Global Ramifications of Dust and Sandstorm Microbiota

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Abstract

Dust and sandstorm events inject substantial quantities of foreign microorganisms into global ecosystems, with the ability to impact distant environments. The majority of these microorganisms originate from deserts and drylands where the soil is laden with highly stress-resistant microbes capable of thriving under extreme environmental conditions, and a substantial portion of them survive long journeys through the atmosphere. This large-scale transmission of highly resilient alien microbial contaminants raises concerns with regards to the invasion of sensitive and/or pristine sink environments, and to human health—concerns exacerbated by increases in the rate of desertification. Further increases in the transport of dust-associated microbiota could extend the spread of foreign microbes to new ecosystems, increase their load in present sink environments, disrupt ecosystem balance, and potentially introduce new pathogens. Our present understanding of these microorganisms, their phylogenic affiliations and functional significance, is insufficient to determine their impact. The purpose of this review is to provide an overview of available data regarding dust and sandstorm microbiota and their potential ramifications on human and ecosystem health. We conclude by discussing current gaps in dust and sandstorm microbiota research, and the need for collaborative studies involving high-resolution meta-omic approaches in conjunction with extensive ecological time-series studies to advance the field towards an improved and sufficient understanding of these invisible atmospheric travelers and their global ramifications.

Key words: dust and sandstorms microbiota, global spread, stress resistant and pathogenic microorganisms, human and ecosystem health, metagenomics and multiomics, monitoring.

Introduction

Dust and sandstorm events inject substantial quantities of foreign microorganisms to downwind atmosphere, terrestrial, and aquatic environments, and are known as one of the most far-reaching vehicles for transport of highly stress resistant and potentially invasive/pathogenic microorganisms across the globe (Kellogg and Griffin 2006; Favet et al. 2013; Smith et al. 2013; Weil et al. 2017). Significant increases in the concentration of bacteria and fungi are commonly detected in dust clouds during sandstorm events (Kellogg and Griffin 2006; Griffin 2007; Vijayakumar et al. 2017; Tang et al. 2018). Since microorganisms are fundamental players in ecosystem processes (Schulz et al. 2013; Bernhard and Kelly 2016; Graham et al. 2016), large-scale transport of highly stress resistant, foreign, and potentially invasive/pathogenic microorganisms could have wide ranging impacts on downwind environments and our health (Griffin and Kellogg 2004; Gonzalez-Martin et al. 2014). African dusts were linked to the meningitis outbreaks in sub-Saharan Africa (Agier et al. 2013; Jusot et al. 2017) and the coral reef decline in the Caribbean (Shinn et al. 2000). Dust storms are known to correlate with increased hospital emergency visits due to asthma exacerbations and other respiratory and cardiovascular complications (Gyan et al. 2005; Mallone et al. 2011; Tam et al. 2012; Lee et al. 2013; Meo et al. 2013). However, the few studies investigating the roles of dust storm microbiota in disease outbreaks found correlation, but did not explore clinical evidence for causal effects (Chen et al. 2010; Rodo et al. 2014; Wang et al. 2016). Although these studies provide a link between sandstorms and disease outbreaks, they were constrained in terms of number and scope.

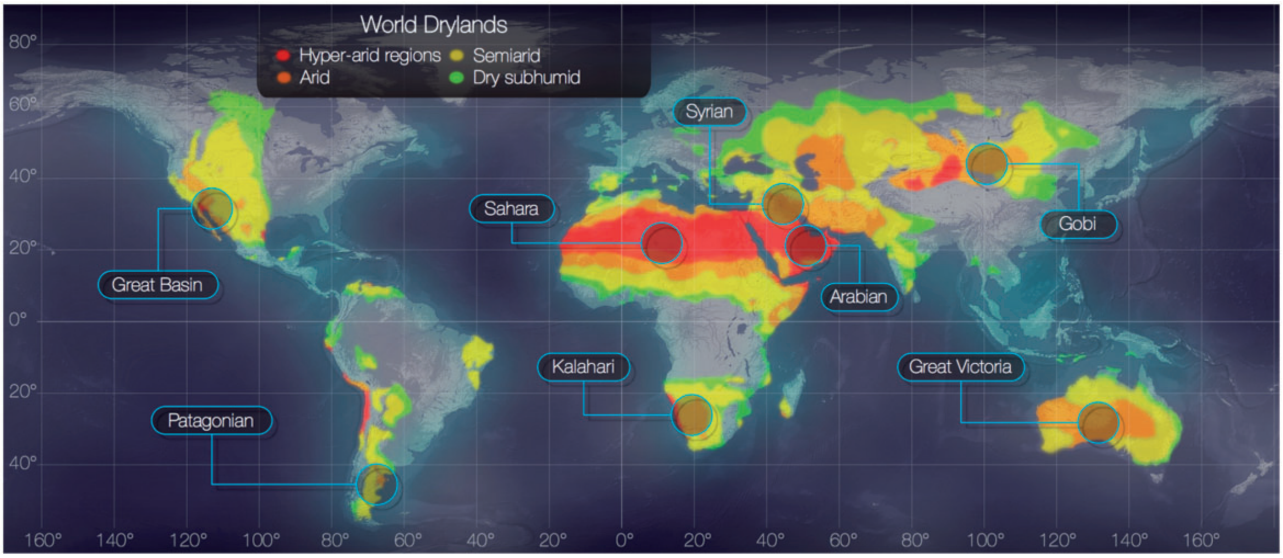

Fig. 1.—World map of drylands. Colors highlight regions with varying degrees of aridity. Major deserts (excluding Antarctica and the Arctic) are annotated. http://www.naturalearthdata.com/, last accessed July 21, 2018.

Expanded study is needed since dust activity is predicted to rise substantially in the future due to global climate changes and anthropogenic causes. The world's drylands have expanded over the past 60 years, and their expansion is projected to continue well into the 21st century (Huang et al. 2017). Dryland regions cover approximately 40% of earth's total landmass (White and Nackoney 2003), and are spread throughout the globe, with the largest percentage localized in Africa and Asia, as shown in figure 1. Increased aridity, frequent draughts, low precipitation, low soil fertility, and excessive anthropogenic exploitations have made dryland soils exceptionally vulnerable to desertification, degradation, and erosion by wind (Fu and An 2002; Maestre et al. 2014; Tao 2014; Zhou et al. 2016). Approximately $12\text{x}10^6$ hectares of arable land is lost annually to desertification, which is 30–35 times greater than expected based on historic rates (UNCCD). Desertification generates new grounds for dust activities (Moulin and Chiapello 2006; McConnell et al. 2007; Johnson et al. 2011; Issanova et al. 2015; Sharma et al. 2015), and could increase microbial load in the atmosphere. The overall escalation in dust activities could alter the equilibrium in sink environments by increasing their share of foreign microbes, extremophiles, and potentially invasive/pathogenic species. It could also spread dust masses beyond present sink environments affecting new ecosystems.

The ramifications of dust and sandstorm microbiota are potentially significant. In order to understand impact, we need to have detailed information on the agents of impact. The research in the field of dust and sandstorm aeromicrobiology and its impact on downwind ecology is still in its infancy. Our current knowledge of these microorganisms and their functional attributes is insufficient to determine a cause and effect relationship between their spread and threats to downwind ecosystems. Understanding the breadth of microbial diversity in dust clouds, their viability, invasiveness/pathogenicity, and their long-term impacts on global ecosystems will require comprehensive, collaborative studies and novel approaches. In recent years, with the advent of culture-independent metagenomics, we are beginning to realize the vast extent of microbial diversity in sandstorm dust clouds and the extent of their reach (Smith et al. 2013; Rosselli et al. 2015; Cha et al. 2017; Maki et al. 2017b; Weil et al. 2017). These novel findings opened our eyes to a frontier of previously unknown microbial diversity, and the research in the field is gaining momentum due to pertinent discoveries. We aim to draw attention to this novel frontier of microbial ecology by examining: 1) The current understanding of dust and sandstorm derived microbiota (DSM), and their global spread; 2) Potential ramifications of DSM on human and ecosystem health; and 3) Perspectives to guide future research towards comprehensive understanding of DSM role at a global level.

Dust and Sandstorm Derived Microbiota (DSM) and Their Global Spread

Dust and Sandstorm Derived Microbiota

The majority of DSM originates from large deserts (Griffin 2007). Deserts are laden with highly stress resistant microorganisms capable of thriving in harsh environmental conditions with restricted water and nutrients availability, extremes of temperatures, and UV irradiation (Kuske et al. 1997; Dose et al. 2001; Varin et al. 2012; Makhalanyane et al. 2015;

Etemadifar et al. 2016). Desert microbiota have increased abundance of genes involved in osmoregulation and dormancy, which likely contribute to their survival in hostile desert soil (Fierer et al. 2012). Microorganisms play significant roles in soil ecosystems, from their vital symbiotic interactions with plants, to their major roles in maintenance of biological soil crust, biodegradation of organic matters, and biogeochemical cycling of nutrients (Ortiz-Castro et al. 2009; Abed et al. 2010; Schulz et al. 2013). Microbial diversity in soil is dependent on its pH, nutrient, and moisture contents (Fierer and Jackson 2006; Clark et al. 2009; Lauber et al. 2009; Angel et al. 2010; Rousk et al. 2010). Some variations exist in the diversity of taxa that dwell in different deserts, with cold arctic deserts bearing lower microbial diversity compared with hot deserts (Pointing et al. 2009; Fierer et al. 2012; Lee et al. 2012). Some of the major bacterial taxa that frequently dwell in desert soil with high relative abundance include Actinobacteria, Bacteroidetes, Proteobacteria, Firmicutes, and cyanobacteria (Fierer et al. 2012; An et al. 2013). Archaea also appear to be equally abundant, the majority of which are chemolithoautotrophic ammonia oxidizers potentially involved in biogeochemical cycling of nitrogen and carbon (Makhalanyane et al. 2015). Desert soil also harbors diverse communities of fungi that can withstand adverse environmental conditions (Chan et al. 2013); some of the most common fungal genera in deserts include *Alternaria, Aspergillus, Cladosporium, and Penicillium* (Conley et al. 2006; Sterflinger et al. 2012; Makhalanyane et al. 2015). Taxonomically diverse selections of viruses were also found, although viral diversity and function in desert ecosystems is poorly understood (Fierer et al. 2007; Zablocki et al. 2016).

In addition to desert microbiome, sandstorms carry large quantities of the airborne microbiota encountered along their intermediate path. By some estimate, a cubic meter of air contains hundreds of thousands of microorganisms (Burrows et al. 2009; Prussin et al. 2015), with a diversity of taxa similar to that found in soil (Franzetti et al. 2011). The majority of these microbes originate from local sources, that is, soil, aquatic environments, plants, and anthropogenic pollution (Maron et al. 2005; Brodie et al. 2007). Some of the more dominant bacterial taxa in air include Proteobacteria, Firmicutes, Bacteroidetes, Actinobacteria, and Cyanobacteria (Bowers et al. 2009; Smith et al. 2013; Lee et al. 2017). Air also harbors diverse communities of fungi including *Cladosporium, Aspergilllus*, and *Penicillium*, some of which are potential allergens (Oh et al. 2014). Archaea including Thaumarchaeota and Euryarchaeota were also found in the air (Frohlich-Nowoisky et al. 2014). DNA sequences from a diversity of viruses, including those related to plant-associated geminiviruses and animal-infecting circoviruses, were also found in air (Whon et al. 2012). Airborne microbiota are known to resist adverse atmospheric conditions (Rothschild and Mancinelli 2001), and the atmosphere is believed to be a source of both beneficial and pathogenic microorganisms (Polymenakou 2012; Nicolaisen et al. 2017).

There is limited data on the extent of microbial diversity and taxonomic details of DSM. These details are required to study the functional and ecological significance of these microbes in their native environments and larger ecosystems.

Global Spread of DSM and Their Wide-Ranging Reach

According to different studies, each year between 0.5 billion and 5 billion tons of dust is injected into the atmosphere (Perkins 2001), the majority of which originate from the Sahara Deserts and Sahel regions in Africa, and the Gobi and Taklamakan Deserts in Asia (Griffin 2007). Sandstorms from the Sahara Deserts transmit roughly a billion tons of dust across the atmosphere, and are considered as one of the major sources of the intercontinental dust transport (Moulin et al. 1997; Griffin 2007). Figure 2 shows NASA satellite images of a strong sandstorm that blew off the west coast of Africa on October 13, 2017, carrying massive amounts of African dusts across the Atlantic Ocean. The dust plume generated from this particular storm stretched for a few thousand kilometers over the Atlantic, and reached the Caribbean within 5–6 days. Sandstorms such as this are common occurrences in the region, and can transport substantial quantities of African dust thousands of kilometers from the source; depending on the strength and direction of the wind, these dust can move westward across the Atlantic Ocean to the Americas and the Caribbean (Prospero and Carlson 1981; Swap et al. 1992; Perry et al. 1997; Prenni et al. 2009), or north and eastward over the Mediterranean Sea to Europe and the Middle East, respectively (Ganor et al. 1991; Franzen et al. 1995; LoyePilot and Martin 1996; Kubilay et al. 2000; Rodríguez et al. 2001). Gobi and Taklamakan Deserts in Asia, the second largest source of long-range dust transport, inject approximately 100–460 Mt/year (Laurent et al. 2006) to 800 Mt/year (Zhang et al. 1997) of dust into the atmosphere (Bishop et al. 2002; Griffin 2007). The dust plumes generated from Asia sandstorms frequently disturb the air quality in East Asia (Iwasaka et al. 1983; Choi et al. 2001; Trochkine et al. 2003), and can reach as far as the Americas (Husar et al. 2001; VanCuren and Cahill 2002), the Alps (Grousset et al. 2003), the Arctic (Huang et al. 2015), and even circle around the globe (Uno et al. 2009). Strong sandstorms originating from African and Asian deserts are known to carry a large enough quantity of dust to affect air quality in destinations thousands of kilometers away from the source (Prospero 1999; Griffin 2007). Considering that one gram of soil can harbour 10^8–10^9 prokaryotes (Whitman et al. 1998), this could translate into transport of trillions upon trillions of microbes into the air and downwind destinations along their intermediate path. Increases in the concentration of microbes in sandstorm dust clouds have been documented extensively by both culture dependent and independent approaches (Kellogg and Griffin 2006; Griffin 2007; Nishimura et al. 2010; Yamaguchi et al. 2014).

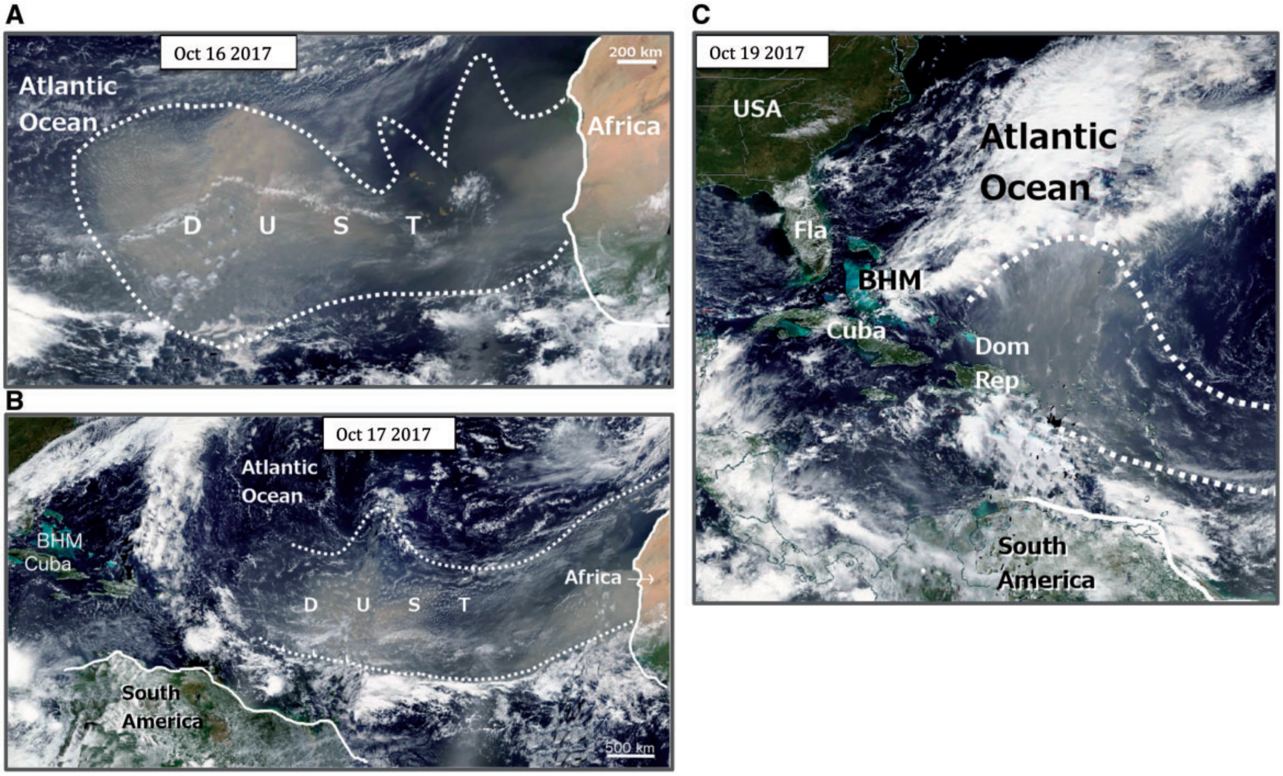

FIG. 2.—A massive sandstorm blows off the west coast of Africa and over the Atlantic Ocean towards the Caribbean, on October 13, 2017. (*A*) A dust plume greater than 2,000 km in length could be seen over the Atlantic Ocean, 3 days later on October 16. (*B*) The dust plume was stretched over 4,000 km by day 4, October 17. The dust clouds reached the Caribbean by day 5 on October 18, covering Dominican Republic (Dom Rep) by October 19 (*C*), and moving towards the Bahamas (BHM) and Florida (Fla.) in the United States (USA). The natural color images were captured with the Moderate Resolution Imaging Spectroradiometer (MODIS) abroad NASA's Satellites. Images courtesy of NASA Earthdata: https://worldview.earthdata.nasa.gov/, last accessed July 21, 2018.

A few studies examined the impact of increased transport of DSM on ambient airborne microbiota in leeward environments. A recent metagenomic analysis of air samples collected during an Asian dust event in South Korea showed a significant increase in the number of bacterial Operational Taxonomic Units (OTU) with significantly different microbial composition including potential human pathogens, compared with control nondust samples (Cha et al. 2017). A similar analysis of air samples in Northern China demonstrated substantial increases in airborne bacterial diversity and concentration in dust versus nondust air samples (Tang et al. 2018). Asian dust was shown to carry substantial increases in the proportion of endospore forming *Bacillus* as well as other bacterial genera including *Modestobacter* (Cha et al. 2016), which are resistant to desiccation and UV irradiation (Gtari et al. 2012). Examination of two transpacific Asian air plumes at Mt. Bachelor Observatory (2.8 km above sea level) in North America revealed a richness of microbiota tantamount to those found in surface environments; the plumes carried increased level of Gram-positive bacteria that included many spore forming species adapted to survive in extreme conditions (Smith et al. 2013). Similarly, analysis of airborne bacterial communities in the free troposphere at high altitude (500–3,000 m above ground level) over the Noto Peninsula in Japan during Asian dust days showed a high diversity of bacteria, dominated by natural-sand/terrestrial-associated taxa including endospore forming *Bacillus* members (Maki et al. 2017a). Hara et al. (2015) isolated a number of UV tolerant endospore forming culturable bacteria in air samples collected over the East China Sea during Asian dust events, demonstrating that dust storms carry viable bacteria.

At present, we do not know exactly what percentage of DSM survives the long journey through the atmosphere. It is also uncertain whether these alien microbial contaminants can adapt to disparate new environmental conditions upon arrival, and if they could significantly alter their new host ecosystems. Findings from a recent culture independent metagenomic study by Weil et al. revealed that a massive sandstorm originating from the Sahara Deserts deposited a large fraction of the entire microbial communities from Saharan soil to snow covered Alpine mountains in Italy (Weil et al. 2017). Within these deposits, the authors found a number of putative pathogens and some of the most highly stress resistant microorganisms ever detected on the planet.

Surprisingly, some of these microorganisms might have survived in the frozen Alpine soil and still remained viable upon melting of the snow (Weil et al. 2017). In a similar study, the snow samples collected at Mont Blanc glaciers (French Alps) during Sahara dust storms showed high indices of bacterial diversity with a dominance of phylotypes commonly found in desert and arid soils (Chuvochina et al. 2011a, 2011b), some of which belonged to genera known to carry resistance to adverse environmental conditions including extreme cold, UV irradiation, and desiccation; these traits could enable them to remain viable during atmospheric transport and subsequently adapt to the snow covered environment despite the physical and physiological stress associated with these events. Comparison of microbial data with their closest relatives in the GenBank identified 15 phylotypes as potential snow colonizers (Chuvochina et al. 2011b). In another study, sandstorm originating from the Sahara Desert was shown to change the bacterial assemblage and composition of a pristine fresh water lake in Austrian Alps, and increased viable bacterial concentration in these waters (Peter et al. 2014). These findings raise significant concerns over invasion and alteration of pristine and sensitive sink environments, and further suggest the spread of human diseases by alien microbial contaminants. However, the prevailing data on sandstorm microbiota is exceedingly sparse and insufficient to estimate the potential global effect exerted by these microorganisms.

Potential Ramifications of DSM on Human and Ecosystem Health

The Impact of DSM on Human Health

A primary concern with the dispersal of microorganisms via sandstorms is the potential impact on human health. A few studies have found correlations between DSM and disease outbreaks, but no major attempts were made to establish cause and affect relationships. The annual meningitis outbreaks in Sahel region of Africa were linked to the occurrence of seasonal changes including high temperatures, dry air, and increased dust activities from African deserts (Sultan et al. 2005; Griffin 2007; Agier et al. 2013; Jusot et al. 2017). Inhalation of hot and dry dusty air is thought to impair host immune response, leading to an increase in the nasopharyngeal carriage of precolonized or airborne bacterial pathogens, their direct aspiration into the lung, and dissemination into blood and brain (Jusot et al. 2017). The potential role of dust borne microbiota in the spread of meningitis in the region, however, is not clear and requires detailed investigations. Interestingly, several OTUs potentially belonging to meningitis pathogens were detected in the Sahara dust deposits within the snow packs in Swiss Alps (Meola et al. 2015). The outbreaks of Kawasaki disease (KD), a serious heart complication acquired in childhood, in Japanese children was linked to *Candida* species found in tropospheric winds originating from China (Rodo et al. 2014). The seasonal occurrence of KD in US children similarly showed a significant association with the strong wind currents that originated from central Asia (Rodo et al. 2011; Rodo et al. 2014). Another infectious disease presumably caused by wind dissemination of microorganisms is Valley Fever, whose fungal causative agents *Coccidioides immitis* and *Coccidioides posadasii* are primarily found in hot and arid desert soil (Kirkland and Fierer 1996). In particular, positive correlations were found between the intensification of sandstorms and the epidemics of Valley Fever in Southern United States in the last decade (Tong et al. 2017). The incidence of measles in Western China was positively correlated with dust events in the region (Ma et al. 2017). The epidemics of pulmonary tuberculosis, a chronic infectious disease of the lung caused by *Mycobacterium tuberculosis*, was similarly linked to Asian dust storms (ADS) in China (Wang et al. 2016). A significant increase in the concentration of ambient influenza type A virus was detected in air samples collected in Taiwan during ADS (Chen et al. 2010); and the highly pathogenic H5N1 avian influenza virus outbreaks in 2003–2005 in Japan and South Korea, positioned downwind of ADS, were potentially caused by increases in the influenza virus load during ADS (Chen et al. 2010). A strong association between increased particulate matter (PM2.5) levels and the risk of acquiring influenza-like illness was reported in Beijing, China across all the age categories studied (Feng et al. 2016). Outbreak of the foot-and-mouth disease (FMD) in Miyazaki, Japan in July–March 2010 which led to the slaughter of 289,000 domestic animals was linked to transport of the FMD virus via yellow sandstorms that originated from China (Maki et al. 2012). Dust events typically lead to increased hospital emergency visits due to asthma exacerbations and other respiratory and cardiovascular complications (Yang et al. 2005; Kanatani et al. 2010; Tam et al. 2012; Meo et al. 2013), but the potential link between sandstorm microbiota and these human health concerns have rarely been investigated even though mounting evidence suggest that microorganisms contribute to the establishment and/or exacerbations of asthma (Glezen et al. 2000; Denning et al. 2006; Hilty et al. 2010; Huang et al. 2011). Airborne dissemination of microorganisms could also greatly increase the range and influence of horizontal gene transfer. This would be particularly problematic when antibiotic resistant genes (ARGs) are acquired by pathogenic microorganisms rendering them resistant to antibiotic treatments (Martinez 2008).

Current data on the potential link between DSM and disease outbreaks show correlation, but are insufficient for establishing causation. Establishing a cause-and-effect relationship between DSM and human health concerns is difficult since the majority of these microorganisms are not yet characterized, and their viability, pathogenic potential, and geospatial distributions remain mostly unknown. A comprehensive database of DSM, environmental metadata, and implementation of disease surveillance strategies in downwind environments are all prerequisites for establishing a clear link between DSM and human health concerns. Surveillance strategies based on emerging biosensor technologies with high sensitivity and specificity for detection of windborne pathogens could provide advanced warning system for at-risk populations (Yoo et al. 2017).

The Impact of DSM on Aquatic Environments

Over two-third of our planet is covered with aquatic ecosystems including oceans, marines, lakes, rivers, and estuaries. Microorganisms are essential players in the natural functioning of these ecosystems from their major roles in biogeochemical cycling of nutrients, to their involvement in food chains through primary productivity, and the sequestration and export of atmospheric CO_2. Dust storms could have significant impacts on these processes through: 1) replenishing of essential nutrients (i.e., P and N) and trace metals (i.e., Fe) needed for growth and propagation of indigenous microorganisms; and 2) deposit of a large supply of foreign microbes, including potentially pathogenic microorganisms.

The majority of previous research on dust impact in aquatic environments primarily examined the influence of dust nutrients on indigenous microorganisms with little to no focus on the potential impact of DSM. These studies suggest that dust nutrients could promote or inhibit propagation of certain species over others depending on the trophic status of marine environments (oligotrophic vs. eutrophic) and the richness/toxicity/anthropogenic content of the dust source (Herut et al. 2005; Paytan et al. 2009; Lekunberri et al. 2010; Romero et al. 2011; Gallisai et al. 2014; Guieu et al. 2014; Westrich et al. 2016). Concomitant with the deposit of nutrients, dust storms can deliver copious supplies of highly stress resistant foreign microorganisms to aquatic environments. In a microcosm bioassay experiment, when dust samples from different deserts with distinct microbial communities were added to presterilized Mediterranean seawater, a significant increase in bacterial production and nitrogen fixation was detected within a short period following dust addition suggesting that dust borne microorganisms were alive and metabolically active (Rahav et al. 2016). Peter et al. (2014) compared the viability, composition, and abundance of bacteria in a fresh water lake in Austrian Alps during rain events influenced by Saharan versus non-Saharan dust days, and showed that the bacterial assemblage and composition in the lake differed significantly between the two events, with Gamma Proteobacteria dominating the Saharan dust intrusion events and Beta Proteobacteria dominating the non-Saharan events. The authors found a rapid increase in bacterial cell count in sterile lake water samples upon addition of the rain from Saharan dust days demonstrating that the bacteria in the wet deposits were alive and able to readily propagate. These studies, although limited in their number, focus, and temporal scope, suggest that sandstorms could significantly impact the makeup of microbial community structures in downwind aquatic environments in part through deposit of large supplies of foreign microorganisms. Intrusion of large quantities of potentially stress resistant foreign microorganisms could affect microbial community interactions and equilibrium in these environments; but the long-term impact or threats to the ecology of pristine settings such as the alpine lakes is not known.

In addition to their predicted impact on ecosystem maintenance and sustainability, dust borne microorganisms could have pathogenic ramifications on aquatic organisms. One of the best studied examples is the potential link between increased dust activities and the rapid decline in the coral reef status in the Caribbean, which receives hundreds of millions of tons of dust from Sahara Deserts annually (Shinn et al. 2000). *Aspergillus sydowii*, the fungal causative agent of Aspergillosis or sea fan disease, was isolated from both the Sahara-derived dust samples in the Caribbean and from the diseased sea fan corals in the region (Weir et al. 2000; Garrison et al. 2003). Later, it was shown that inoculation of healthy sea fans with *Aspergillus* spp. isolated from dust samples in the Caribbean produced Aspergillosis-like disease morphology in the infected corals and the fungi was successfully reisolated from the diseased animals (Weir-Brush et al. 2004). In a tissue culture bioassay, *A. sydowii* was shown to impede the motility of dinoflagellate *symbiodinium*, the coral symbiont that plays essential roles in coral fitness and energy production (Hallegraeff et al. 2014). Considering that coral reefs house some of the most vibrant marine ecosystems, these studies support the notion that escalation in dust activities could have a negative impact on marine health through increased deposit of dust borne pathogens.

Long term monitoring of sandstorm spread using advanced satellite technologies combined with fieldwork analysis of DSM in downwind environments over the Ocean and terrestrial regions, and close observations of infectious outbreaks could reveal more concrete links between pathogenic DSM and major disease outbreaks in aquatic ecosystems.

The Impact of DSM on Agriculture

Long-range transport of atmospheric dust could have both positive and negative implication on plants and agriculture in sink environments. A clear example of the positive impact of intercontinental dust transport is the continuous fertilization of nutrient depleted soils in the Amazon. By transport of nutrients, in particular phosphorus, and topsoil to the Amazon, Sahara sandstorms are believed to be major contributors to the fertility and productivity of the Amazon rainforest (Yu et al. 2015). However, dust storms can also have negative impacts on downwind agriculture through transport of substantial quantities of foreign, stress resistant and/or pathogenic microorganisms, which could potentially change the make-up of soil microbial communities or introduce pathogenic microorganisms to crops and plants. Since modern crops lack genetic diversity and are susceptible to similar set of pathogens, aerial dispersion of plant pathogens and invasive microorganisms by sandstorms could have major implications in agricultural productivity and the global economy. Understanding the mechanisms involved in regional and long-range aerial transport of crop pathogens, and monitoring their spread could help instigate remediation strategies to combat the global spread of plant infectious diseases.

The majority of the studies on aerial dispersal of plant pathogens (phytopathogens) have primarily focused on fungi, since over a thousand species of fungi are responsible for 70% of all known plant diseases (Shi et al. 2016). Fungi form spores that can withstand adverse environmental conditions (Wainwright et al. 2003; Griffin 2004; Sterflinger et al. 2012), enabling them to survive long journeys through the atmosphere (Griffin et al. 2001; Prospero et al. 2005). Several species of fungi known to cause common plant diseases, such as leaf spot, rust, rot, wilt, inhibition of growth, black mold, and early blights, were identified in Asian and African dusts collected thousands of kilometers in sink environments (Yeo and Kim 2002; Kellogg et al. 2004; Wu et al. 2004; Ho et al. 2005; Griffin 2007; Kakikawa et al. 2008; Palmero et al. 2011; Grishkan et al. 2012; Smith et al. 2012). Brown and Hovmøller surveyed the global outbreaks of plant diseases caused by intercontinental dispersion of fungal spores and uncovered a number of fungal diseases that affected plantations of tobacco, coffee, banana, sugarcane, potato, wheat and cereal worldwide (Brown and Hovmoller 2002). Many species of the genus *Puccinia* with well-known long-range wind dispersion patterns are the causative agents of major crop disease outbreaks worldwide. Long distance dissemination of airborne *Puccinia* spores by winds, for example, were responsible for the crop stem rust in the North American continent (Eversmeyer and Kramer 2000), the wheat leaf rust in the Indian subcontinent (Nagarajan and Singh 1990), the sugarcane rust, stem rust, and stripe rust across different continents (Watson and De Sousa 1983; Purdy et al. 1985; Wellings and McIntosh 1990), and the loss of the cereal crops worldwide (Narayanasamy 2011). Other important fungal crop pathogens such as *Hemileia vastatrix* causing the coffee leaf rust (Bowden et al. 1971) and *Phakopsora pachyrhizi* causing the soybean rust (Pan et al. 2006) were introduced to North America by windborne dissemination from Africa and Asia, respectively. Since the long-range spread of crop diseases by pathogenic fungi could cause significant economic downturn and food insecurities globally, effective surveillance and management strategies are needed to halt the spread of infections (Mahaffee and Stoll 2016). Periodic monitoring of air with molecular approaches, such as quantitative PCR (qPCR) to identify specific pathogens and/or culture independent metagenomics to screen the entire airborne microbiota, are powerful tools that could be more commonly implemented to monitor and identify potential threats as early as possible (Nicolaisen et al. 2017). Early pathogen detection would enable implementation of well-informed disease management strategies to combat infections.

Studies on potential long distant aerial spread of plant pathogenic bacteria have not been as extensive as those of fungi. Although a large number of putative bacterial plant pathogens were found in regional and intercontinental dust samples (Griffin et al. 2001; Kellogg et al. 2004; Kakikawa et al. 2008; Chuvochina et al. 2011b; Munday et al. 2013), no evidence of a direct link between the long-range aerial transport of bacteria and the spread of plant infectious diseases has been found. The majority of well-known phytopathogenic bacteria, including *Agrobacterium*, *Xanthomonas*, *Pseudomonas*, *Erwinia*, *Clavibacter*, and *Rhodococcus* species (Francis et al. 2010; Mansfield et al. 2012), do not form endospores, which make them unlikely candidates for long distant transport, unless they possess other mechanisms for resisting adverse atmospheric conditions. Microorganisms can improve their viability in the atmosphere by acting as cloud condensation nuclei (CCN), which can help increase the relative humidity of their surrounding environment, and protect them against desiccation and harmful UV irradiation. The ability to form CCN potentially played a role in the long distant aerial spread of *Erwinia carotovora*, the causal agent of potato blackleg disease, from the source waters off the west coast of the United States (US) to inland destinations in Colorado (US), where the disease was prevalent (Franc 1994). *Pseudomonas syringae*, another known plant pathogen with the ability to act as CCN (Lindow et al. 1982), could use a similar strategy for long-range aerial transport and disease spread. The mechanisms involved in long distance aerial spread of phytopathogenic bacteria warrant closer examination in light of their potential ramifications on disease spread.

Unlike fungi and bacteria, plant viruses usually require vectors for transmission of infection. The main route for transmission of plant viruses is by means of insect vectors including aphids, whiteflies, leafhoppers, beetles, and many other insects (Maramorosch 1980; Agrios 2005; Ng and Perry 2004). Aphids are known to carry and spread a large diversity of viruses including the barley yellow dwarf viruses (BYDV) that affects wide varieties of cereal crops worldwide (Miller and Rasochova 1997; Hall et al. 2010). Plant viruses can also transmit infections by means of infected seeds and pollens (Mink 1993). Little is known about the potential long-range atmospheric transport of plant pathogenic viruses and disease transmission in sink environment, although large number of viral DNA sequences, in particular those belonging to plant associated viruses, have been found in the air (Whon et al. 2012). The identification of airborne plant viral DNA sequences does not necessarily indicate the presence of viable viruses that could transmit infection. Viral particles are particularly sensitive to lengthy exposure to desiccation, extreme temperatures, and UV irradiation (Prussin et al. 2014), and are extremely unlikely to remain viable during long-range atmospheric transport unless they are carried inside host vectors such as plant debris, pollen, bacteria, fungi, or insects. Before any decision can be made regarding the potential ramifications of aerial spread of viral plant pathogens on global agriculture, we need to acquire a more extensive knowledge of the airborne viral community structures, their role in the atmosphere, and the potential mechanisms involved in their viability, virulence, and spread throughout the atmosphere.

Perspectives

Our present knowledge of sandstorm microbiota is limited with regard to their diversity, function, and impact. The majority of our knowledge comes from culture-based studies. By many accounts, over 90% of environmental microbiota cannot be cultured in laboratories; also since microorganisms are grown in isolation in growth culture media, culture-based approaches cannot provide information on microbial community structures in their natural environments. This information is essential for understanding their potential impact on host ecosystems. Regardless of their potential limitations, these studies confirmed that a large number of viable microorganisms, including known and opportunistic human and plant pathogens, are transported via sandstorms (Kellogg and Griffin 2006; Vijayakumar et al. 2017). Culture-based approaches in their current state can only provide a small glimpse into sandstorm-associated microbial diversity and function, unless significant improvements are made to make it possible to grow the majority of environmental microbiota (Vester et al. 2015).

In recent years, with the advent and significant progress in culture-independent metagenomic approaches, we are beginning to realize the vast extent of microbial diversity spread via sandstorms. Table 1 provides a list of some of the most recent publications on dust and sandstorm microbiology, showing that culture independent metagenomics approaches are gaining momentum. As can be seen from the table, the majority of recent studies were conducted on Asian and African dust events, with a few focusing on Arabian and Australian dust storms. Endospore forming, stress resistant microorganisms were commonly found in dust samples from different studies. These studies, although promising, are limited in terms of number and scope, and in particular studies of viral metagenomics is noticeably lacking. Metagenomics could provide the ability to study the entire microbiota and their community composition through direct sequencing and characterization of environmental DNA without the need for prior cultivation. In this paper, we use the term metagenomics to denote both the targeted amplicons sequencing (TAS) and the whole-genome shotgun sequencing (WGS) approaches. Although metagenomics is frequently used in studies of microbiome from different environments, few studies have adopted it for microbial analysis of air and sandstorm samples (Behzad et al. 2015). Culture-independent phylogenetic studies using TAS revealed that surprisingly diverse microbial communities are transported by sandstorm; in particular those by Weil et al. (2017) who showed that a strong sandstorm originating from the Sahara Deserts in Africa deposited a large fraction of the entire desert microbiome to a pristine remote mountain in Italy. In order to understand "impact", we need to more fully characterize microbial diversity and function. Few of the published sandstorm metagenomic studies thus far have provided detailed phylogenetic analysis of sandstorm microbiota at species and strain levels, which is needed for determining the ecological significance and invasiveness/pathogenicity of these microorganisms. This could be due to the sole use of TAS, which is known for its low-resolution power amongst closely related species, sequencing errors, amplification biases, and inability to detect viruses (Hong et al. 2009; Quince et al. 2009; Quince et al. 2011; Wylie et al. 2012; Logares et al. 2014; Sharpton 2014). A more insightful approach, which is not commonly in practice in sandstorm research, is analysis of the entire microbial genomes in the environmental samples using WGS. This approach has significantly improved our understanding of microbial community structure, genes, and function in many environments including marine and soil (Simon and Daniel 2011) and would benefit sandstorm research. Although considerable advances in DNA sequencing platforms and bioinformatics analysis have been made in recent years, the approach still suffers from an inability to completely characterize the entire microbiota in environmental samples mainly due to: 1) inefficient assembly of the entire sample metagenome; and 2) inability to annotate a substantial fraction of these metagenomes since current databases lack representative sequences for many environmental microorganisms. Further improvements in air/dust sample collection (Behzad et al. 2015), DNA extraction methodologies, sequencing approaches and platforms, bioinformatics tools and software, and the availability of larger database of annotated environmental microbiota could help further advance sandstorm metagenomic research. A combined metagenomic and single cell genomic approach could also overcome the current shortcomings of metagenomics by improving the single cell genome and metagenome assembly and annotations (Lasken and McLean 2014). Metatranscriptomics, meta-proteomics, and metabolomics are other omic approaches rarely used in studies of sandstorm aeromicrobiology. The multi-omic approaches could help unravel not only the entire community and their genome makeup but also the functional and ecological significance of these microorganisms in their native environments and global biosphere.

In order to exert impact, DSM needs to survive the long journey across the atmosphere, and continue to remain viable and propagate in their new host ecosystems. On the subject of viability, current culture dependent and independent approaches do not provide accurate representation of the

Table 1
Culture Independent Metagenomic Approaches Are Increasingly Used in More Recent Studies to Detect DSM

Bacteria or Archaea	Fungi	Dust Source	Collection Site	Methods of Identification	Potential Impact	References
Actinobacteria; Bacteroidetes; Proteobacteria; Acidobacteria; Chloroflexi		Asian dust	Northern China	High throughput Metagenomics: 16S rRNA gene sequencing Bacterial abundance: DAPI staining	Human; Agriculture	(Tang et al. 2018)
Deinococcus-Thermus; Chloroflexi; Cyanobacteria; Gemmatimonadetes; Acidobacteria;		Sahara dust Syrian Saudi Arabia	Israel	High throughput Metagenomics: -16S rRNA gene sequencing Bacterial abundance: qPCR	Human	(Gat et al. 2017)
Geodermatophilus; *Bacillus*; *Deinococcus*; *Gemmatimonas;* *Arthrobacter*; *Nocardiodes*; *Rubrobacter*; *Solirubrobacter*	*Aurebasidium*; *Periconia*; *Pleosporaceae*; *Montagnulaceae*; *Embellisia;* *Davidiella*	Sahara dust	Dolomite Alps, Italy	High throughput Metagenomics: -16S rRNA gene sequencing -ITS1 region sequencing for fungi	Human; Agriculture	(Weil et al. 2017)
Dominated by *Bacillus* members		Asian dust	Noto Peninsula, Japan	High throughput Metagenomics: -16S rRNA gene sequencing	N/D	(Maki et al. 2017a)
	Fusarium; *Cladosporium*; *Ulocladium*; *Aspergillus*; *Alternaria*	Arabian dust	Saudi Arabia	Fungal culture	Human	(Vijayakumar et al. 2017)
Bacillus subtilis		Asian dust		Carbon nanotubes (SWCNTs)-based electrochemical biosensor	Human	(Yoo et al. 2017)
-Bacterial Quantity -Bacterial communities		Asian dust	Beijing, China	High throughput Metagenomics: -16S rRNA gene sequencing Bacterial abundance: qPCR	N/D	(Zhen et al. 2017)
Bacillus; Bacillus circulans; Modestobacter; Methylobacterium iners; *Sphingomonas starnbergensis*; *Micrococcus terreus*; *Rubellimicrobium roseum; Rubellimicrobium aerolatum*		Asian dust	Seoul, Korea	High throughput Metagenomics: -16S rRNA gene sequencing	Human	(Cha et al. 2017)
α-proteobacteria; Firmicutes *(Bacilli)*; Bacteroidetes		Asian dust	Mongolia	High throughput Metagenomics: -16S rRNA gene sequencing	N/D	(Maki et al. 2017b)

Gemmatimonadetes; *Adhaeribacter*; *Arthrobacter*; *Bacillus*; *Balneimonas*; *Cellulomonas*; *Geodermatophilus*; *Pontibacter*; *Rubellimicrobium*; *Rubrobacter*; *Sporosarcina*		Sahara dust	Eastern Mediterranean	High throughput Metagenomics: -16S rRNA gene sequencing	Human	(Mazar et al. 2016)
Bacteroidetes; Actinobacteria; Proteobacteria; Firmicutes; *Bacillus* spp.; *Rubellimicrobium* spp.; *Rubellimicrobium mesophilum; R. roseum*		Asian dust	Beijing, China	Culture indepepndent: -DGGE profile of 16S rRNA gene -16S rRNA gene clone library sequencing Bacterial abundance: qPCR	Human; Agriculture	(Yamaguchi et al. 2016)
Bacillus circulans; *Methylobacterium iners;* *Sphingomonas starnbergensis;* *Micrococcus terreus;* *Rubellimicrobium roseum;* *Rubellimicrobium aerolatum*		Asian dust	S. Korea	High throughput Metagenomics: -16S rRNA gene sequencing Bacterial abundance: qPCR	Human	(Cha et al. 2016)
Actinobacteria; Cyanobacteria Acidobacteria; *Bacilli*; γ-proteobacteria; β-proteobacteria; Clostridia; α-proteobacteria; *Deinococci*;		Asian dust	Osaka, Japan	High throughput Metagenomics: -16S rRNA gene sequencing Bacterial abundance: qPCR	N/D	(Park et al. 2016)
	Alternaria; Ulocladium; Aspergillus; Penicillium; Fusarium; Acremonium; Phoma	North Westerly dust	Kuwait	Fungal culture: -Morphology and culture traits -18s rRNA sequencing	Agriculture	(Al-Bader et al. 2016)
Bacillus spp.	*Mycosporium spp*	Arabian dust	Iran	Culture dependent	Human	(Nourmoradi et al. 2015)
Bacillus; Streptococcus; Lactococcus; Anoxybacillus; Corynebacterium; Brevundimonas; *Paracoccus; Sphingomonas;* *Methylobacterium; Caulobacter*	*Aspergillus* spp.	African dust	Sardinia, Italy	High throughput Metagenomics: -16S rRNA gene sequencing Culture dependent: -MALDI-TOF	Human	(Rosselli et al. 2015)
UV-tolerant culturable bacteria: Bacillales; Actinomycetales; Gram positive bacteria with high GC content		Asian dust	Over East China Sea	Culture dependent: -16S rRNA sequencing	N/D	(Hara et al. 2015)

(continued)

Table 1 Continued

Bacteria or Archaea	Fungi	Dust Source	Collection Site	Methods of Identification	Potential Impact	References
Massilia; Planococcus; Carnobacterium; Planomicrobium; Pontibacter; Pedobacter; Lysobacter; Sanguibacter; Ohtaekwangia		Asian dust	China; S. Korea	High throughput Metagenomics: -16S rRNA gene sequencing	Human	(An et al. 2014)
Gemmatimonadetes; Deinococcus-Thermus; Flavobacteriaceae; Chloroflexi; Cytophagaceae; *Oxalobacteriaceae; Comamonadaceae; Myxococcales; Janthinobacterium;* Neisseriaceae; *Neisseria; Streptococcus*		Sahara dust	Swiss Alps	High throughput Metagenomics: -16S rRNA gene sequencing Bacterial abundance: qPCR	Human	(Meola et al. 2015)
Cyanobacteria (*Synechococcus spp.);* Firmicutes (*B. subtilis, B. pumilus);* α-*proteobacteria* (SAR clade and *Sphingomonas* spp.)		Asian dust (Kosa)	Japan	Culture independent metagenomics: -16S rRNA gene clone library sequencing	Human; Animal; Agriculture	(Maki et al. 2014)
	Aspergillus sydowii	Australian dust	Australian coastal waters	Culture dependent: Molecular sequencing	Marine	(Hallegraeff et al. 2014)
α-proteobacteria; Actinobacteria; β-proteobacteria	Dothideomycetes; Tremellomycetes; Mitosporic Ascomycota	Europe; North Africa	Israel	High throughput Metagenomics: -16S rRNA; 18S rRNA sequencing	Human; Agriculture	(Katra et al. 2014)
γ-aproteobacteria; Bacilli;		Sahara dust	Lake Gossenköllesee Austrian Alps	Culture independent metagenomic: -16S rRNA gene clone library sequence In situ growth experiment Bacterial abundance: DAPI	Aqueous ecosystems	(Peter et al. 2014)
Actinobacteria; Bacteroidetes; Archaea: Thaumarchaeota		Sahara dust	Pyrenees, Spain	High throughput Metagenomics: -16S rRNA gene sequencing Microbial abundance: DAPI, FISH	Aqueous ecosystems	(Vila-Costa et al. 2013)
Proteobacteria; Firmicutes (*Bacillus, Sporosarcina)*		Sahara dust	South of Spain	Culture independent metagenomic: -16S rRNA gene clone library sequencing Culture dependent characterization	N/D	(Sánchez de la Campa et al. 2013)
Proteobacteria (Comamonadaceae; Pseudomonadaceae, Enterobacteriaceae); Actinobacteria (Corynebacteriaceae, Streptomycetaceae); Firmicutes (Bacillaceae, Lachnospiraceae,		Transpacific air plumes from Asia	Central Oregon, USA	Culture independent: -16S rRNA gene microarray	N/D	(Smith et al. 2013)

Staphylococcaceae, Streptococcaceae)						
Firmicutes-Bacillaceae; Actinobacteria-Geodermatophilaceae, Nocardiodaceae, Solirubrobacteraceae; Proteobacteria-Oxalobacteraceae, Rhizobiales, Sphingomonadaceae; Bacteroidetes-Cytophagaceae	Ascomycota; Basidiomycota; Chytridiomycota; Microsporidia; Glomeromycota	African dust	Chad, Africa; Cape Verde Islands	High throughput Metagenomics: -16S rRNA gene sequencing Microscopic structure: SEM Culture dependent characterization	Human; Animal; Agriculture	(Favet et al. 2013)
Actinobacteria; Firmicutes (*B. Subtillus*); Proteobacteria;		Asian dust (Kosa)	Mt. Tateyama, Japan	Culture dependent and independent: DGGE- 16S rRNA gene sequencing Physiological culture	Ecosystem; Human	(Maki et al. 2011)
Actinobacteria (*Crossiella cryophilus*); α-Proteobacteria (*Devosia limi*); Deinococcus Thermus (*D. claudionis*); Cyanobacteria (*Anabaena sp.*); Bacteroidetes (*Hymenobacter soli*)		Sahara dust	Mont Blanc glacier (French Alps)	Culture independent metagenomics: -16S rRNA gene clone library sequencing	Ecosystem	(Chuvochina et al. 2011a)
Firmicutes (Bacillus species); Actinobacteria; α-Proteobacteria; Planctomycetes; Deinococcus Thermus		Asian dust	Seoul, Korea	Culture dependent and independent: -DGGE profile of 16S rRNA gene -16S rRNA gene clone library sequencing	N/D	(Jeon et al. 2011)
Bacillus species; Pseudomonas species		Australian dust	Canberra and Melbourne (Australia)	Culture dependent: -DGGE- 16S rRNA sequencing	Human; Plant	(Lim et al. 2011)

Viruses	Dust Source	Collection Site	Methods of identification	Potential Impact	Reference
Wide diversity of DNA and RNA viruses shed from a range of hosts, including animals, arthropods, bacteria, fungi, humans, plants, and protists	Indoor dusts	Indoor	High throughput metagenomics: -Whole genome shotgun sequencing	Human; Animal; Plant	(Rosario et al. 2018)
ssDNA geminivirus-related viruses; circovirus-related sequences; nanoviruses; microphages-related genomes	Ambient air and rainwater samples	Seoul, Korea	High throughput metagenomics: -Whole genome shotgun sequencing Viral enumeration	Plant	(Whon et al. 2012)
Influenza A	Asian dust	Taiwan	Real time qPCR	Human	(Chen et al. 2010)

N/D: Not Determined.

percent-viability of DSM before and upon arrival in destination. Knowledge of microbial viability is essential for determining the spread and propagation of foreign, pathogenic or invasive microorganisms. The presence of DNA sequences belonging to pathogenic microorganisms in environmental metagenome does not necessarily indicate that the pathogen is alive and able to propagate. Culture dependent approaches could provide better metrics for assessment of viability but currently greater than 90% of environmental microbes cannot be cultured using standard culturing media. Dust samples contain diverse groups of microorganisms that propagate in different environmental conditions; whereas some microbes prefer standard conditioned media for growth, others have specific growth requirements that need to be met. A combination of culture dependent and independent methodologies could be employed to circumvent the shortcomings associated with either of the two approaches (Vester et al. 2015). Culturing requirements could be improved by using culture independent multi-omic approaches to obtain information on the complexity of the microbiota in dust samples and their metabolic needs; this information could then be used to design specific culture media formulations to improve percent cultivability of environmental microbiota (Gutleben et al. 2018). This would help resolve questions pertaining to viability, and also advance studies of microbial diversity and function in culture settings.

Since sandstorms are recurring events and their impacts potentially additive, time-series studies are needed to determine potential long-term ramifications of increased DSM transmission on the ecology of downwind ecosystems (Chuvochina et al. 2011b; Weil et al. 2017). These studies could establish microbial fingerprints of various environments and enable tracking variations in microbial patterns in response to different environmental changes, including sandstorms (Faust et al. 2015). Comparative analysis of microbiota and environmental metadata from source and destination environments could enable identification of influential variables, including invasive/pathogenic microorganisms, involved in ecosystem alterations. The ideal settings for such studies would be environments with minimal external influence, and reduced seasonal variability (Hervas et al. 2009; Mladenov et al. 2011).

Time series studies place particular demands on consistency and reproducibility of data since they typical involve collaboration among multiple laboratories. Such collaborations require standardized approaches to enable comparison of data collected across different time and space, by multiple laboratories. Metagenomic approaches are particularly sensitive to variability in methodology; metagenomic studies that use different approaches and protocols generate different outcomes concerning microbial quantity, diversity, and composition (Clooney et al. 2016). Currently there is no consensus within the field on best methodologies, or standardization between multiple laboratories. Standardized Operating

Protocols (SOP) would help unify the methodologies used by all the collaborators involved in the field. These SOPs require considerable investments of time and resources to develop and perfect; however, their use by wider research community could provide long-term benefits that could substantially advance DSM research. Collaborative work, in particular time-series studies, should address potential relationships between global climate changes, expansion of desertification, increased and widespread injection of DSM into downwind ecosystems, and their human health and ecological ramifications.

Conclusions

Dust activities are expected to rise globally due to climate changes and the rise in desertification caused by natural and anthropogenic events. This could lead to a substantial increase in transport of foreign, invasive, and potentially new pathogenic microorganisms that could alter equilibrium balance in downwind ecosystems, remodel pristine environments, and/or affect human and ecosystem health. Previous attempts to make concrete connections between DSM and human and environmental health concerns have been largely unsuccessful due to lack of substantive data. Inadequate knowledge of sandstorm microbiota limits our understanding of their broader significance. In recent years, TAS metagenomic studies have uncovered a large diversity of microbiota in dust clouds but the significance of these findings remains unknown due to the low-resolution power of TAS-based approaches. To gain a better insight into the phylogenetic diversity and functional and ecological significance of DSM, we recommend a combination of high-resolution strategies including WGS metagenomics, single cell genomics, and multiomic approaches in conjunction with improved culture-based methodologies. Given the increased prevalence of these highly stress resistant, diverse, and potentially pathogenic microorganisms in global atmosphere and downwind ecosystems, there is now a clear need for large-scale collaborative efforts to address potential relationships between the widespread injection of DSM in global atmosphere, ecosystem alterations, and global climate changes, through extensive ecological time-series studies.

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