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Chitosan oligosaccharide and *Enteromorpha prolifera* polysaccharides as additives affect the bacterial community and optimize the compost performance

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The yield of agricultural wastes is increasing year by year, and composting is a common and effective strategy. However, the influence of marine-derived carbohydrates such as chitosan oligosaccharide (COS) and *Enteromorpha prolifera* polysaccharides (EPP)—on composting efficiency and microbial dynamics remains poorly understood. Here, we conducted composting experiments using agricultural wastes (cow manure, rice husks, and tomato residues) as substrates, and systematically evaluated the effects of chitosan oligosaccharide (COS) and Enteromorpha prolifera polysaccharides (EPP) supplementation through physicochemical analysis and high-throughput sequencing. These additives not only advanced the thermophilic phase and facilitated compost maturation but also reshaped the composition of the bacterial community in compost piles. By providing suitable microenvironments, the carbohydrates-containing group increased the abundance of thermophilic bacteria such as *Ureibacillus*, *Geobacillus*, and *Ammoniibacillus,* facilitating the degradation and utilization of organic matter. During which, the organic matters loss rates of COS and EPP were 26.61 and 12.66% higher than CK, respectively. By increasing the abundance of *Cellvibrio* and *Flavobacterium* in the cooling phase, carbohydrates-containing additives are expected to promote the conversion of recalcitrant lignocellulosic fibers. Additionally, PICRUSt 2 predictions revealed that carbohydrates addition increased the gene abundance related to amino carbohydrates and nucleotide carbohydrates metabolism, fructose and mannose metabolism, galactose metabolism, and butanoate metabolism in the initial and thermophilic phases, thereby facilitating carbohydrate metabolism. In summary, the addition of carbohydrates-containing additives enhanced the maturity and fertility of compost products and exerted significant regulatory effects on the composition and function of the bacterial community during composting.

KEYWORDS

agricultural wastes, composting performance, bacterial community, metabolic function, co-occurrence network

1 Introduction

The accelerated advancement of agricultural modernization, coupled with rising living standards, has significantly increased the generation of agricultural waste, including crop residues and livestock manure. Current estimates indicate China produces approximately 97 million tons of crop straw and 3.8 billion tons of livestock and poultry manure annually (Ge et al., 2020; Sun et al., 2021). Improper management of these organic wastes may lead to substantial environmental degradation and public health risks (Li et al., 2019). Composting is the current ideal treatment (Wang et al., 2018), which is a complex process that involves the utilization of various microorganisms to drive the conversion of biodegradable organic materials into stable humus-like substances (Cesaro et al., 2015). And the resulting compost products, such as agricultural fertilizers or soil amendments, can not only enhance crop quality but also improve soil structure, increasing its capacity to retain water, heat, air, and nutrients (Wu et al., 2022).

Microorganisms (e.g., bacteria) drive the biological decomposition and play a vital role in the composting process (Wu et al., 2017). For example, bacteria accelerate compost maturation by promoting the breakdown of recalcitrant organic compounds and facilitating nutrient conversion through elevated metabolic activity and extracellular enzyme secretion (Liu X. et al., 2023). Microbial community dynamics during composting exhibit successional patterns that are both shaped by and reciprocally influence key physicochemical parameters, ultimately determining composting efficiency (Meng et al., 2019; Zhong et al., 2020; Hernandez-Lara et al., 2022). Furthermore, microbial co-occurrence patterns can disentangle complex microbial communities and delineate the underlying ecological processes (Banerjee et al., 2016). Network analysis identifies keystone microorganisms that shape community structure and function through node-link interactions (Ai et al., 2023). Monitoring the dynamic changes in microbial community structure, co-occurrence network and metabolic functions during composting is crucial for unraveling the mechanisms of material transformation and enhancing the quality of compost products (Li D. et al., 2023).

However, the long composting time, nitrogen loss, incomplete organic matter decomposition, and low humification degree directly reduce the application value of compost products (Wang et al., 2016; Chen et al., 2023). Several approaches have been proposed to improve the composting process as well as the quality of the finished products, including the addition of physical, chemical and microbial additives (Wu et al., 2019; Zhou et al., 2019; Duan et al., 2020; Wang et al., 2021; Li S. et al., 2023). In recent years, marine carbohydrates, e.g., chitosan oligosaccharides (COS) and *Enteromorpha prolifera* polysaccharides (EPP), which have been widely used in food, medical and livestock and poultry industry (Li et al., 2018; Wang W.-W. et al., 2022; Kim et al., 2024; Li et al., 2024). COS are degradation products obtained from chitin or chitosan in shrimp shells or crab shells through chemical or enzymatic hydrolysis. Previous studies have revealed that COS can not only promote plant growth, enhance their nitrogen fixation capacity and nutrient absorption efficiency but also significantly optimize soil microbial community structures, leading to a substantial increase in the abundance of beneficial bacteria such as *Talaromyces* (Guo et al., 2012; Salachna et al., 2017; Mukhtar Ahmed et al., 2020). EPP are a water-soluble sulfated heteropolysaccharide extracted from *Enteromorpha prolifera*, which have been proven to act as a biostimulant, promoting seed germination, plant growth, and inducing plant defense responses (Battacharyya et al., 2015; Shukla et al., 2016; Mzibra et al., 2018). In addition, EPP could promote root colonization of plant growth-promoting rhizobacteria by serving as an environmental signal for bacterial biofilm formation (Chu et al., 2023). Furthermore, both COS and EPP, being carbon sources to be metabolized by bacteria easily, serve to bolster microbial activity and expedite the decomposition of organic matter. Given the potential role of COS and EPP in regulating microbial structure directly and indirectly, we speculate that the application of COS and EPP to compost would reshape bacterial community, and then impact compost performance. However, it remains unclear how COS and EPP, as compost additives, affect the microbial community characteristics, co-occurrence network and their metabolic functions, as well as composting performance during composting.

Therefore, in this study, composting experiments was conducted with cow manure, rice husks, and tomato residues as substrates, with COS and EPP as additives. The main objectives of this study were to: (1) investigate the effects of COS and EPP on the physicochemical properties of compost; (2) explore the influence of COS and EPP on bacterial community succession during composting using high-throughput sequencing technology, and to analyze the correlation between physicochemical properties and bacterial community dynamics; (3) to identify the core bacteria and interaction of key bacterial community in composting with co-occurrence network analysis; (4) analyze the impact of COS and EPP on the metabolic functionalities of bacterial community through PICRUSt 2 functional prediction.

2 Materials and methods

2.1 Experimental design and sampling

The husks of rice (*Oryza sativa* L.) were provided by Beisenmiao Energy Company. Cow manures were obtained from the local dairy farm in the Jimo District, Qingdao, Shandong Province, China. Tomato residues were collected from a conventional tomato farm located in Jimo District, Qingdao. COS and EPP were provided by Qingdao Seawin Biotech Group. The three components were thoroughly mixed at a wet weight ratio of 5:1:2, and their main physicochemical properties are summarized in Supplementary Table S1. The composting process employed a 60 L airtight stainless steel composting reactor, equipped with a device capable of automatically recording temperature and constructed with double-layer insulated stainless steel. The experiment adopted a bottom ventilation design, with a ventilation device connected to the bottom of the composting reactor. To ensure effective ventilation and oxygen supply, a stainless steel porous sieve plate was placed at the bottom to support the composting materials. Three treatments were set up: (1) rice husks + cow manure + tomato residues (CK); (2) rice husks + cow manure + tomato residues + 0.02% chitosan oligosaccharide (COS); (3) rice husks + cow manure + tomato residues + 0.02% *Enteromorpha prolifera* polysaccharide (EPP). Samples were collected after each turning of the compost pile to ensure uniformity. At each sampling time point, three samples were collected from three different vertical positions and then thoroughly mixed together. Samples were treated following Xie's protocol (Xie et al., 2024). All samples were ground, sieved, thoroughly mixed, and divided into two parts. One sample was stored at 4°C for physicochemical property analysis, while the remaining sample was frozen at −80°C for microbiological analysis. Samples collected on days 0, 2, 8, and 20 were selected to represent the initial, thermophilic, cooling, and maturation stages, respectively.

2.2 Physicochemical analyses

The compost temperature was automatically recorded using a temperature sensor at the center of the compost pile, with a time interval of 1 h. Fresh compost samples were mixed with deionized water at a ratio of 1:10 (w/v) and oscillated at 200 rpm for 30 min. pH and electrical conductivity (EC) were measured with a digital pH meter (pHS-3C, China) and a conductivity meter (DS-307A, China), respectively. The water extract and pak choi seeds were incubated in a constant temperature incubator at 25°C in darkness for 48 h to determine the germination index (GI). The dried sample weighing 1.00 g was transferred to a crucible and then placed in a muffle furnace, where it was incinerated at 550°C for 6 h until a constant weight was achieved. The difference in mass before and after incineration, divided by the mass of the sample before incineration, represented the organic matter content (OM). The sample to be tested reacted with ammonium molybdate to form yellow phosphomolybdate, and the concentration of phosphate ions was determined by measuring the absorbance of the solution. The total carbon (TC) and nitrogen (TN) content of the dried sample were determined using an elemental analyzer (ThermoFisher FlashSmart, USA), and the carbon/nitrogen ratio (C/N) was calculated. Ammonium nitrogen (NH_4^+–N) and nitrate nitrogen (NO_3^-–N) in the compost samples were extracted using a 2 mol/L KCl solution and analyzed using a segmented flow analyzer (Skeleton San++, France). Unfortunately, due to the low concentration of NO_3^-–N, it was not measurable, and therefore not included in the subsequent analysis.

2.3 DNA extraction and high-throughput sequencing

Total microbial DNA was extracted using the FastDNA® Spin Kit for Soil (MP Biomedicals, Solon, USA). A NanoDrop 2000 ultraviolet–visible spectrophotometer was used to measure DNA concentration and purity. The V3–V4 region of the bacterial 16S rRNA gene was amplified using primers 338F (5′-ACTCCTACGGGAGGCAGCAG-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′). The amplified products were subjected to high-throughput sequencing on the Illumina Miseq PE 300 platform by Majorbio Bio-Pharm Technology Co., Ltd. (Shanghai, China).

2.4 Data analysis

All samples for analysis were triplicated and all data was analyzed and visualized in Excel 2019 and OriginPro 2021. One-way analysis of variance (ANOVA) and post-hoc multiple comparison tests were conducted using SPSS 25.0 (SPSS for Windows, version 25.0, USA). Differences with a $p < 0.05$ were considered statistically significant. Based on the MGISEQ bioinformatics platform, sequences were clustered into Operational Taxonomic Units (OTUs) with a 97% similarity threshold. OTU sequences were then annotated against the Silva138/16s_bacteria database. To visually display differences in bacterial community composition among different composting treatments and over time, non-metric multidimensional scaling (NMDS) statistical analysis and plotting were conducted using R (version 3.3.1). Redundancy analysis (db-RDA) based on Bray-Curtis distance matrix was employed to investigate the relationship between bacterial community composition in compost and environmental factors. Spearman correlation analysis was conducted using R (version 3.3.1) with the pheatmap package to reveal the correlation between environmental parameters and the abundance of bacterial community composition (Top 30 genes). PICRUSt 2 was utilized for predicting functional gene profiles based on bacterial 16S rRNA data using the Kyoto Encyclopedia of Genes and Genomes (KEGG) database. The network analysis was performed to explore the co-occurring relationships between the members of bacterial communities using the "WGCNA" and "igraph" R packages. The interactive platform "Gephi" was used to identify the modules (ecological clusters) of microbial taxa.

3 Results and discussion

3.1 Changes in physicochemical properties during composting

Temperature, as one of the crucial indicators in composting, determines the succession of microbial communities and the degradation process of organic matter (Wei et al., 2014). In this study, CK, COS, and EPP reached peak temperatures on the 3rd, 1st, and 2nd days, respectively, with peak temperatures of 57.96°C, 65.12°C, and 63.15°C (Figure 1A). This finding suggested that the addition of marine carbohydrate led to an advance in the thermophilic phase and an increase in peak temperature, especially COS (Zhao et al., 2022). pH is a critical parameter affecting the composting process, influencing microbial nutrient uptake and altering their activity (Cao et al., 2023). As illustrated in Figure 1B, the pH values of all treatments exhibited an initial increase followed by a decrease trend, reaching their peaks on the 2nd day. The pH increase was likely attributed to microbial decomposition of organic nitrogen and reduction of NH_4^+–N, while the subsequent decrease may have been caused by rapid microbial degradation of organic matter, resulting in the accumulation of organic and inorganic acids (Jiang et al., 2015). After composting, the final pH values were 7.78 ± 0.07, 8.22 ± 0.06, and 8.06 ± 0.14, respectively, all within the optimal pH range (5.5–8.5) (Wang Z. et al., 2023). The EC of each treatment exhibited a continuous upward trend, reaching peak values at the end of composting, all exceeding 4 $ms \cdot cm^{-1}$ (Figure 1C), which was related with the ongoing decomposition of organic matter (Liu J. et al., 2023). The GI reflects the phytotoxicity of compost (Cao et al., 2023). As GI values indicated, marine carbohydrates promoted compost maturity, with final values of 104.82 ± 20.83%, 156.12 ± 16.02%, and 119.47 ± 15.48% in CK, COS, and EPP, respectively (Figure 1D), all meeting the security requirements (>80%). The loss rates of organic matters (OMs) for COS and EPP were 51.41 and 37.46%, respectively, higher than 24.80% in CK (Figure 1E). It was speculated that

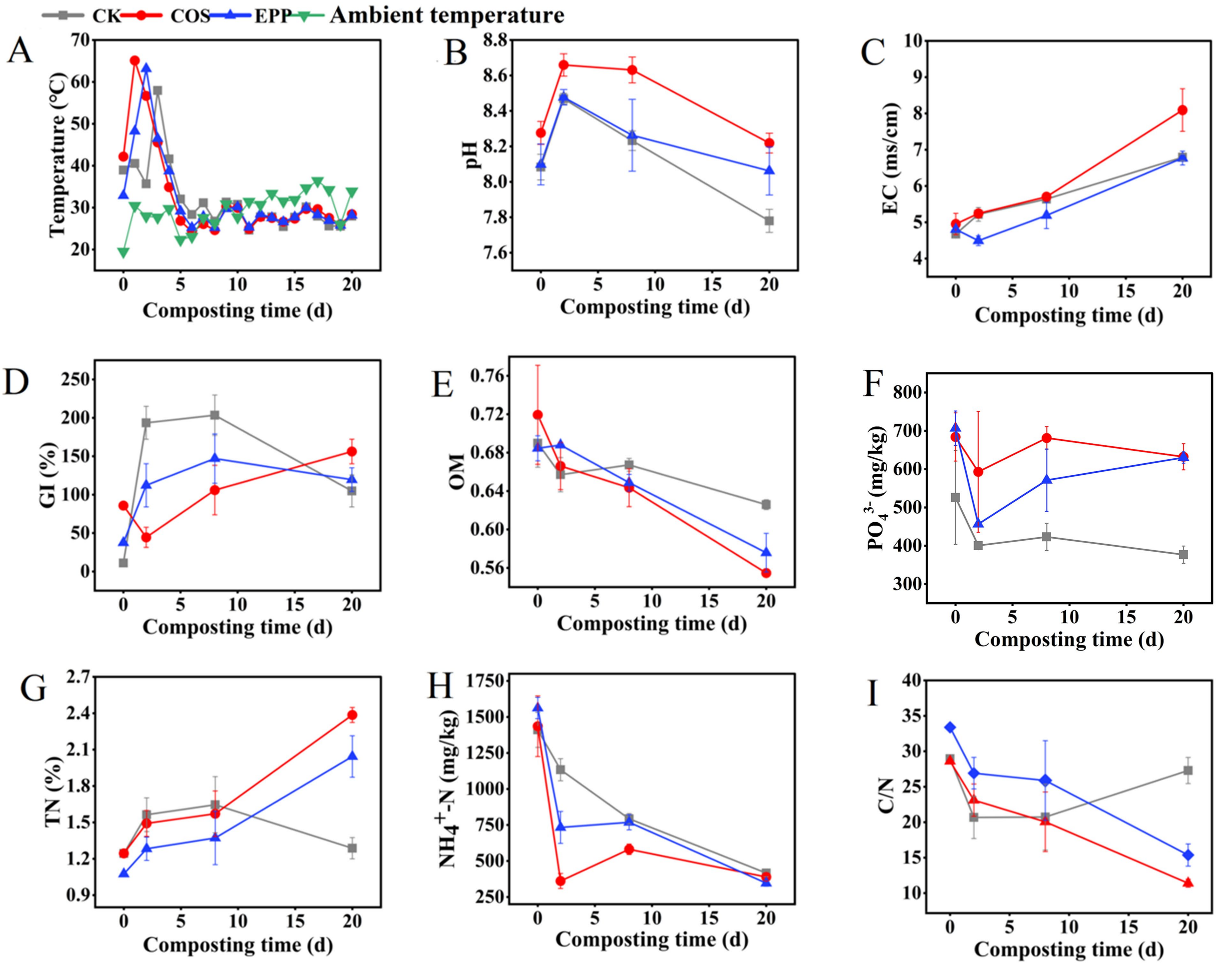


FIGURE 1
Physicochemical properties in different treatments during composting. **(A)** Temperature, **(B)** pH, **(C)** EC, **(D)** germination index (GI), **(E)** organic matter content, **(F)** phosphate content, **(G)** total nitrogen (TN), **(H)** NH_4^+–N, and **(I)** C/N. CK, rice husks + cow manure + tomato residues; COS, rice husks + cow manure + tomato residues + 0.02% chitosan oligosaccharide; EPP, rice husks + cow manure + tomato residues + 0.02% *Enteromorpha prolifera* polysaccharides. Error bars represent standard deviations of triplicate measurements.

carbohydrates provided nutrients to promote microbial metabolism, thereby increasing the degradation rate of organic matter (Zhang et al., 2013). After composting, the content of PO_4^{3-} decreased slightly. Compared with CK, the addition of marine carbohydrates increased the phosphorus content in the compost, possibly because the carbon-containing additives directly drove the phosphorus decarbonating microorganisms to contribute microbial biomass P (Chen P. et al., 2022) (Figure 1F). Compared to the initial stage, the TN concentration of CK, COS, and EPP in the mature stage increased by 3.46, 91.74, and 96.84%, respectively, resulting in a higher TN of final compost in COS and EPP than in CK (Figure 1G). These results indicated that the addition of marine carbohydrates increased the nutrient content of the compost (Zhou et al., 2019). In the initial stage of composting, the decrease rate of NH_4^+-N in the carbohydrates-added group was faster than that in the CK group, which was due to the faster heating rate in the carbohydrates-added group, resulting in more intense NH_3 volatilization. Notably, the CK group exhibited a distinct NH_4^+–N variation pattern: continuous decline until day 2 followed by stabilization through day 8, then rebounding by day 20—contrasting sharply with the carbohydrates-added group pattern of initial rapid decrease followed by slight recovery. This divergence likely stemmed from microbial community restructuring induced by carbohydrate supplementation, thereby promoting NH_4^+–N accumulation (Szliszka et al., 2009) (Figure 1H). Ultimately, all treatments achieved comparable NH_4^+–N reduction levels by day 20. The C/N ratio in composting is an important indicator affecting the nutrient requirements of microorganisms (Cao et al., 2023). C/N < 20 can be considered as the standard for compost maturity (Chen et al., 2021). At the end of composting, the C/N of CK, COS and EPP decreased to 27.29, 11.40, and 15.37, respectively, and all the carbohydrates groups met the requirements of decomposition (Figure 1I).

3.2 Bacterial diversity and community composition during composting

Bacteria, being the most abundant microorganisms during composting, exhibit rapid growth and play a key role in the degradation of nutrients such as carbohydrates and proteins.

Differences in bacterial diversity among different treatments at different stages were observed. The Chao 1 index reflects the richness of bacterial community, while the Shannon index indicates the diversity of bacterial community. Higher values signify greater richness or diversity (Liu et al., 2017; Zhong et al., 2020). As shown in Figure 2A, the richness of bacterial community in the composting process exhibited a trend of initially decreasing and then increasing, and the initial decline may be attributed to a sharp rise in temperature during the first 2 days (Wang Y. et al., 2022). Meanwhile, bacterial diversity showed a continuous increase, indicating microbial adaptation to the environment throughout the composting process, ultimately reaching its highest level in mature compost (Xu et al., 2021; Chen Y. et al., 2022) (Figure 2B). Notably, EPP outperformed COS in promoting microbial richness and diversity, potentially because of COS' antimicrobial activity, though the distinction diminished by day 20 (Liu et al., 2018; Phil et al., 2018; Yin et al., 2020).

Non-metric multidimensional scaling (NMDS) was conducted to analyze β diversity, and the results were shown in Figure 2C. It could be observed that the although composting stage was the primary factor (Han et al., 2022), additives also significantly influenced the bacterial community composition. During composting, the phyla Firmicutes, Proteobacteria, Actinobacteriota, and Bacteroidota are important dominant bacteria in the composting system (Figure 2D). These phyla were widely utilized in agricultural waste treatment (Liu et al., 2017; Wang et al., 2018; Wang G. Y. et al., 2022). During the initial stage, the abundance of Firmicutes was highest, with an increase during the thermophilic phase and a subsequent decrease during the cooling and maturation phases. This pattern was attributed to the predominance of thermophilic bacteria within the Firmicutes phylum, such as the genera *Bacillus*, *Thermobacillus*, and *Ureibacillus* (Zhong et al., 2018) (Figure 2E). These bacteria have the capability to produce heat-resistant endospores and efficiently degrade large molecular organic compounds like cellulose and polysaccharides (Li et al., 2019; Awasthi et al., 2020; Bello et al., 2020). The abundance of Proteobacteria and Bacteroidota was inhibited at high temperatures, resulting in a decrease in abundance, followed by an increase during the cooling and maturation phases. Actinobacteriota exhibited less fluctuation in abundance with temperature changes, suggesting their tolerance to the high temperatures in the composting process. They worked synergistically with Firmicutes in cellulose degradation (He et al., 2022). In addition, except for the initial stage, the relative abundance of Firmicutes in the CK group was lower than in the carbohydrates-containing group (Supplementary Figure S1). This might be due to

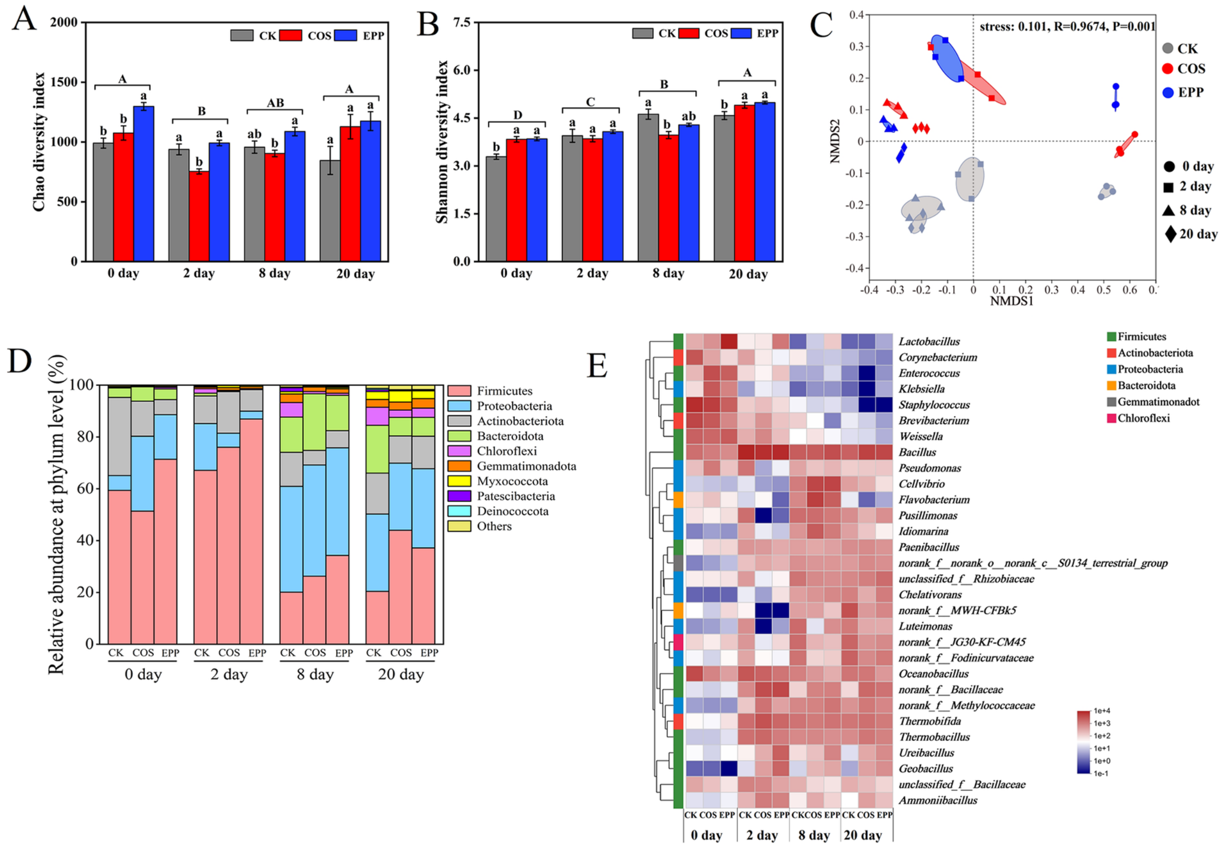


FIGURE 2
Changes in bacterial diversity index and community composition in different treatments during composting. **(A)** Chao 1 diversity index, **(B)** Shannon diversity index. Bars without shared lowercase and uppercase letters indicate significant differences among different additive treatments at each composting time and among different composting time according to Tukey's HSD. **(C)** Non-metric multidimensional scaling (NMDS) analysis of microbial communities based on bray–curtis dissimilarity. **(D)** Phylum level and **(E)** genus level. CK, rice husks + cow manure + tomato residues; COS, rice husks + cow manure + tomato residues + 0.02% chitosan oligosaccharide; EPP, rice husks + cow manure + tomato residues + 0.02% *Enteromorpha prolifera* polysaccharides.

the incorporation of carbohydrates-containing additives, which changed microbial activity by increasing the amount of organic compounds in the heap (Zhong et al., 2018; Bello et al., 2020).

At the genus level (Figure 2E), there were differences in the dominant bacterial genera and their relative abundance among treatments at the initial phase. The dominant genera in the CK group included *Staphylococcus* (27.99%), *Brevibacterium* (14.33%), *Oceanobacillus* (12.35%), *Weissella* (6.67%), and *Bacillus* (4.79%); In group COS, the dominant bacterial genera included *Staphylococcus* (17.99%), *Enterococcus* (11.24%), *Brevibacterium* (8.59%), *Weissella* (5.96%), and *Bacillus* (3.31%); In group EPP, the dominant bacterial genera were *Lactobacillus* (37.04%), *Weissella* (8.15%), *Enterococcus* (7.20%), *Staphylococcus* (7.14%), and *Brevibacterium* (2.49%). It was worth emphasizing that *Lactobacillus* was capable of organic matter degradation and promoted the initiation of composting (Xu et al., 2022). In summary, the addition of carbohydrates-containing additives could alter the composition of initial bacterial communities, indicating a meaningful additive significance (Wang Y. et al., 2022). In the thermophilic phase, the dominant genera in each treatment were *Bacillus* (25.67–34.63%), *Thermobifida* (4.84–10.44%), *Thermobacillus* (3.30–5.69%), and *Oceanobacillus* (4.01–8.98%). *Oceanobacillus* has strong protein hydrolysis ability and participates in the humification of organic matter (Zhang et al., 2020). In addition, there were also relatively high abundances of norank _f_ Bacillaceae in groups COS and EPP. During the cooling phase, compared with CK group, the carbohydrates-added group had more *Cellvibrio* (belonging to the Proteobacteria phylum) and *Flavobacterium* (belonging to the Bacteroidetes phylum). Both *Cellvibrio* and *Flavobacterium* have excellent abilities to utilize polysaccharides, converting recalcitrant lignocellulose into stable humic substances. The addition of carbohydrates-containing additives provided them with a suitable growth environment (He et al., 2022; Wang C. et al., 2022; Wang S. P. et al., 2022). In the maturation stage, the diversity of dominant bacteria decreased, and the abundance of each bacterial taxon tended to be uniform.

Interestingly, the abundance of *Ureibacillus*, *Geobacillus*, and *Ammoniibacillus* increased in the thermophilic stage, with the abundance in the carbohydrates-added group significantly greater than that of CK group. The thermophilic bacterium *Ureibacillus* is one of the main microbial groups responsible for organic matter degradation under high-temperature conditions, and it has been reported in most high-temperature phases of composting trials (Li et al., 2020; Wang Y. et al., 2022). *Geobacillus*, like *Ureibacillus*, is also a thermophilic bacterium that dominates during the high-temperature phase of composting and can prolong this phase (Sarkar et al., 2010; Xu et al., 2022). *Ammoniibacillus*, another thermophilic bacterium, relies on NH_4^+–N as its sole nitrogen source for growth (Sakai et al., 2015; Qiu et al., 2021). In other words, the higher the abundance of *Ammoniibacillus*, the higher the utilization rate of corresponding NH_4^+–N and the less nitrogen loss (Wang N. et al., 2022). The above taxa belong to the thermophilic bacteria of Firmicutes and are closely related to the degradation and utilization of organic matter. The observed results might be attributed to the provision of a more suitable microenvironment for their growth by the addition of carbohydrates-containing additives (Wang et al., 2021; Wang Y. et al., 2022). In summary, the application of carbohydrates additives increased the abundance of microorganisms that could effectively degrade organic matter in compost, thereby promoting the maturity of compost.

3.3 Drivers of microbial communities during composting

Changes of environmental factors drive bacterial community structure succession during composting (Ge et al., 2020). The relationship among samples, environmental factors, and bacterial community was explored using distance-based redundancy analysis (db-RDA). As shown in Figure 3A, in the CK treatment, only two environmental factors, EC ($R^2 = 0.9527$, $p = 0.001$) and NH_4^+–N ($R^2 = 0.8901$, $p = 0.001$), showed significant correlations with bacterial community structure. By contrast, in the COS treatment, eight environmental factors, pH ($R^2 = 0.8001$, $p = 0.002$), EC ($R^2 = 0.8769$, $p = 0.001$), OM ($R^2 = 0.6555$, $p = 0.002$), GI ($R^2 = 0.6347$, $p = 0.02$), TC ($R^2 = 0.6681$, $p = 0.015$), TN ($R^2 = 0.861$, $p = 0.001$), C/N ($R^2 = 0.7644$, $p = 0.002$), and NH_4^+–N ($R^2 = 0.7099$, $p = 0.008$) were significantly correlated with bacterial community structure (Figure 3B). For the EPP treatment, five environmental factors, EC ($R^2 = 0.7443$, $p = 0.011$), OM ($R^2 = 0.8027$, $p = 0.001$), TN ($R^2 = 0.6261$, $p = 0.017$), C/N ($R^2 = 0.5112$, $p = 0.044$), and NH_4^+–N ($R^2 = 0.6507$, $p = 0.019$) exhibited significant correlations with bacterial community structure (Figure 3C). These findings suggested that carbohydrates additives could significantly enhance the correlation between bacterial community and environmental factors. Carbohydrate amendment induces bacterial population shifts, altering community structure and function, thereby modulating the system's environmental responsiveness. Therefore, the observed correlations suggest that carbohydrates additives can play a key role in modulating the relationship between bacterial communities and their surroundings.

The Spearman correlation analysis reflected the relationship between dominant bacteria genera and environmental factors (Figure 3D). It could be seen that the relative abundance of *Ureibacillus*, *Geobacillus*, and *Ammoniibacillus* in the carbohydrates-added group compared with that in the CK group was mainly positively correlated with pH and TN. The Spearman correlation heatmap broadly reflected two clusters of taxa: the first cluster included *Corynebacterium*, *Staphylococcus*, *Enterococcus*, *Lactobacillus*, *Weissella*, *Brevibacterium*, and *Klebsiella*, which were mainly pathogenic bacteria, lactic acid bacteria, and thermosensitive bacteria (Lasaridi et al., 2006; Wang et al., 2014; Tran et al., 2019; Liu et al., 2021; Shangguan et al., 2022; Shi et al., 2022). Their abundance was negatively correlated with EC, GI, and TN, and positively correlated with NH_4^+–N, OM, TC, and C/N. The second cluster included norank_f__Methylococcaceae, *Paenibacillus*, unclassified_f__Rhizobiaceae, *Chelativorans*, *Cellvibrio*, *Pusillimonas*, and *Luteimonas*, which were mainly associated with the degradation of cellulose, lignin, nitrogen-containing compounds, and organic matter (Yin et al., 2017; Wang Y. et al., 2023; Wongkiew et al., 2023; Xie et al., 2023). The correlation of their abundance with environmental factors was exactly opposite to that of the first cluster of genera. This suggested that the bacteria in the first cluster primarily relied on NH_4^+–N, OM, and TC for nutrition and were responsible for TN degradation, while TN primarily supported the nutrition of bacteria in the second cluster and promoted the transformation of NH_4^+–N and the humification of OM. Combining the relative abundance heatmap (Figure 2E), it was observed that the bacteria belonging to the first cluster decreased continuously as composting progresses, while those in the second cluster increased.

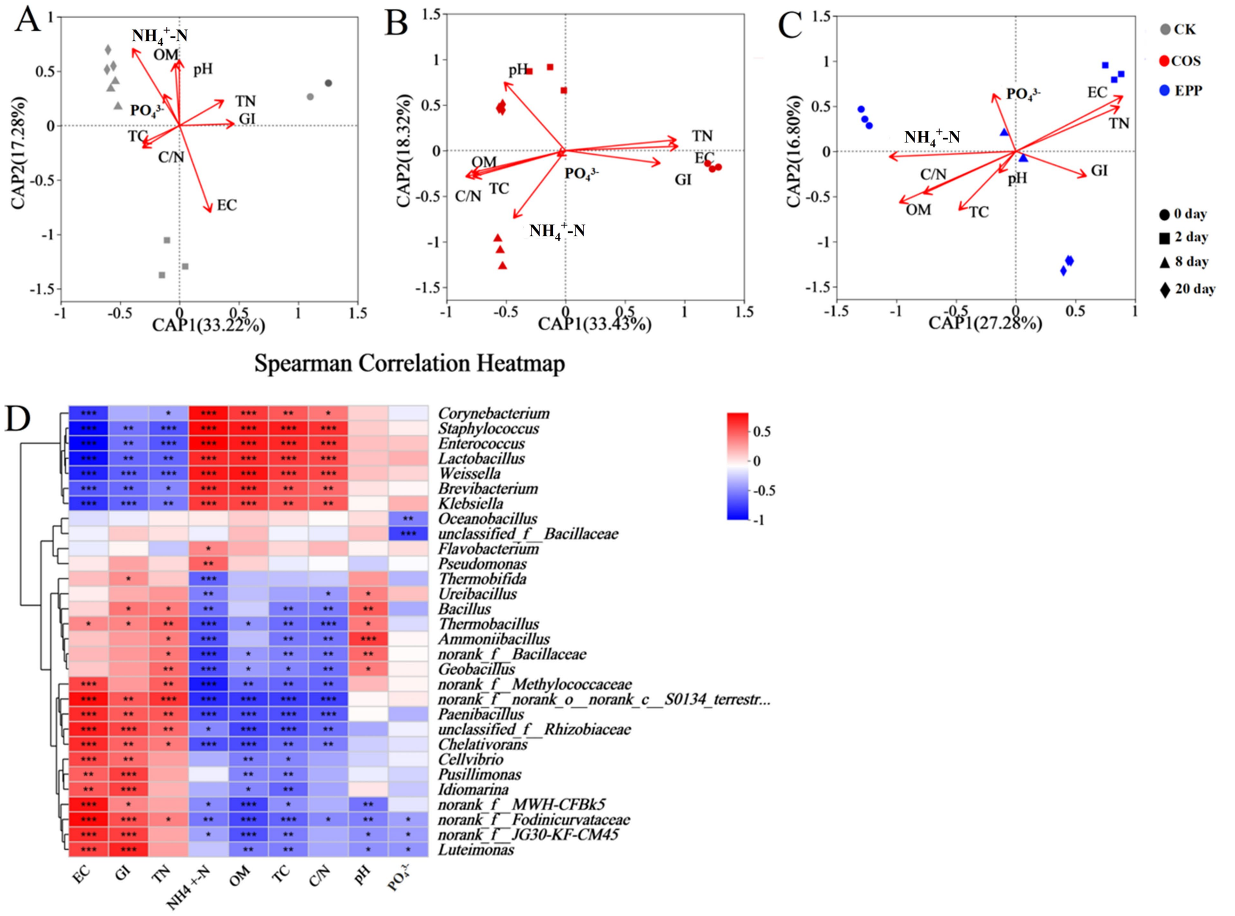


FIGURE 3
Db-RDA of the bacterial community in CK **(A)**, COS **(B)** and EPP **(C)** during composting. **(D)** Spearman's correlation heatmap between compost physicochemical properties and top 30 genera. The value of $p < 0.05$ is marked with "*," $p < 0.01$ is marked with "**," and $p < 0.001$ is marked with "***." CK, rice husks + cow manure + tomato residues; COS, rice husks + cow manure + tomato residues + 0.02% chitosan oligosaccharide; EPP, rice husks + cow manure + tomato residues + 0.02% *Enteromorpha prolifera* polysaccharides.

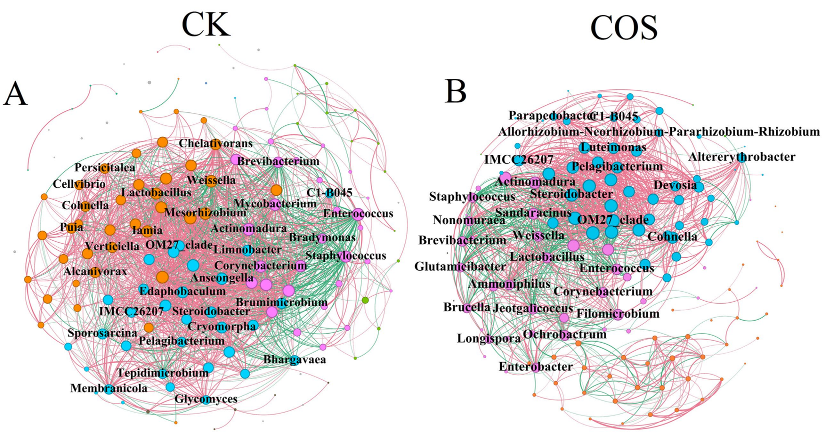
This indicated that significant succession of bacterial community occurred during composting, and the abundance of dominant genera was closely related to environmental factors.

3.4 Bacterial co-occurrence network patterns during composting

The addition of marine polysaccharides affected the co-occurrence network patterns of bacteria during composting (Figure 4; Table 1). Compared to CK, the addition of COS reduced the total number of nodes, total number of edges, and avgD, but increased the avgCC, GD, and proportion of positive edges. The addition of EPP reduced the total number of edges, avgD, and proportion of positive edges, but increased the total number of nodes, avgCC, and GD. In summary, the addition of carbohydrates decreased the total number of edges and avgD, and increased GD, indicating that the addition of carbohydrates weakened the overall associations among bacteria and reduced network complexity, which was also directly reflected in the graph density data. However, the higher avgCC suggested that the addition of carbohydrates could enhance the connections within certain bacterial communities (Li G. et al., 2023).

Keystone taxa are highly connected taxa in microbial communities, which have special and important roles, and their removal can cause drastic changes in community structure and function. The keystone taxa from the highest connectome were *Mesorhizobium* (Lin et al., 2023), *Steroidobacter* (Krishnan et al., 2017), *Edaphobaculum*, *Anseongella* (Wang Y. et al., 2023), *Actinomadura* (Wang Y. et al., 2023) with degrees of 61, 59, 59, 59, 59 in the CK treatment. The COS treatment keystone taxa composed of *Actinomadura*, *Steroidobacter*, *Ammoniphilus*, *Cohnella* (Rastogi et al., 2010) and *Luteimonas* (Yang et al., 2023; Liu N. et al., 2024) with 47, 46, 37, 37, 37 degrees. The EPP treatment keystone taxa composed of *Leuconostoc* (Kot et al., 2014), *Persicitalea*, *Corynebacterium* (Ahmed et al., 2023), *Enterococcus* (Liu S. et al., 2024) and *Proteus* (Shi et al., 2022) with 54, 52, 51, 51, 50 degrees.

Although taxonomic composition of keystone taxa differed in different treatments, the critical bacteria remain those involved in the degradation of organic matter and nitrogen cycling. These potential core bacteria played a crucial role in the maturation of compost, underscoring the importance of enhancing indigenous functional bacteria in compost. Interestingly, the first bacterial cluster mentioned earlier (e.g., *Corynebacterium*, *Enterococcus*, *Staphylococcus*, *Lactobacillus*, *Weissella*, and *Brevibacterium*) exhibited high degree,



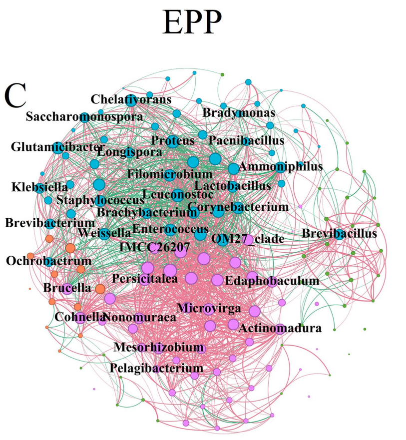


FIGURE 4
Molecular ecological network analysis showing the bacterial co-occurrence pattern during composting. **(A–C)** The bacterial co-occurrence network of different treatments. The colors of the nodes are assigned according to the module. The size of each node is proportional to the degree. Edge thickness is proportional to the weight of each correlation. A red edge indicates a positive interaction between two individual nodes, whereas a green edge indicates a negative interaction. Only nodes whose degree is greater than the average degree of corresponding processing are shown. CK, rice husks + cow manure + tomato residues; COS, rice husks + cow manure + tomato residues + 0.02% chitosan oligosaccharide; EPP, rice husks + cow manure + tomato residues + 0.02% *Enteromorpha prolifera* polysaccharides.

TABLE 1 Key topological features of soil microbial communities under different fertilization treatments.

Treatment	Total nodes	Total edges	Average degree (avgD)	Average clustering coefficient (avgCC)	Average path distance (GD)	Density	Proportion of positive edges
CK	144	1,740	24.167	0.614	2.484	0.169	67.76%
COS	137	1,166	17.022	0.631	3.334	0.125	68.82%
EPP	154	1,609	20.896	0.659	3.088	0.137	65.05%

demonstrating significant linking roles (Supplementary Table S2). These bacterial groups exhibited close interactions with other bacteria during the composting process, performing their main functional roles before gradually disappearing. Considering that this bacterial group included some potential pathogens or antibiotic resistance genes hosts, their disappearance after compost maturation provided a safeguard for compost safety (Wei et al., 2018; Wang B. et al., 2022).

3.5 Prediction of microbial metabolic functions during composting

The changes in bacterial community often lead to alterations in bacterial metabolic functions (Zhou et al., 2019). Bacterial metabolic function was predicted by PICRUSt 2 based on KEGG pathway database. As shown in Figure 5A, most of the predicted functional genes were assigned to metabolic (76.22–78.19%), genetic information processing (6.50–7.23%), environmental information processing (5.89–7.64%), and cellular process (3.71–5.01%) pathways in different composting processes.

As shown in Figure 5B, among the pathways with relative abundances exceeding 1%, the second-level KEGG orthology function predictions encompassed 12 metabolic pathways, 2 environmental information processing pathways, 3 genetic information processing pathways, and 2 cellular processes pathways. The major metabolic pathways included global and overview maps (39.33–40.18%), carbohydrate metabolism (8.62–10.99%), and amino acid metabolism (6.90–8.42%).

Carbohydrate metabolism primarily provides substrates for microbial reproduction and the formation of humic substances through the degradation of cellulose and hemicellulose (Toledo et al., 2017; Yin et al., 2019). It was easy to predict that the addition of marine carbohydrates significantly promoted carbohydrate metabolism. As expected, the gene abundance related to carbohydrate metabolism was higher in group EPP than in group COS, that was, polysaccharides had a more pronounced effect than oligosaccharides in promoting carbohydrate metabolism (Figure 5B).

As illustrated in Figure 5C, the addition of carbohydrates augmented the gene abundance related to amino carbohydrates and nucleotide carbohydrates metabolism, fructose and mannose metabolism, galactose metabolism, and butanoate metabolism during the initial and thermophilic stages of composting. These substrates are readily degradable and can be rapidly consumed during the early stages of composting (Zhong et al., 2020). By modulating the gene abundance associated with the metabolism of arginine, proline, lysine, phenylalanine, and tryptophan, among others, carbohydrates were speculated to reduce bacterial protein synthesis and activity in the amino acid metabolism pathway (Figure 5D) (Zhou et al., 2019).

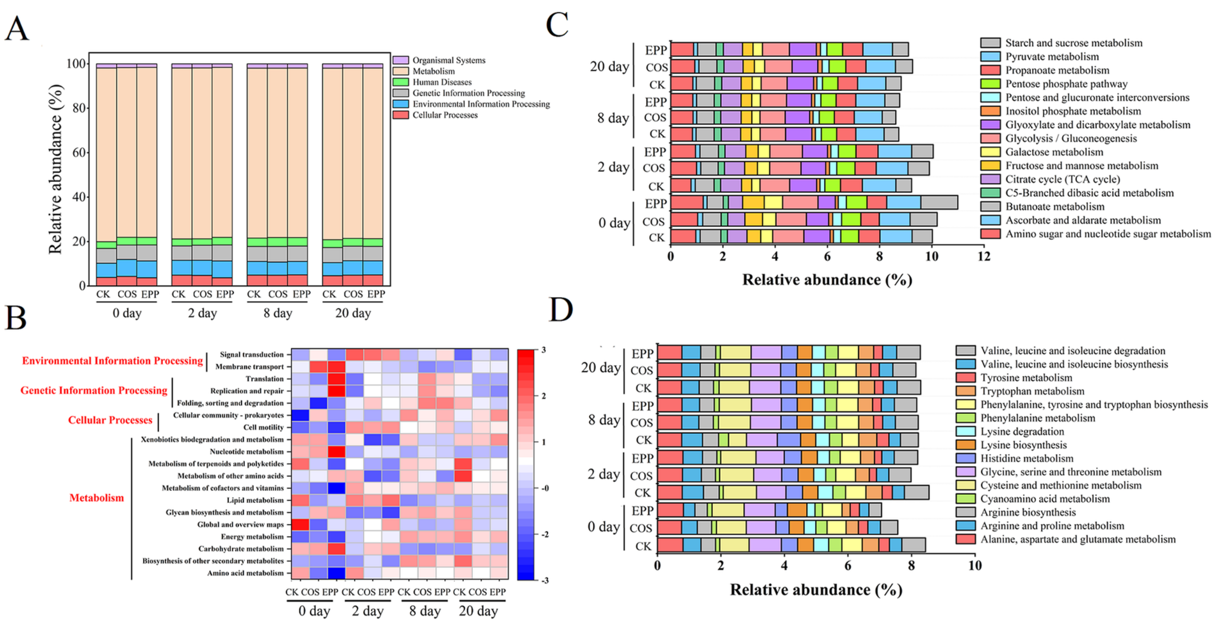


FIGURE 5
Variation of bacterial function profiles in different treatments during composting analyzed by PICRUSt2. **(A)** Relative abundance of KEGG primary function. **(B)** Heatmap showing the changes of bacterial metabolic functions at KEGG level 2. And changes in abundance of carbohydrate metabolism **(C)** and amino acid metabolism **(D)** at each step during composting. CK, rice husks + cow manure + tomato residues; COS, rice husks + cow manure + tomato residues + 0.02% chitosan oligosaccharide; EPP, rice husks + cow manure + tomato residues + 0.02% *Enteromorpha prolifera* polysaccharides.

4 Conclusion

The present study revealed that COS and EPP had significant effects on the physicochemical properties of cow manure and rice husk compost, which could accelerate compost decomposition and promote bacterial community succession, and enhance the correlation of bacterial communities with environmental factors. Specifically, chitosan oligosaccharides outperform *Enteromorpha prolifera* polysaccharides in terms of temperature, TN concentration and GI. EPP exhibited higher influence on microbial diversity and metabolic function. However, they did not contribute to enhancing the complexity of the co-occurrence network. This study provides a theoretical basis for the utilization of chitosan oligosaccharides and *Enteromorpha prolifera* polysaccharides as compost additives to ameliorate agricultural waste composting.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary material.

Author contributions

XYi: Formal analysis, Methodology, Writing – original draft. SC: Formal analysis, Validation, Writing – original draft, Writing – review & editing. GS: Conceptualization, Supervision, Writing – review & editing. GZ: Investigation, Software, Writing – review & editing. GM: Methodology, Supervision, Writing – original draft. SG: Methodology, Software, Writing – original draft. HY: Formal analysis, Visualization, Writing – review & editing. XYo: Conceptualization, Resources, Writing – review & editing. YL: Funding acquisition, Supervision, Writing – review & editing.

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Conflict of interest

XYi, GS, GZ, GM, and SG were employed by Yunnan Tobacco Company Baoshan Company.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The authors declare that no Gen AI was used in the creation of this manuscript.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2025.1563421/full#supplementary-material

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