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Dissimilarity of different cephalosporins on volatile fatty acids production and antibiotic resistance genes fates during sludge fermentation and underlying mechanisms

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ABSTRACT

The distinct influences of cephalosporins (CEPs, *i.e.,* cefamandole nafate and cefpirome sulfate) affiliated to different generations on the volatile fatty acids (VFAs) production and antibiotic resistance genes (ARGs) fates during waste activated sludge (WAS) fermentation were unveiled. The presence of CEPs mainly exhibited negative effects on the total VFAs production (5%–15% reduction), especially the cefamandole nafate, which is quite different to previous understanding. Further investigation revealed that the CEPs contributed to the solubilization and hydrolysis but inhibited the acidification process by affecting the functional microbial populations (*i.e.*, *Tissierella*) and general microbial metabolic activities (*i.e.,* pyruvate metabolism and VFAs biosynthesis). In addition, CEPs (especially the cefpirome sulfate) caused the propagation of ARGs (*i.e., blaTEM*, *tetX* and *mexF*) during WAS fermentation. CEPs enhanced the cell membrane permeability to promote the antibiotics mechanism of efflux pump and the horizontal transfer of ARGs. Also, the CEPs altered the regulatory systems (*i.e.,* two component system) and microbial populations associated with ARGs, resulting in the proliferation of specific ARGs. Overall, the dissimilarity of different CEPs impacts on the WAS fermentation for VFAs production and ARGs variations enlightened the diverse environmental behaviors of anthropogenic pollutants and evoked the caution of ecological risks.

Antibiotics had been developed with various products and utilized for a long history to fight against the pathogens [1,2]. Among them, the β-lactam antibiotics (*e.g.,* cephalosporins (CEPs)) accounted for >50% total used antibiotics [3], and over 50 kinds of CEPs affiliated to different generations have been developed in view of their different antibacterial performance and mechanisms [4]. Only a tiny fraction of consumed antibiotics would be metabolized by humans or animals while most of them (approximately 40%–90%) are released into the environment [5]. They mainly transport to the wastewater treatment facilities and eventually accumulate in waste activated sludge (WAS) due to their poor removal efficiency by conventional wastewater treatment processes [6,7].

The effective WAS disposal is currently prone to adopt the anaerobic fermentation technology for the built-up of carbon-neutral society, by which the organics in WAS could be bioconverted into high-valuable products (*e.g.,* volatile fatty acids (VFAs)) instead of fugitive carbon emission [8]. Previous studies have revealed that antibiotics mainly contributed the solubilization and hydrolysis while inhibited methanogenesis, resulting in the VFAs promotion [9,10]. For example, Chen *et al.* had reported that with the increment of roxithromycin content (0 to 100 mg/kg TSS), the highest VFAs production was improved from 295 mg to 610 mg COD/L [9]. However, how the high concentrated CEPs in WAS would interact and affect the VFAs production is still unknown. In addition, due to their diverse categories, whether the different generation of CEPs exhibit similar or dissimilar impacts on the anaerobic process requires further evaluations.

Meanwhile, the propagation and fates of antibiotics resistance genes (ARGs) induced by massive antibiotics misuse is also undesirable, which causes great ecological risks. On one hand, anaerobic fermentation was proved to remove the ARGs effectively. For example, Tang *et al.* indicated that the alkaline WAS fermentation

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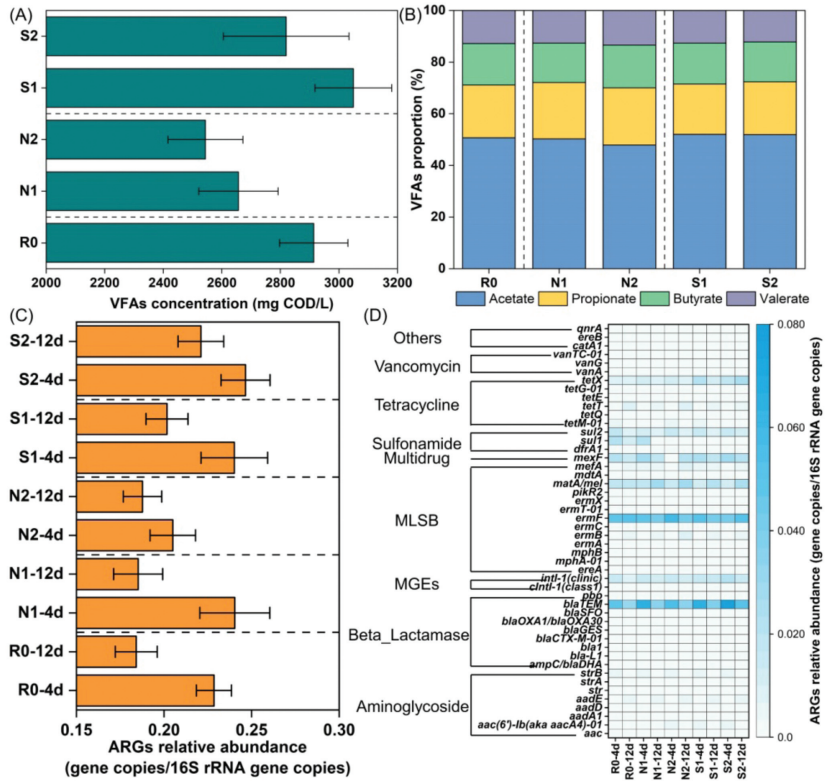

Fig. 1. The variation of (A) VFAs accumulation, (B) VFAs distribution, (C) total ARGs, and (D) specific ARGs in different reactors during WAS fermentation.

reduced the targeted ARGs in the range of 0.42–1.36 log units [10]. Shi *et al.* also found 21.9% of total ARGs reduction during WAS digestion [11]. On the other hand, the presence of antibiotics is expected to induce the intrinsic resistance genetic expressions in microbes, which is one of the main reasons for the massive propagation of ARGs [12]. Unfortunately, the dynamic variations of ARGs during anaerobic fermentation with different antibiotics exposure have yet to be disclosed.

This work mainly evaluated the potential impacts of typical CEPs affiliated to different generation on the VFAs production and ARGs fate simultaneously during WAS fermentation. The associations of different CEPs with the main fermentation steps are unveiled. Also, the dynamic variations of functional microbial profiles (including microbial community structure and genetic traits) responsible for VFAs biosynthesis and ARGs proliferation are analyzed to disclose the interfering mechanisms of CEPs affiliated to different generations. It gives new insights to understand and evaluate the environmental risks of diverse antibiotics.

Cefamandole nafate, as one of the second generation of CEPs against gram-negative bacteria [13], and cefpirome sulfate, as one of the fourth generation of CEPs against gram-positive bacteria, were selected as the representative CEPs due to their wide utilization [4,14]. The cefamandole nafate and cefpirome sulfate were obtained from the Dalian Meilunbio Inc (China). The impacts of different CEPs on the VFAs production and ARGs variation were conducted in 5 identical serum bottles with the feed of 0.3 L WAS. The CEPs level in different was set as follows: 0 (Control, R0), 1 and 5 mg/g TSS cefamandole nafate (namely N1 and N2, respectively), and 1 and 5 mg/g TSS cefpirome sulfate (namely S1 and S2, respectively). The nitrogen with 99.99% purity as the protective gas was purged into different reactors for 5 min to keep the anaerobic environment. The operational conditions were set at 35 °C and 180 rpm in an air-bath shaker. All the reactors were adjusted and maintained at pH 10, which was proven to be the optimal pH for VFAs production and ARGs reduction during WAS anaerobic fermentation [15]. The detailed information for the experiments could be referred to the supporting information.

As shown in Fig. 1A, the highest VFAs reached to 2914 mg COD/L in the control. The presence of cefamandole nafate exhibited dose-dependent effects on the reduction of VFAs yield, in which the highest VFAs was 2656 and 2544 mg COD/L in N1 and N2 reactor, respectively. However, the cefpirome sulfate slightly improved the VFAs generation (3049 mg COD/L) at low level (1 mg/g TSS). It also inhibited the VFAs production (2819 mg COD/L) at high dosage (5 mg/g TSS), but the inhibitory effect was much lower than that of cefamandole nafate at the similar level. But the different CEPs exerted insignificant impacts on the distributions of generated VFAs, and the acetate (47.8%−52.0%) and propionate (19.5%−22.1%) were the predominant VFAs in all the investigated reactors (Fig. 1B).

Generally, in contrast to most of the previously reported enhancing effects of antibiotics on the VFAs production during WAS fermentation [9,10], the CEPs mainly exhibited inhibitory effects on VFAs generation. Moreover, the different generations of CEPs also exhibited distinct impacts on the WAS fermentation efficiency for VFAs yields, which might be mainly ascribed to their distinctive properties.

The ARGs in WAS were evidently reduced in the anaerobic process. For instance, the relative abundance of total ARGs in R0 was reduced by 19.4% from 4 d to 12 d (Fig. 1C), which was consistent with previous study [9]. Also, the relative abundance of total ARGs was decreased in the CEPs reactors but with distinctive downward trends. The residue ARGs abundance in reactors with cefamandole nafate (N1 and N2) at 12 d was similar to that of control (at the ratio of 0.184 to 16S rRNA gene). But the reduction rate of ARGs was obviously slower with the exposure of cefpirome sulfate. The ratio of total ARGs to 16S rRNA gene in S1 and S2 reactors was respectively 0.201 and 0.221. This indicated the positive roles of

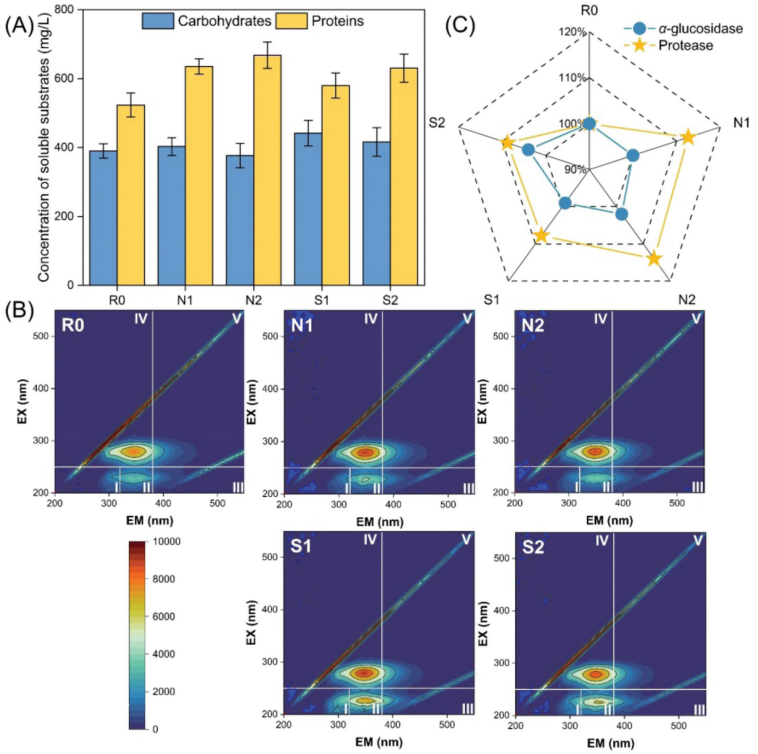

Fig. 2. (A) Concentrations of soluble substrates, (B) relative activities of hydrolytic enzymes, and (C) 3D-EEM characterization of SMP in different reactors.

cefpirome sulfate in promoting the spread of ARGs compared with that of control during WAS fermentation, which evoke to alert the ecological risks.

In view of the specific ARGs (Fig. 1D), the dominant ARGs consisted of *tetX, sul1, sul2, matA/mel, ermF, mexF,* and *blaTEM*, which were the frequently detected ARGs in WAS [12]. Most of these ARGs showed downward trends during the fermentation process, except for *ermF*. However, compared with the control reactor, the different generations of CEPs exhibited different impact on the variation of specific ARGs. For instance, the ratio of *tetX* to 16S rRNA gene was 0.0082 in R0–12d reactor, while slightly decreased to 0.0077 and 0.0070 in N1–12d and N2–12d reactors, respectively. However, it was remarkably increased to 0.0103 and 0.0246 in S1–12d and S2–12d reactors, respectively. Meanwhile, the variation of *blaTEM* also exhibited the similar trend. Nevertheless, the cefamandole nafate and cefpirome sulfate both promoted the spread of *mat/mel*, especially for cefamandole nafate. The ratio of *mat/mel* to 16S rRNA gene was 0.0170 in control reactor at 12d, while improved to 0.0287 and 0.0269 in N1–12d and N2–12d reactors, respectively, and 0.0207 and 0.0240 in S1–12d and S2–12d reactors, respectively. Similar phenomenon was also observed in the variation of *mexF*. Generally, CEPs were not conducive to the removal of certain ARGs during WAS fermentation, especially the cefpirome sulfate.

The solubilization and hydrolysis process was previously considered as the rate-limiting steps for efficient VFAs production during WAS fermentation [17]. As illustrated in Fig. 2A, the contents of soluble carbohydrates and proteins (dominant organics in WAS) were respectively 390.2 and 523.3 mg/L in the control reactor. The presence of CEPs exhibited minor impacts on the solubilization of carbohydrates while significantly promoted that of proteins. For example, the level of soluble carbohydrates in N1 and N2 reactors were 402.9 and 376.8 mg/L, while the proteins were up to 635.2 and 668.2 mg/L, respectively. Further analysis based on 3D-EEM characterization (Fig. 2B) found that the increased proteins were mainly affiliated to tryptophan-like (Region IV) and tyrosine-like compounds (Region II), which were typical proteinaceous matters derived from WAS [16]. Similar results were also observed in the cefpirome sulfate reactors (S1 and S2).

Moreover, the activities of typical hydrolytic enzymes (*i.e.,* α-glucosidase and protease) were characterized to unveil the WAS hydrolysis efficiency in different reactors. The effects of two CEPs on the activities of α-glucosidase were insignificant, while they remarkably improved the activities of protease (Fig. 2C). Compared with the R0, the activities of protease were enhanced by 12.6% and 14.1%, 7.8% and 8.8% in N1 and N2, S1 and S2 reactors, respectively. This indicated the enhanced WAS hydrolysis efficiency with CEPs exposure. The reasons might mainly attribute to the evident increase of bioavailable soluble substrates in the solubilization process, which stimulated the microbial metabolic activities [6]. Overall, the presence of both CEPs enhanced the solubilization and hydrolysis processes, especially the proteins release and hydrolysis, during the WAS fermentation.

The functional anaerobes exhibited essential roles in the biochemical process for VFAs biosynthesis. The major phylas in control reactor included *Firmicutes* (35.2%), *Proteobacteria* (16.4%), *Chloroflexi* (14.2%), *Actinobacteriota* (12.4%), *Bacteroidota* (8.6%), *Acidobacteriota* (7.2%), and *Patescibacteria* (2.5%) (Fig. 3A). However, the presence of CEPs decreased the abundances of *Chloroflexi* (12.1%–13.0%) and *Actinobacteriota* (8.9%–10.5%), which were proved to be the typical acid-forming bacteria [17,18], and the decreasing effect was dose-dependent. This might explain the VFAs reduction with different CEPs, especially at high levels. Interestingly, the CEPs enriched the abundance of Firmicutes. For instance, the relative abundance of *Firmicutes* was increased to 39.6% and 41.6% in N1 and N2 reactors, respectively. The *Firmicutes* were expected to be more tolerant to the adverse environment induced by various pollutants (*e.g.,* heavy metals, pharmaceuticals) [19]. Its increase also manifested the evolution of microbial community structure and their responses to the CEPs exposure.

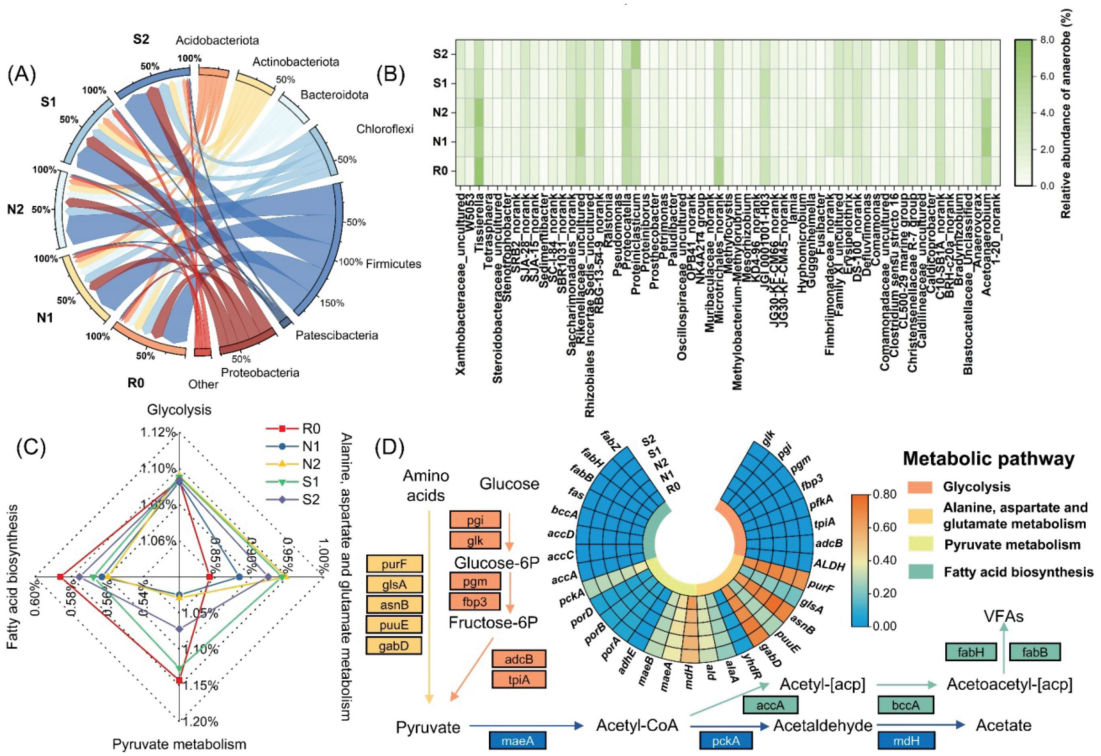

Fig. 3. The relative abundance of dominant microbial community at (A) phylum and (B) genus level, and (C) specific metabolic pathways related with VFAs biosynthesis and (D) corresponding genetic expressions in different reactors.

Further analysis at genus level also found the negative effects of CEPs on the functional fermentative bacteria in WAS anaerobic systems (Fig. 3B). For instance, *Tissierella*, which was the typical fermentative bacteria with the acetic and propionic acids as the main metabolites [20], was decreased from 7.7% in the control to 6.1%, 7.2%, 4.6% and 3.9% in N1, N2, S1 and S2 reactors, respectively. Obviously, the decrease of these key acid-forming bacteria would result in the reduction of VFAs yield. Interestingly, the *Proteocatella* and *Proteiniclasticum*, which were typical proteolytic bacteria with the ability to secrete various proteolytic enzyme [21], were respectively enriched by 9.6%–26.7% and 11.7%–74.5% in the cefamandole nafate and cefpirome sulfate reactors. This was consistent with the enhancement of proteolytic enzymatic activities in the corresponding reactors (Fig. 2B), which might be induced by the increased soluble bioavailable proteins during WAS solubilization.

The metabolic activities and genetic expressing levels related with VFAs biosynthesis were also critical to the ultimate VFAs generation. As shown in Table S2 in Supporting information, the activities of major microbial metabolic pathways were reduced with CEPs. For example, the relative abundances of gene hits related with cell growth and death decreased from 0.61% in control to 0.57%, 0.53%, 0.59% and 0.54% in the N1, N2, S1 and S2 reactors, respectively. Similar results were also found for the energy metabolism and carbohydrates metabolisms pathway. These results indicated the inhibitory effects of CEPs on the microbial metabolic activity. (Although the amino acid metabolism was slightly improved from 10.57% in control to 10.69%–10.75%) in CEPs reactors (consistent with the improvement of soluble proteins and proteolytic bacteria in CEPs-conditioned reactors), it failed to offset the overall reduction of microbial metabolic activities and thus resulted in the ultimate VFAs decrease.

The deep explorations of the substrates metabolisms for VFAs biosynthesis also found similar phenomenon (Figs. 3C and D). The metabolism of alanine, aspartate and glutamate, which were the typical types of amino acids in the WAS [22], was enhanced from 0.84% in the control to 0.88%, 0.95%, 0.94%, 0.92% in N1, N2, S1, and S2 reactors, respectively. Correspondingly, the key genetic expressions (*e.g.*, *glsA*, *asnB*, and *aldA*) were significantly improved by 10.7%–59.1% in the presence of CEPs. However, the variation of glycolysis, which responsible for glucose conversion, was insignificant in different reactors. In addition, the pyruvate metabolism, which was located at the center of VFAs biosynthesis and played essential roles on the acidification [8], was remarkably reduced in the presence of CEPs (decreased from 1.14% in the control to 1.02%–1.03%). Also, the relevant critical genes were remarkably decreased. For example, the relative abundance of *mdH*, which could catalyze a reversible NAD-dependent dehydrogenase reaction involved in central metabolism [6], was reduced from 0.64‰ in R0 reactor to 0.56‰, 0.54‰, 0.55‰, 0.52‰ in N1, N2, S1 and S2 reactors, respectively. Meanwhile, the relative abundance of *porA*, *porB*, and *porD*, which could catalyze the ferredoxin-dependent oxidative decarboxylation of pyruvate [3], were also remarkably reduced in the CEPs reactors. Besides, the metabolic pathway of fatty acids biosynthesis and the related genetic expressions were also observed to be downregulated in the CEPs reactors. Hence, these results implied that the presence of CEPs mainly interfered the pyruvate metabolism for the subsequent VFAs biosynthesis and caused the ultimate VFAs reduction.

As shown in Fig. 4A, the resistance mechanisms of detected ARGs in WAS mainly belonged to the categories of antibiotic deactivate, cellular protection and efflux pump, which accounted for 83.6%–90.3%. Further analysis found that the ARGs affiliated to cellular protection category was reduced by 16.3%–23.5% with the dosage of CEPs in comparison with that of control. This might be associated with severe damage of microbial cells at strong alkaline conditions (pH 10 in this study) [23]. And the CEPs might further deteriorate such situations. In fact, the LDH release, which was frequently used to reflect the membrane disruption [6], was

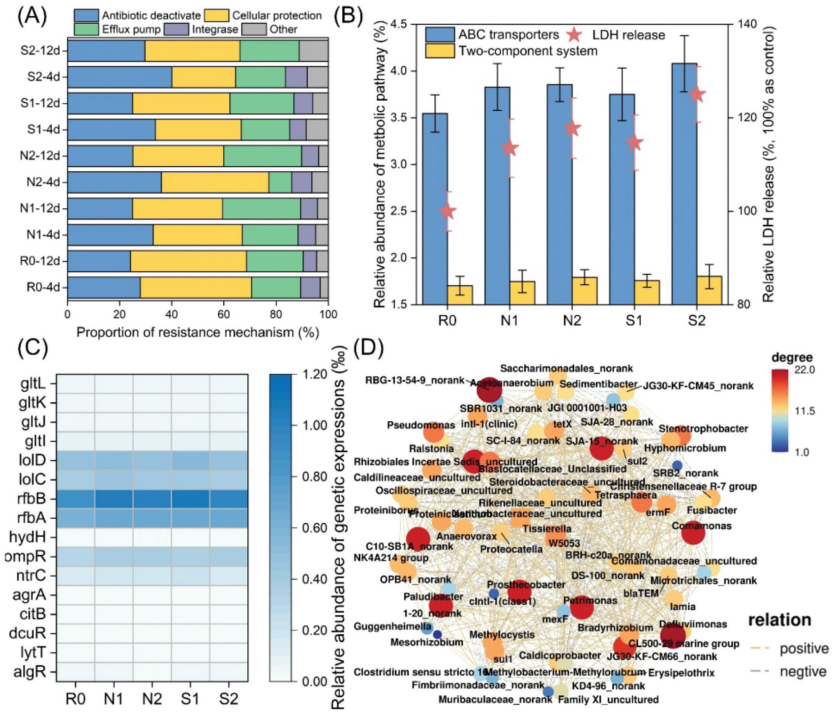

Fig. 4. (A) The variation of ARGs resistance mechanisms and (B) the level of related metabolic pathways and LDH release, (C) relative abundance of corresponding genetic expressions and (D) network analysis of the co-occurrence between ARGs and bacterial genera in different reactors.

respectively increased by 13.5%, 17.8%, 14.7% and 25.1% in N1, N2, S1 and S2 reactors (Fig. 4B) when comparing with that in control. This would undoubtedly reduce the ARGs resistance mechanisms by cellular protection.

On the contrary, the increase of cell permeability might be beneficial to the metabolic pathway of membrane transport [24]. The relative abundance of ABC transporter, which had been reported to be correlated with the cell permeability and ARGs spread [25], was increased from 1.70% in control reactor to 1.75%–1.79% in cefamandole nafate reactors, and 1.76%–1.81% in cefpirome sulfate reactors (Fig. 4B). Consequently, compared with the control (21.6%), the ARGs affiliated to efflux pump category, which stimulate the microorganisms to remove toxic substances from intracellular to extracellular sides [24], were enhanced in CEPs conditioned reactors (29.9%–30.0% by cefamandole nafate and 22.7%–24.5% by cefpirome sulfate). Correspondingly, the *tetX*, *mexF*, and *matA/mel*, which belonged to the efflux pump resistance mechanism, were also observed to be proliferated in CEPs reactors (Fig. 1D).

Moreover, MGEs were considered to be beneficial for the exchange and penetration of ARGs, resulting in the improvement of bacterial antibiotic resistance [26]. As depicted in Fig. 1D, the ratio of total *intI-1(clinic)* to 16S rRNA gene was 0.009 in control reactor at 12 d, while it increased to 0.011 and 0.012 in S1–12d and S2–12d reactor, and further improved to 0.016 and 0.018 in N1 and N2 reactor at 12 d. Hence, the increase of cell permeability might provide more chance to promote the horizontal transfer of ARGs, especially the cefpirome sulfate. It explained the relative higher total ARGs abundance in cefpirome sulfate reactors. Besides, the metabolic intensity of two component system, which could enable bacteria to sense, respond, and adapt to the environment [27], was improved from 1.70% in R0 reactor to 1.75%–1.80% in the reactors with CEPs addition. Also, the crucial keys (*i.e., algR*, *lytT*, *agrA*, *ntrC*, *ompR* and *hydH*), which could control bacterial resistance towards antibiotics, were also observed to be overexpressed in CEPs-conditioned reactor (Fig. 4C). Hence, the CEPs stimulated the microorganisms to respond to undesirable stress, and further contributing to the transition of ARGs. Generally, the CEPs (especially the cefpirome sulfate) could enhance membrane permeability to promote the antibiotics mechanism of efflux pump and the horizontal transfer of ARGs, resulting in the proliferation of specific ARGs

The co-occurrence network analysis revealed the symbiosis pattern of ARGs and microbial populations. As described in the Fig. 4D, *blaTEM* and *tetX* were both positively linked to the genera *Proteocatella* ($P = 0.011$ and 0.024) and *Proteiniclasticum* ($P = 0.023$ and 0.018), which had been found to be enhanced in the CEPs-conditioned reactors, especially the cefpirome sulfate. Clearly, the enrichment of these potential hosts in CEPs reactors would result in the increment of corresponding ARGs. Meanwhile, the dominant *intI-1(clinic)*-associated genera were also *Proteocatella* ($P = 0.024$) and *Proteiniclasticum* ($P = 0.002$), indicating these genera might be the potential host for critical ARGs, and played an essential role on ARGs transition. Hence, although these bacteria accelerate the proteins metabolism, which might be beneficial for the VFAs production, they also played an important role on ARGs proliferation. This might also be the potential reason for relative higher total ARGs in cefpirome sulfate-conditioned reactor, which exhibited higher abundance of *Proteocatella* and *Proteiniclasticum*. Besides, the positive associations of *sul2* with *Xanthobacteraceae_uncultured* ($P = 0.038$) and *ermF* with *Comamonas* ($P = 0.041$), and the negative associations of *mexF* with *Microtrichales_norank* ($P = 0.036$), also showed good agreement with the variation of ARGs and microbial community structure in the corresponding reactors. Overall, CEPs affected the microbial populations as ARGs hosts and ultimately led to the ARGs variations.

In summary, this study revealed the distinct impacts of CEPs with different generations on VFAs generation and ARGs fate during WAS fermentation. On one hand, the CEPs promoted to the solubilization and hydrolysis, while inhibited the acidification and metabolic traits for VFAs biosynthesis, resulting in the decrement of ultimate VFAs production. On the other hand, CEPs (especially the cefpirome sulfate) caused the propagation of ARGs and al-

tered the ARGs resistance mechanisms by changing the cell membrane permeability, regulatory systems and microbial populations associated with ARGs. Overall, the dissimilarity of different CEPs impacts on the WAS fermentation process evokes the caution and reevaluation of the ecological risks of various anthropogenic pollutants.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.cclet.2022.07.004.

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