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Contributions of meat waste decomposition to the abundance and diversity of pathogens and antibiotic-resistance genes in the atmosphere

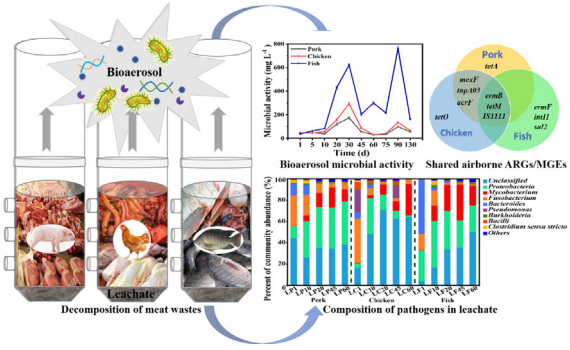
Yun Yu [a], Zhishu Liang [a,b], Wen Liao [a], Zikai Ye [a], Guiying Li [a,b], Taicheng An [a,b,*]

[a] Guangdong Key Laboratory of Environmental Catalysis and Health Risk Control, Guangdong Hong Kong-Macao Joint Laboratory for Contaminants Exposure and Health, Institute of Environmental Health and Pollution control, Guangdong University of Technology, Guangzhou 510006, China
[b] Guangzhou Key Laboratory of Environmental Catalysis and Pollution Control, Key Laboratory of City Cluster Environmental Safety and Green development, Department of Education, School of Environmental Science and Engineering, Guangdong University of Technology, Guangzhou 510006, China

HIGHLIGHTS

- Decomposition of chicken & fish wastes led to high bioaerosol level & activity, respectively.
- High diversity and richness of bacterial community were detected in bioaerosol.
- High diversity and abundance of ARGs were detected in the leachate.
- Aerosolization of bacteria & ARGs in leachate had less relative to their abundance & diversity.
- ARG structures were mainly driven by bacterial community shift in bioaerosol and leachate.

GRAPHICAL ABSTRACT



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ABSTRACT

Airborne transmission of antibiotic-resistance genes (ARGs) in landfill and acquisition of antibiotic resistance by pathogenic bacteria are posing potential threat to human and environmental health. However, little is known about contribution of waste decomposition to airborne ARGs and pathogens during landfilling of household waste. Herein, the dynamic changes of microbial communities and ARGs were comparatively investigated in leachate and bioaerosol during the decomposition of chicken, fish, and pork wastes. Results found that chicken and pork decomposition could result in emitting high abundance of bioaerosol and pathogen, while fish fermentation will lead to high airborne microbial activity. The main pathogens were *Bacilli*, *Burkholderia-Paraburkholderia* and *Mycobacterium* in bioaerosols, but were *Wohlfahrtiimonas*, *Peptoniphilus* and *Fusobacterium* in leachate, suggesting that the ability of aerosolization of bacteria in leachate was independent of their abundance and diversity. Whereas, diversity and relative abundance of ARGs in leachate were significantly higher than bioaerosol. Moreover, the relative abundance of ARGs in leachate and bioaerosols was not completely relevant. The changes of pathogenic community contributed significantly to the prevalence of ARGs in bioaerosol and leachate. The results will define the contribution of household waste decomposition to airborne pathogen and ARG distribution and provide foundation for airborne bacterial exposure risk and control in landfill.

* Corresponding author at: Guangdong Key Laboratory of Environmental Catalysis and Health Risk Control, Guangdong Hong Kong-Macao Joint Laboratory for Contaminants Exposure and Health, Institute of Environmental Health and Pollution control, Guangdong University of Technology, Guangzhou 510006, China.
E-mail address: antc99@gdut.edu.cn (T. An).

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1. Introduction

Bioaerosols are comprised of airborne dispersions of solid or liquid particles that contain bacteria, viruses, fungi under various natural and anthropogenic activities (Garcia-Mena et al., 2016). Particularly, airborne bacteria with sizes ranging from 0.5–10 μm are contributed to a relatively long atmospheric residence time and prefer to attaching onto other particles or forming agglomerates with numerous bacterial cells. Airborne bacteria not only have an important impact on the climate and atmospheric processes, but also function as pathogens of humans, plants as well as animals, transport and attach over large physical scales (Despres et al., 2012). Therefore, the microbial fraction of aerosols presented in both outdoor and indoor environments is of high concern from environmental and public health perspectives.

Currently, increasing researches have been progressing to deeply explore the airborne bacterial pollutions that accompany human activities. Especially, bioaerosol generated from waste operations, such as garbage collection, waste dumping, municipal solid wastes (MSWs) landfilling, and waste disposal at the open site (Agarwal et al., 2016; Akpeimeh et al., 2019; Cyprowski et al., 2019; Neumann et al., 2005). This is mainly attributed to the increasing and high amount of MSWs (2 billion tons) generated annually worldwide, and landfilling is the cheapest and most common means to dispose of them (Braguglia et al., 2018; He et al., 2011; Qi et al., 2013; Renou et al., 2008). Therefore, high levels of bacterial aerosol (1.0×10^3 to 7.2×10^4 CFU m^{-3}) were detected in the offices of municipal landfills (Lis et al., 2004). Breza-Boruta indicated that gram-positive *cocci* and *bacilli* successively accounted for the highest percentage of bacterial aerosols in a municipal landfill in Northern Poland (Breza-Boruta, 2016). Moreover, bioaerosol emitted from landfills is the source of hemolytic bacteria and pathogenic bacteria, and the opportunistic bacteria *Escherichia coli*, *Proteus mirabilis*, *Staphylococcus sciurii*, and *S. xylosus* were commonly found in bioaerosol (Fraczek and Kozdroj, 2016; Kalwasinska and Burkowska, 2013).

Furthermore, MSWs in landfill contain a wide range of antibiotic-resistance genes (ARGs) and pathogens. Besides, other co-existed complex toxic components such as heavy metals, antibiotics, and other organic pollutants might result in the spread of ARGs and antibiotic resistance during landfilling (You et al., 2018). It is because these co-existed pollutants may act as environmental stressors to select antibiotic-resistance bacteria and shape the bacterial communities (Kohanski et al., 2010; Toprak et al., 2011). ARGs may persist even if the selective pressure is removed or the host bacteria have died, which is called the "easy to obtain, not easy to lose" feature (Courvalin, 1994; Mao et al., 2014). Besides, due to the concerted activities of different types of mobile genetic elements (MGEs) that can be transferred within or between DNA molecules and bacterial cells, bacteria can acquire ARGs through horizontal gene transfer, which promotes the spread of resistance (Partridge et al., 2018). Previous studies showed that bacterial community including pathogenic bacteria might contribute to the dissemination of ARGs, besides, MGEs and physicochemical parameters can modify ARG profiles by the combined effects (Li et al., 2018; Zhou et al., 2017). So far, several studies have reported rich distribution of ARGs/MGEs in landfill. For example, high prevalence of ARGs (*sulI* and *tetO*) was detected in refuse samples from different depths within landfill (Song et al., 2016). In addition, 21 ARG types and 526 subtypes were detected in the 19 leachate samples from landfill (Zhao et al., 2018). Furthermore, in the groundwater near a landfill, 171 unique ARGs, 8 MGEs and 15 potential hosts of ARGs were also detected (Chen et al., 2017). High level of ARGs may result in the emission of high amount of antibiotic-resistant bioaerosol and pose a possible health risk to the workers and nearby residents.

A case study shows that 41% and 46% of the total bacteria and gram-negative bacteria in landfill bioaerosol can penetrate deep into the respiratory system, respectively, and pose significant health risks (Akpeimeh et al., 2019). Exposure to bioaerosols in landfills will result in a series of symptoms including diarrhea, ulceration of the skin, lung function decline (Ray et al., 2005), and respiratory diseases such as allergic bronchopulmonary aspergillosis, allergic aspergillus sinusitis, hypersensitive pneumonitis, and organic dust toxic syndrome (Basu et al., 2018; Pearson et al., 2015) to the community and the workers. Therefore, the distribution, characterization, and health risk, as well as the occurrence and abundance of ARGs/MGEs in solid waste, soil, leachate, and bioaerosols has caused increasing attention (Madhwal et al., 2020; Sun et al., 2016; You et al., 2018). However, the emission and dispersal of ARGs/MGEs through bioaerosols generated during landfilling has received limited attention, although dominant ARGs were found in food wastes such as meat (including pork, beef, and fish), fruits, and vegetables (Liao et al., 2019; Rolain, 2013).

To further understand the contributions of domestic waste decomposition to the abundance of bacterial and antibiotic-resistant bioaerosols, three bioreactors were constructed to stimulate the fermentation of various meat wastes, and the aims of this study were mainly focused: 1) to analyze the microbial aerosolization behavior including the size distribution, microbial activity and diversity of bioaerosol during the decomposition of meat wastes; 2) to compare the abundance and diversity of ARGs/MGEs as well as community in bioaerosol with leachate; 3) to figure out the influence of physical and chemical properties on the airborne pathogenic bacteria, ARGs, MGEs during meat wastes decomposition process. This work will not only improve the understanding of bioaerosol aerosolization behavior and antibiotic resistance profiles during MSWs decomposition, but also provide references for the health risk assessment of the anaerobic decomposition process of domestic wastes.

2. Materials and methods

2.1. Lab-scale bioreactor and meat wastes fermentation

Three lab-scale bioreactors (171.8 L, 1.5 m height × 0.4 m i.d) were designed to conduct anaerobic decomposition experiments of pork, chicken and fish wastes, separately. As Fig. S1 shows, the bioreactors made of polymethyl methacrylate were consisted of bioaerosol collector, waste decomposition container, and leachate storage chamber. Besides, a round-hole plate was used to separate wastes and leachate and sensors used to monitor the temperature of the waste pile were placed into waste decomposition container. In addition, similar to our early reactor (Zhang et al., 2020a), 10 cm gravel (8–16 mm i.d) and glass fabric were laid above the plate to block large particles and effectively filter the waste and form effective drainage layer.

Three kinds of raw meat wastes included pork (mixture of pork, lung, head, and liver), whole chicken, and whole fish were bought from Tangde farmers market (Guangzhou, China). Detailed components of the meat wastes are provided in Table S1. Before fermentation at room temperature, meat wastes were cut into 2 cm in diameter and mixed evenly, then loaded into the corresponding bioreactor, which was wrapped with high-density rubber-plastic board to prevent heat loss. Additionally, 500-mL sterile water was added into the bioreactor on day 1 and after leachate sampling. Leachate was circulating with peristaltic pump at the rate of 2.5 L min^{-1} to promote the stabilization process of the waste before collecting on specific days (day 0, 1, 5, 10, 20, 30, 45, 60, 75, 90 and 130). Decomposition process began on July 10, 2019 and was lasted for 130 days.

2.2. Bioaerosol analysis

Bioaerosol was sampled and tested using the FA-1 six-stage impact microbial sampler (Applied Technical Institute of Liaoyang, China) at different decomposition stages of meat wastes. This sampler with six impact disks can separate bioaerosol particles in the following size range according to their aerodynamic diameter: 0.65–1.1 μm, 1.1–2.1 μm, 2.1–3.3 μm, 3.3–4.7 μm, 4.7–7.0 μm, >7.0 μm. Specifically, culturable bacteria were collected and cultivated on nutrient agar medium plates

with 5 mg L^{-1} nystatin to inhibit fungal growth, while the total bacteria were filtered on cellulose acetate membrane (0.22 μm pore size; ANPEL), which was covered upon agar plates used as carrier to stabilize the membrane. The sampling flow rate was 28.3 L min^{-1}, and sampling time was 5 and 30 min for the culturable and total bacteria, respectively. The control samples were implemented with identical methods except for not operating the pump. The detailed depiction of sampling and culturing methods is provided in Supporting Information (SI). The concentration of culturable bacterial bioaerosols was expressed as CFU m^{-3} and calculated using the following equation:

$$Concentration\ (CFU\ m^{-3}) = \frac{TC\ (CFU)}{ST\ (min) \times 28.3 \times 10^{-3}\ \left(m^3\ min^{-1}\right)}$$

where TC is the total colony count and ST is the sampling time.

2.3. Physiochemical property analysis of leachate

Leachate samples (100 mL) were synchronized collected with microbial aerosols during meat waste decomposition and equally divided into two parts. One part was used to extract the DNA for bacterial community and ARG analysis after centrifuged at 12,000 rpm for 8 min; another part was used to conduct the physiochemical property analysis. The water quality parameters, including pH, dissolved oxygen (DO), and electrical conductivity (EC) were determined using pH meter (ST3100, OHAUS, USA), portable dissolved oxygen meter (ST300D/B, OHAUS, USA), and conductivity meter (DDSJ-308A, INESA, China), respectively. Besides, sedimentation rate (SR) and temperature were measured directly and by thermocouple temperature sensor, respectively.

2.4. Microbial activity analysis

The microbial activity of bioaerosol during meat waste decomposition was measured using the fluorescein diacetate (FDA) method reported previously, considering the amount of fluorescein produced by FDA hydrolysis can be directly proportional to the level of microbial activity (Qi et al., 2015). In brief, the shredded bioaerosol membranes were put into 50 mL Erlenmeyer flasks with 10 mL sterilized 0.9% NaCl solution, and the microorganisms were eluted by shaking for 30 min at 37 °C. After mixing with 200 μL FDA working solution, the hydrolysis reaction was initiated at 30 °C under dark conditions. Finally, 500 μL chloroform/methanol mixed solution (2:1 *V*/V) was added to stop the reaction after 150 min (Adam and Duncan, 2001). The fluorescence intensity was measured using fluorescence spectrophotometry (λex = 488 nm, λem = 530 nm) with fluorescein sodium that emitted the same yellow fluorescein as standard. Microbial activity was calculated referring to the sodium fluorescein standard curve and data were corrected by subtracting the blank intensity from the measured values. Blanks were prepared with equal amount of sterile filter membranes using the identical method.

2.5. DNA extraction and ARG quantification

The bioaerosol membranes were disrupted by grinding in liquid nitrogen and subjected to extract DNA using genomic DNA extraction kit (Sangon Biotech, Shanghai, China) following the manufacturer's instruction. DNA concentration and purity were detected using Microvolume UV–Vis Spectrophotometer (NanoDrop one, Thermo Fisher Scientific, USA), while the DNA quality was evaluated using 1% agarose gel electrophoresis. All the DNA extracts were kept at −20 °C until further analysis. Since the DNA concentrations of the bioaerosol from days 75, 90, and 130 were below the detection limit, the following microbial composition and ARG analysis were only conducted for 60 days.

To investigate the ARGs present in the decomposition process of meat wastes, 34 sets of primer (Table S2) including aminoglycoside (*aadA*, *aadE*), macrolides-lincosamids-streptogramins (MLS) (*ermB*, *ermF*, *lnuB*, *mefA*), tetracycline (*tetA*, *tetC*, *tet (36)*, *tetT*, *tetM*, *tetO*, *tet (35)*, *tetX*, *tetW*), sulfonamide (*sul1*, *sul2*, *sul3*), multiple drug resistance (MDR) (*acrB*, *acrF*, *mexF*, *mdtF*), bacitracin (*bacA*), β-lactam (*blaSHV*, *bla0XA10*), and vancomycin (*vanA*, *vanB*) resistance genes as well as MGEs (*intI1*, *intI2*, *intI3*, *tnpA03*, *IS1111*, *IS-CR3*, *IS-26*) were designed on Primer 5, synthesized by TsingKe Biological Technology Co., Ltd. and quantified by qPCR using CFX Connect Real-Time PCR Detection System (Bio-Rad, USA). The detailed amplification methods are shown in SI. The selection of these target ARGs was based on their high abundance and representativeness in domestic waste (Li et al., 2020; Liu et al., 2018; Zhang et al., 2018), while the MGEs were chosen as they can make a big difference in the acquisition, exchange and dissemination of antibiotic resistance (Chen et al., 2019; Li et al., 2018). Relative abundance of the ARGs and MGEs was calculated by normalizing to bacterial 16S rRNA gene, while the absolute gene copy number of ARGs was calculated based on the number of 16S rRNA gene copies according to the reference (Su et al., 2015).

2.6. 16S rRNA gene sequencing and statistical analysis

The extracted DNA was used to amplify the hypervariable V3-V4 region of the bacterial 16S rRNA gene using primers 338F (5- ACTCCTACG GGAGGCAGCAG -3) and 806R (5- GGACTACHVGGGTWTCTAAT -3) according to early reference (Gou et al., 2016). Library preparation and sequencing on the Illumina PE300 platform were performed by Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China). Raw fastq files were quality-filtered and merged by the reported FLASH (version1.2.11) (Yang et al., 2019). The reads were truncated at any site receiving an average quality score < 20 over a 50 bp sliding window, and ambiguous base reads were removed. Operational taxonomic units (OTUs) were bunched in 97% similarity utilizing UPARSE (http://drive5.com/uparse/) (Wang et al., 2017). Bacterial and pathogenic OTUs were taxonomically classified against Silva database and the Human pathogen database, respectively, based on the RDP classifier Bayesian algorithm (Wang et al., 2007). Raw data reported in this study were deposited in the NCBI database with accession number of PRJNA693996.

All data analyses were conducted on the online platform of Majorbio I-Sanger Cloud Platform (www.i-sanger.com) and by IBM SPSS Statistics 22 (Version 22.0. Armonk, NY: IBM Corp., USA). The Kruskal-Wallis H test was used to investigate the difference of bacterial community between each group, and *p* values less than 0.05 was regarded as significant. Spearman correlation between environmental parameters/ARGs/MGEs and the relative abundance as well as the diversity of pathogenic bacteria were analyzed by heatmap. The main bacteria types in bioaerosol and leachate were also determined by principal coordinate analysis based on the Jensen-Shannon Divergence distance algorithm (Kageyama et al., 2018).

3. Results and discussion

3.1. The pollution profile of bacterial bioaerosols during meat decomposition

3.1.1. Culturability and particle size of bacterial bioaerosol

Food wastes could be gradually decomposed and stabilized under the function of diverse microorganisms from aerobic and anaerobic fermentation processes (Wang et al., 2020), which may result in the emission of bioaerosol to the nearby atmosphere. Herein, the concentrations of culturable airborne bacteria released during the anaerobic decomposition of meat wastes were studied. The highest concentration of aerobic or facultative anaerobes was found on day 1 of chicken decomposition (449 CFU m^{-3}), followed by pork (63 CFU m^{-3}) and fish as the lowest (28 CFU m^{-3}) (Fig. 1a). This may be related to the relatively high

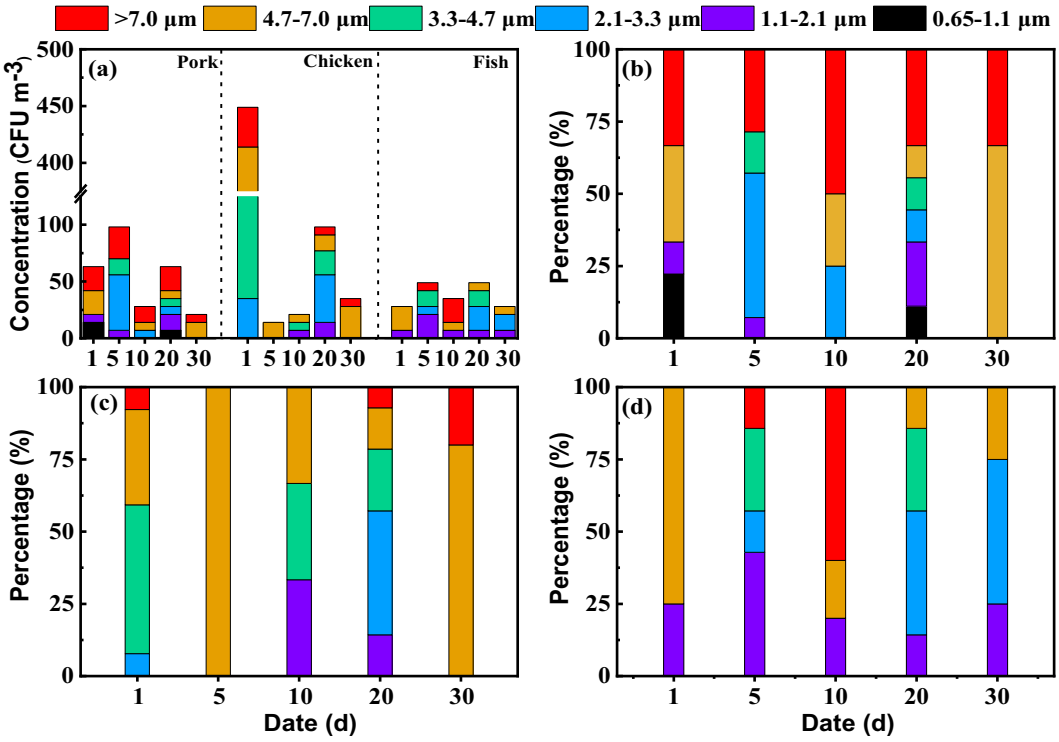

Fig. 1. The concentration **(a)** and size distribution of bioaerosol during the decomposition process of pork **(b)**, chicken **(c)** and fish wastes **(d)**.

abundance of aerobic bacteria such as *Rhodococcus*, *Methylobacterium-Methylorubrum*, and *Brevibacillus* in the chicken bioaerosol on day 1, which were able to be aerosolized and cultivated under aerobic conditions. Moreover, the airborne bacterial concentration from pork and fish decomposition remained below 100 CFU m^{-3}, and was far less than those at a municipal landfill site in Northern Poland (ranged from 134 to 53,800 CFU m^{-3}) (Breza-Boruta, 2016). This may be due to that most airborne bacteria emitted from the anaerobic decomposition of meat wastes cannot be cultivated aerobically.

The particle size distribution of culturable bacteria was further analyzed, and we found that an average of 62.94% of the culturable bacterial bioaerosols collected were larger than 4.7 μm during the decomposition of pork (Fig. 1b), while the highest proportion of bacteria obtained in chicken wastes (an average of 90.48%) was above 2.1 μm (Fig. 1c). However, the average percentage of bioaerosol from fish decomposition with size range of 1.1–2.1 μm (25.43%) and < 4.7 μm (58.29%) was the highest (Fig. 1d) among the three meat wastes. The different size distribution may be due to the properties and composition of meat wastes. Zhao et al. suggested that animals themselves affect the concentrations and size distribution of airborne microorganisms (Zhao et al., 2014). Besides, cells or spores of specific microorganisms may be attached to particles of various sizes and result in different particle size distribution (Predicala et al., 2002). Considering that small-sized particles (< 5 μm) are able to pass through the throat, enter the lower respiratory tract, and deposit in deep of the respiratory tract, especially the particles with size range < 2 μm having the longest retention time in the alveoli

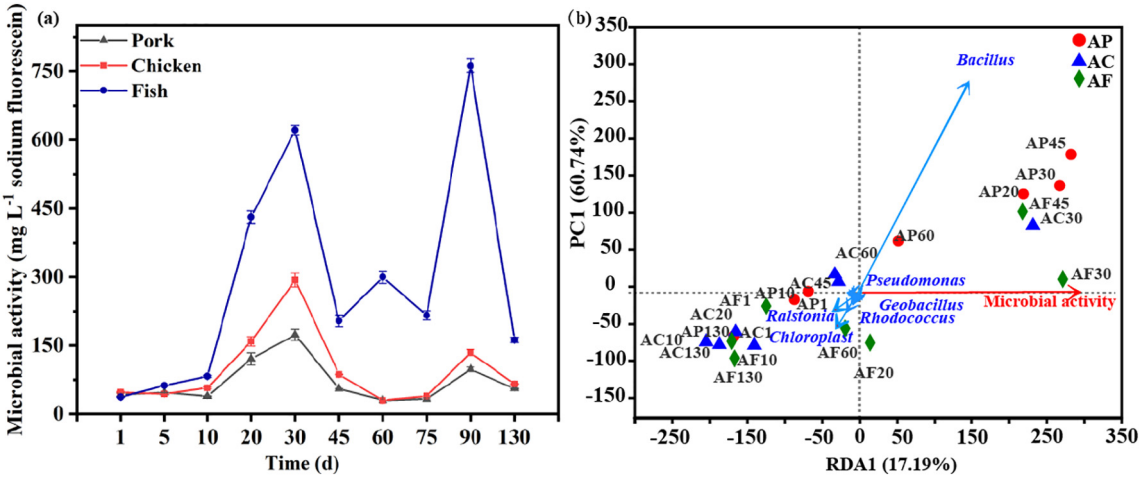

Fig. 2. The total bioaerosol microbial activity detected during the decomposition process of various meat wastes **(a)**. Redundancy analysis (RDA) showing the relationships between airborne bacteria on genus level and the bioaerosol microbial activity **(b)**.

(Pahari et al., 2016), the bioaerosol produced from fish decomposition is more likely to deposit deep of respiratory tract and alveoli, and may cause more harm to people than those of other two meat wastes.

3.1.2. The level of total microbial activity

FDA hydrolysis is catalyzed by three types of extracellular enzymes (lipase, protease, and esterase), and the released fluorescein can reflect the relative activity of metabolic and other processes mediated by microorganisms (Costa et al., 2007; Jaiswal and Pandey, 2019). Therefore, FDA method was used to measure the total activity of microorganisms. As Fig. 2a shows, the average microbial activity of bioaerosol followed the order of pork (69.59 mg L^{-1}) < chicken (95.90 mg L^{-1}) < fish wastes (287.99 mg L^{-1}), suggesting that the bioaerosol emitted from fish wastes may has higher health risk than other two meat wastes. Considering culturable bacteria in fish waste was the lowest, followed by pork and chicken, we concluded that the concentration of culturable bacteria and the total microbial activity were not comparable. This is because except for culturable bacteria, fungi and other unculturable microorganisms in the bioaerosol also contribute to the microbial activity. In addition, the variation tendency of microbial activity of three kinds of meat wastes all presented a similar pattern, which was increased sharply from day 10 to 30, then decreased. The rich nutrients in the meat waste were favorable for the reproduction of microorganisms and resulted in the gradually increased microbial activity. However, with the depletion of nutrients and formation of toxic metabolites, the growth and activity of these microorganisms were inhibited, which may lead to the decrease in the microbial activity of bioaerosol. It was reported that ammonia compounds produced from fish and meat spoilage are toxic for mickle microorganisms (Comi, 2017). Strikingly, further prolonging the decomposition time to day 90 resulted in the increased microbial activity to 98, 135, and 762 mg L^{-1} for pork, chicken, and fish, respectively. This may be attribute to the high relative abundance of *Bacillus* (Fig. 3a). Redundancy analysis (RDA) also showed that microbial activity had a significant positive correlation with *Bacillus*, while the major negative correlations were linked with the dominant bacteria including *Chloroplast*, *Ralstonia*, and *Rhodococcus* in bioaerosol (Fig. 2b). This result was also supported by previous reports that *Bacillus* is an important bacterium which can produce multiple enzymes including lipase, protease, and esterase (Hasan et al., 2006; Odu and Akujobi, 2012). For instance, *Bacillus licheniformis* VSG1 can simultaneously produce protease and lipase responsible for FDA hydrolysis (Sangeetha et al., 2010).

Besides, the size distribution of the microbial activity level during the meat waste decomposition was also evaluated. As Fig. S2 shows, the bioaerosol with the size >3.3 μm had higher activity than other sizes with an average percentage of 55.84%, 58.94%, and 64.30% for pork, chicken, and fish wastes, respectively. This maybe because large particles can serve as the energy and carbon sources for the survival of airborne microorganisms (Clements et al., 2014). Besides, the proportions on day 20 (73.44% and 53.48%), 30 (68.33% and 71.60%), and 90 (70.16% and 67.47%) of fish and chicken decomposition were higher than those on other days. This suggested that high microbial activity was attributed to the enrichment of bioaerosol with the size >3.3 μm, especially on day 30 and 90 of fish and chicken waste decomposition. However, further exploring microbial communities of bioaerosol was needed to figure out the reason for the different distribution of microbial activity.

3.1.3. The composition of pathogenic bacteria during meat waste decomposition

The bacterial communities between bioaerosol and leachate samples were compared using the 16S rRNA sequencing technique to figure out the contribution of meat waste decomposition to the abundance and diversity of airborne microorganisms. We found that, at 97% 16S rRNA gene sequence similarity, 1512 OTUs were detected in all samples. Higher Shannon index or lower Simpson index in the bioaerosol than the corresponding leachate samples indicated higher airborne bacterial community diversity (Table S3). Moreover, as raw meat waste

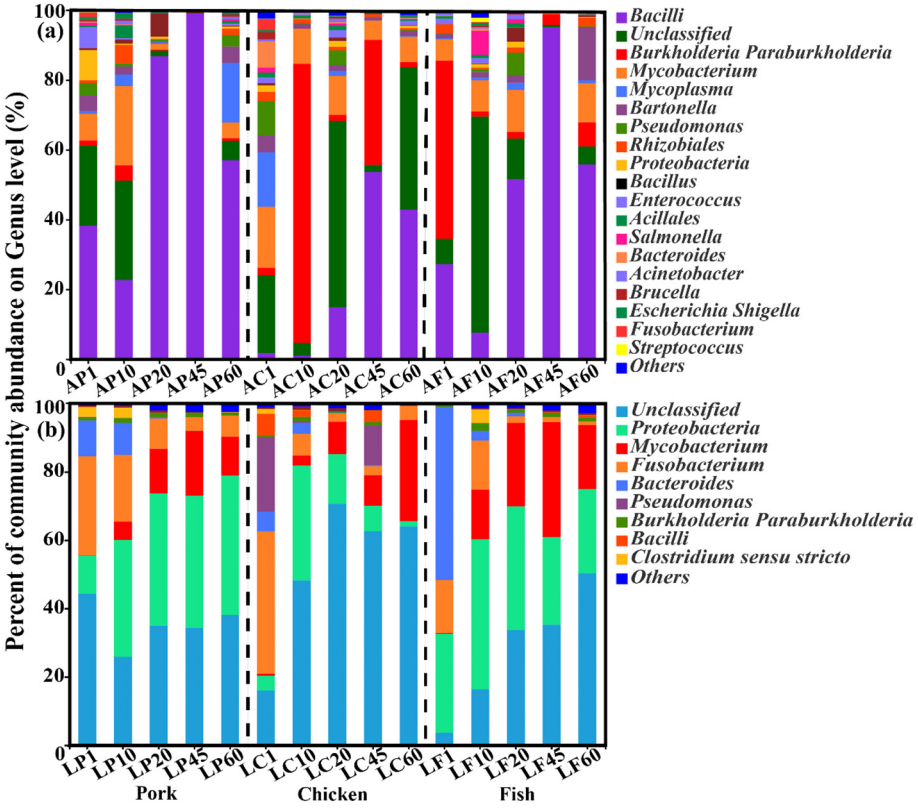

Fig. 3. The compositions of pathogenic bacteria on genus level in bioaerosol **(a)** and leachate **(b)** during the decomposition process of pork, chicken and fish wastes.

decomposition progressed, the diversity of bacterial community in the leachate increased firstly then leveled off, while the airborne bacterial community behaved differently. To be specific, the diversity of airborne bacterial community decreased as the decomposition time of pork waste increased from day 1 to 45, while an increased diversity was detected at the early phase of chicken and fish decomposition (day 20), and then decreased. Additionally, an increased diversity was also observed from days 45–50 decomposition duration with the highest diversity detected on day 1, 10, and 20 of pork, fish, and chicken fermentation. These indicated the inconsistent diversity of bacterial communities between the leachate and bioaerosol samples. Besides, the average richness of bioaerosol was also higher than the relevant leachates samples as revealed by the Ace, Chao, Sobs index of alpha diversity especially on day 1 of pork, day 1 and 20 of chicken, day 10 of fish decomposition (Table S3). Previous study has reported that a constant and high content of bioaerosol have detected in the confined spaces that host confined animal feeding operations (swine barns, dairy farms, poultry, etc.), where the bioaerosol sources are numerous and vary with time and spaces (Mbareche et al., 2017). Analysis of variance of Ace index indicated that no difference was found in the richness of bacterial community between meat types or decomposition times, although there were significant differences between leachate and bioaerosol samples (MANOVA; $R = 0.355$; $P < 0.05$).

Regarding bacterial abundance, Firmicutes and Proteobacteria were found to be the two dominating phyla in the bioaerosol and the proportion of Firmicutes continued to increase as the decomposition progresses (Fig. S3a). This was consistent with the results obtained by Zhang et al. that Firmicutes is the predominant phylum during the whole decomposition process of meat wastes (mixture of fish, pork, chicken) (Zhang et al., 2020a). At the genus level, *Bacillus* was found to be the dominant taxa in bioaerosol samples during meat waste decomposition. Besides, *Ralstonia* and *Chloroplast* were also prevalent in the atmosphere of chicken and fish waste decomposition (Fig. S4a). Among them, *Bacilli*, *Burkholderia-Paraburkholderia,* and *Mycobacterium* were found to be the main airborne dominant pathogens (Fig. 3a). For example, *Burkholderia* belonging to phylum Proteobacteria can cause cystic fibrosis to humans and animals (Pan et al., 2019). In brief, the abundance of *Bacilli* increased from day 10 to day 45 for pork (23.01%–99.11%), fish (7.54%–95.24%), and chicken wastes (0.56%–53.64%), respectively, while decreased only in chicken waste from day 45 (53.64%–43.27%). However, further prolonging decomposition time to day 60 resulted in decreased abundances of *Bacilli* for all the meat wastes, indicating that the decomposition of meat wastes would decrease the health risk of *Bacilli*. By the analysis of PcoA based on JSD distance algorithm, we found that bioaerosol samples can be classified into four enterotypes, and most belong to the *Bacillus* (Fig. S5a), indicating its prevalence in the atmosphere. As similar to the reference, *Bacillus* spp. is the most predominant strain present in the compost (Partanen et al., 2010).

Similarly, the relative abundance of Firmicutes and Proteobacteria were also found to be the highest in the leachate samples for all meat wastes (Fig. S3b). However, different from the bioaerosol samples, *Wohlfahrtiimonas*, *Peptoniphilus*, and *Fusobacterium* were observed to be the dominant genera in the leachate of pork sample. Whereas, chicken and fish have obtained high abundance of *Peptoniphilus* and *Wohlfahrtiimonas*, respectively (Fig. S4b). Besides, the dominant pathogens were also different, with high abundance of pathogenic bacteria such as *Proteobacteria*, *Mycobacterium*, *Fusobacterium*, and *Bacteroides* detected in leachates for all meat wastes (Fig. 3b). The prevalence of these pathogens might suggest that high health risk regarding *Mycobacterium tuberculosis* is a deadly pathogen and has emerged as drug-resistant strain (Schon et al., 2017). Moreover, nontuberculous *mycobacteria* are characterized by moderate pathogenicity (Tortoli, 2014). By typing analysis at the genus level, we found that the leachate samples could be classified into three enterotypes, and each enterotype was respectively dominated by *Wohlfahrtiimonas*, *Peptoniphilus*, and *Bacteroides* (Fig. S5b). Overall, the quite different bacterial community structure between leachate and bioaerosol revealed that the ability of aerosolization of bacteria does not completely rely on their abundance and diversity.

Comparatively, a total of 190 shared bacteria genera (occupying 42.32%–54.29% of total bacteria) were found in bioaerosol samples (Fig. 4a), while only 73 shared bacteria genera (accounting for 57.48%–74.49% of total bacteria) were detected in the leachate samples (Fig. 4b), suggesting that more bacteria were shared by bioaerosol than leachate. Among 675 and 162 bacteria on the genus level detected in bioaerosol and leachate, respectively, 123 bacteria were co-shared (Fig. 4c). The shared numbers in pork (90 bacteria) were highest, followed by chicken (80 bacteria) with fish (54 bacteria) as the lowest (Fig. 4d-f), indicating that the bacteria in pork wastes have a higher

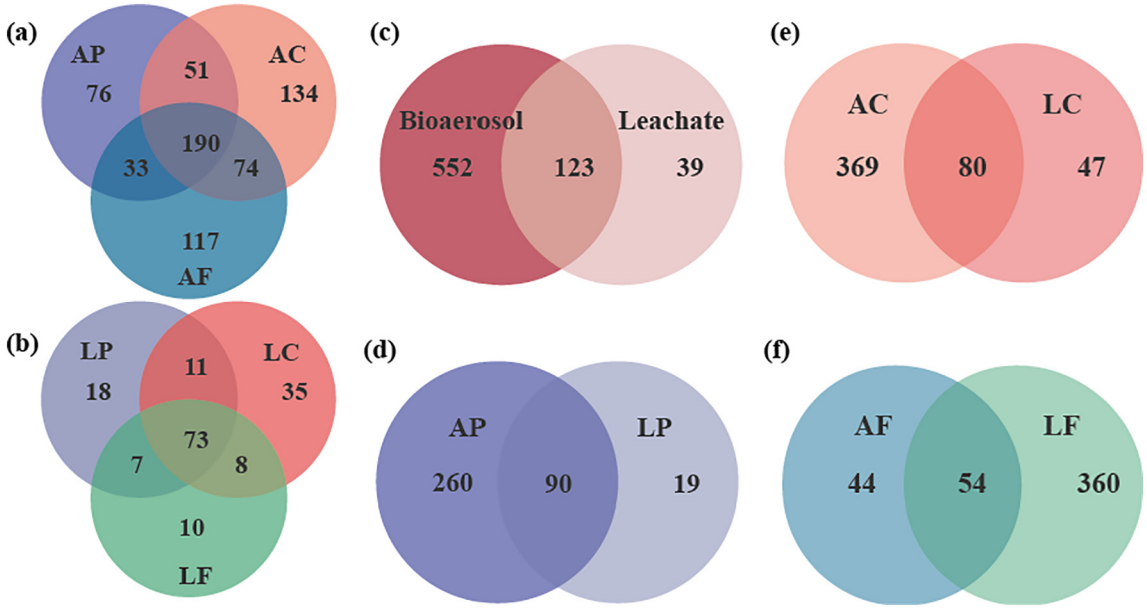

Fig. 4. Venn diagram showing the shared bacteria community on genus level among the bioaerosol **(a)** and leachate samples **(b)**, and between bioaerosol and leachate samples **(c)**, as well as between pork **(d)**, chicken **(e)**, and fish **(f)** wastes from bioaerosol and leachate, respectively.

potential for aerosolization. However, it has to be mentioned that more genera (414 bacteria) were detected in the leachate of fish wastes than other wastes (Fig. 4f). This may be due to the rich endogenous enzymes and fragile organization of fish, which is favorable for the bacteria on/in fish body to decompose the nutrition components (such as lipid and protein) and therefore lead to the rapid propagation of bacteria (Wu et al., 2019). Besides, the abundant intestinal microorganisms in fish wastes will also result in high microbial diversity in the leachate (Delbarre-Ladrat et al., 2006). For the dominant pathogens, 7 kinds of pathogenic bacteria including *Bacilli*, *Burkholderia-paraburoholderia*, *Mycobacterium*, *Bacteroides*, *Pseudomonas*, *Fusobacterium*, and *Proteobacteria* were shared by the bioaerosol and leachate (Fig. S6), suggesting that they were prone to be aerosolized. But the shared pathogens have different evolution trends. For example, the abundance of *bacilli* decreased from day 1 to 60 in leachate of chicken and pork wastes, but increased in the corresponding bioaerosol samples. While for *Mycobacterium*, an opposite trend was found. For fish wastes, the relative abundance of *bacilli* and *Mycobacterium* were both increased with the increase of fermentation time. Therefore, in future research endeavors, more work should be carried out to elucidate why some bacteria like *Bacillus* can be easily aerosolized while others like *Fusobacteriota* and *Peptoniphilus* cannot. These works will be very useful for the assessment of the potential risk of bioaerosol respiratory exposure.

3.2. The abundance of ARGs and MGEs in bioaerosol and leachate

As Fig. 5a shows, among 34 ARGs/MGEs detected, a total of 7, 7, and 6 subtypes of ARGs/MGEs were detected in the bioaerosol of pork, chicken, and fish wastes, respectively. And two airborne ARGs (*ermB* and *tetM*) and one MGEs (*IS1111*) were shared by three meat wastes. The absolute abundance of these genes ranged from 8.79×10^4 to 1.97×10^5 and 4.57×10^4 to 9.22×10^5 copies m^{-3} for pork and chicken, respectively, of which were no significant difference in the order of magnitude (KW tests, $P > 0.05$). Among these ARGs, the *tetM* gene was the most prevalent, especially on day 10 of chicken fermentation (8.00×10^5 copies m^{-3}). This may be due to the prevalence of *Burkholderia Paraburkholderia* (78.67%). Previous studies have reported a strong significant association between *Burkholderia-Paraburkholderia* and tetracycline resistance genes (Liang et al., 2020a), and *Burkholderia cepacia* complex species have

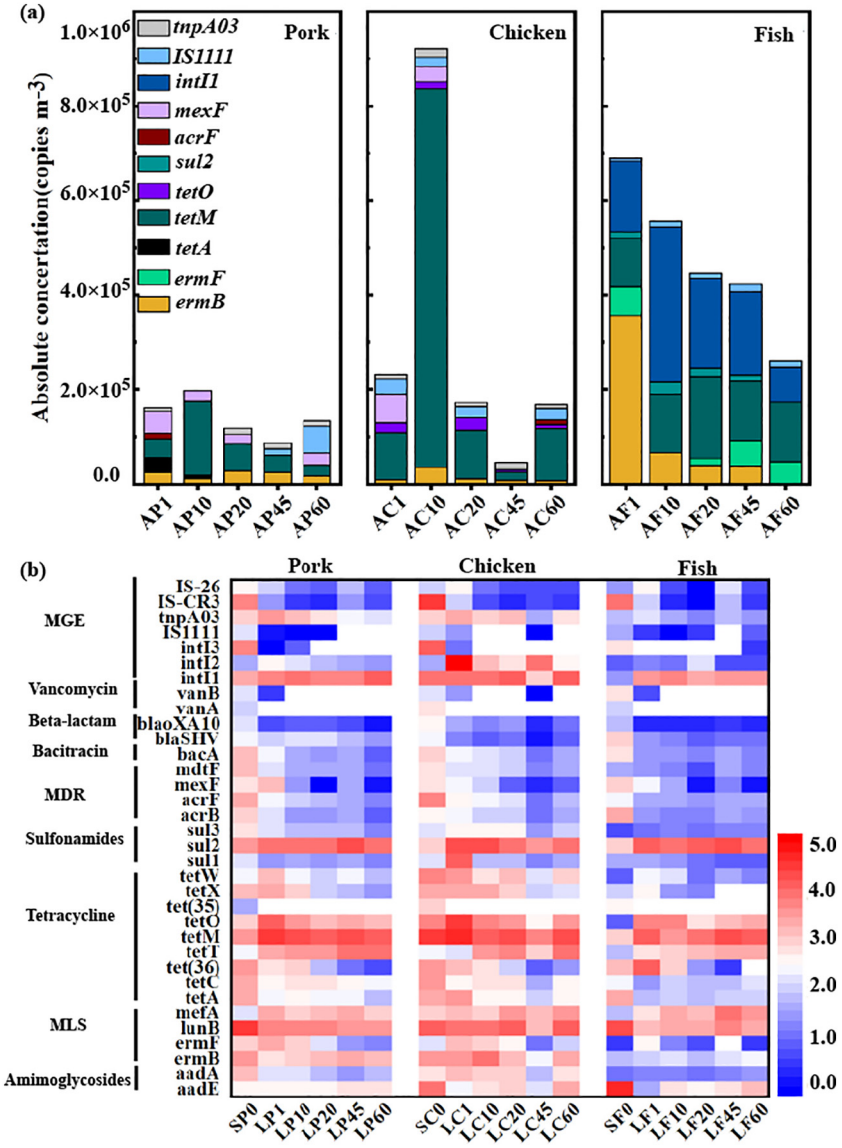

Fig. 5. The absolute concentrations of airborne ARGs/MGEs during the decomposition process of various meats **(a)**. Heatmap of the relative abundance of ARGs/MGEs in the raw meat and the leachate of fermented meat wastes (b). The color change from dark blue to dark red represents the transition from low to high relative abundance. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

become resistant to a large range of antibiotics including tetracycline (Alswat, 2020). Besides, according to a previous study that tetracycline residues in the chicken were up to 8148 μg kg^{-1} and they will trigger the formation and spread of bacterial resistance (Salama et al., 2011; Sivagami et al., 2020), we concluded that the prevailing of *tetM* may connect with tetracycline residues in chicken wastes.

Comparably, the abundance of antibiotic resistance bioaerosol was higher than that in fish with *ermB* as the most dominant, followed by *tetM*. Moreover, their abundance decreased from 6.90×10^5 to 2.61×10^5 copies m^{-3} from days 1 to 60 decomposition time, suggesting that meat decomposition would decrease the abundance of airborne ARGs. This is consistent with a previous study that anaerobic digestion can effectively reduce the copy number of ARGs such as *tetM*, erm*F*, and *sul2* (Sui et al., 2016). Besides, high abundance of *intI1* and *IS1111* were also detected, especially in fish. To be specific, with the decomposition of pork and fish waste increased to day 60, the abundance of *IS1111* increased to 5.74×10^4 and 1.39×10^4 copies m^{-3} respectively, while the abundance of *intI1* was decreased to 7.32×10^4 copies m^{-3} for fish wastes. This indicating that the existence of transfer, retention, and spread of antibiotics resistance in bioaerosol regarding ARGs might horizontally transfer through MGEs (Lin et al., 2018).

In comparison, the diversity and relative abundance of ARGs and MGEs in the leachate were significantly higher (Fig. 5b). In specific, sulfonamides (*sul2*), tetracyclines (*tetM*, *tetO*, *tetT*), MLS (*mefA*, *lnuB*) resistance genes were found to be the most abundant genes, which was consistent with dominant ARGs found in mixed meat decomposition in the early reference (Liang et al., 2020b). Besides, MGEs (*intI1*) maintained high abundance during the decomposition of meat wastes, revealing the possibility of ARGs spread. Different from the bioaerosol samples, the leachate from chicken waste had higher relative abundance of ARGs than that from pork and with fish as the least. This suggested that high abundance of ARGs in the leachate was not certainly resulted in high emission of antibiotic resistance bioaerosol. A previous study has also demonstrated that the relative abundance or diversity of ARGs in aerosols was different from that in biogas digestate (Zhang et al., 2020b). Moreover, in the decomposition process of three meat wastes, variation trends of these ARGs in the leachate were also different. A total of 34.38% ARGs increased during the pork decomposition, while 28.13% showed a trend of first decreased and then increased. For the leachate from chicken wastes, 62.50% ARGs increased and then decreased, while in leachate of fish wastes, 43.75% of ARGs decreased, increased, and then decreased in order with ongoing. Overall, the decomposition of meat wastes markedly decreased the tetracycline, MLS, and aminoglycoside resistance genes as well as MGEs, especially compared with the predominant ARGs/MGEs in raw meat including *lnuB* (pork and fish), *aadE* (fish), *IS-CR3* and *tetM* (chicken) (Fig. 5b). However, it must mention that after 60-day fermentation, high relative abundance of *sul2*, *tetM*, *tetT*, *intlI*, and *lnuB* were also detected (Fig. 5b), suggesting that they may eventually contaminate the receiving water and soil. This hypothesis was confirmed by Zhang et al., who found that the predominant ARGs/MGEs in the effluent-receiving soil and surface water of leachate treatment plant were *intI1*, *sul2* and tetracycline resistance genes, which were 1 to 2 orders of magnitude higher than those in other natural bodies (Zhang et al., 2016).

In a word, different ARGs have diverse potential to be released into the atmosphere. For the dominant ARGs/MGEs in leachate, *tetM* and *intI* could easily emit to the atmosphere through aerosol dispersion, while *lnuB*, *sul2*, *tetO*, and *tetT* cannot/hard to be aerosolized. Strikingly, high abundance of *ermB* was detected in the bioaerosol of fish fermentation even though it was not the dominant ARGs in the leachate, indicating that the relative abundance of ARGs in leachate and aerosols was not completely relevant. Therefore, to control the spread of antibiotic-resistant bioaerosols, future work should also focus on revealing which and how ARGs would aerosolize from wastewater such as leachate.

3.3. Relationships of pathogenic bacteria with environmental factors and the ARG prevalence

Microbial decomposition of meat wastes will be affected by the change of environmental factors including pH, dissolved oxygen, EC, temperature, and SR. As shown in Table S4, the pH value was found to be initially decreased and then increased as all three kinds of meat waste decomposition progressed from day 1 to 45 and then to day 60. A similar evolution curve of pH value in leachate across waste decomposition was observed by Liu et al., who found that pH value first decreased due to the production of carboxylic acid in the anaerobic acid phase and then increased because of the conversion of carboxylic acid to CH_4 and CO_2 in methanogenic phase (Liu et al., 2018). Although no major variation of EC was observed during the fermentation of pork and chicken wastes, significant higher and increased EC was detected in fish wastes, indicating that the decomposition of fish would result in the release of salt ions. Besides, the SR in fish wastes was also higher, suggesting that fish waste was decomposed faster than chicken and pork. This was possibly attributed to the rich intestinal microorganisms in fish waste, which are responsible for the decomposition of fish proteins and lipids (Delbarre-Ladrat et al., 2006).

The spearman correlations among environmental parameters (temperature, SR, EC, pH, dissolved oxygen), ARGs/MGEs, and the top 30 pathogenic bacteria in bioaerosol and leachate at the genus level were analyzed. As Fig. 6a shows, some airborne ARGs conferring resistance to tetracycline (*tetM*, *tetA*), MDR (*mexF*), and MGEs (*IS1111*) were found positively correlated with the pathogenic bacteria ($p < 0.05$). Specifically, *Corynebacteriales* and *Bacillales* were strongly positively correlated with *tetM* gene ($p < 0.001$), indicating that they may be the hosts of *tetM*. Besides, *tetM* gene was also positively related to *Staphylococcus*. Early study has demonstrated that *Staphylococcus aureus* from raw meat including turkey, chicken, beef, and pork has high levels of antibiotic resistance especially tetracycline than that from antibiotic-free chicken samples (Haskell et al., 2018). Notably, most pathogenic bacteria have no correlation with temperature and SR, except for *Bacilli* and *Enterococcus*, which were positively and negatively correlated with SR, respectively.

In contrast, a significant correlation was found between airborne pathogenic bacteria and seven ARGs/MGEs (aminoglycosides, MLS, tetracycline, sulfonamides, MGE, beta-lactam, and vancomycin resistance genes) as well as EC ($p < 0.05$) (Fig. 6b). In detail, *Escherichia-shigella*, *Clostridium_sensu_stricto_7*, *Fusobacterium*, *Bacteroides* were positively correlated with *aadA*, *ermF*, *tet(36)*, *tetO*, *tetX*, *mexF*, *blaSHV*, and *tnpA-03* ($p < 0.01$), suggesting that these pathogens may be the possible hosts harboring ARGs in meat wastes. Previous study has reported that tetracycline-resistant *E. coli also* bore *sul3* and *aadA* genes (Blau et al., 2018). Meanwhile, negative correlations were also identified between *Mycoplasma*, *Mycobacterium*, *Lactobacillales*, *Enterococcus*, *Streptococcus* and *ermF*, *tet(36)*, *tetO*, *tetX*, *tetW*, *mexF*, *vanB*, *tnpA-03* ($p < 0.01$). This may be due to the competition of these species for limited resources (van Elsas et al., 2012), resulting in the decreased ARGs abundance. The above results showed that the succession of ARGs in both bioaerosol and leachate was mainly driven by a shift of pathogenic bacteria host.

4. Conclusions

In this study, the emission of ARGs and pathogens through aerosolization during 130-day anaerobic decomposition process of meat wastes were comprehensively characterized by comparing with leachate samples. The concentration of culturable airborne bacteria was highest in chicken than other two meat wastes and decreased with decomposition progressed. The bioaerosol from fish fermentation has smaller aerodynamic size, but their microbial activity was higher than chicken and with pork wastes as the lowest. The diversity and richness of bacterial community in the bioaerosols were higher with *Bacilli*, *Burkholderia-*

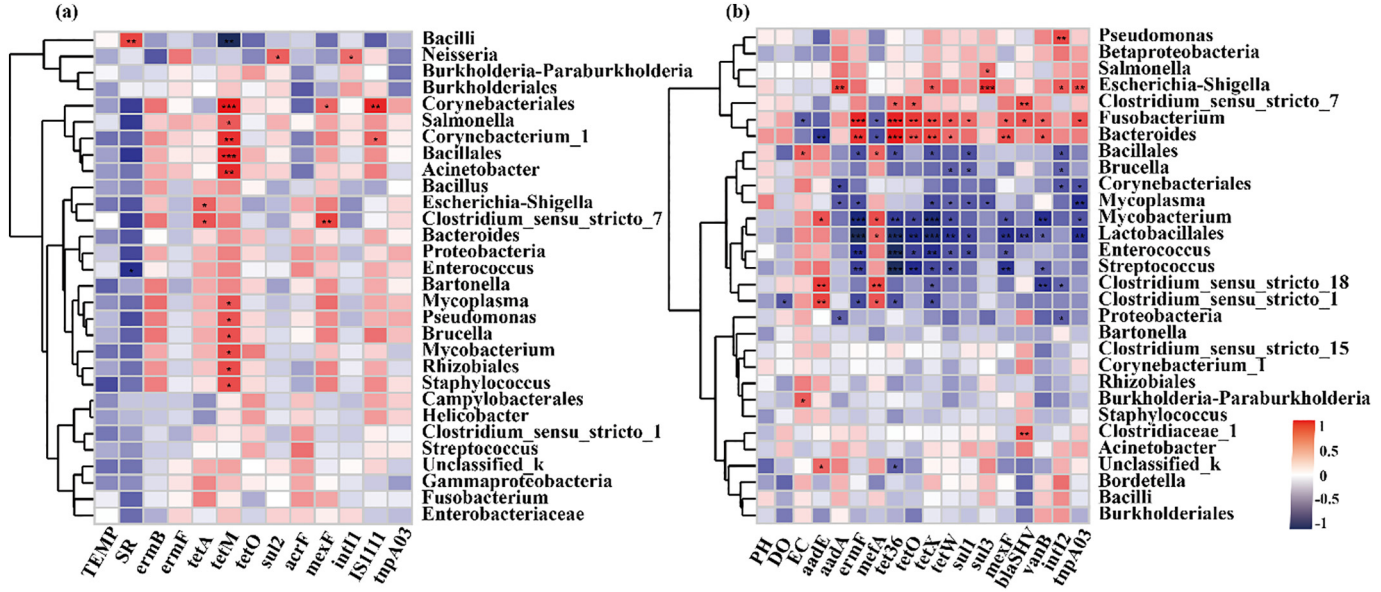

Fig. 6. Spearman correlations among the top 30 pathogenic bacteria at the genus level and environmental parameters (TEMP: temperature; SR: sedimentation rate; EC: electrical conductivity) as well as typical ARGs/MGEs in bioaerosol **(a)** and leachate **(b)**. The correlation was stronger when more asterisks ($0.01 < p^{*} \leq 0.05$, $0.001 < p^{**} \leq 0.01$, and $p^{***} < 0.001$) were used. The color transition from blue to white then to red indicated an increased abundance. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Paraburkholderia, and *Mycobacterium* as the main airborne pathogens, while the leachate samples were dominated by *Wohlfahrtiimonas*, *Peptoniphilus*, and *Fusobacterium*, suggesting that ability of aerosolization of bacteria in the leachate does not rely on their abundance and diversity. In contrast, the diversity and abundance of ARGs/MGEs in the bioaerosol were lower than that in the leachate. To be specific, the bioaerosols were found to be dominated by *tetM*, *ermB*, and *intI*, while the prevalence of *sul2, tetM, tetO, tetT, mefA, lnuB, intI1* were detected in the leachates, indicating that the relative abundance of ARGs in the leachate and aerosols is not completely relevant. Besides, the significant correlation between ARGs and pathogens in the bioaerosol and leachate suggested that ARG structures were mainly driven by the bacterial community shift. Overall, these results will provide useful information for the management of microbial exposure risk involving waste treatment.

CRediT authorship contribution statement

Yun Yu: Methodology, Formal analysis, Writing-original draft.
Zhishu Liang: Methodology, Formal analysis.
Wen Liao: Methodology, Data curation.
Zikai Ye: Investigation.
Guiying Li: Writing- Reviewing and Editing.
Taicheng An: Conceptualization, Supervision.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.147128.

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