Biogeochemical cycles and health implications potentially mediated by active dust-borne bacteria

Pengfei Hu¹, Yehonatan Sharaby¹, Ji-Dong Gu², Adi Radian¹, and Naama Lang-Yona¹

¹Technion Israel Institute of Technology ²Guangdong Technion-Israel Institute of Technology

August 21, 2023

Abstract

Understanding microbial migration and survival mechanisms in dust events can elucidate genetic and metabolic exchange between environments and help predict the atmospheric pathways of ecological and health-related microbial stressors. Dust-borne microbial communities have been previously characterized, but the impact of active bacteria within transported communities remains limited. Here, we analyzed samples collected during dust events in Israel, using amplicon sequencing of the 16S rRNA genes and transcripts. Different air trajectories and wind speeds were associated not only with microbial community composition variations but also with those of active bacteria. Active dust-borne bacteria exhibited positive interactions, including highly active carbon and nitrogen cycling bacteria, potential degraders of heavy metals and organic compounds, biofilm-forming, and pathogenic bacteria. This study provides insights into the potential interactive relationships and survival of active microorganisms within the extreme dust environment.

Introduction

Airborne microorganisms disperse across continents and oceans, facilitating genomic and metabolic exchanges across different ecosystems. Moreover, they can significantly impact not only aquatic, atmospheric and terrestrial ecosystems, but also human health (Riselyet al. 2018; Lang-Yona et al. 2020; Gat et al.2021). Extensive research has focused on dust-borne microbial diversity including bacteria, eukaryotes, archaea, and viruses (Aalismail et al. 2019), with the majority of bacterial group, with predominance of Actinobacteriota, Bacteroidota, Firmicutes and Proteobacteria (Aalismailet al. 2019; Elmassry et al. 2020; Gat et al. 2021; Erkorkmaz et al. 2023). Bacillus species were detected in Asian dust events and in several East Asian countries (An et al.2013; Maki et al. 2014), and are known for spore-forming, which provide protection and enabling long-distance atmospheric transport (Wainwright et al. 2003a; Griffin 2004; An et al. 2013).

Dust storms facilitate extensive transport of microbiota across vast distances, subjecting them to harsh conditions (Goudie *et al.*2006). Therefore, both viable and non-viable microorganisms are present within the dust-transported microbiota. Distinguishing between active and inactive microbes offers meaningful ecological insights into microbial survival strategies and their interactions with the dust environment (Schuerger et al. 2006). A few studies have utilized ribosomal RNA (rRNA) sequencing to characterize the active airborne bacterial community (Blazewicz et al. 2013; Santl-Temkiv et al. 2018; Erkorkmaz et al. 2023), focusing primarily on the active microbial community structure in relation to environmental factors such as air mass origination, atmospheric particulate matter ($\lt 10 \mu m$; PM10), and particle-size (Erkorkmaz et al.2023). However, the potential influence of geochemical elemental cycles (e.g., carbon, nitrogen and sulfur) and the possible interaction mechanism within microbial communities remained elusive. Exploring these aspects could provide valuable insights into the survival and transportation of active microorganisms within the challenging dust macro-environment. Furthermore, it may provide deeper understanding of the impact of the dust microbiome on global biogeochemical cycles.

In this study we investigate dust-borne bacterial communities by utilizing high-throughput amplicon sequencing of the rRNA gene and transcript to characterize these communities and construct a preliminary understanding of elemental cycles and microbial interactions among the active dust-borne microorganisms. This research shed light on their survival strategies and transportation in dust events.

Materials and Methods

Sampling. Dust event (DE) samples were collected during March and April of 2022. Before sampling, 30 seconds blank sample was taken to ensure proper sampling and check for any contaminations. Air samples were collected on a sterile single-packed filter (S-Pac, Millipore, Massachusetts, US) at 14 L/min for ~6-6.5 hours, during both day and night (Table 1). The samples were stored at -80 for nucleic acid extraction.

Meteorological conditions and backward trajectory analyses. Data on wind speed, direction, temperature, and relative humidity were obtained from a nearby station (https://ims.gov.il/en). The origin of sampled dust was determined by calculating back trajectories using the hybrid single-particle Lagrangian integrated trajectory model (HYSPLIT; https://www.ready.noaa.gov/HYSPLIT_traj.php). Each back trajectory was computed for 48 hours at three different altitudes (50, 100, and 500 meters above ground level).

DNA/RNA extraction, amplification, and sequencing. The DNA/RNA extraction was performed using the ZymoBIOMICS DNA/RNA Kit (Zymo research, California, US), utilized with high-yield improvements according manufacturer protocols. The DNA extracts were stored at -80 °C, while RNA were promptly utilized for complementary DNA (cDNA) synthesis. The remaining RNA was kept at -80 °C. For cDNA synthesis, the Qiagen's QuantiTect Reverse Transcription Kit (Cat $\#$: 205313, Hilden, Germany) was employed. The total cDNA reaction of 20 μL consisted of 1x reverse transcription (RT) enzyme, 4 μL of RT mix, 1 μL of random primer mix, and 5 μL of RNA extract. Thermocycling was performed using the MiniAmp Plus Thermocycler (Applied Biosystems, Thermo Fisher Scientific, Massachusetts, US). The thermocycling program included 25.0°C for 3 min, 45°C for 10 min, 85°C for 5 min, and 10°C until the process was terminated. The cDNA samples were stored at -20°C for subsequent analysis.

The bacterial 16S rRNA gene and 16S rRNA were amplified using the primers CS1 515F - CS2 926R targeting the biodiversity and active community compositions (Walters et al. 2016). The amplification was performed in a 25 μL reaction volume containing a polymerase mix of 12.5 μL, 400 nM of each primer, 5 μ L of DNA/cDNA template, and water. The cycling program consisted of an initial denaturation step at 95.0ºC for 1 min, 30 cycles of 95ºC for 15 sec, 55ºC for 15 sec, 72ºC for 10 sec, and a final extension at 72ºC for 10 min. PCR products were verified on 1% agarose gel, and the triplicates were pooled. Gel visualization was performed using a ChemiDOCTM MP Imaging System (BioRad, California, US).

High-throughput sequencing and taxonomic analysis.High-throughput sequencing was conducted at the at the Technion - Israel Institute of Technology, Haifa, using the Illumina Miniseq platform, with a sequencing depth of 100 kbp per sample. Sequences analysis was performed using QIIME2. Raw data from each sample were introduced into QIIME2 for quality control following the standard procedure (Bolyenet al. 2019). Specifically, raw sequences were denoised and filtered for invalid reads, mitochondrial sequences, and chloroplast sequences contamination using the software packages DADA2 (Callahanet al. 2016) and Deblur (Hanshew et al. 2013; Rowan-Nashet al. 2019). After quality control, taxonomic assignment of the amplicon sequence variants (ASVs) was performed using dada2 against the SILVA 138.1 reference database (Quastet al. 2012). Biodiversity was assessed using Chao1, Abundance-based Coverage Estimator (ACE), Shannon, and Simpson indices, as well as principal component analysis (PCoA) were calculated using the Vegan package after normalizing the sequence number of the 16S rRNA gene. Statistical significance between groups was calculated using Permutational multivariate analysis of variance (PERMANOVA). Venn diagram was contracted using the ggvenn package. The sequence data has been deposited in the NCBI GenBank Database under the accession number: PRJNA982604.

Network construction of active microorganisms. The interactions within the core dust microbial communities were investigated using a network of the active microorganisms by calculating Spearman correlation coefficients between genera (Barberán et al. 2012; Varsadiyaet al. 2021). Microorganisms from the top five phyla were merged at the genus level, as pre-determined from 16S rRNA result. A two-by-two correlation matrix (Table S3) was generated using the "Hmisc" package in R (Varsadiya et al. 2021). The false discovery rate (FDR) controlling procedure was used to calculate p -values, and the Benjamini-Hochberg method was applied for correction (Benjamini & Hochberg 2018). Correlation coefficients with an absolute value of 0.6 or greater, or -0.6 or less was defined as the cut-off for a meaningful co-occurrence network, with p -values < 0.01 . Network visualizations were generated using the "igraph" package in R (Csardi & Nepusz 2006). In the undirected network, nodes represent genera and edges represent correlations between nodes.

Results

The microbial communities from three different dust storms (during both day and nighttime) were analyzed for co-existence, and biogeochemical contributions of active dust-borne microorganisms.

Environmental Variables.

Substantial day-night fluctuations in relative humidity (RH) and temperature were observed during the dust events (Table 1). These factors are known to influence the viability of microbial communities (Aarnink et al. 2015; Dannemiller et al. 2017; Haineset al. 2020). Daytime events exhibited lower RH levels than nighttime. It has been shown that bacteria can endure and travel within 40-80% RH range (Aarnink *et al.* 2015), indicating conducive environmental conditions during the sampled dust-events for their survival and migration (Table 1).

Table 1 also shows the favorable temperature range (within 10-30) for long-distance microorganism survival (Aarnink et al. 2015), supporting microbial translocation with the dust events. Notably, DE-II displayed significant daytime-nighttime wind speed difference $(7.78 \text{ m/s} \text{vs. } 3.38 \text{ m/s})$, respectively). Wind speed has been linked with dust generation and bacteria transportation (Fujiyoshi et al. 2017; Ulrich 2021; Sorkheh et al. 2022; Erkorkmaz et al. 2023), possibly explaining the observed microbial composition variation during this event.

The distinct origins of the three dust events were revealed by air-mass backward trajectories (Fig. S1). On March 29, 2022, the air mass mainly originated from the mainland (DE-I D & N). On April 6, 2022, it crossed the Mediterranean Sea from west to south and reached Haifa (DE-II D & N). On April 25, 2022, the air mass primarily originated from the northwest (DE-III.D & N). Interestingly, DE-III.D had a mixed origin, with inland source at 500 meters above ground (Fig. S1).

Dust-borne microbial community characterization. Each dust sample yielded at least 1893 highquality ASVs in 16S rRNA gene and 1667 in 16S rRNA. In DE-I and III, daytime samples displayed lower biodiversity compared to the nighttime, whereas in DE-II, daytime samples presented higher biodiversity (Table 1). However, based on PCoA and PERMANOVA analysis showed no significant differences in betadiversity among events (Fig. 1A). The Venn diagram revealed three core ASVs shared among the six groups (Fig. 1B). However, the shared microorganisms were closely associated with the dust origin. For example, DE-II and III daytime samples shared 44 core ASVs (Table S1), accounting for 20.21% and 10.23% of the microbial communities, respectively. This aligns with air mass back trajectories of these events (Fig. S1), indicating a significant exposure of the air-mass to Mediterranean Sea environment, likely leading to shared microorganisms, including those associated with the marine environment (e.g.,Prochlorococcus sp.). The remaining microbial composition differences may stem from the additional east origins of DE-III air-mass.

The relative abundance was calculated by averaging the ASVs of two sequenced sample replicates. The airborne bacterial populations analyzed from the 16S rRNA gene were composed of several bacterial types (Table S1 and Fig. 1). The predominant ASVs identified in the dust samples belonged to the phyla Proteobacteria, Bacteroidota, and Actinobacteriota. Cyanobacteria and Firmicutes, common in marine and terrestrial environments, were also detected in the dust samples with some variation. Specifically, Proteobacteria accounted for 90% and 80% in DE-II and III daytime samples, reducing to 79 and 63% during daytime, respectively. In contrast, the trend was opposite in DE-I. (Fig. 1C). Predominant taxonomic groups within Proteobacteria included Comamonadaceae (13.10% in DE-I \Box D, 28.55% in DE-I \Box N), Pseudoalteromonas (22.66 % in DE-II \Box - D), Alteromonas(9.07 % in DE-I_N, 31.93% in DE-II_D, 15.50 % in DE-III_D) and Sphingomonas (7.97%) in DE-II₋D, 14.12% in DE-II₋N, 20.18% in DE-III₋D, 3.54 % in DE-III₋N). These genera are common in marine environments, aligning with back trajectory analysis indicating Mediterranean Sea influence (Fig. S1). Bacteroidota emerged as the second dominant phylum in all three night sampling events, (11.65% in DE-I_N, 16.84% in DE-II_N, 11.71 % in DE-III_N), in contrast to the lower values in daytime samples (3% in DE-II.D, 6% in DE-III.D) compared to nighttime samples (16.84% and 11.71% in DE-II.N and III.N). Actinobacteriota constituted 21.13% of the microbial composition in DE-I D samples, but less than 10% in other samples, except DE-III_N (12%) .

Table S4 shows that the dominant family in DE-I₋D was Comamonadaceae (13.10%), while in DE-I_{-N} it was only 1.69%. In DE-II and III daytime samples, Alteromonas (31.93% in DE-II) and Sphingomonas(20.18% in DE-III), were the dominant microorganisms, which are common marine microorganisms (Yoon *et al.* 2003; Romanenko et al.2007). Conversely, nighttime samples were primarily dominated by Comamonadaceae (28.55% in DE-II) and Frankiales (6.48% in DE-III).

Bioactive dust-borne microbial community. To investigate the core active microbial community within dust events, we further analyzed the 16S rRNA (Table S2). In general, Proteobacteria dominated the 16S rRNA libraries, which reflects its likely abundance as an active phylum in the dust samples (Fig.2A). The abundance of other active microbial groups was less consistent compared to the 16S rRNA gene library. For example, DE-LD samples had a higher abundance of active Firmicutes, Cyanobacteria and Actinobacteriota than Bacteroidota. In DE-I N night sample, active Actinobacteriota and Firmicutes also exceeds Bacteroidota, but there was an abrupt increase in the abundance of active Cyanobacteria. This may be attributed to the nighttime short air path through the Mediterranean Sea (Fig. S1). In DE-II, active microorganisms were consistent with 16S rRNA gene results, but active Bacteroidota was less abundant in night samples of this dust event, despite its higher abundance in the 16S rRNA gene results. In DE-III daytime samples the active microorganisms were primarily clustered within Bacteroidota, Actinobacteriota and Firmicutes, with a relatively lower abundance of Proteobacteria. Specifically, Actinobacteriota and Firmicutes displayed relatively high activity, compared to a relatively low abundance of Actinobacteriota and Firmicutes in DE-III₋D 16S rRNA gene results (Fig. 2A). In contrast, night samples showed no significant variation.

Genus-level analysis shows diverse abundances of microorganisms within and between dust events (Fig. 2B). In DE-I daytime, Staphylococcus, Chroococcidiopsis and Cutibacterium exhibited relative abundances $> 5\%$. followed by Actinetobacter , Corynebacterium and Methylobacterium with $> 2\%$ relative abundance. DE-I nighttime had highly active Oleibacter, Hymenobacter, Chroococcidiopsis, Bergeyella, Staphylococcus (2 -5% relative abundance). Interestingly, in DE-II active *Oleibacter* also displayed high abundance during daytime (24.13%) , however this dynamic shifted during nighttime, where *Alteromonas* became the prevailing active microorganism (13.33%). In DE-III, Bacillus emerges as the predominant active microorganism (6.02%) , with night samples dominated again by *Alteromonas* (14.26%) . These findings collectively suggest varying active microbial compositions in different dust events.

Potential survival strategies of active dust-borne microorganisms. Adaptation strategies of microorganisms for surviving harsh conditions include mutual feeding and the formation of protective measures against environmental stressors (Haruta & Kanno 2015; Yinet al. 2019; Thakur et al. 2022). Notably, such interactions appear to be prevalent within the core active microorganism communities of the sampled dust events (Fig. 2C). The cycling of essential elements, such as carbon and nitrogen, play a crucial role in the survival of microorganisms in unfavorable environments (Yan et al. 2008; Bollmann et al. 2013; Aasfar et al. 2021; Jawaharraj et al. 2021; Sahoo et al. 2021; Aronsonet al. 2023). Our analysis revealed the presence of highly active microorganisms engaged in carbon and nitrogen metabolism, suggesting a positive element cycle within the community. Methylobacterium ,Geodermatophilus , Bacillus and Dietzia contribute to carbon availability through organic compound biodegradation (Zhanget al. 2013; Yoshikawa et al. 2017; Venil et al.2021; Kong et al. 2022; Sandhu et al. 2022; Yao et al. 2022). Pseudomonas exhibited metabolic activity across all samples, suggesting active heterotrophic nitrification and aerobic denitrification processes over the dust particulates (Zhang et al. 2022). Additionally, the highly active Corynebacterium ,Mucilaginibacter and Acinetobacter convert inorganic nitrogen compounds into ammonia and nitrate (Madhaiyan et al.2010; Lee *et al.* 2016; Shelly *et al.* 2021; Amrutha & Nampoothiri 2022), providing a stable nitrogen source for the microbial community.

Biodegradation potential of microorganisms carried over dust particles. High levels of dust particles can lead to adverse health effects associated with the presence of heavy metals, organic pollutant particles and harmful minerals carried in the wind during dust events (Liu et al. 2004; Tian et al. 2019; Aili *et al.*2022). Microorganisms possessing the ability to transform and utilize these pollutants might have the advantages of thriving in polluted dust events. Our 16S rRNA analysis revealed pollutant-degrading genera, including Comamonas (Lu et al. 2022), Sphingomonas(Zhou et al. 2022), Comamonadaceae (Fahy et al.2006) and Acinetobacter (Tesso et al. 2019) in Proteobacteria, as well as Hymenobacter (Guo et al. 2020) and Frankiales (Wang et al. 2021) in Bacteroidota, andBacillus (Ikram et al. 2022) in Firmicutes. These microorganisms have the potential to degrade a wide range of organic pollutants.

The genus *Staphylococcus* demonstrated consistent activity across all samples (Fig. 2B) and its close interactions with other genera (Fig. 2C) suggests its key role in dust-borne community. Different Staphylococcus species are known for their tolerance to high salt concentrations and arid conditions, enabling their survival and long-distance traveling during dust events (Tsai et al. 2011; Kozajda et al. 2019; Feng et al. 2022). Additionally, certain Staphylococcus species can induce quorum sensing (Lyon & Novick 2004; Otto 2009), promoting inter-bacterial communication and collaboration through signaling molecules, supporting coexisting bacterial adaptation in unstable environments (Gobbetti et al.2007; Novick & Geisinger 2008). Moreover, Staphylococcus species (Hou et al. 2018), along with Cutibacterium , Bacillus , and Paenibacillus (Timmusk et al. 2019; Arnaouteli et al. 2021; Coenye et al. 2022), have been found to release extracellular polymeric substances, supporting biofilm formation, nutrient supply, and attachment in the community.

Discussion

In this study we aimed to explore the active microbial communities within dust events, to better understand their traits in the environment and to human and the ecology.

Our result illustrates that distinct trajectories and wind speeds induce significant variations in microbial composition of active microbiota. This is in correspondence with previous studies exploring these effects on the metagenomic community composition (Gat *et al.* 2017).

Diurnal shifts in biodiversity patterns were observed and are likely due to air-mass exposure to the Mediterranean Sea environment. There is relatively little research on diurnal shifts in bioaerosols, with Saari et al (2015) utilizing fluorescent technology to monitor their concentration variations between day and night (Saari et al.2015), Hu et al (2020) exploring diurnal pathogens diversity in the urban environment (Hu et al. 2020), and Gusareva et al (2019) exploring variations in airborne community composition showing a robust diurnal repetitive dynamics in the tropical air ecosystem (Gusareva et al. 2019). To the best of our knowledge, diurnal variations in microbial composition have not been explored in dust events to date and may allow a better understanding of the dynamics of the microbial migration along the dust transport.

Investigating active microorganisms allows exploring interactions between different active communities. These interactions encompass collaborative metabolic processes such as carbon and nitrogen metabolism, the degradation of organic compounds and heavy metals, and the promotion of microbial biofilm formation through quorum sensing. Other studies have explored dust contribution to nutrient cycles such as N_2 fixation through diazotrophs in dust (Rahav et al. 2016; Rahav et al. 2018). Our findings not only shed light on the potential survival strategies of active microorganisms during dust events but also uncover their inherent ability for active genetic and metabolic exchanges across various ecosystems.

Prolonged exposure to airborne dust particles can result in various health issues, including conjunctivitis, meningitis, and coccidioidomycosis (Aghababaeian et al. 2021). Nevertheless, the causing factors are not fully understood. While a range of potential pathogenic microorganisms have been identified during dust events, their viability remains unknown.

Of particular note is Staphylococcus , consistently detected in nearly all samples, suggesting its widespread presence during dust events. This species reported to be abundant (Kakikawa et al.2008) and active (White et al. 2020) in other dust events. Beyond its activity in the microenvironment, certain Staphylococcusspecies are associated with human pathogens (Balasubramanian et al. 2017; Vestergaard et al. 2019), that could induce dust-associated health effects.

Another key genus in our dust samples was the spore-forming Bacillus, which includes potential traits such as biomineralization (Keren-Paz et al. 2022), biofilm formation (Maet al. 2017), and toxicity (Azarkar & Zare Bidaki 2016). Other studies have managed to detect and isolate *Bacillus* species in dust and other high-altitude samples, and it is hypothesized that their survival is due to sporulation abilities (Wainwright et al.2003b; Griffin 2004; Yoo et al. 2019).

In conclusion, our findings demonstrate positive interactions among active dust-borne microorganisms, facilitating element cycling, pollutant degradation, and biofilms formation. These interactions likely play a vital role in microorganism survival and adaptation in the challenging dust environment, while also potentially influencing broader phenomena like biogeochemical cycling and implications for human health. Further exploration could shed light on microbial resilience and adaptation in extreme environments and may pave the way for novel insights into the broader implications of these versatile microorganisms.

Acknowledgements

The authors gratefully acknowledge support from Prof. Yigal Erel for providing sampling instrumentation, and from Ms. Ariel Tastassa for support in sample collection.

References

1.

Aalismail, N.A., Ngugi, D.K., Diaz-Rua, R., Alam, I., Cusack, M. & Duarte, C.M. (2019). Functional metagenomic analysis of dust-associated microbiomes above the Red Sea. Sci Rep , 9, 13741.

2.

Aarnink, A., Hoeksma, P., Venglovsky, J., Gregova, G. & Čornejová, T. (2015). Effects of temperature and relative humidity on the survival of airborne bacteria. In: XVII International Congress on Animal Hygiene.

3.

Aasfar, A., Bargaz, A., Yaakoubi, K., Hilali, A., Bennis, I., Zeroual, Y. et al. (2021). Nitrogen Fixing Azotobacter Species as Potential Soil Biological Enhancers for Crop Nutrition and Yield Stability. Frontiers in Microbiology , 12.

4.

Aghababaeian, H., Ostadtaghizadeh, A., Ardalan, A., Asgary, A., Akbary, M., Yekaninejad, M.S. et al. (2021). Global Health Impacts of Dust Storms: A Systematic Review. Environ Health Insights , 15, 11786302211018390.

5.

Aili, A., Xu, H. & Zhao, X. (2022). Health Effects of Dust Storms on the South Edge of the Taklimakan Desert, China: A Survey-Based Approach.*International journal of environmental research and public health* , 19.

6.

Amrutha, M. & Nampoothiri, K.M. (2022). In silico analysis of nitrilase-3 protein from Corynebacterium glutamicum for bioremediation of nitrile herbicides. Journal of Genetic Engineering and Biotechnology , 20,

51. 7.

An, S., Couteau, C., Luo, F., Neveu, J. & DuBow, M.S. (2013). Bacterial Diversity of Surface Sand Samples from the Gobi and Taklamaken Deserts.Microbial Ecology , 66, 850-860.

8.

Arnaouteli, S., Bamford, N.C., Stanley-Wall, N.R. & Kovács, Á.T. (2021). Bacillus subtilis biofilm formation and social interactions.Nature Reviews Microbiology , 19, 600-614.

9.

Aronson, H.S., Clark, C.E., LaRowe, D.E., Amend, J.P., Polerecky, L. & Macalady, J.L. (2023). Sulfur disproportionating microbial communities in a dynamic, microoxic-sulfidic karst system. bioRxiv, 2023.2003.2026.534238.

10.

Azarkar, Z. & Zare Bidaki, M. (2016). A case report of inhalation anthrax acquired naturally. BMC Research Notes , 9, 141.

11.

Balasubramanian, D., Harper, L., Shopsin, B. & Torres, V.J. (2017). Staphylococcus aureus pathogenesis in diverse host environments.Pathog Dis , 75.

12.

Barberán, A., Bates, S.T., Casamayor, E.O. & Fierer, N. (2012). Using network analysis to explore cooccurrence patterns in soil microbial communities. The ISME Journal , 6, 343-351.

13.

Benjamini, Y. & Hochberg, Y. (2018). Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing.Journal of the Royal Statistical Society: Series B (Methodological) , 57, 289- 300.

14.

Blazewicz, S.J., Barnard, R.L., Daly, R.A. & Firestone, M.K. (2013). Evaluating rRNA as an indicator of microbial activity in environmental communities: limitations and uses. The ISME Journal , 7, 2061-2068.

15.

Bollmann, A., Sedlacek, C.J., Norton, J., Laanbroek, H.J., Suwa, Y., Stein, L.Y. et al. (2013). Complete genome sequence of Nitrosomonas sp. Is79, an ammonia oxidizing bacterium adapted to low ammonium concentrations. Standards in genomic sciences , 7, 469-482.

16.

Bolyen, E., Rideout, J.R., Dillon, M.R., Bokulich, N.A., Abnet, C.C., Al-Ghalith, G.A. et al. (2019). Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. Nature Biotechnology , 37, 852-857.

17.

Callahan, B.J., McMurdie, P.J., Rosen, M.J., Han, A.W., Johnson, A.J.A. & Holmes, S.P. (2016). DADA2: High-resolution sample inference from Illumina amplicon data. Nat Methods , 13, 581-583.

Coenye, T., Spittaels, K.-J. & Achermann, Y. (2022). The role of biofilm formation in the pathogenesis and antimicrobial susceptibility of Cutibacterium acnes. Biofilm , 4, 100063.

19.

Csárdi, G. & Nepusz, T. (2006). The igraph software package for complex network research.

20.

Dannemiller, K.C., Weschler, C.J. & Peccia, J. (2017). Fungal and bacterial growth in floor dust at elevated relative humidity levels.Indoor Air , 27, 354-363.

21.

Elmassry, M.M., Ray, N., Sorge, S., Webster, J., Merry, K., Caserio, A.et al. (2020). Investigating the culturable atmospheric fungal and bacterial microbiome in West Texas: implication of dust storms and origins of the air parcels. FEMS Microbes , 1.

22.

Erkorkmaz, B.A., Gat, D. & Rudich, Y. (2023). Aerial transport of bacteria by dust plumes in the Eastern Mediterranean revealed by complementary rRNA/rRNA-gene sequencing. Communications Earth \mathcal{B} Environment , 4, 24.

23.

Fahy, A., McGenity, T.J., Timmis, K.N. & Ball, A.S. (2006). Heterogeneous aerobic benzene-degrading communities in oxygen-depleted groundwaters. FEMS Microbiology Ecology , 58, 260-270.

24.

Feng, Y., Ming, T., Zhou, J., Lu, C., Wang, R. & Su, X. (2022). The Response and Survival Mechanisms of Staphylococcus aureus under High Salinity Stress in Salted Foods. Foods (Basel, Switzerland) , 11.

25.

Fujiyoshi, S., Tanaka, D. & Maruyama, F. (2017). Transmission of Airborne Bacteria across Built Environments and Its Measurement Standards: A Review. Front Microbiol , 8, 2336.

26.

Gat, D., Mazar, Y., Cytryn, E. & Rudich, Y. (2017). Origin-Dependent Variations in the Atmospheric Microbiome Community in Eastern Mediterranean Dust Storms. Environ Sci Technol , 51, 6709-6718.

27.

Gat, D., Reicher, N., Schechter, S., Alayof, M., Tarn, M.D., Wyld, B.V. et al. (2021). Size-Resolved Community Structure of Bacteria and Fungi Transported by Dust in the Middle East. Frontiers in Microbiology , 12.

28.

Gobbetti, M., De Angelis, M., Di Cagno, R., Minervini, F. & Limitone, A. (2007). Cell–cell communication in food related bacteria.International Journal of Food Microbiology , 120, 34-45.

29.

Griffin, D. (2004). Terrestrial Microorganisms at an Altitude of 20,000 m in Earth's Atmosphere. Aerobiologia , 20, 135-140.

Guo, L., Dai, Z., Guo, J., Yang, W., Ge, F. & Dai, Y. (2020). Oligotrophic bacterium Hymenobacter latericoloratus CGMCC 16346 degrades the neonicotinoid imidacloprid in surface water. AMB Express , 10, 7.

31.

Gusareva, E.S., Acerbi, E., Lau, K.J.X., Luhung, I., Premkrishnan, B.N.V., Kolundžija, S. et al. (2019). Microbial communities in the tropical air ecosystem follow a precise diel cycle. Proc Natl Acad Sci U S A, 116, 23299-23308.

32.

Haines, S.R., Siegel, J.A. & Dannemiller, K.C. (2020). Modeling microbial growth in carpet dust exposed to diurnal variations in relative humidity using the "Time-of-Wetness" framework. Indoor Air , 30, 978-992.

33.

Hanshew, A.S., Mason, C.J., Raffa, K.F. & Currie, C.R. (2013). Minimization of chloroplast contamination in 16S rRNA gene pyrosequencing of insect herbivore bacterial communities. Journal of microbiological methods , 95, 149-155.

34.

Haruta, S. & Kanno, N. (2015). Survivability of Microbes in Natural Environments and Their Ecological Impacts. Microbes and environments , 30, 123-125.

35.

Hou, J., Veeregowda, D.H., van de Belt-Gritter, B., Busscher, H.J. & van der Mei, H.C. (2018). Extracellular Polymeric Matrix Production and Relaxation under Fluid Shear and Mechanical Pressure in Staphylococcus aureus Biofilms. Appl Environ Microbiol , 84.

36.

Hu, Z., Liu, H., Zhang, H., Zhang, X., Zhou, M., Lou, L. et al.(2020). Temporal discrepancy of airborne total bacteria and pathogenic bacteria between day and night. Environmental Research , 186, 109540.

37.

Ikram, M., Naeem, M., Zahoor, M., Hanafiah, M.M., Oyekanmi, A.A., Islam, N.U. et al. (2022). Bacillus subtilis: As an Efficient Bacterial Strain for the Reclamation of Water Loaded with Textile Azo Dye, Orange II. International journal of molecular sciences , 23.

38.

Jawaharraj, K., Sudha Dhiman, S., Bedwell, S., Vemuri, B., Islam, J., Sani, R.K. et al. (2021). Electricity from methane by Methylococcus capsulatus (Bath) and Methylosinus trichosporium OB3b.Bioresource Technology , 321, 124398.

39.

Kakikawa, M., Kobayashi, F., Maki, T., Yamada, M., Higashi, T., Chen, B.et al. (2008). Dustborne microorganisms in the atmosphere over an Asian dust source region, Dunhuang. Air Quality, Atmosphere & Health , 1, 195-202.

40.

Keren-Paz, A., Maan, H., Karunker, I., Olender, T., Kapishnikov, S., Dersch, S. et al. (2022). The roles of intracellular and extracellular calcium in Bacillus subtilis biofilms. iScience , 25, 104308.

Kong, X., Dong, R., King, T., Chen, F. & Li, H. (2022). Biodegradation Potential of Bacillus sp. PAH-2 on PAHs for Oil-Contaminated Seawater.Molecules (Basel, Switzerland) , 27.

42.

Kozajda, A., Jeżak, K. & Kapsa, A. (2019). Airborne Staphylococcus aureus in different environments-a review. Environmental science and pollution research international , 26, 34741-34753.

43.

Lang-Yona, N., Öztürk, F., Gat, D., Aktürk, M., Dikmen, E., Zarmpas, P. et al. (2020). Links between airborne microbiome, meteorology, and chemical composition in northwestern Turkey. Science of the Total Environment , 725, 138227.

44.

Lee, J.H., Kim, M.S., Kang, J.W., Baik, K.S. & Seong, C.N. (2016). Mucilaginibacterpuniceus sp. nov., isolated from wetland freshwater.International Journal of Systematic and Evolutionary Microbiology , 66, 4549-4554.

45.

Liu, L.Y., Shi, P.J., Gao, S.Y., Zou, X.Y., Erdon, H., Yan, P. et al. (2004). Dustfall in China's western loess plateau as influenced by dust storm and haze events. Atmospheric Environment , 38, 1699-1703.

46.

Lu, Q., Sun, X., Jiang, Z., Cui, Y., Li, X. & Cui, J. (2022). Effects of Comamonas testosteroni on dissipation of polycyclic aromatic hydrocarbons and the response of endogenous bacteria for soil bioremediation. Environmental science and pollution research international , 29, 82351-82364.

47.

Lyon, G.J. & Novick, R.P. (2004). Peptide signaling in Staphylococcus aureus and other Gram-positive bacteria. Peptides , 25, 1389-1403.

48.

Ma, W., Peng, D., Walker, S.L., Cao, B., Gao, C.-H., Huang, Q. et al. (2017). Bacillus subtilis biofilm development in the presence of soil clay minerals and iron oxides. NPJ Biofilms Microbiomes, 3, 4.

49.

Madhaiyan, M., Poonguzhali, S., Lee, J.-S., Senthilkumar, M., Lee, K.C. & Sundaram, S. (2010). Mucilaginibacter gossypii sp. nov. and Mucilaginibacter gossypiicola sp. nov., plant-growth-promoting bacteria isolated from cotton rhizosphere soils. International Journal of Systematic and Evolutionary Microbiology , 60, 2451-2457.

50.

Maki, T., Puspitasari, F., Hara, K., Yamada, M., Kobayashi, F., Hasegawa, H. et al. (2014). Variations in the structure of airborne bacterial communities in a downwind area during an Asian dust (Kosa) event. Science of The Total Environment , 488-489, 75-84.

51.

Novick, R.P. & Geisinger, E. (2008). Quorum Sensing in Staphylococci.Annual Review of Genetics , 42, 541-564.

Otto, M. (2009). Staphylococcus epidermidis–the 'accidental' pathogen. Nature reviews. Microbiology , 7, 555-567.

53.

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P.et al. (2012). The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic Acids Research , 41, D590-D596.

54.

Rahav, E., Ovadia, G., Paytan, A. & Herut, B. (2016). Contribution of airborne microbes to bacterial production and N2 fixation in seawater upon aerosol deposition. Geophys Res Lett , 43, 719-727.

55.

Rahav, E., Paytan, A., Mescioglu, E., Galletti, Y., Rosenfeld, S., Raveh, O. et al. (2018). Airborne Microbes Contribute to N2 Fixation in Surface Water of the Northern Red Sea. Geophys Res Lett , 45, 6186-6194.

56.

Risely, A., Waite, D.W., Ujvari, B., Hoye, B.J. & Klaassen, M. (2018). Active migration is associated with specific and consistent changes to gut microbiota in Calidris shorebirds. Journal of Animal Ecology , 87, 428-437.

57.

Romanenko, L.A., Uchino, M., Frolova, G.M., Tanaka, N., Kalinovskaya, N.I., Latyshev, N. et al. (2007). Sphingomonas molluscorum sp. nov., a novel marine isolate with antimicrobial activity. Int J Syst Evol Microbiol , 57, 358-363.

58.

Rowan-Nash, A.D., Korry, B.J., Mylonakis, E. & Belenky, P. (2019). Cross-Domain and Viral Interactions in the Microbiome.Microbiology and Molecular Biology Reviews , 83, e00044-00018.

59.

Saari, S., Niemi, J., Ro¨nkko¨, T., Kuuluvainen, H., Ja¨rvinen, A., Pirjola, L. et al. (2015). Seasonal and Diurnal Variations of Fluorescent Bioaerosol Concentration and Size Distribution in the Urban Environment. Aerosol Air Qual Res , 15, 572-581.

60.

Sahoo, K.K., Goswami, G. & Das, D. (2021). Biotransformation of Methane and Carbon Dioxide Into High-Value Products by Methanotrophs: Current State of Art and Future Prospects. Frontiers in Microbiology , 12.

61.

Sandhu, M., Paul, A.T. & Jha, P.N. (2022). Metagenomic analysis for taxonomic and functional potential of Polyaromatic hydrocarbons (PAHs) and Polychlorinated biphenyl (PCB) degrading bacterial communities in steel industrial soil. Plos one , 17, e0266808.

62.

Santl-Temkiv, T., Gosewinkel, U., Starnawski, P., Lever, M. & Finster, K. (2018). Aeolian dispersal of bacteria in southwest Greenland: their sources, abundance, diversity and physiological states. FEMS Microbiology Ecology , 94.

Shelly, Y., Kuk, M., Menashe, O., Zeira, G., Azerrad, S. & Kurzbaum, E. (2021). Nitrate removal from a nitrate-rich reverse osmosis concentrate: Superior efficiency using the bioaugmentation of an Acinetobacter biofilm. Journal of Water Process Engineering , 44, 102425.

64.

Sorkheh, M., Asgari, H.M., Zamani, I. & Ghanbari, F. (2022). The Relationship Between Dust Sources and Airborne Bacteria in the Southwest of Iran. Environmental Science and Pollution Research , 29, 82045-82063. 65.

Tesso, T.A., Zheng, A., Cai, H. & Liu, G. (2019). Isolation and characterization of two Acinetobacter species able to degrade 3-methylindole. PLoS One , 14, e0211275.

66.

Thakur, N., Singh, S.P. & Zhang, C. (2022). Microorganisms under extreme environments and their applications. Current Research in Microbial Sciences , 3, 100141.

67.

Tian, L., Yang, C., Zhou, Z., Wu, Z., Pan, X. & Clements, A.C.A. (2019). Spatial patterns and effects of air pollution and meteorological factors on hospitalization for chronic lung diseases in Beijing, China. Science China Life Sciences , 62, 1381-1388.

68.

Timmusk, S., Copolovici, D., Copolovici, L., Teder, T., Nevo, E. & Behers, L. (2019). Paenibacillus polymyxa biofilm polysaccharides antagonise Fusarium graminearum. Scientific Reports , 9, 662.

69.

Tsai, M., Ohniwa, R.L., Kato, Y., Takeshita, S.L., Ohta, T., Saito, S.et al. (2011). Staphylococcus aureus requires cardiolipin for survival under conditions of high salinity. BMC Microbiol , 11, 13.

70.

Ulrich, R. (2021). Bacteria in the wind. Nature Reviews Earth $\mathcal B$ Environment, 2, 823-823.

71.

Varsadiya, M., Urich, T., Hugelius, G. & Bárta, J. (2021). Fungi in Permafrost-Affected Soils of the Canadian Arctic: Horizon- and Site-Specific Keystone Taxa Revealed by Co-Occurrence Network.Microorganisms , 9.

72.

Venil, C.K., Malathi, M. & Devi, P.R. (2021). Characterization of Dietzia maris AURCCBT01 from oilcontaminated soil for biodegradation of crude oil. 3 Biotech , 11, 291.

73.

Vestergaard, M., Frees, D. & Ingmer, H. (2019). Antibiotic Resistance and the MRSA Problem. Microbiol Spectr , 7.

74.

Wainwright, M., Wickramasinghe, N.C., Narlikar, J.V. & Rajaratnam, P. (2003a). Microorganisms cultured from stratospheric air samples obtained at 41 km. FEMS Microbiology Letters , 218, 161-165.

75.

Wainwright, M., Wickramasinghe, N.C., Narlikar, J.V. & Rajaratnam, P. (2003b). Microorganisms cultured from stratospheric air samples obtained at 41 km. FEMS Microbiol Let , 218, 161-165.

76.

Walters, W., Hyde, E.R., Berg-Lyons, D., Ackermann, G., Humphrey, G., Parada, A. et al. (2016). Improved bacterial 16S rRNA gene (V4 and V4-5) and fungal internal transcribed spacer marker gene primers for microbial community surveys. Msystems , 1, e00009-00015.

77.

Wang, B., Kuang, S., Shao, H., Wang, L. & Wang, H. (2021). Anaerobic-petroleum degrading bacteria: Diversity and biotechnological applications for improving coastal soil. Ecotoxicology and Environmental Safety , 224, 112646.

78.

White, J.K., Nielsen, J.L., Larsen, C.M. & Madsen, A.M. (2020). Impact of dust on airborne Staphylococcus aureus' viability, culturability, inflammogenicity, and biofilm forming capacity. International Journal of Hygiene and Environmental Health , 230, 113608.

79.

Yan, Y., Yang, J., Dou, Y., Chen, M., Ping, S., Peng, J. et al.(2008). Nitrogen fixation island and rhizosphere competence traits in the genome of root-associated $\langle i \rangle$ Pseudomonas stutzeri $\langle i \rangle$ A1501. Proceedings of the National Academy of Sciences , 105, 7564-7569.

80.

Yao, Z., Seong, H.J. & Jang, Y.-S. (2022). Degradation of low density polyethylene by Bacillus species. Applied Biological Chemistry , 65, 84.

81.

Yin, W., Wang, Y., Liu, L. & He, J. (2019). Biofilms: The Microbial "Protective Clothing" in Extreme Environments. International journal of molecular sciences , 20.

82.

Yoo, K., Han, I., Ko, K.S., Lee, T.K., Yoo, H., Khan, M.I. et al.(2019). Bacillus-Dominant Airborne Bacterial Communities Identified During Asian Dust Events. Microbial ecology , 78, 677-687.

83.

Yoon, J.H., Kim, I.G., Kang, K.H., Oh, T.K. & Park, Y.H. (2003). Alteromonas marina sp. nov., isolated from sea water of the East Sea in Korea. Int J Syst Evol Microbiol , 53, 1625-1630.

84.

Yoshikawa, M., Zhang, M. & Toyota, K. (2017). Biodegradation of Volatile Organic Compounds and Their Effects on Biodegradability under Co-Existing Conditions. Microbes and environments , 32, 188-200.

85.

Zhang, M., Li, A., Yao, Q., Xiao, B. & Zhu, H. (2022). Pseudomonas oligotrophica sp. nov., a Novel Denitrifying Bacterium Possessing Nitrogen Removal Capability Under Low Carbon–Nitrogen Ratio Condition.Frontiers in Microbiology , 13.

86.

Zhang, Y., Wang, F., Wei, H., Wu, Z., Zhao, Q. & Jiang, X. (2013). Enhanced biodegradation of poorly available polycyclic aromatic hydrocarbons by easily available one. International Biodeterioration $\mathcal B$ Biodegradation , 84, 72-78.

Zhou, M., Liu, Z., Wang, J., Zhao, Y. & Hu, B. (2022). Sphingomonas Relies on Chemotaxis to Degrade Polycyclic Aromatic Hydrocarbons and Maintain Dominance in Coking Sites. Microorganisms , 10.

Figure captions

Figure 1. Abundance of Bacterial Phyla in Dust Samples. (A)Principal coordinate analysis of dust samples collected during three dust events using Weighted UniFrac metrics. (B) Venn diagram illustrating the shared microbes Amongst the sampled dust events. Both day (D) and night (N) samples are analyzed. (C) The top 13 abundant phyla, ranked by average abundance, as represented in percentages for each dust sample.

Figure 2. Abundance and interactions of active dust-borne bacteria. (A) Comparison of abundances of the top five phyla in dust events based on 16S rRNA gene (DNA) and 16S rRNA (cDNA) libraries. (B) Heatmap presenting the predominant active genera within the top five phyla. (C) Visualization of the interactions between different genera of the microbial community.

Figure 1.

Figure 2.

Table 1. Sampling parameters, meteorological conditions, and dust microbiome diversity parameters during sampled dust events. The relative humidity (RH), temperature, wind speed and directions, as well as air sampling time, duration and rate are denoted. The different α-diversity values (Observe ASVs, Chao1, Abundance-based Coverage Estimator; ACE, Shannon, Simpson) are listed per the different samples.

		Samplingura-	Samplinglow	rates	Air vol-			Wind speed	Wind di-				
ID	Sample Samplingimes date	$(UTC+2)h)$	tion	(L) min^{-1})	ume (m^3)	R _H (%)	Temperature $(^{\circ}C)$	s^{-1})	recti- $\text{on} (°)$	Observe ASVs	Chao1 ACE		Sha
Blank \bf{I}	$29 -$ Mar- 2022	11:40	$0.008\,$	14.00	0.007	$26.15\,$	$22.22\,$	4.63	122.87	$\overline{}$			
$DE-$ $I_{\neg}D_{\neg}a$ $DE-$	$29 -$ Mar- $2022\,$	11:45 \equiv 18:00	6.25	14.00	$5.25\,$	$26.15\,$	22.22	4.63	122.87	$82\,$	89.80	89.53	$3.83\,$
$L_{\rm D.b}$ DE- I.N.a	$30-$ Mar-	$0:00 -$ 6:00	$6.00\,$	14.00	$5.04\,$	$55.05\,$	16.75	$5.08\,$	166.57	$88\,$ 111	$91.06\,$ 126.40	$\boldsymbol{93.75}$ 124.28	3.79 4.11
$DE-$ I_N_b	$2022\,$									116	134.00	136.21	4.04
Blank $\rm II$	$06-$ Apr- $2022\,$	$10:55\,$	$0.008\,$	14.00	0.007	$61.41\,$	$20.63\,$	7.78	244.08	$\frac{1}{2}$			\overline{a}
\rm{DE} $\rm ILD_a$ \rm{DE} ILD_b	$06-$ Apr- $2022\,$	11:00 \sim 17:00	$6.00\,$	14.00	$5.04\,$	61.41	$20.63\,$	7.78	244.08	$79\,$	100.43	103.95	3.06
$DE-$ $\rm{II} _N_a$ \rm{DE} II.N.b	$07 -$ Apr- $2022\,$	$0:00 -$ 06:00	$6.00\,$	14.00	$5.04\,$	88.62	15.06	$3.38\,$	213.16	132 $22\,$	142.34 22.00	148.81 22.00	$3.83\,$ 2.46
Blank $\rm III$	$25-$	10:55	$0.008\,$	14.00	$0.007\,$	$50.51\,$	25.57	$2.05\,$	127.22	43 $\frac{1}{2}$	$43.25\,$ \overline{a}	43.69 $\overline{}$	2.86 $\overline{}$
$DE-$	Apr- $2022\,$ $25 -$	11:00	6.00	14.00	$5.04\,$	50.51	25.57	$2.05\,$	127.22	125	136.81	145.21	3.18
III - D_a $DE-$ III -	Apr- $2022\,$	\equiv 17:00											
D_b										168	201.44	197.15	4.02

17

