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ENVIRONMENTAL BIOTECHNOLOGY

Seasonal dynamics of bacterial composition and functions in biological treatment of coking wastewater

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Abstract

Seasonal dynamics of bacterial composition and functions were demonstrated for the biological fluidized-bed bioreactors combined in the anoxic/aerobic1/aerobic2 (AOO) coking wastewater (CWW) treatment sequences. The bacterial composition and functions in the CWW activated sludge samples were revealed by 16S rRNA genes amplicon sequencing. *Thiobacillus, Cloacibacterium, Alkaliphilus* and *Pseudomonas* were determined as core genera with seasonal changes. Mutable microbial community composition fluctuated in different seasons in same bioreactor. Distributions of predicted KEGG pathways along four seasons consistently demonstrated enrichment in biodegradation of carbon- and nitrogen-containing compounds. The major contaminants were removed from CWW by biochemical pathway of xenobiotics biodegradation and metabolism. This Level 2 pathway mainly owned the Level 3 pathways of benzoate degradation, drug metabolism-other enzymes, drug metabolism-cytochrome P450, metabolism of xenobiotics by cytochrome P450, and aminobenzoate degradation. The RDA results showed that dissolved oxygen with seasonal fluctuation was the main parameter shaping the microbial community. The observed dynamics within the microbial community composition, coupled with the maintained stability of CWW treatment efficiencies and a consistent profile of microbial functional pathways, underscore the presence of functional redundancy in the AOO bioreactors. The study underscored stable and effective operational performances of bioreactors in the AOO sequences, contributing the knowledge of microbiological basics to the advancement of CWW biological treatment.

Key points

- *Seasonal fluctuations of bacterial composition described for the AOO system.*
- *Seasonal distributions of metabolic functions focused on carbon and nitrogen removal.*
- *Functional redundancy was revealed in the AOO microbial community.*

Keywords Coking wastewater · Seasonal dynamics · Bacterial community · Functional profiling · 16S rRNA genes

Introduction

Coking wastewater (CWW), originating from coal coking, coke quenching and coal liquefaction, represents an industrial wastewater of poor biodegradation and high toxicity for its complex composition including NH_3, cyanides (CN^-), phenolic compounds, and polycyclic aromatic hydrocarbons (PAHs) (Tamang and Paul 2022). These pollutants are harmful for biological and ecosystem's health (Li et al. 2023a; Pathak et al. 2023). For example, phenols and PAHs can cause genotoxicity, cardiotoxicity and skeletal development toxicity for aquatic and botanic creatures (Li et al. 2023a; Liu et al. 2017). Ammonia brings the biological toxicity (Wu et al. 2020). CN^- is a typical inorganic pollutant, with damage to human cardiac and central nervous systems.

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Moreover, CWW's contaminants can pollute the soil, preventing the land recycle (Li et al. 2023b). Therefore, CWW, with serious environmental risk, must be duly treated before discharge (Pathak et al. 2023).

At present, bioprocess technology stands as a prevalent methodology for CWW treatment (Zhou et al. 2020). The biological treatment is the core for CWW process and relies upon its intricate prokaryotic microbial community, resulting in highly efficient removal of pollutants at a low cost (Zhang et al. 2022a). Therefore, microbial community is an important component to determine the operational efficiency of CWW biological treatment (Chu et al. 2021). The spectrum of biological processes are employed in CWW treatment encompasses diverse bioreactor combinations, such as anaerobic/aerobic (AO), anaerobic1/anaerobic2/aerobic (AAO), anaerobic/aerobic1/aerobic2 (AOO), anaerobic/oxic1/hydrolytic/oxic2 (AOHO) and oxic1/hydrolytic/oxic2 (OHO) (Zhu et al. 2019). The AOO fluidized-bed sequence biodegrades the major CWW pollutants and achieves stable pollutants removal efficiency with good performance (Zhu et al. 2016). The functions of AOO bioreactors consist of denitrification and nitrogen removal in the bioreactor A, metabolism of organic matters in the bioreactor O1, and nitrification and biodegradation of residual pollutants in the bioreactor O2. Besides, internal recycling facilitates the transfer of nitrified liquid from the bioreactor O2 to A, while nitrite in the bioreactor O1 is also refluxed to A, expediting nitrogen removal at low energy consumption (Ou et al. 2014). Previously, *Pseudomonas*, *Comamonas*, *Thiobacillus*, *Nitrosomonas* and *Nitrosospira* were reported for the organic carbon degradation and nitrogen removal in the AOO system and the microbial community and functions in the AOO bioreactors have been studied statically, although its temporal dynamics is lacking (Zhu et al. 2016).

The structure of microbial community exhibits notable variability throughout the course of a year with influencing factors encompassing temperature, character of contaminants, and operational parameters (Peces et al. 2022). Seasonal factors are recognized as particularly consequential in perturbing the bacterial composition of activated sludge (AS) (Zhang et al. 2018), potentially instigating substantial alterations in removal efficiency (Suransh et al. 2023). Microbial community were proven to go through a seasonal dynamics in wastewater treatment and some dominant species displayed an obvious seasonal dynamics pattern in different seasons (Zhang et al. 2018; Sun et al. 2021; Peces et al. 2022), subsequently affecting the quality of released wastewater (Soares-Castro et al. 2019). The nitrogen removal groups change markedly in different seasons, especially the nitrifying community (Datta et al. 2011; Wang et al. 2016). *Thauera*、*Pseudomonas* and *Longilinea* express high sensitivity for seasonal change (Xu et al. 2022). Sludge foaming is also a problem to reduce treatment efficiency throughout the changing seasons in wastewater (Wang et al. 2016). The microbial community composition of municipal wastewater changes along with the seasons changes in temperature and wastewater compound of the influent (Nomoto et al. 2018). However, microbial community in CWW may have a different response for seasonal dynamics, especially facing the stable influent produced from industrial process. The CWW treatment efficiency, similarly, is affected by seasonal microbial fluctuations (Kim et al. 2007; Kim 2013). However, a critical gap of CWW microbial community obtained with high-throughput sequencing method limits the comprehensively microbial investigation in seasonal dynamics. Consequently, an in-depth study of AOO system microbial community composition in its dynamics becomes imperative, offering valuable insights for the enhancement of treatment methodology.

16S rRNA genes amplicon sequencing is regarded as the standard method for the investigation of microbial diversity (Klindworth et al. 2013). The highly conserved regions and highly variable regions of 16S rRNA genes lead the detection for bacterial taxonomy (Nossa et al. 2010). The Illumina MiSeq sequencing is able to uncover the rare biosphere with low per base costs and short read length (Zhu et al. 2016). PICRUSt2 is designed to predict the bacterial functions according to 16S rRNA genes amplicon data, with more accurateness than PICRUSt1 (Douglas et al. 2020). The community functions were predicted by PICRUSt2 via marker gene sequencing profiles based on the MetaCyc database. The good correlation of PICRUSt2 with shotgun metagenomics sequencing has been proven by studies (Chen et al. 2024; Yang et al. 2023). PICRUSt2 shows no disadvantage comparing with other commonly used tools (Sun et al. 2020; Douglas et al. 2020). Also, PICRUSt2 predictions are prevalent and help for the meaningful findings in environmental researches, especially in wastewater treatment (Tsukamoto et al. 2023; Wang et al. 2023; Xu et al. 2023).

This study delves into the seasonal dynamics and functions of microbial communities in the full-scale AOO bioreactors' sequence in CWW treatment. Standard methods were employed in the analysis of the efficiency of contaminants removal. The process operation characteristics were monitored under conditions of extensive and stable operation. The diversity and composition of microbiota was delineated by 16S rRNA genes amplicon sequencing, while the microbial functions were predicted using PICRUSt2. The objectives of this study were to (1) distinguish the seasonal dynamics in pollutants removal efficiency, (2) identify the microbial consortia with their functions in the seasonal successions, and (3) discern the relationships between environmental factors and microbial consortia.

Materials and methods

Full-scale AOO bioreactors combination

The full-scale AOO CWW treatment installation schematically shown in Fig. 1 is located at the premises of Songshan Iron and Steel Corporation, Shaoguan, Guangdong Province, China. The treatment plant has continuously operated for fifteen years at a CWW processing capacity of 1680 ± 80 m^3/day. To enhance operational resilience against unexpected disturbances, two independent parallel bioreactor sequences were built, being named the South and the North lines.

Collection and analysis of sludge and water samples

The AS samples were taken from the South and North lines in duplicate on March 30, May 29, October 13, 2021, and January 8, 2022, representing the spring, summer, autumn and winter samples, respectively. Every sample was meticulously preserved in ice-boxes and transported to the laboratory. The volume of two to three mL of each sample was used to form cell pellets by centrifugation at 12,000 g for ten minutes at 4 °C. The 120 mM sodium phosphate buffer at pH 8.0 was used to rinse and prepare the cell pellets for storage at -20 °C for further DNA extraction.

For the supernatant liquid analyses, the AS samples were centrifuged at 3,500 g for three minutes to separate the solids. The supernatants analyses revealed pertinent pollutant characteristics, including the chemical oxidation demand (COD), 5-day biochemical oxygen demand (BOD_5), contents of NH_3, phenolic compounds, sulfides, CN^-, thiocyanate (SCN^-), total nitrogen (TN), total phosphorus (TP), total organic carbon (TOC), dissolved oxygen (DO) and pH. Analytical methods were consistent with those outlined by Zhang et al. (2022a, b).

Operational parameters at the AOO treatment of CWW

For intensifying the mass transfer, an internal-loop multiphase airlift fluidized bed bioreactors were designed and commissioned at the enterprise (Wei et al. 2000). The AOO bioreactors exhibited an excellent stability in seasonal dynamics: throughout the long operation, all bioreactors maintained stable temperature within the range of 24 to26°C (Supplementary File Table S1). The pH values in the bioreactors A, O1, and O2 averaged 7.69–7.96, 7.19–7.33 and 7.04–7.14, with DO of 0.12–0.21, 1.42–1.62 and 2.90–3.22 mg L^{-1}, respectively. The detailed operational parameters were given in Supplementary File Table S1.

PCR amplification and MiSeq sequencing

Genomic DNA from microorganisms was extracted with the powerSoil™ DNA isolation kit (Mobio Laboratories, USA) in strict adherence to the manufacturer's instructions. High-quality DNA extracts from each sample subsequently undergone PCR-amplification using the primers F515 (5'-GTGCCAGCMGCCGCGGTAA-3') and R806 (5'-GGACTACVSGGGTATCTAAT-3') as described by Deng et al. (2020).

Sequence processing

The PCR products were defined through Illumina MiSeq. Samples were individually barcoded to enable multiplex sequencing in this study. The raw data underwent preprocessing and manipulation by Mothur (v1.35.1) (Schloss et al. 2009) in conjunction with QIIME (v 1.7) pipelines (Caporaso et al. 2010). Operational taxonomic units (OTUs) were demarcated at 97% sequence similarity and a RDP classifier was applied for taxonomic classification by default. Microbial alpha-diversity and Good's coverage were statistically analyzed by Mothur and QIIME. Functional predictions of microbial communities were accomplished by q2-picrust2 (2021.11_0), a QIIME2 plugin of PICRUST2 (Douglas et al. 2020).

Data analysis

Box plot of alpha-diversity, bubble plot of xenobiotics biodegradation and metabolism distribution and bar graph of major phyla and genera were delineated by ImageGP (Chen

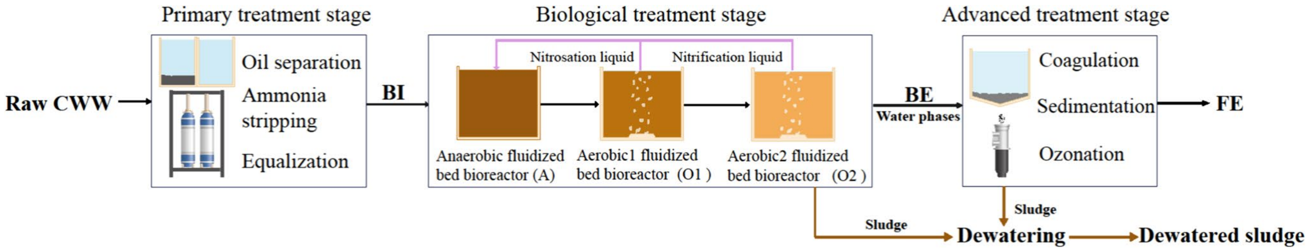


Fig. 1 Schematic outline of the AOO coking wastewater treatment sequence. ^{a} *BI* biological influent, *BE* biological effluent

et al. 2022) and Chiplot (https://www.chiplot.online/). The distribution of Level 2 metabolism pathways, rarefaction curves, principal co-ordinates analysis (PCOA, with the closer distance of Bray Curtis) and redundancy analysis (RDA) were generated utilizing diverse R packages.

Results

AOO seasonal performance

Twelve CWW quality indices were measured to evaluate the functional stability of the AOO combination across the seasons (Table S2). All indices achieved removals surpassing 95% except for TN in all samples. Moreover, the removals remained stable in all four seasons. Notably, the bioreactor A demonstrated, among the total removal from BI to BE, the highest removals of TN and CN^- with average of 38.04% and 65.39%, respectively. In the bioreactor O1, substantial removals of COD, BOD_5, phenols and SCN^- were observed with average 56.87%, 76.67%, 77.65%, and 48.60%, respectively. The bioreactor O2 exhibited efficient nitrification, removing NH_3 for 73.71%.

Biodiversity analysis of the sequences

A total of 17,763 OTUs were retrieved from 624,537 effective sequences in all AS samples. The sequences were assigned into various OTUs (3% nucleotide cut-off) by RDP Classifier. Based on OTUs, the alpha-diversity indices of each sample were listed in Supplementary File Table S3 and Fig. 2. The values of Good's coverage showcased an average of 98.54%, affirming the sequencing depth's representation of the main of 16S rRNA genes. The rarefaction curves further supported this depth assessment (Supplementary File Fig. S1). The Chao 1 of richness and the Shannon's (H') as well as Simpson's (1-D) diversity indices were analyzed (Lemos et al. 2011). On the seasonal scale, the tendency of Chao 1 showed no significant difference in bioreactors (Supplementary File Table S4). The lowest Shannon's (H′) and Simpson's (1-D) indices were exhibited in the bioreactor A, which made them remarkably different from those in bioreactors O1 and O2. By winter, bioreactor A demonstrated remarkably higher Shannon's (H′) and Simpson's (1-D) indices than by other seasons.

PCoA was conducted to evaluate the beta-diversity of microbial communities in the samples (Fig. 3). Evidently, winter samples (Win-A, Win-O1 and Win-O2) differed distinctly from those in other seasons, underscoring a disparate winter microbial community composition. Conversely, in the bioreactor A, Spr-A, Sum-A and Aut-A were grouped together. Bioreactors O1 and O2 showed seasonal similarity (Fig. 3), grouping of Spr-O1, Sum-O1 and Aut-O1, and Spr-O2, Sum-O2 and Aut-O2, respectively. Besides, samples taken from the North and South lines were consistent, indicating seasonal similarity in microbial community composition.

Seasonal dynamics of microbial community composition

In the bioreactors of the AOO combination, identified bacterial OTUs dominated at an average of 99.79%. The study delved into the seasonal variations of microbial community structure in the AOO bioreactors, focusing on the phylum and genera levels of the classified OTUs (Fig. 4 and Supplementary File Fig. S2). At the phylum level, eighteen major phyla were distinguished in all samples, including five subphyla of *Proteobacteria*—*Alphaproteobacteria*, *Betaproteobacteria*, *Epsilonproteobacteria*, *Deltaproteobacteria* and *Gammaproteobacteria*. In each bioreactor, the dominant phyla comprised certain share variable with seasons. Notably, the phyla compositions were obviously divergent in winter, aligning with PCoA results. Among subphyla of *Proteobacteria*, *Alphaproteobacteria*, *Betaproteobacteria* and *Gammaproteobacteria* dominated and fluctuated in seasons in all three bioreactors. During wintertime, the share of *Betaproteobacteria* increased in every bioreactor, while *Gammaproteobacteria* decreased in the bioreactors A and O1 (Fig. 4a and b). *Firmicutes* and *Bacteroidetes* emerged as the steadily subdominant phyla in the bioreactors A and O1, respectively. By winter, *Bacteroidetes* became the subdominant phylum in the bioreactor O2 instead of *Planctomycetes* (Fig. 4c).

At the genera level, thirty major genera were identified in the AOO bioreactors across all seasons. In the bioreactor A, *Pseudomonas*, *Alkaliphilus* and *Campylobacter* were identified as the top three dominant genera in spring, summer and autumn with the average relative abundancy of 5.66%, 5.19% and 3.08%, respectively, whereas *Thiobacillus* genera with its abundancy of 5.12% dominated in winter (Fig. 4d) followed by *B-42* with 2.62%, and *Pseudomonas* with 2.29%. In the bioreactor O1, the dominant genera abundances appeared to significantly fluctuate in seasons. Thus, *Corynebacterium* (5.13%), *Cloacibacterium* (1.61%) and *Ochrobactrum* (1.30%) dominated in spring, whereas certain quantitative changes were observed in summer: *Corynebacterium* (2.57%), *Limnohabitans* (1.13%) and *Ochrobactrum* (0.97%) comprised the leading trio. By the fall, the dominance picture changed qualitatively, showing *Limnohabitans* (1.52%), *Thiobacillus* (1.10%) and *Pseudomonas* (0.77%) dominant. In turn, *Thiobacillus* (16.67%), *Cloacibacterium* (7.01%) and *Thauera* (1.20%) dominated in the active sludge by winter (Fig. 4e). In the bioreactor O2, the abundance of *Thiobacillus* ranged from 16.44% to 34.28%, and stood out

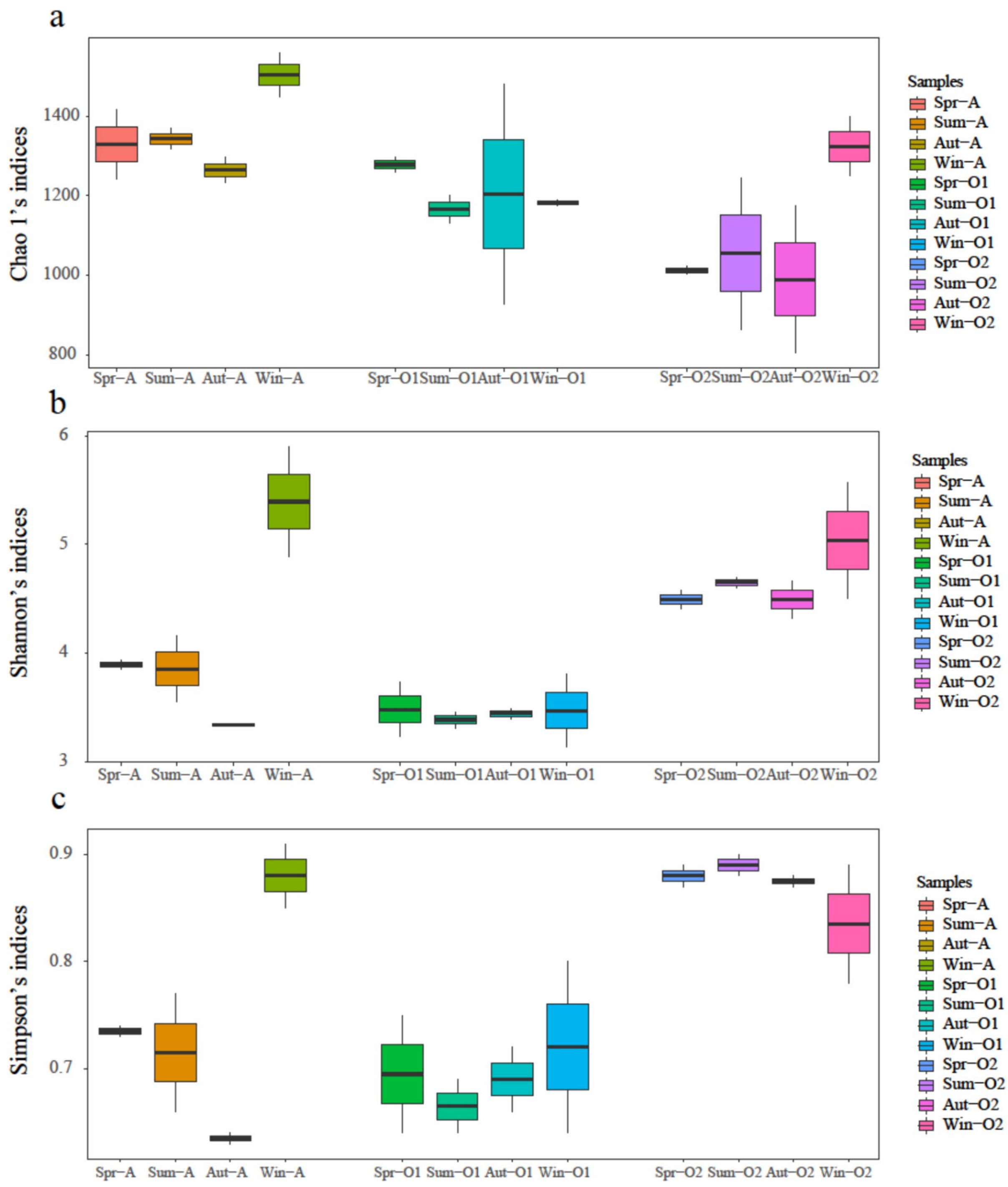


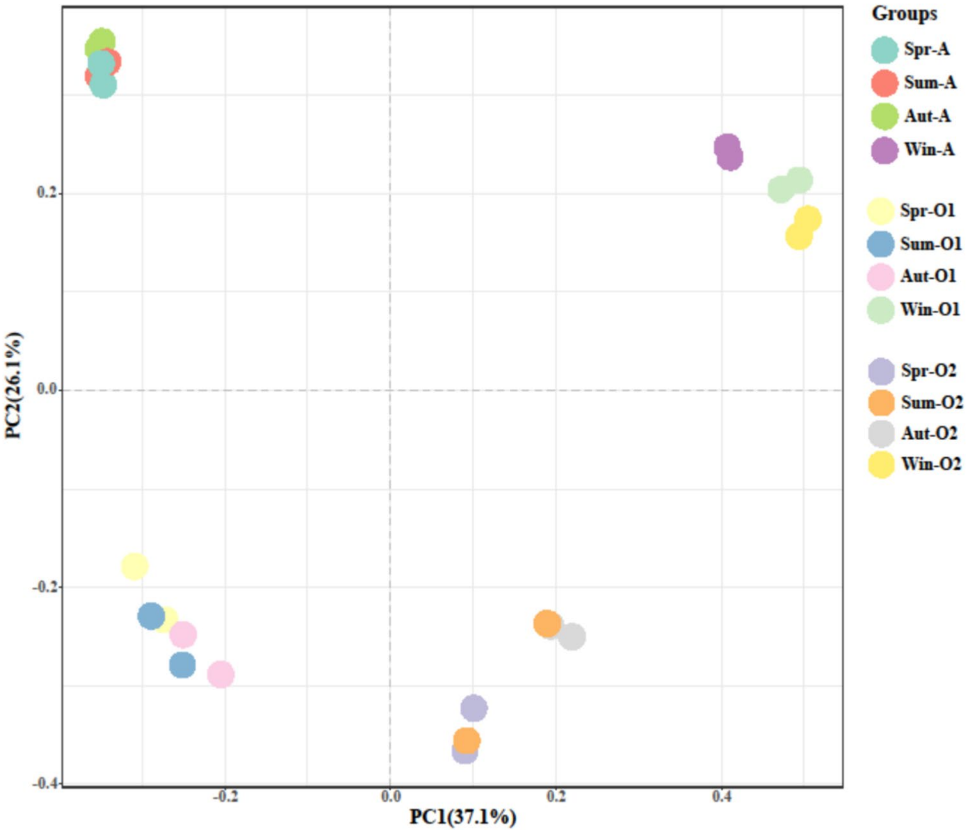
Fig. 2 Calculations of Chao 1's (**a**), Shannon's (H') (**b**) and Simpson's (1-D) (**c**) indices in the AOO bioreactors. [a] *Spr* Spring, *Sum* Summer, *Aut* Autumn, *Win* Winter, *A* anaerobic bioreactor sample, *O1* aerobic1 bioreactor sample, *O2* aerobic2 bioreactor sample

as the predominant genus across all seasons (Fig. 4f). *Rhodoplanes* (0.62%—0.90%) was also the important genus with stable abundances along all seasons, while *Nitrospira* (0.62%—2.69%) showed a burst in winter. The other obvious surges in winter were observed with *B-42* (0.01%-1.17%) and *Thauera* (0.21%-1.14%).

Potential functions profiling

Functional microbiota contents in the AOO bioreactors were predicted using q2-picrust2 with the microorganisms' assessment using the Nearest Sequenced Taxon Index (NSTI). Lower NSTI values indicated a closer association

Fig. 3 The PCoA analysis of microbial communities among the samples



with the sequenced genomes (Gao et al. 2016). In this study, the NSTI values in the AOO bioreactors across the seasons ranged from 0.169 to 0.085, surpassing, e.g., soil inhabitants (0.170) (Zhang et al. 2022a). This establishes the obtained sequencing data as suitable for scrutinizing PICRUST2 predictions.

According to KEGG database, metabolism of Level 1 pathways was related to the performance and rate of microbial removal of pollutants. The AOO bioreactors were enriched with eleven Level 2 pathways of the Level 1 metabolism pathway, encompassing carbohydrate metabolism, amino acid metabolism, energy metabolism and xenobiotics biodegradation and metabolism, among others (Fig. 5).

Xenobiotics biodegradation and metabolism was an important pathway for the pollutants removal (Zhu et al. 2019), which was further analyzed in Level 3 pathways. Twenty-one Level 3 pathways within xenobiotics biodegradation and metabolism were unveiled, featuring, among others, benzoate degradation, drug metabolism-other enzymes, drug metabolism-cytochrome P450, metabolism of xenobiotics by cytochrome P450 and aminobenzoate degradation (Fig. 6). Nitrotoluene degradation supplanted aminobenzoate degradation, claiming the fifth-highest position in the bioreactor O2. These pathways exhibited harmonized seasonal patterns across various seasons in each AOO bioreactor.

Correlations between environmental factors and the major genera

In a quest to examine the correlations of chosen environmental variables (physicochemical characteristics and operational parameters) on the major genera and shed light on the predominating variables impacting the microbial community, RDA was conducted (Fig. 7). The interpretation rates of the two axes were 51.46% and 19.48%, respectively. Several major genera demonstrated robust correlations with the environmental variables, such as the content of pollutants. *Thiobacillus*, *Cloacibacterium* and *Corynebacterium* exhibited inverse relationships with concentrations of the key pollutants – phenolic compounds, COD, TN, CN^-, SCN^- and NH_3. In contrast, *Alkaliphilus*, *Pseudomonas* and *Campylobacter* displayed positive correlations with concentrations of these pollutants. These relationships pointed to the biodegradability potential of identified genera in pollutants removal. In addition, the content of phenolic compounds surfaced as the foremost environmental factor exerting a profound impact on the microbial community composition in the AOO bioreactors.

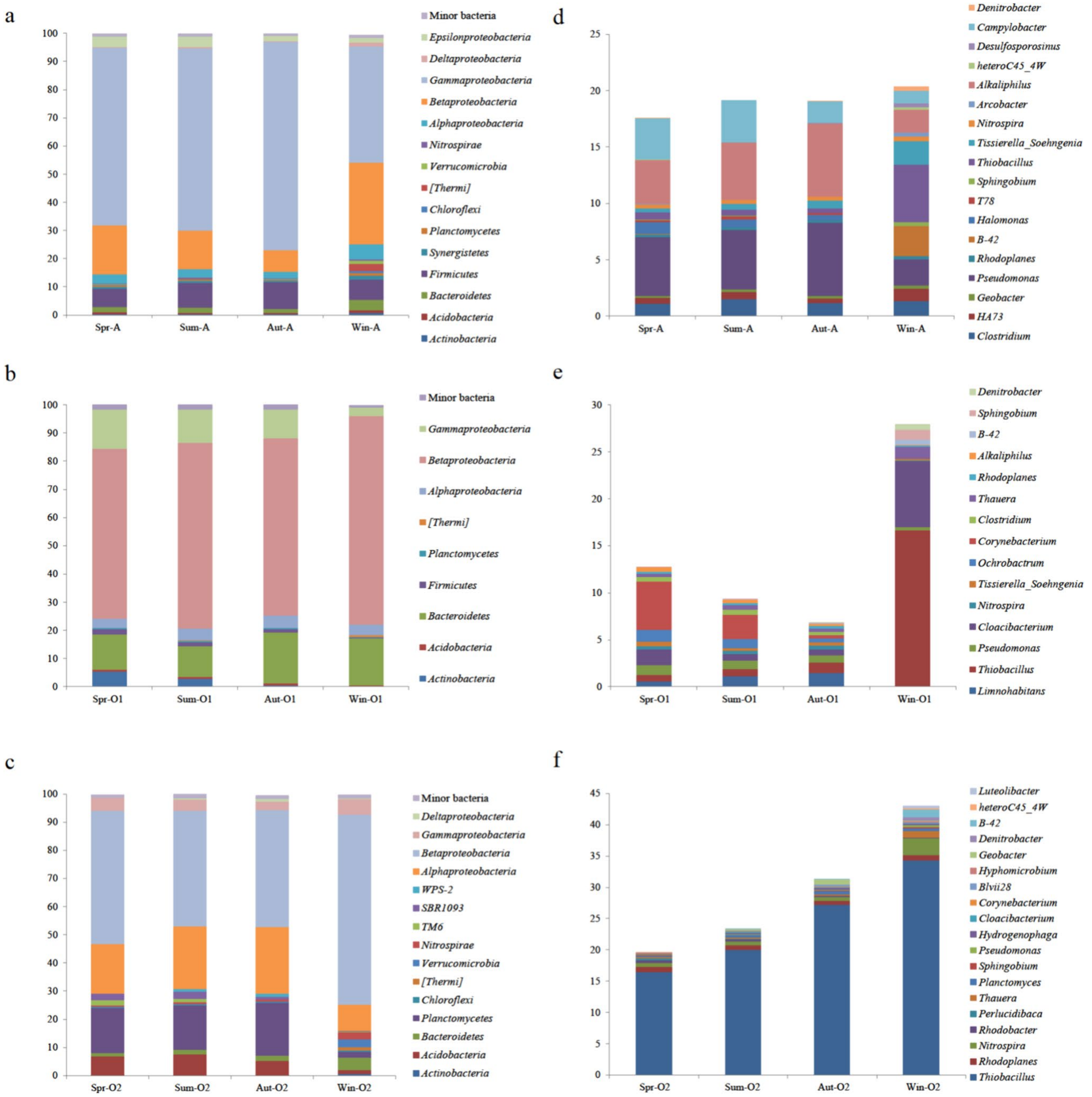


Fig. 4 Seasonal distribution of the major phyla and genera in the AOO bioreactors. Phylum level in the bioreactors A (**a**), O1 (**b**), and O2 (**c**), and genus level in the bioreactors A (**d**), O1 (**e**), and O2 (**f**). Average relative abundances > 0.5% were regarded as major phyla, average relative abundances > 0.3% were regarded as major genera

Discussion

Microbial diversity can be used to represent the individual, number and distribution of microorganisms in a microbial community. Diverging from CWW quality indices stable round the year, tendencies in biodiversity in the AOO bioreactors displayed a notable variability across the seasons, particularly in the bioreactor A. In this bioreactor, Shannon's and Simpson's indices by winter showed exceptional elevation comparing to those in other seasons. The anaerobic bioreactor A worked being loaded with heavily polluted raw CWW, resulting in poor biodegradation and high residual toxicity, which was also observed earlier (Kim et al. 2008; Shi et al. 2017). This environmental stress made the varying microbial community and diversity in the bioreactor A. The ascent diversities in winter are also observed in textile

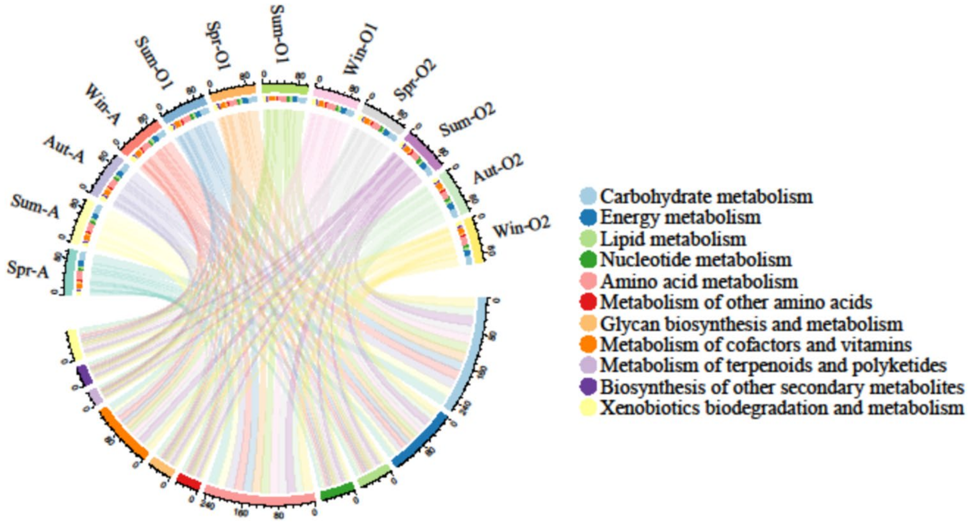


Fig. 5 Distributions of Level 2 pathways of metabolism in the AOO bioreactors

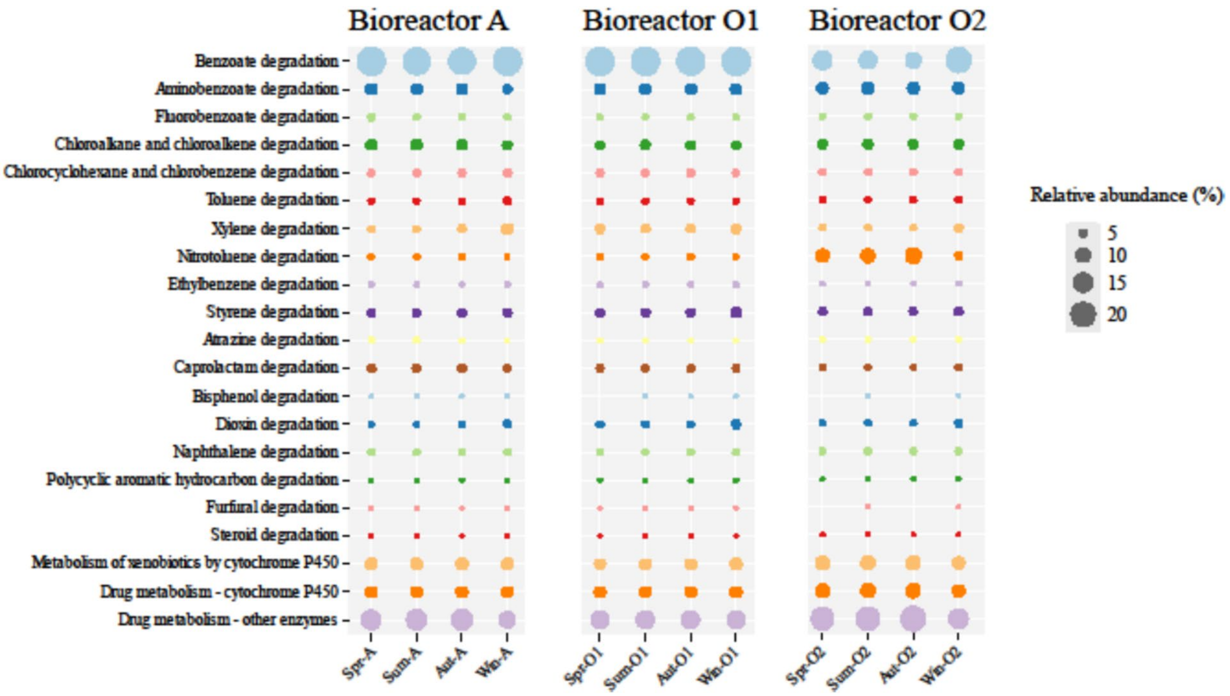


Fig. 6 Distributions of xenobiotics biodegradation and metabolism in the AOO bioreactors

dyeing wastewater treatment (Xu et al. 2022). On the other hand, the Chao 1 richness indices exhibited no significant seasonal variation, affirming the relatively stable bacterial members with flexible abundances. This suggests certain taxa gaining predominance during the environmental perturbations and contributing to the stable performance of CWW treatment.

As for the beta-diversity, the winter samples manifested a clustered and distinct character of microbial communities compared to those of other seasons, revealing a more pronounced impact of seasonal factors than variations among bioreactors. Conversely, in spring, summer and autumn, samples from each bioreactor were grouped together. The South China region experiences a tropical and subtropical monsoon climate (Liu et al. 2011; Zhang et al. 2022b) with warm conditions lasting from March to September. Consequently, spring, summer and autumn may be considered as a long hot season, exhibiting comparable sweltering climate, while winter stands out for

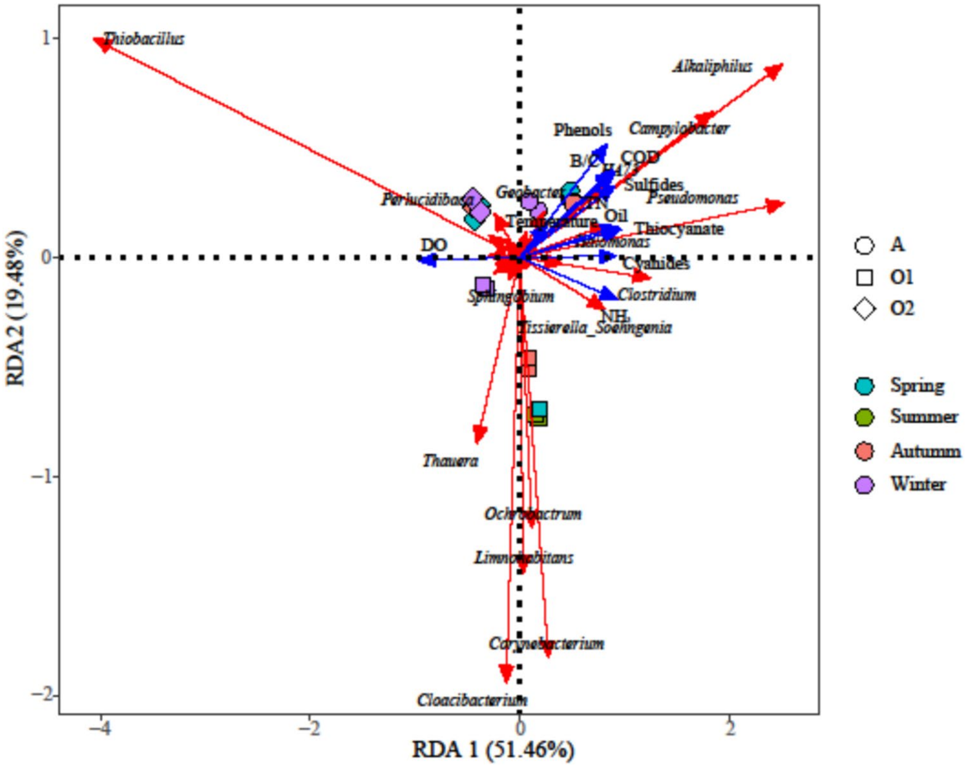


Fig. 7 The correlations between major genera and environmental variables in the AOO bioreactors within seasonal dynamics. Arrows indicate the direction and magnitude of environmental factors (blue) associated with genera (red). ^{a} *B/C*-COD/BOD

its marked coldness. This climatic variation resulted in distinct beta-diversity in winter compared to other seasons.

Considering the stable water temperature throughout the four seasons, some other variations may cause the distinct alpha and beta diversities of bacterial community in winter. For the oxic bioreactors, O1 and O2, weak ultraviolet ray in winter can slack its lethality for microbe (Ye et al. 2021). Moreover, aeration in these oxic bioreactors can pump cold air into liquid phase, which decreases the temperature in a way and increases the DO in wastewater, intensifying the activity of microbe and increasing their diversity (Ferro et al. 2020). On the other hand, the internal recycling from the bioreactor O2 sending the wastewater with higher DO was considered to change the microbial diversity in the anaerobic bioreactor A of winter. In this condition, some vulnerable members gained the advantage and some dominant anaerobic groups were inhibited (Gaio et al. 2023), so the bioreactor A could achieve higher diversity in winter.

The composition of microbial community in the AOO bioreactors displayed a fluctuant seasonal pattern, which was also observed in the winter bacterial composition being distinct from those in other seasons according to the PCoA result. In the bioreactor A, the highest number of major genera in winter aligned with the alpha-diversity patterns, reflecting the relatively amenable environment. Smaller number of main genera comprised mainly of *Pseudomonas*, *Alkaliphilus*, and *Campylobacter*, were characteristic for spring, summer and autumn. *Pseudomonas*, known for its denitrification capacity (Mozumder et al. 2021), aligns with the observed TN removal in this bioreactor. *Alkaliphilus*, identified as an anaerobic alkaliphilic and fermentative acidogenic species, producing hydrogen sulfide in the existence of sulfur compounds in the sea (Xie et al. 2014; Postec et al. 2021), signifies a vital role in sulfur biodegradation. *Campylobacter* has been reported as a pathogenic bacteria (Ma et al. 2023), hinting a heathy risk for CWW treatment workers. Despite a decrease in abundance by winter, these genera still maintained sufficient abundances (1.10%-2.29%) and contributed to the system performance, making them key genera in the bioreactor A. *Thiobacillus* experienced a surge in winter, assuming a predominant role as a relay of denitrifying bacteria. Besides, *Thiobacillus* plays a key role in pollutants biodegradation, attributed to refractory organics removal, such as phenol and SCN^{-}, while concurrently executing denitrification (Yuan et al. 2020). *Thiobacillus*, demonstrated good performance at low temperature (Trouve et al. 1998), was found in winter environments elsewhere (Yi et al. 2021; Chen et al. 2023), justifying its abundance in the bioreactor A by winter. In the bioreactor A, however, the main bacterial groups performed the denitrification throughout all seasons.

In the bioreactor O1, genera abundances underwent seasonal fluctuations. In spring, *Corynebacterium*, *Cloacibacterium* and *Ochrobactrum* were of their highest abundances. *Corynebacterium*, identified in anaerobic/aerobic biological system for CWW treatment, was reported for biodegradation of phenol and PAHs (Lors et al. 2004; Joshi et al. 2016). *Cloacibacterium* is associated with the degradation of complex organic contaminants in aquatic habitats (Behnami et al. 2018), also removing nitrogen (Han et al. 2020). *Ochrobactrum* is associated with biodegradation of phenol and PAHs (Jayashree et al. 2014; Pugazhendi et al. 2017). In summer, however, *Ochrobactrum* was displaced at the subdominant genus level with *Limnohabitans*, which is potentially engaged in autotrophic nitrite oxidation (Zhuang et al. 2020). *Corynebacterium* and *Ochrobactrum* were the first- and third-abundant genera in summer with their abilities of organics biodegradation. In autumn, *Limnohabitans*, *Thiobacillus* and *Pseudomonas* became the major genera. *Pseudomonas* at its stable abundance of 0.77%-1.06% with the exception of 0.33% in winter was earlier assigned for denitrification, as well as for degradation of phenol, naphthalene and hydrocarbons (Li et al. 2018; Mallick and Chakraborty 2019). The important genus of *Thiobacillus* exhibited stable moderate abundances in spring, summer and autumn, while showing its elevated abundance in winter. *Cloacibacterium* also underwent an increase in winter, as well as *Sphingobium* and *Thauera*. Both of them were known as aromatic compound degraders (Mao et al. 2010; Zhang et al. 2012; Zhou et al. 2015). *Thauera* has been identified as a low-temperature-tolerant strain (Zhou et al. 2021). In contrast to bioreactor A, in bioreactor O1 the abundance of the main genera varied significantly, although the alpha-diversities showed no obvious changes. Due to the poor biodegradation in the bioreactor A, toxic pollutants remain at high concentrations impacting the bacterial community in the bioreactor O1: bacteria remain active maintaining a stable aerobic microbial community, and, thus, sustaining stable operation. Additionally, *Thiobacillus* continued to leverage its advantage adaption from the bioreactor A to winter conditions. Although the seasonal factors caused a serious impact on the microbial community composition, the bacteria managed with the most of contaminants removal to provide the performance of the bioreactor O1.

The microbial composition in the bioreactor O2 containing CWW of low load and toxicity showed the dominant shared genera across all seasons with dynamics of seasonal changes, including *Thiobacillus*, *Rhodoplanes* and *Nitrospira*. *Thiobacillus*, with its consistent predominance in winter, underscored its pivotal position in the AOO system. *Rhodoplanes* showed its stable dominance throughout all seasons with the capability in biodegradation of phenolic compounds, SCN^- and sulfides (Wu et al. 2021). The nitrite-oxidizing bacteria (NOB) *Nitrospira* went through a burst in winter, contributing to TN removal through nitrification (How et al. 2020). Given the minor presence of ammonia-oxidizing bacteria (AOB) in all samples, a family level analysis was conducted (Fig. S2). The major family of *Nitrosomonadaceae* was identified as AOB (Zhu et al. 2019). Both *Nitrospira* and *Nitrosomonadaceae* demonstrated higher abundances in winter, determined by the reduced inhibition from competitive microorganisms (Kim et al. 2007). Although the abundances of *Nitrospira* and *Nitrosomonadaceae* were relatively low in spring, summer and autumn, the strong expression of nitrification genes had been reported, explaining stable nitrification in these seasons (Yu and Zhang 2012). *Thauera* appeared as major genera in winter, indicating its importance. In the bioreactor O2, the dynamic microbial communities showed their steady functions in nitrification and refractory organics removal. However, the varying seasonal abundances of nitrifying bacteria pointed to their possible susceptibility along the seasons, requiring more studies focused on this aspect.

Due to the pronounced PCoA aggregation of bioreactors in winter, a comparative analysis of microbial communities was conducted for this season. Despite the distinct function of each bioreactor, three genera, *Thiobacillus*, *Denitrobacter* and *B-42*, were found to be omnipresent. Especially, *Thiobacillus* absolutely dominated in winter samples of the three bioreactors aggravating this cluster. The shared genera underscore their pivotal role for the CWW treatment in the cold season. In summary, the microbial community composition in the AOO bioreactors exhibited pronounced seasonal dynamics, although the changes maintained the functions of the sludge keeping strict CWW discharge standards as a result of stable operations. By the other words, microbial communities exhausted all available feed resources in CWW, adapting the microbial composition to the seasonal changes.

The seasonal function dynamics exhibited a consistent pattern in Level 2 pathways distributions in which the top four are carbohydrate metabolism, amino acid metabolism, energy metabolism and metabolism of cofactors and vitamins. This observation aligns with the expected correlation between these pathways and microbial activity. Energy metabolism, including nitrogen and sulfur metabolism, consistently maintained the abundance ranging from 12.20%to 15.07% along all seasons, indicating the AOO system's robust and stable capability in nitrogen and sulfur removal. Similar resilience was also observed in the distribution of Level 3 pathways of xenobiotics biodegradation and metabolism across the seasons. Among the Level 3 pathways, benzoate degradation, drug metabolism-other enzymes, drug metabolism-cytochrome P450, metabolism of xenobiotics by cytochrome P450, aminobenzoate degradation, and nitrotoluene degradation emerged as major contributors to the biodegradation of phenols and other organic contaminants (Zhu et al. 2019). Therefore, the functions of microbiota in each bioreactor remain stable in seasons and are consistent in nitric and carbonic pollutants removal.

The RDA analysis results showed specific information between bacterial functions and environmental factors. CWW indicators of COD, phenols and CN^- had a negative correlation with *Thiobacillus*, *Thauera*, *Limnohabitans*, *Corynebacterium*, *Cloacibacterium* and *Ochrobactrum* in the first or second axes, hinting the biodegradation of pollutants. Among of these genera, *Ochrobactrum*, *Limnohabitans* and *Corynebacterium* showed a positive relationship with NH_3, which produced NH_3 for subsequent denitrification by biodegrading nitrogen pollutants. Totally, *Thiobacillus*, *Cloacibacterium*, *Corynebacterium*, *Alkaliphilus*, *Pseudomonas* and *Campylobacter* exhibited direct relationships with environmental factors in the AOO system. The *Thiobacillus*, *Cloacibacterium*, *Alkaliphilus* and *Pseudomonas* were present in the AOO bioreactors for all four seasons, being determined as core genera supporting the operation in seasonal dynamics. Interestingly, the DO showed a stronger relationship with genera than the temperature. Because the solubility of DO decreases with increasing water temperatures (Jane et al. 2021), the bacterial community seems to be mainly impacted by DO, which is changed by temperature under seasonal dynamics. Generally, the water temperature kept stable throughout the four seasons, but aeration would bring outside air into liquid phase, leaving a fluctuation of temperature and DO. In the current CWW biological treatment system, DO is an essential parameter to shape different functions of bioreactors. Therefore, variation of water temperature caused from seasonal dynamics can change the DO level to impact microbial community. For subsequent development of CWW treatment, DO may be one of the most important parameters to consider.

The observed dynamics within the microbial community composition, combining with the maintained stability of CWW treatment efficiencies and a consistent profile of microbial functional pathways, suggest the presence of functional redundancy in the AOO system, i.e., the system's strong adaptability to seasonal variations, emphasizing its vital role in maintaining stable operations throughout the year. Functional redundancy has been reported in the researches of wastewater process (Chen et al. 2020; Zhang et al. 2018), but evidence is lacking in CWW. In winter, *Thiobacillus* and *Thauera* with winter adaptability gained obvious advantages in the AOO system, performing carbon and nitrogen removal. The same functions were performed by *Limnohabitans*, *Corynebacterium*, *Cloacibacterium* and *Ochrobactrum* in spring, summer and autumn. Although they seasonally succeed with fickle abundances, the same functions were maintained in AOO bioreactors. The toxic substances of CWW often caused AS disintegration, which could be prevented by the resistance and resilience of functional redundancy, provided by unique microbial community composition (Muñoz-Palazon et al. 2019; Suarez et al. 2022). Based on functional redundancy, the AOO system can be subsequently improved to be more stable and better processing in COD load. Overall, the seasonal dynamics in the microbial community contents and functions were revealed in tight connection with functional redundancy in the AOO system. The main conclusions of seasonal bacterial composition and functions dynamics in the AOO bioreactors include:

1. The microbial community compositions in the AOO bioreactors exhibited substantial seasonal changes.
2. *Thiobacillus, Cloacibacterium, Alkaliphilus and Pseudomonas* were determined as core genera in the AOO bioreactors.
3. In seasons, the predicted functional genes were enriched in the pathways associated with metabolism of nitric and carbonic contaminants.
4. The analogous distributions of the Level 1 metabolism pathways and fluctuating microbial community composition revealed the functional redundancy and composition diversity.

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Author contributions BS, CW, and SZ conceived and designed the experiments. ZT, XX, and SZ collected the samples. ZT, ZG, and YL performed the experiments. ZT, CW, JX, and JD analysed the data. JX provided the reagents, materials and analytic tools. ZT wrote the manuscript. SP, WC, and SZ reviewed and edited the manuscript. All authors edited and approved the paper.

Data availability The sequences have been deposited in the NCBI Sequence Read Archive under the accession number SRX1056084 and SRR9651087.

Declarations

Conflict of interest The authors declare that they have no competing interests.

Human and animal rights and informed consent This article does not contain any studies with human participants or animals performed by any of the authors.

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