



Effect of Indian monsoon on the glacial airborne bacteria over the Tibetan Plateau



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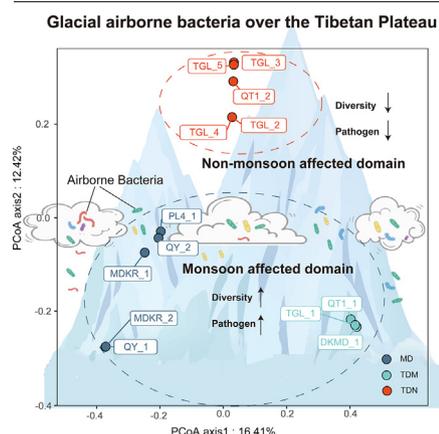
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HIGHLIGHTS

- Atmospheric circulation influences glacial airborne bacteria on the Tibetan Plateau.
- Indian monsoon increases glacial airborne bacterial diversity.
- Indian monsoon and westerly carry distinct bacterial communities.
- Indian monsoon can carry a higher relative abundance of potential bacterial pathogens.

GRAPHICAL ABSTRACT



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ABSTRACT

The glacier of the Tibetan Plateau (TP) is influenced by the Indian monsoon and continental westerlies. Wind flow can carry a variety of bacteria and disperse across the TP. Once these bacteria are colonized to the glacier surface, they could affect the biogeochemical cycle of the glacial ecosystems. However, very few studies have focused on the relationships between these airborne bacteria and atmospheric circulation over glaciers of the TP. Here we studied the diversity, taxonomic composition, and community structure of airborne bacteria on six TP glaciers using 16S rRNA gene sequencing. The results revealed an increase in the airborne bacterial diversity over the glaciers under the effect of the Indian monsoon. Airborne bacteria were dominated by *Proteobacteria*, *Firmicutes*, *Bacteroidetes*, and *Actinobacteria*, while relative abundances of *Bacteroidetes* and *Firmicutes* were significantly higher under the influence of the Indian monsoon in the southern and central of the TP, respectively. Moreover, significantly different airborne bacterial community structures were observed over glaciers under the influence of the Indian monsoon, which could be explained by the increased community stochasticity. In addition, the Indian monsoon increases the diversity and relative abundance of potential pathogens, which includes the most notorious bacteria such as *Pseudomonas fluorescens*, *Staphylococcus aureus*, and *Clostridium butyricum*. Our results revealed for the first time that atmospheric circulation influences the composition of airborne bacteria over the glaciers on the TP, this may provide critical insights into the distinct microbial community structure and function in glaciers across the TP.

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1. Introduction

Glacier surface hosts abundant and diverse microbes. These microbes are responsible for the cycling of vital nutrients (Stibal et al., 2012) and they also have the potential to influence the melting rate of the glacier by reducing surface albedo (Sommers et al., 2019). In addition, biological processes at the glacier surfaces amplify the impacts of climate warming on glaciers (Irvine-Fynn et al., 2012). Thus, microbes are important components of glacier ecosystems (Edwards et al., 2020). Studies have shown that biological processes on glacier surfaces are influenced by aerosol deposition (Stibal et al., 2012), however, the sources of microbial deposition remain unclear.

Microbes are important components of bioaerosol (Burrows et al., 2009b). It can be atomized from almost any surface (Smets et al., 2016), and then be emitted into the atmosphere. Moreover, bacteria can be carried and dispersed over long distances via wind flow (Maki et al., 2018; Yoo et al., 2017), which efficiently links microbial communities across continents, islands, and oceans (Bowers et al., 2009; Fröhlich-Nowoisky et al., 2016). Once deposited on the Earth's surface, these airborne bacteria may impact the development and succession of microbial communities (Maki et al., 2011; Stern et al., 2021). This influence is particularly important for fragile ecosystems like glaciers. Earlier research has demonstrated that bacteria can be globally transported by wind flow and influences the composition of microorganisms in downwind ecosystems (Hervas et al., 2009). Transpacific wind has been shown to disperse microorganisms across continents (Smith et al., 2013). This kind of long-range transportation of airborne microbial can affect the diversity of Antarctic soils (Archer et al., 2019). In addition, one study documented that the microbes uplifted during dust storms can survive long-range transport in the atmosphere and colonize high-altitude snow (Chuvochina et al., 2011). Therefore, airborne bacteria can be an important source of the microbes in glacier ecosystem. Although connections between atmospheric circulation and bacteria transportation have been observed (Romano et al., 2019), these studies primarily focused on a single location or a small geographical scale, the distribution of airborne bacteria at the regional scale remains elusive.

Tibetan Plateau (TP) possesses the largest area of glaciers outside of the polar regions (Liu et al., 2017). A diverse microbial community has been identified on glacier surface, and the microbial biogeochemical cycle has a great impact on downstream ecosystems through glacial meltwater (Edwards et al., 2020; Liu et al., 2021). However, the source of glacier surface microbes remain unclear. Nevertheless, aerosol deposition is considered an important source of microbes on glacier surface. In summer, the TP is controlled by the Indian monsoon and the westerly (Thompson et al., 2018; Yao et al., 2012). Many studies have demonstrated that the monsoon and westerly play important roles in delivering aerosols, including black carbon, brown carbon, and organic pollutants (Kang et al., 2019; Luthi et al., 2015). However, whether there are differences in airborne bacteria composition remains unclear. Indian monsoon and westerly-driven air masses have different sources with distinct ecosystem types and are likely to carry distinct microbial compositions. Thus, we hypothesize that the Indian monsoon will carry significantly different microbial communities from the westerly. To test this, we collected aerosol samples over six glaciers of the TP during June to August, and investigated their airborne bacteria diversity, taxonomic composition, and community structure.

2. Material methods

2.1. Sampling sites and sample collection

The TP glaciers are controlled by the interplay of the Indian monsoon and the westerly (Yao et al., 2012). The TP can be roughly divided into three climate domains, south of 30°N is mainly affected by Indian monsoon, as the monsoon domain; the north of 35°N is mainly affected by westerly, as the westerlies domain; while the region between 30°N and 35°N is considered to be the transition domain, which is under the control of a shifting

climate between the Indian monsoon and the westerly (Wang et al., 2016; Yao et al., 2013).

Aerosol samples were collected at six different glaciers on the Tibetan Plateau (Fig. 1), three of which were located at the monsoon domain (Parlung No. 4, Qiangyong, and Mengdakangri Glaciers), and the other three were located at the transition domain (Qingtang No. 1, Dongkemadi, and Tanggula Glaciers) of the TP (Fig. 1). The Parlung No. 4 Glacier (PL4, 29.26° N, 96.93° E; 4664 m above sea level (m a.s.l)) is nearly 8 km long and covers an area of about 11.7 km² (Yang et al., 2011). It is located in the upper Parlung-Zangbu River Basin, southeast TP, where the Indian monsoon intrudes through the Brahmaputra Valley. The Qiangyong Glacier (QY, 28.89° N, 90.23° E; 4884 m a.s.l) is located between the Himalayan ranges and the Yarlung Zangbo River in the southern TP (Tian and Tian, 2019). The length of the QY Glacier is 4.9 km, the maximum width is 2.8 km, and the area is 7.7 km² (Luo et al., 2003). Mengdakangri Glacier (MDKR, 28.47° N, 90.60° E; 5408 m a.s.l) is located on the mid-eastern section of the Himalayas. It is 3.1 km long and covers an area of 2.46 km² (Gao et al., 2017). PL4, QY, and MDKR glaciers are controlled by the Indian monsoon from June to August. Qingtang No. 1 (QT1), Dongkemadi (DKMD), and Tanggula (TGL) glaciers are located in the transition domain, which is affected by westerly with strong monsoon event influence in summer. QT1 glacier (33.17° N, 88.42° E; 5726 m a.s.l) located in the eastern Qiangtang Plateau of the central Tibetan Plateau, it is a small (2.4 km²) glacier of about 2 km in length. Its climate is influenced by both monsoon and westerly (Li et al., 2017). DKMD (33.03° N, 92.03° E; 5284 m a.s.l) and TGL Glacier (33.11° N, 92.03° E; 5255 m a.s.l) are located on the northern slope of Tanggula Mountain, in the central TP (Zhou et al., 2011). The DKMD glacier is 5.4 km long with an area of 14.63 km² (Zhou et al., 2011), while the TGL glacier is 2.8 km long, 0.5 to 0.6 km wide with a surface area of 1.7 km².

Due to weather conditions and logistic limitations, one to four samples were collected at each glacier. A total of 13 samples were collected during the 2018 and 2019 monsoon seasons (June–August) (Table S1). Samples were collected using pre sterilized polycarbonate filters with a pore size of 0.2 μm (GTTP04700) and a sterilized Swinnex 47 mm filter holder (Millipore SX0004700) connected to an air pump (the flow rate was approximately 2.5 Lmin⁻¹) lasts 48–144 h (Qi et al., 2021). Blank controls were exposed through a sampler that did not collect air. Samplers were mounted at the glacial terminus, 1.5 m above the ice. All filters were transported within 30 h in an insulated container at 4 °C to the Lab in Lhasa and then were transported frozen to a laboratory in Beijing. After entering the laboratory, the samples were kept frozen at –20 °C for laboratory analysis.

2.2. Back-trajectory analysis

A ten-day backward trajectory was computed by using the Hybrid Single-Particle Lagrangian Integrated Trajectory (HYSPPLIT) model and Global Data Assimilation System meteorological data at 500 m above ground level and visualized with Meteoinfo (Choufany et al., 2021). This method has been used to determine the source of air masses, establish the source-sink relationship, and analyze the geographic source, path, and altitude of aerosol from the ground. In addition, the length of the trajectory indicates the speed of the air mass. The geographic region where air masses fly at low altitudes within the planetary boundary layer is considered to be the likely source area of the collected material (Péguilhan et al., 2021).

2.3. DNA extraction, PCR amplification, Illumina sequencing and processing of Illumina sequencing data

The holders were opened and polycarbonate membranes were removed in a PC2 certified laboratory. Total DNA was extracted from the 0.2 μm polycarbonate films by using the UltraClean Soil DNA kit (MoBio, San Diego, CA) according to the manufacturer's instructions. The V4-V5 region of the bacterial 16S rRNA genes was amplified in triplicate with the primer set 515F/907R (515F: 5'-GTGCCAGCMGCCGCGG-3'; 907R: 5'-CCGTCA

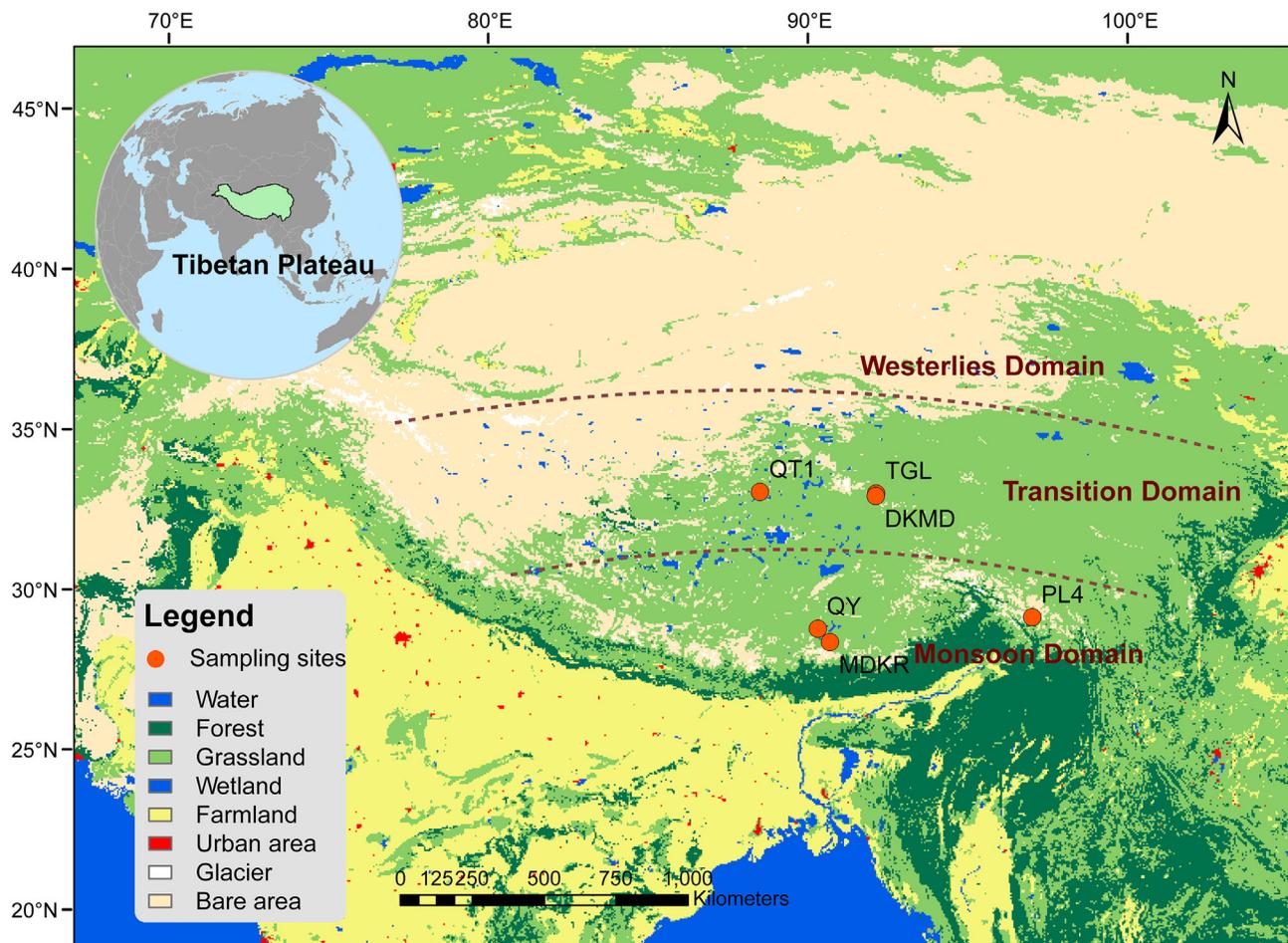


Fig. 1. Map showing the ecosystems and the sampled locations. The glaciers sampled include: Parlung No. 4 Glacier (PL4), Qiangyong Glacier (QY), Mengdakangri Glacier (MDKR), Qingtang No. 1 Glacier (QT1), Dongkemadi Glacier (DKMD) and Tanggula Glacier (TGL) on the Tibetan Plateau. Dashed lines indicate the boundaries of westerly and monsoon influences (Thompson et al., 2018).

ATTCMTTTRAGTTT-3') (Fang et al., 2017). PCR reactions were performed in a volume of 50 μ l containing 25 μ l $2 \times$ Premix Taq (Takara Biotechnology, Dalian Co. Ltd., China), 1 μ l of each primer (10 mM) and 3 μ l DNA (20 ng/ μ l) template in a volume of 50 μ l. The reaction was carried out by the thermocycling program: 5 min at 94 $^{\circ}$ C for initialization; 30 cycles of 30 s denaturation at 94 $^{\circ}$ C, 30 s annealing at 52 $^{\circ}$ C, and 30 s extension at 72 $^{\circ}$ C; followed by 10 min final elongation at 72 $^{\circ}$ C. Finally, sequencing of the bacterial 16S rRNA gene clone libraries were performed using an Illumina MiSeq Sequencer (Illumina, San Diego, CA) with a paired-end strategy (2×250 bp) provided by Guangdong Magigene Biotechnology Co. Ltd. (Guangzhou, China). Reads created in this study have been uploaded to the NCBI SRA database (BioProject accession number PRJNA808868).

Taxonomic analysis of raw sequences were processed using the Quantitative Insights into Microbial Ecology pipeline (QIIME2; version 2021.04) (Almeida et al., 2018; Caporaso et al., 2010). In brief, for all sequenced sample, raw paired-end sequences were imported into Qiime2, the demultiplexed and quality filtered by q2-demux and DADA2 denoise plugin (Callahan et al., 2016). The result of high-quality sequences were clustered as amplicon sequence variants (ASVs) at 99% identity for downstream diversity and taxonomic analysis. The taxonomic assignment of the ASVs was performed against the SILVA v132 as the database (Quast et al., 2012) using q2-feature-classifier plugin which based on a pre-trained Naïve Bayes classifier on SILVA 99% OTU database (version 138) trimmed to the V4-V5 regions of the 16S rRNA gene. To standardize the uneven sequencing depth, all samples were randomly subsampled to the smallest library sizes, which is 16,210. After taxonomy had been assigned, non-

bacterial ASVs (such as the chloroplast, mitochondria, archaea, and unclassified) sequences were removed from the subsequent analysis.

2.4. Statistical analyses

The alpha-diversity indices (Shannon and Chao1 indices) were calculated in the R environment. Kruskal-Wallis one way analysis of variance was used to test for the significance of the differences between different domains. Distance-based community analyses were calculated based on Bray-Curtis dissimilarities. The beta-diversity statistical analyses were tested using PERMANOVA (permutational multivariate analysis of variance) based on Bray-Curtis dissimilarities and 999 permutations (Kusstatscher et al., 2020). All analyses were carried out using the vegan and ggplot2 (Ginestet, 2011) packages under the R environment (Grunsky, 2002). The presence of potential pathogens was identified by comparing the 16S gene sequences against the bacterial pathogens database (Wardeh et al., 2015) using BLAST (Boratyn et al., 2013). Only ASVs with 100% identical and 100% coverage were retained.

3. Results

3.1. Sources of air masses on the Tibetan Plateau

Ten-day backward trajectory plots of the air masses of the samples indicated that 13 aerosol samples can be divided into three groups based on air mass history. PL4_1, QY_1, QY_2, MDKR_1 and MDKR_2 samples were located in the monsoon domain (MD), ten-day back trajectories showed

that air masses were predominately originated from the Indian continent (Bangladesh, India, and Nepal) and Indian Ocean. These air masses traveled at a low altitude (500 m) before reaching the sampling sites (Fig. 2A).

QT1_1, TGL_1 and DKMD_1 samples were located in the transition domain and were affected by monsoon (TDM) at the time of sampling, ten-day back trajectories showed a similar air mass backtrace history as for MD samples,

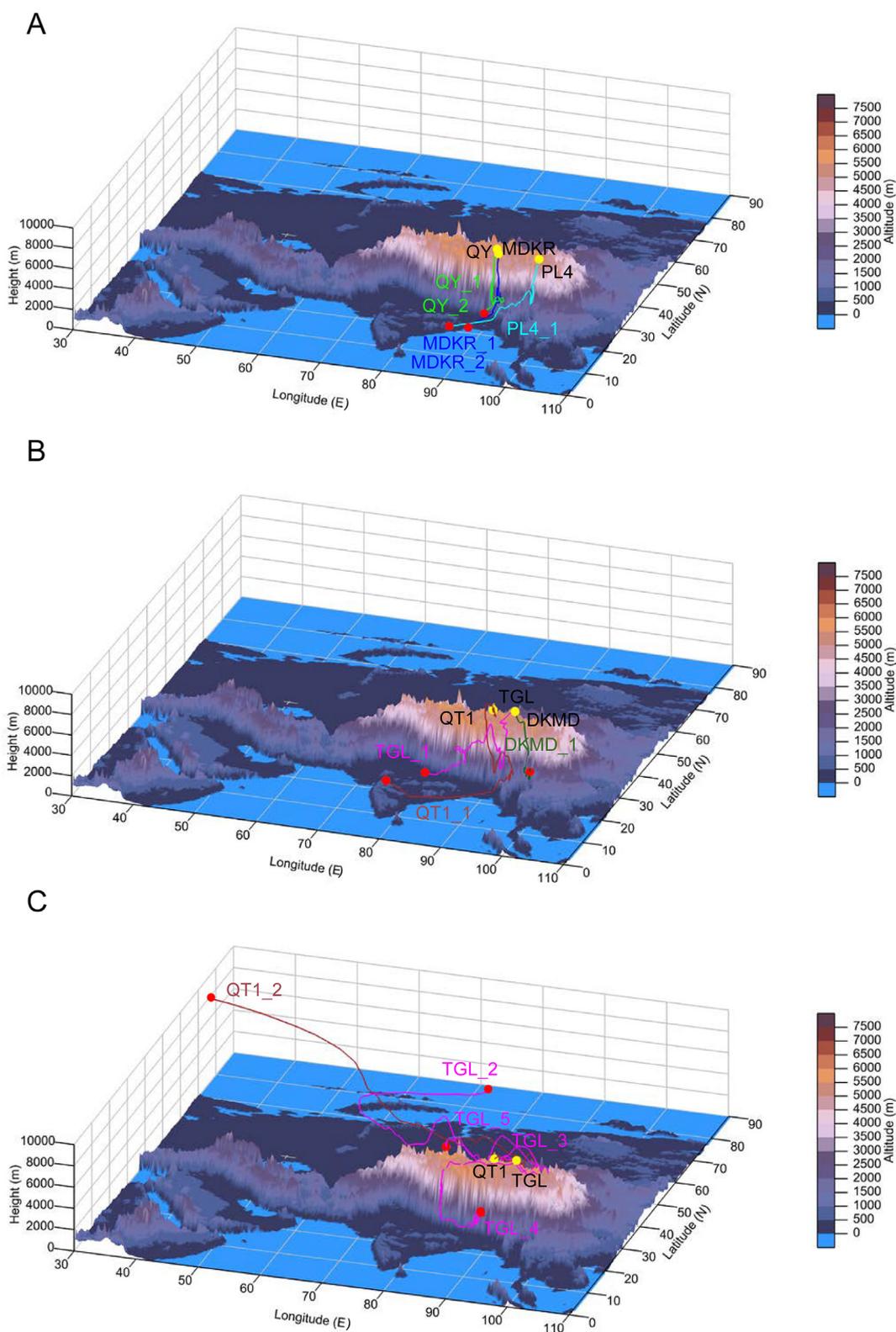


Fig. 2. Ten days backward trajectory at 500 m above the ground level from Hybrid Single-Particle Lagrangian Integrated Trajectory (HYSPPLIT) model in MD (A), TDM (B) and TDN (C) samples. Yellow dots indicate the final position (sampled locations) of the backward trajectory, and red dots indicate the start position of the backward trajectory. The trajectories of different glaciers are shown with different colored. Monsoon domain (MD), Transition domain affected by monsoon (TDM), Transition domain not affected by monsoon (TDN), Parlung No. 4 Glacier (PL4), Qiangyong Glacier (QY), Mengdakangri Glacier (MDKR), Qingtang No. 1 Glacier (QT1), Dongkemadi Glacier (DKMD) and Tanggula Glacier (TGL).

and they were all influenced by the Indian continental and Ocean air masses before reaching the sampling sites (Fig. 2B). In comparison, QT1_2, TGL_2, TGL_3, TGL_4 and TGL_5 samples were also located in transition domain, but were not affected by the monsoon. Instead, the air masses traveled from west to east at a high altitude (1500–6000 m) over the Xinjiang Autonomous Region and even over Europe before reaching the sampling sites (Fig. 2C), therefore were termed transition domain samples not affected by the monsoon (TDN). Although the backward track of TGL_4 originated from Nepal, but the air mass traveled was at a high altitude from west to east after entered the Tibetan Plateau, and the ecosystem it passed through was mostly same with TDN samples, so it was classified as TDN group (Fig. 2C).

3.2. Bacterial diversity of the aerosol sample over the Tibetan glaciers

There were 3185 ASVs identified across all samples. The Shannon diversity ranged from 5.02 to 7.99 (mean = 6.64) and the Chao1 index varied from 128 to 517 (mean = 260). The Shannon diversity of the MD samples was similar to the TDM samples (Kruskal-Wallis, $P = 0.25$). In addition, the Shannon diversity of both MD and TDM was significantly higher compared with TDN samples ($P = 0.016$ and 0.036 , Fig. 3). The Chao1 index of the MD samples was similar to the TDM samples ($P = 0.14$), whereas both those of MD and TDM samples were significantly higher compared with TDN samples ($P = 0.008$ and 0.036 , Fig. 3).

3.3. Spatial variation of airborne bacterial taxonomic composition and community structure in glaciers over the Tibetan Plateau

Taxonomic analysis at the phylum level revealed that *Proteobacteria* (43%), *Firmicutes* (10%), *Bacteroidetes* (9%), and *Actinobacteria* (8%) were dominant across all samples (Fig. 4). There was no significant difference observed at the phylum level across the MD, TDN, and TDM, except *Bacteroidetes* and *Firmicutes*. The relative abundance of *Bacteroidetes* was significantly higher in MD and TDN samples than in TDM samples (Kruskal-Wallis, $P = 0.036$), while that of *Firmicutes* was significantly higher in TDM samples than in MD samples ($P = 0.036$; Fig. S1A). Comparison of *Firmicutes* and *Bacteroidetes* ASVs at the order level showed that *Lactobacillales* and *Flavobacteriales* were responsible for the difference observed (Fig. S1B and C). More specifically, the significant differences were mainly observed in *Lactococcus sp.*, which accounted for 65% of the *Lactobacillales* ASVs. The relative abundance differences of *Bacteroidetes* were mainly due to *Flavobacteriales*, and the dominated species were

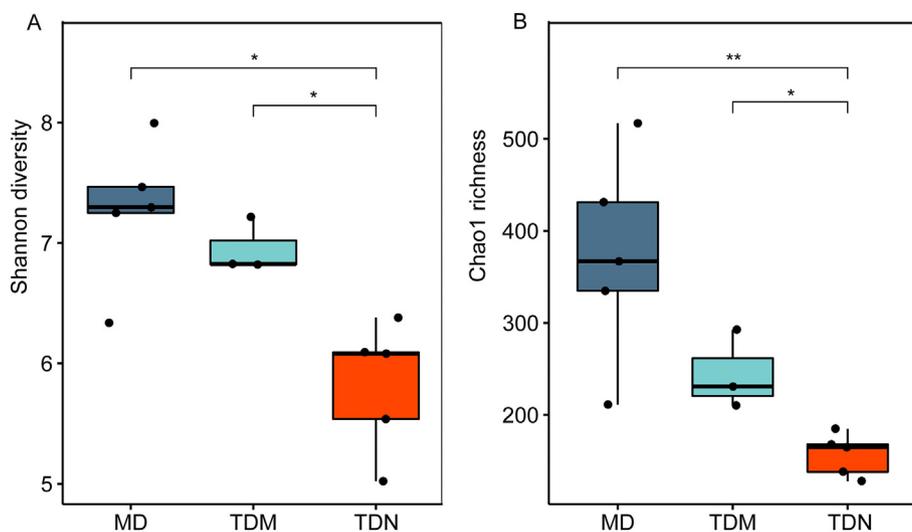


Fig. 3. Comparison of bacterial alpha-diversity indices Shannon diversity (A) and Chao1 richness (B) indices in MD, TDM and TDN samples. The box stretches from the 25th percentile to the 75th percentile with medium values marked. Significance is tested using the Kruskal-Wallis test, with $P < 0.05$ considered significant. *** $P < 0.001$, ** $P < 0.01$ and * $P < 0.05$. Monsoon domain (MD), Transition domain affected by monsoon (TDM), and Transition domain not affected by monsoon (TDN).

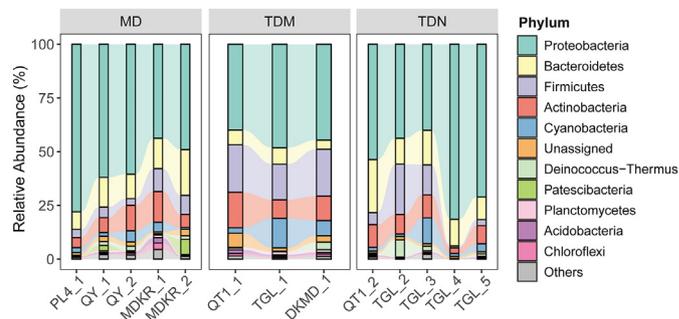


Fig. 4. Relative abundances of bacterial 16S rRNA gene sequences at the phylum level (relative abundance >2%) in all glacier aerosol samples across MD, TDM and TDN. Monsoon domain (MD), Transition domain affected by monsoon (TDM), and Transition domain not affected by monsoon (TDN).

identified to be *Flavobacterium sp.*, which accounted for 70% of the *Flavobacteriales* by relative abundance.

Principal coordinate analysis (PCoA) based on Bray-Curtis dissimilarity revealed three clusters of aerosol samples. Cluster I comprised MD samples, while cluster II and III comprised transition domain samples under the influence of monsoon (TDM) and without the influence of monsoon (TDN), respectively (Fig. 5A). Significantly bacterial community structure differences were identified across the three groups (PERMANOVA, $P = 0.021$, Table S2), while the community similarity between MD and TDM ($P = 0.021$) samples were higher than those between TDN samples ($P = 0.009$).

The community assembly of MD samples was dominantly explained by stochastic processes (64%, Fig. 5B), while the deterministic processes only explained 34%. In comparison, the community assembly of transition domain samples was dominantly explained by deterministic processes (56% and 68%). However, significant differences were observed between the TDM and TDN samples. For TDM samples, the stochastic processes explained 44%, which is significantly higher than the TDN samples (32%, Fig. 5B).

3.4. Potential pathogens

Potential pathogens were identified by comparing sequences against the infectious disease database. A total of 23 bacterial ASVs were identified to be potential pathogens, and they were identified as *Pseudomonas fluorescens*, *Pantoea agglomerans*, *Acinetobacter calcoaceticus*, *Lactobacillus*

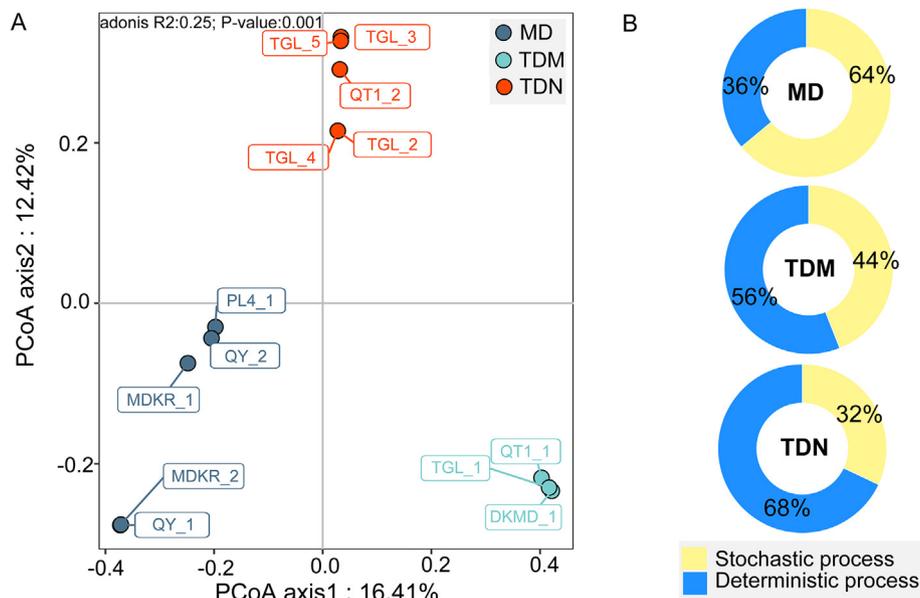


Fig. 5. Principal coordinates analysis based on the Bray-Curtis dissimilarity (A) and the contribution of the ecological processes that determined community assembly of the bacterial community (B). Monsoon domain (MD), Transition domain affected by monsoon (TDM), and Transition domain not affected by monsoon (TDN).

sp., *Staphylococcus lugdunensis*, *Staphylococcus aureus*, *Moraxella osloensis*, *Stenotrophomonas maltophilia*, *Fusobacterium nucleatum* subsp. *vincentii*, *Bacillus thuringiensis*, *Achromobacter piechaudii*, *Sphingomonas paucimobilis*, *Capnocytophaga sputigena*, *Aeromonas veronii*, *Clostridium butyricum*. Of the pathogens detected, 44% were observed in MD samples, an additional 52% were observed in TDM samples, while only 4% were identified in TDN samples (Table S3). The potential pathogens accounted for 0.7% of all 16S rRNA gene sequences across all samples, and their relative abundance was similar in MD (4.93%) and TDM samples (5.49%, Kruskal-Wallis, $P = 0.21$; Fig. S2), while they were both significantly higher than those of TDN samples (0.03%, $P = 0.002$ and $P < 0.001$, respectively, Fig. S2).

4. Discussion

4.1. Spatial variations of glacier airborne bacterial diversity in glaciers over the Tibetan Plateau

In this study, Shannon and Chao1 diversity indices in MD samples were similar to the TDM samples, both of them were significantly higher compared with TDN samples (Fig. 3). Both MD and TDM samples were affected by the Indian monsoon, thus this suggests that the Indian monsoon may increase the airborne bacterial diversity. Airborne bacterial diversity is the result of the influence of air mass sources (Qi et al., 2021; Tang et al., 2018) and the ecosystems that the air mass moves over (Fröhlich-Nowoisky et al., 2016). For MD and TDM samples, the airborne bacteria were carried by the Indian monsoon from the India (Fig. 2A and B). In addition, the Indian monsoon travels at low altitude before reaching the sampling sites (Fig. 2A and B), thus it may pick up microbes from the ecosystems on the path of air mass travels, assisting the dispersal of soil-borne bacteria to glacier environment (Li et al., 2020). Indian monsoon travels over diverse ecosystems including meadow, shrub, and forest (Fig. 1). The diverse source of microorganisms can enhance the diversity of microbes carried by the Indian monsoon.

For TDN samples, the air mass was mainly influenced by the westerly. The air mass predominately traveled at a high altitude (Fig. 2C). The drier, harsher atmospheric environment with stronger UV radiation suggest the airborne microbes could be subjected to a stronger selection process (Pan et al., 2021), which could greatly limit the diversity of bacterial that survived. This is similar to the study in the Arctic region, where microorganisms in the Arctic atmosphere were exposed to extremely low

temperatures and hurricane-strength winds, extreme exposure to UV radiation, and extremely low levels of nutrients, resulting in a lower diversity compared with that in urban areas (Cuthbertson et al., 2017). Moreover, a study on the Antarctic airborne bacteria suggests that strong selection occurs during atmospheric transport, limiting the airborne microbes input into the Antarctic continent (Archer et al., 2019). Furthermore, the westerly mainly travels through simple ecosystems such as deserts and sparse grasslands (Figs. 1 and 2C), further limiting the diversity of bacteria dispersed.

4.2. Glacial airborne bacteria community assembly over the Tibetan Plateau

The airborne bacteria samples were grouped into three clusters: MD, TDM, and TDN (Fig. 5A). MD and TDM samples were more similar compared with TDN samples, which could be attributed to the influence of the Indian monsoon. The air masses of MD and TDM moved in a similar trajectory from the Indian continent into the Tibetan plateau (Fig. 2A and B). Thus, these air masses could carry similar microbes from the ecosystems along the path of air mass (Burrows et al., 2009a; Qi et al., 2021). This has been evidenced by the Fröhlich-Nowoisky et al. (2016) that different ecosystems can emit distinct airborne microbes. In comparison, TDN samples were mainly influenced by the westerly air masses, which carry distinct microorganisms from the Indian monsoon due to the different sources of air mass and ecosystems they move over (Figs. 1 and 2C). Thus, different atmospheric circulation impacts both the diversity and relative abundance of aerosol bacteria, which may subsequently impact the microbial ecosystems on the glacier surface. Furthermore, the sampling time was different for aerosol samples of TDM and TDN (Table S1). However, the bacterial communities in the aerosol were clustered by the influence of atmospheric circulation, but not by sample time (Fig. 5A). Therefore, this confirms the vital roles Indian monsoon in shaping the bacterial community structure in aerosol over the Tibetan glaciers.

The bacterial community assembly of Indian monsoon domain (MD) and transition domain (TDN and TDM) samples were dominantly explained by stochastic and deterministic processes, respectively (Fig. 5B). The high contribution of determinism to the microbial community in transition domain samples could be explained by the longer distance traveled (and hence the longer retention time in the atmosphere). Microbes in the atmosphere are subjected to strong UV radiation, low temperature and moisture (Cuthbertson et al., 2017), which greatly increase the selection pressure (Bottos et al., 2014). This is evidenced by the prolonged exposure to UV irradiation greatly reduces the survival rate of airborne bacteria (Pan et al.,

2021). The influence of the Indian monsoon increased the influence of stochasticity in both monsoon domain samples (MD) and transition domain samples influenced by the monsoon (TDM samples, Fig. 5B). Indian monsoon carries a diverse range of bacteria, whose deposition is affected by dispersal limitation (Qi et al., 2021), which is typically considered a stochastic process (Ning et al., 2020). Thus, the random dispersal of bacteria over the glacier explained the increased stochasticity observed.

4.3. Variation of airborne bacterial taxa and potential bacterial pathogens in glaciers over the Tibetan Plateau

Airborne bacteria were dominated by *Proteobacteria*, *Firmicutes*, *Bacteroidetes*, and *Actinobacteria* (Fig. 4). This is consistent with the dominant airborne bacteria identified globally, including the high-elevation sites (Bowers et al., 2012) and the low troposphere (Bowers et al., 2009; González-Toril et al., 2020; Pearce et al., 2010). In the present study, the relative abundance of *Firmicutes* was significantly higher in TDM samples (Fig. S1A). *Firmicutes* are probably well adapted to atmospheric life for their ability to form endospores in low nutrient conditions (Galperin, 2013). Furthermore, they can even multiply in dust particles when nutrients are available (Tang et al., 2018). The difference in *Firmicutes* relative abundance was attributed to *Lactobacillales* (Fig. S1A and C, predominately *Lactococcus* sp.). The genus *Lactococcus* was commonly identified in dairy products (Bolotin et al., 2001). This is consistent with the intensive pasture activity in central Tibet (Li et al., 2019).

The relative abundance of *Bacteroidetes* was significantly higher in MD samples than in TDM samples, and the differences were mainly attributed to the *Flavobacteriales* (Fig. S1A and B), and the dominated species were identified as *Flavobacterium* sp. Members of the genus *Flavobacterium* have been isolated from a wide range of habitats such as freshwater, river sediments, seawater, soils, cropland, and glaciers (Dong et al., 2013; Ekwe and Kim, 2018; McCammon and Bowman, 2000). This is consistent with the complex ecosystems and frequent human activities in the path of the Indian monsoon.

The identified bacterial pathogens can affect a diverse range of hosts including plants, fish, arthropods, amphibians, birds, mammals, and humans (Table S3). The relative abundances of potential bacterial pathogens in MD and TDM samples were similar, and were both significantly higher than that in TDN samples (Fig. S2). Therefore, the Indian monsoon not only increases airborne bacterial diversity, but also increase the diversity and relative abundance of potential pathogens, which also includes the most notorious bacteria such as *P. fluorescens* (Schwartz et al., 2006), *S. aureus* (Myles and Datta, 2012), and *C. butyricum* (Lee et al., 2008). MD and TDM samples were both affected by the Indian Monsoon, and the areas affected by the Indian monsoon were more populated than that by the westerlies (Rumpf et al., 2017). This could be due to the higher abundance of pathogenic microbes in urban air than in rural (Nanclares Castaneda et al., 2020). The higher population and greater density explain the higher prevalence of airborne pathogens. The dispersal of potential pathogens on glacier surface could make Tibetan glaciers a reservoir for hazardous bacteria. Snow as a pathogen reservoir has also been demonstrated by the identification of pathogens in glacier surface snow (Ji et al., 2021). These potential pathogens could be released into downstream ecosystems through glacier meltwater, and impact the health of plants, animals, and humans.

5. Conclusion

Our results revealed that the Indian monsoon and westerly carry distinct bacterial populations and affected the airborne bacteria over the glaciers of the monsoon and westerly affected domains. These distinct bacteria could be responsible for the distinct microbial community observed on the glacier surface, which affects the biogeochemical cycling of elements and impact the health of downstream ecosystems during glacier melting. Thus, our study provides novel insights into the establishment and evolution of microbial ecosystems in Tibetan glaciers.

CRedit authorship contribution statement

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

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.154980>.

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