



Review

Atmospheric transport and mixing of biological soil crust microorganisms

Steven D. Warren^{1,*} and Larry L. St. Clair²

¹ US Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, Utah, USA

² Brigham Young University, Department of Biology (Emeritus Professor) and M.L. Bean Life Science Museum (Emeritus Curator), Provo, Utah, USA

* **Correspondence:** Email: Steven.Warren@usda.gov.

Abstract: Biological soil crusts (BSCs) are created where a diverse array of microorganisms colonize the surface and upper few millimeters of the soil and create a consolidated crust. They were originally described from arid ecosystems where vascular vegetation is naturally sparse or absent. They have since been discovered in all terrestrial ecosystems. Where present, they perform a variety of important ecological functions, including the capture and accumulation of water and essential plant nutrients, and their release in forms useful to vascular plants. They also stabilize the soil surface against wind and water erosion. BSC organisms include fungi (free-living, lichenized, and mycorrhizal), archaea, bacteria (cyanobacteria and chemotrophic and diazotrophic bacteria), terrestrial algae (including diatoms), and bryophytes (mosses and worts). BSC organisms reproduce primarily asexually via thallus or main body fragmentation or production of asexual spores that are readily dispersed by water and wind. Asexual and sexual propagules of BSC organisms are commonly lifted into the air with vast quantities of dust from the world's arid areas. BSC organisms and/or their propagules have been detected as high as the stratosphere. Some have also been detected in the mesosphere. Airborne dust, microorganisms, and their propagules contribute to the formation of essential raindrop and snowflake nuclei that, in turn, facilitate precipitation events. While airborne in the atmosphere, they also reflect the sun's rays passing laterally through the troposphere and stratosphere at dawn and dusk, often causing brilliant colors at sunrise and sunset.

Keywords: aerobiology; fungi; archaea; bacteria; terrestrial algae; bryophytes; dust; ecological roles

1. Introduction

Biological soil crusts (BSCs) are comprised of diverse and highly integrated communities of microorganisms that effectively occupy and stabilize soil surfaces against the forces of wind and water erosion. Generally, their environmental parameters vary in soil chemistry, texture, and structure depending on the specific combination of organisms present and local environmental conditions. Organisms commonly comprising BSC communities include various combinations or subsets of fungi (free-living, lichenized, mycorrhizal), archaea, bacteria (cyanobacteria, and chemoheterotrophic and diazotrophic bacteria), terrestrial algae (including diatoms), and bryophytes (mosses and worts) [1]. BSCs and their component organisms have global distributions, occurring ubiquitously anywhere that aridity and/or disturbance have reduced vascular plant cover, but are best developed and recognized in arid and semiarid environments where competing vascular plant cover is naturally limited [2–4]. The composition and ecological functions of BSCs in arid environments have been well-documented, and are discussed below.

In soils with large and/or numerous pores, i.e., those with a sand content that exceeds ~80%, cyanobacteria, fungal hyphae, filamentous terrestrial algae, and root-like structures produced by lichenized fungi and bryophytes, and polysaccharide exudates produced by cyanobacteria and fungal hyphae tend to clog or obstruct soil pores, thus limiting water infiltration. However, in soils with a sand content of less than ~80%, BSC filaments, soil binding exudates, and roots and/or root-like structures contribute to the formation of stable soil aggregates, thus increasing the number and size of soil pores and, thereby, enhancing water infiltration, redistribution, and storage [5].

BSC organisms contribute to soil surface stability in three ways. First, the presence of larger and more vertical vegetative structures such as those produced by lichen and moss thalli tend to dissipate the kinetic energy of wind, falling raindrops, and surface flow of water, thus reducing the potential for soil erosion [6,7]. Second, even where such vegetative structures are absent, many BSC communities contribute to an irregular soil surface micro-topography that dissipates the velocity of wind and water flow. Third, BSCs contribute to the mechanical and chemical aggregation of soil particles, particularly in soils with finer texture. For example, bryophyte rhizoids, lichen rhizines, fungal hyphae, filamentous cyanobacteria and algae typically form a dense living mesh that stabilizes soil particles [8–10]. Extracellular polysaccharide exudates produced by some BSC organisms, particularly cyanobacteria, also contribute to the formation of soil aggregates. McCalla (1946) [11] was among the first to show that soil aggregates formed in association with bryophytes, algae, and fungi were more resistant to erosion by rainfall than aggregates formed through physical processes without the stabilizing influence of BSC organisms. Osborn (1952) [12] subsequently demonstrated that the occurrence of a cyanobacteria-dominated soil crust in deteriorated rangeland habitats significantly reduced splash erosion by raindrops. Furthermore, Osborn (1952) [12] showed that greater rainfall intensity was required to initiate splash erosion on crusts dominated by bryophytes and lichens than on cyanobacteria-dominated crusts or bare ground. The presence of BSC organisms significantly contributes to both the living cover and the irregular structure of the soil surface, thus causing water to pool on the surface of BSC dominated soils, and facilitating increased infiltration and subsequent storage of water in sub-surface soil pores [5].

BSC organisms also contribute to the accumulation, fixation, and processing of a variety of soil nutrients, ultimately making them available to the associated vascular plants [13]. For example, free-

living and symbiotic diazotrophic bacteria and archaea fix atmospheric nitrogen, some of which is subsequently taken up by vascular plants [14]. Photoautotrophic BSC organisms fix and store organic carbon while co-occurring prokaryotic decomposers and saprophytic fungi extract energy from decaying organic matter, and thus cycle carbon as CO₂ back into the atmosphere [15]. Essential micronutrients are also accumulated, stored, and released by BSC organisms [16,17], including Ca, Cu, Fe, K, Mg, Mn, Na, and Zn, among others [18]. The contributions of BSC organisms to the community-level availability of mineral nutrients is directly related to their capacity to bind with fine soil particles. Negatively charged clay particles, bind to the gelatinous sheaths and polysaccharide exudates produced by cyanobacteria as well as the hyphae of free-living and symbiotic fungi that, in turn, bind with and accumulate positively charged essential mineral nutrients [10]. The weathering of essential minerals from rock substrata is enhanced by the production and release of weak organic acids produced by some BSC organisms, particularly lichen mycobionts [19,20]. Polysaccharide exudates produced by cyanobacteria act as chelating agents, sequestering and releasing micronutrients [21,22]. Considered together, improved water infiltration into the soil profile, soil stabilization against the action of wind and water erosion, and the enhanced accumulation and availability of essential nutrients, combine to provide critical support for the establishment and survival of vascular plant seedlings [23–25]. Results may vary depending on the nature and timing of critical events and processes.

The various BSC microorganismal groups share several common characteristics, including tolerance to desiccation, extreme temperatures, and ultraviolet (UV) solar radiation, as well as production and excretion of various soil-binding chemistries, preferential utilization of asexual reproduction, a pattern of aerial dispersal over impressive global distances, and a universal vulnerability to various kinds of anthropogenic disturbances. Beyond those already described, BSC communities perform several other essential community level ecological functions, including the enhancement of vascular plant seed germination and seedling survival [26–28]. Many BSC organisms are photoautotrophic (e.g., cyanobacteria, eukaryotic algae, and bryophytes) which fix, accumulate, and distribute organic carbon in a variety of forms and in connection with various community-level processes. Other BSC groups (e.g., free-living and symbiotic diazotrophic bacteria and archaea) fix atmospheric nitrogen and release organic nitrogen into the soil environment.

In addition to arid environments where BSCs were originally described, they are also abundant in semiarid climates, particularly in vascular plant communities dominated by shrubs with significant inter-shrub spaces commonly occupied by BSC communities. Some BSC organisms, particularly bryophytes, also commonly occur beneath the shrub canopy [29,30]. This type of community structure minimizes competition for direct sunlight while generally providing for a more equitable distribution of other essential resources. Biological soil crusts are also known to occur on the sand dunes and beaches of both lakes and oceans [31–36]. They have been reported to occur on as mine spoils [37,38].

The authors of the present paper have each been involved in various aspects of BSC research for 40+ years each. However, beginning in 2018, they began a new line of investigation regarding aerobiology and passive restoration of BSC communities [39]. This adjustment in research direction was initiated with the intent of exploring answers to previously unanswered questions about how BSC propagules are effectively and broadly distributed across earth landscapes. There are interesting similarities in the taxonomic composition and diversity of BSC organisms in widely disparate geographic locations, including at bipolar, intercontinental, and interhemispheric scales. While BSCs have generally been reported from arid and semiarid habitats globally, the authors have observed or

collected BSCs throughout most of the United States, including Florida and Hawaii, which are seldom considered arid. They have also seen or collected them in Chile, England, Germany, and Iceland. They are also aware of collections from many other parts of the world that are neither arid nor semiarid. They finally arrived at the conclusion that BSC organisms are not limited to arid and semiarid environments. Indeed, they are geographically universal. However, how they are transported and distributed on a global scale is poorly understood – a question that is the focus of this paper. They have explored this question to a limited degree previously [1,39]. The intent with this paper is to address the issue in more detail by specifically exploring patterns and processes of aerial dispersal on a global scale. Some novel and poorly documented functions of BSC organisms are described in the following two sections.

2. Cloud condensation, raindrop, and ice nuclei

In 1978, a student from Montana, USA flew over a farm field collecting air samples while attempting to obtain samples of a bacterium that might also serve as cloud and ice nuclei while airborne. The idea lay dormant for 30+ years but has now reemerged. *Pseudomonas* and other microorganisms are now commonly recognized as cloud and ice nucleating agents [40]. BSC organisms and their propagules are now recognized for the critical role they play as cloud condensation nuclei, and raindrop and ice nuclei in the atmosphere [41–43]. Specifically, fungi [44,45], archaea [46], bacteria [47–49], algae [50,51], and bryophyte fragments [52] have been identified as frequent, viable contributors to cloud condensation and ice nucleation. Clouds form as moist air reaches a saturation point and condenses onto small solid airborne particles, thus forming tiny droplets that initiate cloud formation [53] eventually increasing in size until they fall as precipitation. In cold climates, bioaerosol particles serve as ice nuclei, contributing to the formation of snowflakes [54,55]. BSC organisms often reach the atmosphere with airborne dust and, in combination, they serve as condensation nuclei [57,58], as can pollen [59], smoke particulates [60–62], and sea salt aerosols [63–65]. The presence of condensation nuclei is essential, without which there would be no precipitation [66].

3. Aesthetics of airborne BSC organisms at dawn and dusk

Most of us, at one time or another, have noticed the colors of the sky at dawn and/or dusk. These color patterns result from the presence of dust, along with airborne microorganisms, and other particulates suspended in the atmosphere that scatters the sun's rays [67,68]. The process is referred to as Rayleigh scattering [69] where sunlight passes obliquely through the relatively thin (~50 km) band composing the troposphere and stratosphere where most dust and microorganisms accumulate. This effect often results in a variety of spectacular colors at sunrise and sunset [70–72]. Early in the morning and late in the evening, as the sun rises or sets, its rays traverse a much greater horizontal distance (hundreds or thousands of kilometers) than at mid-day when they traverse vertically only from the top of the stratosphere to the Earth's surface (a mere 50 km), encountering an abundance of solid atmospheric particles including dust and airborne microorganisms. As the distance increases, it is increasingly scattered [74] by concentrated airborne particles.

4. How BSC organisms become airborne

Biological soil crust organisms living at or near the soil surface are susceptible to being dislodged and subsequently suspended by wind [74–76]. Given their small size and minimal weight, they are easily suspended and transported. Because reproduction by BSC organisms is largely asexual [1], asexual spores and thallus fragments are even smaller and lighter. Laminar airflow over an unconsolidated soil surface can easily dislodge BSC organisms. As the wind encounters rocks, vegetation, and other surface features, turbulent airflow occurs, lifting BSC organisms and their reproductive propagules farther from the surface. Warm air rises, carrying the lightweight particles even higher. In arid areas, where BSCs often occur, dust devils, or tornadic bodies of rotating air, can lift dust and associated BSC organisms up to a height of 2 km [77]. All BSC organisms, once airborne, are ubiquitous or nearly ubiquitous inhabitants of the atmosphere, at least through the stratosphere, e.g., fungi [45,78], archaea [79,80], bacteria [81,82], algae [83,84], and bryophytes [85,86].

5. Characteristics of bioaerosols

Bioaerosols, or airborne microorganisms, collected from the Earth's atmosphere include essentially all groups of BSC organisms, including archaea, bacteria, fungi, algae, and bryophytes in the form of sexual and/or asexual propagules, including spores, group-specific specialized reproductive structures, or thallus fragments, all of which have been shown to regenerate viable organisms [87]. They include both unicellular and multicellular organisms that range in size from <1 µm and larger [88]. Given the small size and weight of BSC propagules, they are easily suspended and carried aloft by surface winds – depending on wind speed and air temperature parameters [88]. Airborne microorganisms have also been shown to pass through multiple generations while airborne [89].

Bioaerosols often accompany wind-eroded sediment from windstorms as reported from various parts of the world [90]. Dust and accompanying BSC organisms may be transported by wind on scales ranging from centimeters to thousands of kilometers, a process that has been ongoing for at least a millennium [91]. Primary sources of dust arriving in the mid-latitudinal United States are transported by western trade winds blowing from the Taklamakan and Gobi Deserts of China and Mongolia [92–94] via the Pacific Dust Express, so named by the National Aeronautics and Space Administration [95,96]. Dust originating in Asian deserts is deposited in western North America [97–99]. Dust and accompanying microorganisms arriving in the Caribbean and the southeastern United States generally originate from the east, specifically the Saharan Desert via the Saharan Air Layer [100–102].

Dust generally originates from arid landscapes and/or areas of disturbed or otherwise destabilized soil surfaces. Dust originating in the deserts of Northern Africa routinely arrives in the Caribbean and southeastern United States, bringing with it an impressive array of bacterial and fungal propagules [103,104]. At a conservative estimate of 10,000 microorganisms per gram of soil, that would be equivalent to 10 quadrillion microbes. While UV radiation from the sun may kill some microbes during the 5–7 day journey across the Atlantic Ocean, a huge number makes landfall in the Americas [103]. Worldwide, billions of tons of dust and vast numbers microorganisms are aerosolized

each year [105]. Dust storms from different parts of the world transport unique microbial communities [106].

Dust storms and sandstorms also carry billions of microbes that come from harsh environments and survive the stressful journey of thousands of kilometers through the troposphere [107]. Airborne dust commonly originates in all arid areas of Earth. In addition to the Asian and Saharan Deserts, dust is commonly reported from the North American arid areas of the Mojave, Sonoran, Chihuahuan, and Great Basin Deserts [108,109], the Namib Desert of southwestern Africa [110], the Great Victoria Desert of Australia [111], the Atacama Desert of western South America [112,113], and interior Antarctica [114,115].

6. Reproduction of BSC organisms

Warren et al. (2019b) [1] reported that while specific modes of reproduction vary between BSC organisms, many groups demonstrate both sexual and asexual reproductive patterns. Asexual processes such as fission, cloning, budding, mitotic cell division, formation of specialized asexual spores, and thallus fragmentation represent the most common reproductive approaches across BSC organismal groups. Asexuality among BSC organisms is not a negative alternative to sexual reproduction. Indeed, asexually reproducing microbial communities are known to reproduce successfully even at low population densities, while also demonstrating impressive potential for both diversity and rarity [116]. BSC prokaryotes and eukaryotes with dominant haploid generations, readily express genetic variation through mutations, thus providing the genetic raw material essential for developing potentially valuable adaptations through natural selection. Eukaryotic BSC organismal groups commonly reproduce a variety of both sexual and asexual propagules. Sexual reproductive cycles among eukaryotic BSC organisms follow a basic pattern involving alternation of haploid and diploid generations with a wide variety of group specific patterns. Cycling between haploid and diploid generations is accomplished by the meiotic division of the diploid generation followed by the fusion of sex cells produced mitotically by the haploid generation. Among eukaryotic BSC organisms, in addition to mutations, meiosis also produces a significant source of genetic variation through generic recombination essential for the evolution of useful adaptations by natural selection. Almost exclusively, BSC reproductive propagules (both sexual and asexual) are dispersed aerially, often over impressive distances [117] – between countries, climates, continents, hemispheres, and poles.

7. Atmospheric structure

The Earth's atmosphere is organized conceptually by the National Aeronautics and Space Administration (NASA) and the global astrophysicist community into multiple concentric regions or layers based on approximate distances from the Earth's surface, i.e., the troposphere, stratosphere, mesosphere, thermosphere, and exosphere (https://www.nasa.gov/mission_pages/sunearth/science/atmosphere-layers2.html). The troposphere, the first atmospheric layer, extends from the Earth's surface up to approximately 12 km. Most weather phenomena, including convection, turbulence, and clouds occur in the troposphere layer, although some phenomena may extend into the next layer or lower stratosphere. Generally, bands of circumpolar trade winds in the troposphere occur between 30 °north and 30 °south latitudes, straddling the equator, and blow from east to west. As those winds reach 30 ° north or south latitude, they are

affected by the Coriolis force [118], a phenomenon related to the rotational pattern of the planet that causes the winds to reverse direction between 30 ° and 60 ° north or south latitudes. The winds reverse again between 60 ° north and south latitude and the respective poles. The trade winds derive their name from the role they played in intercontinental commercial trade via windblown sailing ships on the world's oceans many years ago. Jet streams generally occur in the tropopause, the boundary layer between the top of the troposphere and the bottom of the stratosphere; they are meandering air currents reaching speeds of 110+ mph (177+ kph) (<https://scijinks.gov/jet-stream/>). They generally blow from west to east, and meander between continents and hemispheres. Air temperatures in the troposphere generally decline with altitude.

The next atmospheric layer is the stratosphere. It is located above troposphere, beginning at about 12 km and extending to approximately 50 km above the Earth's surface. The stratosphere is minimally susceptible to vertical mixing, and lies in horizontal strata, hence the name *stratosphere*. Wind speeds in the stratosphere can reach 220 km per hour (130 mph). Occasionally, tropospheric and the stratospheric air-masses mix, particularly when strong Polar-night Jet Oscillations correspond to the strong downward movement of stratospheric air-masses, typically associated with significant increases in stratospheric ozone levels [119]. Due to low humidity conditions, there are generally few clouds in the stratosphere. There are no storms or turbulence there to mix the air, so cold, heavy air is at the bottom of the layer and warm, lighter air is at the top. The stratosphere is perhaps most noteworthy for the presence of the ozone layer located about 25 km above the Earth's surface. This is the layer where approximately 90% of atmospheric ozone is concentrated. The ozone layer absorbs much of the solar ultra-violet (UV) radiation from the sun and protects life on Earth from the harmful effects associated with prolonged exposure to UV radiation.

Above the stratosphere is the mesosphere. It begins at about 50 km altitude and extends to about 80 km above the Earth's surface. The mesosphere is the coldest atmospheric layer. At the top of the mesosphere, the temperature falls to a low of -90 °C. Most meteors approaching the Earth's surface from outer space vaporize in this layer. Knowledge about the mesosphere is limited due to accessibility issues associated with sampling methods.

Above the mesosphere is the thermosphere which begins at about 80 km altitude and ends at about 700 km altitude. As the name implies, temperatures in the thermosphere are very hot, reaching 2,000 °C or higher. The northern and southern lights, or aurora borealis and aurora australis, respectively, occur in the thermosphere as charged particles (electrons) collide with oxygen and nitrogen molecules, exciting them to higher energy states and emitting photons or light (https://pwg.gsfc.nasa.gov/polar/telecons/archive/PR_E-PO/Aurora_flyer/aurora-flyer_p2.doc.pdf).

The exosphere is the outermost layer of the atmosphere, beginning at about 700 km altitude and ranging up to about 1000 km above the Earth's surface. This atmospheric layer serves as the transition zone between the Earth's atmosphere and outer space, and reaches temperatures of up to 1,700 °C. Only the lightest gases occur in the exosphere, i.e., helium, hydrogen, traces of carbon dioxide, and elemental oxygen. The density of the exosphere is so low that it is difficult to determine where this layer ends and outer space begins.

8. The occurrence of BSC organisms in the atmospheric layers

The atmosphere is considered by some to be the ‘last extreme environment’, due in large part to temperature extremes and high levels of ultraviolet radiation particularly in the upper portions of the earth’s atmosphere [120]. Nevertheless, biological material is considered universally present in the atmosphere [121]. All groups of BSC microorganisms have been found as airborne propagules up to at least the mid-stratosphere [84,122,123]. Although diverse groups of bacteria and fungi have been collected from the troposphere [124], they have also been collected from a wide range of elevations in the stratosphere over India using hot air balloons [125]. The density of microbes in the troposphere varies little between the lower troposphere ($2\text{--}5 \times 10^5$ cells/m³) and the tropopause (1×10^6 cells/m³), but declined to 8×10^4 cells/m³ in the stratosphere at 35–38 km altitude [126]. Chen et al. (2012) [127] measured airborne microorganisms near ground level in Guangzhou, China during the summer and found markedly greater concentrations of bacteria than of fungi. Spores of two strains of yeast (fungi) from a high elevation site in the Atacama Desert survived stratospheric balloon flights into the upper stratosphere (severe desiccation, low atmospheric pressure, low temperature, and high UV exposure) [128]. Viable bacteria and fungi are also reported to occur in a stratospheric transoceanic bridge between Asia and North America [78,129]. Bacterial taxa collected from below and above the tropopause, an area corresponding to the upper tropospheric and lower stratospheric layers of the atmosphere, were highly similar [130]. When exposed to conditions typical of the upper stratosphere - including reduced atmospheric pressure, low temperatures, extreme desiccation, and high levels of UV radiation, 99.9% of *Bacillus subtilis* spores were killed [131]. Nicholson et al. (2000) [132] reported similar results. In contrast, bryophytes propagules have been shown to tolerate all extraterrestrial stresses except for UV radiation [133], suggesting that UV radiation may be the critical factor limiting global atmospheric transport of BSC propagules [131]. The ozone layer is located in the mid-stratosphere and serves to attenuate most UV radiation, suggesting that the possibility of viable bacteria occurring above that layer is unlikely. However, at least some species of lichens have been shown to survive UV exposure [134]. A number of studies have demonstrated the presence of both bacteria and fungi in the stratosphere. It is likely that bacteria can survive conditions in the upper stratosphere [135], although it is not clear if the samples were collected above or below the ozone layer [136]. Moist vegetative shoots of three or four species of bryophytes have been shown to survive after two hours in the harsh conditions of the stratosphere while showing initial stages of regeneration, suggesting the potential for wide-range aerial dispersal by bryophytes [137].

9. Biosphere

The biosphere defines the physical and functional limits of life on Earth and was originally thought to have an upper atmospheric limit of about 12 km above the Earth’s surface, thus within the troposphere. The biosphere likely originated billions of years ago and included ancient prokaryotes such as bacteria and archaea, all capable of surviving without molecular oxygen. Over time, some groups of prokaryotes likely evolved the capacity to use sunlight to synthesize simple sugars by extracting hydrogen from water and carbon and oxygen from carbon dioxide, and subsequently releasing the oxygen from the water into the atmosphere as O₂. These photosynthetic prokaryotes were abundant, and over time, changed the chemical environment of the biosphere by contributing a

significant amount of molecular oxygen to the atmosphere – a condition that ultimately resulted in conditions suitable for sustaining new and more complex forms of life on the Earth. Recently, the vertical dimensions of the biosphere have been reevaluated and some have suggested that those portions of the atmosphere protected by the ozone layer of the stratosphere may also be part of the biosphere [138]. As exploration of the stratosphere above the ozone layer and into the mesosphere has increased, a growing number of viable airborne microorganisms have been collected and identified from the upper stratosphere and lower mesosphere [135,139]. It has been suggested that the dark pigments in cells from these parts of the atmosphere could protect resident cells from the harmful effects of UV radiation [140].

After being exposed for 2 weeks to Mars-like conditions (severe desiccation, high UV radiation, and temperature extremes) on the surface of an Earth-orbiting FOTON-M2 Russian satellite, dormant lichens were found to have remained dormant, with no ultrastructural changes in either symbiont, and thalli generally remaining viable as measured by chlorophyll fluorescence [141]. The International Space Station (ISS) orbits the Earth at approximately 400 km (250 mi) above the Earth, within the thermosphere (85–690 km). Dust samples collected from the ISS have been stored for 12 years, and still contain viable bacteria and fungi [142], suggesting the possibility of extraterrestrial BSC organisms. Cosmic dust samples were collected from the surface of the ISS by a crew member during a spacewalk. These samples were subsequently analyzed for bacterial DNA and a gram-negative bacterium of the genus *Delfia* was identified. This bacterium was genetically similar to a gram-negative bacillus collected in surficial microlayers from the Barents and Kara sea coastal zones in Russia [143].

10. Ozone hole

In 1957, the British Antarctic Survey began to monitor ozone levels at the Halley Bay ground station in Antarctica with the intent of better understanding ozone concentrations at ground level and in the atmosphere above the station. Since the mid-1970s, NASA has used satellites to monitor atmospheric ozone. In 1985, scientists first reported what they assumed was a ‘hole’ or a depleted area in the ozone layer of the stratosphere over the South Pole [144–146]. That discovery led to worldwide panic, with fears of high levels of skin cancer in humans caused by increased UV radiation associated with depletion of the ozone layer. Consequently, the global ‘Montreal Protocol on Substances That Deplete the Ozone Layer’ was signed in 1987, phasing out the production and use of chlorofluorocarbons (CFCs) and halons that were thought to be the leading causes of ozone depletion. A subsequent decline of 98% in the production and use of ozone depleting substances was correlated with a reversal of the depletion pattern associated with the hole in the ozone layer over Antarctica [148]. However, at least part of the ozone layer depletion pattern may be attributed to a significant relationship with the polar vortex, as a longer, stronger, and later breakup time of the polar vortex each year has also been connected to ozone depletion [148].

An opportunity exists to research the consequences of a reduced ozone layer by studying the impact of increasing levels of UV radiation on BSC organisms *in situ*. Due to the ‘ozone hole’ in the stratosphere above Antarctica, scientists have been investigating the impact of increasing UV levels on various life forms, including BSC organisms. Initial results showed that many of the organisms have adapted by developing a cryptoendolithic growth habit [149], increasing the production of

enzymatic antioxidants [150], and producing UV-absorbing/screening pigments and carotenoids [151–153]. Some BSC organisms have also been shown to reduce UV impact through the formation of clumps or aggregates [154]. Some BSC organisms have evolved adaptations to counteract the negative effects of increased exposure to ultraviolet radiation by (1) moving vertically up or down in the substrate column to avoid stressful exposure to UV radiation, and (2) evolving molecular repair mechanisms in situations where UV exposure is unavoidable [155]. Whether these adaptations arose before or after the discovery of the ozone hole is unknown, but the issue does raise questions about whether the ozone hole is strictly a recent phenomenon. Some have suggested that the ozone hole is a Black Swan event, i.e., a rare, improbable, and unpredictable outlier event [156,157]. Indeed, it seems several important questions remain unanswered. First, and most relevant to this paper, are questions about whether the UV-related defensive adaptations employed by BSC organisms and other microorganisms are new or have existed for millennia. Second, is the question of whether the first appearance of the ozone hole was truly novel, or whether it was a recurring phenomenon that grew and subsided regularly on a time scale much longer than modern humankind can imagine.

Regardless of the answers to these questions, while the Antarctic ozone hole is shrinking, possibly due to implementation of the Montreal Protocol, a large hole recently opened in the Arctic, possibly caused by cold temperatures and the strong vortex at the North Pole [158]; <https://science.nasa.gov/nasa-reports-arctic-stratospheric-ozone-depletion-hit-record-low-march>). This, plus the fact that the Arctic ozone layer appears to thin at least once per decade, seems to call into question the previously reported rationale for the human-related cause of the Antarctic ozone hole. It is quite possible that the occurrence and strength of the polar ozone layer is strongly influenced by the polar vortex [148].

11. Conclusion

Biological Soil Crusts (BSCs) occur where small, often microscopic, living organisms occupy and stabilize the upper few millimeters of the soil. First recognized and described in arid areas, they have since been identified globally, wherever aridity and/or physical disturbance have left at least portions of the soil surface bare. Biological organisms associated with BSCs typically include archaea, bacteria (cyanobacteria, and chemoheterotrophic and diazotrophic bacteria), fungi (free-living, lichenized, and mycorrhizal), and bryophytes (mosses and worts). They provide essential ecological services including soil stabilization against wind and water erosion, and the acquisition, distribution, and storage of soil water and essential nutrients used by vascular plants. From where and how they are transported to viable habitats raises important questions seldom seriously considered by BSC aficionados. BSC organisms are readily dislodged from arid or disturbed soil surfaces. BSC organisms are transported globally via trade winds in the troposphere (150 – 900 m altitude) and jet streams in the tropopause (6,000 – 15,000 m altitude) and are subsequently deposited globally. Most airborne organisms reproduce asexually via asexual spores, thallus fragments, specialized reproductive structures generated by fission/budding and mitotic cell division among eukaryotic groups. Most airborne propagules are accompanied by windborne dust from distant locales such as the Saharan and Asian deserts, and other arid regions around the world. Together, the microorganisms and dust particles play an essential role as cloud and condensation nuclei, without which precipitation as rain or snow

would be eliminated. The particles also play a critical role in scattering the sun's rays to create colorful sunrises and sunsets.

Acknowledgments

This research was supported in part by the USDA Forest Service, Rocky Mountain Research Station. The findings and conclusions in this publication are those of the author(s) and should not be construed to represent any official USDA or U.S. government policy.

Conflict of interest

All authors declare no conflicts of interest in this paper.

References

1. Warren SD, Clair LLS, Stark LR, et al. (2019) Reproduction and dispersal of biological soil crust organisms. *Frontiers in Ecology and Evolution* 7: 344.
2. Warren SD Ecological role of microphytic soil crusts in arid ecosystems[C]//Microbial diversity and ecosystem function: proceedings of the IUBS/IUMS Workshop held at Egham, UK, 10–13 August 1993. CAB INTERNATIONAL, 1995: 199–209.
3. Belnap J, (2013) Biological soil crusts: structure, function, and management. Berlin: Springer Science & Business Media.
4. Belnap J, Weber B, Büdel B (2016) Biological soil crusts as an organizing principle in drylands. Biological soil crusts: an organizing principle in drylands. Springer, Cham. 3–13.
5. Warren SD (2001) Synopsis: influence of biological soil crusts on arid land hydrology and soil stability. Biological soil crusts: Structure, function, and management. Springer, Berlin, Heidelberg. 349–360.
6. Belnap J, (2001) Biological soil crusts and wind erosion. Biological soil crusts: Structure, function, and management. Springer, Berlin, Heidelberg, 339–347.
7. Fick SE, Barger N, Tatarko J, et al. (2020) Induced biological soil crust controls on wind erodibility and dust (PM₁₀) emissions. *Earth Surf Proc Land* 45: 224–236.
8. Tisdall JM, OADES JM (1982) Organic matter and water-stable aggregates in soils. *J Soil Sci* 33: 141–163.
9. Schulten JA (1985) Soil aggregation by cryptogams of a sand prairie. *Am J Bot* 72: 1657–1661.
10. Belnap J, Gardner JS (1993) Soil microstructure in soils of the Colorado Plateau: the role of the cyanobacterium *Microcoleus vaginatus*. *Great Basin Nat* 1993: 40–47.
11. McCalla TM (1946) Influence of some microbial groups on stabilizing soil structure against falling water drops. *Soil Sci Soc Am Pro* 11: 260–263.
12. Osborn B (1952) Range soil conditions influence water intake. *J Soil Water Conserv* 7: 128–132.
13. Gao GL, Ding GD, Wu B, et al. (2014) Fractal scaling of particle size distribution and relationships with topsoil properties affected by biological soil crusts. *Plos One* 9: e88559.
14. Weber B, Wu D, Tamm A, et al. (2015) Biological soil crusts accelerate the nitrogen cycle through large NO and HONO emissions in drylands. *Proc Natl Acad Sci* 112: 15384–15389.

15. Elbert W, Weber B, Burrows S, et al. (2012) Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nat Geosci* 5: 459–462.
16. Loope WL, Gifford GF (1972) Influence of soil microfloral crust on select properties of soils under pinyon-juniper in southwestern Utah. *J Soil Water Conserv* 17: 164–167.
17. Kleiner EF, Harper KT (1972) Environment and community organization in grasslands of Canyonlands National Park. *Ecology* 53: 299–309.
18. Harper KT, Pendleton RL (1993) Cyanobacteria and cyanolichens: can they enhance availability of essential minerals for higher plants? *Great Basin Nat* 53: 59–72.
19. Metting B, (1991) Biological soil features of semiarid lands and deserts. Pages 257–293 in Skujiņš J [ed.] Semiarid lands and deserts. Marcel Dekker: New York.
20. Edwards HGM, Villar SEJ, Seaward MRD, et al. 2004. Raman spectroscopy of rock biodeterioration by the lichen *Lecidea tessellata* Flörke in an arid desert environment, Utah, USA, 229–240, In St. Clair LL, Seaward MRD (Eds.), Biodeterioration of Stone Surfaces: Lichens and Biofilms as Weathering Agents of Rocks and Cultural Heritage. Dordrecht, the Netherlands: Kluwer Academic Publishers.
21. Lange W (1974) Chelating agents and blue-green algae. *Can J Microbiol* 20: 1311–1321.
22. Lange W (1976) Speculations on a possible essential function of the gelatinous sheath of blue-green algae. *Can J Microbiol* 22: 1181–1185.
23. St Clair, LL, Well BL, Johansen JR, et al. (1984) Cryptogamic soil crusts: enhancement of seedling establishment in disturbed and undisturbed areas. *Reclam Reveg Res* 3: 129–136.
24. Li XR, Jia XH, Long LQ, et al. (2005) Effects of biological soil crusts on seed bank, germination and establishment of two annual plant species in the Tengger Desert (N China). *Plant Soil* 277: 375–385.
25. Zhang Y, Arad ótir AL, Serpe M, et al. (2016) Interactions of biological soil crusts with vascular plants. Chapter 19 in Belnap J, Weber B and Büdel B. [Eds.] Biological soil crusts: an organizing principle in drylands, Ecological studies 226. Springer: Cham, Switzerland.
26. Deines L, Rosentreter R, Eldridge DJ, et al. (2007) Germination and seedling establishment of two annual grasses on lichen-dominated biological soil crusts. *Plant Soil* 295: 23–35.
27. God ónez-Alvarez H, Mor ón C, Rivera-Aguilar V (2012) Germination, survival and growth of three vascular plants on biological soil crusts from a Mexican tropical desert. *Plant Biology* 14: 157–162.
28. Song G, Li X, Hui R (2017) Effect of biological soil crusts on seed germination and growth of an exotic and two native plant species in an arid ecosystem. *PLoS One* 12: e0185839.
29. Warren SD, St Clair LL, Johansen JR, et al. (2015) Effects of prescribed fire on biological soil crusts in a Great Basin juniper woodland. *Rangeland Ecol Manage* 68: 241–247.
30. Warren SD, Rosentreter R, Pietrasiak N (2020) Biological soil crusts of the Great Plains. *Rangeland Ecol Manage* in press
31. Smith SM, Abed RMM, Gercia-Pichel F (2004) Biological soil crusts of sand dunes in Cape Cod National Seashore, Massachusetts, USA. *Microbial Ecol* 48:200–208.
32. Thiet RK, Boerner REJ, Nagy M, et al. (2005) The effect of biological soil crusts on throughput of rainwater and N into Lake Michigan sand dune soils. *Plant Soil* 278: 235–251.

33. Zellman KL (2014) Changes in vegetation and biological soil crust communities on sand dunes stabilizing after a century of grazing on San Miguel Island, Channel Islands National Park, California. *Monogr West N Am Naturalist* 7: 225–245.
34. Schulz K, Mikhailyuk T, Dreßler M, et al. (2016) Biological soil crusts from coastal dunes at the Baltic Sea: cyanobacterial and algal biodiversity and related soil properties. *Microbial Ecol* 71: 178–193.
35. Mikhailyuk T, Glaser K, Tsarenko P, et al. (2019) Composition of biological soil crusts from sand dunes of the Baltic Sea coast in the context of an integrative approach to the taxonomy of microalgae and cyanobacteria. *Eur J Phycol* 54: 263–290.
36. Schaub I, Baum C, Schumann R, et al. (2019) Effects of an early successional biological soil crust from a temperate coastal sand dune (NE Germany) on soil elemental stoichiometry and phosphatase activity. *Microbial Ecol* 77: 217–229.
37. Shubert LE, Starks TL (1980) Soil-algal relationships from surface mined soils. *Brit Phycol J* 15: 417–428.
38. Spröte R, Fischer T, Veste M, et al. (2010) Biological topsoil crusts at early successional stages on Quaternary substrates dumped by mining in Brandenburg, NE Germany. *Geomorphologie* 16: no. 4
39. Warren SD, Clair LLS, Leavitt SD (2019) Aerobiology and passive restoration of biological soil crusts. *Aerobiologia* 35: 45–56.
40. Evans Ogden L (2014) Life in the clouds. *BioScience* 64: 861–867.
41. Bowers RM, Lauber CL, Wiedinmyer C, et al. (2009) Characterization of airborne microbial communities at a high-elevation site and their potential to act as atmospheric ice nuclei. *Appl Environ Microb* 75: 5121–5130.
42. Delort A M, Vařilingom M, Amato P, et al. (2010) A short overview of the microbial population in clouds: in atmospheric chemistry and nucleation processes. *Atmos Res* 98: 249–260.
43. Fan J, Leung LR, Rosenfeld D, et al. (2017) Effects of cloud condensation nuclei and ice nucleating particles on precipitation processes and supercooled liquid in mixed-phase orographic clouds. *Atmos Chem Phys* 17: 1017–1035.
44. Hassett MO, Fischer MWF, Money NP (2015) Mushrooms as rainmakers: how spores act as nuclei for raindrops. *PloS One* 10(10): e0140407.
45. Woo C, An C, Xu S, et al. (2018) Taxonomic diversity of fungi deposited from the atmosphere. *The ISME J* 12: 2051–2060.
46. Fröhlich-Nowoisky J, Kampf CJ, Weber B, et al. (2016) Bioaerosols in the Earth system: Climate, health, and ecosystem interactions. *Atmos Res* 182: 346–376.
47. Bauer H, Giebl H, Hitzenberger R, et al. (2003) Airborne bacteria as cloud condensation nuclei. *J Geophys Res: Atmos* 108(D21).
48. Morris CE, Georgakopoulos DG, Sands DC (2004) Ice nucleation active bacteria and their potential role in precipitation. *J de Physique IV Fr* 121: 87–103.
49. Lazardis M (2019) Bacteria as cloud condensation nuclei (CCN) in the atmosphere. *Atmosphere* 10: 786.
50. K Sharma N, K Rai A, Singh S (2006) Meteorological factors affecting the diversity of airborne algae in an urban atmosphere. *Ecography* 29: 766–772.

51. Tesson SVM, Šantl-Temkiv T (2018) Ice nucleation activity and aeolian dispersal success in airborne and aquatic microalgae. *Front Microbiol* 9: 2681
52. Wynn-Williams DD (1990) Ecological aspects of Antarctic microbiology. Chapter 3 in Marshall, K.C. [Ed], *Advances in Microbial Ecol* 11. Plenum Press: New York
53. Byers HR (1949) Condensation nuclei and precipitation. *J Meteorolo* 6: 363.
54. Christner BC, Morris CE, Foreman CM, et al. (2008) Ubiquity of biological ice nucleators in snowfall. *Science* 319: 121465.
55. Moffett BF (2015) Ice nucleation in mosses and liverworts. *Lindbergia* 38: 14–16.
56. Georgia Institute of Technology (2011) Cloud formation: insoluble dust particles can form cloud droplets that affect global and regional climate. ScienceDaily 13 Oct 2011. www.sciencedaily.com/releases/2011/10/111013113814.html
57. Karydis VA, Kumar P, Barahona D, et al. (2011) On the effect of dust particles on global cloud condensation nuclei and cloud droplet number. *J Geophys Res* 116: D23204.
58. Kerminen VM, Paramonov M, Anttila T, et al. (2012) Cloud condensation nuclei production associated with atmospheric nucleation: a synthesis based on existing literature and new results. *Atmos Chem Phys* 12: 12037–12059.
59. Pope FD (2010) Pollen grains are efficient cloud condensation nuclei. *Environ Res Lett* 5: 044015.
60. Holle RL (1971) Effects of cloud condensation nuclei and surface sources during south Florida droughts. *J Appl Meteorol* 10: 62–69.
61. Kobziar LN, Pingree MRA, Larson H, et al. (2018) Pyroaerobiology: the aerosolization and transport of viable microbial life by wildland life. *Ecosphere* 9: article e02507.
62. Mirskaya E, Agranovski IE (2020) Generation of viable bacterial and fungal aerosols during biomass combustion. *Atmosphere* 11: 313.
63. Orellana MV, Matrai PA, Leck C, et al. (2011) Marine microgels as a source of cloud condensation nuclei in the high Arctic. *Proc Natl Acad Sci* 108: 13612–13617.
64. Sanchez KJ, Chen CL, Russell LM, et al. (2018) Substantial seasonal contribution of observed biogenic sulfate particles to cloud condensation nuclei. *Sci R* 8: 3235.
65. Jiang B, Wang D, Shen X, et al. (2019) Effects of sea salt aerosols on precipitation and upper troposphere / lower stratosphere water vapour in tropical cyclone systems. *Sci R* 9: 15105.
66. Sheil D (2018) Forests, atmospheric water and an uncertain future: the new biology of the global water cycle. *Forest Ecosyst* 5: article 19.
67. Reguera, G. 2012. The colors of the microbial rainbow. <https://schaechter.asmblog.org/schaechter/>
68. Pointing S (2019) Microbes connect the earth, sea and sky. Nature Research: Microbiology: 21 Nov. <https://go.nature.com/2KFhB>
69. Zagury F (2012) The color of the sky. *Atmos Climate Sci* 2: 510–517.
70. University of Wisconsin-Madison. 2007. What determines sky's colors at sunrise and sunset? ScienceDaily, <https://www.sciencedaily.com/releases/2007/11/071108135522.htm>
71. Fiegl A (2013) Red sky at night: the science of sunsets. National Geographic <https://www.nationalgeographic.com/news/2013/10/131027-sunset-sky-change-color-red-clouds-science/>
72. Corfidi SK (2014) The colors of sunset and twilight. <https://www.spc.noaa.gov/publications/corfidi/sunset/>

73. Ballantyne C (2007) Fact or fiction?: Smog creates beautiful sunsets. *Sci Am* 12 July 2007.
74. Gardner T, Acosta-Martinez V, Calderón FJ, et al. (2012) Pyrosequencing reveals bacteria carried in different wind-eroded sediments. *J Environ Qual* 41:744–753.
75. Abed RMM, Ramette A, Hübner V, et al. (2012) Microbial diversity of eolian dust sources from saline lake sediments and biological soil crusts in arid Southern Australia. *Fems Microbiol Ecol* 80: 294–304.
76. Elliott DR, Thomas AD, Strong CL, et al. (2019) Surface stability in drylands is influenced by dispersal strategy of soil bacteria. *J Geophys Res: Biogeosciences* 124: 3403–3418.
77. Ives RL (1947) Behavior of dust devils. *Bulletin American Meteorological Society* 28: 168–174
78. Smith DJ, Griffin DW, Schuerger AC (2010) Stratospheric microbiology at 20 km over the Pacific Ocean. *Aerobiologia* 26: 35–46.
79. DasSarma P, Laye VJ, Harvey J, et al. (2016) Survival of halophilic Archaea in Earth's cold stratosphere. *Int J Astrobiology* 16: 321–327.
80. DasSarma P, DasSarma S (2018) Survival of microbes in Earth's stratosphere. *Curr Opin Microbiol* 43: 24–30.
81. Barberán A, Ladau J, Leff J W, et al. (2015) Continental-scale distributions of dust-associated bacteria and fungi. *PNAS* 112: 5756–5761.
82. Burrows SM, Elbert W, Lawrence MG, et al. (2009) Bacteria in the global atmosphere – Part 1: Review and synthesis of literature data for different ecosystems. *Atmos Chem Phys* 9: 9263–9280.
83. Sharma NK, Rai AK, Singh S, et al. (2007) Airborne algae: their present status and relevance. *J Phycol* 43: 615–627.
84. Tesson SVM, Skjøth CA, Šantl-Temkiv T, et al. (2016) Airborne microalgae: Insights, opportunities, and challenges. *Appl Environ Microb* 82: 7.
85. Frahm JP (2008) Diversity, dispersal and biogeography of bryophytes (mosses). *Biodivers Conserv* 17: 277–284.
86. Lönnell N (2014) Dispersal of bryophytes across landscapes. Stockholm University, Department of Ecology, Environment and Plant Sciences. PhD Thesis, 41 p.
87. Löndahl J (2014) Physical and biological properties of bioaerosols. Chapter 4 in Jonsson, O., Olofsson, G., and Tjærnhage, T. [Eds] *Bioaerosol Detection Technologies. Integrated Analytical Systems*. Springer-Verlag: New York.
88. Clauß M (2015) Particle size distribution of airborne microorganisms in the environment-a review. *Landbauforsch Appl Agric Forestry Res* 65: 77–100.
89. Womack AM, Bohannon BJM, Green JL (2010) Biodiversity and biogeography of the atmosphere. *T Roy Soc A* 365: 3645–3653.
90. Acosta-Martinez V, Van Pelt S, Moore-Kucera J, et al. (2015) Microbiology of wind-eroded, sediments: current knowledge and future. *Aeolian Res* 18: 99–113.
91. He Y, Zhao C, Song M, et al. (2015) Onset of frequent dust storms in northern China. *Sci R* 5: 1711.
92. Yongxiang H, Xiaomin F, Tianliang Z, et al. 2008. Long range trans-Pacific transport and deposition of Asian dust aerosols. *J Environ Sci* 20: 424–428.
93. Yumimoto K, Eguchi K, Uno I, et al. 2010. Summertime trans-Pacific transport of Asian dust. *Geophys Res Lett* 37: L18815.

94. Guo J, Lou M, Miao Y, et al. (2017) Trans-Pacific transport of dust aerosols from East Asia: Insights gained from multiple observations and modeling. *Environ Pollut* 230: 1030–1039.
95. Barry PL (2001) The Pacific Dust Express. https://science.nasa.gov/science-news/science-at-nasa/2001/ast17may_1
96. Doherty OM, Riemer N, Hameed S (2008) Saharan mineral dust transport into the Caribbean: observed atmospheric controls and trends. *J Geophys Res* 113: DO7211.
97. Chen KY (2010) The northern path of Asian dust transport from the Gobi Desert to North America. *Atmospheric and Oceanic Science Letters* 3: 155–159.
98. Creamean JM, Spackman JR, Davis SM, et al. (2014) Climatology of long-range transported Asian dust along the West Coast of the United States. *J Geophys Res: Atmosarchaeapheres* 119: 171–185.
99. Liu L, Guo J, Gong H, et al. (2019) Contrasting influence of Gobi and Taklimakan Deserts on the dust aerosols in western North America. *Geophys Res Lett* 46: 9064–9071.
100. Dunion JP, Velden CS (2004) The impact of the Saharan Air Layer on Atlantic cyclone activity. *B Am Meteorol Soc* 85: 353–365.
101. Strong JDO, Vecchi GA, Ginoux P (2015) The response of the tropical Atlantic and west African climate to Saharan dust in a fully coupled GCM. *J Climate* 28: 7071–7092.
102. Di Liberto T (2018) Dust from the Sahara Desert stretches across the tropical Atlantic Ocean in late June / early July 2018. National Oceanic and Atmospheric Administration. [Climate.gov/print/832174](https://climate.gov/print/832174)
103. Kellogg CA, Griffin DW (2003) African dust carries microbes across the ocean: Are they affecting human and ecosystem health? United States Geological Survey Open-File Report 03–028.
104. Kellogg CA, Griffin DW, Garrison VH, et al. (2004) Characterization of aerosolized bacteria and fungi from desert dust events in Mali, West Africa. *Aerobiologia* 20: 99–110.
105. Griffin D W, Kellogg C A, Garrison V H, et al. (2002) The global transport of dust: an intercontinental river of dust, microorganisms and toxic chemicals flows through the Earth's atmosphere. *Am Sci* 90: 228–235.
106. Gat D, Mazar Y, Cytryn E, et al. (2017) Origin-dependent variations in the atmospheric microbiome community in eastern Mediterranean dust storms. *Environ Sci Technol* 51: 6709–6718.
107. Behzad H, Mineta K, Gojobori T (2018) Global ramifications of dust and sandstorm microbiota. *Genome Biol Evol* 10: 1970–1987.
108. Dregne HE (1984) North American deserts. In: El-Baz, F. (Ed), Deserts and arid lands. Remote sensing of earth resources and environment. 1. Springer: Dordrecht
109. Achakulwisut P, Shen L, Mickley LJ (2017) What controls springtime fine dust variability in the western United States? Investigating the 2002–2015 increase in fine dust in the U.S southwest. *J Geophys Res: Atmos* 122: 12449–12467.
110. Chazette P, Flamant C, Totems J, et al (2019) Evidence of the complexity of aerosol transport in the lower troposphere on the Namibian coast during AEROCLO-sA. *Atmos Chem Phys* 19: 14979–15005.

111. Nguyen HD, Riley M, Leys J, et al. (2019) Dust storm event of February 2019 in central and east coast of Australia and evidence of long-range transport to New Zealand and Antarctica. *Atmosphere* 10: 653.
112. Azua-Bustos A, González-Silva C, Fernández-Martínez M Á, et al. (2019) Aeolian transport of viable microbial life across the Atacama Desert, Chile. *Sci R* 9: 11024.
113. Li J, Wang F, Michalski G, et al. (2019) Atmospheric deposition across the Atacama Desert, Chile: Composition, source distribution, and interannual comparisons. *Chem Geol* 525: 435–446.
114. Aarons SM, Aciego SM, McConnell JR, et al. (2019) Dust transport in Taylor Glacier, Antarctica, during the last interglacial. *Geophys Res Lett* 46: 2261–2270.
115. Kavan J, Dagsson-Waldhauserova P, Renard JB, et al. (2018) Aerosol concentration in relationship to local atmospheric conditions on James Ross Island, Antarctica. *Front Earth Sci* 6: 207.
116. Herren CM (2019) Asexual reproduction can account for the high diversity and prevalence of rare taxa observed in microbial communities. *Appl Environ Microb* 85: e01099–19.
117. Mayol E, Arrieta J M, Jiménez M A, et al. (2017) Long-range transport of airborne microbes over the global tropical and subtropical ocean. *Nature Commun* 8: 201.
118. Persson, A. 1998. How do we understand the Coriolis force? *B Am Meteorol Soc* 79: 1373–1385.
119. Peters DHW, Schneidereit A, Karpechko AY (2018) Enhanced stratosphere/troposphere coupling during extreme warm stratospheric events with strong polar-night jet oscillation. *Atmosphere* 9: 467.
120. Aguilera Á, de Diego-Castilla G, Osuna S, et al. 2018. Microbial ecology in the atmosphere: the last extreme environment. In: Extremophilic microbes and metabolites diversity bioprospecting and biotechnological applications. IntechOpen, London. doi: <http://dx.doi.org/10.5772/intechopen.81650>
121. Jaenicke R, Matthias-Maser S, Gruber S (2007) Omnipresence of biological material in the atmosphere. *Environ Chem* 4: 217–220.
122. Laaka-Lindberg S, Korpelainen H, Pohjamo M (2003) Dispersal of asexual propagules in bryophytes. *J Hattori Bot Lab* 94: 319–330.
123. Fröhlich-Nowoisky J, Pickersgill DA, Després VR, et al. (2009) High diversity of fungi in air particulate matter. *Proc Natl Acad Sci* 106: no. 31.
124. Bowers RM, Clements N, Emerson JB, et al. (2013) Seasonal variability in bacterial and fungal diversity of the near-surface atmosphere. *Environ Sci Technol* 47: 12097–12106.
125. Narlikar JV, Wickramasinghe NC, Wainwright M, et al. (2003) Detection of microorganisms at high altitudes. *Curr Sci* 85: 23–29.
126. Bryan NC, Christner BC, Guzik TG, et al. (2019) Abundance and survival of microbial aerosols in the troposphere and stratosphere. *ISME J* 13: 2789–2799.
127. Chen X, Ran P, Ho K, et al. (2012) Concentrations and size distributions of airborne microorganisms in Guangzhou during summer. *Aerosol Air Qual Res* 12: 1336–1344.
128. Pulschen AA, de Araujo GG, de Carvalho ACSR, et al. (2018) Survival of extremophilic yeasts in the stratospheric environment during balloon flights and in laboratory simulations. *Appl Environ Microb* 84: e01942–18.
129. Smith DJ, Timonen HJ, Jaffe DA, et al. (2013) Intercontinental dispersal of bacteria and archaea by transpacific winds. *Appl Environ Microb* 79: 1134–1139.

130. Smith DJ, Ravichandar JD, Jain S, et al. (2018) Airborne bacteria in the Earth's lower stratosphere resemble taxa detected in the troposphere: Results from a new NASA Aircraft Bioaerosol Collector (ABC). *Front Microbiol* 9: article 1752.
131. Smith DJ, Griffin DW, McPeters RD, et al. 2011. Microbial survival in the stratosphere and implications for global dispersal. *Aerobiologia* 27: 319–332.
132. Nicholson WL, Munakata N, Horneck G, et al. (2000) Resistance of *Bacillus* endospores to extreme terrestrial and extraterrestrial environments. *Microbiol Mol Biol Rev* 64: 548–572.
133. Huwe B, Fiedler A, Moritz S, et al. 2019. Mosses in low orbit: Implications for the limits of life and the habitability of Mars. *Astrobiology* 19: 221–232.
134. Trest MT, Will-Wolf S, Keuler R, et al. (2015) Potential impacts of UV exposure on lichen communities: A pilot study of *Nothofagus dombeyi* trunks in southernmost Chile. *Ecosyst Health Sus* 1: article 14.
135. Wainwright M, Alharbi S, Wickramasinghe NC (2006) How do microorganisms reach the stratosphere? *Int J Astrobiology* 5: 13–15.
136. Langematz A (2019) Stratospheric ozone: down and up through the Anthropocene. *ChemTexts* 5: 8.
137. Studlar SM, Eddy C, Spencer J (2007) Survival of four mosses from West Virginia after two hours in the stratosphere. *Evansia* 24: 17–21.
138. Horneck G, Klaus DM, Mancinelli RL (2010) Space microbiology. *Microbiol Mol Biol Rev* 74: 121–156.
139. Wainwright M, Wickramasinghe NC, Narlikar JV, et al. (2003) Microorganisms cultured from stratospheric air samples obtained at 41 km. *Fems Microbiol Lett* 218: 161–165.
140. Imshenetsky AA, Lysenko SV, Lach SP (1979) Microorganisms of the upper layer of the atmosphere and the protective role of their cell pigments. *Life Sci Space R* 17: 105–110.
141. Sancho LG, De la Torre R, Horneck G, et al. 2007. Lichens survive in space: results from the 2005 LICHENS experiment. *Astrobiology* 7: 143–454.
142. Mora M, Perras A, Alekhova TA, et al. (2016) Resilient microorganisms in 12-year old dust samples of the International Space Station – survival of the adaptation specialists. *Microbiome* 4: 65.
143. Grebennikova TV, Syroeshkin AV, Shubralova EV, et al. (2018) The DNA of bacteria of the world ocean and the Earth in cosmic dust at the International Space Station. *Sci World J* 2018: 7360147.
144. Farman JC, Gardiner BG, Shanklin JD (1985) Large losses of total ozone in Antarctica reveal seasonal C10x/NOx interaction. *Nature* 315: 307–210.
145. Bhartia PK, McPeters RD (2018) The discovery of the Antarctic Ozone Hole. *Cr Geosci* 350: 335–340.
146. Solomon S (2019) The discovery of the Antarctic ozone hole. *Nature* 575: 46–47.
147. Ritchie H, Roser M (2020) Ozone layer. <https://ourworldindata.org/ozone-layer>
148. Zhang Y, Li J, Zhou L (2017) The relationship between polar vortex and ozone depletion in the Antarctic stratosphere during the period 1979–2016. *Adv Meteorol* 2017: 3078079.
149. Onofri S, Barreca D, Selbmann L, et al. (2008) Resistance of Antarctic black fungi and cryptoendolithic communities to simulated space and Martian conditions. *Stud Mycol* 61: 99–109.

150. Monsalves MT, Ollivet-Besson GP, Amenabar MJ, et al. (2020) Isolation of a psychrotolerant and UV-C-resistant bacterium from Elephant Island, Antarctica with a highly thermoactive and thermostable catalase. *Microorganisms* 8: 95.
151. Romanovskaya VA, Tashirev B, Shilin NA, et al (2011) Resistance of Antarctic microorganisms to UV radiation. *Mikrobiologichnyi Zhurnal* 73: 3–8.
152. Waterman MJ, Nugraha AS, Hendra R, et al. (2017) Antarctic moss bioflavonoids show high antioxidant and ultraviolet-screening activity. *J Nat Prod* 80: 2224–2231.
153. Reis-Mansur MCPP, Cardoso-Rurr JS, Silva JVMA, et al. (2019) Carotenoids from UV-resistant Antarctic *Microbacterium* sp. LEMMJ01. *Sci R* 9: 9554.
154. Yang Y, Itahashi S, Yokobori S, et al. (2008) UV-resistant bacteria isolated from upper troposphere and lower stratosphere. *Biol Sci Space* 22: 18–25.
155. Ehling-Schulz M, Scherer S. (1999) UV protection in cyanobacteria. *Eur J Phycol* 34: 329–338.
156. Taleb NM (2007) *The Black Swan*. Random House Publishing, New York
157. Ferrari, M. 2009. Anticipating the climate black swan. <https://energycentral.com/c/pip/anticipating-climate-black-swan>
158. Witze A (2020) Rare ozone hole opens over the Arctic – and it's big. *Nature* 580: 18–19.



AIMS Press

© 2021 the Author(s), licensee AIMS Press. This is an open access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0>)