

# Large-Scale Dust–Bioaerosol Field Observations in East Asia

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**KEYWORDS:**

Atmosphere;  
Aerosols;  
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**ABSTRACT:** The long-range transport of bioaerosols by dust events significantly impacts ecological and meteorological networks of the atmosphere, biosphere, and anthroposphere. Bioaerosols not only cause significant public health risks, but also act as efficient ice nuclei for inducing cloud formation and precipitation in the hydrological cycle. To establish risk management for bioaerosol impacts on the Earth system, a large-scale investigation of bioaerosols must be performed under different environmental conditions. For this purpose, a Dust–Bioaerosol (DuBi) field campaign was conducted to investigate the distribution of bioaerosols by collecting ~950 samples at 39 sites across East Asia from 2016 to 2021. Concentrations and community structures of bioaerosols were further analyzed using fluorescence microscopic observations and high-throughput DNA sequencing, and these factors were compared to environmental factors, such as  $PM_{10}$  and aridity. The results indicated that microbial concentrations at dryland sites were statistically higher than those at humid sites, while the microbe-to-total-particle ratio was statistically lower in drylands than in humid regions. Microbial cells per microgram of  $PM_{10}$  decreased when  $PM_{10}$  increased. The proportion of airborne particles at each site did not vary substantially with season. The richness and diversity of airborne bacteria were significantly higher in drylands than in semiarid regions, while the community structures were stable among all sampling sites. The DuBi field campaign improves our understanding of bioaerosol characteristic variations along the dust transport pathway in East Asia and the changes of bioaerosols under the trend of climate warming, supporting the efforts to reduce public health risks.

**SIGNIFICANCE STATEMENT:** We first conducted large-scale Dust–Bioaerosol (DuBi) field observations in East Asia from 2016 to 2021. We used unified sampling and analysis methods to collect 950 samples at 39 sites and analyzed bioaerosols' concentration and community structure. This study aims to find the relationship between bioaerosols with atmospheric particles and aridity, which fills gaps in the field. These results improve our understanding of bioaerosols' impacts on ecological and meteorological networks of the atmosphere, biosphere, and anthroposphere. The comprehensive observations will promote prediction of bioaerosol change under the trend of climate warming, supporting the efforts to reduce global climate, ecological security, and public health risks in the future.

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**B**ioaerosols, including bacteria, fungi, pollen, viruses, and plant and animal fragments, are dominant in the atmosphere (Després et al. 2012; Fröhlich-Nowoisky et al. 2016). Atmospheric circulations can suspend bioaerosols in the atmosphere for many days and, therefore, carry them for long distances. In far downwind environments, transportation of bioaerosols impact public health and indirectly influence climate change. Some bacteria, such as *Pseudomonas*, *Erwinia*, *Pantoea*, and *Xanthomonas* species, are thought to initiate ice-cloud formation with high ice nucleation activities (Bauer et al. 2003; Fröhlich-Nowoisky et al. 2016; Hill et al. 2017; Pratt et al. 2009; Yankofsky et al. 1981). Other gram-negative bacteria can initiate the formation of water clouds as cloud condensation nuclei (Bauer et al. 2003; Möhler et al. 2007). In addition, recent studies have revealed that aerosols spread several respiratory diseases, such as coronavirus disease 2019 (COVID-19), measles, tuberculosis, and influenza (Hoseinzadeh et al. 2013; Huang et al. 2020; Jiang et al. 2021; Kutter et al. 2018; Lane et al. 2020). The prevalence and risks of asthma, allergies, and respiratory diseases are enhanced by bacteria, fungi, and viruses in the atmosphere (Kim et al. 2018). Overall, the roles of bioaerosols in many disciplines such as climate and human health are important and significant (Shen and Yao 2022).

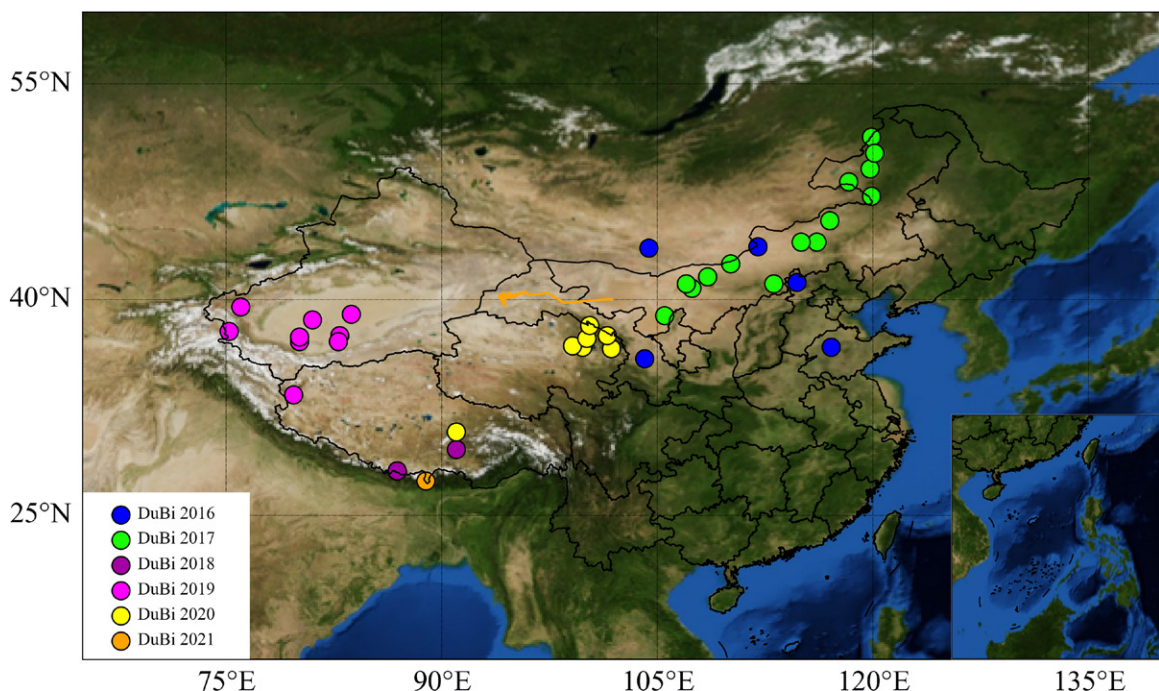
Furthermore, events from arid and semiarid regions not only reduce visibility but also possibly carry several pathogens to human health. For example, some surveys in Kansas and the western part of China suggested that dust events could have contributed to the dispersion of the measles epidemic (Brown et al. 1935; Ma et al. 2017). And Wang et al. (2023) found that spectroscopic lidar system their built could pick up the robust fluorescence signal emitted by dust aerosols, which showed the dust contains bioaerosols. Additionally, some bacterial genera, *Mycobacterium* and *Brucella*, in dust samples of Middle East arid areas have been demonstrated to cause respiratory diseases and brucellosis (Soleimani et al. 2020). The mineral-dust transported from large desert areas carries large amounts of microorganisms over long distances (Du et al. 2023; Liu et al. 2022; Qi et al. 2023). The Asian dust originating from the Taklimakan Desert circulates even around Earth within 13 days through the upper troposphere (Uno et al. 2009). Dust events are known to increase microbial communities and concentrations in the atmosphere of dust sources and transported environments (Chen et al. 2020; Hara and Zhang 2012; Jeon et al. 2011; Maki et al. 2014, 2018; Puspitasari et al. 2015; Tang et al. 2018), and airborne microbial particles are reported to be strongly related to inorganic aerosols. For example, there are significant correlations of bacterial concentrations to several anthropogenic and natural dust mineral particles, such as  $PM_{2.5}$  (particulate matter with aerodynamic diameter  $< 2.5 \mu m$ ),  $PM_{10}$  (particulate matter with aerodynamic diameter  $< 10 \mu m$ ), and coarse particles (Santos-Burgoa et al. 1994; Hara and Zhang 2012; Liu et al. 2019).

Bioaerosol samplings have been carried out at various sites worldwide, and the impact of seasonal, meteorological elements and atmospheric components to bioaerosols has also

been frequently researched in the past (Bowers et al. 2012; Dong et al. 2016; Du et al. 2018; Ghosh et al. 2015; Herrero et al. 1996; Huang et al. 2023; Sousa et al. 2008; Wu et al. 2012; Xie et al. 2018b; Xie et al. 2020; Xu et al. 2021; Zhai et al. 2018; Zhen et al. 2017). However, there are few studies investigating bioaerosol distributions under several atmospheric and underlying surface conditions using unified methods in large scale (especially at dust sources and transport paths), and the focus on bioaerosols and aridity were less noticed in previous studies (Tignat-Perrier et al. 2019; Xie et al. 2018b). Due to the climate change, the desertification risks are projected to increase with high confidence and East Asia will be greatly affected (Mirzabaev et al. 2019). Considering the vast arid and semiarid areas in East Asia, and the large population in downwind regions, the potential threat from bioaerosols is relatively high in East Asia. In this study, to understand the East Asian distribution of bioaerosols related to climate and ecosystems, we performed the Dust–Bioaerosol (DuBi) field campaign at 39 sites across East Asia from 2016 to 2021 to investigate the dynamics of bioaerosol concentration and community structure that are influenced by environmental factors (aridity index) and aerosols ( $PM_{10}$ ). The microbe communities in the samples were analyzed through advanced analysis methods, which were combined with microscopic observations and high-throughput DNA sequencing. The bioaerosol samples were collected during the period from 2016 to 2021 based on unified sampling, which have large temporal and spatial research scales and can facilitate comparative analysis from multiple areas collected samples. The statistical relationships demonstrate the distribution of bioaerosols presented at different levels of aridity and atmospheric pollution, contributing to better understanding of possible public health threats under climate change.

### Sampling sites and methodology

**Observation sites.** The DuBi observation sites were located throughout northern China, and most of them were in the dust source and transport pathway of East Asia, with small areas on the Tibetan Plateau (Fig. 1). There are several underlying surface types at the sampling sites: desert, grassland, wetland, cropland, alpine meadow, urban, etc. (Table S1).



**Fig. 1.** Distribution of the sampling sites during the DuBi field campaign from 2016 to 2021 over East Asia. Colored circles represent the locations of the sampling sites, and the orange line represents the track of the aircraft for the bioaerosol investigation in the upper troposphere in summer 2021.

Figure S1 in the supplemental material uses the Hybrid Single-Particle Lagrangian Integrated Trajectory (HYSPLIT) model to investigate the transport paths of dust storms over a period in March 2021, and it can be seen that the dust paths by the HYSPLIT model overlap considerably with the distribution of the sampling sites. Most of the DuBi sites are situated on the source and transport pathways of East Asian Dust, except some of the sites on the Tibetan Plateau. Due to most of the DuBi sites are concentrated in arid and semiarid regions of China, we expand the range of aridity index (adding more arid and wetter sites) and increase samples size to ensure more reliable statistical results. Apart from the samples collected at these sites in Fig. 1, some samples from China, Japan, and Mongolia were also used in this paper. These samples are listed in Table S2. During the study period, a total of 950 DuBi samples were collected at the 39 sampling sites, but samples were not all analyzed in this study.

**Bioaerosol sampling.** The bioaerosol samplers designed by Maki et al. (2010, 2013) and Tang et al. (2018) were used for the samplings during the DuBi campaign. The bioaerosol samples were collected on sterilized 0.2  $\mu\text{m}$  pore-size polycarbonate filters (Whatman 111106 and GTTP01300) in a Swinnex 13 mm filter holder (Millipore SX0001300), which were connected to an air pump (AS ONE MAS-1, Japan). Before the experiments, all filters are sterilized by using 75% alcohol, ultraviolet light (30 min), and autoclaving (120°C for 20 min). The bioaerosol samplers were installed at a height of approximately 1.5 m above ground level during field observations (Figs. 2a–f).

In addition, the complex laboratory processes required for membrane sampling, fluorescence microscopy analysis, and 16S rRNA gene sequencing are mainly used to analyze collected samples for obtaining bioaerosols' concentration and community structure in this study. The sampling times and locations were listed in Table S1 in supplemental material. The DuBi observation sites were more extensive, and some samples were even collected from remote and harsh environment areas. Thus, it was very difficult to collect and maintain samples for long periods at these sites due to the harsh weather and lack of electricity and household goods. And due to the high cost in terms of human and financial resources, continuous sampling for more than one year was difficult, even at other sites with good conditions. But if we have more opportunities and resources, we will conduct more field observation experiments in the future.

**Fluorescence microscopy analysis.** A variety of methods and instruments can be used to detect, test, and analyze bioaerosols. This study used DAPI-stained and fluorescence microscopy to count the bioaerosols concentration. Under ultraclean conditions, 250  $\mu\text{L}$  of 4% paraformaldehyde solution was added to the filter to fix for more than an hour, and then the solution was removed and rinsed with sterile ultrapure water. Then, 250  $\mu\text{L}$  of 10  $\mu\text{g mL}^{-1}$  DAPI (4',6-diamidino-2-phenylindole, D9542, Sigma) was added to stain the samples for 15 min. Afterward, clean the stained solution following the previously mentioned cleaning step.

We removed the treated filter membrane, added a drop of nonfluorescent immersion oil (IMMOIL-F30CC, Olympus) to the slide, placed the membrane on it, added another drop of immersion oil, covered it with a coverslip, and then pressed it firmly. The samples were observed using a fluorescence microscope (Olympus, BX53 and DP72) with UV excitation light in the wavelength range of 340–390 nm. Notably, the bioaerosols in this study refer to DAPI-stained blue-green and presenting cellular form microbial particles, and the calculation formula listed in Eq. (1) in the supplemental material was used for bioaerosol concentration. This method has been widely used in many previous studies (Dong et al. 2016; Gong et al. 2019, 2020; Li et al. 2017; Maki et al. 2019b; Tang et al. 2018; Xie et al. 2018a; Yin et al. 2021).

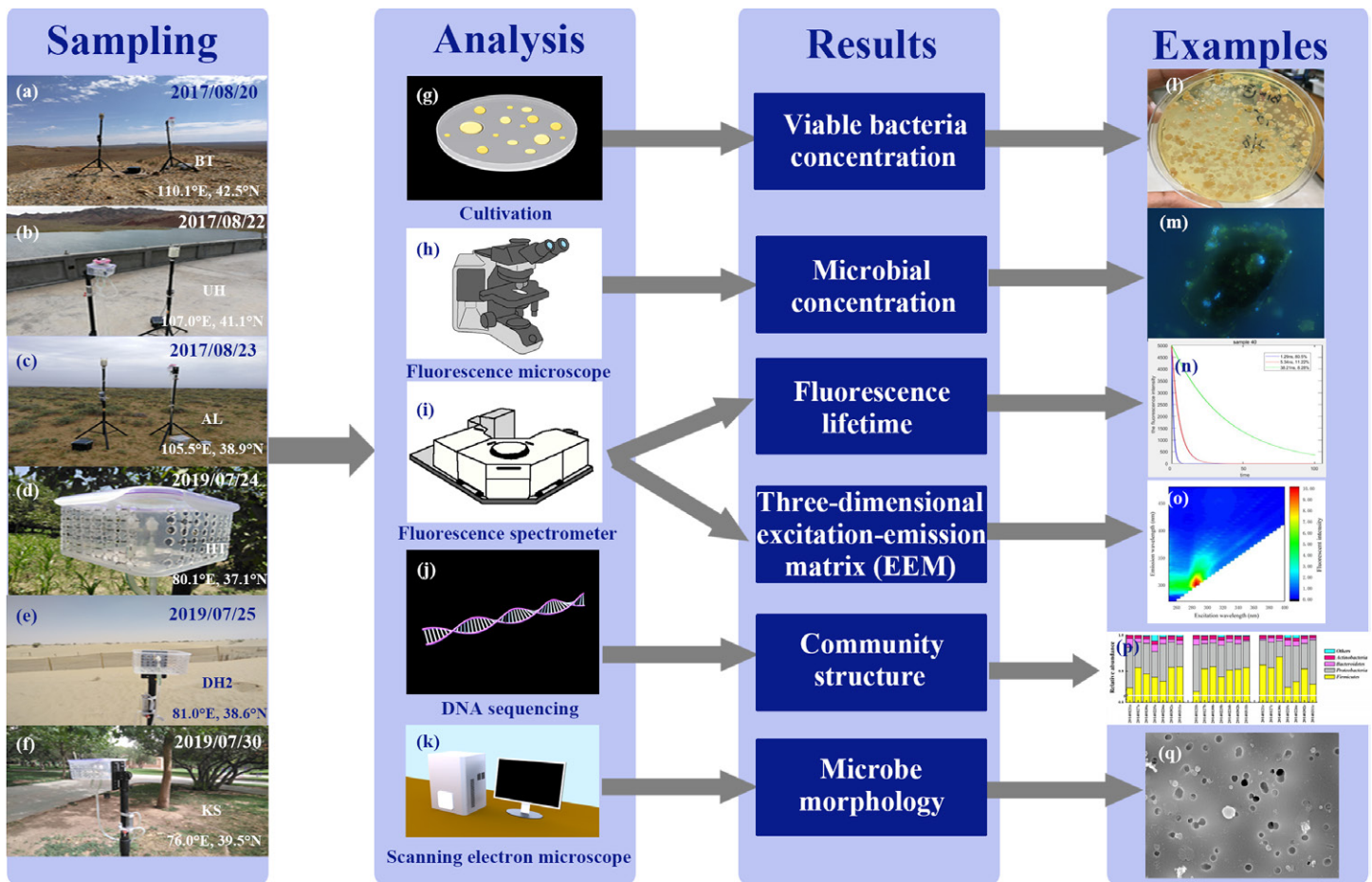


Fig. 2. Unified methods for sampling and analysis of bioaerosols during the DuBi field campaign from 2016 to 2021. (a)–(f) The scene, time, longitude, and latitude information of several DuBi sampling experiments. (g)–(k) The analytical methods and instruments. (l)–(q) Examples of the results. Some subgraphs are with reference to some instruments, such as (h) Olympus BX53 of Olympus Corporation, (i) FLS980 of Edinburgh Instruments, (k) CUBE-II Smart Benchtop Scanning Electron Microscope of EmCrafts Corporation. And examples (l) and (p) are quoted from Mendis et al. (2018) and Xu et al. (2017), respectively. In this study, fluorescence microscopy analysis and DNA sequencing methods were mainly used.

Four kinds of particles were demonstrated in Fig. S2 in the supplemental material. Based on the fluorescence microscopic observations, the particles were classified into blue, yellow, white, and black. The blue and blue–green particles were DAPI-stained microbial cells (excitation light at a wavelength of 365 nm), the white particles were mineral particulate matter, and the black particles were black carbon (Kepner and Pratt 1994; Maki et al. 2013). Yellow particles are thought to be DNA-free aerosols (Kepner and Pratt 1994), while Mostajir et al. (1995) indicated that organic matter in coastal seawater was observed as yellow particles. And the particles with water-soluble salts can also appear to be yellow–green (Liu et al. 2023). Furthermore, the yellow–green particles in most arid and semiarid DuBi samples are presented in mineral dust in the form of grain. The composition of yellow particles is complex. Therefore, the yellow particles in this paper refer to mineral dust containing water-soluble salts and organic matter.

**16S rRNA gene sequencing.** The bacterial diversity and community structures were analyzed using 16S rRNA gene sequencing. Bacterial DNA was extracted using the UltraClean Soil DNA kit (MoBio, San Diego, CA) by following the manufacturer’s instructions. During PCR amplification, the hypervariable V4-V5 region of the 16S rRNA gene was determined using 515F and 907R primers (Caporaso et al. 2012). Taxonomic analyses of raw sequences were performed using ultrafast sequence analysis (USEARCH). The taxonomic assignment

of the amplicon sequence variants (ASVs) was performed against the SILVA v132 reference database (Quast et al. 2012). The raw sequences in this study were uploaded to the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) database (BioProject accession number PRJNA1054501).

A diversity index is a quantitative measure that reflects the number of types (such as species) in a dataset and simultaneously considers the evenness of the basic entities (such as individuals) among these types. The alpha-diversity indices (Shannon and Chao1 indices) were calculated in the R environment. The Games–Howell test is a nonparametric post hoc analysis approach for performing multiple comparisons for two or more sample populations. It was used to test the significance of the differences between the different groups. Distance-based community analyses were calculated based on Bray–Curtis dissimilarity. The beta-diversity statistical analyses were tested using permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis dissimilarity and 999 permutations. All analyses were conducted using the *vegan* and *ggplot2* packages in the R environment.

***HYSPLIT model.*** The HYSPLIT model is a complete system for calculating simple air parcel trajectories, as well as complex transport, dispersion, chemical transformation, and deposition simulations, and it continues to be one of the most extensively used atmospheric transport and dispersion models in the atmospheric sciences community (<https://www.ready.noaa.gov/HYSPLIT.php>). Many studies have simulated the East Asian dust transport pathway by HYSPLIT (Ganbat and Jugder 2019; Huang et al. 2015; Maki et al. 2019b; Shin et al. 2015; Zhao et al. 2022). In this study, the HYSPLIT model was also used to determine the trajectories of dust transport paths in East Asia. The dust transport path map cases for the two East Asian starting points on 14 March 2021 are listed in Fig. S1 in the supplemental material.

***PM<sub>10</sub> dataset and aridity index.*** The PM<sub>10</sub> mass concentration data in China were obtained from the China National Urban Air Quality Real-Time Publishing Platform (<https://air.cnemc.cn:18007/>). The PM<sub>10</sub> air quality index (AQI) data in Japan were obtained from the Real-Time AQI website (<https://aqicn.org/city/>).

Typically, dryland extent is determined by the aridity index, which can be calculated as the ratio of precipitation (PRE; unit: mm) to potential evapotranspiration (PET; unit: mm) (Mirzabaev et al. 2019). The PRE and PET dataset was obtained from the CRU TS4.05: Climatic Research Unit (CRU) Time-Series (TS) version 4.05 of high-resolution gridded data of month-by-month variation in climate (January 1901–December 2020), (<https://catalogue.ceda.ac.uk/uuid/c26a65020a5e4b80b20018f148556681>; University of East Anglia Climatic Research Unit et al. 2021).

As reported by the Intergovernmental Panel on Climate Change (IPCC), aridity is a long-term climatic feature, characterized by low precipitation or available water (Mirzabaev et al. 2019). And the aridity index was applied to distinguish lands. The geographical distribution in this study were simply classified as arid (aridity index  $\leq 0.2$ ), semiarid ( $0.2 < \text{aridity index} \leq 0.65$ ), and humid (aridity index  $> 0.65$ ) (Mirzabaev et al. 2019). And most of the sampling sites are located in arid and semiarid regions. Arid regions exhibit characteristics of low precipitation, wide daily temperature ranges, strong solar radiation, high evaporation, and unfavorable for plants growing. And in semiarid regions, precipitation is slightly higher than that in arid areas, but also have fragile ecological environment. There are dust events in arid and semiarid regions. In addition, the sites in Japan are located in humid areas with abundant rainfall and vegetation, which is quite different from the climate and land cover in arid and semiarid regions.

Most of the sampling sites were divided into six categories depending on their geographical locations and aridity index. From west to east in Fig. 3 in the next section, they are referred to as Dunhuang (DH), Qinghai and Yuzhong (QH-YZ), Tsogt-Ovoo and Dalanzadgad in Mongolia

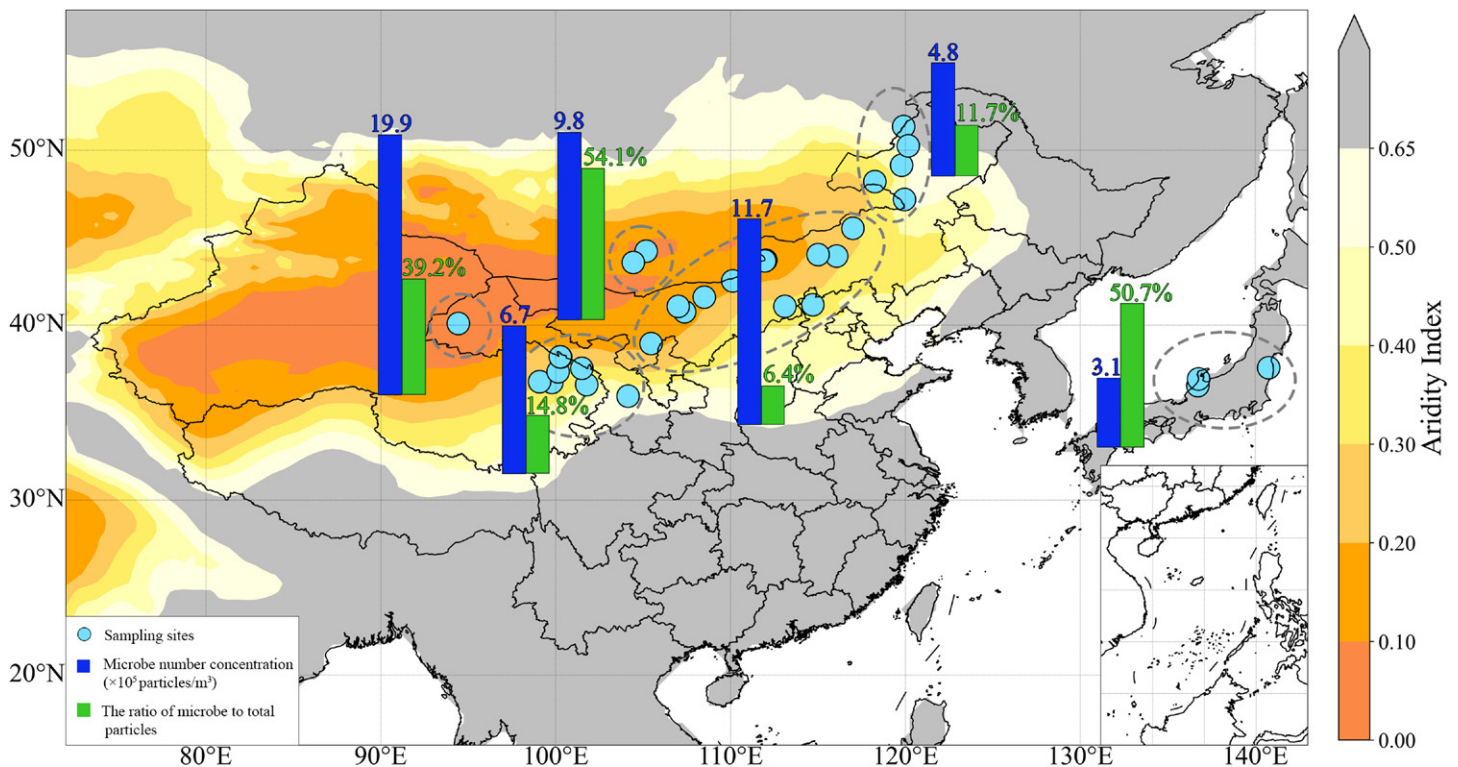


Fig. 3. Mean microbial cell concentrations and the ratios of the microbes to total particles change in different parts of East Asia. The blue circles represent the sampling sites of the DuBi field observations and those in Dunhuang, China; Japan; and Mongolia. The blue bars represent the average microbial cell concentration at adjacent sites within the gray dashed oval, while the green bars show the ratio of microbes to total particle concentration. There are three land surface types according to the 2001–20 average aridity index: arid (aridity index  $\leq 0.2$ ), semiarid ( $0.2 < \text{aridity index} \leq 0.65$ ), and humid (aridity index  $> 0.65$ ).

(TO-DZ), central Inner Mongolia and Zhangbei (IM-ZB), eastern Inner Mongolia (East-IM), and sites in Japan (JP). The DH and TO-DZ are in arid regions. The IM-ZB sites correspond to mixed arid and semiarid regions. The QH-YZ and East-IM groups are in semiarid regions, and the sites in JP are in humid regions as these belong to coastal areas.

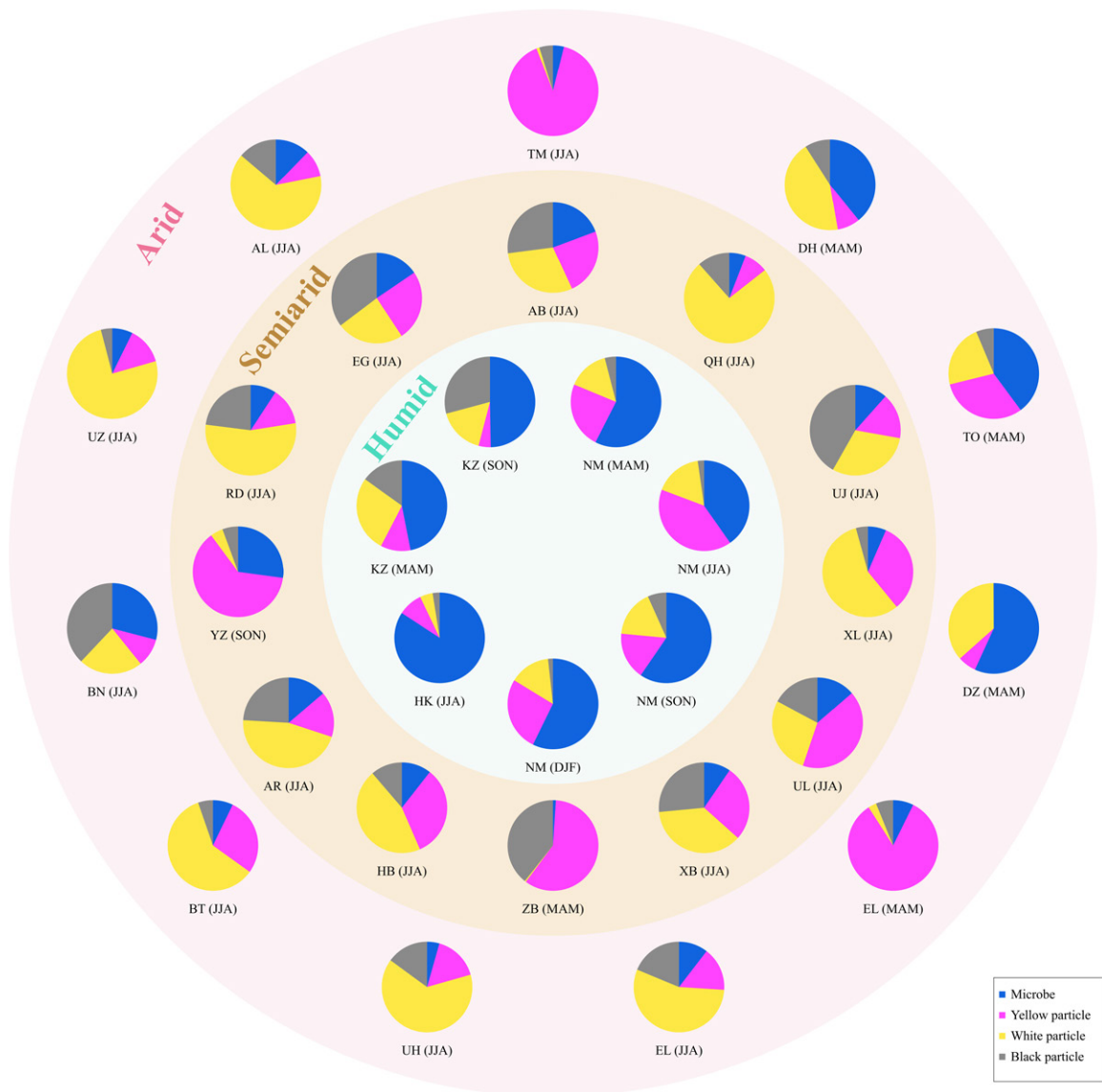
## Results and discussion

**Concentration of bioaerosols in East Asia.** First, according to location and aridity, the sites are divided into several groups to understand the approximate distribution and variation of mean bioaerosol concentrations and percentages at different scales in East Asia. Most of the DuBi field observation sites are in arid and semiarid regions in northern China and Mongolia, and some of these sites are in natural areas with minimal human activity. While other sites are humid and belong to Japan as shown in Fig. S1, these sites are located on the source and transport path of East Asia dust. Due to the harsher environment in many sites, it was difficult to collect the sampling for longer periods.

The microbial cell concentrations and the ratio of microbes to total particles varied among the sampling sites in East Asia (Fig. 3). In the arid regions, the microbial cell concentrations and the microbial ratios in DH and TO-DZ exceeded  $9.0 \times 10^5$  particles  $\text{m}^{-3}$  and 30%, respectively. Kakikawa et al. (2009) estimated approximately  $4 \times 10^6$  microbial cells in  $0.7 \text{ m}^{-3}$  air in Dunhuang aerosol samples in August 2007. Similar experiments at Tsogt-Ovoo during March and April 2015 also indicated that the microbial cell concentrations fluctuated by approximately  $10^4$ – $10^5$  particles  $\text{m}^{-3}$  during the nondust periods, while they increased to more than  $10^6$  particles  $\text{m}^{-3}$  during dust events (Maki et al. 2017). The cell concentrations of airborne microorganisms in arid areas consistently range from  $10^5$  to  $10^6$  cells  $\text{m}^{-3}$  and increase to higher values during dust events.

In terms of the observation results, except for the arid sampling sites, the microbial cell concentrations and ratios at the other four groups of sites (IM-ZB, QH-YZ, East-IM, and JP) showed some patterns of change. The mean concentration of microbial cell mean concentrations was higher at drier sites: IM-ZB ( $1.17 \times 10^6$ ) > QH-YZ ( $6.7 \times 10^5$ ) and East-IM ( $4.8 \times 10^5$ ) > JP ( $3.1 \times 10^5$ ). The ratios of microbes to total particles showed the opposite trend: IM-ZB (6.4%) < QH-YZ (14.8%) and East-IM (11.7%) < JP (50.7%). The microbial cell concentrations were higher in drier regions, while the ratios of microbes to total particles were higher in humid regions.

**Portion of bioaerosols in total suspended particles.** The aridity index averaged over 20 years were classified at all sampling sites into three types (Fig. 4). At the humid sites, microbe particles usually accounted for the majority of the four kinds of particles. For the widely distributed arid and semiarid sampling sites, the proportional patterns of the four kinds of particles differed. However, it was also determined that yellow and white particles that



**Fig. 4.** Percentage of four particles at sampling sites during the DuBi field campaign and sampling time in the different seasons (MAM: March–May, spring; JJA: June–August, summer; SON: September–November, autumn; DJF: December–February, winter). The outer circle (red) is arid, the inner circle (green) is humid, and the middle circle (yellow) is semiarid. The site names are abbreviated and can be found in Tables S1 and S2 in the supplemental material.



contain mineral dust were usually present in large proportions. The proportional pattern of the four particles in the atmosphere was changed due to the variations in geographic location and aridity. In terms of seasonal changes in proportions, seasonal variations were less frequently observed at NM and KZ. In the samples of EL, yellow and white particles containing mineral dust were dominant in spring and summer, while black carbon and microorganisms occupied a small proportion. Thus, the proportion of particles in the atmosphere at each site was not varied substantially with the season.

Generally, yellow and other particles mix with each other in arid and semiarid regions. This mixing is due to the arid climate, abundant sources of dust, and weak wet deposition processes. In the BN, DH, TO, and DZ samples, the microbial cell ratios were high, possibly because local animal husbandry, agriculture, and dust events increased airborne bacteria. DAPI-stained microorganisms were reported to increase during dust events in Tsogt-Ovoo and Dalanzadgad in 2015 and 2016 (Maki et al. 2017, 2019a).

The concentrations of yellow, white, and black particles increased in correspondence with the increase in microbial particles (Fig. 5). This finding indicates that overall, microbial particle concentrations and the other three kinds of particles were usually synchronized in their variation.  $PM_{10}$  mass concentration and the total particles are two different variables reflecting the content of particulate matter in the atmosphere; the former represents the mass concentration of particles with aerodynamic diameter  $< 10 \mu\text{m}$ , while the latter is used to characterize the number concentration without size limitation. There was also a negative correlation between  $PM_{10}$  and the ratio of microbial concentrations to  $PM_{10}$  in Fig. 6. Although the particle number concentration and  $PM_{10}$  mass concentration are two different variables, it can be inferred that the rate of increase of the sum of the other three particles was faster than that of the microbes.

**Effects of aridity and  $PM_{10}$  on bioaerosol concentration.** After the statistical analysis, the microbial cell concentrations were negatively related to the aridity index ( $R^2 = 0.09, p < 0.001$ ), while the relations of the ratio of microbes to total particles and the aridity index were positive ( $R^2 = 0.38, p < 0.001$ ) (Figs. 6a,b). This result suggests that drier regions often had higher microbial cell concentrations and lower microbial ratios to total particles. Hara and Zhang (2012) and Tang et al. (2018) reported that dust mineral particles are vectors that carry high amounts of microorganisms in dry climates and loose surfaces in arid and semiarid regions.

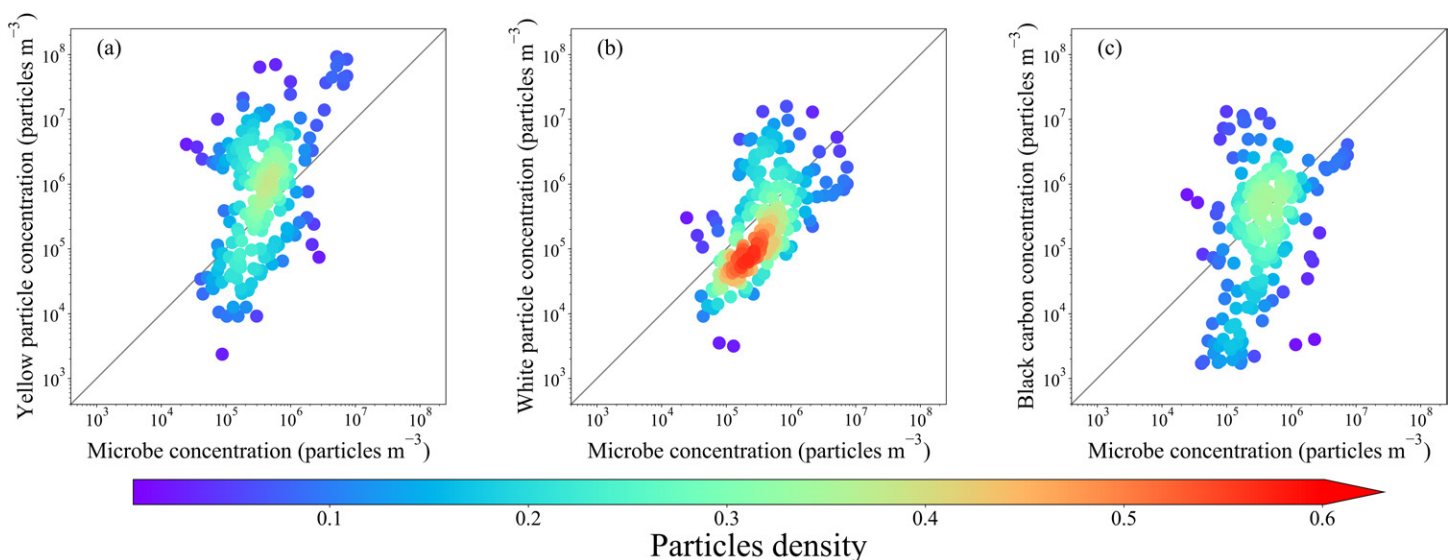
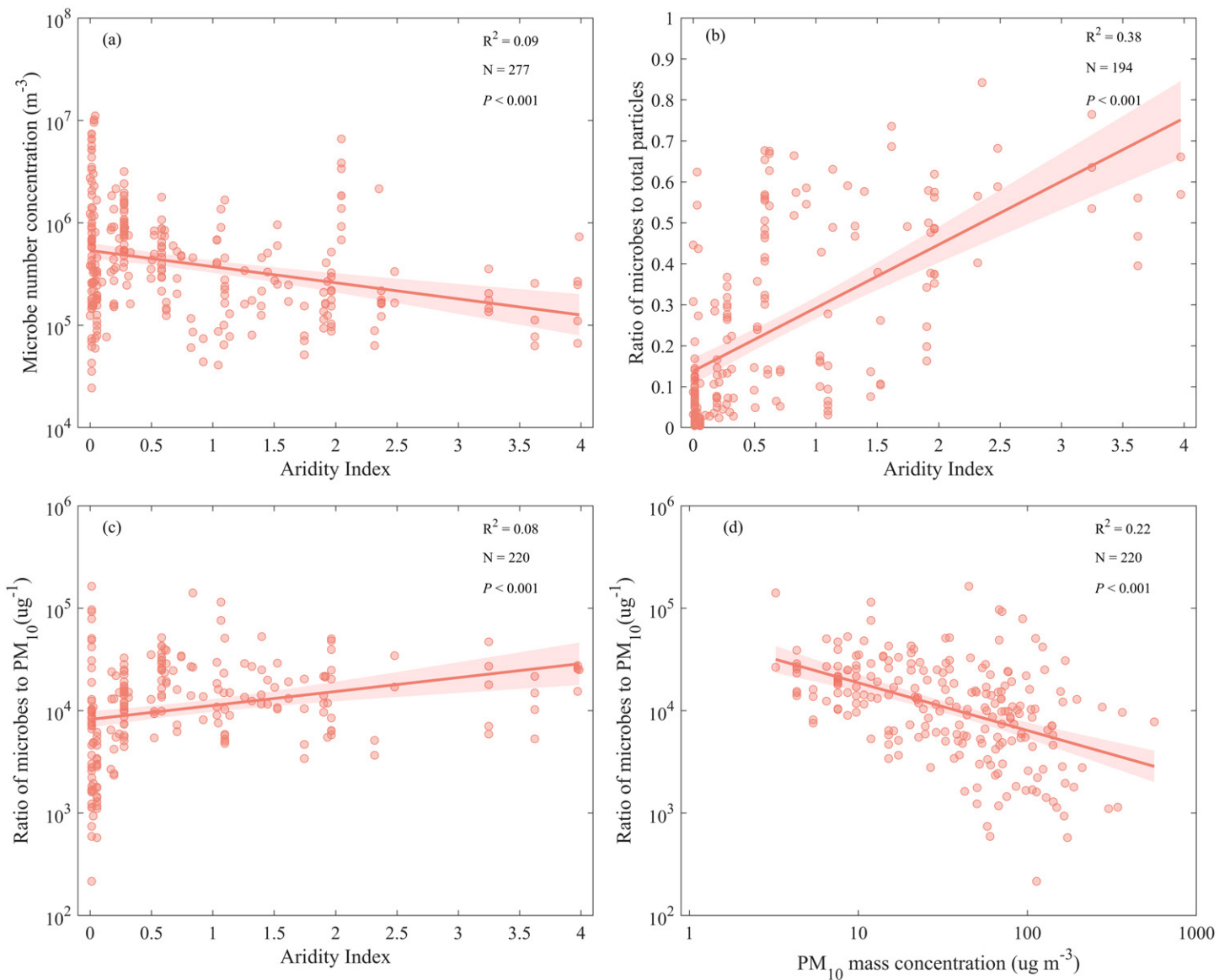


Fig. 5. Relation between microbe particles and the other three types of particles observed by fluorescence microscopy during the DuBi field campaign.



**Fig. 6.** Effects of monthly aridity index and  $PM_{10}$  mass concentration on microbes and the capacity of particles carrying microbes, respectively. The red lines are the fitted lines, and the red shaded areas are the 95% confidence intervals.

We surmised that microbe and microbe-attached particles were more likely to suspend in more arid areas. Therefore, the total concentrations of microorganisms were relatively high in the arid areas, while the microbial ratio among particulate matter was lower.

The airborne microbial cells were aerosolized mostly in the accompanying mineral particles (Zhai et al. 2018). The microbial cell ratio to  $PM_{10}$  mass concentration can be considered as a measure of the ability to  $PM_{10}$  that contained microbial cells. The co-relations of the ratio of microbes to  $PM_{10}$  and the aridity index and  $PM_{10}$  concentrations were weak positive ( $R^2 = 0.08$ ,  $p < 0.001$ ) and negative ( $R^2 = 0.22$ ,  $p < 0.001$ ), respectively, after the statistical analysis (Figs. 6c,d).

Many studies have demonstrated a positive correlation between airborne microbial cell concentrations and  $PM_{10}$  and coarse particle concentrations (Santos-Burgoa et al. 1994; Hara and Zhang 2012; Wu et al. 2012; Liu et al. 2019), and this study shows the correlation between  $PM_{10}$  and its ability to contain bioaerosols. According to the above results, the microbial cells per microgram of  $PM_{10}$  decreased when  $PM_{10}$  increased. In other words, when the atmosphere becomes dirty, the ability of  $PM_{10}$  to contain microbes is reduced. It could be speculated that other particles increased more rapidly when all particles increased.

However, it must be noted that in addition to the aridity index and  $PM_{10}$ , many other factors (e.g., temperature, humidity, precipitation, wind speed and direction, solar radiation, emissions, atmospheric components, season, and human activities) can affect the bioaerosol concentration and community structure in the atmosphere. In this study, we focused on the relationships between these two variables and bioaerosols, and the long duration of the sampling experiments that passed significance tests and are the evidence of these associations.

**Community composition, diversity, and structure of bioaerosols.** For the analyses using the aridity index and field observations, a total of 122 aerosol samples were obtained from eight sampling sites for which sequencing data were obtained and classified into two regions: arid and semiarid, whose subsurface types were dominated by bare ground and sparse grassland, respectively. The airborne bacterial compositions at the phylum level in all samples were dominantly composed of members of Proteobacteria (55%), Firmicutes (15%), Actinobacteria (13%), and Bacteroidetes (9%) (Fig. 7). Almost all samples have similar airborne bacterial compositions, except for those of YZ and EL, which contained local bacterial populations. Large dust events carry bacteria and disperse them over long distances via wind flow (Maki et al. 2019b). Moreover, Huang et al. (2008) and Tang et al. (2018) found that airborne bacteria transported by dust events could significantly change the atmospheric bioaerosol content in downwind ecosystems. Thus, atmospheric transport can cause similar community compositions to occur among different sampling sites. However, since the YZ and EL samples were collected during dust-free events, local bacterial species were thought to be dominant.

A total of 7,901 ASVs were obtained from all samples. The Shannon diversity and Chao1 indices of the EL samples were significantly higher than those of the DH, IM, QH, and YZ samples (Games–Howell test,  $p < 0.05$ , Figs. 8a,b). The ZB and YZ samples had similar Shannon diversity values, which were significantly higher than those of the DH and QH samples (Games–Howell test,  $p < 0.05$ , Fig. 8a). The observations showed that the aerosols in the arid regions contained high diversities of airborne bacterial communities in comparison to those in the semiarid regions (Games–Howell test,  $p = 0.005$ , Figs. 8c,d). Airborne bacterial diversity is known to be influenced by aerosol components originating from local arid terrestrial ecosystems (Qi et al. 2021; Zhai et al. 2018) and distant air masses (Qi et al. 2022). Aerosol emissions depend on land surface conditions, such as the compositions of vegetation cover (Zhou et al. 2021) and the wind forces imposed on the land (Šantl-Temkiv et al. 2022). In addition, soil dust from bare land increases the chances of bacteria entering the atmosphere (Mu et al. 2020). The bacterial populations in bare ground soil could be easily transported

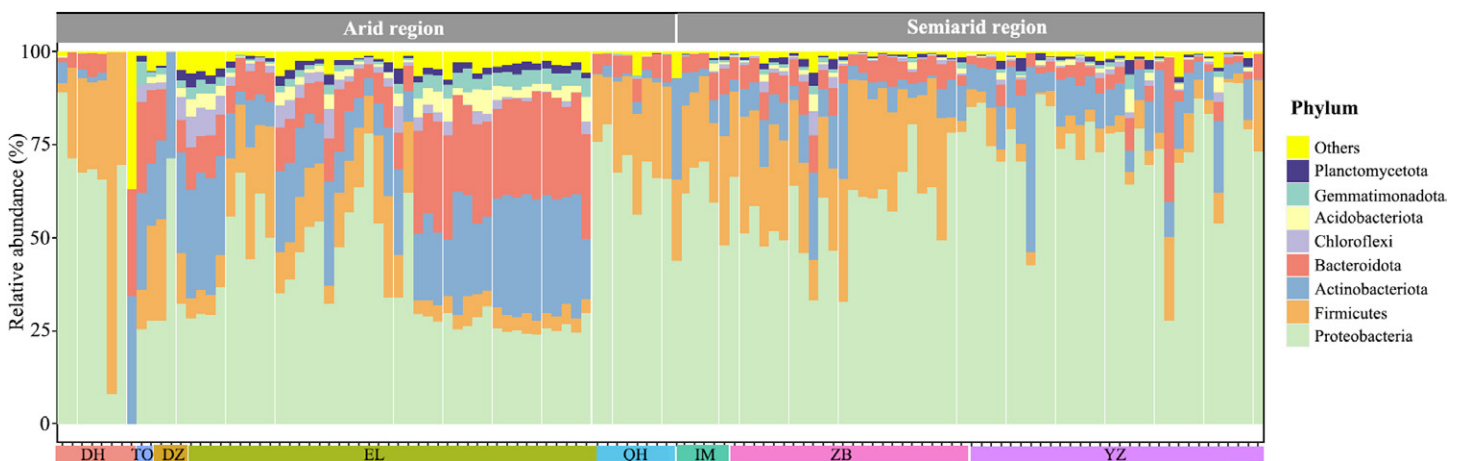
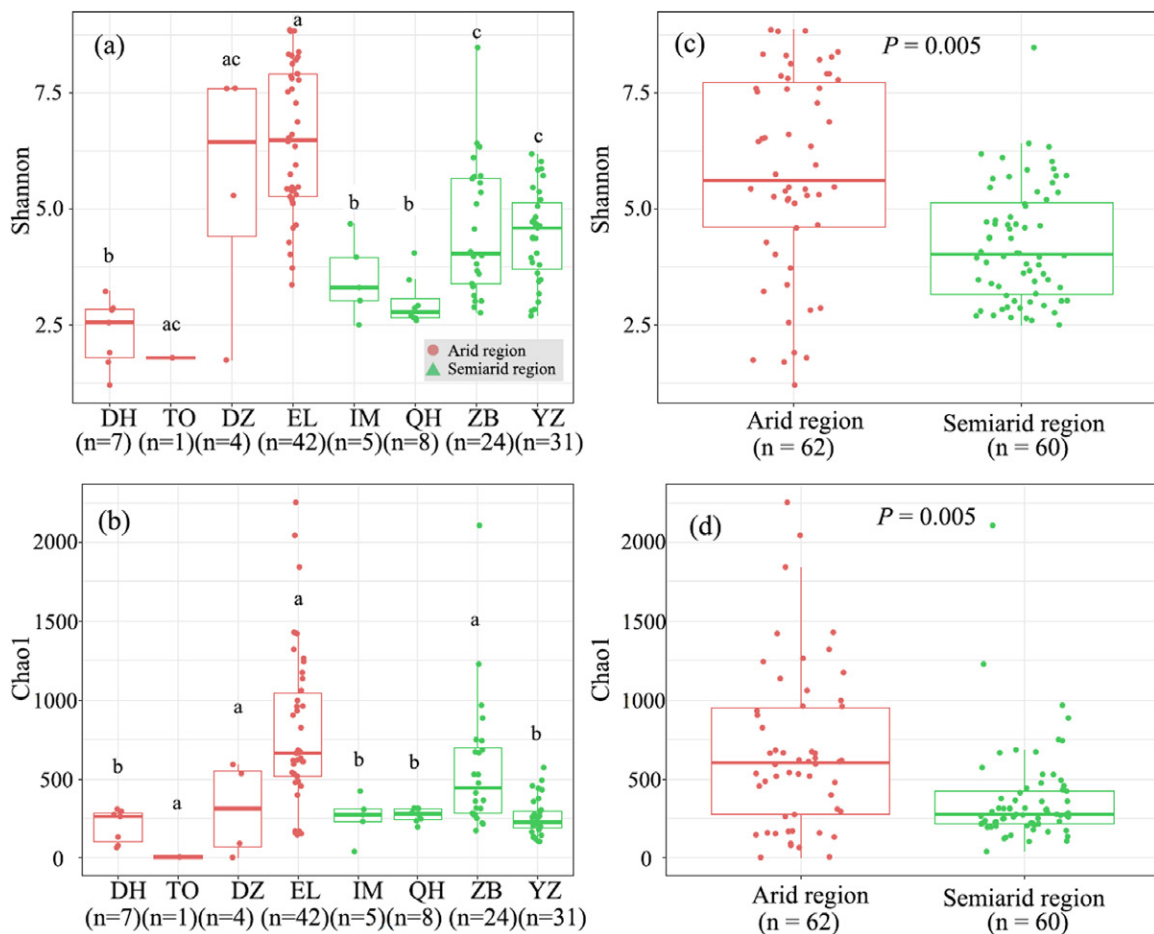


Fig. 7. Relative abundances of bacterial 16S rRNA gene sequences at the phylum level (relative abundance > 2%) in the aerosol samples across the different sampling sites and regions during the DuBi field campaign.



**Fig. 8.** Comparison of bacterial Shannon diversity at different (a) sampling sites and (c) regions and the Chao1 richness at different (b) sampling sites and (d) regions during the DuBi field campaign. Significance was tested using the Games–Howell test, with  $p < 0.05$  is considered significant. The significant differences in the subgroups are denoted by (a)–(c).

to the atmosphere by the upward blowing of desiccated soil particles (Burrows et al. 2009). However, since grasses covering sparse grasslands protect soil bacteria from being transported into the atmosphere, the bacterial communities in semiarid regions are less diverse than those in other regions (Zhou et al. 2021). Moreover, in the sand-desert environments of DH, the low diversity of terrestrial bacteria reduces the diversity of airborne bacteria (Rao et al. 2015).

A principal coordinate analysis (PCoA) of the Bray–Curtis dissimilarity revealed that the samples at DH, DZ, EL, IM, QH, TO, and ZB sites were closely clustered with each other, while the samples at YZ site formed a separate cluster from the other samples (PERMANOVA,  $p = 0.001$ , Fig. 9a). Although the community structures of airborne bacteria seem to be different between arid and semiarid regions, the YZ samples from both regions remained in a single cluster. Some samples in ZB were still clustered with the arid region samples, but they belonged to the semiarid region samples on the PCoA coordinate (PERMANOVA,  $p = 0.001$ , Fig. 9b). Dust transport is expected to mix airborne bacterial communities from several sampling sites regardless of ground conditions. Furthermore, transported dust can also carry pathogens and allergens, potentially impacting the health of downwind populations and ecosystems (Jones and Brosseau 2015).

### Summary and outlook

Bioaerosols are related to the interactions among the atmosphere, hydrosphere, biosphere, and anthroposphere; hence, they have significant impacts on the Earth system. However, their influence mechanisms on climate, environment, and human health, especially in relation

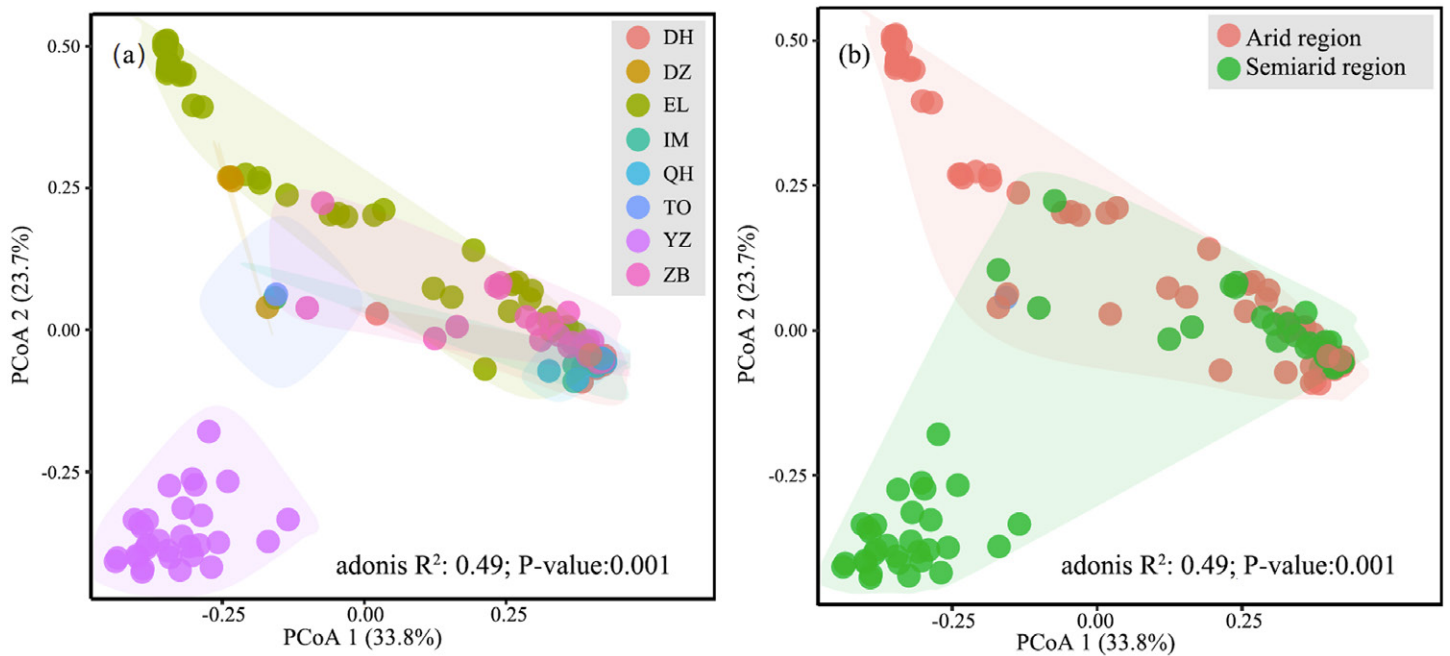


Fig. 9. Principal coordinate analysis based on the Bray–Curtis dissimilarity at different (a) sampling sites and (b) regions during the DuBi field campaign.

with aridity, are still unclear because of limited information on the spatial–temporal distribution of bioaerosol characterization. In this study, the DuBi field campaign led by Lanzhou University in China was performed at 39 sites across East Asia from 2016 to 2021 to rigorously investigate the quantitative and qualitative characteristics of bioaerosols using the unified methods at large scale.

Many previous studies have studied how several meteorological and environmental factors can affect the concentration and community structure of bioaerosols. This study focuses on the statistical correlation between bioaerosols and the aridity index and  $PM_{10}$  concentration. In more arid regions, there are usually higher microbe concentrations and lower microbe ratios than those in humid areas. The richness diversities of the airborne bacteria were also significantly higher in drylands than in semiarid regions. And for the amount of bioaerosol in a single gram of  $PM_{10}$ , it is higher in moist and cleaner atmospheres. These results suggest characteristics of bioaerosols under varying aridity and atmosphere particulate matter content conditions.

It is worth mentioning that the experiments in this study were limited due to the lack of financial, material, and human resources, and some samples were collected at some harsh sites. And continuous observations at many sites in large scale for more than one year were hard to accomplish. If available, we will continue to improve the experiment by adding long-time and multiple sampling of arid deserts in East Asia continuing to prove the above experiments' results.

As a whole, the bioaerosol investigation through the DuBi field campaign will improve our understanding and assessment of the links between bioaerosol with aridity and atmospheric particulate matter in the Earth–atmospheric system. These comprehensive observations will also support efforts to reduce global climate, ecological security, and public health risks in the future.

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**Data availability statement.** Datasets of the DuBi field campaign are available upon request from the lead contact. The observation  $PM_{10}$  mass concentration in China can be downloaded from the China National Urban Air Quality Real-time Publishing Platform (<https://air.cnemc.cn:18007/>), and  $PM_{10}$  Air Quality Index (AQI) data in Japan are from Real-time Air Quality Index (AQI) website (<https://aqicn.org/city/>) are all freely available. The precipitation and potential evaporation dataset used to calculate the aridity index can be acquired from the CRU TS4.05: Climatic Research Unit (CRU) Time-Series (TS) version 4.05 of high-resolution gridded data of month-by-month variation in climate (January 1901–December 2020), (<https://catalogue.ceda.ac.uk/uuid/c26a65020a5e4b80b20018f148556681>, University of East Anglia Climatic Research Unit et al. 2021). The data are available free of charge at the above websites.

## References

- Bauer, H., H. Giebl, R. Hitznerberger, A. Kasper-Giebl, G. Reischl, F. Zibuschka, and H. Puxbaum, 2003: Airborne bacteria as cloud condensation nuclei. *J. Geophys. Res.*, **108**, 4658, <https://doi.org/10.1029/2003JD003545>.
- Bowers, R. M., I. B. McCubbin, A. G. Hallar, and N. Fierer, 2012: Seasonal variability in airborne bacterial communities at a high-elevation site. *Atmos. Environ.*, **50**, 41–49, <https://doi.org/10.1016/j.atmosenv.2012.01.005>.
- Brown, E., S. Gottlieb, and R. Laybourn, 1935: Dust storms and their possible effect on health: With special reference to the dust storms in Kansas in 1935. *Public Health Rep.*, **50**, 1369–1383, <https://doi.org/10.2307/4581653>.
- Burrows, S. M., T. Butler, P. Jöckel, H. Tost, A. Kerkweg, U. Pöschl, and M. G. Lawrence, 2009: Bacteria in the global atmosphere – Part 2: Modeling of emissions and transport between different ecosystems. *Atmos. Chem. Phys.*, **9**, 9281–9297, <https://doi.org/10.5194/acp-9-9281-2009>.
- Caporaso, J. G., and Coauthors, 2012: Ultra-high-throughput microbial community analysis on the Illumina HiSeq and MiSeq platforms. *ISME J.*, **6**, 1621–1624, <https://doi.org/10.1038/ismej.2012.8>.
- Chen, X., D. Kumari, and V. Achal, 2020: A review on airborne microbes: The characteristics of sources, pathogenicity and geography. *Atmosphere*, **11**, 919, <https://doi.org/10.3390/atmos11090919>.
- Després, V. R., and Coauthors, 2012: Primary biological aerosol particles in the atmosphere: A review. *Tellus*, **64B**, 15598, <https://doi.org/10.3402/tellusb.v64i0.15598>.
- Dong, L., and Coauthors, 2016: Concentration and size distribution of total airborne microbes in hazy and foggy weather. *Sci. Total Environ.*, **541**, 1011–1018, <https://doi.org/10.1016/j.scitotenv.2015.10.001>.
- Du, P., R. Du, W. Ren, Z. Lu, and P. Fu, 2018: Seasonal variation characteristic of inhalable microbial communities in PM<sub>2.5</sub> in Beijing city, China. *Sci. Total Environ.*, **610–611**, 308–315, <https://doi.org/10.1016/j.scitotenv.2017.07.097>.
- , Z. Huang, S. Tang, Q. Dong, J. Bi, X. Yu, and Q. Gu, 2023: Long-term variation of dust devils in East Asia during 1959–2021. *J. Geophys. Res. Atmos.*, **128**, e2022JD038013, <https://doi.org/10.1029/2022JD038013>.
- Fröhlich-Nowoisky, J., and Coauthors, 2016: Bioaerosols in the Earth system: Climate, health, and ecosystem interactions. *Atmos. Res.*, **182**, 346–376, <https://doi.org/10.1016/j.atmosres.2016.07.018>.
- Ganbat, G., and D. Jugder, 2019: Observations and transport modeling of dust storm event over Northeast Asia using HYSPLIT: Case study. *E3S Web Conf.*, **99**, 02002, <https://doi.org/10.1051/e3sconf/20199902002>.
- Ghosh, B., H. Lal, and A. Srivastava, 2015: Review of bioaerosols in indoor environment with special reference to sampling, analysis and control mechanisms. *Environ. Int.*, **85**, 254–272, <https://doi.org/10.1016/j.envint.2015.09.018>.
- Gong, J., J. Qi, and H. Li, 2019: Distribution of total microbes in atmospheric bioaerosols in the coastal region of Qingdao (in Chinese). *Huan Jing Ke Xue*, **40**, 3477–3488.
- , —, B. E., Y. Yin, and D. Gao, 2020: Concentration, viability and size distribution of bacteria in atmospheric bioaerosols under different types of pollution. *Environ. Pollut.*, **257**, 113485, <https://doi.org/10.1016/j.envpol.2019.113485>.
- Hara, K., and D. Zhang, 2012: Bacterial abundance and viability in long-range transported dust. *Atmos. Environ.*, **47**, 20–25, <https://doi.org/10.1016/j.atmosenv.2011.11.050>.
- Herrero, B., M. A. Fombella-Blanco, D. Fernandez-Gonzalez, and R. M. Valencia-Barrera, 1996: The role of meteorological factors in determining the annual variation of *Alternaria* and *Cladosporium* spores in the atmosphere of Palencia, 1990–1992. *Int. J. Biometeor.*, **39**, 139–142, <https://doi.org/10.1007/BF01211226>.
- Hill, T., P. DeMott, F. Conen, and O. Möhler, 2017: Impacts of bioaerosols on atmospheric ice nucleation processes. *Microbiology of Aerosols*, D. Anne-Marie and A. Pierre, Eds., Wiley, 195–219, <https://doi.org/10.1002/9781119132318.ch3a>.
- Hoseinzadeh, E., M. R. Samarghande, S. A. Ghiasian, M. Y. Alikhani, and G. Roshanaie, 2013: Evaluation of bioaerosols in five educational hospitals wards air in Hamedan, during 2011–2012. *Jundishapur J. Microbiol.*, **6**, e10704, <https://doi.org/10.5812/jjm.10704>.
- Huang, J., P. Minnis, B. Chen, Z. Huang, Z. Liu, Q. Zhao, Y. Yi, and J. K. Ayers, 2008: Long-range transport and vertical structure of Asian dust from CALIPSO and surface measurements during PACDEX. *J. Geophys. Res.*, **113**, D23212, <https://doi.org/10.1029/2008JD010620>.
- Huang, Z., J. Huang, T. Hayasaka, S. Wang, T. Zhou, and H. Jin, 2015: Short-cut transport path for Asian dust directly to the Arctic: A case study. *Environ. Res. Lett.*, **10**, 114018, <https://doi.org/10.1088/1748-9326/10/11/114018>.
- , —, Q. Gu, P. Du, H. Liang, and Q. Dong, 2020: Optimal temperature zone for the dispersal of COVID-19. *Sci. Total Environ.*, **736**, 139487, <https://doi.org/10.1016/j.scitotenv.2020.139487>.
- , and Coauthors, 2023: Bioaerosols in the atmosphere: A comprehensive review on detection methods, concentration and influencing factors. *Sci. Total Environ.*, **912**, 168818, <https://doi.org/10.1016/j.scitotenv.2023.168818>.
- Jeon, E. M., H. J. Kim, K. Jung, J. H. Kim, M. Y. Kim, Y. P. Kim, and J.-O. Ka, 2011: Impact of Asian dust events on airborne bacterial community assessed by molecular analyses. *Atmos. Environ.*, **45**, 4313–4321, <https://doi.org/10.1016/j.atmosenv.2010.11.054>.
- Jiang, J., M. Yao, J. Hwang, and C. Wang, 2021: Bioaerosol: A key vessel between environment and health. *Front. Environ. Sci. Eng.*, **15**, 49, <https://doi.org/10.1007/s11783-021-1422-6>.
- Jones, R. M., and L. M. Brosseau, 2015: Aerosol transmission of infectious disease. *J. Occup. Environ. Med.*, **57**, 501–508, <https://doi.org/10.1097/JOM.0000000000000448>.
- Kakikawa, M., and Coauthors, 2009: Dustborne microorganisms in the atmosphere over an Asian dust source region, Dunhuang. *Air Qual., Atmos. Health*, **1**, 195–202, <https://doi.org/10.1007/s11869-008-0024-9>.
- Kepner, R. L., and J. R. Pratt, 1994: Use of fluorochromes for direct enumeration of total bacteria in environmental samples: Past and present. *Microbiol. Rev.*, **58**, 603–615, <https://doi.org/10.1128/mr.58.4.603-615.1994>.
- Kim, K. H., E. Kabir, and S. A. Jahan, 2018: Airborne bioaerosols and their impact on human health. *J. Environ. Sci.*, **67**, 23–35, <https://doi.org/10.1016/j.jes.2017.08.027>.
- Kutter, J. S., M. I. Spronken, P. L. Fraaij, R. A. M. Fouchier, and S. Herfst, 2018: Transmission routes of respiratory viruses among humans. *Curr. Opin. Virol.*, **28**, 142–151, <https://doi.org/10.1016/j.coviro.2018.01.001>.
- Lane, M. A., and Coauthors, 2020: Bioaerosol sampling of a ventilated patient with COVID-19. *Amer. J. Infect. Control*, **48**, 1540–1542, <https://doi.org/10.1016/j.ajic.2020.07.033>.
- Li, H., J. Qi, L. Dong, and D. Gao, 2017: Influence of dust events on the concentration and size distribution of microorganisms in bioaerosols (in Chinese). *Huan jing Ke xue*, **38**, 3169–3177.
- Liu, Q., Z. Huang, Z. Hu, Q. Dong, and S. Li, 2022: Long-range transport and evolution of Saharan dust over East Asia from 2007 to 2020. *J. Geophys. Res. Atmos.*, **127**, e2022JD036974, <https://doi.org/10.1029/2022JD036974>.
- Liu, T., and Coauthors, 2019: Bioaerosol concentrations and size distributions during the autumn and winter seasons in an industrial city of central China. *Aerosol Air Qual. Res.*, **19**, 1095–1104, <https://doi.org/10.4209/aaqr.2018.11.0422>.
- , and Coauthors, 2023: Identification of coexistence of biological and non-biological aerosol particles with DAPI (4',6-diamidino-2-phenylindole) stain. *Particology*, **72**, 49–57, <https://doi.org/10.1016/j.partic.2022.02.009>.
- Ma, Y., J. Zhou, S. Yang, Y. Zhao, and X. Zheng, 2017: Assessment for the impact of dust events on measles incidence in western China. *Atmos. Environ.*, **157**, 1–9, <https://doi.org/10.1016/j.atmosenv.2017.03.010>.
- Maki, T., and Coauthors, 2010: Phylogenetic analysis of atmospheric halotolerant bacterial communities at high altitude in an Asian dust (KOSA) arrival region, Suzu City. *Sci. Total Environ.*, **408**, 4556–4562, <https://doi.org/10.1016/j.scitotenv.2010.04.002>.
- , K. Hara, M. Yamada, F. Kobayashi, H. Hasegawa, and Y. Iwasaka, 2013: Epifluorescent microscopic observation of aerosol. *Earozoru Kenkyu*, **28**, 201–207, <https://doi.org/10.11203/jar.28.201>.

- , F. Puspitasari, K. Hara, M. Yamada, F. Kobayashi, H. Hasegawa, and Y. Iwasaka, 2014: Variations in the structure of airborne bacterial communities in a downwind area during an Asian dust (Kosa) event. *Sci. Total Environ.*, **488–489**, 75–84, <https://doi.org/10.1016/j.scitotenv.2014.04.044>.
- , and Coauthors, 2017: Variations in the structure of airborne bacterial communities in Tsogt-Ovoo of Gobi desert area during dust events. *Air Qual., Atmos. Health*, **10**, 249–260, <https://doi.org/10.1007/s11869-016-0430-3>.
- , and Coauthors, 2018: Long-range-transported bioaerosols captured in snow cover on Mount Tateyama, Japan: Impacts of Asian-dust events on airborne bacterial dynamics relating to ice-nucleation activities. *Atmos. Chem. Phys.*, **18**, 8155–8171, <https://doi.org/10.5194/acp-18-8155-2018>.
- , and Coauthors, 2019a: Vertical distributions of airborne microorganisms over Asian dust source region of Taklimakan and Gobi Desert. *Atmos. Environ.*, **214**, 116848, <https://doi.org/10.1016/j.atmosenv.2019.116848>.
- , and Coauthors, 2019b: Aeolian dispersal of bacteria associated with desert dust and anthropogenic particles over continental and oceanic surfaces. *J. Geophys. Res. Atmos.*, **124**, 5579–5588, <https://doi.org/10.1029/2018JD029597>.
- Mendis, H. C., V. P. Thomas, P. Schwientek, R. Salamzade, J.-T. Chien, P. Waidyarathne, J. Kloepper, and L. De La Fuente, 2018: Strain-specific quantification of root colonization by plant growth promoting rhizobacteria *Bacillus firmus* I-1582 and *Bacillus amyloliquefaciens* QST713 in non-sterile soil and field conditions. *PLOS ONE*, **13**, e0193119, <https://doi.org/10.1371/journal.pone.0193119>.
- Mirzabaev, A., and Coauthors, 2019: Desertification. *Climate Change and Land: An IPCC Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security, and Greenhouse Gas Fluxes in Terrestrial Ecosystems*, P. R. Shukla et al., Eds., IPCC, 249–343, <https://doi.org/10.1017/9781009157988.005>.
- Möhler, O., P. J. DeMott, G. Vali, and Z. Levin, 2007: Microbiology and atmospheric processes: The role of biological particles in cloud physics. *Biogeosciences*, **4**, 1059–1071, <https://doi.org/10.5194/bg-4-1059-2007>.
- Mostajir, B., J. R. Dolan, and F. Rassoulzadegan, 1995: A simple method for the quantification of a class of labile marine pico- and nano-sized detritus: DAPI Yellow Particles (DYP). *Aquat. Microb. Ecol.*, **9**, 259–266, <https://doi.org/10.3354/ame009259>.
- Mu, F., Y. Li, R. Lu, Y. Qi, W. Xie, and W. Bai, 2020: Source identification of airborne bacteria in the mountainous area and the urban areas. *Atmos. Res.*, **231**, 104676, <https://doi.org/10.1016/j.atmosres.2019.104676>.
- Pratt, K. A., and Coauthors, 2009: *In situ* detection of biological particles in cloud ice-crystals. *Nat. Geosci.*, **2**, 398–401, <https://doi.org/10.1038/ngeo521>.
- Puspitasari, F., T. Maki, G. Shi, C. Bin, F. Kobayashi, H. Hasegawa, and Y. Iwasaka, 2015: Phylogenetic analysis of bacterial species compositions in sand dunes and dust aerosol in an Asian dust source area, the Taklimakan Desert. *Air Qual., Atmos. Health*, **9**, 631–644, <https://doi.org/10.1007/s11869-015-0367-y>.
- Qi, J., Z. Huang, T. Maki, S. Kang, J. Guo, K. Liu, and Y. Liu, 2021: Airborne bacterial communities over the Tibetan and Mongolian Plateaus: Variations and their possible sources. *Atmos. Res.*, **247**, 105215, <https://doi.org/10.1016/j.atmosres.2020.105215>.
- , M. Ji, W. Wang, Z. Zhang, K. Liu, Z. Huang, and Y. Liu, 2022: Effect of Indian monsoon on the glacial airborne bacteria over the Tibetan Plateau. *Sci. Total Environ.*, **831**, 154980, <https://doi.org/10.1016/j.scitotenv.2022.154980>.
- , and Coauthors, 2023: Aridification alters the diversity of airborne bacteria in drylands of China. *Atmos. Environ.*, **315**, 120135, <https://doi.org/10.1016/j.atmosenv.2023.120135>.
- Quast, C., E. Priesse, P. Yilmaz, J. Gerken, T. Schweer, P. Yarza, J. Peplies, and F. O. Glöckner, 2012: The SILVA ribosomal RNA gene database project: Improved data processing and web-based tools. *Nucleic Acids Res.*, **41**, D590–D596, <https://doi.org/10.1093/nar/gks1219>.
- Rao, S., Y. Chan, D. C. Bugler-Lacap, A. Bhatnagar, M. Bhatnagar, and S. B. Pointing, 2015: Microbial diversity in soil, sand dune and rock substrates of the Thar Monsoon Desert, India. *Indian J. Microbiol.*, **56**, 35–45, <https://doi.org/10.1007/s12088-015-0549-1>.
- Šantl-Temkiv, T., P. Amato, E. O. Casamayor, P. K. H. Lee, and S. B. Pointing, 2022: Microbial ecology of the atmosphere. *FEMS Microbiol. Rev.*, **46**, fuac009, <https://doi.org/10.1093/femsre/fuac009>.
- Santos-Burgoa, C., I. Rosas, and A. Yela, 1994: Occurrence of airborne enteric bacteria in Mexico City. *Aerobiologia*, **10**, 39–45, <https://doi.org/10.1007/BF02066745>.
- Shen, F., and M. Yao, 2022: Bioaerosol nexus of air quality, climate system and human health. *Natl. Sci. Open*, **2**, 20220050, <https://doi.org/10.1360/nso/20220050>.
- Shin, S. K., D. Müller, C. Lee, K. H. Lee, D. Shin, Y. J. Kim, and Y. M. Noh, 2015: Vertical variation of optical properties of mixed Asian dust/pollution plumes according to pathway of air mass transport over East Asia. *Atmos. Chem. Phys.*, **15**, 6707–6720, <https://doi.org/10.5194/acp-15-6707-2015>.
- Soleimani, Z., P. Teymouri, A. Darvishi Boloorani, A. Mesdaghinia, N. Middleton, and D. W. Griffin, 2020: An overview of bioaerosol load and health impacts associated with dust storms: A focus on the Middle East. *Atmos. Environ.*, **223**, 117187, <https://doi.org/10.1016/j.atmosenv.2019.117187>.
- Sousa, S. I. V., F. G. Martins, M. C. Pereira, M. C. M. Alvim-Ferraz, H. Ribeiro, M. Oliveira, and I. Abreu, 2008: Influence of atmospheric ozone, PM10 and meteorological factors on the concentration of airborne pollen and fungal spores. *Atmos. Environ.*, **42**, 7452–7464, <https://doi.org/10.1016/j.atmosenv.2008.06.004>.
- Tang, K., and Coauthors, 2018: Characterization of atmospheric bioaerosols along the transport pathway of Asian dust during the Dust-Bioaerosol 2016 Campaign. *Atmos. Chem. Phys.*, **18**, 7131–7148, <https://doi.org/10.5194/acp-18-7131-2018>.
- Tignat-Perrier, R., A. Dommergue, A. Thollot, C. Keuschnig, O. Magand, T. M. Vogel, and C. Larose, 2019: Global airborne microbial communities controlled by surrounding landscapes and wind conditions. *Sci. Rep.*, **9**, 14441, <https://doi.org/10.1038/s41598-019-51073-4>.
- University of East Anglia Climatic Research Unit, I. C. Harris, P. D. Jones, and T. Osborn, 2021: CRU TS4.05: Climatic Research Unit (CRU) Time-Series (TS) version 4.05 of high-resolution gridded data of month-by-month variation in climate (Jan. 1901–Dec. 2020). NERC EDS Centre for Environmental Data Analysis, accessed 10 March 2022, <https://catalogue.ceda.ac.uk/uuid/c26a65020a5e4b80b20018f148556681>.
- Uno, I., and Coauthors, 2009: Asian dust transported one full circuit around the globe. *Nat. Geosci.*, **2**, 557–560, <https://doi.org/10.1038/ngeo583>.
- Wang, Y., Z. Huang, T. Zhou, J. Bi, and J. Shi, 2023: Identification of fluorescent aerosol observed by a spectroscopic lidar over northwest China. *Opt. Express*, **31**, 22157, <https://doi.org/10.1364/OE.493557>.
- Wu, Y.-H., C.-C. Chan, G. L. Chew, P.-W. Shih, C.-T. Lee, and H. J. Chao, 2012: Meteorological factors and ambient bacterial levels in a subtropical urban environment. *Int. J. Biometeor.*, **56**, 1001–1009, <https://doi.org/10.1007/s00484-011-0514-6>.
- Xie, W., Y. Li, W. Bai, J. Hou, T. Ma, X. Zeng, L. Zhang, and T. An, 2020: The source and transport of bioaerosols in the air: A review. *Front. Environ. Sci. Eng.*, **15**, 44, <https://doi.org/10.1007/s11783-020-1336-8>.
- Xie, Z., Y. Li, R. Lu, W. Li, C. Fan, P. Liu, J. Wang, and W. Wang, 2018a: Characteristics of total airborne microbes at various air quality levels. *J. Aerosol Sci.*, **116**, 57–65, <https://doi.org/10.1016/j.jaerosci.2017.11.001>.
- , and Coauthors, 2018b: Characteristics of ambient bioaerosols during haze episodes in China: A review. *Environ. Pollut.*, **243**, 1930–1942, <https://doi.org/10.1016/j.envpol.2018.09.051>.
- Xu, C., and Coauthors, 2017: Bacterial characterization in ambient submicron particles during severe haze episodes at Ji'nan, China. *Sci. Total Environ.*, **580**, 188–196, <https://doi.org/10.1016/j.scitotenv.2016.11.145>.
- , and Coauthors, 2021: Diverse bacterial populations of PM2.5 in urban and suburb Shanghai, China. *Front. Environ. Sci. Eng.*, **15**, 37, <https://doi.org/10.1007/s11783-020-1329-7>.



- Yankofsky, S. A., Z. Levin, T. Bertold, and N. Sandlerman, 1981: Some basic characteristics of bacterial freezing nuclei. *J. Appl. Meteor.*, **20**, 1013–1019, [https://doi.org/10.1175/1520-0450\(1981\)020<1013:SBCOBF>2.0.CO;2](https://doi.org/10.1175/1520-0450(1981)020<1013:SBCOBF>2.0.CO;2).
- Yin, Y., J. Qi, J. Gong, and D. Gao, 2021: Distribution of bacterial concentration and viability in atmospheric aerosols under various weather conditions in the coastal region of China. *Sci. Total Environ.*, **795**, 148713, <https://doi.org/10.1016/j.scitotenv.2021.148713>.
- Zhai, Y., X. Li, T. Wang, B. Wang, C. Li, and G. Zeng, 2018: A review on airborne microorganisms in particulate matters: Composition, characteristics and influence factors. *Environ. Int.*, **113**, 74–90, <https://doi.org/10.1016/j.envint.2018.01.007>.
- Zhao, X., K. Huang, J. S. Fu, and S. F. Abdullaev, 2022: Long-range transport of Asian dust to the Arctic: Identification of transport pathways, evolution of aerosol optical properties, and impact assessment on surface albedo changes. *Atmos. Chem. Phys.*, **22**, 10389–10407, <https://doi.org/10.5194/acp-22-10389-2022>.
- Zhen, Q., Y. Deng, Y. Wang, X. Wang, H. Zhang, X. Sun, and Z. Ouyang, 2017: Meteorological factors had more impact on airborne bacterial communities than air pollutants. *Sci. Total Environ.*, **601–602**, 703–712, <https://doi.org/10.1016/j.scitotenv.2017.05.049>.
- Zhou, S.-Y.-D., H. Li, M. Giles, R. Neilson, X. Yang, and J. Su, 2021: Microbial flow within an air-phyllosphere-soil continuum. *Front. Microbiol.*, **11**, 615481, <https://doi.org/10.3389/fmicb.2020.615481>.