component analysis (**D**) of volatile compounds in northeastern sauerkrauts during fermentation. CS: control with spontaneous fermentation; LB: sauerkraut inoculated with *Levilactobacillus brevis*.

days 10 and 20, CS was located in the second quadrant and the correlation with volatile compounds was not strong. These results are helpful to understand the differences between the volatile profiles in sauerkrauts.

3.6. Sensory evaluation

In Fig. 5A, inoculation with *L. brevis* can promote the formation of aroma, sourness, and gloss of sauerkraut, while reduce the off-odor, astringency, fresh cabbage odor, and fracturability. Compared with CS, LB has more flavor metabolites such as esters, volatile acids, and lactic acid, so the aroma and sourness of sauerkraut were significantly ($P < 0.05$) improved, and the off-odor and astringency were covered. Moreover, the fermentation time of sauerkraut was also shortened, so the fresh cabbage odor was reduced. Spoilage bacteria such as *Pseudomonas* can produce pigments (brown and yellow) to reduce the gloss of sauerkraut (Caldera et al., 2016). Inoculation with *L. brevis* can inhibit the growth of spoilage bacteria in sauerkraut fermentation system, thus improving the gloss of sauerkraut and the acceptance of consumers. Meanwhile, pectinase produced by *L. brevis* also accelerated the decomposition of pectin, resulting in a decrease in the fracturability of sauerkraut (Fan, Huang, & Wang, 2022). Moreover, Zhang et al. (2023) found that *L. brevis* could improve the color and sensory acceptability of radish paocai, similar to the results of this study.

The correlation between volatile compounds and sensory attributes was established by performing Spearman's analysis. As shown in Fig. 5B, aldehydes, alcohols, esters, acids, alkanes, ketones, and other compounds had significant ($P < 0.05$) positive correlations with aroma and sourness. Alcohols, esters, ketones, acids, and aldehydes are considered to be the important volatile compounds in sauerkraut, which contribute to the formation of characteristic aroma and sourness (Hu et al., 2021). Isothiocyanates, phenols, and olefins had significant ($P < 0.05$) positive correlations with astringency, fresh cabbage odor, saltiness, and off-odor. As the breakdown product of glucosinolates, isothiocyanates can provide characteristic pungent and sulfurous odors to *Brassica* and play an important role in forming flavor (Xu et al., 2020). Phenols and olefins have also been detected in sauerkraut in the other study, but the mechanism by which they affect the sensory attribute formation of sauerkraut still needs to be explored in depth (He et al., 2020). The above results suggest that the formation of volatile compounds may be a key factor in enhancing the sensory attribute of sauerkraut.

3.7. Correlation between bacterial communities, nitrite, and flavor metabolites

As shown in Fig. 5C, the relative abundance of 10 core bacterial genera (the top 10 in relative abundance) and the contents of nitrite, organic acids, and volatile compounds were selected to calculate Spearman's correlation coefficients. The results revealed that nitrite had significant positive correlations with *Pseudomonas*, *Acinetobacter*, *Chryseobacterium*, *Serratia*, *Erwinia*, *Pantoea*, *Rhizobium*, and *Sphingobacterium*, whereas, *Lactobacillus* and *Stenotrophomonas* had significant negative correlations with nitrite. This indicates that most of the core bacterial genera (a total of eight) may promote nitrite accumulation in northeastern sauerkraut. However, except for *Lactobacillus*, the roles of other bacteria on nitrite accumulation have not been extensively studied

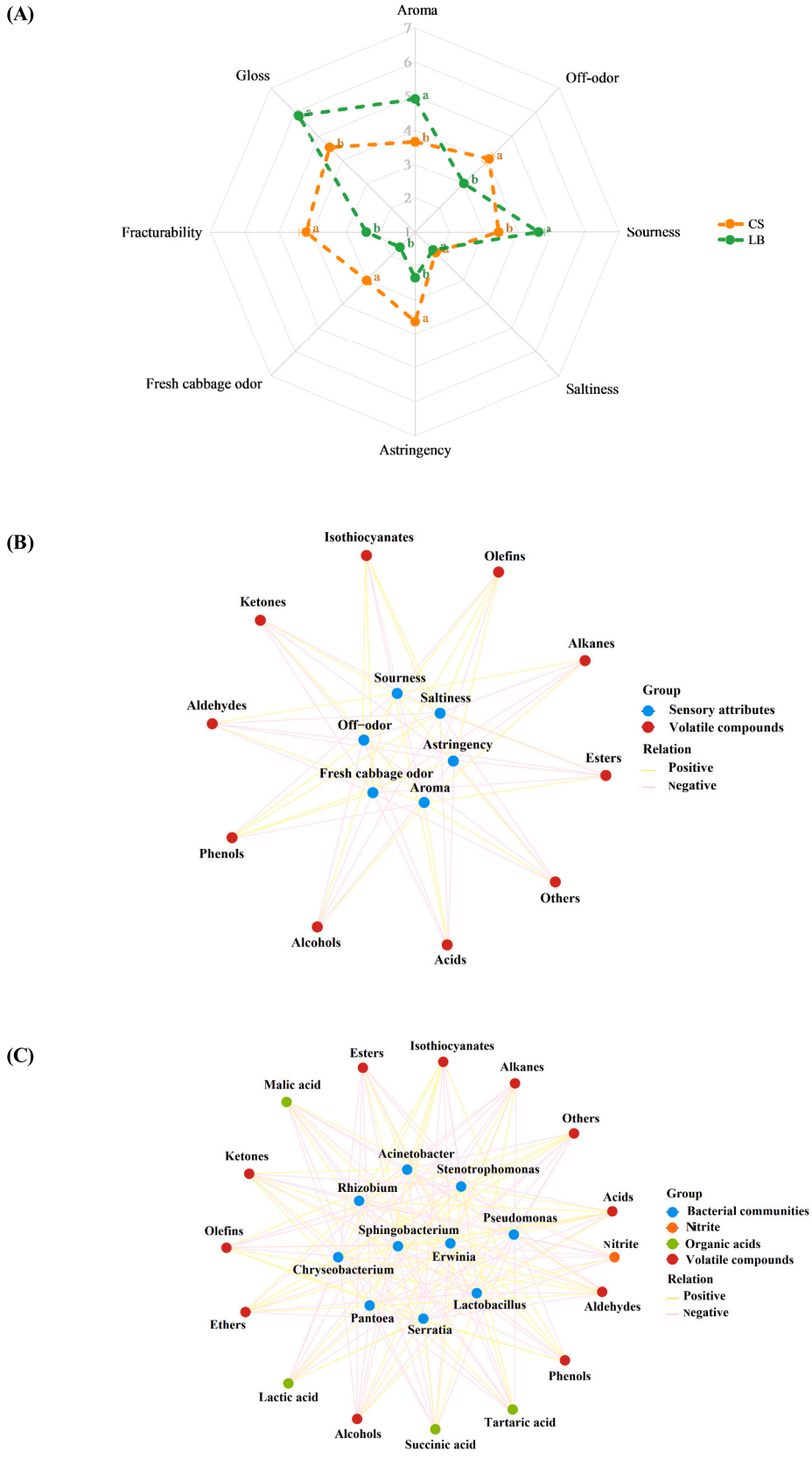

Fig. 5. Sensory evaluation (**A**) and Spearman's correlation network of sensory attributes and volatile compounds (**B**) and 10 core bacteria at the genus level, nitrite, organic acids, and volatile compounds (**C**) of northeastern sauerkrauts. Different lowercase letters (a-b) indicate significant differences between the different treatments for the same sensory attribute ($P < 0.05$). CS: control with spontaneous fermentation; LB: sauerkraut inoculated with *Levilactobacillus brevis*.

in fermented vegetables. On the one hand, *Lactobacillus* (*L. brevis*) produces acid compounds to inhibit the growth of bacteria containing nitrate reductase; on the other hand, it produces nitrite reductase and denitrifying enzymes to reduce the content of nitrite (Song, Zhao, Wang, Han, & Zhou, 2021).

The production of organic acids and volatile compounds is closely related to bacterial communities in sauerkraut. *Lactobacillus*, *Serratia*, and *Stenotrophomonas* had significant positive correlations with succinic acid, lactic acid, tartaric acid, and malic acid, whereas *Erwinia* had significant positive correlations with lactic acid. *Lactobacillus* is the main bacteria to produce organic acids and contributes greatly to the formation of organic acids in fermented vegetables (Liu et al., 2023). Malic acid and succinic acid are crucial metabolites of the TCA cycle. Inoculation with *Lactobacillus* (*L. brevis*) may accelerate the TCA cycle through carbohydrate consumption and affect the production of relevant metabolites. However, the role of bacteria in regulating the production of succinic acid and malic acid needs to be further verified. Moreover, *Pseudomonas*, *Chryseobacterium*, *Pantoea*, *Rhizobium*, and *Sphingobacterium* had significant positive correlations with aldehydes; *Lactobacillus*, *Serratia*, and *Stenotrophomonas* had significant positive correlations with alcohols and alkanes; *Lactobacillus*, *Acinetobacter*, and *Serratia* had significant positive correlations with esters; *Pseudomonas*, *Chryseobacterium*, *Lactobacillus*, *Rhizobium*, *Stenotrophomonas*, and *Sphingobacterium* had significant positive correlations with acids; *Acinetobacter*, *Pseudomonas*, *Chryseobacterium*, *Pantoea*, *Rhizobium*, and *Sphingobacterium* had significant positive correlations with isothiocyanates; *Acinetobacter*, *Lactobacillus*, *Serratia*, *Erwinia*, and *Pantoea* had significant positive correlations with ketones; *Lactobacillus*, *Acinetobacter*, *Serratia*, *Erwinia*, and *Pantoea* were significantly positively correlated with olefins. *Lactobacillus* is the core functional bacteria for promoting the formation of volatile compounds during vegetable fermentation (Hu et al., 2021). However, the roles of other bacteria in flavor formation have not been extensively studied in fermented vegetables. In this study, *Lactobacillus* (*L. brevis*) had the most positive correlations with volatile compounds, and significantly positive correlations with alcohols, esters, alkanes, acids, ketones, phenols, and olefins. Although correlation analysis can help to identify potential correlations, since most volatile compounds are secondary metabolites, preliminary correlation analysis may not prove the specific contribution of bacterial communities to the production of volatile compounds in sauerkraut; thus, the mechanism causing correlations needs to be further investigated. The above results showed that *Lactobacillus* (*L. brevis*) has the most positive correlation with volatile compounds and organic acids, and is considered as the core functional bacterium to generate the unique flavor of northeastern sauerkraut.

4. Conclusions

Inoculation with *L. brevis* accelerated the acidification of northeastern sauerkraut, shortened the fermentation time, and promoted nitrite degradation, which enhanced the safety of sauerkraut. *L. brevis* inoculation enhanced the growth of *Lactobacillus* and inhibited some spoilage bacteria such as *Pseudomonas* and *Acinetobacter*. *L. brevis* inoculation also promoted the production of organic acids and volatile compounds, which enhanced flavor and sensory attributes development during sauerkraut fermentation. These findings prove that *L. brevis* may have potential as a starter for sauerkraut production and provide a valuable reference for the extensive application of *L. brevis* in fermented vegetables.

CRediT authorship contribution statement

Jiawang Wang: Writing – original draft, Methodology. **Xin Liu:** Data curation, Investigation. **Jiaqi Liu:** Methodology. **Yumeng Sui:** Data curation. **Weihua Yu:** Investigation. **Baohua Kong:** Project administration, Funding acquisition. **Qian Chen:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships in this paper.

Data availability

Data will be made available on request.

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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.2024.101408.

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