Airborne bacterial communities over the Tibetan and Mongolian Plateaus: variations and their possible sources

Jing Qi[a,d,h], Zhongwei Huang[b,*], Teruya Maki[c], Shichang Kang[e,f,g], Junming Guo[e], Keshao Liu[d,g], Yongqin Liu[d,f,g,h]

[a] School of Life Sciences, Lanzhou University, Lanzhou 730000, China
[b] Key Laboratory for Semi-Arid Climate Change of the Ministry of Education, College of Atmospheric Sciences, Lanzhou University, Lanzhou 730000, China
[c] College of Science and Engineering, Kanazawa University, Kakuma 920-1192, Japan
[d] Key Laboratory of Tibetan Environment Changes and Land Surface Processes, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, China
[e] State Key Laboratory of Cryosphere Science, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China
[f] CAS Center for Excellence in Tibetan Plateau Earth Sciences, Beijing 100101, China
[g] University of Chinese Academy of Sciences, Beijing 100049, China
[h] Frontier Center for Eco-environment and Climate Change in Pan-third Pole Regions, Lanzhou 730000, China

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ABSTRACT

The transportation of atmospheric bacteria is increasingly recognized as an important factor that affects bacterial diversity in natural environments as well as human health. However, few studies have investigated airborne bacterial biodiversity in extremely remote, arid, and cold environments, such as desert and alpine areas, which may contain ambient bacteria transported by air masses. In this study, atmospheric aerosol samples were collected from the southern slope of the Himalayas, the southern Tibetan Plateau and the Mongolian Plateau to analyze the diversity of airborne bacteria and its relationship to environmental factors. The results show that the bacterial communities in all samples were predominantly composed of Proteobacteria, Actinobacteria, Firmicutes, and Bacteroidetes. Furthermore, the community structures of airborne bacteria exhibited significant differences among the collected sample, these differences mainly depended on meteorological parameters (P values < 0.01). In particular, the aerosol samples over the Tibetan Plateau showed the lowest diversity among the three regions. This suggests that the variability in airborne bacterial communities is determined by meteorological parameters and long-range transportation. Our study provides new information about airborne bacterial community composition in extreme environments and its large-scale spatial variability.

1. Introduction

As an important component of bioaerosols, airborne bacteria originate from terrestrial and aquatic environments and are carried through the free troposphere to downwind regions, combining with mineral particles and organic debris during transport (Burrows et al., 2009; Kakikawa et al., 2009; Maki et al., 2017a; Pearce et al., 2009; Sattler et al., 2001). Airborne bacteria actively participate in the physical and chemical processes of the atmosphere (Fröhlichnowoisky et al., 2016), such as the formation of ice nuclei (IN) and cloud condensation nuclei (CCN), and thereby influence climatic change, i.e., precipitation, cloud dynamics and solar-radiation regulation (Amato et al., 2005; Augustinbauditz et al., 2016; Harrison et al., 2018; Jones and Harrison, 2004; Kakikawa et al., 2009; Kunert et al., 2018; Peng et al., 2019; Sahu and Tangutur, 2014). During cloud formation,

bacteria can attach to particles or be carried into cloud droplets to be deposited back to the land by either dry or wet deposition, respectively (Monteil et al., 2014). The deposition of airborne bacteria has a potential impact on the diversity and function of atmospheric and terrestrial ecosystems (Delort et al., 2010). These bacteria can also play an important role in geochemical cycling, agricultural productivity, ecosystem dynamics, and human health (Mbareche et al., 2018; Perrino and Marcovecchio, 2016; Reinmuthselzle et al., 2017; Sahu and Tangutur, 2014; Smets et al., 2016).

Most bacterial communities in the atmosphere are comprised of four main phyla: Actinobacteria, Bacteroidetes, Firmicutes, and Proteobacteria (Cuthbertson et al., 2017). However, at the genus level, airborne bacteria are variable, depending on their adaptation to environmental conditions. Moreover, variations in meteorological parameters (e.g., wind speed, wind direction, temperature, and relative
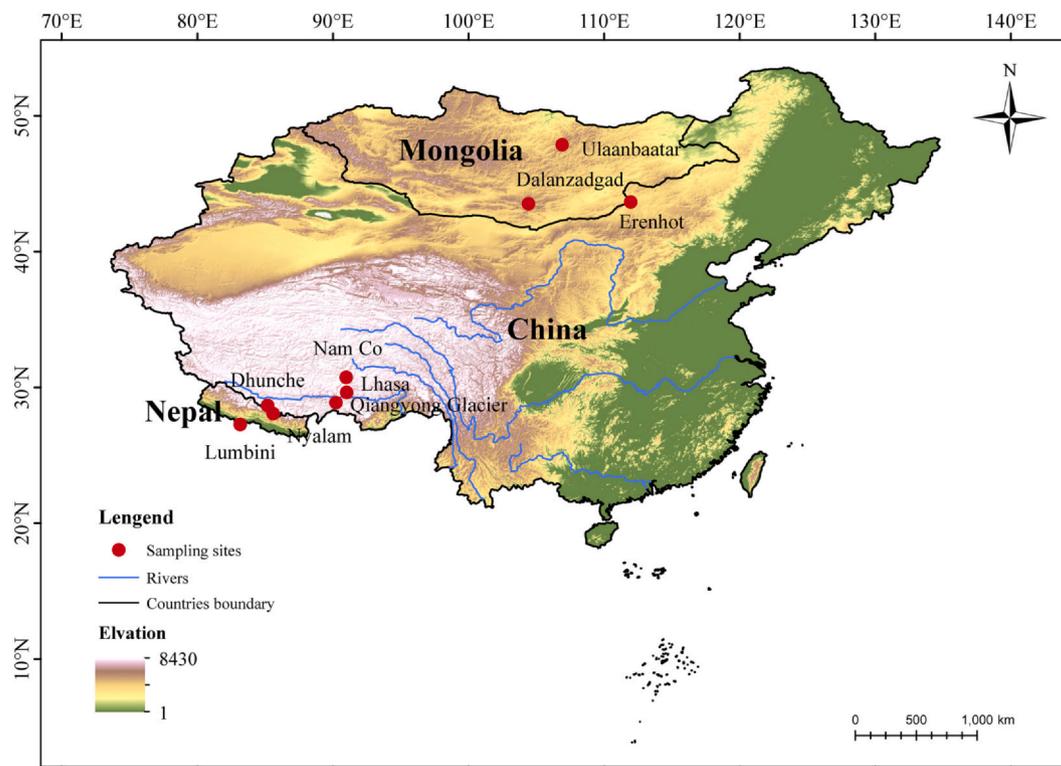

Fig 1. Sampling locations of airborne bacteria in three countries, Nepal (Lumbini and Dhunche), China (Lhasa, Nam Co, Qiangyong Glacier, Nyalam, and Erenhot) and Mongolia (from Dalanzadgad to Ulaanbaatar). The contour colors represent elevation of the region.

humidity) (Bowers et al., 2012; Jones and Harrison, 2004; Seifried et al., 2015) and sampling location (Bowers et al., 2011a; Bowers et al., 2011b; Burrows et al., 2009; Pearce et al., 2010) can directly affect the composition of the airborne bacterial community. Between the North and Baltic Seas the airborne bacterial communities were strongly affected by temperature, wind direction, and sample location (Seifried et al., 2015). Airborne bacterial populations in western Oregon, U.S.A. were positively correlated with temperature and negatively correlated with relative humidity across all four seasons (Tong and Lighthart, 2000). Li et al. (2018) also found that relative humidity was a key factor that significantly affected the airborne bacterial communities. Moreover, Uetake et al. (2019) suggested that bacterial community composition and diversity were affected by local meteorology, especially relative humidity and wind speed, while long-range transport, from oceans or continents, was not the principal determinant controlling local airborne bacterial communities. However, Hervas and Casamayor (2009) found that the bacterial community composition of the surface film of a remote high mountain lake was influenced by airborne bacteria from dust deposited on the surrounding snow pack. In the wake of recent discoveries, there is a growing interest in investigating the transport of airborne bacteria via air masses over long distances.

In East Asia, westerly winds blowing at high altitudes are reported to carry microbial particles over long distances. Airborne bacterial communities in the upwind regions of these winds are important for understanding the long-range transport processes of airborne bacteria and their influences on ecosystem dynamics, human health, and climate change in downwind areas. Airborne bacterial concentrations, which generally range from 10^4 to 10^6 particles·m^{-3} (Cuthbertson et al., 2017), increase to higher concentrations of 10^7 to 10^9 particles·m^{-3}, during dust events originating from the Gobi and Taklimakan Deserts (Maki et al., 2017b). Tang et al. (2018) found that the dominant members of airborne bacterial communities over northern China were transported from the Gobi Desert by Asian dust events. Other studies also corroborate the transport of similar taxonomic bacteria from Asian desert areas by westerly winds (Maki et al., 2017a; Maki et al., 2017b).

Mescioglu et al. (2019) demonstrated that airborne bacterial diversity is positively correlated with the mineral dust content in aerosols. African dust events increased the diversity of airborne bacterial communities (Romano et al., 2019). Long-range transport and local winds affect the airborne bacterial composition (Innocente et al., 2017). Although these westerly winds also carry air masses over alpine regions, such as the Himalayas and the Tibetan Plateau, the airborne bacteria over such regions have not been investigated, and their long-range transport is still unclear. Accordingly, we expect that the airborne bacteria in these two areas possess different ecological characteristics due to the impacts of westerly winds (desert and alpine) and may potentially influence the ecosystems and public health in downwind areas.

Here, aerosol samples were collected from alpine (southern slope of the Himalayas : SH and southern Tibetan Plateau : STP) and desert (the Mongolian Plateau : MP) regions, and the airborne bacterial communities were compared among the three regions to evaluate the potential influences of local terrestrial meteorological factors and air mass movements on airborne bacterial dynamics. We estimated the air mass sources using the Hybrid Single Particle Lagrangian Integrated Trajectories (HYSPLIT) model and the meteorological data obtained during the sampling periods. Bacterial community structures were analyzed using high-throughput sequencing targeting bacterial 16S rRNA genes.

2. Materials and methods

2.1. Sampling locations

The Tibetan Plateau (TP) has the world's highest average elevation (average 4,000 m above sea level), and some of its surface features even reach the mid-troposphere (Yao et al., 2012). The Himalayas are a crucial and sensitive area, as the dynamics of atmospheric circulation playing a role in meteorology and the climate at regional and global scales (Kang et al., 2010). As the southern border of the TP, the Himalayas block marine moisture transport to the TP, and high

precipitation caused by the Indian monsoon occurs on the southern side of the Himalayas. The Mongolian Plateau (MP) is another region that is sensitive to climate change in Asia; it includes the Inner Mongolia Autonomous Region of China and the Mongolian People's Republic. The MP contains arid and semiarid regions controlled by the westerlies and the east Asian monsoon, respectively (Chen et al., 2008). The daily precipitation values of SH, STP and MP are 0.13, 2.97, and 1.03 mm, respectively. The daily mean TOA incident solar radiation values are 29.77, 40.09 and 32.64 MJ·m^{-2}, respectively. The average wind speeds were 1.44, 2.02 and 6.48 m·s^{-1}, respectively, during the sampling period (Table S1).

2.2. Sample collection

Aerosol samples were collected from nine sites in the three regions during 2013 and 2016, as shown in Fig 1. The seasons were classified as winter, spring (pre-monsoon), summer (monsoon) and autumn (post-monsoon) (Chen et al., 2019). Both aerosol samples in SH and MP were sampled in the non-monsoon season and were mainly affected by westerly winds. Sampling periods in the STP took place during the monsoon season, which was affected by the Indian monsoon. At this time, the influence of westerly winds was weak, and the effect of up-drafts was obvious. Two sites in Nepal (Lumbini and Dhunche) were located on the southern slope of the Himalayas (SH). One site in China (Nyalam) was located in a valley of the Himalayas. Lumbini, Dhunche, and Nyalam, which are in close geographic proximity, were grouped and referred to as the southern slope of the Himalayas (SH). The site in Lumbini was located on the roof of the Lumbini International Research Institute, a Buddhist library in Lumbini in the Rupandehi district. Lumbini city has received worldwide attention for its poor air quality due to tourism and vehicular traffic. The site in Dhunche was located at Langtang National Park in Rasuwa district, which is rural (or very small town) and surrounded by agricultural land (Tripathee et al., 2014). The Nyalam site was located in a valley of the Himalayas and is characterized by agriculture and yak husbandry. Nyalam is located on the Chinese border, adjacent to Nepal. One 24-hour sample was collected in April 2013 at Lumbini (Lb) and Dhunche (Dc), while at Nyalam (Nm), one 24-hour sample was collected in December 2013.

Four samples were collected at three sampling sites in the southern Tibetan Plateau (STP), i. e., Lhasa city, beside Nam Co Lake, and at Qiangyong Glacier, in the summer of 2016. Two aerosol samples (Ls1 and Ls2) were collected for 72 hours on the roof of a building at the Institute of Tibetan Plateau Research in June 2016. These samples were collected by a particle size separation sampler, in which Ls2 was located in the upper layer and Ls1 was the filtered sample in the lower layer. At Nam Co Station for Multisphere Observation and Research, Chinese Academy of Sciences, one sample (NC) was collected over 111 hours in July 2016. Nam Co is a sparsely populated, remote, high-elevation region that has a variety of landscapes, including mountains, glaciers, lakes, rivers, and grasslands. The site on Qiangyong Glacier is at the end of the glacier, where a single 72-hour sample (Qy) was collected in July 2016.

Six samples were collected from three sites on the Mongolian Plateau (MP); one site was in China (Erenhot), and two sites were in Mongolia (Dalanzadgad and Ulaanbaatar). The sampling site in Erenhot was located to the northwest of the residential area and at a distance from this area. Three samples were taken from Erenhot (Erh1 to Erh3) for 24 hours in April 2016. The samples (DU1 to DU3) from Mongolia were collected from a car for one hour along the road across the Gobi Desert between Dalanzadgad and Ulaanbaatar in May 2016 (Tang et al., 2018).

In the field, all samples were collected using presterilized polycarbonate filters with a pore size of 0.2 μm (Whatman 111106) and a sterilized Swinnex 13 mm filter holder (Millipore SX0001300) connected to an air pump for 1–120 hours, according to the air quality conditions (Tang et al., 2018). Duplicate filters for each collected

sample were used for DNA extraction for the subsequent bacterial community analyses. Before sampling, all the filters were sterilized by autoclaving at 121°C for 20 min. To avoid contamination, the sampling filter holders and the materials used to change the filters were treated with 75% ethanol every day, and masks were worn during filter operation. Samples collected from SH and STP were transported by car to the nearby laboratory in Lhasa in an insulated container with ice. The samples collected from MP were stored in a –20°C refrigerator during the fieldwork campaign, and kept frozen at –80°C in the laboratory before analysis.

2.3. Meteorological data and the HYSPLIT model

The meteorological data used in this study were obtained from the European Center for Medium-Range Weather Forecasts (https://apps.ecmwf.int/datasets/data/interim-full-daily; last access: 15 February 2019). We downloaded meteorological data for the sampling periods, including 2-meter temperature (Temperature), sunshine during (SD), precipitation, TOA incident solar radiation (TOA), albedo and wind speed (Table S1).

To determine the origin of the air mass, backward trajectories of all sampled air masses were conducted using the National Oceanic and Atmospheric Administration (NOAA) HYSPLIT model. According to the sample time, we calculated the monthly seven-day backward trajectory cluster analysis (commonly used in bioaerosol studies) of the air masses at 1000 m above ground level at the sampling sites (Xu et al., 2014). This method of clustering is used to cluster air trajectory data by speed and direction. Calculations started on the seventh day of every sampling month and continued every 6 hours for 23 days.

2.4. DNA extraction and bacterial 16S rRNA gene amplification and Illumina MiSeq sequencing

Genomic DNA (gDNA) was extracted from the aerosol samples using sodium dodecyl sulfate, proteinase K, and lysozyme and purified by phenol-chloroform extraction as previously described (Maki et al., 2008). The V4 region of the bacterial 16S rRNA genes was amplified with the uniquely tagged primer pair 515F (5´-Seq A-GTGCCAGCMGC CGCGGTAA-3´) and 806R (5´-Seq B GGACTACHVGGGTWTCTAAT-3´) (Caporaso et al., 2012), where Seq A and Seq B represent the nucleotide sequences delimited by the second set of PCR primers. The detailed process has been described by Maki et al. (2017a). Each PCR contained 25 μL 2x Premix Taq DNA polymerase (Takara Biotechnology, Dalian Co. Ltd., China), 3 μL DNA template (20 ng μL^{-1}), 1 μL each primer (10 μM), and 20 μL nuclease-free water. PCR products of the triplicate reaction samples were pooled and quantified with PicoGreen staining. The sample libraries were generated with purified PCR products. A MiSeq 500 cycles kit was used for 2 × 250 bp paired-end sequencing. The 16S rRNA gene sequences were submitted to the NCBI SRA database (BioProject accession number: PRJNA645037 and PRJNA648253). We also downloaded SAMN07758520, SAMN07758528, SAMN07758529 and SAMN07758530.

2.4.1. Processing of Illumina sequencing data

The overlapping paired-end sequences from the sequencing run were assembled with FLASH, and poor-quality sequences were filtered out before demultiplexing based on barcodes (Magoc and Salzberg, 2011).We processed the sequences using the QIIME pipeline (v1.8). Briefly, bacterial reads were truncated at any location containing more than three consecutive bases receiving a quality score < 20, and any reads containing one or more ambiguous base calls were removed from the analysis. In addition, truncated reads with < 75% (of the raw read length) consecutive high-quality base calls were discarded. Sequences were then clustered into OTUs at 97% pairwise identity with the uclust algorithm (Edgar, 2010). Singleton OTUs (consisting of only one read) were removed from the downstream analysis. A bacterial alpha

diversity estimate, the Shannon diversity, was calculated by using the QIIME script 'alpha_diversity.py'. The taxonomic identity of each representative sequence was determined against the Greengenes database (v13.8) (DeSantis et al., 2006). After the taxonomies had been assigned, OTUs that were affiliated with chloroplast, archaeal and unclassified sequences were removed from the subsequent analysis.

2.5. Statistical analysis

The Kruskal-Wallis test was performed to compare the differences in bacterial α-diversity among SH, STP and MP. Spearman's rank correlations were used to determine the relationships between α-diversity indices and environmental variables. Hierarchical cluster analysis of the relative abundance of OTUs was performed with the complete linkage method on the chi-square distance between samples. Analysis of similarity (ANOSIM) was performed to evaluate the overall differences in the bacterial community structures based on Bray-Curtis dissimilarity metrics (Liu et al., 2014). A distance-based multivariate linear model (DISTLM) based on weighted UniFrac distance was performed using the DISTLM_forward3 program to determine which environmental variables significantly explained the observed similarity among samples (McArdle and Anderson, 2001). The relationship between the relative abundance of bacteria and environmental factors was studied by Spearman rank correlation analysis. The "Venn Diagram" package was used to construct a Venn diagram to show the potential relationships between bacterial communities in different sites at the OTU level (Chen and Boutros, 2011). SIMPER (similarity percentage) analysis, implemented in the PAST software (http://folk.uio.no/ohammer/past), was used to identify the taxa primarily responsible for the dissimilarity among the three locations using a contribution cutoff of > 1% (Liu et al., 2017).

3. Results

3.1. Sources of air masses during sampling

To identify the possible sources of airborne bacteria, the backward trajectories were classified as the air-mass patterns of the SH, STP and MP. Among the three sites at SH, the fast-flowing cluster 1 (33%) of the air mass trajectories at Lumbini originated from Pakistan and India in the west and moved eastward, while the remaining slow-flowing cluster 2 (67%) of air masses originated from the southern India (Fig 2A). The clustering results at the Dhunche and Nyalam sites were very similar; Nepal was the most active source region contributing 91% and 82% of the air masses, and the other minor source was from Pakistan, contributing 9% and 18%, respectively (Fig 2B and C). During the sampling period at STP, air-mass trajectory clusters originating from the south moved eastward to Lhasa with a pair of fast-flowing clusters, 7 (73%) and 8 (27%) (Fig 2D). At the Nam Co and Qiangyong Glacier sites, clusters 9 (86%), 11 (60%) and 12 (40%) mainly originated from Nepal and India, but cluster 10 (14%) which originated from the west and moved eastward (Fig 2E and F). The last three points are from MP. Russia was the active source region at the Erenhot, Dalanzadgad and Ulaanbaatar sites, for clusters 13 (55%), 14 (26%), 15 (19%), 16 (75%), 17 (25%), 18 (72%) and 19 (28%), respectively (Fig 2G, H and I).

3.2. Community composition and diversity of airborne bacteria

The compositions of airborne bacterial communities were investigated based on 16S rDNA sequences. A total of 875,133 high-quality sequences were obtained, with 13,972 to 107,911 reads (mean = 67,317, n = 13) per sample. The results show that the bacterial communities of aerosol samples were predominantly composed of eight phyla accounting for over 91% of the amplicon sequences from all aerosol samples, including Bacteroidetes, Actinobacteria, Proteobacteria, Firmicutes, Acidobacteria, Gemmatimonadetes,

Chloroflexi and Planctomycetes (relative abundance > 2% in at least one sample) (Fig 3A). The airborne bacterial communities of the three regions included different relative abundances of dominant groups. Both SH and MP samples were dominated by three phyla, Actinobacteria, Proteobacteria and Bacteroidetes, with mean relative abundances ranging from 19% to 34%, while Actinobacteria (39%), Proteobacteria (31%) and Firmicutes (19%) were the three most abundant phyla in the STP samples (Fig 3B).

The relative abundances of dominant bacterial phyla were related to meteorological parameters. The relative abundances of Acidobacteria, Gemmatimonadetes, and Planctomycetes were negatively correlated with altitude and TOA but positively correlated with wind speed (Spearman's rank correlation, all $P < 0.05$, Fig S1). In particularly, the relative abundances of Bacteroidetes, Acidobacteria and Chloroflexi exhibited a negative correlation with temperature, but that of Actinobacteria was positively correlated with temperature ($P < 0.05$). Only the relative abundance of Acidobacteria showed a positive correlation with surface albedo (Spearman's rank correlation, $P < 0.05$ Fig S1).

The alpha diversity index, the Shannon index, varied from 3.8-10.2 (Table 1) with the average values for SH, STP and MP of 7.70, 7.63, and 5.99, respectively. The Shannon index showed no significant differences among the aerosol samples from SH, STP, and MP (Kruskal-Wallis test, $P = 0.38$ Fig 4). However, the Shannon index was significantly related to altitude (Spearman's rank correlation, r = -0.556, $P < 0.048$ Table 2).

The richness of airborne bacterial OTUs varied among the three regions, with the largest value in the SH samples and the smallest in the STP samples. The OTU numbers of the SH, STP and MP samples were 4627, 3318 and 3464, accounting for 46.4%, 33.3% and 34.7% of the total number of OTUs, respectively (Fig 5). There was low OTU overlap between the STP and MP regions, with only 1.1% (109) shared OTUs, while 4.6% (462) of OTUs overlapped between SH and STP, and 5.3% (532) overlapped between SH and MP. The proportion of common OTUs in samples from all three regions was 1.7% (168).

3.3. Variations in bacterial community composition

Cluster analysis, based on the Bray–Curtis distance across samples, clearly revealed differences in the airborne bacterial communities among the three regions (Fig 6). The pattern was also confirmed by dissimilarity tests, showing that location was an important determinant of the bacterial community composition (MRPP, ANOSIM and perMANOVA, all $P < 0.05$, Table 3).

To better assess the effects of meteorological variables on the bacterial community variations among the three regions, we used DISTLM to minimize autocorrelation between the variables. Airborne bacterial community composition was significantly related to wind speed ($P = 0.002$), altitude ($P = 0.004$), albedo ($P = 0.044$) and TOA ($P = 0.018$). The cumulative variation explained was 73.3% (Table 4).

Based on the SIMPER analysis results we identified 10 OTUs (contribution to dissimilarity > 1%) that contributed to the variation in airborne bacterial community composition among the SH, STP and MP samples. These 10 OTUs accounted for 26.14% of the overall bacterial sequences and belonged to Proteobacteria, Actinobacteria, and Bacteroidetes (Fig 7). Four Actinobacteria OTUs contributed the most to the overall difference (11.96%) among the SH, STP and MP samples, followed by Bacteroidetes (5 OTUs, 7.36%) and finally Proteobacteria (1 OTU, 6%). In particular, OTUs belonging to the genera *Rhodococcus* and *Flavobacterium* were mainly detected in the SH samples (Fig 7). Sequences of *Blastomonas*, *Rosea*, and *Mycobacterium* species predominantly appeared in the STP air samples. The OTUs of MP samples were dominated specifically by sequences from the genus *Segetibacter* and the family *Chitinophagaceae*.
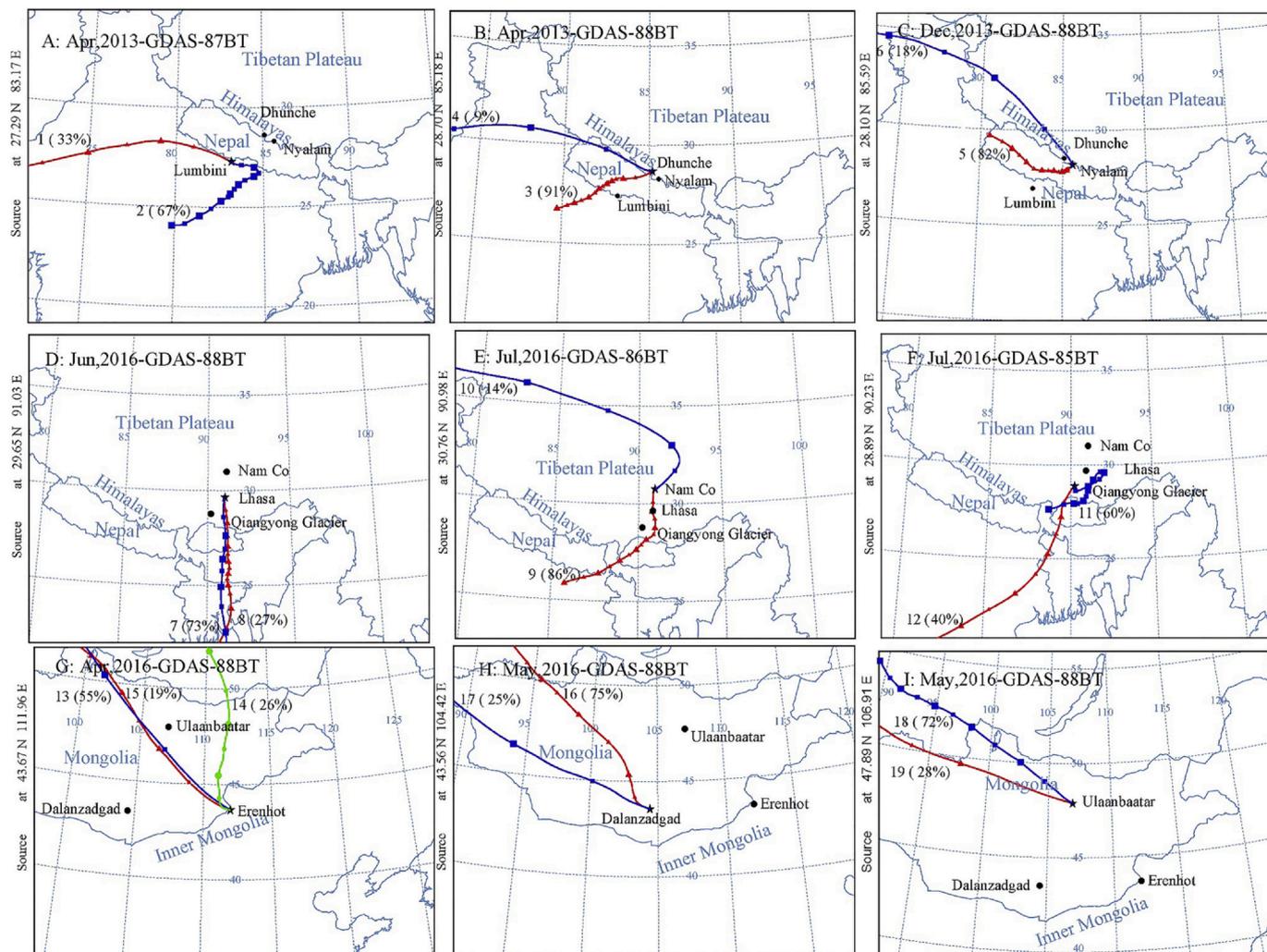
Fig 2. Mean seven days backward trajectory at 1000 m above ground level from HYSPLIT model during the sampling period, which can be classified to the three patterns of air masses such as SH (A-C), STP (D-F), and MP (G-I) at (A) Lumbini, (B) Dhunche, (C) Nyalam, (D) Lhasa, (E) Nam Co, (F) Qiangyong Glacier, (G) Erenhot, (H) Ulaanbaatar and (I) Dalanzadgad.

SH: southern slope of the Himalayas, STP: southern Tibetan Plateau, MP: Mongolian Plateau, BT: backward trajectories.

The sampling site is the end point of the air-mass trajectory marked with a black star. Other sites are marked with black points. Backward trajectories of different clusters in every site are marked with different colors. The numbers in each panel indicate the percentages of monthly trajectories with the movement.

4. Discussion

4.1. Characteristics of the airborne bacterial communities

The airborne bacterial community compositions in the aerosol samples collected at the southern slope of the Himalayas (SH), on the southern Tibetan Plateau (STP), and on the Mongolian Plateau (MP) were predominantly composed of the phyla Proteobacteria, Actinobacteria, Bacteroidetes and Firmicutes. However, the bacterial community structures showed significant differences among the SH, STP and MP samples (MRPP, ANOSIM and perMANOVA, all $P < 0.05$, Table 3). The phylum Actinobacteria (39%) was dominant in the samples from STP, the site with the highest TOA value (Fig 3B, Table S1), suggesting their higher ultraviolet (UV) resistance (John et al., 2011). The surface waters of 10 mountain lakes in the Tyrolean Alps (Austria) were found to contain high amounts of Actinobacteria, which was significantly correlated with the ambient levels of solar UV radiation (Warnecke et al., 2005). Members of Actinobacteria frequently dominate high-altitude habitats, such as the littoral wetland of Lake Nam Co on the TP (28.6~29.3% in total sequences) (Yun et al., 2014), as well as ice cores (Yao et al., 2008) and snow over the glaciers of the TP (Liu et al., 2009).

The relative abundance of Firmicutes was higher in the STP samples than in the SH and MP samples (Fig 3B). This can be explained by their ability to form spores in low nutrient conditions. Their spores can resist the extreme environmental stressors at high altitude and under desiccation conditions (Galperin, 2013). Smith et al. (2018) also found that Firmicutes represented the majority of bacteria in aerosol samples collected at high altitudes during aircraft ascents or descents (0.3 to 11 km). Likewise, Firmicutes were the most abundant group in ten hot springs (4,600 m above sea level) in central and central-eastern Tibet (Huang et al., 2011). Therefore, we speculated that the high altitude and strong UV radiation influenced the bacterial community composition in the STP samples. These findings suggest that the Actinobacteria and Firmicutes sequences that dominated in the STP samples may originate from natural environments around the Tibetan region.

The bacterial taxa responsible for the majority of the variance in community composition were linked with the various ecosystems involved in our study. Most notably, the genera *Blastomonas* (Proteobacteria), *Rosea* (Actinobacteria) and *Mycobacterium* (Actinobacteria), which were enriched in STP (Fig 7), are able to survive in extreme environments. Many members of the genera
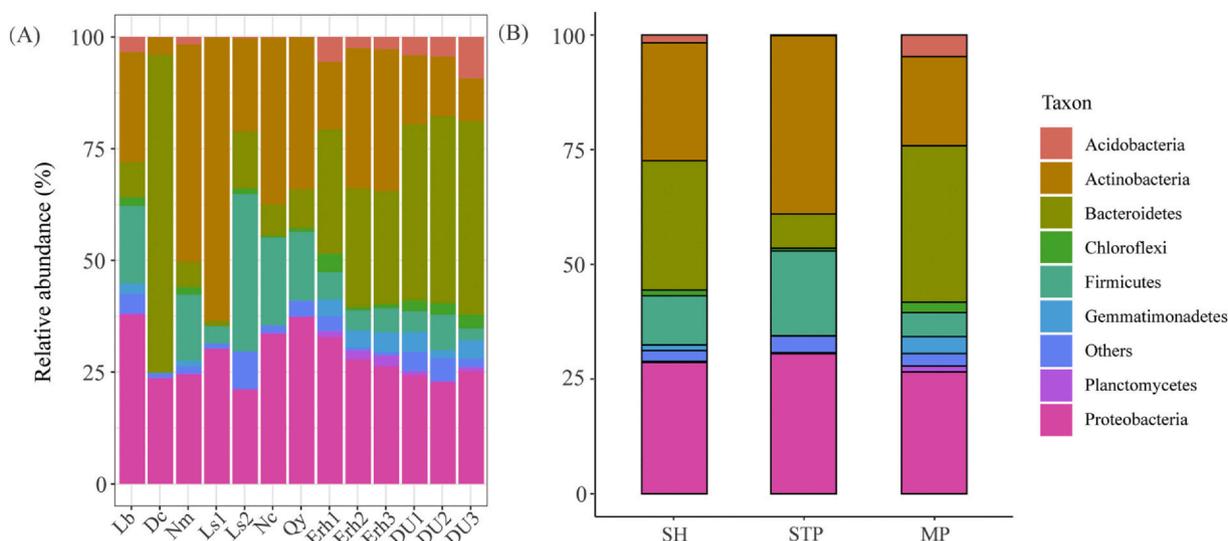
Fig 3. Relative abundance of bacterial 16S rRNA genes sequences at the phylum level (> 2%) in all aerosol samples (A) and at three regions, SH (southern slope of the Himalayas), STP (southern Tibetan Plateau) and MP (Mongolian Plateau) (B).
Relative abundances are based on the proportional frequencies of DNA sequences that could be classified at the phylum level.

Table 1
Information on the sampling locations and the alpha-diversity values of all aerosol samples.

Country	Location	Sample name	Region	Date	Sampling duration (h)	Latitude(°N)	Longitude(°E)	Altitude(m)	Shannon
Nepal	Lumbini	Lb	SH	2013/4/19	24	27.29	83.17	100	10.18
	Dhunche	Dc	SH	2013/4/25	24	28.70	85.18	2051	4.69
China (TP)	Nayalam	Nm	SH	2013/12/25	24	28.10	85.59	4166	7.63
	Lhasa	Ls1	STP	2016/6/22	72	29.65	91.03	3600	3.78
	Lhasa	Ls2	STP	2016/6/22	72	29.65	91.03	3600	8.39
	Nam Co	NC	STP	2016/7/7	111	30.76	90.98	4730	5.75
	Qiangyong Glacier	Qy	STP	2016/7/27	72	28.89	90.23	4800	6.05
China (IM)	Erenhot	Erh1	MP	2016/4/1	24	43.67	111.96	957	9.19
	Erenhot	Erh2	MP	2016/4/7	24	43.67	111.96	957	7.24
	Erenhot	Erh3	MP	2016/4/8	24	43.67	111.96	957	7.42
Mongolia	R-DzToUb	DU1	MP	2016/5/5	1	Dz:43.56	Dz:104.42	Dz:1489	7.13
	R-DzToUb	DU2	MP	2016/5/5	1	Ub:47.89	Ub:106.91	Ub:1302	8.02
	R-DzToUb	DU3	MP	2016/5/5	1				7.19

TP: Tibetan Plateau, IM: the inner Mongolia Autonomous Region, R-DzToUb: a road between Dalanzadgad and Ulaanbaatar.
SH: southern slope of the Himalayas, STP: Southern Tibetan Plateau, MP: Mongolian Plateau.

Blastomonas and *Rosea* have been isolated from lake water (Xiao et al., 2015), coastal waters (Sheu et al., 2017), seawater (Liang et al., 2016; Meng et al., 2017), and saline soils (David Castro et al., 2017). Some isolates of the genus *Mycobacterium* have been obtained from soil (Zhang et al., 2012). As previously described, the Indian monsoon which can carry air masses originating from the ocean, can affect the TP (Fig 2D), and local emissions, such as the extensive distribution of lakes in the TP (Zhang et al., 2017), contribute part of the airborne bacterial communities. The dominant genus *Segetibacter* (Bacteroidetes) and family *Chitinophagaceae* (Bacteroidetes) in the MP samples (Fig 7) have been isolated from soil samples (Dahal et al., 2017; Kim Mincheol et al., 2013) The Mongolian plateau is clearly affected by Asian dust events. The family *Chitinophagaceae* has also been isolated from hot springs, exhibiting resistance to high temperature (Hanada et al., 2014). However, the dominant *Rhodococcus* (Actinobacteria) and *Flavobacterium* (Bacteroidetes) species in the SH samples (Fig 7), are ubiquitous bacteria found in many different environments, including leaf surfaces (Kämpfer et al., 2013), soil (Nguyen and Kim, 2016), freshwater (Chen et al., 2013), glacial ice (Dong et al., 2012) and high-altitude lakes (Li et al., 2014; Van Trappen et al., 2004), Their presence is related to the complex local emissions from the surrounding geographical environment and human activities at SH (Fig 2A, B, and C).

4.2. Potential effects of local and long-range transportation on airborne bacterial diversity

The airborne bacterial communities in the STP samples showed low diversity (Fig 4), and local meteorological parameters, especially altitude, had significant relationships with alpha diversity (Table 3). As the high altitude of the Tibetan Plateau results in lower temperatures, lower allochthonous inputs of organic matter and strong solar radiation (Liu et al., 2017), the conditions select for bacterial species that are resistant to harsh environmental conditions; this is similar to the relatively low airborne bacterial diversity in Arctic regions that exhibit extremely low temperatures, hurricane strength winds, seasonal freeze–thaw cycles, strong UV radiation, and extremely low nutrient levels (Cuthbertson et al., 2017). In addition, the frequent precipitation events (rain, hail, and snow) that occur on the TP during the monsoon season wash out suspended particles from the atmosphere, resulting in low airborne bacterial diversity. Ice-nucleating bacteria within a cloud induce precipitation and thus cause their own deposition (Amato, 2012). Studies on airborne bacteria along the coast (Murata and Zhang, 2014) and on snow at altitudes of 2,450 m on Mt Tateyama found that the amount of bacteria in air decreased as the airborne bacteria were deposited (Maki et al., 2018). Harsh habitat conditions together with the high precipitation in the monsoon season caused the relatively low
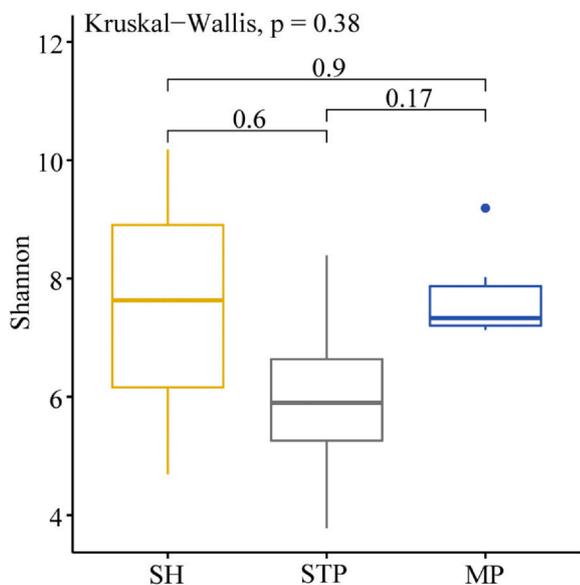
Fig 4. Comparison of alpha-diversity indices (Shannon) among the southern slope of the Himalayas (SH), southern Tibetan Plateau (STP) and Mongolian Plateau (MP).

Table 2

Spearman's rank correlation (r) between alpha-diversity values and environmental factors of aerosol samples.

Factors	Shannon	
	r	P
Altitude	-0.556	**0.048**
Temperature	-0.033	0.914
SD	-0.216	0.478
Precipitation	-0.407	0.168
TOA	-0.443	0.130
Albedo	-0.216	0.479
Wind speed	0.094	0.760

Temperature: 2 meter air temperature, SD: sunshine duration, TOA: TOA incident solar radiation, Data in bold indicates significant correlations.

diversity at the STP.

The difference in community composition between SH and STP is smaller than between SH and MP (Table 3). This may be due to their geographic proximity of SH and STP, which may allow the air masses that affect them to frequently mix with each other (Fig 2B, C, E and F). Wind speed was positively related to bacterial beta diversity (Table 4). The schematic diagram in Fig. 8 outlines can explain the effect of air-masses transport on air conditions at the sampling region, suggesting that air-mass transport may also have an effect on the airborne bacterial beta diversity. Although the Himalayas have been believed to be a "barrier" to the atmospheric transport of particles (Gong et al., 2014), some aerosol particles can pass over this obstruction (Wang et al., 2015). Studies have also reported that pollutants emitted in the Indo-Gangetic Plain and central Asia may be transported to the TP (Cong et al., 2015a). The local meteorological conditions and regional atmospheric flow processes facilitate the penetration of the carbonaceous aerosols from South Asia throughout the Himalayas (Cong et al., 2015b). The accumulated atmospheric pollution at the southern foot of the Himalayas can be transported to the inner TP through valleys or be lifted by advection over the Himalayas (Kang et al., 2019). Due to the daytime up-valley wind and a down-valley wind on the Himalayan slopes, aerosols can move over the mountain ridge (5,000 m) and undergo trans-Himalayan transport. In addition to the above studies, a recent study (Gong et al., 2019) demonstrated that aerosols can also be
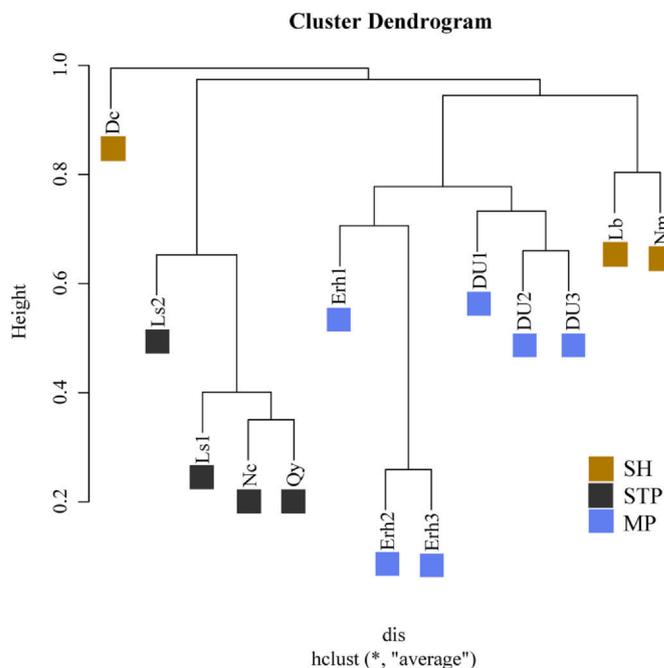

Fig 5. Venn diagram showing the number of shared OTUs among the three regions, SH (southern slope of the Himalayas), STP (southern Tibetan Plateau) and MP (Mongolian Plateau).
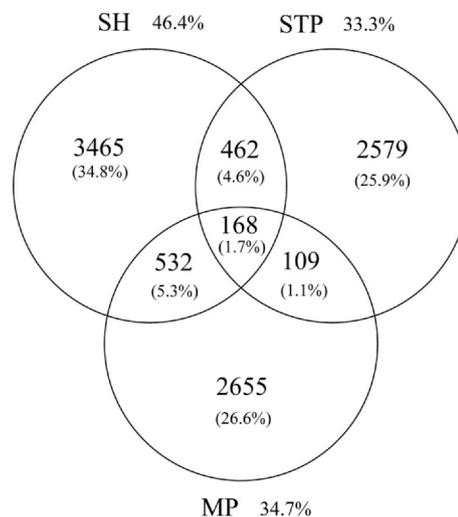

Fig 6. Cluster analysis of the airborne bacterial communities into three regional groups: SH (southern slope of the Himalayas), STP (southern Tibetan Plateau) and MP (Mongolian Plateau). The dendrogram was obtained from an unweighted pair-group average algorithm (UPGMA) based on Bray–Curtis distance.

transported to the STP along valleys and that the transport flux is 2-3 times higher than that across the mountain ridge.

In contrast to their dissimilarity test results, a greater number of OTUs were shared between SH and MP than between SH and STP (Fig 5). During the non-monsoon season, the SH and STP samples were mainly carried by westerly air masses, suggesting the potential for the long-range transport of similar bacteria. However, the STP samples are mainly affected by the Indian monsoon, and the westerly wind effect is weakened. Recent studies have reported that microorganisms are abundant in the upper atmosphere, particularly downwind of arid regions, where winds mobilize large amounts of topsoil and dust (Smith et al., 2013). A study on the land surface of the STP during the spring identified a strong source of sensible heat that warms the surface air

Table 3

Bray-Curtis distance-based dissimilarity tests of the airborne bacterial communities among SH, STP and MP.

Communities	MRPP[a]		ANOSIM[b]		Adonis[c]	
	δ	P	R	P	R²	P
MP VS. SH	0.079	**0.012**	0.852	**0.016**	0.272	**0.011**
MP VS. STP	0.639	**0.006**	1.000	**0.004**	0.460	**0.008**
SH VS. STP	0.694	**0.025**	0.704	**0.027**	0.418	**0.029**

SH: southern slope of the Himalayas, STP: Southern Tibetan Plateau, MP: Mongolian Plateau; Data in bold indicate significant correlations.

[a] MRPP, multiresponse permutation procedure. MRPP is a nonparametric procedure that depends on the internal variability of the data.

[b] ANOSIM, analysis of similarities.

[c] Nonparametric multivariate analysis of variance with the Adonis function.

Table 4

Distance-based multivariate linear model of bacterial community structures showed percentage of variation explained by environmental factors (sequential tests, 999 permutations).

Factors	Pseudo-F	P	Percent variation explained	Cumulative variation explained
Wind speed	2.992	**0.002**	0.214	0.214
Altitude	2.043	**0.004**	0.133	0.347
Albedo	1.638	**0.044**	0.101	0.448
TOA	1.733	**0.018**	0.098	0.546
SD	1.005	0.519	0.057	0.603
Precipitation	1.588	0.091	0.083	0.686
Temperature	0.869	0.558	0.047	0.733

TOA: TOA incident solar radiation, SD: sunshine duration, Temperature: 2 meter temperature, Data in bold indicates significant correlations.

(Ma et al., 2011) allowing the dust aerosols emitted from this region to be brought to the upper troposphere. The geographical characteristics of the TP are thought to cause the long-range zonal dust transport around the Northern Hemisphere by westerly winds. Finally, a cyclonic circulation in the upper troposphere develops over East Asia as a result of the TP warming, and the forced downdrafts facilitate dust deposition (Xu et al., 2018; Yuan et al., 2019).

5. Conclusion

This study demonstrated that the airborne bacterial communities over the Tibetan and Mongolian Plateaus were primarily dominated by the members of Proteobacteria, Actinobacteria, Bacteroidetes and Firmicutes; these bacteria are affected by meteorological parameters and are thought to originate from regional environments or be carried by westerly wind patterns. High relative abundances of Actinobacteria and Firmicutes were found in the airborne bacterial communities of STP, while the diversity of the bacterial communities of STP was the lowest among those of the three regions. In addition, the movement of air masses (along with microbial cells) has potential impacts on the variations in airborne bacterial communities in downwind areas such as the Mongolian Plateau. Our study provides new information on airborne bacterial community compositions in extreme environments and its spatial variability over large-scale areas. However, the long-range transport processes of airborne bacteria across the Himalayas and to Mongolia and other regions are still unclear. Future work will need to integrate molecular surveys of airborne bacterial communities with atmospheric chemical transport models across more extensive sample sets in order to more confidently determine bacterial sources and map their atmospheric trajectories over extended time periods.
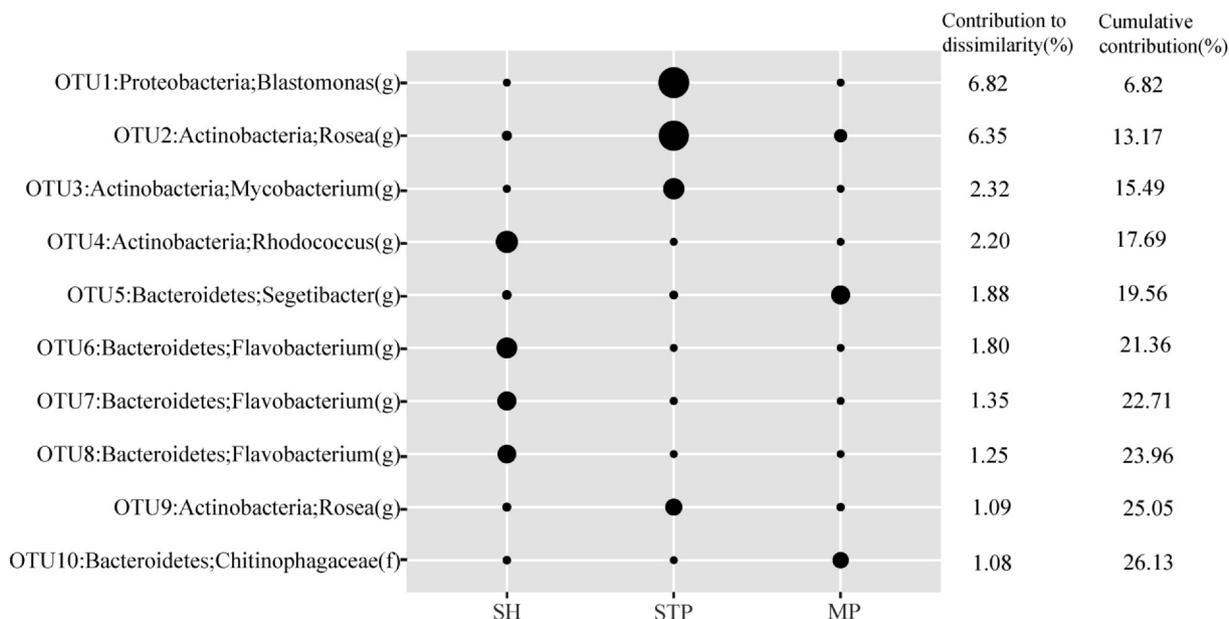
Fig 7. Taxonomic categories of the 10 representative OTUs that specifically dominate air samples of SH (southern slope of the Himalayas), STP (southern Tibetan Plateau), and MP (Mongolian Plateau), with their relative contributions to community dissimilarities. The diameters of circles indicate the relative abundances of OTUs, at the average values of each region (square root transformed).
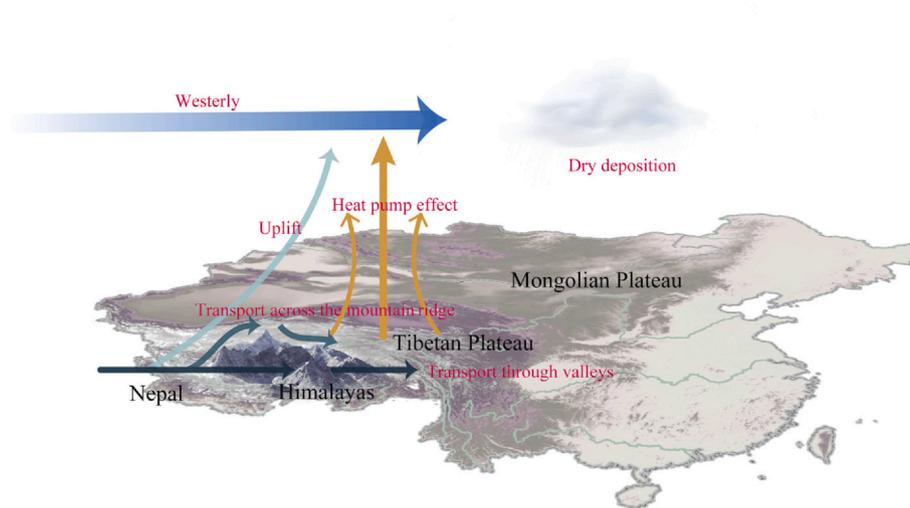
Fig 8. Schematic diagram illustrating airborne bacterial transportation over the sampling region.

Declaration of Competing Interest

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.atmosres.2020.105215.

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