Frontiers of Environmental Science & Engineering
2025, 19(6): 75 https://doi.org/10.1007/s11783-025-1995-6

RESEARCH ARTICLE

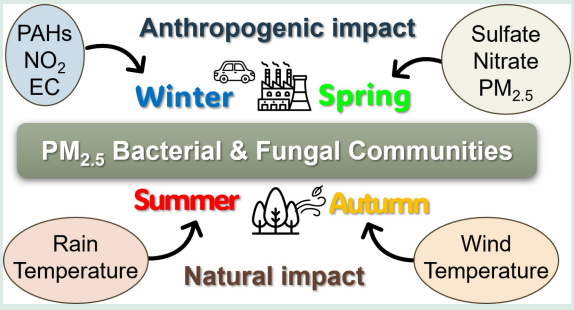
Impact of seasonal variability and atmospheric compositions on the bacterial and fungal communities of $PM_{2.5}$ in Seoul, Republic of Korea

Sookyung Kang, Ji Yi Lee, Kyung-Suk Cho ✉

Department of Environmental Science and Engineering, Ewha Womans University, Seoul 03760, Republic of Korea

HIGHLIGHTS

- In spring and winter, $PM_{2.5}$ microbial communities were mainly affected by chemicals.
- In summer and autumn, meteorological factors greatly influenced $PM_{2.5}$ microbiome.
- $PM_{2.5}$ microbial diversity in winter and spring were negatively impacted by chemicals.
- Bacteria's most prevalent function is metabolism, while fungi's is saprotroph.
- Metabolism was highest in spring, with dominant genera showing a positive relation.



ABSTRACT: This study examined particulate matter with a diameter of 2.5 μm or less ($PM_{2.5}$) samples to investigate seasonal shifts in bacterial and fungal communities in Seoul, Republic of Korea. To assess these variations and the influence of environmental factors, DNA was extracted from $PM_{2.5}$ samples and subjected to sequencing analysis. The results showed distinct seasonal changes in microbial communities. *Pseudarthrobacter* dominated in winter, *Arthrospira* in spring, *Rhodococcus* in summer, and *Pelomonas* in autumn among the bacterial communities, while *Candida* in winter, *Coprinopsis* in spring, and *Cutaneotrichosporon* in both summer and autumn were prevalent in fungal communities. Bacterial richness peaked in spring, whereas fungal richness was highest in winter. These shifts were driven by environmental factors: air pollutants and chemical compositions had a greater influence in winter and spring, while meteorological conditions, such as temperature and humidity, were dominant in summer and autumn. Functional gene analysis revealed a prevalence of metabolic pathways essential for microbial survival, with fungi showing a higher proportion of saprotrophs, particularly in spring. This comprehensive analysis, considering a wide range of environmental factors including meteorological conditions, air pollutants, and atmospheric organic compounds such as polyaromatic hydrocarbons (PAHs) and dicarboxylic acids (DCAs), provides novel insights into the dynamic relationships between environmental factors and microbial communities in $PM_{2.5}$, highlighting the significant role of anthropogenic influences. This research advances our understanding of atmospheric microbial

✉ Corresponding author. E-mail: kscho@ewha.ac.kr
Article history: Received 8 October 2024, Revised 10 March 2025, Accepted 20 March 2025, Available online 20 April 2025

ecosystems and their seasonal dynamics.

KEYWORDS: Airborne microbiome, Chemical composition, Microbial functions, $PM_{2.5}$, Seasonal effect, Seoul

1 Introduction

Particulate matter with a diameter of 2.5 μm or less ($PM_{2.5}$) has been a subject of sustained concern owing to its potential harm to human health (Jung et al., 2019; Tucker, 2000; Ting et al., 2022). It causes various health conditions, including respiratory diseases, respiratory infections, chronic obstructive pulmonary disease, lung cancer, heart diseases, and in severe cases, even death (Di et al., 2017; Bu et al., 2021; Yang et al., 2022). Typically, it is composed of heavy metals, carcinogenic atmospheric organic compounds, and microorganisms, which contribute to these diseases (Alghamdi et al., 2014). The composition and concentration of heavy metals, carcinogenic atmospheric organic compounds, and microorganisms within $PM_{2.5}$ can vary depending on the season, and this variation in $PM_{2.5}$ constituents can lead to different health effects that vary seasonally (Zheng et al., 2005; Alghamdi et al., 2014; Du et al., 2018a; Pan et al., 2025). Additionally, gaseous air pollutants, such as O_3, NO_2, and SO_2, exhibit complex interactions with $PM_{2.5}$, affecting human health (Crouse et al., 2015).

The concentration and composition of these gaseous air pollutants and the ions, atmospheric organic compounds, and organisms within $PM_{2.5}$ can vary depending on the season (Boreson et al., 2004; Zheng et al., 2005; Zhang et al., 2010; Cao et al., 2022). For example, a study conducted in Beijing, China in 2000 reported that carbonaceous aerosols in $PM_{2.5}$ were highest in January (winter), whereas SO_4^{2-}, NO_3^-, and NH_4^+ were highest in July (summer) (Zheng et al., 2005). Additionally, another study conducted in Nanjing, China, in 2019, reported that sugars in $PM_{2.5}$ and NO_2 concentrations were highest in winter (Cao et al., 2022). Further, a survey conducted in urban areas in 2002–2003 found that SO_4^{2-}, NO_3^-, NH_4^+, Cl^-, and elemental carbon (EC) in $PM_{2.5}$ were highest in summer (Boreson et al., 2004).

Studies have reported seasonal variations in the microbial communities of $PM_{2.5}$ in regions with distinct seasonal characteristics. For example, a study reported changes in the microbial communities in $PM_{2.5}$ collected over 14 months in Colorado, USA, with variations in the source environment, with the highest diversity observed in summer and spring (Bowers et al., 2013). An analysis of the $PM_{2.5}$ microbial communities in Beijing, China, in 2014 revealed seasonal variations in the bacterial and fungal community composition in this region, with microbes thriving the most in summer and pathogenic bacteria and fungi being most abundant in winter (Du et al., 2018a). In another study, Du et al. (2018b) observed the seasonal variation in the dominant phylum in $PM_{2.5}$ samples in Beijing in 2016, with Actinomycetota (Actinobacteria) being most abundant in both summer and winter, and Firmicutes and Proteobacteria being dominant in fall. Additionally, among the fungal class, Dothideomycetes were most abundant in winter, with Sordariomycetes and Eurotiomycetes also dominating during this season. Wang et al. (2021) reported that the bacterial abundance in $PM_{2.5}$ in Xi'an and Linfen, China, was highest in fall, whereas the fungal abundance peaked in summer. Additionally, the comparison of the relative abundance of bacteria revealed that Actinobacteria dominated the bacterial community in fall, whereas Firmicutes dominated in summer; for the fungal community, Basidiomycota dominated both in summer and fall (Wang et al., 2021).

Despite the existence of studies on the seasonal characteristics of $PM_{2.5}$ microbial communities and the various factors influencing these communities, there are few to no studies specifically focusing on Seoul (Bowers et al., 2013; Du et al., 2018a; 2018b; Wang et al., 2021). This makes it crucial to gather data from various regions, such as Seoul, to identify general trends across different areas. Additionally, there is a significant lack of research on the influence of atmospheric organic compounds on microbial community structure. Particularly, the effects of atmospheric organic compounds such as PAHs on microbial communities remain underexplored. Therefore, this study, which includes an analysis of the influence of atmospheric organic compounds, provides valuable insights by investigating the bacterial and fungal communities in atmospheric $PM_{2.5}$ samples collected in Seoul in 2018. We examined their correlations with various environmental factors, including meteorological factors, pollutants, ions, and atmospheric organic compounds. This research focused on the following key research questions: (i) Does the composition of $PM_{2.5}$ microbial communities vary seasonally? (ii) How do the impacts of different types of environmental factors on $PM_{2.5}$ microbial

communities differ by season? (iii) Does natural or anthropogenic influence play a more significant role in shaping community structure with changing seasons? (iv) How does the functions of $PM_{2.5}$ microbial communities differ seasonally? The findings of this study will provide insight into the changes in $PM_{2.5}$ microbial communities with seasonal variations, particularly in relation to environmental factors. They will shed light into how human activities impact $PM_{2.5}$ microbial communities and offer insights into the differences in the genetic functions of $PM_{2.5}$ microbial communities across different seasons. This information will contribute to our understanding of the complex interactions between microbial communities and environmental conditions, which is essential for addressing the public health concerns related to $PM_{2.5}$ and expanding our knowledge on microbial dynamics in the atmosphere.

2 Materials and methods

2.1 Samples and data collection

For this study, $PM_{2.5}$ samples were collected in the Korean Environmental Industry & Technology Institute building (37.61°N, 126.930°E), Seoul, Republic of Korea. The $PM_{2.5}$ samples were collected from the roof of the six-story building, approximately 20 m high, over a period of 23 h, from 10 AM to 9 AM the following day. The climate of Seoul varies notably with season: mild and occasional yellow dust winded spring, hot and humid summer, cool and clear autumn, cold and dry winter. A total of 75 $PM_{2.5}$ samples were collected from January to November 2018. Sampling was conducted across different seasons: 20 samples were collected during winter (January 16th to February 8th), 20 samples during spring (March 16th to April 5th), 20 samples during summer (August 20th to September 12th), and 15 samples during autumn (November 5th to November 19th). The $PM_{2.5}$ samples were collected using quartz filters (Tissuequartx-2500QAT-UP, 8 × 11 inch, Pall®, New York), which were sterilized at 550 °C for 12 h. The samples were collected at a flow rate of 1000 L/min for 23 h using high-volume air samplers (HV-RW, SIBATA, Japan & 6070V-2.5, Tisch, USA). After sampling, the collected $PM_{2.5}$ samples were stored at –20 °C until microbiological and chemical analysis. Information on the meteorological data, pollutant gas, and ions was obtained from the Korea Environment Corporation (Table S1). The data of the chemical components (atmospheric organic compounds) were obtained from a previous paper analyzing the same $PM_{2.5}$ samples (Kang, 2021) (Table S1).

2.2 Microbial analysis

For the microbial analysis, each of the sample filters was cut into a 6 cm^2 size and placed, with their dusty side inside, in 5 mL–Eppendorf tubes. DNA was extracted from each individual $PM_{2.5}$ filter collected on each sampling day. Thereafter, a total of 1.5 mL of corrosive buffer solution, containing a mixture of sodium hydroxide, potassium hydroxide, and ethanolamine, along with 25 μL of Proteinase K provided by the NucleoSpin eDNA Water kit (MACHEREY-NAGEL, Germany), was added into the 5-mL centrifuge tube. To evenly wet the sample filters, the tubes were rocked at 90 r/min for 20 min, after which all tubes, containing the solution and filter, were moved into a 5 mL-syringe and injected into a bead tube. During this process, care was taken to prevent the damage of the filter. Subsequent steps were performed following the protocol of a NucleoSpin eDNA Water kit (MACHEREY-NAGEL, Germany) (Kang and Cho, 2023).

The V3-V4 regions of the bacterial 16S rRNA gene were amplified by PCR using the primer set amp-515F (5′-TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGGTGCCAGCMGCCGCGGTAA-3′) and amp-806R (5′-GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG GGACTACHVGGGTWTCTAAT-3′) (Hugerth et al., 2014; Lee et al., 2019). The bacterial amplification procedure was performed as follows: 94 °C for 3 min, 35 cycles at 94 °C for 45 s, 58 °C for 60 s, 72 °C for 90 s, and 72 °C for 10 min. The target gene for fungi was the ITS2 gene, and the primer set, amp-ITS3 target mix3 (5′-TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGCTAGACTCGTCACCGATGAAGAACGCAG-3′) and amp-ITS4 (5′-GTCTCGTGGGCTCGG AGATGTGTATAAGAGACAG TCCTCCGCTTATTGATATGC-3′), was used for PCR (Bellemain et al., 2010; Tedersoo et al., 2015). The fungal PCR program was performed under the following condition: 95 °C for 3 min; 35 cycles at 95 °C for 30 s, 58 °C for 30 s, 72 °C for 30 s, followed by 10 min at 72 °C. The concentration and band size of the PCR product were examined using gel electrophoresis with 1.5% agarose gel. To obtain the DNA library, each of the products was purified with NucleoSpin® Gel and PCR Clean-up Kit (Macherey-Nagel GmbH), and indexed by amplifying with each combination of primer set (N701-N712 and S501-S507) (Lee et al., 2019). The indexing PCR products were run on a 2% agarose gel, and

appropriately-sized bands were cut and purified with QIAquick Gel extraction kit (Qiagen Inc., Valencia, CA, USA). The purified samples were diluted to similar concentration and pooled in a tube to a similar quantity to achieve DNA library. The concentration was examined using a Molecular Imager Gel Doc XR + Imaging System (BIO-RAD, CA, USA), Nanodrop 200c Spectrophotometer (Thermo Fisher Scientific, MA, USA), and CFX96 Real-time system C1000 Touch Thermal Cycler (BIO-RAD, CA, USA). The total sequences of the DNA library were analyzed using the Illumina MiSeq sequencing platform by Macrogen Inc. (Seoul, South Korea).

The complete set of sequence reads was subjected to analysis using Quantitative Insights into Microbial Ecology (QIIME) (Gregory Caporaso et al., 2010). Sequences falling below 250 bp or exceeding 350 bp were eliminated using the FLASH software (Magoč et al., 2011). Noise data and the OTU clustering process were performed using the *De Novo* approach and the CD-HIT program (Schloss et al., 2009). The following OTU clustering procedure was performed to analyze the sequencing data. First, short reads were removed from the raw sequences, and long tails were trimmed. The filtered reads were clustered at 100% identity using CD-HIT-DUP, during which chimeric sequences were identified and removed. Secondary clusters were then recruited into primary clusters, and noise sequences in clusters of size x or below were removed based on statistically calculated x values. Finally, the remaining representative sequences were clustered at a 97% similarity threshold. Through this process, we established high-quality OTUs and provided reliable data for biodiversity analysis. The outcome of the sequencing process was determined using UCLUST, and compared against the RDP database for 16S rDNA. To assess the α-diversity, the Chao1, Shannon index, and Simpson index were calculated using QIIME (Caporaso et al., 2010). The obtained bacterial and fungal community sequences have been submitted to the National Center for Biotechnology Information (NCBI) Sequence Read Archive, with accession numbers SRP456353, SRP456560, SRP436939, and SRP436979.

Blank samples were prepared using quartz filters that were sterilized at 550 °C for 12 h, the same way as the samples collected. However, after DNA extraction and PCR by the same manners, there was no PCR amplification.

2.3 Chemical analysis

The data on the organic compounds (DCAs, fatty acids (FAs), PAHs, sugars, and alkane) were obtained from a previous paper analyzing the same $PM_{2.5}$ samples (Kang, 2021) (Table S1). To determine the concentrations of atmospheric organic compounds , a gas chromatograph/mass spectrometer (7890B GC and 6977A MS, Agilent) was employed. Internal standardization was applied for the analysis of PAHs, DCAs, FAs, and sugars. The surrogate standards used in the analysis included Phenanthrene-d10, Fluoranthene-d10, Chrysene-d12, Perylene-d12, Benzo(ghi)perylene-d12 for PAHs; Succinic acid-d6 for DCAs; Myristic acid-d27 for FAs; and Levoglucosan-d13 for sugars. The filters, containing a mix of these surrogate compounds, were placed in 125 mL amber vials, filled with a DCM/MeOH (3:1, v/v) solvent, and subjected to two rounds of 30-min ultrasonication. The extracted solvent was then evaporated using a TurboVapII evaporator at 40 °C until the total volume was reduced to 10 mL. The extracts were filtered through 0.45 μm pore-sized filters (Acrodisc 25 mm Syringe Filter, Pall) and further concentrated to 500 μL using a needle concentrator (TS-18821, Reacti-therm) with a gentle nitrogen (N_2) stream at 40 °C. The concentration of non-polar atmospheric organic compounds, such as PAHs, was determined via GC/MS, while other atmospheric organic compounds required derivatization. For this process, 50 μL of each extracted sample was evaporated at 40 °C for 30 min using a nitrogen stream. Afterward, 50 μL of 99% N, O-Bis(trimethylsilyl)trifluoroacetamide (BSTFA) with 1% trimethylchlorosilane and 50 μL of pyridine were added, followed by vortexing for 40–50 s. The mixture underwent derivatization by heating at 75 °C for 90 min on a hot plate, and then the samples were analyzed using GC/MS.

The National Institute of Environmental Research (NIER, Republic of Korea) provided concentration data for the inorganic fraction. Ion concentrations (sulfate (SO_4^{2-}), nitrate (NO_3^-), chloride (Cl^-), ammonium (NH_4^+)) were measured using ion chromatography, while sodium (Na^+), potassium (K^+), magnesium (Mg^{2+}), and calcium (Ca^{2+}) were analyzed via ion chromatography and atomic absorption/emission spectrophotometry. $PM_{2.5}$ concentrations were measured using a gravimetric method, and concentrations of other air pollutants were measured with the following methods: the pulse UV fluorescence method for SO_2, the non-dispersive infrared method for CO, the chemiluminescent method for NO_2, and the UV photometric method for O_3.

2.4 Statistical analysis

To identify seasonal variation in the bacterial and

fungal community structure, as well as the effect of environmental factors, various statistical analysis methods were employed. The environmental factors considered meteorologic data, air pollutants ($PM_{2.5}$, O_3, NO_2, CO, SO_2, organic carbon (OC), and elemental carbon (EC)), ions (SO_4^{2-}, NO_3^-, Cl^-, Na^+, NH_4^+, K^+, Mg^{2+}, Ca^{2+}), and atmospheric organic compounds (DCAs, FAs, PAHs, sugars, and alkane). To understand the effect of the seasonal variation in environmental factors on the bacterial and fungal distribution, canonical correlation analysis was performed using CANOCO 4.5 software (Microcomputer Power, Ithaca, NY, USA). Pearson coefficients between environmental factors and the seasonal dominant genera were calculated using corrplot and Hmisc package in R version 3.6.3 (R Core Team, Austria). To analyze the correlation between environmental factors and seasonal alpha-diversity indices, Spearman coefficients were calculated in R. The variations in the bacterial and fungal alpha-diversity during different seasons were evaluated using one-way analysis of variance (ANOVA) in R. Functional prediction of the bacterial communities was performed using the Tax4Fun2, which can be found in the Kyoto Encyclopedia of Genes and Genomes (KEGG) database in R (Wemheuer et al., 2020). Functional redundancy prediction of fungal communities was conducted using the microeco based on FUNGuild database in R (Liu et al., 2021).

3 Results and discussion

3.1 Seasonality of $PM_{2.5}$ bacterial and fungal community structures

In the 2018 Seoul $PM_{2.5}$ samples, the most commonly found bacteria overall were Proteobacteria, Actinobacteria, Firmicutes, Cyanobacteria, and Bacteroidetes (Fig. 1(a)), which are consistent with commonly observed bacterial phyla in the atmosphere (Seifried et al., 2015; Park et al., 2020; Wei et al., 2020; Kang and Cho 2022). However, the relative abundance of $PM_{2.5}$ bacteria in this study varied with season. In winter, Proteobacteria, Actinobacteria, and Firmicutes held the highest proportions, whereas Cyanobacteria, Actinobacteria, and Proteobacteria were the most dominant phyla in spring. The differences were more pronounced at the genera level than at the phyla level. *Pseudarthrobacter* and *Janthinobacterium*, which were dominant genera in winter, have been isolated from Antarctic soil (Shivaji et al., 1991; Kit et al., 2020; Shin et al., 2020; Kim and Seo, 2023). Among the dominant spring bacteria, *Arthrospira* has been previously found in aquatic environments, such as lakes and coastal wetlands (Mussagy et al., 2006; Dong et al., 2015; Misztak et al., 2021), whereas *Mycolicibacterium* has been identified in various environments, such as peat bogs, bays, and soils (Nouioui et al., 2019; Dahl et al., 2021; Ou et al., 2023). *Rhodococcus*, *Pelomonas*, and *Acinetobacter*, which were dominant during summer and autumn, have been found in diverse habitats, including soil, freshwater, and even human bodies. The composition of $PM_{2.5}$ bacterial communities differed significantly across seasons, with dominant bacteria in each season originating not only from soil but also from various other environments. This implies that bacteria dominating each season originate from diverse media, suggesting a stronger influence of seasonal environmental α-diversity rather than terrestrial origins, underscoring the substantial impact of seasonal variations on bacterial dominance.

To comprehend the microbial community characteristics of $PM_{2.5}$, the α-diversity indices of the microbial communities were determined (Table S2). α-Diversity indices serve as indicators of community structure, reflecting the environmental conditions of atmosphere as microbial habitats. Chao1 reflects richness, Shannon index indicates diversity, and Gini-Simpson index portrays evenness (Basualdo, 2011; Thukral et al., 2019). The seasonal variations in community structures were also confirmed through α-diversity indices (Fig. S2). The results of ANOVA analysis indicated significant differences in Chao1 and Shannon index between the four seasons. The highest richness was observed during spring, whereas diversity peaked during winter. Both indices reached their lowest points in summer, which is similar to the trend of the seasonal α-diversity indices reported for Xi'an and Linfen (Wang et al., 2021). Previous study reported that the α-diversity indices of bacterial communities were lowest during winter and highest in spring (Wang et al., 2021). This discrepancy could be attributed to variations in the $PM_{2.5}$ concentrations, with their samples reaching up to 312 μg/m^3, indicating higher $PM_{2.5}$ levels than that considered in this study and substantial differences in the seasonal $PM_{2.5}$ concentrations (Wang et al., 2021). In this study, the maximum $PM_{2.5}$ concentration was 108 μg/m^3, and the seasonal differences, except for summer, were not as pronounced as in the previous study (Table S1). Despite the relatively minor differences in the $PM_{2.5}$ concentrations, the observed variations in the diversity indices of $PM_{2.5}$ bacterial communities imply that the bacterial diversity in this study was significantly

influenced by various environmental factors beyond $PM_{2.5}$ concentrations. Therefore, to investigate the impact of a wide range of environmental factors, this study analyzed the influence of meteorological conditions, air pollutants, and chemical composition, including both atmospheric organic and ionic components, on microbial community structure. The results of this analysis are discussed in the following sections.

For the $PM_{2.5}$ fungal communities, Ascomycota was dominant during winter and spring, whereas Basidiomycota prevailed during summer and autumn (Fig. 1(b)). In contrast, previous studies conducted in Beijing, China, reported the > 90% dominance of Ascomycota throughout all seasons (Du et al., 2018a; 2018b). However, a research conducted in Xi'an reported similar trends in the variation on the fungal communities as this study (Wang et al., 2021). Previous studies have highlighted the dominance of Basidiomycota in forest soil environments, as well as its prevalence in continental atmospheric samples compared to marine environments (Fröhlich-Nowoisky et al., 2012; Weber et al., 2013; Womack et al., 2015). The richness and diversity were higher during winter and spring (Fig. S1). The comparison of previous studies regarding fungal α-diversity revealed that the fungal diversity of $PM_{2.5}$ samples collected from Mt. Tai in China was higher in winter compared to summer (Xu et al., 2017). The fungal richness and diversity of samples collected in Beijing, China were highest in winter and lowest in summer, indicating marked seasonal variations (Du et al., 2018a; 2018b). However,

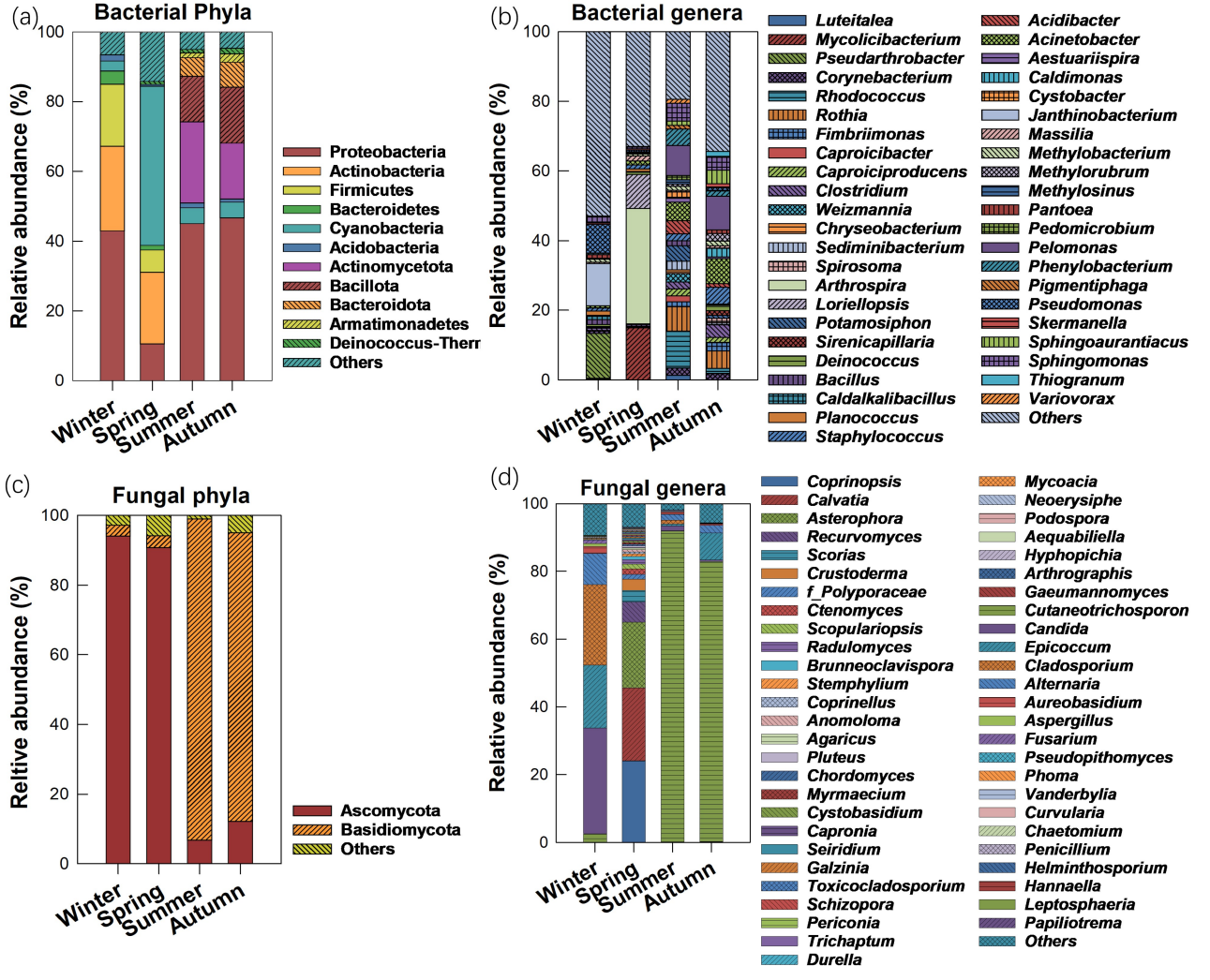


Fig. 1 Seasonal variation in the relative abundance of (a) bacterial phyla, (b) bacterial genera, (c) fungal phyla, and (d) fungal genera in particulate matter with a diameter of 2.5 μm ($PM_{2.5}$) samples.

according to previous studies, the fungal richness in Xi'an, was higher in summer, and the diversity was higher in autumn, whereas in Linfen, both the richness and diversity were higher in summer (Wang et al., 2021). Since wind speed and rainfall affect fungal abundance, they also influence fungal richness and diversity. (Aira et al., 2013; Xu et al., 2017). In this study, wind speed and air pressure exhibited a significant correlation with the fungal diversity during winter (Fig. 3(a)). Excessively low wind speeds (< 2 m/s) are known to limit fungal dispersion due to sedimentation effects, whereas abundant vegetation in the direction of wind flow might increase atmospheric fungal abundance (Xu et al., 2017). Reports on the α-diversity of fungal communities seem to display varying trends based on the region and sampling time. However, differences in the values across seasons have been consistently reported, suggesting the contribution of seasonal factors to the differences. This study also observed varied diversity indices across seasons, highlighting seasonal differences in the $PM_{2.5}$ fungal community structures influenced by various environmental factors.

In Fig. S3, we present the temperature, microbial α-diversity indices, $PM_{2.5}$ levels, OC/EC ratios, and atmospheric organic compounds categorized by sampling date. Our findings indicate that both microbial diversity indices and the concentrations of $PM_{2.5}$ and atmospheric organic compounds were elevated during the winter and spring seasons. This suggests that the high levels of $PM_{2.5}$ and atmospheric organic compounds during these periods may have a significant impact on the structure of $PM_{2.5}$ microbial communities. These observations are further confirmed through various statistical analyses presented in the subsequent sections.

3.2 Seasonal communities of bacteria in response to environmental factors

To interpret the impact of environmental factors on the clustering structure of $PM_{2.5}$ microorganisms at the genus level with a change in season, CCA was performed (Fig. 2). During winter, the $PM_{2.5}$ bacterial community appeared to be significantly influenced by pollutants and atmospheric organic compounds (Fig. 2). In Seoul, winds tend to blow from the north during the winter. Since heating systems that involve burning wood are commonly used in areas located north of Seoul, the overall concentration of air pollutants is generally higher, which may have also impacted the $PM_{2.5}$-associated bacteria. In the Republic of Korea, $PM_{2.5}$ concentrations exhibit a distinct seasonal pattern, showing high levels during winter (December to February) and in March (Allabakash et al., 2022; Lee et al., 2024). This is attributed to factors such as the influx of $PM_{2.5}$ from abroad, increased fossil fuel usage, and the downward movement of the atmospheric boundary layer during winter (Lee et al., 2024). In summer, the concentration of $PM_{2.5}$ significantly decreases due to the cleansing effects of precipitation, while in autumn, the levels of most pollutants are relatively low (Allabakash et al., 2022; Park, 2021).

To analyze the correlation between the $PM_{2.5}$ microbial community structure and various environmental factors, the Spearman coefficients between the α-diversity indices of microbial communities and environmental factors were calculated and plotted in Fig. 3. The α-diversity indices exhibited a negative correlation with most pollutants, whereas the top three dominant bacterial genera displayed a positive correlation ($p < 0.05$) (Figs. 3 and S2). This suggests the possible utilization of pollutants as nutrients by some dominant bacteria or a certain level of resistance, as these nutrients might not be accessible for other minor species, thus impacting the α-diversity negatively (Fan et al., 2019). In winter, higher pollutant concentrations correlated with the increased dominance of certain bacterial species but reduced diversity, emphasizing the role of pollutants as significant determinants of microbial community structure. Additionally, the CCA analysis revealed the significant influences of PAHs and sugars on the composition of winter $PM_{2.5}$ bacterial communities (Fig. 2(a)). All atmospheric organic compounds exhibited significant negative correlations with diversity indices ($p < 0.05$). Further, PAHs, known for their carcinogenic properties and primarily arising from human activities, were likely interconnected with pollutants, particularly during the influential winter period (Ghosal et al., 2016). Sugars, serving as microbial constituents and nutrients, likely exhibited a close relationship. Additionally, DCAs, the largest component of the atmospheric organic compounds, displayed the strongest negative correlation with winter bacterial diversity, but exhibited a significant positive correlation with the top three dominant bacterial genera (*Pseudarthrobacter*, *Janthinobacterium*, and *Pseudomonas*) ($p < 0.05$) (Figs. 3(a) and S2(a)). The primary emission sources of DCAs include fossil fuel combustion, biomass burning, vehicular exhaust, or atmospheric secondary organic aerosols (SOA) resulting from photochemical reactions (Kawamura and Bikkina, 2016). In the atmosphere, biogenic hydrocarbons, such as isoprene, might contribute to DCAs production, and this may involve the metabolism of hydrocarbon gases that contribute to

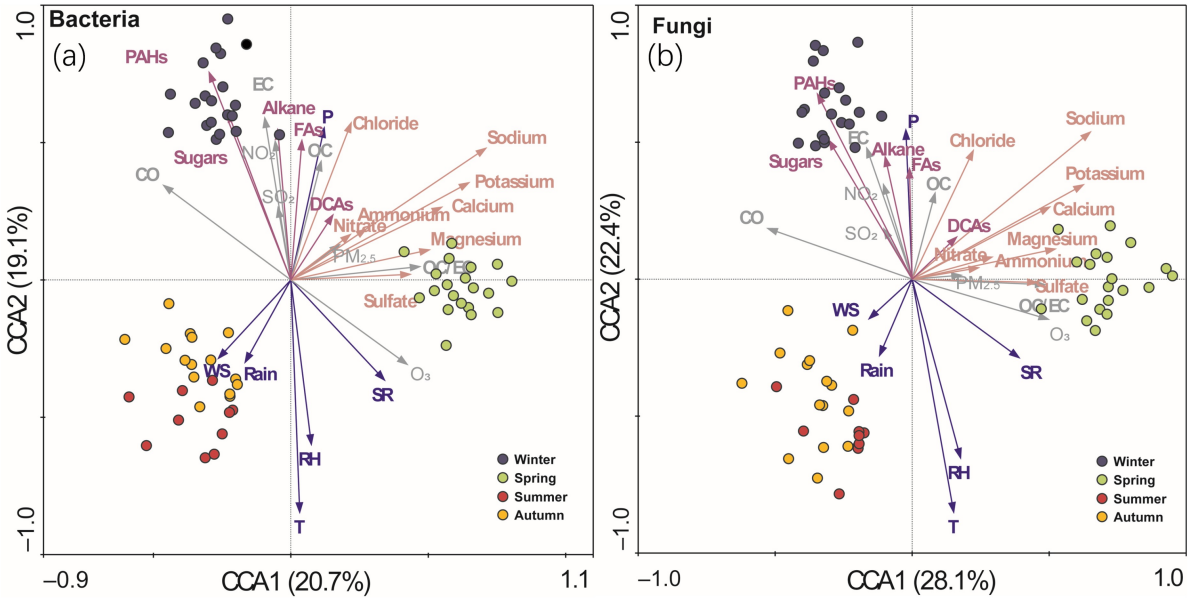


Fig. 2 Canonical correlation analysis (CCA) results showing the distribution of environmental factors and $PM_{2.5}$ microbial communities at the genus level. (a) Bacterial community, (b) fungal community (DCAs, dicarboxylic acids; FAs, fatty acids; PAHs, poly aromatic hydrocarbonsp; WS, wind speed; T, temperature; RH, relative humidity; SR, solar radiation).

DCAs formation by specific microbes (Shennan, 2006; Kawamura and Bikkina, 2016). Although the α-diversity indices exhibited a negative correlation with pollutants ($PM_{2.5}$, NO_2, CO, SO_2, OC, EC), three dominant bacteria (*Pseudarthrobacter*, *Janthinobacterium*, *Pseudomonas*) exhibited a positive correlation with pollutants ($p < 0.05$). Since the winds blowing from the north of Seoul come from land where people live rather than from the sea, the impact of these winds on Seoul's atmosphere in winter is more likely to be influenced by human activities than by marine factors. Additionally, the CCA analysis highlighted the significant influence of PAHs and pollutants (EC, NO_2), indicating a more pronounced anthropogenic impact than natural influences on the winter $PM_{2.5}$ bacterial community.

In spring, pollutants ($PM_{2.5}$, O_3) and ions exhibited a close relationship with the structure of the $PM_{2.5}$ bacterial community (Fig. 2(a)). The correlation between the α-diversity indices of the $PM_{2.5}$ bacterial community and environmental factors (pollutants, ions) differed in spring and winter (Figs. 3(a) and 3(b)), with a comparatively weaker correlation observed in spring compared to winter. The dominant genera in spring, particularly *Atrhrospira* and *Mycolicibacterium*, displayed contrasting correlations with most environmental factors, particularly with Na^+, where *Atrhrospira* showed a positive correlation, and *Mycolicibacterium* showed a negative correlation ($p <$ 0.05) (Fig. S2b). *Atrhrospira* is known as an alkaliphilic cyanobacterium primarily found in soda lakes characterized by high pH, Na^+ concentration, solar light intensity, and temperature (Berry et al., 2003). Consistent with these characteristics, this study observed a positive correlation between *Arthrospira* and Na^+, temperature, and solar radiation. Generally, Cyanobacteria exhibit Na^+ extrusion through an ATP-dependent primary sodium pump (Berry et al., 2003). *Mycolicibacterium* displayed a positive correlation with NO_3^-, an inorganic nitrogen source predominantly utilized by microbes (Lundberg et al., 2004). *Mycolicibacterium* produces assimilatory nitrate reductase, which is involved in the reduction of NO_3^- to NO_2^- (Tan et al., 2020). Thus, this study confirmed the close association between the spring bacterial community structure and dominant species with ions. Ions, such as Na^+, K^+, Mg^{2+}, Ca^{2+}, primarily originate from natural sources, such as sea salts or forest-derived mineral dust, whereas SO_4^{2-} and NO_3^- originate largely from anthropogenic sources (Warneck, 2000). The $PM_{2.5}$ bacterial community structure in spring was significantly influenced by pollutants ($PM_{2.5}$, O_3) and ions originating from both natural sources (Na^+, K^+, Mg^{2+}, Ca^{2+}) and anthropogenic sources (SO_4^{2-}, NO_3^-, NH_4^+) (Figs. 2(a) and 5(b)). Hence, the influential environmental factors shaping the $PM_{2.5}$ bacterial community structure in spring were primarily attributed to anthropogenic impacts, with the simultaneous co-

existence of natural impacts.

During summer and autumn, the $PM_{2.5}$ bacterial community structure displayed close associations with meteorological factors, such as precipitation and wind speed (Fig. 2(a)). The examination of the correlation between dominant bacteria and environmental factors during these seasons revealed the strong positive relation between *Rhodococcus*, *Pelmonas*, and *Acinetobacter* and temperature in summer ($P < 0.01$) (Fig. S2(c)). Particularly, *Pelmonas* displayed a negative correlation with temperature during autumn ($p > 0.05$), whereas *Acinetobacter* showed a significant positive relationship during both summer and autumn ($p < 0.01$) (Fig. S2(d)). In contrast, *Rothia* exhibited a significant positive correlation with temperature only during autumn ($p < 0.01$). Hence, this study confirmed the seasonal variation in the correlation between the same bacteria and environmental factors. Given the temperature range of 21–31 °C in summer and 5–15 °C in autumn, *Pelmonas* seemed to thrive at temperatures below 15 °C but comparatively less so at 21 °C or higher. In contrast, *Rothia* appeared to thrive more in the temperature range of 21–31 °C. Additionally, *Rothia aeria* has been associated with Infective Endocarditis in Korea, indicating its pathogenic potential (Kim et al., 2014). Given its activity within the human body temperature range, we presumed it exhibited a positive relationship with temperatures above 21 °C. As each microorganism has an optimal growth temperature, temperature is considered the most critical meteorological factor (Zhai et al., 2018; Šantl-Temkiv et al., 2022). However, as temperature not only directly affects microorganisms but also influences atmospheric chemical reactions, the optimal temperature for microbial diversity in the atmosphere remains unclear (Zhai et al., 2018; Šantl-Temkiv et al., 2022). In this study, the α-diversity indices of $PM_{2.5}$ bacterial communities during summer and autumn were strongly influenced by wind speed and precipitation, whereas dominant bacteria were significantly affected by temperature. Consequently, during summer and autumn, which are meteorologically sensitive seasons, bacterial communities appeared to be more influenced by natural impacts than anthropogenic impacts.

3.3 Seasonal communities of fungi in response to environmental factors

Similar to the bacterial community, the $PM_{2.5}$ fungal community in winter exhibited close associations with atmospheric organic compounds, such as PAHs and Alkanes, along with pollutants, such as NO_2 (Fig. 2(b)). In winter, the fungal α-diversity index showed a non-significant Spearman correlation with PAHs, and the top three dominant genera also displayed no significant Spearman correlation with PAHs. (Figs. 3(a) and S2(a)). However, compared to Spearman correlation, the CCA analysis, which examined the multivariate relationships between groups, depicted linear relationships between individual variables, displayed a notably high correlation with PAHs (Fig. 2(b)). The CCA analysis is a method for measuring the relationships between multidimensional variables, enabling complex group correlations, compared to the simple linear relationships between single variables depicted by Spearman correlation (Borga, 2001; Härdle and Simar, 2015). Therefore, despite the lower Spearman correlation with α-diversity indices, it can be inferred that PAHs exerted a significant influence on the fungal community group comprising over 1%. It is known that PAHs, which are recognized as major atmospheric organic compounds, are harmful to the environment owing to their carcinogenic, mutagenic, toxic, and genotoxic properties (Mallick et al., 2011). They are mainly produced from the incomplete combustion of fossil fuels and organic matter (Li et al., 2019b), and exhibit toxicity toward microorganisms, potentially disrupting their growth (Li et al., 2019b; Zhou et al., 2022). However, despite this inhibitory effect on the growth of microorganisms, certain microorganisms can utilize PAHs in their metabolic activities (Cerniglia, 1997; Zhou et al., 2022). Through co-metabolism or the formation of enzyme-substrate complexes, microorganisms can either utilize PAHs as a carbon source or enzymatically degrade them (Liu et al., 2017). Fungi, through bioremediation processes, can either completely degrade PAHs or transform them into less hazardous compounds, indicating their ecological significance owing to their ability to break down these compounds (Cerniglia, 1997). Although the Spearman correlation coefficient between *Alternaria* and PAHs was low in this study, it exhibited a highly significant positive correlation ($p < 0.001$) (Fig. S2a), aligning with previous research reporting its ability to efficiently remove PAHs (Álvarez-Barragán et al., 2021). In winter, the fungal community displayed a close association with pollutants, particularly showing a strong correlation with NO_2 and EC (Fig. 2(b)). This is consistent with the findings of previous studies that reported NO_2 as a significant atmospheric pollutant affecting the structure of fungal communities within particulate matter (PM) (Ho et al., 2005; Alghamdi et al., 2014; Pan et al., 2020). Particularly, during winter, the microbial impact of NO_2 can be substantial owing to increased fuel combustion and reduced atmospheric convection. Additionally, OC is composed

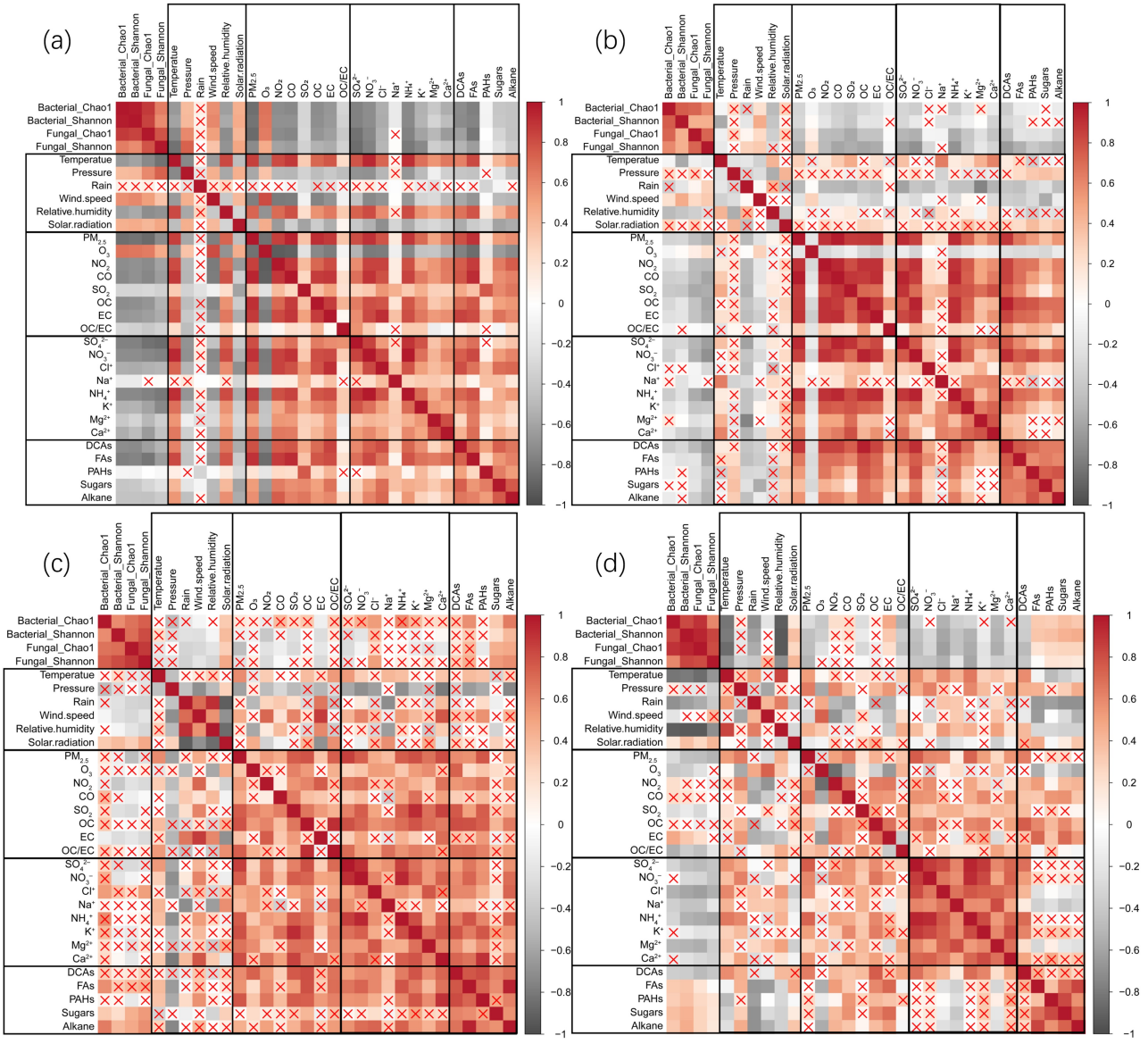


Fig. 3 Seasonal Spearman correlation analysis between microbial diversity indices and environmental factors in: (a) winter, (b) spring, (c) summer, and (d) autumn. DCAs, dicarboxylic acids; FAs, fatty acids; PAHs, poly aromatic hydrocarbons; Red '×' mark denotes statistical insignificance at a significance level of 0.05.

of particulate matter derived not only from fossil fuel but also from biological activities, including biogenic sources such as plant debris and microbial processes, which contribute to biogenic secondary OC (SOC) (Cao et al., 2004; Han et al., 2009; Meng et al., 2020). In contrast, EC comprises graphite-like particles produced from the incomplete combustion of fossil fuels or biomass (Cao et al., 2004; Han et al., 2009; Meng et al., 2020). It possesses high solar radiation absorption capabilities and adsorption sites, which enhance catalytic processes (Cao et al., 2004; Han et al., 2009). These traits enable its participation in chemical reactions with gaseous pollutants, such as NO_2 and SO_2, contributing to global warming (Cao et al., 2004). Therefore, the fungal community structure within winter $PM_{2.5}$, influenced significantly by PAHs, EC, and NO_2, reflects a substantial anthropogenic impact.

The fungal community in spring was closely associated with OC/EC, pollutants ($PM_{2.5}$, O_3) and ions (NO_3^-, SO_4^{2-}, Mg^{2+}) (Fig. 2(b)). The OC/EC ratio can provide insights into the sources and contributions of organic carbon, helping to differentiate between anthropogenic and biogenic origins of OC (Wang et al.,, 2019; Zeng and Wang, 2011). A higher OC/EC

ratio may indicate a more significant influence from biogenic sources particularly during periods of heightened biological activity (Wang et al., 2019; Zeng and Wang, 2011). In spring, increased solar radiation enhances photochemical reactions in the atmosphere, promoting the oxidation of VOCs and increasing the formation of SOC (Huang et al., 2023). This increase in SOC formation can elevate OC concentrations, resulting in a higher OC/EC ratio, which may influence the microbial community in spring (Huang et al., 2020). Additionally, rising temperatures during spring can enhance microbial decomposition activities, contributing to OC production (Shigyo et al., 2019). Furthermore, increased plant activity in spring may affect the microbial community and the OC/EC ratio, as the growth of plants leads to greater root exudation, which stimulates soil microbial activity (Shigyo et al., 2019). The increase in biogenic VOC emissions from plants further promotes SOC formation (Huang et al., 2023).

Pollutants, excluding ozone, and ions, excluding sodium, showed negative correlations with fungal richness and diversity indices in spring (Fig. 3(b)). These findings indicate that anthropogenic activities heavily influenced the fungal community structure in spring. NO_3^- and SO_4^{2-} are the primary components of secondary inorganic aerosols, a major component of atmospheric particles (Lin and Cheng, 2007; Hung and Hoffmann, 2015). In the atmosphere, NO_3^- typically exists as ammonium nitrate (NH_4NO_3), and is formed through the gas reaction of NO_2 to produce HNO_3, which reacts with NH_3 to form NO_3^- particulates, linking NO_2 and NO_3^- (Lin and Cheng, 2007). Additionally, SO_4^{2-} is produced by the oxidation of SO_2 gas (Hung and Hoffmann, 2015). The correlation analysis results in Fig. 3(b) indicate the positive relationships between NO_3^- and SO_4^{2-} and $PM_{2.5}$, NO_2, and SO_2, indicating their association with air pollutants. However, O_3 exhibited a negative relationship with NO_2 and a positive correlation with the α-diversity indices of the fungal community (Fig. 3(b)). This is contrary to the known toxicity of O_3 to microbes, as it is known to hinder microbial growth (Li et al., 2019a). This discrepancy might be linked to NO_x, as NO reacts with O_3 to form NO_2, potentially reducing O_3 concentration owing to urban NO_x emissions (Alghamdi et al., 2014). Therefore, rather than a direct positive impact of O_3 on microbial community diversity, these results suggest a complex interplay of atmospheric components, which resulted in such correlations. The spring samples demonstrated a significant relationship with atmospheric pollutants, indicating the substantial impact of air pollutants on the fungal community, suggesting a significant anthropogenic influence.

In summer and autumn, the fungal community was significantly influenced by meteorological factors, particularly wind speed and precipitation (Fig. 2(b)). Fungal α-diversity indices exhibited a significant negative correlation with both wind speed and precipitation in summer, whereas in autumn, a substantial negative correlation was predominantly observed with precipitation ($p < 0.05$) (Figs. 3(c) and 3(d)). The negative correlation with the α-diversity can be attributed to the increased microbial washout due to rainfall (Wiśniewska et al., 2022). Furthermore, rainfall-induced alterations in the ion concentrations (Ca^{2+}, Mg^{2+}, K^+) and pH, along with changes in the concentration of organic carbon, were speculated to modify microbial habitats, potentially influencing community structures (Peter et al., 2014). Three out of the top four dominant species remained consistent in summer and autumn (Figs. S2(c) and 2(d)). *Cutaneotrichosporon* exhibited a positive relationship with precipitation during both seasons, whereas *Alternaria* showed a negative correlation. In a total suspended particles (TSP) study conducted in Tianjin, China, during the summer of 2018, *Cutaneotrichosporon* was identified as a dominant species (Niu et al., 2021), with higher occurrences in rainy samples compared to non-rainy samples. In Xi'an, however, during the winter transition from 2018 to 2019, *Cutaneotrichosporon* emerged as the dominant species. Despite the different seasons, the discovery of *Cutaneotrichosporon* during similar periods in the North-east Asia region was notable. *Alternaria* is recognized as a dry-air spore, thriving in warm and low humidity conditions (Peternel et al., 2004; Stępalska and Wołek, 2005). Hence, its dominance and negative association with precipitation during summer and autumn in this study can be considered consistent with previous findings. Investigations on bioaerosols in Granada also reported a significant negative correlation between *Alternaria* and precipitation (Sabariego et al., 2000). The $PM_{2.5}$ fungal community during summer and autumn appeared heavily influenced by weather conditions, suggesting a more substantial natural impact compared to anthropogenic influence.

3.4 Seasonal microbial function dynamics

Understanding the functionality of atmospheric microbes enabled predictions of how these microbes utilize atmospheric components and the potential impact of microbial metabolic activities on the atmospheric environment. Therefore, in this study,

functional pathways of $PM_{2.5}$ bacterial community genes were predicted using the KEGG database (Fig. 4). Within KEGG Level 3, metabolism pathways accounted for over 70%, followed by environmental information processing with approximately 10% and cellular processes with approximately 6.5%. These findings are consistent with results obtained from a study conducted in Xi'an and Linfen, during a nearly identical period (Wang et al., 2021). In this study, metabolism pathways constituted the highest proportion within $PM_{2.5}$ bacterial communities during spring, whereas prior study observed the highest proportion during autumn (Wang et al., 2021). However, considering that both spring and autumn provide suitable conditions for microbial habitation, such as favorable temperatures in both seasons, they share similarities. Our study indicated that the richness and diversity were greater in spring compared to autumn, suggesting that spring might offer a more conducive environment for microbial activities involving various substances. Examining the Top 20 KEGG Level 2 pathways shown in Fig. 4(b) indicates that during spring, the $PM_{2.5}$ bacterial community during spring, significant proportions were occupied by pathways, such as global and overview maps, carbohydrate metabolism, amino acid metabolism, lipid metabolism, and xenobiotics biodegradation and metabolism. Among the dominant spring bacterial genera mentioned previously, *Mycolicibacterium*, *Acinetobacter*, and *Loriellopsis* exhibited notable positive correlations with these pathways (Fig. S4b). Particularly, *Mycolicibacterium* and *Acinetobacter* had high correlation with amino acids metabolism. *Mycolicibacterium*, a non-pathogenic organism, engages in tryptophan biosynthesis, a process not conducted by mammals (Chen et al., 2020; Czubat et al., 2020). *Acinetobacter*, when provided with phenylalanine as a single carbon source, catalyzes the reaction of phenylacetic acid to 2-hydroxyphenylacetic acid in amino acid metabolism (Keil et al., 1983). Staphylococcus aureus, a commensal bacterium, has been known to act as a pathogen in humans, leading to outbreaks in hospital or community settings (Shinefield and Ruff 2009).

The functional analysis of $PM_{2.5}$ fungal community genes was conducted using the FUNGuild database, analyzing fungal functional groups based on the concept of ecological guilds (Nguyen et al., 2016) (Fig. 5). When classified based on the trophic modes, Saprotroph was observed as the predominant fungal group throughout all seasons, with minimal variation. The most diverse functional distribution (with 14 modules) was observed in spring. In both winter and spring, the percentage occupied by a single function was lower, suggesting a more even distribution of the functions collectively. This is consistent with the higher α-diversity values observed during winter and spring. However, considering the trophic mode of the dominant fungi, the spring-dominant fungi, including *Calvatia, Scorias*, *Crustoderma*, *Ctenomyces*, and *Radulomyces*,

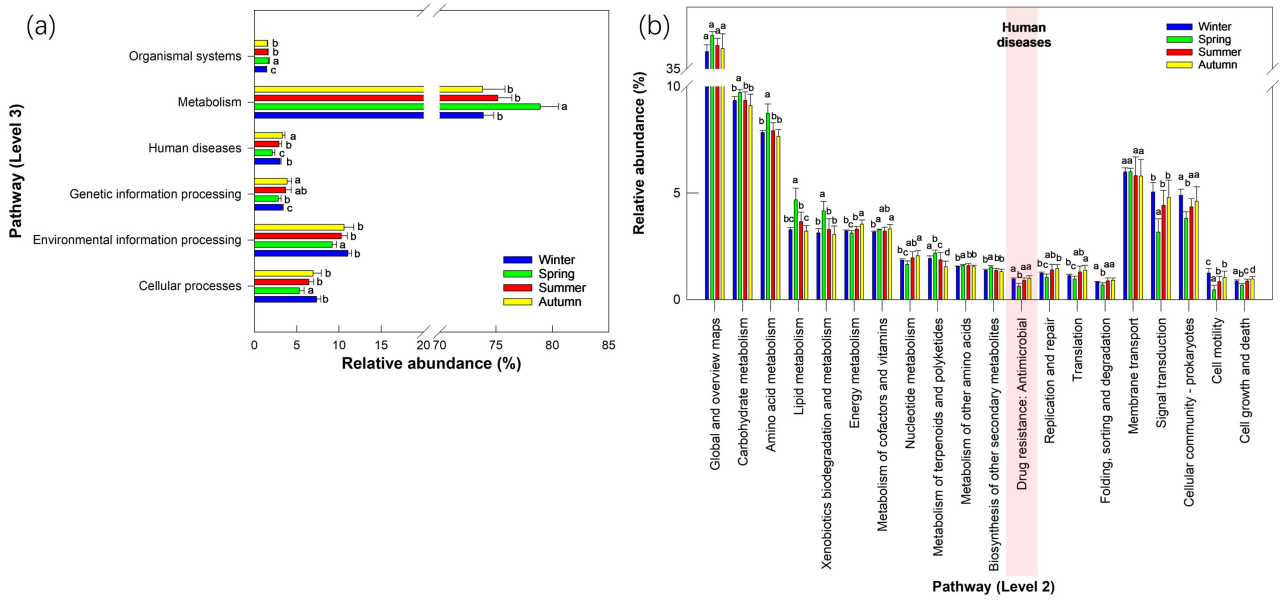


Fig. 4 Seasonal KEGG pathway analysis for $PM_{2.5}$ bacterial community. (a) Pathways (Level 3) based on the KEGG database, (b) Top20 pathways (Level 2) based on the KEGG database ($p < 0.05$).

were all identified as saprotrophs (Table S3). Saprotrophic fungi obtain nutrients through extracellular digestion, playing an ecologically significant role by decomposing dead organic matter, such as wood or plant debris (Asiegbu and Kovalchuk, 2021). It is speculated that the minor fungal communities within spring $PM_{2.5}$ use various trophic modes. Examining the Guilds based on FUNGuild database revealed that $PM_{2.5}$ fungi in Seoul in 2018 displayed a higher proportion of plant pathogens (Fig. 5), and the dominant fungi groups in all seasons except spring were largely comprised of plant pathogens and endophytes (Table S3). Endophytes refer to microbes residing within plants without causing explicit diseases (Asiegbu and Kovalchuk, 2021). This strong association of $PM_{2.5}$ fungal communities with plants aligns with reports identifying soil and plants as significant sources of bioaerosols (Qi et al., 2020; Xie et al., 2021). Particularly, fungal spores are reported to be heavily influenced by plant growth and weather conditions (Qi et al., 2020; Xie et al., 2021). Although microbial thriving and growth may be limited in low temperatures, such as winter, long-term survival is feasible (Qi et al., 2020). Moreover, fungal

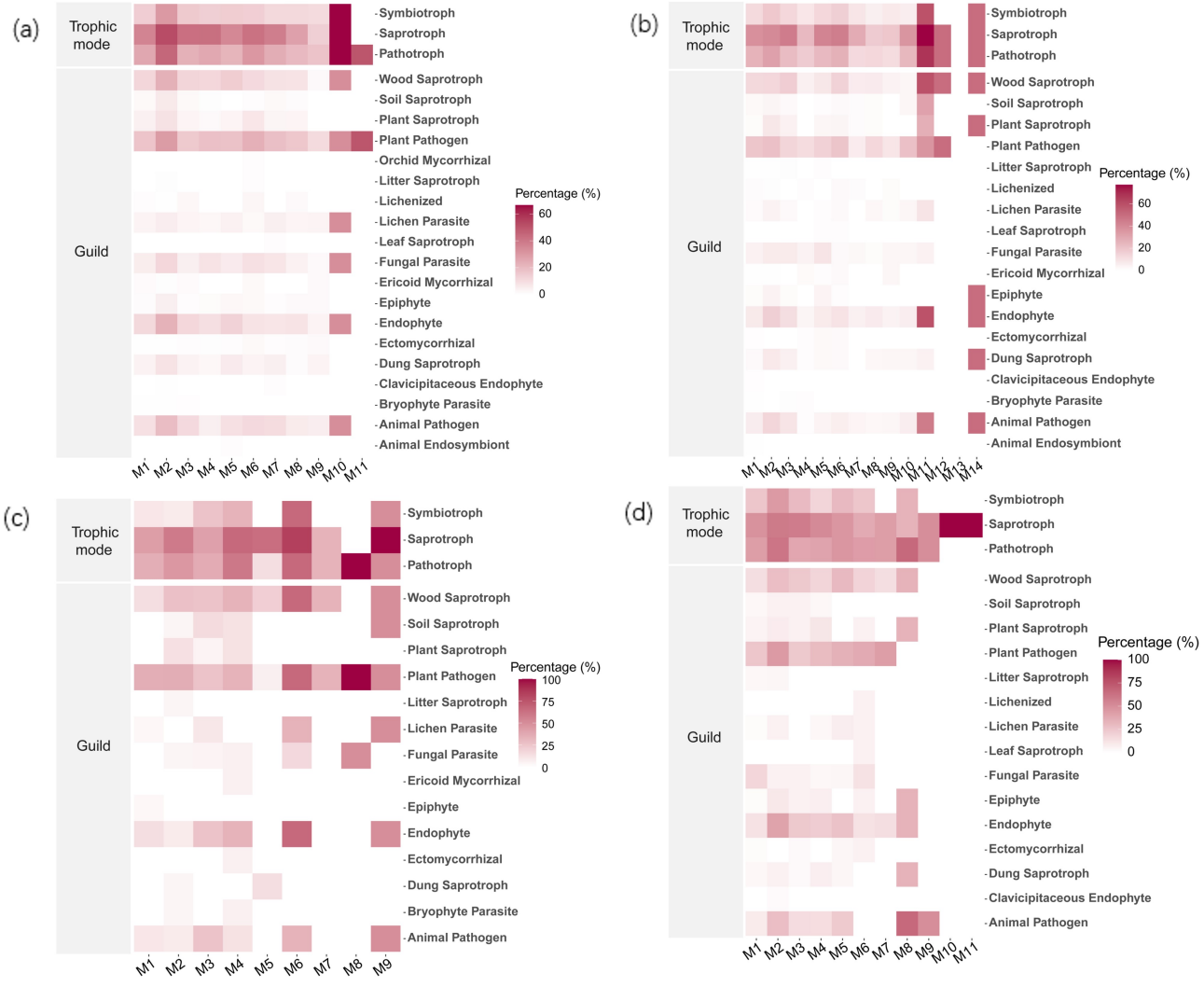


Fig. 5 Seasonal heatmap demonstrating functional redundancy of airborne fungal communities in (a) winter, (b) spring, (c) summer, and (d) autumn. The *X*-axis indicates modules (M) which represent groups of interacting entities within a functional network of fungi and share similar functions or ecological roles. (Module: a set of functionally related genes or pathways that collectively perform a specific biological role or function within an ecosystem or biological system. In the context of functional redundancy analysis, modules help to assess the resilience and stability of microbial communities by indicating how multiple genes or pathways can compensate for each other's loss. The greater the number of modules, the more functional redundancy is provided, enhancing adaptability to environmental changes and overall health).

communities originating from soil, plants, or oceans, and transported into the atmosphere are more likely to adhere to particles, which could enhance their survival (Xie et al., 2021; Kang and Cho, 2022). Therefore, it is plausible that more diverse fungi survived during periods of high $PM_{2.5}$ concentration in winter and spring.

3.5 Limitation

This study aims to analyze the seasonal variation of $PM_{2.5}$ microbial communities. In Fig. 2, the explained variance ratio of CCA1 and CCA2 is approximately 20%, which is considered low; however, microbial communities exhibited distinct seasonal differences, and each environmental factor was categorized into varying positions during the analysis. Previous studies utilizing constrained ordination methods, such as CCA and RDA, have similarly reported relatively low variance in the analysis of atmospheric microbes and environmental factors (Lee et al., 2017; Li et al., 2018; Xue et al., 2023). Given this context, the variation observed in this study has been interpreted as indicative of seasonal differences related to $PM_{2.5}$ microbes. It is important to note that the complexity of atmospheric conditions and the various factors influencing the proliferation of $PM_{2.5}$ microbes have been insufficiently addressed in existing literature. Therefore, this study conducted a correlation analysis across seasons in Fig. 3, emphasizing the observed differences to aid in the readers' understanding. While conclusions were drawn by categorizing the findings into natural and anthropogenic factors, it should be recognized that the sources of the analyzed constituents do not strictly adhere to this binary classification. The primary objective of this research was to analyze overall seasonal trends, leading to straightforward conclusions. However, it is essential to consider that meteorological elements categorized as natural factors can also significantly influence the emissions of air pollutants identified as anthropogenic factors. Thus, environmental factors do not exert merely primary effects on microbial communities; rather, they can have secondary and tertiary complex influences as well. This study has not fully explored such complexities, indicating a need for further research.

Future studies should investigate these multifaceted interactions by incorporating a broader range of environmental variables and exploring their collective impact on microbial diversity within the atmospheric context. Moreover, longitudinal studies examining these relationships could provide deeper insights into how seasonal changes and varying environmental conditions affect the dynamics of $PM_{2.5}$ microbial communities over the years.

4 Conclusions

This study analyzed the microbial dominance and diversity indices of $PM_{2.5}$ samples collected in Seoul in 2018 to identify seasonal variations in airborne bacterial and fungal communities. Bacterial Chao1 peaked in spring, whereas the bacterial Shannon index peaked in winter, with both indices being lowest in summer. Similarly, both Chao1 and Shannon indices for the fungal communities were higher in winter and spring. The seasonal environmental factors influencing $PM_{2.5}$ bacterial communities indicated a significant anthropogenic impact in winter owing to the presence of pollutants and atmospheric organic compounds. In spring, $PM_{2.5}$ and ions (Na^+, NO_3^-) experienced a complex mix of anthropogenic and natural impacts. Summer and autumn showcased meteorological factors, such as precipitation and wind speed, suggesting a predominant natural impact. For fungal communities, considerable influence from atmospheric organic compounds (PAHs, Alkanes), as well as pollutants (EC, NO_2) was observed in winter. In contrast, spring exhibited a significant influence from $PM_{2.5}$, NO_3^-, and SO_4^{2-}, indicating a strong anthropogenic impact in both seasons. Summer and autumn exhibited meteorological factors, particularly wind speed and precipitation, highlighting a larger natural impact. Predicting the seasonal function of microbial genes revealed that metabolism pathways dominated the bacterial community, with spring exhibiting the highest proportion, indicating a thriving environment for microbes during spring. A prevalence of Saprotrophs was observed in the fungal community in all seasons, with spring displaying 14 modules, indicating diverse functional distribution. This significance of this study resides in the investigation of the atmospheric microbial communities in regions with distinct seasonal climate variations, such as Seoul, and providing valuable insights into the behavior of atmospheric bacterial and fungal communities in response to various environmental factors, thus contributing essential data to the atmospheric ecosystem.

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

Acknowledgements This study was supported by the National research Foundation of the Republic Korea (NRF) grant funded by the Republic of

Korea government, the Ministry of Science and ICT (MSIT) (No. 2022R1A2C2006615 and RS2023-00217228). This research was supported by the Particulate Matter Management Specialized Graduate Program through the Republic Korea Environmental Industry & Technology Institute (KEITI) funded by the Ministry of Environment (MOE).

Electronic Supplementary Material Supplementary material is available in the online version of this article at https://doi.org/10.1007/s11783-025-1995-6 and is accessible for authorized users.

References

Aira M J, Rodríguez-Rajo F J, Fernández-González M, Seijo C, Belén E R, Abreu I, Gutiérrez-Bustillo M, Pérez-Sánchez E, Oliveira M, Recio M, et al. (2013). Spatial and temporal distribution of Alternaria spores in the Iberian Peninsula atmosphere, and meteorological. International Journal of Biometeorology, 57: 265–274

Alghamdi M A, Shamy M, Redal M A, Khoder M, Awad A H, Elserougy S (2014). Microorganisms associated particulate matter: a preliminary study. Science of the Total Environment, 479–480(1): 109–116

Allabakash S, Lim S, Chong K S, Ymada T J (2022). Particulate matter concentrations over South Korea: impact of meteorology and other pollutants. Remote Sens, 14(4849): 1–26

Álvarez-Barragán J, Cravo-Laureau C, Wick L Y, Duran R (2021). Fungi in PAH-contaminated marine sediments: cultivable diversity and tolerance capacity towards PAH. Marine Pollution Bulletin, 164(112082): 1–12

Asiegbu F O, Kovalchuk A (2021) Chapter 1 — An introduction to forest biome and associated microorganism. Forest Microbiology. San Diego: Academic Press

Basualdo C V (2011). Choosing the best non-parametric richness estimator for benthic macroinvertebrates databases. Revista de la Sociedad Entomológica Argentina, 70(1−2): 27–38

Bellemain E, Carlsen T, Brochmann C, Coissac E, Taberlet P, Kauserud H (2010). ITS as an environmental DNA barcode for fungi: an *in silico* approach reveals potential PCR biases. BMC Microbiology, 10(1): 1–9

Berry S, Bolychevtseva Y V, Rögner M, Karapetyan N V (2003). Photosynthetic and respiratory electron transport in the alkaliphilic cyanobacterium *Arthrospira* (Spirulina) platensis. Photosynthesis Research, 78(1): 67–76

Boreson J, Dillner A M, Peccia J (2004). Correlating bioaerosol load with $PM_{2.5}$ and PM_{10cf} concentrations: a comparison between natural desert and urban-fringe aerosols. Atmospheric Environment, 38(35): 6029–6041

Borga M (2001). Canonical correlation: a tutorial. On Line Tutorial, 4(5): 1–12

Bowers RM, Clements N, Emerson JB, Wiedinmyer C, Hannigan MP, Fierer N (2013) Seasonal variability in bacterial and fungal diversity of the near-surface atmosphere. Environmental Science & Technology, 47(21): 12097–12106

Bu X, Xie Z, Liu J, Wei L, Wang X, Chen M, Ren H (2021). Global $PM_{2.5}$-attributable health burden from 1990 to 2017: estimates from the Global Burden of disease study 2017. Environmental Research, 197(111123): 1–9

Cao J J, Lee S C, Ho K F, Zou S C, Fung K, Li Y, Watson J G, Chow J C (2004). Spatial and seasonal variations of atmospheric organic carbon and elemental carbon in Pearl River Delta Region, China. Atmospheric Environment, 38(27): 4447–4456

Cao M, Chen M, Ge P, Cui Y, Li W (2022). Seasonal variation, source contribution, and impact factors of biogenic organic aerosols in $PM_{2.5}$ in Nanjing, China. Science of the Total Environment, 843: 156875

Cerniglia C E (1997). Fungal metabolism of polycyclic aromatic hydrocarbons: past, present and future applications in bioremediation. Journal of Industrial Microbiology & Biotechnology, 19(5−6): 324–333

Chen Y, Jia H, Liu R, Che S, Zhang Q, Bartlam M (2020). Structure of subunit I of the anthranilate synthase complex of *Mycolicibacterium smegmatis*. Biochemical and Biophysical Research Communications, 527(1): 37–41

Crouse D L, Peters P A, Hystad P, Brook J R, van Donkelaar A, Martin R V, Villeneuve P J, Jerrett M, Goldberg M S, Pope C A III, et al., (2015). Ambient $PM_{2.5}$, O_3, and NO_2 exposures and associations with mortality over 16 years of follow-up in the Canadian census health and environment cohort (CanCHEC). Environmental Health Perspectives, 123(11): 1180–1186

Czubat B, Minias A, Brzostek A, Żaczek A, Struś K, Zakrzewska-Czerwińska J, Dziadek J (2020). Functional disassociation between the protein domains of MSMEG_4305 of *Mycolicibacterium smegmatis* (*Mycobacterium smegmatis*) *in vivo*. Frontiers in Microbiology, 11(2008): 1–15

Dahl J L, Gatlin W III, Tran P M, Sheik C S (2021). *Mycolicibacterium nivoides* sp. Nov isolated from a peat bog. International Journal of Systematic and Evolutionary Microbiology, 71(3): 1–6

Di Q, Wang Y, Zanobetti A, Wang Y, Koutrakis P, Choirat C, Dominici F, Schwartz J D (2017). air pollution and mortality in the medicare population. New England Journal of Medicine, 376(26): 2513–2522

Dong S, Chen J, Wang S, Wu Y, Hou H, Li M, Yan C (2015). Draft genome sequence of cyanobacteria *Arthrospira* sp. TJSD091 isolated from seaside wetland. Marine Genomics, 24: 197–198

Du P, Du R, Ren W, Lu Z, Fu P (2018a). Seasonal variation characteristic of inhalable microbial communities in $PM_{2.5}$ in Beijing city, China. Science of the Total Environment, 610–611: 308–315

Du P, Du R, Ren W, Lu Z, Zhang Y, Fu P (2018b). Variations of bacteria and fungi in $PM_{2.5}$ in Beijing, China. Atmospheric Environment, 172: 55–64

Fan X Y, Gao J F, Pan K L, Li D C, Dai H H, Li X (2019). More obvious air pollution impacts on variations in bacteria than fungi and their co-occurrences with ammonia-oxidizing

microorganisms in $PM_{2.5}$. Environmental Pollution, 251: 668–680

Fröhlich-Nowoisky J, Burrows S M, Xie Z, Engling G, Solomon P A, Fraser M P, Mayol-Bracero O L, Artaxo P, Begerow D, Conrad R, et al. (2012). Biogeography in the air: fungal diversity over land and oceans. Biogeosciences, 9: 1125–1136

Ghosal D, Ghosh S, Dutta T K, Ahn Y (2016). Corrigendum: current state of knowledge in microbial degradation of polycyclic aromatic hydrocarbons (PAHs): a review. Frontiers in Microbiology, 7(1369): 1–27

Caporaso J G, Kuczynski J, Stombaugh J, Bittinger K, Bushman F D, Costello E K, Fierer N, Peña A G, Goodrich J K, Gordon J I, et al. (2010). QIIME allows analysis of high-throughput community sequencing data. Nature Methods, 7(5): 335–336

Han S, Kondo Y, Oshima N, Takegawa N, Miyazaki Y, Hu M, Lin P, Deng Z, Zhao Y, Sugimoto N, Wu Y (2009). Temporal variations of elemental carbon in Beijing. Journal of Geophysical Research, 114(D23202): 1–16

Härdle WK, Simar L (2015). Applied Multivariate Statistical Analysis. Berlin: Springer

Ho H M, Rao C Y, Hsu H H, Chiu Y H, Liu C M, Chao H J (2005). Characteristics and determinants of ambient fungal spores in Hualien, Taiwan, China. Atmospheric Environment, 39(32): 5839–5850

Huang H, Yin X, Tang Y, Zou C, Li J, Yu C, Zhu F (2023). Seasonal distribution and source apportionment of chemical compositions in $PM_{2.5}$ in Nanchang, Inland area of East China. Atmosphere 14(1172): 1–19

Huang Y, Zhang L, Li T, Chen Y Yang F (2020). Seasonal variation of carbonaceous species of $PM_{2.5}$ in a small city in Sichuan Basin, China. Atmosphere, 11(1286): 1–15

Hugerth L W, Wefer H A, Lundin S, Jakobsson H E, Lindberg M, Rodin S, Engstrand L, Andersson A F (2014). DegePrime, a program for degenerate primer design for broad-taxonomic-range PCR in microbial ecology studies. Applied and Environmental Microbiology, 80(16): 5116–5123

Hung H M, Hoffmann M R (2015). Oxidation of gas-phase SO_2 on the surfaces of acidic microdroplets: implications for sulfate and sulfate radical anion formation in the atmospheric liquid phase. Environmental Science & Technology, 49(23): 13768–13776

Jung M I, Son S W, Kim H C, Kim S W, Park R J, Chen D (2019). Contrasting synoptic weather patterns between non-dust high particulate matter events and Asian dust events in Seoul, South Korea. Atmospheric Environment, 214(116864): 1–10

Kang M K (2021) Source apportionment of organic carbons in PM2.5 using the positive matrix factorization model: characterization of secondary organic aerosols at Seoul, Korea using SOA tracers. Thesis for the Master Degree. Seoul: Ewha Womans University

Kang S, Cho K S (2022). Microbial metagenome of airborne particulate matter: methodology, characteristics, and influencing parameters. Microbiology and Biotechnology Letters, 50(2): 165–192

Kang S, Cho K S (2023). Optimization of DNA extraction and PCR conditions for fungal metagenome analysis of atmospheric particulate matter. Microbiology and Biotechnology Letters, 51(1): 99–108

Kawamura K, Bikkina S (2016). A review of dicarboxylic acids and related compounds in atmospheric aerosols: molecular distributions, sources and transformation. Atmospheric Research, 170: 140–160

Keil H, Tittmann U, Lingens F (1983). Degradation of aromatic carboxylic acids by *Acinetobacter*. Systematic and Applied Microbiology, 4(3): 313–325

Kim I, Seo T (2023). *Pseudarthrobacter humi* sp. nov., an actinobacterium isolated from soil. International Journal of Systematic and Evolutionary Microbiology, 73(1)

Kim U J, Jeong E, Kim J E, Jang M O, Kang S J, Jang H C, Park K H, Jung S I, Shin J H (2014). *Rothia aeria* infective endocarditis: a first case in Korea and literature review. Annals of Laboratory Medicine, 34: 317–320

Kit I, Tan P, Foong C P, Tiang Tan H, Lim H, Zain N A A, Chie Tan Y, Choong Hoh C, Sudesh K (2020). Polyhydroxyalkanoate (PHA) synthase genes and PHA-associated gene clusters in *Pseudomonas* spp. and *Janthinobacterium* spp. isolated from Antarctica. Journal of Biotechnology, 313(10): 18–28

Lee J Y, Park E H, Lee S, Ko G, Honda Y, Hashizume M, Deng F, Yi S, Kim H (2017). Airborne bacterial communities in three East Asian cities of China, South Korea, and Japan. Scientific Reports, 7(5545): 1–8

Lee YY, Hong S, Cho KS (2019) Design and shelf stability assessment of bacterial agents for simultaneous removal of methane and odors. Journal of Environmental Science and Health, Part A, 54(9), 906–913

Lee U J, Kim M J, Kim E J, Lee D W, Lee S D (2024). Spatial distribution characteristics and analysis of $PM_{2.5}$ in South Korea: a geographically weighted regression analysis. Atmosphere, 15(69): 1–18

Li H, Shan Y, Huang Y, An Z, Xu G, Wei F, Zhang G, Wu W (2019a). Bacterial community specification in $PM_{2.5}$ in different seasons in Xinxiang, Central China. Aerosol and Air Quality Research, 19(6): 1355–1364

Li W, Yang J, Zhang D, Li B, Wang E, Yuan H (2018). Concentration and community of airborne bacteria in response to cyclical haze events during the fall and midwinter in Beijing, China. Frontiers in Microbiology, 9(1741): 1–12

Li X, Qu C, Bian Y, Gu C, Jiang X, Song Y (2019b). New insights into the responses of soil microorganisms to polycyclic aromatic hydrocarbon stress by combining enzyme activity and sequencing analysis with metabolomics. Environmental Pollution, 255(113312): 1–9

Lin Y C, Cheng M T (2007). Evaluation of formation rates of NO_2 to gaseous and particulate nitrate in the urban atmosphere. Atmospheric Environment, 41(9): 1903–1910

Liu C, Cui Y, Li X, Yao M (2021). microeco: an R package for data mining in microbial community ecology. FEMS Microbiology

Ecology, 97(255): 1–9

Liu SH, Zeng GM, Niu QY, Liu Y, Zhou L, Jiang LH, Tan X, Xu P, Zhang C, Cheng M (2017). Bioremediation mechanisms of combined pollution of PAHs and heavy metals by bacteria and fungi: a mini review. Bioresource Technology, 224: 25–33

Lundberg J O, Weitzberg E, Cole J A, Benjamin N (2004). Nitrate, bacteria and human health. Nature Reviews Microbiology, 2(681): 593–602

Magoč T, Salzberg S L (2011). FLASH: fast length adjustment of short reads to improve genome assemblies. Bioinformatics, 27(21): 2957–2963

Mallick S, Chakraborty J, Dutta T K (2011). Role of oxygenases in guiding diverse metabolic pathways in the bacterial degradation of low-molecular-weight polycyclic aromatic hydrocarbons: a review. Critical Reviews in Microbiology, 37(1): 64–90

Meng J, Liu X, Hou Z, Yi Y, Yan L, Li Z, Cao J, Li J, Wang G (2020). Molecular characteristics and stable carbon isotope compositions of dicarboxylic acids and related compounds in the urban atmosphere of the North China Plain: implications for aqueous phase formation of SOA during the haze periods. Science of the Total Environment, 705: 13526

Misztak A E, Waleron M, Furmaniak M, Waleron M M, Bazhenova O, Daroch M, Waleron K F (2021). Comparative genomics and physiological investigation of a new *Arthrospira/Limnospira* strain O9.13F isolated from an alkaline, winter freezing, Siberian Lake. Cells, 10(3411): 1–25

Mussagy A, Annadotter H H, Cronberg G (2006). An experimental study of toxin production in *Arthrospira fusiformis* (Cyanophyceae) isolated from African waters. Toxicon, 48(8): 1027–1034

Nguyen N H, Song Z, Bates S T, Branco S, Tedersoo L, Menke J, Schilling J S, Kennedy P G (2016). FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecology, 20: 241–248

Niu M, Hu W, Cheng B, Wu L, Ren L, Deng J, Shen F, Fu P (2021). Influence of rainfall on fungal aerobiota in the urban atmosphere over Tianjin, China: a case study. Atmospheric Environment: X, 12(100137): 1–13

Nouioui I, Sangal V, Cortés-Albayay C, Jando M, Igual J M, Klenk H P, Zhang Y Q, Goodfellow M (2019). *Mycolicibacterium stellerae* sp. nov., a rapidly growing scotochromogenic strain isolated from *Stellera chamaejasme*. International Journal of Systematic and Evolutionary Microbiology, 69(11): 3465–3471

Ou Y, Zhou J L, Jia Y, Liang M, Hu H, Ren L (2023). Complete genome of *Mycolicibacterium phocaicum* RL-HY01, a PAEs-degrading marine bacterial strain isolated from Zhanjiang Bay, China. Marine Genomics, 69(101019): 1–4

Pan Y, Luo L, Xiao H, Zhu R, Xiao H (2020). Spatial variability of inhalable fungal communities in airborne $PM_{2.5}$ across Nanchang, China. Science of the Total Environment, 746: 141171

Pan Y, Zuo Z, Huang X, Zhu R (2025). Airborne fungal communities are more susceptible to anthropogenic activities than bacteria. Journal of Environmental Sciences, 149: 564–573

Park E H, Heo J, Kim H, Yi S M (2020). The major chemical constituents of $PM_{2.5}$ and airborne bacterial community phyla in Beijing, Seoul, and Nagasaki. Chemosphere, 254(126870): 1–10

Park S (2021). Seasonal variations of fine particulate matter and mortality rate in seoul, korea with a focus on the short-term impact of meteorological extremes on human health. Atmosphere, 12(151): 1–15

Peter H, Hörtnagl P, Reche I, Sommaruga R (2014). Bacterial diversity and composition during rain events with and without Saharan dust influence reaching a high mountain lake in the Alps. Environmental Microbiology Reports, 6(6): 618–624

Peternel R, Čulig J, Hrga I (2004). Atmospheric concentrations of *Cladosporium* spp. and *Alternaria* spp. spores in Zagreb (Croatia) and effects of some meteorological factors. Annals of Agricultural and Environmental Medicine, 11(2): 303–307

Qi Y, Li Y, Xie W, Lu R, Mu F, Bai W, Du S (2020). Temporal-spatial variations of fungal composition in $PM_{2.5}$ and source tracking of airborne fungi in mountainous and urban regions. Science of the Total Environment, 708: 1135027

Sabariego S, Díaz de la Guardia C, Alba F (2000). The effect of meteorological factors on the daily variation of airborne fungal spores in Granada (Southern Spain). International Journal of Biometeorology, 44: 1–5

Šantl-Temkiv T, Amato P, Casamayor E O, Lee P K H, Pointing S B (2022). Microbial ecology of the atmosphere. FEMS Microbiology Reviews, 46: 1–18

Schloss P D, Westcott S L, Ryabin T, Hall J R, Hartmann M, Hollister E B, Lesniewski R A, Oakley B B, Parks D H, Robinson C J, et al. (2009). Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. Applied and Environmental Microbiology, 75(23): 7537–7541

Seifried J S, Wichels A, Gerdts G (2015). Spatial distribution of marine airborne bacterial communities. MicrobiologyOpen, 4(3): 475–490

Shennan J L (2006). Utilisation of C_2–C_4 gaseous hydrocarbons and isoprene by microorganisms. Journal of Chemical Technology and Biotechnology, 81(3): 237–256

Shin Y, Lee B H, Lee K E, Park W (2020). *Pseudarthrobacter psychrotolerans* sp. Nov., a cold-adapted bacterium isolated from Antarctic soil. International Journal of Systematic and Evolutionary Microbiology, 70(12): 6106–6114

Shinefield H R, Ruff N L (2009). Staphylococcal infections: a historical perspective. Infectious Disease Clinics of North America, 23(1): 1–15

Shigyo N, Umeki K, Hirao T (2019) Seasonal dynamics of soil fungal and bacterial communities in cool-temperate Montane Forests. Frontiers in Microbiology, 10(1944): 1–14

Shivaji S, Ray M K, Kumar G S, Reddy G S N, Saisree L, Wynn-Williams D D (1991). Identification of *Janthinobacterium fividum* from the soils of the islands of Scotia Ridge and from Antarctic peninsula. Polar Biology, 11(4): 267–271

Stępalska D, Wołek J (2005). Variation in fungal spore

concentrations of selected taxa associated to weather conditions in Cracow, Poland, in 1997. Aerobiologia, 21(1): 43–52

Tan W, Liao T H, Wang J, Ye Y, Wei Y C, Zhou H K, Xiao Y, Zhi X Y, Shao Z H, Lyu L D, et al. (2020). A recently evolved diflavin-containing monomeric nitrate reductase is responsible for highly efficient bacterial nitrate assimilation. Journal of Biological Chemistry, 295(15): 5051–5066

Tedersoo L, Anslan S, Bahram M, Põlme S, Riit T, Liiv I, Kõljalg U, Kisand V, Nilsson R H, Hildebrand F, et al. (2015). Shotgun metagenomes and multiple primer pair-barcode combinations of amplicons reveal biases in metabarcoding analyses of fungi. MycoKeys, 10: 1–43

Thukral A K, Bhardwaj R, Kumar V, Sharma A (2019). New indices regarding the dominance and diversity of communities, derived from sample variance and standard deviation. Heliyon, 5(e02606): 1–15

Ting Y C, Young L H, Lin T H, Tsay S C, Chang K E, Hsiao T C (2022). Quantifying the impacts of $PM_{2.5}$ constituents and relative humidity on visibility impairment in a suburban area of eastern Asia using long-term *in-situ* measurements. Science of the Total Environment, 818: 151759

Tucker W G (2000). Overview of $PM_{2.5}$ sources and control strategies. Fuel Processing Technology, 65: 379–392

Wang S, Liu W, Li J, Sun H, Qian Y, Ding L, Ma H, Li J (2021). Seasonal variation characteristics of bacteria and fungi in $PM_{2.5}$ in typical basin cities of Xi'an and Linfen, China. Atmosphere, 12(809): 1–17

Wang Y, Pavuluri C M, Fu P, Li P, Dong Z, Xu Z, Ren H, Fan Y, Li L, Zhang Y L, et al., (2019). characterization of secondary organic aerosol tracers over Tianjin, North China during summer to autumn. ACS Earth and Space Chemistry, 3(10): 2339–2352

Warneck P (2000) Chemistry of the Natural Atmosphere, 2nd ed. San Diego: Academic Press

Weber C F, Vilgalys R, Kuske C R (2013). Changes in fungal community composition in response to elevated atmospheric CO_2 and nitrogen fertilization varies with soil horizon. Frontiers in Microbiology, 4: 1–14

Wei M, Liu H, Chen J, Xu C, Li J, Xu P, Sun Z (2020). Effects of aerosol pollution on $PM_{2.5}$-associated bacteria in typical inland and coastal cities of Northern China during the winter heating season. Environmental Pollution, 262: 114188

Wemheuer F, Taylor J A, Daniel R, Johnston E, Meinicke P, Thomas T, Wemheuer B (2020). Tax4Fun2: prediction of habitat-specific functional profiles and functional redundancy based on 16S rRNA gene sequences. Environmental Microbiome, 15(1): 1–12

Wiśniewska K A, Śliwińska-Wilczewska S, Lewandowska A U (2022). Airborne microalgal and cyanobacterial diversity and composition during rain events in the southern Baltic Sea region. Scientific Reports, 12: 2029

Womack A M, Artaxo P E, Ishida F Y, Mueller R C, Saleska S R, Wiedemann K T, Bohannan B J M, Green J L (2015). Characterization of active and total fungal communities in the atmosphere over the Amazon rainforest. Biogeosciences, 12(21): 6337–6349

Xie W, Li Y, Bai W, Hou J, Ma T, Zeng X, Zhang L, An T (2021). The source and transport of bioaerosols in the air: a review. Frontiers of Environmental Science & Engineering, 15(3): 1–19

Xu C, Wei M, Chen J, Zhu C, Li J, Lv G, Xu X, Zheng L, Sui G, Li W, et al., (2017). Fungi diversity in $PM_{2.5}$ and PM_1 at the summit of Mt. Tai: abundance, size distribution, and seasonal variation. Atmospheric Chemistry and Physics, 17(18): 11247–11260

Xue F, Yang Y, Lai S, Xiao Y, Yao Y, Zhang Y, Zou S (2023). Airborne microbiomes at a subtropical island in southern China: importance of the northwest and southeast monsoons. Atmospheric Environment, 307(119): 842

Yang Z, Mahendran R, Yu P, Xu R, Yu W, Godellawattage S, Li S, Guo Y (2022). Health effects of long-term exposure to ambient $PM_{2.5}$ in Asia-Pacific: a systematic review of cohort studies. Current Environmental Health Reports, 9(2): 130–151

Zhai Y, Li X, Wang T, Wang B, Li C, Zeng G (2018). A review on airborne microorganisms in particulate matters: composition, characteristics and influence factors. Environment International, 113: 74–90

Zhang Y Y, Müller L, Winterhalter R, Moortgat G K, Hoffmann T, Pöschl U (2010). Seasonal cycle and temperature dependence of pinene oxidation products, dicarboxylic acids and nitrophenols in fine and coarse air particulate matter. Atmospheric Chemistry and Physics, 10(16): 7859–7873

Zeng T, Wang Y (2011). Nationwide summer peaks of OC/EC ratios in the contiguous United States. Atmospheric Environment, 45(3): 578–586

Zheng M, Salmon L G, Schauer J J, Zeng L, Kiang C S, Zhang Y, Cass G R (2005). Seasonal trends in $PM_{2.5}$ source contributions in Beijing, China. Atmospheric Environment, 39(22): 3967–3976

Zhou Q, Fu K, Hu X, Li X, Lai Z, Yuan P (2022). Relationships between airborne microbial community diversity, heating supply patterns and particulate matter properties. Journal of Environmental Chemical Engineering, 10: 107309