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Relative viability proxy of airborne prokaryotic microorganisms at the Southeastern Mediterranean coastal Sea

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The atmosphere plays a fundamental role in transporting airborne prokaryotes across the oceans and land. Despite the harsh atmospheric conditions, a considerable fraction of the airborne prokaryotic microorganisms survive the journey and remain viable upon deposition, and can affect the receiving environment. Here, we provide the first estimate of potential viability proxy for airborne prokaryotic cells at the Southeastern Mediterranean coast in 22 events during 2015, representing marine and terrestrial air-mass trajectories and a significant dust storm event. This was assessed using sequence amplicons of the small subunit ribosomal RNA gene (SSU rRNA) jointly with other complementary measurements. To estimate the relative viability in our dataset we used the ratio between the abundance of the bacterial SSU rRNA transcripts in a given sampling date and the lowest measured value (23.7.2015) as a measure of a relative viability proxy. The abundance of prokaryotes SSU rRNA transcripts ranged from ~500 to 11,000 copies m^3, with ~2-fold higher relative viability proxy in marine-origin aerosols than predominantly terrestrial atmospheric trajectories. The relative viability proxy of prokaryotes was low during the peak of an intense and prolonged dust storm, and increased by ~1.5-fold in the subsequent days representing background conditions (<1700 ng Al m^{-3}). Furthermore, we show that anthropogenic/toxic trace-metals (Cu/Al, Pb/Al) negatively correlates with potentially viable airborne prokaryotes in marine trajectory aerosols, whereas mineral dust load (Al, Fe proxy) positively affect their potential viability proxy. This may suggest that airborne prokaryotes associated to marine trajectories benefit from a particle-associate lifestyle, enabling relatively higher humidity and supply of nutrients attributed to mineral dust particles.

KEYWORDS

viable airborne prokaryotes, aerosols, trace-metals, Southeastern Mediterranean, dust

Introduction

Aerosol deposition provide external nutrients that contribute to phytoplankton/bacterial growth and activity in the surface layers of the ocean (Moore et al., 2009; Tsagaraki et al., 2017). Experimental results, however, show that aerosol addition do not consistently induce the expected nutrient fertilization effect on phytoplankton/bacteria (Hill et al., 2010; Guieu et al., 2014; Torfstein et al., 2017). Several processes may contribute to this lack of response, including differences in the chemical composition of aerosols and associated release of macro and micro-nutrients (Moore et al., 2013) and toxic elements (Paytan et al., 2009; Després et al., 2012; Jordi et al., 2012). Specifically, variability in the ambient natural assemblages of organisms at different locations and during different seasons may also result in variable responses to atmospheric deposition (Gallisai et al., 2014). Transport and deposition of dust during storms, or the frequency and intensity of the pulses of deposition, may also contribute to the observed variability in ecosystem responses (Giovagnetti et al., 2013). Another factor that may contribute to the observed variability, which has been far less investigated, is the supply of airborne microorganisms upon aerosols deposition to the surface water (Polymenakou, 2012; Peter et al., 2014; Rahav et al., 2016a), resulting in unique interaction with the *in situ* microbial communities (Mescioglu et al., 2019b; Fragola et al., 2021; Peng et al., 2021).

Airborne prokaryotic microorganisms were often neglected as a microbial habitat and a significant ecological vector (Kellogg and Griffin, 2006; Polymenakou, 2012; Mayol et al., 2014). This is partly due to the assumption that most microorganisms in aerosols die while in the atmosphere, before their deposition, as a result of inhospitable conditions including exposure to solar UV-radiation, desiccation, and/or due to low nutrients availability or high levels of toxic constituents (Griffin, 2007). Yet, many bacterial phylum can form spores that protect the cells from desiccation, heat, acidity, radiation, and nutrient-poor conditions (Tang, 2009). Moreover, many bacteria are highly pigmented, which may help shield the cells from damaging radiation levels (Kellogg et al., 2004; Fahlgren et al., 2010). Clouds, fog, smoke and desert dust particles can also shed airborne bacteria from damaging UV radiation (Hara and Zhang, 2012). Evidently, atmospheric aerosols contain bacteria, archaea, algae, viruses, fungi, and pollen originating from land (Kellogg and Griffin, 2006; Griffin et al., 2007) or the ocean (Prospero et al., 2005; Flores et al., 2020). Airborne microorganisms were identified in almost every aerosol sample collected over aquatic and terrestrial environments (Leck and Bigg, 2005; Favet et al., 2013; Yahya et al., 2019), usually ranging from ~10^3 to ~10^7 cells per m^3 of air (Mayol et al., 2017; Rahav et al., 2019; Alsante et al., 2021), and were shown to contribute to bacterial production, primary production, N_2 fixation and viral infections (Peter et al., 2014; Rahav et al., 2018; Rahav et al., 2020). Understanding the parameters that determine the survival of airborne microorganisms is of great ecological significance and may shed light on microbial dispersion throughout the world's oceans.

The Southeastern Mediterranean Sea is a semi-enclosed oligotrophic basin (Siokou-Frangou et al., 2010; Sisma-Ventura et al., 2021), subjected to relatively high input of aerosols originated from neighboring deserts (Herut et al., 2002; Guieu et al., 2014). The aerosols could have different atmospheric transport routes dominated by marine and/or terrestrial paths (Rahav et al., 2019). Previous indirect evidences suggest that airborne microbes can become active following deposition in Southeastern Mediterranean seawater (e.g., Rahav et al., 2018), highlighting the need to quantify their viability and better understand their biochemical role.

Here, we proxy the potential viable airborne prokaryotic microbes (bacteria and archaea) in naturally occurring aerosols and during an extreme dust event in the Southeastern Mediterranean coastal Sea in 22 events over 2015. We hypothesized that terrestrial air-mass trajectories or dust storm events will have relatively lower viable prokaryotic microorganisms upon deposition in seawater. Contrary, marine air-mass trajectories, which likely contain a larger fraction of sea-spray derived prokaryotes, will be more protected from the hostile atmospheric conditions and thus have a relatively higher viable airborne cells.

Material and methods

Bioaerosols collection

Aerosols were collected onto sterile 0.22-µm polycarbonate filters (PALL) using a custom-made high-volume sampler with a collection rate of 40 $m^3 h^{-1}$ (Figure 1). Aerosols were collected over a few hours (4–6 h) to minimize prokaryotes RNA degradation, accumulate sufficient amount of genetic material and prevent prokaryotic cell damage caused by prolonged filtration (Hu et al., 2017). The sampler was placed ~22 m above sea level at the shoreline of the Southeastern Mediterranean Sea (Lat. 32.28″N, Lon. 34.9″E). A total of 22 sampling events were undertaken between February and December 2015 thus covering different seasonal conditions. Three filters were collected in parallel; one for RNA extractions, the second for airborne prokaryotes abundance measurements, and the third as an unused blank placed on the aerosol sampler without any pumping. For some samples ($n = 14$), bacterial production measurements were also undertaken from a fourth filter pumped in parallel.

Trace-metals and $PM_{2.5}$ measurements

Total suspended particles in air (TSP) were sampled in parallel at the same location using a high-volume sampler at a

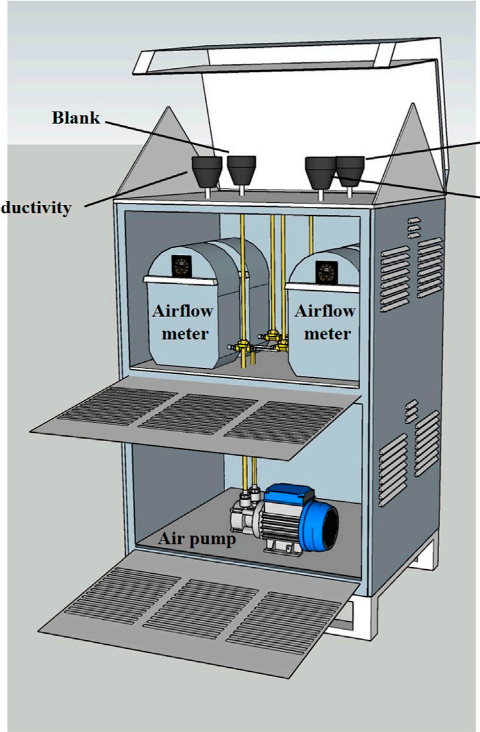

FIGURE 1
An illustration showing the custom-made high-volume sampler (40 m^3 h^{-1}, 4–6 h in each sampling event) and the experimental setup used to collect aerosols. The sampler was located ~22 m above sea level at the Southeastern Mediterranean coast. The collected filters were later processed for measuring the potential viability proxy of airborne prokaryotes and their abundance (n = 22). Blank filters placed on the filter holder without pumping was also collected and analyzed in each sampling event. Filters were collected throughout 2015.

constant flow rate of 60 m^3 h^{-1}. After collection, a subsample of the Whatman 41 filters was dried in a desiccator for 24 h before being reweighed. Al, Fe, Pb, and Cu were measured after total digestion with hydrogen fluoride (Herut et al., 2001) following the procedure of ASTM (1983) by an atomic absorption spectrometer Agilent 280FS AA and graphite furnace Agilent 240Z AA.

Suspended particulate matter smaller than 2.5 µm ($PM_{2.5}$) were collected every 5 min using a low-volume sampler (Thermo Scientific Ambient Particulate Monitor, TEOM® 1400ab; Precision: ±1.5 µg m^3 (1-h average).

Air mass backward trajectories

Air mass backward trajectory analyses arriving at 10–250 m altitudes were computed using the HYSPLIT model (http://ready.arl.noaa.gov/HYSPLIT_traj.php). The GDAS 0.5-degree meteorology data was used to run the backward trajectories using a vertical velocity motion. The aerosols were classified to terrestrial or marine origin based on their main route 3 days prior their arrival to the Southeastern Mediterranean coast (Figure 2).

Airborne prokaryotes abundance

One filter from each event was suspended in 0.22-µm filtered Southeastern Mediterranean costal seawater containing microscopy-grade glutaraldehyde solution (Sigma-Aldrich G7651, final concentration 0.2%). Then, the tube was sonicated for 1 min in a bath sonicator (Symphony) and mixed vigorously for additional 2 min to remove all prokaryotic cells from the filter. Before analyses, triplicate 100 µl aliquots were stained with SYTO9 (1:10^5 *v:v*) for 10 min in the dark, and heterotrophic prokaryotes cells were counted using an Attune®Acoustic Focusing Flow Cytometer (Applied Biosystems) equipped with 488 and 405-nm lasers at a rate of 25 µl min^{-1} using a discrimination threshold of green fluorescence and forward-scatter. Additional unstained triplicate samples were also run for cyanobacterial abundance determination using the orange and red fluorescence, side-scatter and on forward-scatter discriminations. The total airborne cell count is set as the sum of heterotrophic prokaryotes and cyanobacteria. Size beads of ~1 µm (Polysciences) were run with blank seawater every five samples.

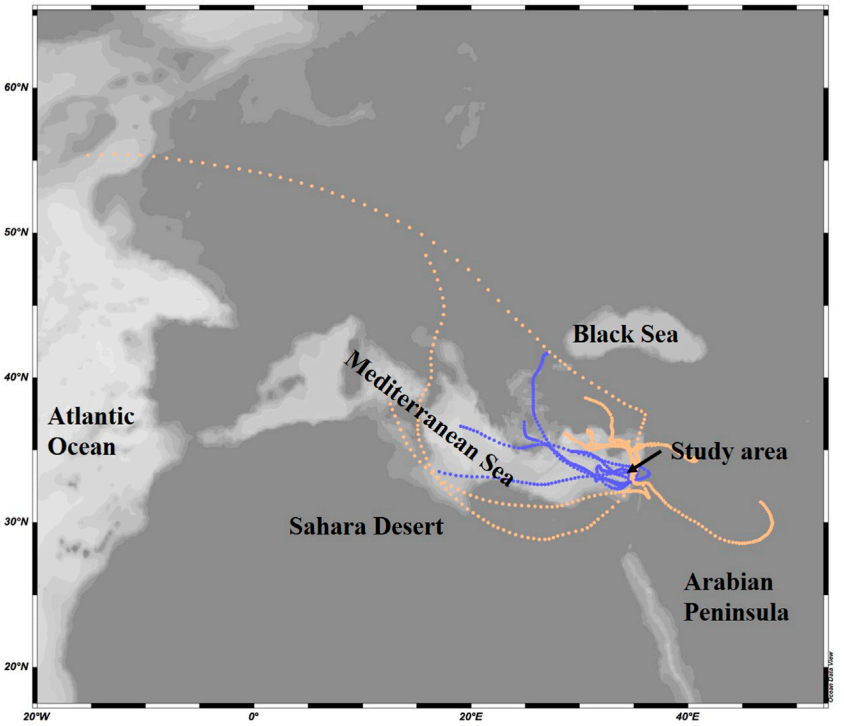

FIGURE 2
Representative marine (blue) and terrestrial (peach) origin of air mass trajectories arriving the Southeastern Mediterranean Sea at 10 m altitude in 2015. The trajectories show the 3-days atmospheric route prior collection.

Molecular extraction and SSU rRNA gene copy number

Collected aerosols on filters were placed in an RNA-later solution (Thermo-Fisher AM7023) and snap-frozen in liquid nitrogen and stored in −80°C until they were processed within a few weeks/months. RNA was extracted from the filters using the mirVana RNA isolation kit (Ambion) as instructed by the manufacture. A high capacity cDNA reverse transcription kit (Applied Biosystems) was used to generate cDNA molecules. The small subunit ribosomal RNA (SSU rRNA) gene copy number was determined using a SYBR green-based quantitative real-time PCR (Applied Biosystems) analyses with the broadly conserved bacterial primers 331F (TCCTACGGGAGGCAGCAGT) and 518R (ATTACCGCGGCTGCTGG). Previous studies showed the validity of these primers for RT-qPCR assays (Bräuer et al., 2011; Gat et al., 2017).

Evaluating the relative viability-proxy of airborne bacteria

Estimate of the “relative viability proxy” of airborne microbial cells was defined here as the ratio between the abundance of the SSU rRNA gene copy number in a given sampling date and the value for 23 July 2015 that represent reference conditions with the lowest levels of total prokaryotes cells and Al per m^3 air (Supplementary Table S1). We based our proxy on the assumption that the physiological state of prokaryotes is regulated by the expression of ribosomal RNA (Klumpp and Hwa, 2009). Note, however, this approach assumes that the average rRNA copies per airborne bacterial cell between samples/sampling dates is similar.

Results

Aerosols deposition in the Southeastern Mediterranean coastal seawater during the year 2015 ranged from 2 mg m^{-2} d^{-1} to as high as 209 mg m^{-2} d^{-1} during a dust storm in early September 2015, thus exceeding the previously reported maximal daily average flux of ~140 mg m^{-2} d^{-1} in this area (Lawrence and Neff, 2009). Airborne prokaryotes abundance ranged from 800 to 21,000 cells m^{-3}, with the highest values measured in early September 2015 during an intense dust storm arriving from the North-East (Supplementary Table S1 and discussion below). The abundance of bacterial SSU rRNA transcripts ranged from 524 to 10,985 copies m^3 (Figure 3A).

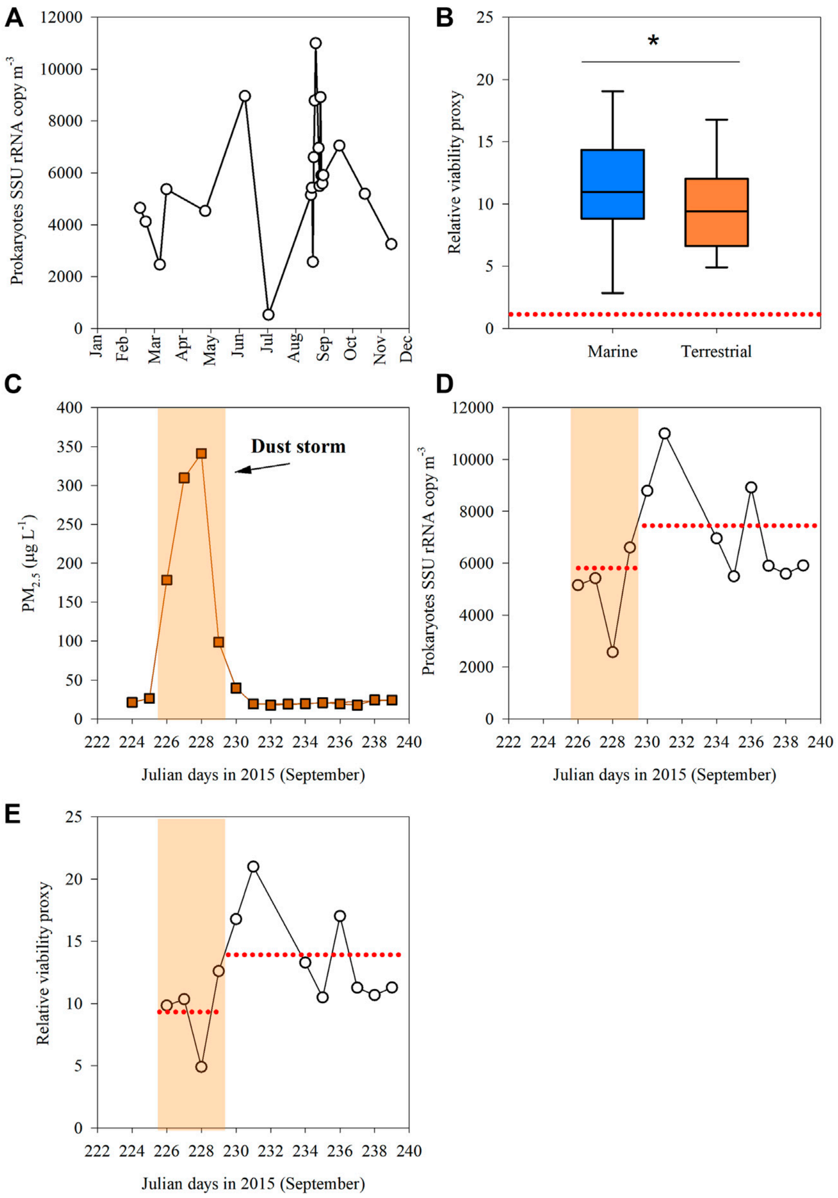

FIGURE 3
(A) Small subunit ribosomal RNA gene (SSU rRNA) copies per cubic meter of air determined by RT-qPCR analysis; **(B)** The "relative viability proxy" of airborne prokaryotic cells in respect to their atmospheric path using air-mass backward trajectory analyses. **(C)** The temporal dynamics of PM$_{2.5}$ through 2015; **(D)** SSU rRNA gene copies during a storm (8–12 September 2015) and 8 days afterwards (13–21 September 2015); and **(E)** The "relative viability proxy" for airborne prokaryotes during the dust-storm event and following days. The dash red line in panel **(B)** signifies the relative baseline conditions with the lowest levels of total prokaryotes cells and Al per m^3 air (23 July 2015). The dash red line in panels **(D,E)** show the averaged value in a given period. The yellowish background signifies the dust storm duration.

We used the abundance of bacterial SSU rRNA transcripts in 23 of July 2015 as a reference (baseline), representing the lowest ranked dataset value and particulate Al levels in air (see "Material and Methods"). We thus evaluate the change/enrichment as a "relative viability proxy," which ranges from 1 (reference) to ~21 (Figure 3B). A significantly higher relative viability proxy was found in marine-origin aerosols as compared to aerosols associated with a dominant terrestrial trajectory (Figure 3B, *t*-test, $p = 0.03$). The average enrichment in marine-origin aerosols was 13.4 ± 3.7 as compared to 8.6 ± 2.8.

Throughout the dust storm event (Julian day 226–229), both the Al (~13,000–69,000 ng m^{-3}, Supplementary Table S1) and the PM$_{2.5}$ (~200–350 µg L^{-1}) levels were significantly higher compared to the lower levels of Al (<1700 ng m^{-3}) and PM$_{2.5}$

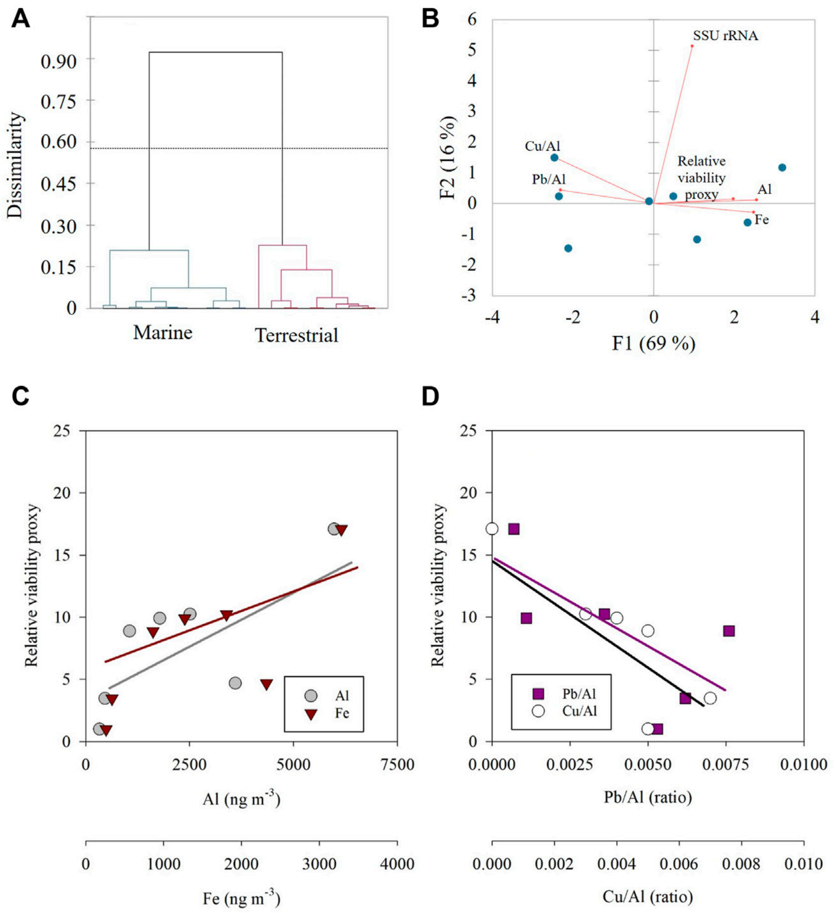

FIGURE 4
(A) An agglomerative hierarchical clustering (AHC) dendrogram showing the dissimilarities (Euclidean distance) between aerosols with marine (green) and terrestrial (red) origin; **(B)** Principle component analysis (PCA) of the marine-origin trajectories; **(C,D)** The relationship between the relative potentially viable airborne prokaryotes and Al (grey), Fe (dark red), Pb/Al (dark pink) and Cu/Al (white) in marine-origin aerosols [corresponds to panel **(B)**].

(<40 µg L^{-1}) measured in the following 8 days (t-test, $p < 0.001$, Figure 3C, Supplementary Table S1) and are considered similar to background conditions in this marine area (Herut et al., 1999). The abundance of bacterial SSU rRNA transcripts during the storm ranged from 5,150 to 8,790 copies m^3 and increased to as high as ~11,000 copies m^3 the following days after the storm had settled (Figure 3D). The concurrent relative viability proxy for the airborne prokaryotes during the dust storm was ~9 ± 3, significantly lower than afterwards, ~14 ± 4 (t-test, $p = 0.03$, Figure 3E) or from the annual average of ~12 ± 4 (t-test, $p = 0.04$).

An agglomerative hierarchical clustering (AHC) analysis, which considers the prokaryotic cell abundance and RNA transcripts, showed that the marine-origin samples significantly differ from aerosols of a dominant terrestrial trajectory (Figure 4A). In the marine-origin aerosols a significant negative correlation was calculated between Pb/Al or Cu/Al and the relative potential viability of airborne prokaryotes, while in the terrestrial-origin aerosols a less clear trend was observed (Supplementary Figure S1). Fe or Al (proxy for mineral dust particles) were positively correlated in both marine (Figures 4B–D; $p < 0.05$) and terrestrial-origin aerosols, noting the limited number of observations.

A limited number of aerosol samples were also collected and analyzed for airborne prokaryotes genetic diversity; one during the intense dust storm (8 September 2015, Julian day 226) and the other under background conditions a few days afterwards (20 September 2015, Julian day 238). The prokaryotic microbial beta-diversity was overall similar between the "dust" and the "background" filters (Supplementary Figure S2). Proteobacteria, *Actinobacteria* and *Firmicutes* were the most dominant bacterial phyla (Supplementary Figure S2A). The most dominant prokaryote within the phylum Proteobacteria was alpha-proteobacteria (~80% of ASVs) followed by beta-proteobacteria (~10%), gamma-proteobacteria (~5%), and delta-proteobacteria (~3%) (Supplementary Figure S2B). Within the order taxonomic level, in the dust filters bacillales, frankiales, and *Cytophagales* were the most abundant; ~10% of ASVs each. *Clostridia* and *Chromatiales* were present in the dust filters but not in the background, comprising 2%–3% each. In the background filter bacillales comprised ~20% of the ASVs, which is double than found in the dust filter. Within the family taxonomic level, bacillaceae comprised ~23% of all ASVs in the background filter, while only ~4% in the background. *Rhodobacteraceae* comprised ~7% in the background and ~4% in the dust filters, and the geodermatophilaceae relative ASV abundance was 5-fold higher in the dust (~5%) than the background (~1%) filters. Other differences in microbial beta diversity between filters were minor and insignificant.

Discussion

Aerosol's origin and trace-metals affect airborne prokaryotic viability proxy

The physiological state of prokaryotes is indirectly regulated by ribosomal RNA transcription (Klumpp and Hwa, 2009), implying the more SSU rRNA gene copies per cell, the more active they are. Based on this assumption, our results suggest that some airborne prokaryotes indeed remain viable during atmospheric transport (Figures 3A,B), in agreement with previous reports (Womack et al., 2010; DeLeon-Rodriguez et al., 2013). A higher relative viability proxy for airborne prokaryotes was found in marine-origin aerosols, suggesting that humidity in the air is an important factor contributing to their ability to survive in the atmosphere (Leck and Bigg, 2005). Indeed, airborne prokaryotes with marine origin are often embedded in transparent gel-like polymers which protect them from desiccation, and provide them with sustaining nutrients (Aller et al., 2005; Leck and Bigg, 2005; Cunliffe and Murrell, 2009). In agreement, a recent study reported on high concentrations of transparent exopolymer particles in aerosol particles at the tropical Atlantic Ocean (Pinxteren et al., 2022). Moreover, a high percent of airborne prokaryotes in cloud-water/precipitation remain viable during atmospheric transport (Hill et al., 2007; Murata and Zhang, 2016; Stopelli et al., 2017).

We observed that in marine aerosols the relative viability proxy of airborne prokaryotes is affected by certain trace metal concentrations (Figures 4B–D). The negative effect of Cu/Al and Pb/Al (Figure 4D) was attributed to the potential toxicity of these anthropogenic trace metals. The positive relationships between the relative viability proxy and Fe or Al concentrations in air, as proxies for mineral dust content (Figure 4C, Supplementary Figure S1), may be linked to the release of some associated nutrients or the positive role of the particle's micro-environment. This suggest that airborne prokaryotes may benefit from a particle–associated lifestyle through attachment to particles, especially under humid (marine) conditions. Indeed, large aggregates/particles were shown to protect airborne microbes through shielding from UV, especially over water which also reduces humidity stress (Dowd and Maier, 2000). Moreover, it is possible that the particle-associated microbes utilize micro and macronutrient directly from the particle surface, thereby can remain active and possibly grow. Furthermore, respiration of particle-associated airborne microbes can create a low oxygen micro-zones, as often found on large marine particles (Klawonn et al., 2015), thus "enable"/"ease" the survival of anoxic bacteria during atmospheric transport which is essentially aerial. Indeed, oxygen-sensitive prokaryotes (facultative or obligate) are routinely found on dust samples (Katra et al., 2014; Gat et al., 2017). For example, bacillaceae (order: Bacillales, Phylum: Firmicutes), which comprised 10%–20% of the ASV's on an order level (Supplementary Figure S2A) and 4%–23% in a family taxonomic level (Supplementary Figure S2C), are considered facultatively anaerobic. While we do not have a direct/specific quantification on their viability, it is reasonable to assume that some of them survive in the atmosphere, especially given that many of them form endospores (Secaira-Morocho et al., 2020). Currently, we cannot state which bacterial phylotypes remained viable during atmospheric transport and were actively growing or involved in specific cellular pathways. This question could be investigated by sequencing efforts of the airborne ribosomal 16S RNA transcripts as well as other specific genes of interest (Alsante et al., 2021). One such gene could be *nifH* as airborne diazotrophs are routinely found in dust samples (Foster et al., 2009), which, in turn, may fix N_2 upon deposition in seawater (Rahav et al., 2018).

Viability proxy of airborne prokaryotes during an extreme dust storm event

The dust storm that arrived at the Southeastern Mediterranean Sea in early September 2015 (starting 7 September 2015) was substantial and relatively prolonged (Rahav et al., 2016b). Estimated increase in inorganic nutrients to the surface seawater were ~185 nM NO_3+NO_2 and ~1.5 nM PO_4 (Rahav et al., 2016b), which are up to 50% higher than the typically reported values in this system during the summer (Kress et al., 2019). The concurrent *in-situ* chlorophyll-*a* concentration and primary productivity rates increased only moderately a few days after aerosol deposition (Rahav et al., 2016b), suggesting the % of viable airborne bacteria, who can become active upon deposition (Rahav et al., 2018), was relatively low in this specific and unique event. Our results, based on the relative viability proxy analysis, overall agrees with this notation that airborne prokaryotes during the dust storm were "less" active than in "typical" (clear-sky) days. The low levels of the relatively viability proxy during the dust event may be attributed to anthropogenic inhibitors carried by the dust, mainly metals and organic pollutants. Thus, transport time, the presence of pollutants and the chemical reactions on surface particles during the dust event probably impacted the microbial viability, yet further research is needed to assess how physical and chemical microhabitats impacts microorganism functionality (Alsante et al., 2021). Moreover, given the acidic conditions in the atmosphere and clouds (Pye et al., 2020), trace-metals leachability and thus potential toxicity may increase (Koçak et al., 2007). It is therefore not surprising that the relative viability proxy for airborne prokaryotes and potentially toxic trace metals display a negative relationship (Figure 4D). Marine trajectory aerosols, with potentially higher pH (seawater are typically basic, pH = ~8.15), will likely result in lower trace-metals leachability and thus lower toxicity to airborne prokaryotes, resulting in their higher relative viability (Figure 3B).

In addition to bacillaceae (see above), frankiales and *Cytophagales* were the most dominant bacterial groups in the dust samples (Supplementary Figure S2). Frankiales (Phylum: Actinobacteria) has high G-C content in their DNA, enabling them to survive (and likely also to remain active) in a wide range of niches, including the atmosphere (Kellogg and Griffin, 2006). Another abundant prokaryote in air is cytophagaceae (order: *Cytophagales*, phylum: Bacteroidota). Members of this bacterial order are well-known remineralizers of organic matter, and are widely dispersed in top-soils, freshwater and surface seawater (Sun et al., 2018; Rubin-Blum et al., 2022). While we cannot say the percent of viable cells within these bacterial phylotypes, in light of their cellular characteristics it is reasonable to hypothesize they are also the dominant groups among the viable cells.

Techniques to assess airborne microbial viability—The plot thickens

The relatively few aero-microbiology studies over the ocean are mostly based on genetic diversity (Mayol et al., 2017; Mescioglu et al., 2019a), culture or spore-counting techniques (Griffin et al., 2001; Womack et al., 2010; Fernandez et al., 2019), microscopic approaches (DeLeon-Rodriguez et al., 2013), measuring specific metabolic/catabolic microbial processes such as bacterial productivity, N_2 fixation and amino-acid synthesis (Rahav et al., 2018; Ruiz-Jimenez et al., 2021), and/or by looking at airborne cell's RNA expression (DeLeon-Rodriguez et al., 2013; Ruiz-Jimenez et al., 2021 and this study). Each approach has its pros and cons (reviewed in Alsante et al., 2021), but neither of them directly quantifies how many airborne microbes remain viable during their atmospheric transport and which taxa are more likely to survive. Here, we used rRNA transcripts quantification as a proxy for a relative consideration of this scientific challenge throughout a representative year in a coastal marine area subjected to high aerosol deposition (Herut et al., 2016). While we cannot directly calculate the actual % viability of the airborne prokaryotic cells, our result provides the first relative change in the potential viability of airborne prokaryotes during an extreme dust storm event and the days afterwards presenting background conditions, and thus a relative estimate of the potential viability at the Southeastern Mediterranean Sea. We warrant that complimentary approaches such as "live-dead" staining of airborne prokaryotes (e.g., based on membrane integrity or other redox-based vitality approaches), and/or collection of airborne cells into sterile seawater containing RNA-later preservation solution, are required to better quantify % viable cells. Moreover, comparing sequences of 16S rRNA gene (DNA level) and transcript (RNA level) may provide valuable information on the prokaryotes identity and which phylotypes remained viable during atmospheric transport. Understanding the factors that influence airborne bacterial abundance and viability in the atmosphere is an important missing component for further insight into microbial biogeography, connectivity/spreading and diversity (Hervas et al., 2009; Fröhlich-Nowoisky et al., 2016). Such information can also benefit the parameterization of model simulations of bacterial emissions and dispersal (Burrows et al., 2013). Moreover, climate change and desertification projections suggest an increase in dust loads and storm events boosting transoceanic/marine transport, and therefore increasing the ecological significance of airborne prokaryotic microorganisms. We note that much further studies are needed to understand the factors and mechanisms impacting bio-aerosols viability.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://www.ncbi.nlm.nih.gov/, RX272470.

Author contributions

Conceived and designed the experiment: ER. Performed the experiment: ER and BH. Analyzed the data: BH, AP, and ER.

Contributed reagents/materials/analysis tools: BH and ER. Wrote the paper: AP, BH, and ER.

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Conflict of interest

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.900977/full#supplementary-material

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