Environmental Microbiome

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Daily turnover of airborne bacterial communities in the sub-Antarctic

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Abstract

Colonization of remote ecosystems by new microorganisms poses a significant threat to the diversity and function of native microbial communities. In the polar regions, including Antarctica, airborne microbial communities are shaped by environmental and climatic factors, which are changing rapidly. However, the specific drivers of microbial community composition and diversity in these regions remain poorly understood. This study explores the daily dynamics of airborne bacterial communities over South Georgia, a large and remote sub-Antarctic Island, and evaluates the influence of environmental factors, local microbiomes, and sampling methodology. Over two weeks, near-surface air samples were collected from coastal and higher-altitude (200 m a.s.l) sites using different air samplers. The Coriolis Compact sampler, run for longer durations, captured higher diversity, while the Coriolis Micro provided high-quality snapshots during shorter sampling windows. Results showed rapid daily turnover in community composition (up to 90%) alongside a stable core microbiome (10–20%). Coastal microbial communities were shaped by local microbiomes, especially wildlife-associated taxa, whereas high-altitude communities were more variable, suggesting influence from long-range microbial dispersal. Environmental factors, including wind direction, temperature, and rainfall, also significantly shaped community structure. These findings highlight the dynamic nature of airborne microbiomes in the sub-Antarctic.

Keywords Antarctica, Aerobiology, Dispersal, Bacteria, Biodiversity, South Georgia

Introduction

The dispersal of microorganisms through the atmosphere has been a long-standing area of research, with significant implications for agriculture, medicine, and ecosystem dynamics. While the study of airborne microbes dates back to Louis Pasteur's pioneering experiments on spontaneous generation [14, 51], recent technological advances, such as high-throughput sequencing and modern air samplers, have enabled unprecedented insights into the complexities of microbial dispersal and biogeography in the atmosphere [59, 76].

Polar regions are particularly important for understanding microbial dispersal due to their extreme isolation and role in regulating global climate through mechanisms like the albedo effect and greenhouse gas cycling [48]. They are often regarded as pristine

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environments with low biomass and low biodiversity due to their extreme remoteness and associated specific mechanisms of environmental isolation, such as the Polar Dome in the Arctic [6] and the oceanic Antarctic Circumpolar Current and atmospheric West Wind Drift [5, 11], separating them from warmer mid-latitude air masses. However, in recent years, these views have been challenged by technological advances that have enabled more detailed studies, revealing not only unexpectedly high microbial biodiversity hotspots but also significant resilience and adaptation to extreme polar conditions [27, 28]. While studies have shown that polar environments are more diverse than previously thought, the role of microbial dispersal, particularly long-range aerial transport, in shaping this diversity is still not fully understood. Further investigation is needed, especially regarding how airborne microbes disperse to and within Antarctica and the extent to which aerial transport influences local biodiversity and ecosystem function [54].

Recent studies have shown that, despite its low contained biomass, the air around Antarctica and the Southern Ocean hosts distinct microbial communities [32, 43, 53]. Some of these microbial genera, such as *Psychrobacter*, *Shewanella* and *Tepidimonas*, appear uniquely adapted to the challenges of aerial dispersal, showcasing traits such as psychrophilic and extremophilic adaptations that enable them to survive and persist in the harsh, cold, and variable atmospheric conditions [2, 43]. These findings suggest that Antarctic airborne microbial communities are not simply passively transported but may be actively adapted to or be selected for airborne dispersal. Although the study of airborne bacteria in and around Antarctica is still in its infancy, recent studies have suggested significant spatial differences in microbial communities and confirmed the importance of aerial transport [2, 10, 43, 53].

In line with large-scale initiatives such as the Earth Microbiome Project (terrestrial) [20], the Global Ocean Sampling (GOS) program [58] and the TARA Oceans expedition (marine) [64], several ambitious programs have been established to investigate the diversity and distribution of airborne microorganisms in the Antarctic and Southern Ocean [2, 10, 69], including the Antarctic Circumnavigation Expedition (ACE) in 2016/17 [43]. These studies revealed significant temporal and spatial variations in airborne microbial communities across the Southern Ocean and into lower-latitude regions. There have also been coordinated global efforts to characterize airborne communities at the global scale [3, 45, 67].

While these studies offer much higher resolution than previously possible, they remain limited by short timescales, often relying on moving vessels or sampling isolated points across large geographic areas. Single-time-point and single-location studies have been invaluable in establishing foundational knowledge, yet they provide only a snapshot of these complex microbial dynamics that shape aerial biodiversity. It is now evident that global aerial biodiversity can fluctuate significantly across long (seasonal) [30, 68], medium (days) [18] and very short (hours) temporal scales [22]. Consequently, to fully characterize aerobiological patterns, it is essential to distinguish persistent community structures from transient fluctuations, capturing both stable and variable components over time. Understanding aerobiology in Antarctica requires comprehensive, long-term studies to determine how microbial communities fluctuate over time and what factors drive these changes.

To address the need for longer-term, high-resolution studies of aerobiology in extreme environments, we conducted a daily time-series sampling on the remote sub-Antarctic Island of South Georgia. We sampled near-surface air continuously at sea-level and at a higher-altitude (200 m a.s.l) location to capture the passage of several distinct weather systems, using high-resolution sampling technology. This allowed us to document the temporal variation in airborne microbial diversity across the sites. Globally, there is no standardized methodology for sampling airborne microbial communities. Among the widely used methods are the Coriolis micro (wet) and Welch pumps [54], though many other methods also exist (reviewed in Dybwad et al. [16] and Mainelis [41]). In polar regions, one limitation of the Coriolis micro is that the sampling water freezes at low temperatures, although other solutions can be used to avoid freezing [2]. To address this freezing issue, we also tested the Coriolis compact (dry), which operates with a dry cone, making it a suitable alternative for freezing environments. In this study, we also compared air sampling methodologies to evaluate their performance and potential biases, and to identify the most suitable approach for cold, remote ecosystems. Overall, our aim was to improve our understanding of near-surface airborne microbial dispersal dynamics and assess how local microbiomes and environmental conditions shape microbial community composition in sub-Antarctic air. Specifically, we addressed the following research questions: (1) How does airborne microbial community composition vary over time and across two different altitudes? (2) To what extent do local or distant microbiomes (e.g., from soil, water, and wildlife) contribute to airborne microbial communities? (3) How do environmental conditions such as temperature, wind, and precipitation influence airborne microbial diversity and turnover? And in so doing, (4) how different air sampling methods perform in capturing airborne microbial diversity?

Materials and methods

South Georgia

A total of 60 air samples and 5 rainfall samples were collected on South Georgia, an isolated island in the South Atlantic sector of the Southern Ocean and one of the largest sub-Antarctic islands located approximately 2,000 km north-east of the Antarctic Peninsula and 2,000 km east of Tierra del Fuego at the tip of South

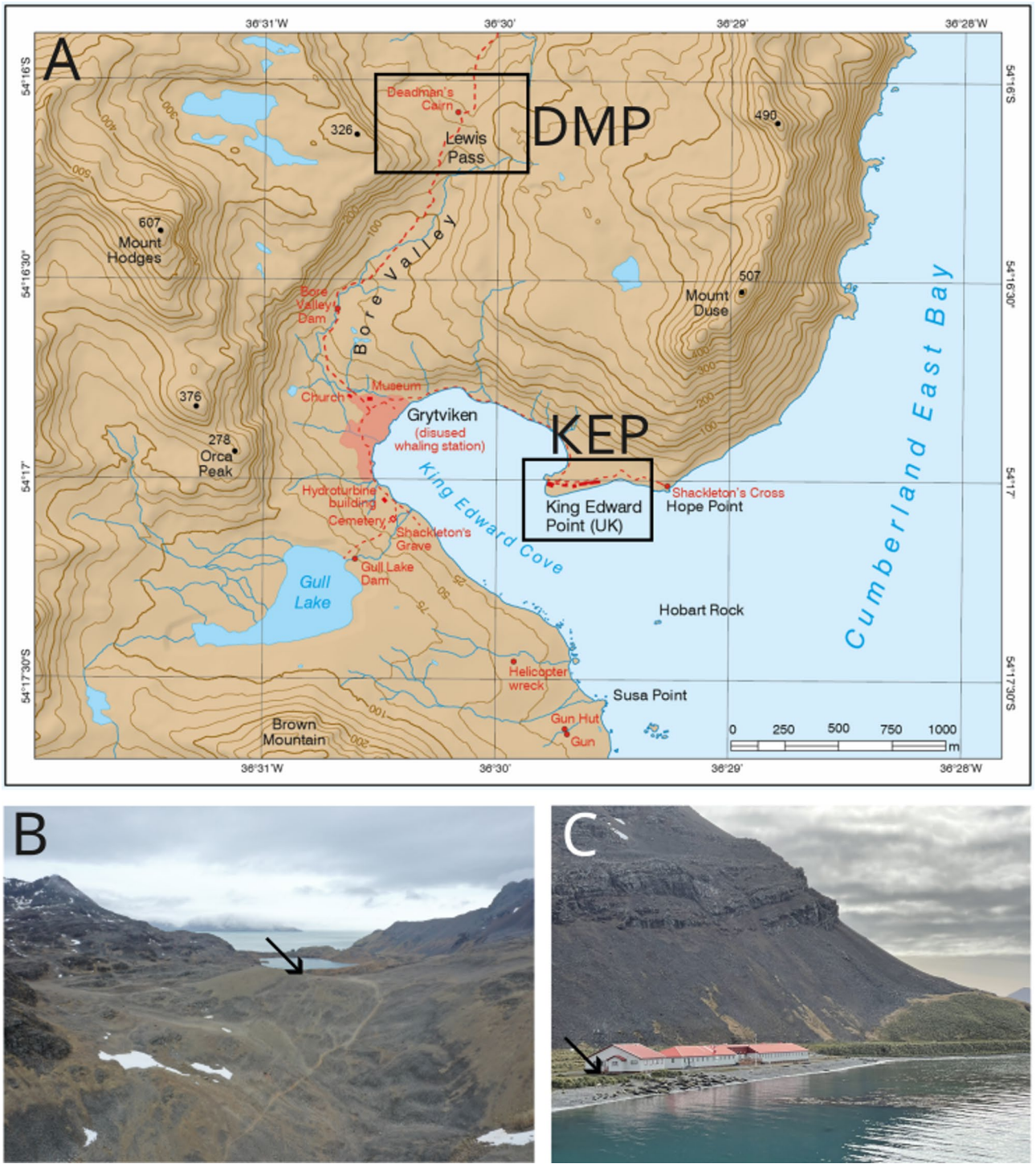

Fig. 1 (**A**) Map of the King Edward Cove region on South Georgia, highlighting the sampling sites at Deadman's Cairn (DMP) and King Edward Point (KEP). (**B**) Oblique aerial view of the DMP sampling site, with arrow indicating the sampling location on the pass. ©John Dickens (**C**) Oblique aerial view of the KEP sampling site near the coast, with arrow marking the sampling location. ©John Dickens

America. Sampling took place between 13 and 25 October 2021 (Fig. 1).

Of these, 23 air samples were collected at Deadman's Cairn, Lewis Pass (DMP; 54° 16'05" S, 36° 30'20" W), an inland site situated ~ 200 m above sea level on a roughly North/South orientation and ~ 1 km from the coast (Fig. 1b, c). The remaining 42 samples were obtained at King Edward Point, East Cumberland Bay (KEP; 54° 17'02" S, 36° 29'75" W), a coastal site approximately 3 m above sea level.

Air and rainfall sample collection

At DMP (no external power), two different methods were applied for air sample collection. Dry samples were collected using a Bertin Coriolis compact sampler (Bertin Technologies, Montigny-le-Bretonneux, France), operated at a flow rate of 50 L min^{-1} for 180 min. Wet samples were collected using a Bertin Coriolis micro sampler (Bertin Technologies), with collection cones filled with sterile DNase- and RNase-free H_2O (Thermo Fisher Scientific), and the sampler run at a flow rate of 300 L min^{-1} for 180 min. At DMP, the samplers were run for 180 min due to limited battery life.

At KEP, three different air sampling methods were employed. The micro (wet) and compact (dry) Coriolis samplers, as described above, were each run for 6 h. Access to electricity allowed us to double the sampling time as an additional method comparison. We also collected dry samples using a membrane filtration apparatus with a Welch WOB-L vacuum pump (Welch, Mt. Prospect, IL, USA) generating a flow rate of 20 L min^{-1}. The pump was connected via tubing to a Sartorius filtration unit (Göttingen, Germany) containing a 47 mm × 0.2 µm pore size cellulose nitrate membrane filter (GE Healthcare Life Sciences, Chicago, IL, USA). Due to the low flow rate of the pump, these samples were collected over a 24-hour period.

Sterile sampling cones were used for both Coriolis instruments. At each site, the instruments were assembled, cleaned with molecular water and operated with a sampling cone to perform decontamination, after which a sterile cone was installed for sample collection. Negative controls included molecular water samples. For the pump, filters attached to the instruments served as negative controls.

Rainfall samples were collected only at KEP using a sterile funnel cleaned with ethanol and subsequently filtered through 0.22 µm nitrocellulose filters (Merck Millipore, Germany) with a sterile Sartorius filtration unit (Sartorius, Groningen, Germany).

All samples were immediately stored at -80 °C after collection and transported to the United Kingdom under the same conditions for further analysis.

Environmental data

Meteorological data were obtained from the Grytviken Automatic Weather Station and included wind direction, wind speed, temperature and pressure. For each sample collected at KEP and DMP, meteorological data were recorded for the duration of sampling, and the conditions were averaged to generate a summary of parameters corresponding to each sample.

DNA extraction and 16 S amplicon sequencing

In total, 60 air samples and 5 rainfall samples were collected in this study. Samples collected on filter substrates were dissected into quarters using an ethanol- and flame-sterilized scalpel within a sterile Petri dish inside a Class II microbiological safety cabinet. Each quarter filter was then placed directly into a labelled bead tube for DNA extraction. For water-based (Coriolis) samples stored in collection cones or Falcon tubes, the contents were transferred to sterile 15 mL Falcon tubes and centrifuged at 5000 ×g for 20 min. Following centrifugation, the supernatant was removed, leaving 1 mL of liquid in which the pellet was resuspended. This 1 mL suspension was then transferred directly into a labelled bead tube for extraction. Coriolis compact samples were resuspended in 1 ml sterile molecular biology grade water and vortexed for 60 s before transfer directly into a labelled bead tube for extraction.

DNA was extracted from each sample using the Qiagen PowerSoil kit (Qiagen, Hilden, Germany) following the manufacturer's protocol. Extracted DNA was stored at -20 °C and subsequently submitted to the NU-OMICS sequencing facility at Northumbria University, Newcastle, for Illumina MiSeq sequencing. 16 S rRNA gene libraries were prepared using the universal primers 515 F and 806R [35] to amplify the V4 region. Amplicons were generated using high-fidelity AccuPrime DNA polymerase (Invitrogen, Carlsbad, CA, USA), purified using the AMPure magnetic bead capture kit (Agencourt, Beckman Coulter, MA, USA), and quantified with a QuantIT PicoGreen fluorometric kit (Invitrogen). Purified amplicons were then pooled in equimolar concentrations using a SequalPrep plate normalization kit (Invitrogen), and the final library concentration was determined via a SYBR Green quantitative PCR (qPCR) assay. The libraries were mixed with Illumina-generated PhiX control libraries and genomic libraries, denatured using fresh NaOH, and sequenced on an Illumina MiSeq V2 platform (500 cycles).

Amplicon bioinformatic processing

Amplicon sequences were processed using the DADA2 pipeline [9]. Forward and reverse read pairs were quality-filtered and trimmed, with forward reads truncated at 230 bp and reverse reads at 200 bp. No ambiguous

bases were allowed, and each read was required to have fewer than two expected errors based on quality scores. Amplicon sequence variants (ASVs) were independently inferred from the forward and reverse reads of each sample using run-specific error rates. Reads were then dereplicated, merged, and screened for chimeras. Taxonomic classification was performed against the SILVA v138 database [55, 80] using the ribosomal database project (RDP) naïve Bayesian classifier [73].

Metagenomic sequencing and bioinformatic processing

A subset of 8 air sample and 3 rainfall sample DNA extracts were submitted to the NU-OMICS sequencing facility at Northumbria University, Newcastle, for Illumina NextSeq shotgun sequencing. These samples were selected as they had sufficient DNA for metagenomic sequencing. The DNA libraries were prepared using the Nextera XT DNA Library Prep Kit following the manufacturer's instructions. Sequencing was performed on an Illumina NextSeq system (Illumina Inc., USA) using V2.5 300-cycle chemistry.

Raw paired-end metagenomic sequencing reads were preprocessed using the BBMap toolkit [8] to ensure high-quality data for analysis. The workflow included repairing inconsistent read pairings, trimming adapter sequences based on a reference adapter file, removing low-quality bases, filtering out reads with low average quality scores, and eliminating contaminant sequences, such as PhiX control reads. This preprocessing ensured that the final dataset consisted of high-quality, contaminant-free reads suitable for downstream analyses. After preprocessing, reads were taxonomically assigned using Kraken2, with bacterial reads filtered using Krakentools [39]. Gene annotation for each bacterial sample output from Krakentools was performed using DIAMOND and MEGAN [7, 25]. The samples were compared in MEGAN, functional and taxonomic tables were extracted in biom format, and statistical analyses were carried out in R.

Statistical analyses

All statistical analyses were performed in the R environment using primarily a combination of the phyloseq [47] and vegan [13] packages, and visualised using ggplot2 [75]. The dataset al.so included 3 sterile water controls, 4 extraction kit controls, 2 Miseq negative controls and 2 Miseq positive controls. The sterile cone and filter controls had insufficient DNA for sequencing. The microdecon package [46] identified 57 potential contaminants, resulting in 12,167 assigned ASVs across all 65 samples (± 47,548 reads per sample).

To compare instrument performance, we calculated the volume of air captured per sample and assessed alpha diversity using the 'plot_richness' function in phyloseq. Linear models were applied to evaluate changes in richness related to the volume of air sampled. Ratios of alpha diversity per litre of sampled air were calculated, and instruments were compared using ANOVA, followed, when significant, by Tukey's HSD tests. Raw read counts were normalised to relative abundances (i.e., the proportion of each taxon within a sample) and used to build a PCoA with Bray-Curtis distance to compare community composition, tested with adonis. Finally, we calculated the proportion of each phylum per litre of air sampled and compared instruments using ANOVA and Tukey's HSD tests.

To investigate the effects of sampling location, we removed r ainfall and vacuum pump samples to focus on the Coriolis samples (both instruments). We calculated alpha diversity values, normalised the reads for beta diversity assessment and calculated the PCoA as described above. We used the microeco package [38] to identify differentially abundant taxa with ALDEX2 (Kruskal-Wallis). We used the ggvenn_pq function in the MiscMetabar package [65] to identify shared ASVs across locations. We built time-decay models to evaluate the similarity in communities over time with Bray-Curtis dissimilarity. We also classified ASVs based on their detection frequency across samples based on the number of days of presence. Categories were common (> 70% of samples), frequent (50–70%), occasional (10–50%), and rare or transient (< 10%). To evaluate the influence of environmental factors on microbial communities, we averaged the environmental conditions to correspond to each sample's duration and time frame. We used the distance-based redundancy analysis (db-RDA) and the adonis function to evaluate the impact of each variable on community composition. We calculated taxa-environment correlations with Spearman coefficients, with fdr correction of the p-values.

To investigate the influence of rainfall events on microbial communities, we focused on KEP samples and conserved rain and air samples before, during and after rainfall events. The same analyses of alpha and beta diversity and differential analysis as described above were conducted.

Metagenomic taxonomic and functional tables were extracted from MEGAN, and similar analyses of alpha and beta diversity of functional genes, were performed.

Global database

The South Georgia samples were integrated into the global database of soil, marine, and air samples described in Malard et al. [43]. This database was updated to widen the geographic and ecosystem range and is available on FigShare. We calculated alpha diversity measures and built an NMDS on normalized counts to investigate microbial community composition. To determine the potential origin of South Georgia ASVs, we performed a

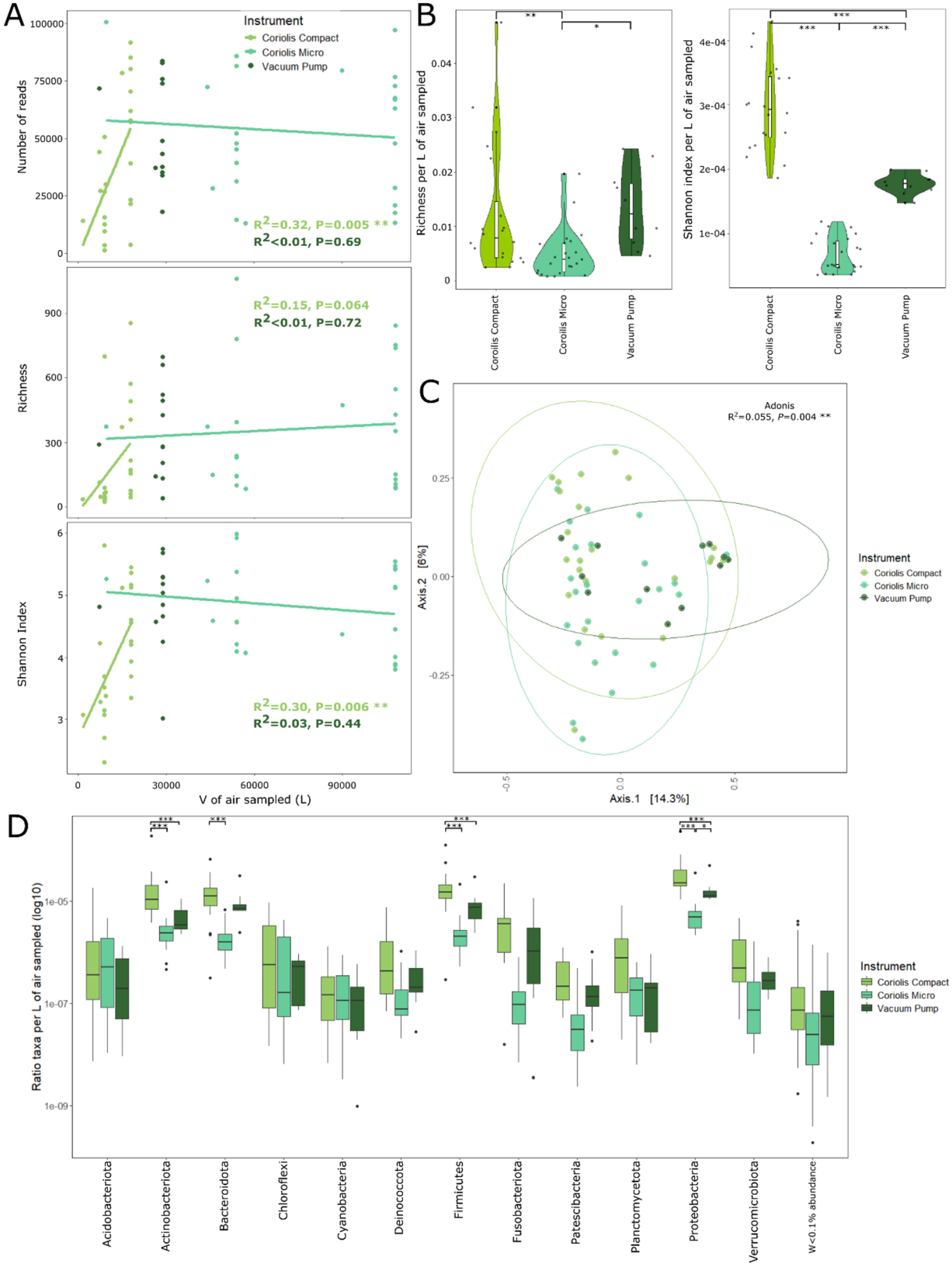

Fig. 2 (See legend on next page.)

(See figure on previous page.)

Fig. 2 (**A**) Changes in read number, richness, and diversity with increasing volume of air sampled. Each colour represents a different sampling instrument, and linear models were fitted for the compact and Coriolis micro (not applicable for the pump). (**B**) Richness and diversity per litre (L) of air sampled for each instrument. Outliers were removed, and differences were calculated using ANOVA followed by Tukey's HSD test with Bonferroni correction. (**C**) PCoA of community composition by sampling instrument, calculated using Bray-Curtis dissimilarity. Differences were assessed with Adonis. (**D**) The ratio of taxa identified by each instrument per L of air sampled. Differences were determined using ANOVA and Tukey's HSD test with Bonferroni correction

source tracking analysis using the FEAST package [61]. In this analysis, the global database served as the source of ASVs, with the South Georgia samples as the sink. Differences between the source origins and South Georgia samples were tested using ANOVA followed by Tukey's HSD tests.

Results

Sampling methods are complementary

In this study, we compared the performance of the Coriolis micro (wet), Coriolis compact (dry), and Welch vacuum pump to assess their impact on sequencing reads, microbial richness, diversity, and community composition. The Coriolis samplers ran for 1 to 6 h, while the pump ran for 24 h (with one 6-hour exception). Results show that the Coriolis compact (dry) captured significantly higher microbial richness and diversity per litre of air than both the Coriolis micro (wet) and the vacuum pump [Fig. 2A, B]. Notably, read numbers, ASV richness, and diversity increased with sampling time only for the Coriolis compact. Sampling for at least 6 h with the Coriolis compact was necessary to achieve results comparable to the other methods [Fig. 2A]. Community composition also differed slightly between instruments (Adonis $R^2 = 0.06$, $p = 0.004$) [Fig. 2C], with the Coriolis compact consistently capturing higher proportions of Actinobacteriota, Bacteroidota, Firmicutes, and Proteobacteria compared to the other samplers [Fig. 2D].

Sampling location matters

To assess the influence of sampling location on airborne microbial communities, we focused exclusively on data from the Coriolis samplers. While alpha diversity was statistically similar between the coastal site (KEP) and the higher-altitude site (DMP) (Fig. S1), community composition differed markedly, reflecting distinct environmental influences at each site (Fig. 3A). In common with other polar studies, the dominant airborne microbial groups across all samples included Proteobacteria, Actinobacteria, Bacteroidota, and Firmicutes, with day-to-day variation in relative abundance (Fig. 3B, C). However, the differential abundance analysis (Aldex2) revealed significant compositional shifts between sites (Fig. S2A, B). At DMP, the community was enriched in Acidobacteriota, WPS-2 (Candidatus Eremiobacterota), Armatimonadota, and Chloroflexi, while KEP samples were enriched in Deinococcota. Genus-level differences also emerged, with a notable presence of peat-associated genera such as *Bryobacter*, *Granulicella*, *Acidiphilum*, and *1174-901-12* (related to nitrogen-fixing Beijerinckiaceae) at DMP. In contrast, KEP samples contained genera associated with soil and permafrost (*Arthrobacter*, *Psychrobacter*, *Pseudoarthrobacter*), glaciers (*Polaromonas*, *Psychrobacter*), marine environments (*Marinifilum*, *Sporosarcina*), and hosts (*Peptinophilus*, *UCG-005*, *Bacteroidetes*, *Ornithobacterium*).

In total, 2,919 ASVs were unique to DMP, 4,167 to KEP, and only 816 ASVs were shared, yet those shared ASVs accounted for 57% of total relative abundance, suggesting a common airborne core dominated by prevalent taxa (Fig. S3). When filtering for ASVs present in at least 50% of all samples, only eight ASVs remained, primarily consisting of *Psychrobacter* and host-associated microorganisms (living on or within a host organism), indicating low overlap in community structure between sites. Accounting for the potential instrument bias, we reduced that threshold to 25% of all samples, resulting in 92 shared ASVs, including additional environment-related microbes (e.g., *Acidiphilum*, *Deinococcus*, *Sphingomonas*, *Halomonas*, *Marinifilum*) and host-related microbes (e.g., *Faecalibacterium*, *Ornithobacterium*, *Streptococcus*).

Temporal variability of communities

Airborne microbial communities over South Georgia exhibited pronounced daily fluctuations in ASV relative abundance (Fig. 4A). Linear models showed high dissimilarity between consecutive days at the high-altitude DMP site, while samples from the coastal KEP site were more similar over time (Fig. 4B). This indicates greater community turnover and instability at DMP compared to the more compositionally stable KEP site. To further explore these dynamics, ASVs were classified based on their detection frequency across samples as common (>70% of samples), frequent (50–70%), occasional (10–50%), and rare/transient (<10%). This classification confirmed that KEP harboured a larger and more stable temporal core microbiome of common taxa shared across samples, compared to DMP, which was dominated by occasional and transient taxa, reflecting greater variability.

At KEP, rare and transient taxa accounted for an average of 35% of the relative abundance, while occasional taxa comprised 30–35%, frequent taxa contributed 21–30%, and common taxa made up only 5–9%. In contrast, frequent and common taxa were far less abundant at DMP, representing only 9–16% and 6–7% of relative

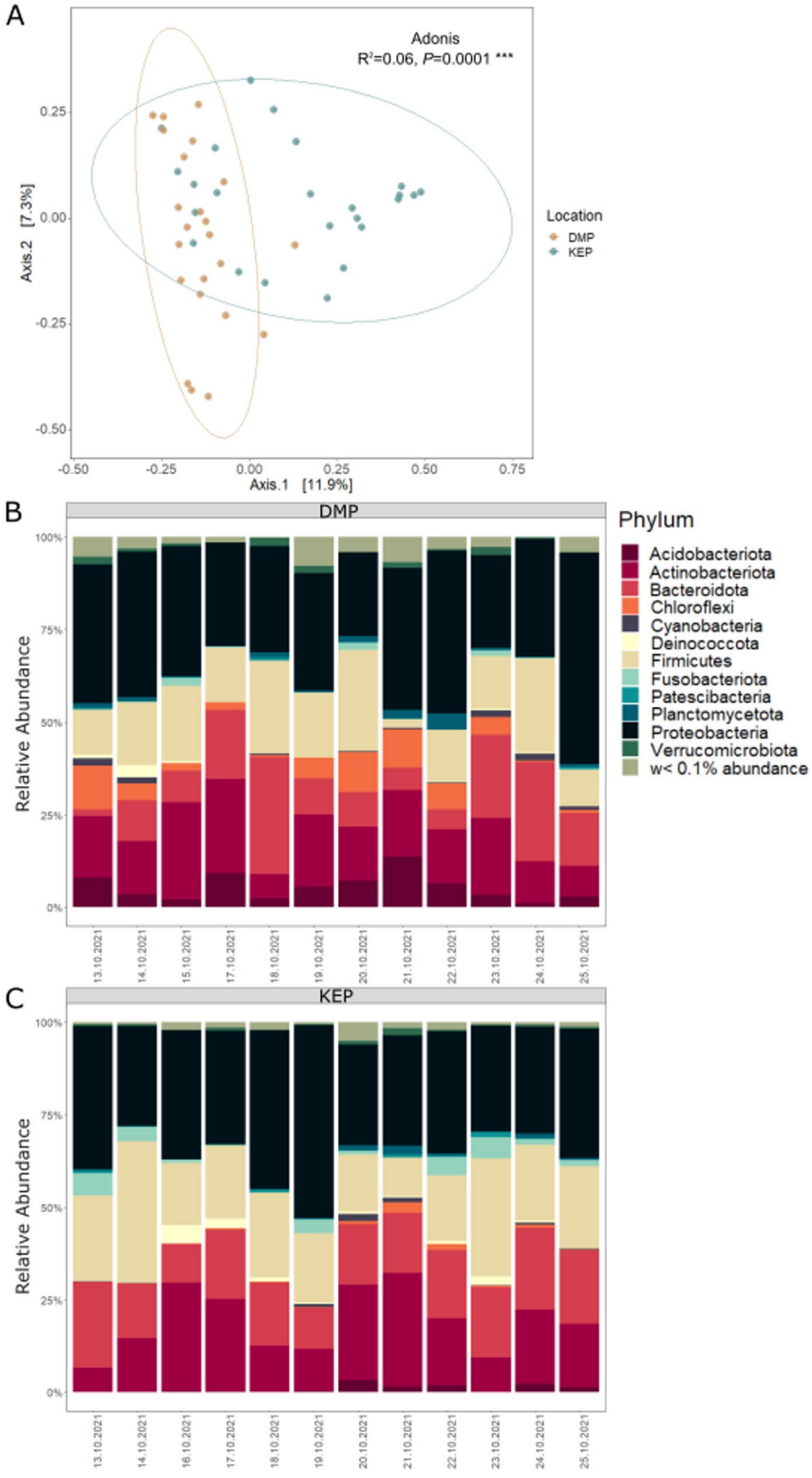

Fig. 3 (**A**) PCoA showing community composition differences between DMP and KEP samples, highlighting the presence of distinct microbial communities at each location. (**B**, **C**) Day to day relative abundance of bacteria at the phylum level differentiated by location

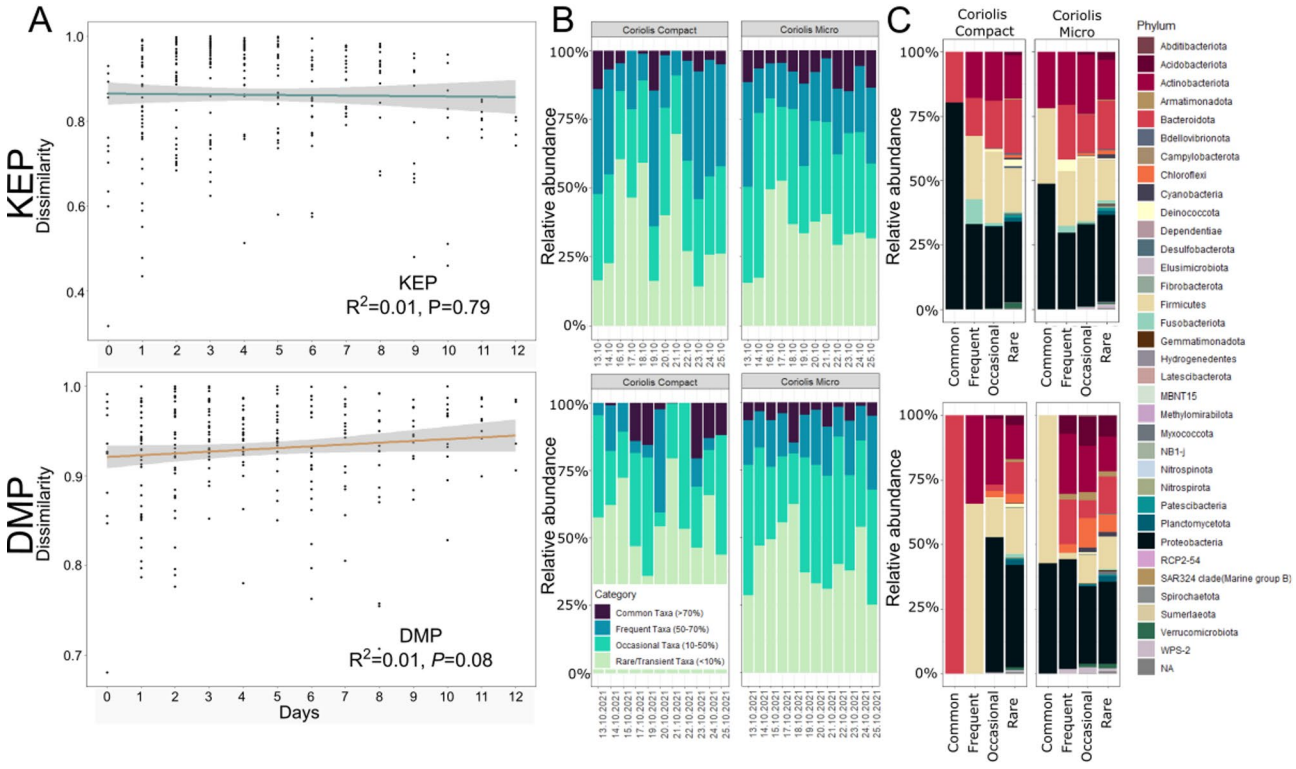

Fig. 4 (**A**) Bray-Curtis dissimilarity between samples, shown across a distance matrix of days between samples. (**B**) Classification of taxa frequency shown by instrument, sampling day and location. (**C**) Relative abundance of ASVs at the phylum level, displayed for each category, sampling instrument and location

abundance, respectively. Instead, occasional taxa constituted 28–36%, and rare/transient taxa dominated, contributing 42–56%, depending on the sampling instrument (Table S1). DMP only had 5 common taxa present in over 70% of samples (Table S2), classified as a *Acidiphilum*, *Staphylococcus*, *Cloacibacterium* and *Clostridium*. At KEP, 7 were classified as common, including *Psychrobacter*, *Romboutsia*, *Knoellia*, *Humibacillus*, *Staphylococcus* and *Bacteroides* (Fig. 4C, Supplementary Data 1). These suggest associations from local microbiomes and host-associated taxa. When considering 50% of samples, at DMP, 43 ASVs were identified in over 50% of samples, with the Coriolis micro identifying more frequent ASVs. These were predominantly extremophiles such as *Psychrobacter*, *Acidiphilium*, *Halomonas*, and *Polymorphobacter*, as well as soil-associated taxa like *Nakamurella*, *Mycobacterium*, *Granulicella*, and *Humibacillus*. In contrast, 79 ASVs were detected in over 50% of the samples at KEP with similar levels of identification between instruments. Like DMP, these included environmental taxa such as *Psychrobacter*, *Polaromonas*, *Marinifilum*, *Knoellia*, and *Paenisporosarcina*. Additionally, host-associated microorganisms, including *Facklamia* (Firmicutes), *Romboutsia* (Firmicutes), and *Faecalibacterium* (Firmicutes), were detected at KEP. These taxa constitute the most stable components of the airborne microbiome over South Georgia. The number of transient taxa at each sampling site was high and therefore, more diversity was captured within this category.

Environmental drivers influence community composition

We collected hourly data on temperature, wind speed, wind direction, and pressure, then averaged these variables for each sampling period. There was no significant collinearity among the environmental variables (Fig. S4). Throughout the sampling period, wind patterns were predominantly from the north or south, with northerly winds generally warmer and stronger than southerly winds. To assess the influence of environmental conditions on airborne microbial community composition, a distance-based redundancy analysis (dbRDA) was performed. The model explained 64.2% of the observed variation in community composition (Fig. S5), indicating a strong environmental influence. PERMANOVA (adonis) results further confirmed that sample location, average temperature, air pressure, and wind direction were significant drivers of microbial community structure (Table 1).

Taxa-environment correlation analysis revealed distinct associations between specific microbial genera and environmental parameters (Fig. 5). Several soil-associated taxa, including *Haliangium*, *Chthoniobacter*, *Spirosoma*, and *Microvirga*, were positively correlated with elevated

Table 1 Results of the PERMANOVA analysis examining the impact of environmental variables on microbial community composition. The significance levels are indicated as follows: * $p < 0.05$, ** $0.001 < p \leq 0.05$, *** for $p \leq 0.001$

Variable	R^2	Pr(> F)
Location	0.035	0.0011 **
Sampling duration	0.023	0.10
L of air sampled	0.023	0.12
Average temperature	0.033	0.0037 **
Average pressure	0.035	0.0032 **
Average wind speed	0.021	0.22
Main wind direction	0.027	0.031 *
Residuals	0.75	

temperatures. Additionally, polar-associated taxa such as *Paenisporosarcina* and *Parablastomonas*, previously identified in Antarctic glaciers and Arctic glacial till, also increased under warmer conditions. Some taxa, including *Terrabacter* and *Parablastomonas*, were associated with higher wind speeds and prevailing northerly winds, suggesting potential long-distance transport. In contrast, *Spirosoma* and *Microvirga* correlated strongly with high-pressure systems, indicating that atmospheric stability may also shape microbial persistence.

Conversely, southerly winds were associated with a greater diversity of genera, encompassing both environmental and host-associated taxa. *Glaciecola* and *Desulforhopalus*, known psychrophiles found in cold environments, as well as *Dasania* and *Bizonia*, identified in marine Arctic ecosystems, were prevalent under these conditions. In addition to these environmental taxa, a significant presence of host-associated microorganisms was detected, likely influenced by proximity to the human settlement at King Edward Point (KEP), the abandoned whaling station at Grytviken, and large nearby colonies of wildlife, including elephant seals, fur seals, penguins, and seabirds. Specifically, *Facklamia*, previously reported in elephant seal pups, was more abundant under southerly conditions. Similarly, *Edwardsiella* and *Alistipes*, both linked to the gut microbiomes of elephant seals and penguins, were detected in air samples, further highlighting the influence of local wildlife and environmental drivers on airborne microbial community composition.

Rainfall events change airborne communities

Rainfall events had a measurable impact on airborne microbial communities. During the study, rain was sampled on three separate days, yielding five rainfall samples collected alongside simultaneous air samples. Microbial analysis revealed that rainfall samples exhibited higher richness and distinct community composition compared to air samples collected during the same period (Fig. S6). Interestingly, air samples collected before and after rainfall consistently displayed higher richness than those collected during rainfall, suggesting that rainfall temporarily reduced airborne microbial diversity. Despite this, a substantial overlap in microbial taxa was observed, with 947 ASVs shared between air and rain samples, accounting for 58% of the total relative abundance. However, the differential abundance analysis indicated no specific taxa were significantly enriched in the rainfall samples compared to air.

South Georgia– a potential hotspot of microbial diversity?

Air samples collected over South Georgia (SG) exhibited greater richness and microbial diversity compared to samples from the surrounding Southern Ocean (SO) (Fig. S7, S8). Despite this higher diversity, community composition analyses revealed a high degree of similarity between SG and SO air samples (Fig. S7, S8), suggesting shared microbial inputs likely driven by atmospheric circulation. Similarly, rainfall samples from South Georgia were richer and more diverse than those from the Southern Ocean, with notable differences in community composition. Non-metric multidimensional scaling (NMDS) analysis further revealed distinct clustering by sample type, separating marine, terrestrial, rainfall, and air communities (Fig. 6). Importantly, while SG and SO air samples clustered closely, indicating overlap in airborne microbial assemblages, global air samples formed a separate cluster, showing the unique microbial signature of the Southern Ocean region.

To assess potential sources contributing to airborne microbial diversity over South Georgia, a source tracking analysis was performed. The results indicated that approximately 20% of ASVs in air samples originated from terrestrial sources, increasing to 45% in rainfall samples. Marine sources accounted for 5% of ASVs, while 25% matched ASVs previously identified in air samples from both global and Southern Ocean datasets. Notably, up to 50% of ASVs remained unassigned to any known source in the database.

Functional potential of airborne microbial communities

Shotgun metagenomics was performed on a subset of samples, which included 4 air samples from DMP, 4 air samples from KEP, and 3 rainfall samples. Compared to the amplicon data, the metagenomic profiles revealed lower relative abundances of Firmicutes and Bacteroidota, likely reflecting differences in sequencing resolution and the smaller sample size. Therefore, no significant taxonomic differences were detected between sampling locations in the metagenomic dataset (Fig. S9).

Analysis of functional gene categories, based on SEED annotations, showed that most genes were associated with core cellular functions, including metabolism, energy production, protein processing, and stress response, defence, and virulence pathways. Differential

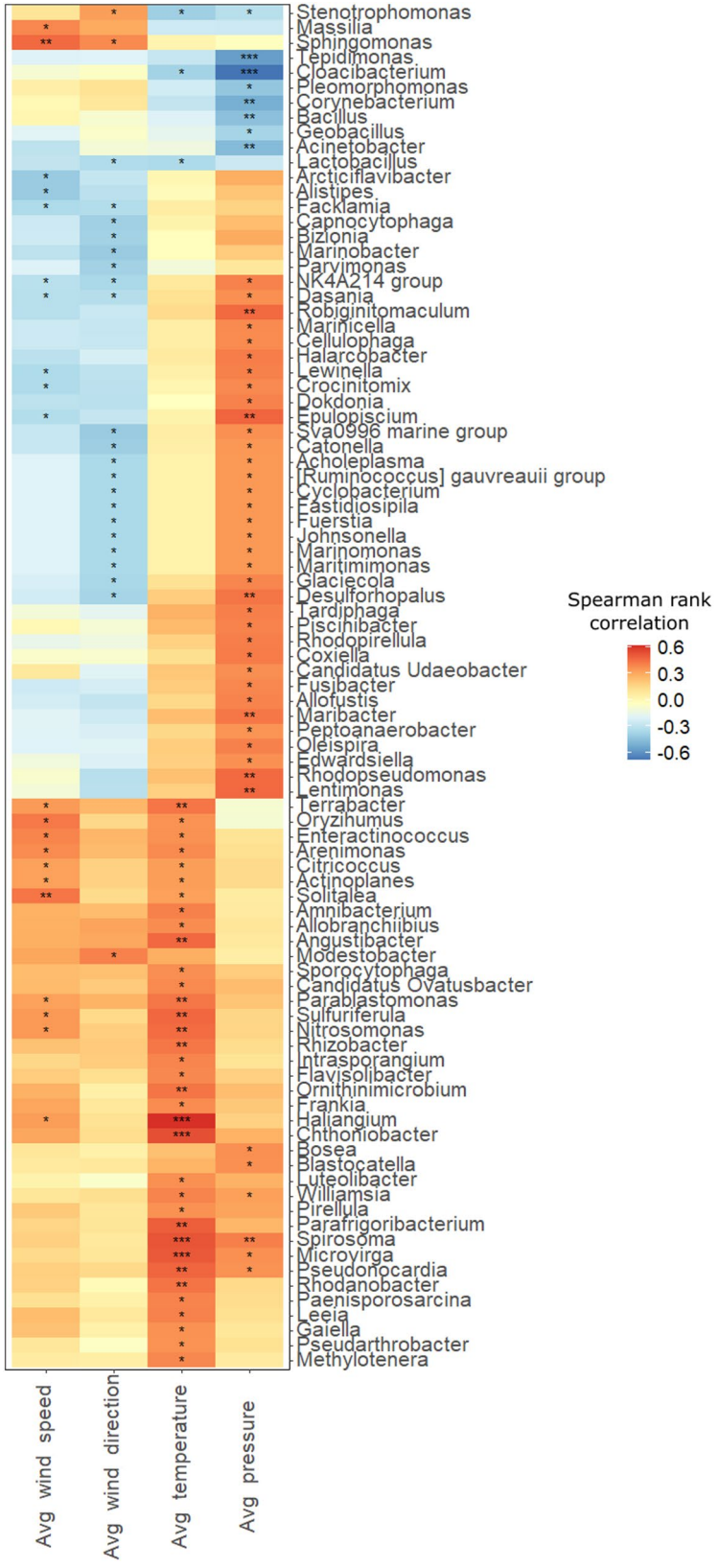

Fig. 5 Heatmap of Spearman rank correlations between environmental factors and taxa. P-values were adjusted using the False Discovery Rate (FDR), with only significant correlations shown. The significance levels are indicated as follows: * $p < 0.05$, ** $0.001 < p \leq 0.05$, *** for $p \leq 0.001$

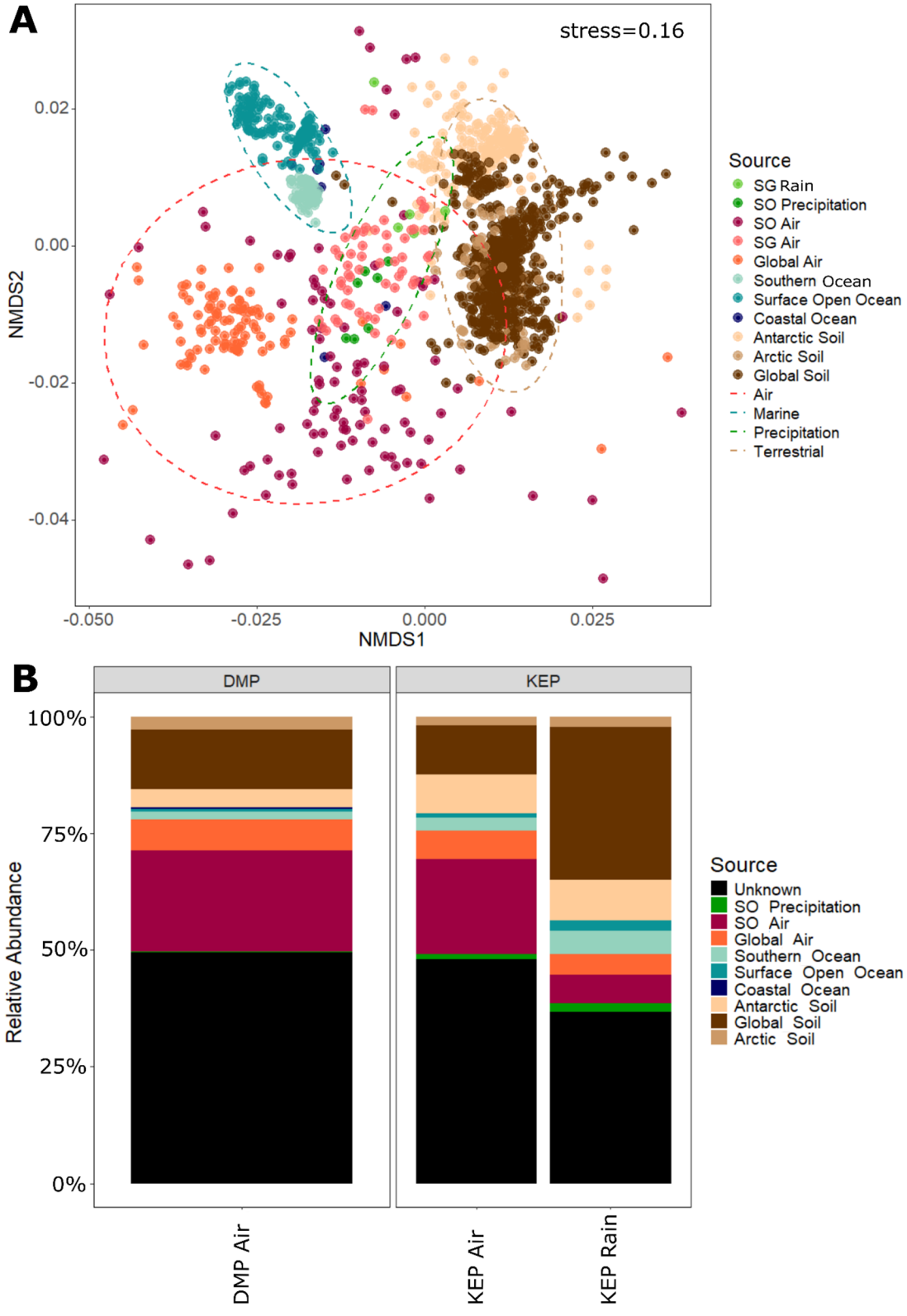

Fig. 6 (**A**) Visualization of community dissimilarity using non-metric multidimensional scaling (NMDS) of the Bray-Curtis distance between air, rainfall, marine, and soil bacterial communities. (**B**) Mean potential origin of ASVs across each South Georgia sample air and rainfall sample by sampling location

abundance analysis (ALDEx2) detected no significant differences in functional gene profiles between air and rainfall samples (Fig. S10). Among the stress response genes, over 50% were linked to antibiotic and toxic compound resistance, highlighting the potential for these airborne microbes to tolerate environmental pressures. Additionally, approximately 20% of stress-related genes were associated with heat and cold shock responses, reflecting adaptations to fluctuating and extreme atmospheric conditions. Focusing on metabolism annotations, phosphate-related genes were the most abundant, accounting for about 50% of metabolic functions, followed by sulphur metabolism genes (30%) and nitrogen metabolism genes (20%) (Fig. S11).

Discussion

This study provides a high-resolution analysis of daily airborne bacterial community turnover, potential microbial sources, and the performance of different sampling methodologies. Our findings demonstrate that the Coriolis compact (dry) and Coriolis micro (wet) samplers offer complementary strengths, each suited to specific environmental conditions and deployment needs. While the Coriolis micro provides high-quality samples over short durations, making it ideal for rapid deployments, it is less suitable for freezing environments due to the risk of liquid freezing. In contrast, although the Coriolis compact is less effective over short durations, it exhibited higher microbial richness and diversity per litre of air when operated for six hours or longer. This makes it particularly suitable to use in cold and remote regions where prolonged sampling is necessary due to low airborne biomass. Together, these results highlight the value of employing multiple sampling strategies to capture the full complexity of airborne microbial communities and reinforce the need for standardized protocols to improve data comparability across studies.

The study further demonstrates the significant influence of sampling location on airborne microbial community composition, despite similar alpha diversity between sites. The dominant bacterial phyla—Proteobacteria, Actinobacteria, Bacteroidota, and Firmicutes—are commonly found in airborne microbial communities across the globe [3, 81], including over the Southern Ocean and Antarctica [10, 43, 69]. However, variations in less abundant but ecologically relevant phyla, such as Acidobacteriota, WPS-2, Armatimonadota, and Chloroflexi at DMP, and Deinococcota at KEP, illustrate distinct environmental influences.

At the higher-altitude site (DMP), the community was dominated by soil-related microorganisms such as *Acidiphilum*, *Granulicella*, and *Bryobacter*. This likely reflects the site's more isolated and terrestrial setting, where inputs from surrounding soils and exposed rock surfaces are the primary sources of airborne microbes. The reduced presence of vegetation and limited animal activity at this elevation, further supports the predominance of terrestrial taxa and suggests minimal influence from marine or host-associated sources. In contrast, KEP exhibited a broader range of taxa, including soil-related and cold-adapted taxa, such as *Arthrobacter*, *Pseudoarthrobacter*, *Psychrobacter* and *Polaromonas*, which are commonly found in polar ecosystems [12, 15, 19, 57, 62, 63], as well as marine-associated taxa such as the family *Marinifilaceae*, previously identified in sea-ice and Antarctic sediments [74, 84], and host-associated taxa such as *Ornithobacterium* identified in Antarctic bird colonies [79]. These results highlight the complexity of assessing local microbial inputs. The observed diversity is likely driven by the site's proximity to a mosaic of habitats including seabird and seal colonies, tundra vegetation, glacial outflows, and marine ecosystems, which collectively contribute to the heterogeneity of airborne microbial sources. This underscores the strong influence of landscape and local microbiomes in shaping near-surface airborne microbial communities, consistent with broader findings that these communities are shaped by surrounding ecosystems. For example, studies have shown that oceanic sources influence microbial communities [36, 45], as well as terrestrial inputs such as soil [3]. Similarly, forests release plant-associated microbes, including fungal spores and bacteria from leaf surfaces [40] while urban areas exhibit high prevalence of human-associated taxa [81]. In our study, DMP exhibited a stronger terrestrial signal while KEP showed greater influence from nearby wildlife and marine ecosystems. This pattern was further supported by the source-tracking analysis which identified Antarctic soils (15%) and the Southern Ocean (5%) as contributors to 20% of the airborne microorganisms detected over South Georgia. An additional 25% of taxa were previously identified in Southern Ocean air or over Antarctica, although their precise origins remain unclear.

Antarctic studies have also found similar results of local or unknown microorganism in the atmosphere [24, 53]. In South Georgia, some taxa of unknown origin are likely to be host-associated taxa, either from humans or wildlife, which are not represented in the global database used for source tracking. For instance, *Faecalibacterium*, a gut-associated taxon [44] and *Ornithobacterium*, identified in penguin microbiomes [50, 79], were detected in the airborne samples. Additionally, *Facklamia*, a taxon identified in elephant seals [23], and *Edwardsiella* and *Alistipes*, linked to the gut microbiomes of penguins and elephant seals [31, 37] were also observed. We also identified *Staphylococcus*, *Cloacibacterium*, *Clostridium* and *Romboutsia* in over 70% of samples both at KEP and DMP, which were not classified as contaminants based

on our controls. Given the island's high wildlife population, their presence in the South Georgia airborne microbiome is not unexpected. For instance, *Staphylococci* are a major group of highly adaptable bacteria associated with humans, mammals and birds but also free-living in the environment [21]. In Antarctica, they are associated with Skua birds, different species of seals, and penguins [72], which might explain their high prevalence in these air samples. These findings support our conclusion that near-surface airborne bacterial communities in South Georgia are shaped by local microbiomes and wildlife.

While some of these taxa, such as *Polaromonas* and *Facklamia*, may originate from local ecosystems, others are likely the result of long-distance dispersal. Transported over vast distances by upper-atmospheric currents, microbes are often dispersed during major events such as dust storms, wildfires, and volcanic eruptions [34, 42, 70]. For instance, Asian dust events have been shown to transport microorganisms to North America and even the Arctic [82]. In the Southern Ocean, the Antarctic Circumpolar Current and West Wind Drift serve as a selective barrier, restricting the movement of certain microbes from lower latitudes while allowing others to pass through [43]. There is evidence of bi-polar biogeographic distributions in microorganisms, likely facilitated by long-distance dispersal and specific metabolic adaptations [28, 33, 52]. These large-scale transport mechanisms underscore the atmosphere's role as a dynamic conduit for microbial exchange, shaping global biogeography and ecosystem connectivity with potential impacts on biogeochemical cycles. In our study, the source tracking analysis identified 5% of ASVs from non-Antarctic air, up to 5% from non-Antarctic marine samples and 15% from non-Antarctic terrestrial samples (up to 65% in rainfall samples), implying long-distance origins. DMP exhibited more ASVs from non-Antarctic sources, suggesting more impact from long-distance transport and terrestrial sources.

In our study, up to 90% of airborne microbial composition changed daily, while 10–20% remained relatively consistent over time. This stable temporal core microbiome was primarily composed of extremophiles, such as *Psychrobacter*, *Halomonas*, *Acidiphilium*, *Polymorphobacter*, *Polaromonas*, *Deinococcus*, and *Paenisporosarcina*, along with soil-associated taxa like *Nakamurella*, *Mycobacterium*, *Granulicella*, and *Humibacillus*, and host-associated microorganisms, including *Facklamia*, *Romboutsia*, and *Faecalibacterium*. Several of these taxa, including *Psychrobacter*, *Acidiphilium*, *Enhydrobacter*, *Deinococcus*, and *Pseudomonas*, can be considered core airborne microbes in South Georgia, and have also been identified in distant atmospheric environments and even cloud water, where they may remain metabolically active [1, 2]. These microorganisms are well-adapted to the extreme conditions of the atmosphere, with some favouring cold environments (e.g., *Psychrobacter*), while others exhibit resistance to high radiation levels (e.g., *Deinococcus*) [78]. Despite exposure to harsh atmospheric conditions, airborne microorganisms can remain metabolically active and potentially influence atmospheric processes. A notable example is their role in ice nucleation, where certain bacteria and microalgae facilitate the formation of ice crystals in clouds, thus influencing rainfall patterns. Studies have shown that approximately 17% of airborne isolates, including taxa such as *Chlorophyceae* and *Stramenopiles*, exhibit ice nucleation activity at temperatures as low as -15 °C [66]. Some bacteria and fungi, such as *Pseudomonas*, can also facilitate ice formation [29], impacting cloud properties and rainfall. This highlights the significant yet often overlooked role of airborne microbes in atmospheric processes. In this study, metagenomic analyses revealed that a significant portion of genes within these communities were associated with stress responses, including resistance to antibiotics and toxic compounds, as well as mechanisms to cope with temperature fluctuations. These adaptations are crucial for survival in the extreme conditions encountered during atmospheric transport [49]. Moreover, airborne microbes harboured genes involved in the metabolism of essential elements such as phosphorus, sulphur, and nitrogen, suggesting their potential role in atmospheric nutrient cycling, with downstream effects on terrestrial and aquatic ecosystems upon deposition. This could be particularly relevant in nutrient-limited polar environments, where atmospheric inputs may subsidise local ecosystems. The repeated detection of this temporal core microbiome across different days and sites implies selective atmospheric filtering or regular reseeding from consistent environmental reservoirs [56]. Ecologically, such a core microbiome likely acts as a stabilizing framework for airborne microbial communities, supporting essential ecosystem functions (e.g., nutrient processing, ice nucleation). In analogy with core microbiomes in host-associated systems [56, 71, 77], these environmental core taxa may define community resilience, modulate broader ecological dynamics, and serve as sensitive indicators of long-term environmental change [4, 60].

Taken together, these results reveal clear differences in the temporal stability and daily turnover of airborne bacterial communities between the two sampling sites. The coastal KEP site exhibited greater compositional stability and a stronger signal from local microbiomes and wildlife while the high-altitude DMP site was characterized by higher daily turnover and a community dominated by transient and occasional taxa, suggesting greater influence from long-distance atmospheric transport. Despite this variability, both sites retained a small core microbial community, emphasizing the dynamic nature of airborne

microbial assemblages in the sub-Antarctic and the critical role of local microbiomes in shaping community composition. These findings emphasize the need to distinguish transient microbial fluctuations from a persistent airborne core when monitoring aerobiomes.

Given these site-specific differences, understanding the environmental drivers that shape airborne microbial communities is essential for interpreting their composition and dispersal patterns. The fact that environmental conditions, including temperature, wind speed, wind direction, and rainfall, play a pivotal role in shaping airborne microbial communities, with temperature and wind patterns influence both community composition and microbial source contributions [67, 83], is in line with what we observed on South Georgia. The taxa-environment analysis revealed strong correlations between specific taxa and prevailing weather conditions, reinforcing the idea that atmospheric microbial assemblages are shaped not only by local microbiome inputs but also by meteorological dynamics. In this study, we observed that northerly winds, generally warmer and stronger, were associated with soil-related taxa such as *Haliangium*, *Chthoniobacter*, *Spirosoma*, and *Microvirga*, as well as cold-adapted microbes like *Paenisporosarcina* and *Parablastomonas*, commonly found in Antarctic and Arctic glacial environments. The association of *Terrabacter* and *Parablastomonas* with high wind speeds (Fig. 5) suggests that these taxa may be transported from terrestrial sources, supporting the role of wind-driven dispersal. Furthermore, *Spirosoma* and *Microvirga* were correlated to high atmospheric pressure, suggesting that stable weather systems may influence microbial persistence in the atmosphere. In contrast, southerly winds, which were colder and weaker, were associated with a broader diversity of microbial taxa, including marine and host-associated groups. Psychrophilic bacteria such as *Glaciecola* and *Desulforhopalus*, as well as Arctic marine-associated genera like *Dasania* and *Bizonia*, were more abundant under these conditions, indicating a stronger influence of oceanic sources. Additionally, host-associated taxa—such as *Facklamia*, *Edwardsiella*, and *Alistipes*, previously identified in elephant seals and penguins—were enriched under southerly wind conditions, further suggesting contributions from regional wildlife concentrations. These results indicate that wind patterns and associated environmental conditions influence the transient airborne microbiome and may also affect the long-range transport and persistence of certain taxa in the atmosphere. Our analysis of rainfall samples further highlights the impact of weather on microbial community composition. Rainfall samples displayed higher microbial richness and distinct community compositions compared to air samples collected on the same days. This difference may result from contributions from higher atmospheric layers, which are more influenced by long-distance dispersal. Supporting this, the source-tracking analysis revealed that up to 65% of ASVs in rainfall samples originated from non-Antarctic sources. This finding aligns with previous observations highlighting differences between airborne and rainfall microbial communities [17, 43], and supports the washout hypothesis, where rain removes aerosolized microorganisms leading to drops in microbial diversity and richness [26]. These dynamic interactions highlight the complex role of weather in microbial transport and deposition, with implications for ecosystem seeding and nutrient inputs.

Conclusions

This study highlights some stability within the complex and dynamic nature of airborne microbial communities in South Georgia, revealing their richness and diversity compared to global airborne microbiomes. The presence of host-associated taxa, likely originating from the region's abundant wildlife, alongside a dominant terrestrial microbial community, underscores the influence of local ecosystems on the near-surface airborne microbial composition. The continuous deposition of these airborne microbes on the island, especially through rainfall, emphasizes the potential for rapid shifts in microbial communities, particularly in the face of ongoing climate change altering precipitation patterns, wind regimes and local niche characteristics. By documenting both the transient and more stable microbial taxa, this research provides valuable insights into the variability of the near-surface airborne microbiota in response to environmental factors. Taken together, these findings position South Georgia as a potential aerobiological diversity hotspot, characterized by very high bacterial diversity shaped by local terrestrial and marine microbiomes as well as long-range atmospheric transport. These findings not only highlight the importance of South Georgia as a potential biodiversity hotspot but also lay a temporal baseline for future studies of interannual variability and its potential as an important location for continued monitoring. As climate change continues to reshape ecosystems across the globe, understanding the dynamics of airborne microbial communities is crucial for predicting broader implications for ecosystem health, biogeochemical cycles, and biodiversity conservation.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40793-025-00745-y.

Supplementary Material 1

Supplementary Material 2

Acknowledgements
We thank the assistance King Edward Point staff who supported our work in 2021 as well as the crew of the staff and scientists of both the BAS station at KEP and the FPVMV Pharos who transported us to Grytviken. Special thanks to John Dickens for his help on the field and the UAV photos of our sampling sites. We thank Luke Cockerton for his technical assistance in performing DNA extractions. Sequencing was completed in NU-OMICS DNA Sequencing Research Facility at Northumbria University. All samples were collected under the appropriate sampling permits.

Author contributions
LM: field sampling, data acquisition, writing, review & editing; PC: review & editing; DAP: conceptualization, field sampling, writing, review & editing.

Funding
Open access funding provided by University of Geneva. Fieldwork was supported by the British Antarctic Survey, SLIDE Project, NERC-CASS-196.

Data availability
The raw weather data was extracted hourly from https://legacy.bas.ac.uk/cgi-bin/metdb-form-2.pl?tabletouse=U_MET.GRYTVIKEN_AWS%26complex=1%26idmask=....%26acct=u_met%26pass=weather to include temperature, pressure, wind speed and wind direction between October 13th and 25th 2021. The raw DNA sequences from this project are deposited on NCBI's SRA under the BioProject PRJNA1219563, accession numbers SRR32239408 to SRR32239477. The ASV table, taxonomy table and metadata (including weather data) associated to the air and precipitation samples are available on FIGSHARE: https://figshare.com/projects/Aerobiology_of_the_Southern_Ocean/140588 The global ASV table and associated taxonomy and metadata are available on FIGSHARE: https://figshare.com/projects/Global_database_of_environmental_bacterial_communities/236774 The metagenomics raw data are deposited on NCBI's SRA under the Bioproject PRJNA1107129.

Declarations

Competing interests
The authors declare no competing interests.

Received: 2 April 2025 / Accepted: 21 June 2025
Published online: 18 July 2025

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