

## Aridification alters the diversity of airborne bacteria in drylands of China

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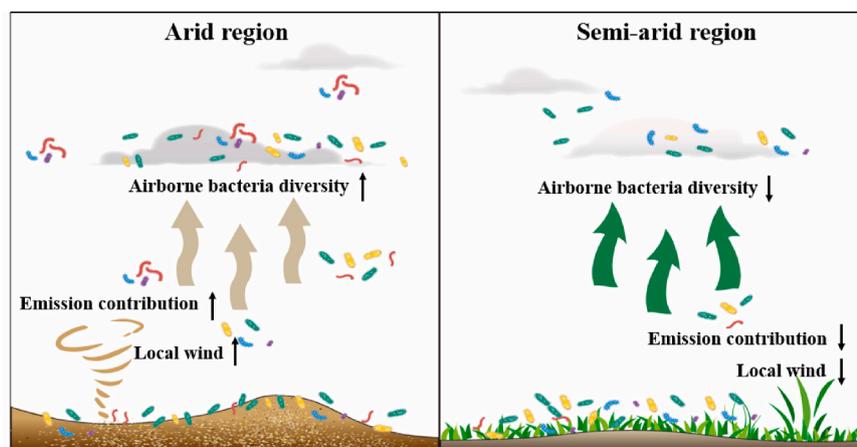
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### HIGHLIGHTS

- Bacterial diversity in the atmosphere was lower than that in terrestrial ecosystems.
- Drought significantly increases the diversity of bacteria in the atmosphere.
- The contribution of terrestrial bacteria to the atmosphere increases during drought.

### GRAPHICAL ABSTRACT



### ARTICLE INFO

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### ABSTRACT

Dryland ecosystems, which vary sensitively to drought owing to climate change and human activities, frequently cause large-scale aeolian dispersal of terrestrial-mineral and biological particles. To date, very few studies have focused on the atmosphere-land exchange of bacteria in drylands. To understand the bacterial transport from the terrestrial environment to the atmosphere over drylands, soil and aerosol samples were collected at 19 sites in arid and semi-arid regions across drylands of China in the summer of 2017. The 16S rRNA gene sequencing revealed that the bacterial diversity in the atmosphere was significantly lower than that in terrestrial ecosystems for all the collected samples. Moreover, bacterial diversity in the atmosphere increases in arid regions compared to semi-arid regions, while those of the terrestrial environment were maintained regardless of the region. Additionally, the terrestrial bacterial sources contributed to the airborne bacteria more significantly in arid regions than those in semi-arid regions (accounting for  $10.0 \pm 1.1\%$  and  $3.5 \pm 1.1\%$ , respectively). The arid

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conditions tended to enhance the atmospheric emissions of *Chloroflexi*, while the members of *Bacteroidetes* were dominant in both the atmospheres of the semi-arid and arid regions. The differences in bacterial community structures between the terrestrial and atmospheric ecosystems are thought to depend on the ground surface characteristics such as vegetation and terrestrial substrates. Meteorological drought may alter terrestrial characteristics, which regulate airborne bacterial dispersal from dryland to its downwind regions, suggesting that more attention should be paid to the bacterial roles in the biology-health-climate process in the future.

## 1. Introduction

Land degradation causes serious issues in Asia and reduces the land capacity that provides ecosystem goods, services, and functions in China (Zhuge et al., 2019). The regions facing the most severe problems of land degradation are located in northern China (Wang et al., 2015), where there are large areas of fragile and unstable dryland ecosystems (Hu et al., 2021a; Wang et al., 2017). Dryland ecosystems include arid and semi-arid regions characterized by low precipitation and soil fertility (de-Bashan et al., 2022). The period of moisture deficiency relative to the average values in a region causes meteorological droughts, which have frequently increased to severe levels in the 21st century (Zou et al., 2005). Increasing meteorological drought can have significant impacts on the structure and functioning of dryland ecosystems (Neff et al., 2008; Prospero et al., 2012). Meteorological drought can reduce soil organic carbon and exacerbate the loss of soil microbial diversity (Jiao et al., 2021a, 2021b; Maestre et al., 2015b). It can even lead to weakened plant-microbe interactions and increased incidence of certain soil diseases (de Vries et al., 2018; Hu et al., 2021b), which may seriously affect dryland ecosystem functions (Huang et al., 2016; Li et al., 2015). In addition, drought-induced catastrophic weather phenomena, such as dust events (Jalali et al., 2021) promotes airborne microbial dispersal among spatially separated natural ecosystems (Kellogg and Griffin, 2006). Thus, microbial dispersal profoundly impacts downwind ecosystems (Maki et al., 2015), the global atmosphere (Behzad et al., 2018; Huang et al., 2006), and human health (Pointing and Belnap, 2014).

Bacteria are the main components of bioaerosols, accounting for more than 80% of their total composition (Yan et al., 2022). Because bacteria can be aerosolized from the surface of almost all ecosystems (Smets et al., 2016), terrestrial ecosystems are considered primary emission sources of airborne bacteria (Burrows et al., 2009). In addition, aerosol generation at the terrestrial/atmosphere interface is thought to be one of the main mechanisms of microbial transport to the atmosphere (Joung et al., 2017). However, the microbial emission processes are regulated by variable factors of interface ground surfaces (Santil-Temkiv et al., 2022), such as the vegetation-cover composition (Zhou et al., 2021) and soil viscosity (Joung et al., 2017). The surface soils contribute to the atmospheric microbial emission at 1–8% (Mu et al., 2020). Furthermore, relationships between land-use types and airborne bacteria have been observed (Bowers et al., 2010). Stochastic and extrinsic forces caused by meteorological drought, causing dust and wildfires (Gonzalez-Toril et al., 2020), affect the dispersal of many bacterial species in ecosystems (Lowe and McPeck, 2014). Earlier research has demonstrated that high-energy wind conditions can mobilize significant amounts of terrestrial particles into the atmosphere (Gillies et al., 1996; Qian et al., 2002). Moreover, large dust events dispersed bacteria over long distances via high-altitude wind (Maki et al., 2019), contributing substantially to the bioaerosol content in the downwind atmosphere (Huang et al., 2008; Tang et al., 2018). However, previous studies have focused mainly on the airborne bacterial distributions in drylands without the terrestrial bacterial database. Therefore, microbial species transported from local soil to the atmosphere remain unclear even under meteorological drought conditions. Thus, the field investigations comparing the terrestrial and atmospheric bacterial communities among different arid-level drylands are required to understand the soil ecosystem variations caused by meteorological drought, which contribute to airborne bacterial dispersions.

In drylands of China, which is located at the margin of the global dust belt (Gobi Desert), dust events frequently occur (Jalali et al., 2021), and semi-arid regions rapidly develop into arid regions due to meteorological drought conditions (Griffin-Nolan et al., 2019; Huang et al., 2014). To investigate the contribution of atmosphere-terrestrial exchange in arid and semi-arid regions, we collected the aerosol and soil samples across drylands of China in August 2017. Bacterial community structures were compared between ecosystems (atmosphere and local soil) and regions (arid and semi-arid), and then the bacterial transports abundances were further quantified from terrestrial to atmospheric ecosystems.

## 2. Materials and methods

### 2.1. Field campaign and sampling

The arid and semi-arid regions of Inner Mongolia in drylands of China are dominated by plateaus, most of which are over 1000 m above sea level (Table S1). In these regions, dust events, due to frequent wind blowing and periodic droughts, damage ecosystems in some regions, seriously affecting human productivity and life (Wang et al., 2015). In this study, aerosol samples were collected 1.5 m above the ground at 19 sites across Inner Mongolia in drylands of China, along with the soil samples (Fig. 1). The sampling sites were located approximately 2.5–5 km away from residential areas. We use the datasets of normalized difference vegetation index (NDVI) values, aridity index (AI), google map observations and field observations (Dias et al., 2016), classified all sampling sites into two groups: arid regions (NDVI between 0 and 0.3, AI < 0.2, bare soil), and semi-arid regions (NDVI > 0.3, 0.2 ≤ AI < 0.5, sparse grassland) (Salinas-Zavala et al., 2017). Detailed information regarding the sampling sites is provided in Table S1 and Fig. S1.

Samples were conducted under sunny conditions, eliminating the influence of particular meteorological events. One to three samples were collected at each site according to weather conditions and logistic limitations. A total of 33 samples were collected in August 2017 (Table S1). Polycarbonate filters (0.2 μm pore-size; GTTP01300) were set in a sterilized Swinnex 13 mm filter holders (Millipore SX0001300) and aerosols were collected onto the filter using an air pump with a flow of approximately 2.5 L min<sup>-1</sup> for 4–12 h (Qi et al., 2021). The soil samples from each site were mixed with 20 soil drills of 5 cm in diameter and collected in sterile self-sealing bags. The aerosol and soil samples were kept frozen at –20 °C in a laboratory before further analysis.

### 2.2. High-throughput sequencing and statistical analysis

Genomic DNA (gDNA) was extracted from the aerosol and soil samples using the phenol-chloroform method (Maki et al., 2017). During polymerase chain reaction (PCR) amplification, the hypervariable V4 region of the 16S rRNA gene was studied using 515F and 806R primers with tag sequences (Caporaso et al., 2012). The PCR amplicons were used for high throughput sequencing using a MiSeq Genome Sequencer with MiSeq Reagent Kit V2 (Illumina, CA, USA) (Maki et al., 2017). Each sample had paired-end sequences with a read length of >250 bp, which were grouped based on tag sequences. Blank controls were used for the DNA extraction and PCR amplification. These negative controls yielded no PCR amplicons, indicating that the experimental procedure was contamination free.

Taxonomic analyses of raw sequences were performed using the Quantitative Insights into Microbial Ecology pipeline (QIIME2; version 2021.04) (Almeida et al., 2018; Caporaso et al., 2010). Briefly, raw paired-end sequences were imported into QIIME2 for all sequenced samples, demultiplexed, and quality filtered with q2-demux and DADA2 denoise plugins (Callahan et al., 2016). The high-quality sequence results were clustered as amplicon sequence variants (ASVs) with 99% identity for downstream analysis. The taxonomic assignment of the ASVs was performed using the SILVA (v132) reference database (Quast et al., 2013). After taxonomic determination, non-bacterial ASV sequences (such as chloroplasts, mitochondria, archaea, and unclassified sequences) were excluded from subsequent analyses. The raw sequences were uploaded to the NCBI SRA database (BioProject accession number PRJNA1011030).

Alpha-diversity indices (Shannon and Chao1 indices) were calculated, and Wilcoxon tests of variance were used to analyze the significant difference between different ecosystems (atmosphere and soil) and regions (arid and semi-arid). Distance-based community analyses were based on Bray-Curtis dissimilarities. We performed non-metric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities and 999 permutations (Kusstatscher et al., 2020). All analyses were performed using the ‘vegan’ and ‘ggplot2’ (Ginestet, 2011) packages in R (Grunsky, 2002). A source tracker was used to identify the specific contribution of the local surface soil to airborne bacterial communities (Knights et al., 2011).

### 2.3. Meteorological data

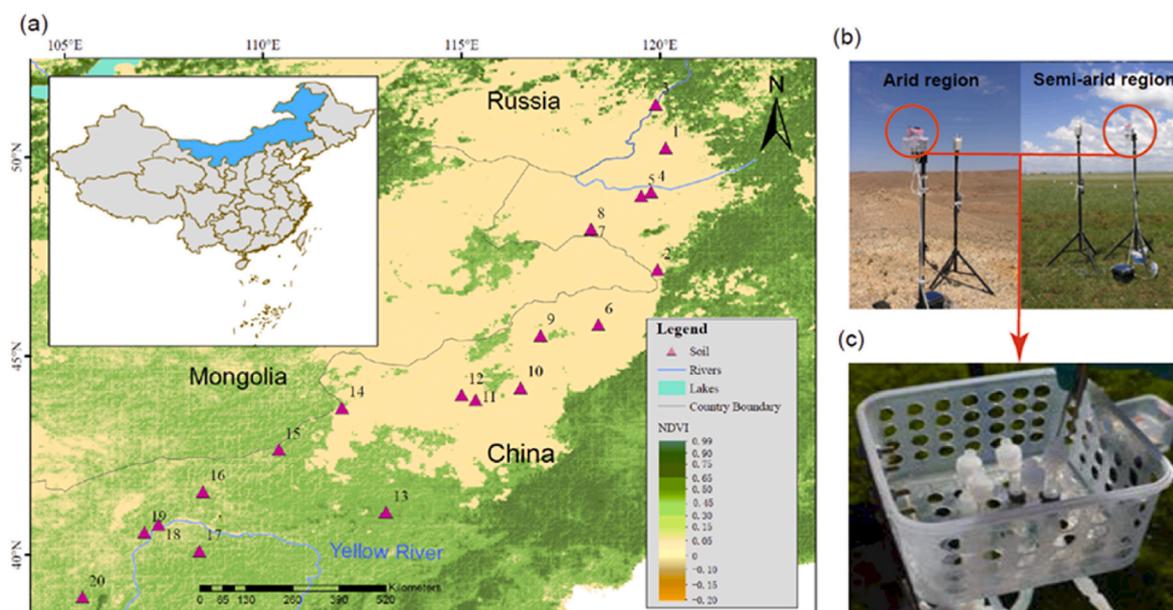
The geographic classification of drylands is based on aridity index (AI), which can be calculated as the ratio of precipitation (PRE, unit: mm) to Potential Evapotranspiration (PET, unit: mm) (Beštáková et al., 2022). The PRE and PET dataset is from the Climatic Research Unit year-by-year variation of selected climate variables by country version 4.05, January 2011–December 2020 ([https://data.ceda.ac.uk/badc/cru/data/cru\\_cy/cru\\_cy\\_4.05/data](https://data.ceda.ac.uk/badc/cru/data/cru_cy/cru_cy_4.05/data)). The classification of AI is arid ( $AI \leq 0.2$ ) and semi-arid ( $0.2 < AI \leq 0.65$ ) regions (Beštáková et al., 2022). The normalized difference vegetation index (NDVI) in 2017 download from moderate resolution imaging spectroradiometer (MODIS, <https://modis.gsfc.nasa.gov/data/dataproduct/mod13.php>) was used to

reaffirm the classification of arid ( $0 \leq NDVI \leq 0.3$ ) and semi-arid ( $NDVI > 0.3$ ) regions (Gu et al., 2007). In addition, meteorological data is acquired through automatic weather stations. Mean daily temperature values ranged from 16.1 to 25.8 °C, and mean wind speeds ranged from 0.2 to 9.1 m s<sup>-1</sup>.

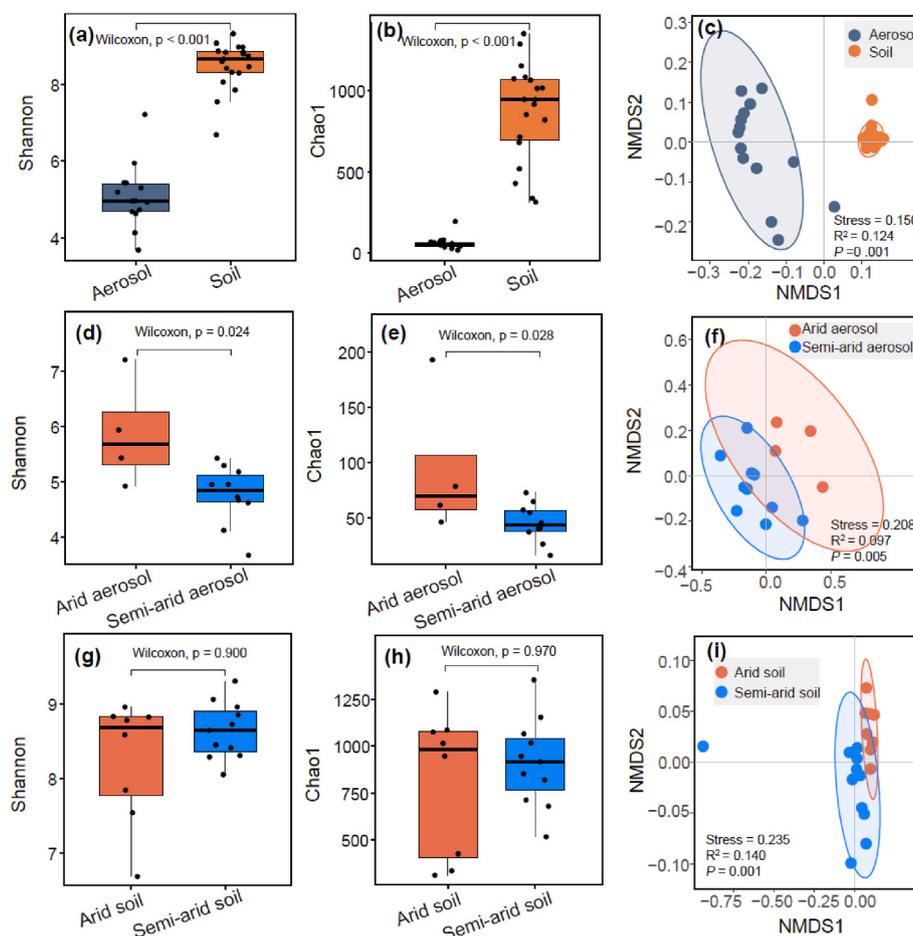
## 3. Results and discussion

### 3.1. Bacterial diversity and community structure in the atmosphere and land

The sequencing database obtained from the aerosol and soil samples was composed of 8920 ASVs. The numbers of ASV in the soil samples of the arid and semi-arid regions were 5760 and 3778, respectively, and those of in the aerosol samples were reduced to 354 and 337, respectively (Fig. 4b). In addition, the Shannon diversity and Chao1 indices in the aerosol samples showed values ranging from 3.7 to 5.9 (mean = 5.0) and from 21 to 191 (mean = 56), respectively, which were significantly lower (Wilcoxon,  $P < 0.001$ , Fig. 2a and b) than those of the soil samples ranging from 7.7 to 9.6 (mean = 8.7) and from 281 to 1289 (mean = 825), respectively. The atmospheric stressors, such as stronger UV radiation and desiccation, can damage the bacterial cells transported from the soil ecosystem to the atmosphere (Pan et al., 2021). Some populations of airborne bacteria can maintain viabilities under the selection process by stressors, consequently limiting bacterial diversity in the atmosphere (Qi et al., 2022). Therefore, the atmospheric environment is not conducive to the growth and reproduction of bacterial communities (Santl-Temkiv et al., 2022). In addition, the alpha diversity of bacteria varied between the arid and semi-arid regions. The Shannon diversity and Chao1 indices of the aerosol samples were significantly higher in arid regions than in semi-arid regions (Wilcoxon,  $P = 0.028$ , Fig. 2d and e), whereas those of the soil samples were similar between arid and semi-arid regions (Wilcoxon,  $P = 0.900$  and  $0.970$ , Fig. 2g and h). Atmospheric bacterial diversity is known to vary in the correspondence with the surrounding habitat of ground surfaces, such as vegetation, and the aerosols-terrestrial exchange with surface ecosystems (Zhao et al., 2022). Moreover, the similar soil characteristics of arid and semi-arid regions would maintain the same bacterial diversity in the soil ecosystem. Low soil moisture (Maestre et al., 2015a), limited vegetation cover (Indoitu et al., 2012), and loose soil in arid regions are thought to



**Fig. 1.** Map of the 19 sampling sites in the drylands of China showing the normalized difference vegetation index (NDVI) (a). The bioaerosols sampler was used in the arid and semi-arid regions (b) and the aerosols were collected on the filters in the filter folders (c).



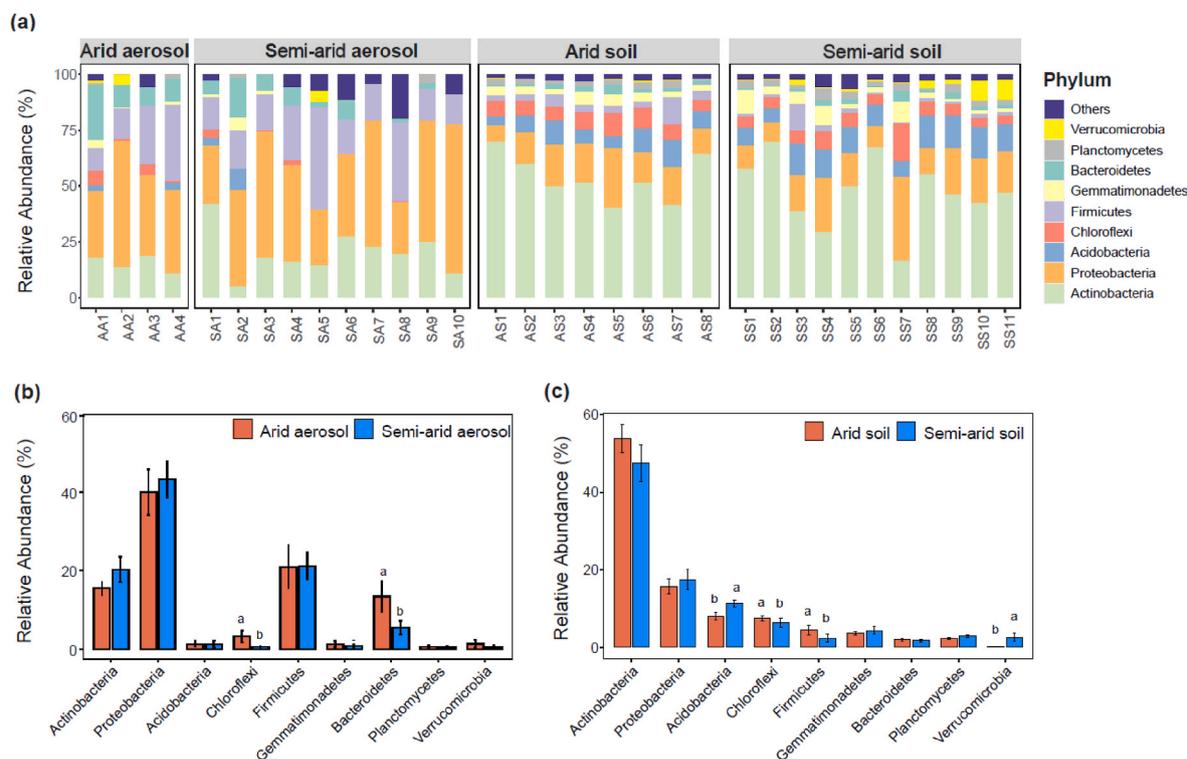
**Fig. 2.** The bacterial diversities (Shannon and Chao1 indices) and community structures (non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities) in the aerosol and soil samples (a–c). Each ecosystem sample of aerosol (d–f) and soil (g–i) was compared between the arid and semi-arid regions. The box ranges from the 25th percentile to the 75th percentile and the cross-bars in the box show medium values.

induce the bacterial transport from the ground surfaces to the atmosphere. Large amounts of mineral particles emissions from the arid drier soils induce the bacterial transports to the atmosphere during dust events under an external wind force (Li et al., 2021).

On the NMDS coordinates of the Bray–Curtis dissimilarity, the bacterial compositions in the aerosol and soil samples each formed cluster (PERMANOVA,  $P = 0.001$ , Fig. 2c). The atmosphere and soil ecosystems have different bacterial community structures owing to the screening mechanisms of bacterial populations from the soil to the atmosphere (Smith et al., 2013). Research has shown that different ecosystems, such as terrestrial, marine, forest, and industrial areas, have specific microbes (Fröhlich-Nowoisky et al., 2016). The bacterial compositions in the atmosphere varied in correspondence to the atmospheric circulation and connectivity more dynamically in comparison to those of the soil samples (Fig. 2c). In addition, the NMDS coordinates showed that the aerosol-sample clusters were separated distinctly between the arid and semi-arid regions (PERMANOVA,  $P = 0.005$ , Fig. 2f), and the soil samples also differed between the arid and semi-arid regions (PERMANOVA,  $P = 0.001$ , Fig. 2i). The different environments between the arid and semi-arid regions would change the bacterial community structures in the aerosol and soil samples (Maestre et al., 2015a). In extremely arid regions, the wind blowing during dust events easily carries high amounts of bacteria affecting downwind environments (Maki et al., 2018).

### 3.2. Bacterial taxonomy composition and exchange in the atmosphere and land

The bacterial taxonomic compositions in the aerosol samples were predominantly composed of the members of the phyla *Proteobacteria* (42.3%), *Firmicutes* (21.2%), *Actinobacteria* (19.0%), and *Bacteroidetes* (7.8%) (Fig. 3a), and those of the soil samples were dominated by the members of the phyla, *Actinobacteriota* (50.2%), *Proteobacteria* (16.8%), *Acidobacteria* (10.0%), and *Chloroflexi* (6.9%). The relative abundances of *Chloroflexi* and *Firmicutes* in the soil samples was significantly higher in the arid region than that in the semi-arid region (Fig. 3c). Soil environments were frequently dominated by the relative abundance of *Chloroflexi* and *Firmicutes* members (Coban et al., 2022), which can resist desiccation by developing a thick peptidoglycan layer (Battistuzzi and Hedges, 2009) and producing endospores (Nicholson et al., 2000). Furthermore, the aerosol samples contained significantly higher abundances of *Chloroflexi* sequences in the arid regions than in the semi-arid regions (Fig. 3b) because of differences in the soil characteristics, such as high temperatures, low moisture, and no vegetation (Coban et al., 2022). *Chloroflexi* in the arid-region soil had higher abundances than that in the semi-arid regions (Fig. 3c), suggesting that this bacterial population is more likely released into the atmosphere under frequent and strong wind blowing. The *Bacteroidetes* sequences in the soil samples exhibited similar abundances in arid and semi-arid regions (Fig. 3c), whereas those of the aerosol samples were significantly higher in arid regions than in semi-arid regions (Fig. 3b). *Bacteroidetes* members are generally detected as dominant species in the atmosphere and are passively emitted from the soil surface into the atmosphere under



**Fig. 3.** The relative abundances of bacteria in the aerosol and soil samples, which were collected in the arid and semi-arid regions. The bacterial taxonomic compositions at the phylum level (relative abundance >1%) in the aerosol and soil samples (a). The relative abundances of some bacterial phyla in the aerosol (b) and soil (c) samples were compared between the arid and semi-arid regions. Significant differences between regions are indicated by a and b ( $P < 0.05$ ). Error bars were calculated for each sample number in the aerosol and soil samples in the arid and semi-arid regions.

external dust events (Fröhlich-Nowoisky et al., 2016). In addition, the some species of *Bacteroidetes* are known to attach to coarse particles and frequently remain in the atmosphere for a long time (Maki et al., 2017). The attachment of *Bacteroidetes* members to coarse particles supports the tolerance against UV radiation and desiccation in the atmosphere (Qi et al., 2021).

### 3.3. Contribution of terrestrial source to airborne bacteria

Source tracking results showed that the soil sources of airborne bacteria were significantly higher in arid regions than that in semi-arid regions ( $P = 0.014$ , accounting for  $10.0 \pm 1.1\%$  and  $3.5 \pm 1.1\%$ , respectively, Fig. 4a). Moreover, the DNA sequencing analyses also revealed that the overlapped ASV between the aerosol and soil samples was 46 ASVs in the arid regions, whereas there were only 13 ASVs in the arid regions (Fig. 4b). Previous studies have found that the terrestrial bacterial communities are thought to be natural source of airborne bacteria (Xie et al., 2021), and the bacteria originating from surface soil occupy the airborne bacteria at the relative abundances ranging from 1 to 8% (Mu et al., 2020). However, our study further revealed that the soil sources of airborne bacteria are more abundant in arid regions. The emission of terrestrial bacteria is closely related to vegetation coverage, soil moisture and wind speed. Vegetation cover is known to regulate aerosol emissions from the ground terrestrial surface (Zhou et al., 2021) with several soil viscosities (Joung et al., 2017). Therefore, arid areas with low vegetation cover are more likely to emit dust with bacteria. In addition, lower soil moisture in arid regions facilitate dust events from ground surfaces, thus, increasing bacterial transport into the atmosphere (Mu et al., 2020). Study has been found that bacterial cells attached to mineral particles can be transported into the atmosphere by wind blowing (Burrows et al., 2009; Liu et al., 2019). It is proved that high wind speeds can enhance the movement of microorganisms from the soil and surface into the air (Wei et al., 2019). For example, mountainous

and urban regions with higher wind speeds in autumn released more bacterial abundances into the atmosphere (Qi et al., 2020). Furthermore, the transport conditions from surface soil to airborne bacteria may vary seasonally due to agricultural activities in autumn, increasing the frequency of airborne bacterial transports (Mu et al., 2020). The sampling sites of this study were near the arid region of China (the Gobi Desert), where dust event frequently occurs (Jalali et al., 2021) and promotes the diffusion of airborne microorganisms in spatially separated natural ecosystems (Kellogg and Griffin, 2006). Model simulation has shown that the world's major deserts can inject about 0.5–1 billion tons of dust into the atmosphere every year (Perkins, 2001). Dust events that import bacteria into the atmosphere and travel long distances with the dust plumes may carry large numbers of bacteria into the plume's path (Murata and Zhang, 2016). In summary, large quantities of arid soil can be transported by dust winds for thousands of kilometers (Kellogg and Griffin, 2006) and increase airborne bacterial abundances in downwind areas during dust events (Griffin et al., 2006; Maki et al., 2019; Tang et al., 2018). Transported dusts may also carry pathogens and allergens, potentially impacting the health of human downwind (Jones and Brosseau, 2015).

## 4. Conclusions

To evaluate atmosphere-terrestrial exchange in the arid and semi-arid regions, we analyzed the bacterial communities in the aerosol and soil samples from 19 sites across drylands of China. The results showed that airborne bacterial diversity and community structures varied greatly between the arid and semi-arid regions, owing to ground-surface characteristics such as vegetation cover. The airborne bacterial diversity was significantly higher in the arid regions than that in the semi-arid regions, and the airborne bacterial communities originated from the soil in the arid regions ( $10.0 \pm 1.1\%$ ) more than that in the semi-arid regions ( $3.5 \pm 1.1\%$ ). Moreover, the bacteria carried by dust winds

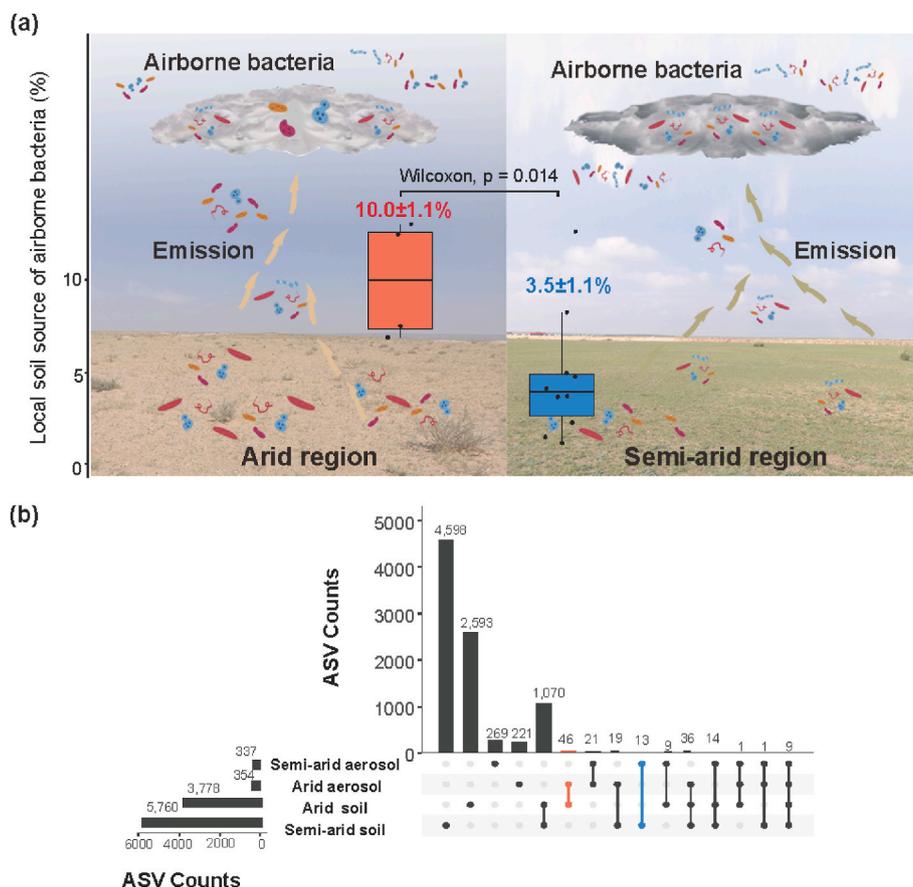


Fig. 4. Upper panel: contribution of local soil sources to airborne bacteria in arid and semi-arid regions, respectively (a). Lower panel: 16S rRNA gene amplicon sequence variants (ASVs) count occurrence of bacterial taxa for aerosol and soil in arid and semi-arid regions (b).

may potentially impact the downwind-microbial ecosystems. The bacterial sequencing database will help to evaluate the bacterial community variations in dryland environments and provide additional insights into the response of soil bacterial communities to meteorological drought. Thus, the bacterial emissions from the earth ground surfaces into the atmosphere should be estimated and contribute to the simulation of the global environment-climate-health model.

**CRedit authorship contribution statement**

**Jing Qi:** Writing – original draft, Formal analysis, Visualization. **Zhongwei Huang:** Conceptualization, Funding acquisition, Writing – review & editing, Project administration. **Fanli Xue:** Writing – review & editing. **Zhaokui Gao:** Investigation. **Teruya Maki:** Writing – review & editing. **Zhihao Zhang:** Data curation, Formal analysis. **Keshao Liu:** Writing – review & editing. **Mukan Ji:** Writing – review & editing. **Yongqin Liu:** Writing – review & editing.

**Declaration of competing interest**

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

**Data availability**

Data will be made available on request.

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**Appendix A. Supplementary data**

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.atmosenv.2023.120135>.

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