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Aerobiology and passive restoration of biological soil crusts

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Abstract Biological soil crusts (BSCs) exist commonly on soil surfaces in many arid and semiarid areas, and disturbed soil surfaces in more mesic environments. BSCs perform many essential ecological functions. Substantial resources have been invested trying to restore or replace BSCs that have been damaged by anthropogenic disturbances, with various levels of success. The nexus of sciences related to BSC establishment and restoration, and to aerobiology suggests that crusts are established and re-established naturally via commonly occurring ecological processes. Formation of BSCs can be accelerated by implementing traditional or novel land rehabilitation techniques that create near-surface turbulence that facilitates the deposition of airborne BSC organisms. Sexual and asexual propagules of BSC organisms are found naturally in the atmosphere and are transported up to very long distances between continents and hemispheres. Whether restoration of BSCs occurs naturally in this fashion, or through efforts to produce and disseminate artificial inoculants, success is ultimately moderated and governed by the timing and frequency of adequate precipitation relative to the arrival of viable propagules on suitable substrates at appropriate times of year. For the greatest ecological and economic benefit, we suggest that efforts should focus on minimizing the scope and scale of unnecessary anthropogenic disturbance to BSC communities.

Keywords Cyanobacteria · Algae · Lichens · Bryophytes · Airborne · Reclamation · Arid lands

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1 Introduction

Biological soil crusts (BSCs; Fig. 1a) develop when various combinations of diminutive cyanobacteria, algae, lichenized and non-lichenized fungi and/or bryophytes occupy the surface and upper few millimeters of the soil. Historically, they have been referred to as cryptobiotic, cryptogamic, microbiotic, microfloral, microphytic and organogenic crusts. They can be present in a wide range of ecological, successional, and climatic conditions when and where disturbance and/or aridity have resulted in opportunities for colonization. However, they are most prevalent in arid and semiarid ecosystems where vascular plant cover and diversity are characteristically low, leaving large areas available for colonization by some combination of the organisms mentioned above. The

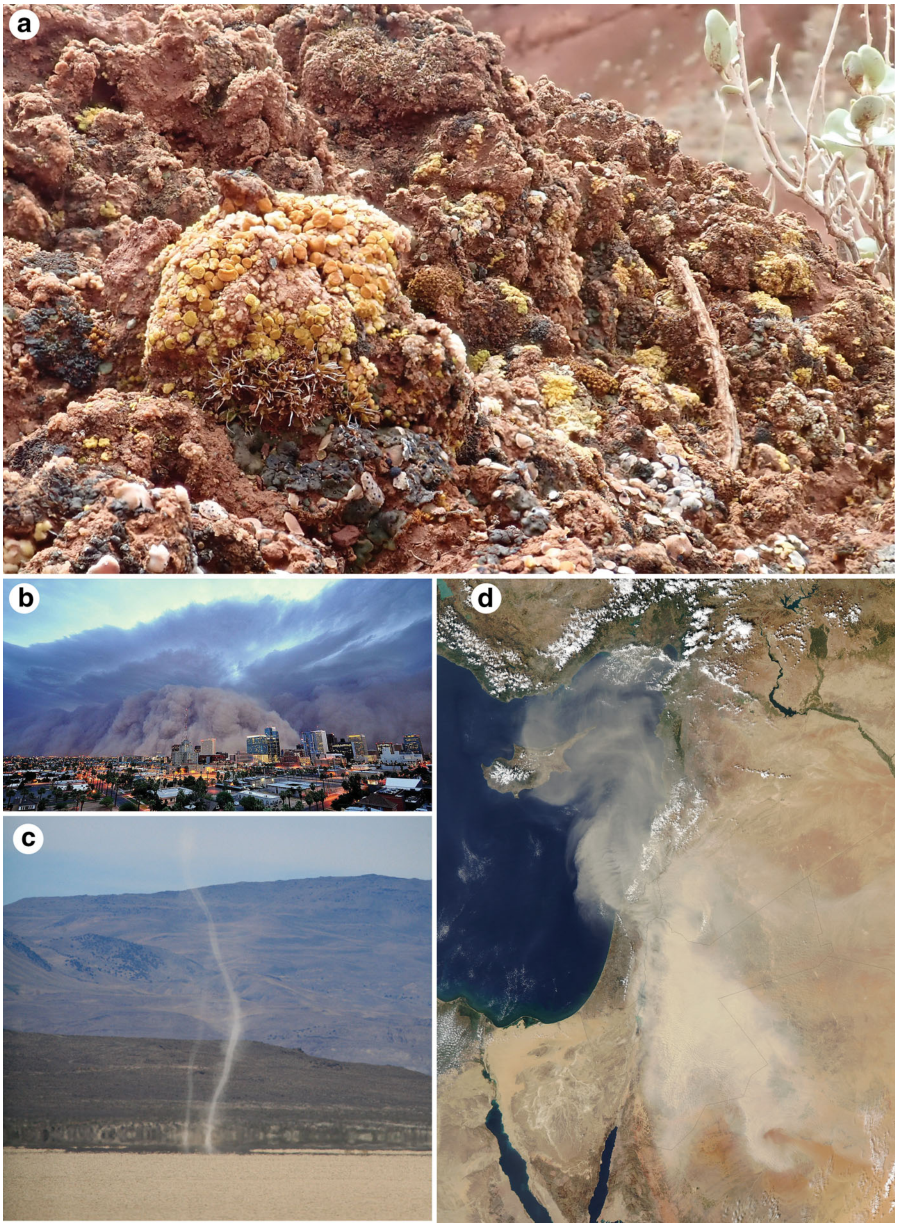

Fig. 1 Biological soil crust communities (BSC) and potential factors leading to atmospheric mixing and dispersal. **a** A well-developed BSC on the Colorado Plateau in southeastern Utah, USA; **b** Dust storm in the southwestern USA created by summer monsoon thunder cells (source: https://commons.wikimedia.org/wiki/File:Dust_storm_clouds_gathering.jpg); **c** a strong vertical vortices or 'dust devils' in western North America (source: (https://www.flickr.com/photos/jurvetson/888064641); and **d** satellite image of a dust storm extending from Saudi Arabia to Turkey in 2011 (source: https://earthobservatory.nasa.gov/images/52305/dust-storm-in-the-middle-east)

diversity and distribution of BSC components in extreme environments is striking. For example, at least 18 species of cyanobacteria have been documented in the soils of Death Valley National Monument in the Mojave Desert, USA, where surface temperatures can reach 88 °C (Durrell 1962). At the opposite end of the temperature spectrum, BSC communities are common in interior Antarctica, where soil temperatures seldom exceed 0 °C (Green and Broady 2001). BSCs are also present in the hyper-arid Atacama Desert of northern Chile (Patzelt et al. 2014), where average annual precipitation, depending on latitude, elevation, and distance from the Pacific coast, can be less than 1 mm.

The ecological roles of BSCs are many and varied and include the collection, accumulation, and cycling of essential airborne and soil nutrients, redistribution of precipitated water, and soil formation and stabilization (Warren 1995; Belnap and Lange 2001; Chen et al. 2009; Weber et al. 2016b). BSCs, and their ecological functions, can be disturbed by a variety of anthropogenic factors, including, but not limited to, livestock trampling (Warren and Eldridge 2001), off-road vehicular traffic (Wilshire 1983; Webb et al. 1988), military operations (Warren 2014), mining (Spröte et al. 2010), and fire (Johansen 2001). In spite of the overall importance of BSCs and the well-documented effects of disturbance on these communities, restoring degraded habitats has received proportionately less attention. While important perspectives on BSCs rehabilitation have been previously summarized (Belnap and Eldridge 2001; Bowker 2007; Chiquoine et al. 2016), the role of aerobiology and passive restoration has not been adequately considered. Here, we provide an up-to-date perspective incorporating principles of aerobiology and passive dispersal into the BSC restoration paradigm. In addition to directing future research, reflection on the broad scope of BSC restoration can improve our perspective of how to effectively manage important dryland regions.

2 Artificial restoration

It may seem intuitive to attempt to restore BSCs by inoculating disturbed sites with crust organisms, but such applications have been relatively rare. St. Clair et al. (1986) inoculated small plots with a soil slurry made by stripping BSCs from intact areas, mixing them with water, and applying them to sites damaged by wildfire. Belnap (1993) stripped crusts from an intact area and used them as a dry inoculant on small plots where the original crust had been removed. The inoculation of soil in petri dishes with dry and slurried inocula, plus additions of water up to five times per week, and sewage sludge, produced limited soil crust re-establishment (Maestre et al. 2006). Bu et al. (2014) inoculated soil in a greenhouse study with BSCs that had been stripped from intact areas in the field in an attempt to accelerate crust restoration. They found that frequent watering of the crusts in that setting enhanced growth, but field trials were not conducted. In the Mojave Desert, USA, a somewhat similar approach was attempted using crusts composed of cyanobacteria, lichens, and bryophytes that had been salvaged from a road construction site and subsequently stored for 2 years (Chiquoine et al. 2016). Cole et al. (2010) transplanted soil cores with intact bryophyte crusts in the Mojave Desert, USA. The cover and density of the bryophytes declined after transplantation, but at rates similar to the parent population, suggesting that annual declines are natural even in intact populations. In most of the aforementioned cases, inoculation hastened recovery of BSC organisms, particularly in controlled laboratory settings, with some recovery also in field studies. However, while the results were promising, the destruction of BSCs in one area to provide inoculants for another area is counterproductive in the context of large-scale arid land reclamation. Use of salvaged crusts from construction sites is promising for limited areas (Chiquoine et al. 2016). Providing sufficient supplemental water for successful large-scale reclamation in arid environments has been difficult, costly, and only minimally feasible.

Related research has investigated the potential for ex situ laboratory-grown BSC amendments for use in inoculating disturbed areas (Zhao et al. 2016; Bowker and Antoninka 2016). For example, Buttars et al. (1998) incorporated laboratory-grown cyanobacteria into alginate pellets. However, the cyanobacteria were unable to escape intact pellets. Crushing the pellets and applying them to moistened soil in the laboratory resulted in significant increases in cyanobacterial biomass, frequency, and nitrogen fixation. Incorporation of cyanobacteria into starch pellets was not successful due to poor survival during the pelletization process (Howard and Warren 1998). Kubečková et al. (2003) also grew cyanobacteria and immobilized it on hemp cloth. Laboratory trials indicated improved growth compared to alginate pellets, but in four of five field trials, there was no significant crust recovery. The general lack of success with artificial crust recovery was attributed, at least in part, to the placement of the inoculants on the soil surface where some species of cyanobacteria can be negatively affected by incident UV radiation (Castenholz and Garcia-Pichel 2012). If sensitive species occur at a depth of 1–2 mm, UV radiation is attenuated (Dor and Danin 2001). When cyanobacterial inoculants have been applied to the soil surface, rather than incorporated into the surface layer of the soil, mortality has been high. Moss protonema transplanted into the sands of the Gurbantunggut Desert of China from laboratory-grown mosses has seen some success when supplemented with liquid growth media (Xu et al. 2008). Mosses have been successfully propagated in the laboratory with frequent watering and fertilization (Antoninka et al. 2016), although field trials have not been conducted. The addition of laboratory-grown cyanobacteria to polyvinyl alcohol and a liquid soil tackifier appeared to accelerate the formation of a biocrust in a laboratory setting (Park et al. 2017).

Although some degree of success has been noted, large-scale field trials have not been attempted, and successful ex situ growth is not ubiquitous across BSC components. While we, too, have been invested in the challenge, the level of success to date, the amount of water required, and the per-acre costs have caused us to wonder whether these approaches merit further consideration in arid areas, except in critical situations where cost is not a constraint. One experience with artificial restoration highlights our concerns and lends credence to our doubts. While working in the Great Basin west of Salt Lake City, Utah, using fragments of hemp cloth embedded with dried cyanobacteria, we treated plots that had been burned by a wildfire. After one season, the chlorophyll content of the soil had increased to a level that exceeded untreated plots, suggesting success. We began to prepare a manuscript to announce the success. In the process, we decided to evaluate the plots after a second year to further document progress. However, after the second year, the untreated plots had improved to a state equal to the treated plots. Confused, we began to try to determine potential reasons. In the process, we recalled that the site had experienced frequent dust devils during the intervening period. That led us to conclude that natural passive restoration had likely occurred.

3 Passive restoration

The fact that BSCs are found in almost all environments, ranging from mesic to hyper-arid, and from temperate to extremely hot or cold, justifies the question as to how crust organisms became so spatially and climatically dispersed in the first place, and if the same processes are still operating. In general, as post-disturbance succession takes place, the initial colonizers tend to be large filamentous cyanobacteria (Belnap and Eldridge 2001). As the surface becomes stabilized, next to appear are the smaller cyanobacteria and green algae. They are often followed by small lichens propagated by vegetative diaspores. Where climatic conditions permit, larger lichens and mosses appear in later successional communities (Dümig et al. 2013). The distribution and successful establishment of these organisms is governed both by historical and contemporary factors (Leavitt and Lumbsch 2016).

Estimates of the time required for natural recovery of BSCs following disturbance have varied widely depending on the nature, periodicity, extent, and spatial and temporal distribution of the disturbance, and soil and climatic conditions. Dojani et al. (2011) reported significant recovery to a level beyond the pre-disturbance condition within 1 year (one moist season) on the Succulent Karoo semi-desert of South Africa where the upper 10 mm of the soil surface was removed. Five years following one-time human trampling, Cole (1990) noted a nearly complete recovery of visible BSC cover, although the complex pinnacled surface micro-topography attributable to many crusts had not recovered to pre-disturbance levels. Read et al. (2011) labeled as 'surprisingly fast' the recovery of biological soil crusts following livestock removal from an area that had been previously heavily disturbed by livestock grazing in Australia. Anderson et al. (1982) estimated that 14–18 years were adequate for recovery of a BSC following exclusion of livestock grazing in the cool Great Basin Desert, USA. In contrast, there was little evidence of recovery during the first 10 years following cessation of grazing at another Great Basin Desert location (Jeffries and Klopatek 1987). Recovery lagged 20 years following burning of a shrub community in the transition zone between the Great Basin and Mojave Deserts in southwestern Utah, USA (Callison et al. 1985). Belnap (1993) estimated that full recovery of BSCs in the Great Basin Desert, including visual as well as functional characteristics, could require as long as 30–40 years for the cyanobacterial component, 45–85 years for lichens, and 250 years for mosses. Fifty-six years following abandonment of a military training camp in the Sonoran Desert, USA, a cyanobacterial crust had not recovered to levels typical of adjacent undisturbed areas (Kade and Warren 2002). In the Mojave Desert, USA, according to measurements taken inside and outside of tank tracks created during training for World War II, and assuming a worst-case linear trajectory scenario, full recovery of the cyanobacterial component of the BSC was estimated to require up to 85–120 years (Belnap and Warren 2002).

Similar temporal patterns of BSC recovery following disturbance have been recorded in other regions. In

Australia, near complete recovery was documented after 20 years on pastures that had been grazed moderately, while heavily grazed pastures recovered at a much slower rate (Read et al. 2011). Eldridge and Ferris (1999) suggested that at least 60 years would be required for full recovery of lichens at a nuclear test site in the Great Victoria Desert of Australia. In an extreme case, Lalley and Viles (2008) estimated that full recovery of lichens in badly disturbed truck ruts in the hyper-arid Namib Desert could take up to 530 years without climatic or anthropogenic intervention. It is important to note, however, that the rate of recovery is likely dependent on the arrival of viable propagules onto suitable substrates at times consistent with adequate moisture. Such conditions may occur only infrequently in the drier and hotter arid zones. We have personally witnessed significant recovery of crust organisms within 2 years following wildfire in the Great Basin Desert, USA, when suitable conditions prevailed.

Regardless of the timeframe required, recovery is dependent on several factors: (1) arrival of suitable propagules, (2) existence of an appropriate substrate on which to establish, including soil texture and chemistry, and (3) timing of the arrival of propagules in relation to cyclical soil moisture conditions suitable for establishment. The failure of any one of the necessary components may substantially delay successful re-establishment.

4 Aerobiology

As early as 1846, Charles Darwin collected dust from surfaces of HMS Beagle during one of his voyages of exploration, and reported 17 different organisms (Darwin 1846). Almost a century and a half following Darwin's original discovery, on an ocean voyage from the Polish Antarctic Station on King George Island, South Shetland Island to Gdynia, Poland, scientists intended to collect pollen grains daily on blotter paper. In addition to pollen, however, the scientists commonly found abundant non-lichenized fungal spores, lichen thallus fragments, isidia, and soredia in all samples, indicating widespread distribution of airborne lichen propagules very long distances from terrestrial environments (Harmata and Olech 1991). Meier and Lindbergh (1935) collected airborne organisms from a fixed-wing aircraft on a flight over the Arctic from Maine to Denmark. Near the same time as the Polish discovery, the field of aerobiology was established, originally emphasizing studies of airborne fungi, bacteria, and viruses associated with respiratory diseases from indoor environments (Benninghoff 1991).

Subsequently, the field began to evaluate other potential airborne allergens including protozoans, minute arthropods, algae, and cyanobacteria in the atmosphere, and began to evaluate the seasonality and other factors affecting their presence. As a consequence, the presence of large numbers of cyanobacteria and algae have been documented as present in indoor and outdoor airborne environments ranging from low to high altitudes above the Earth (Schlichting 1969; Lee and Eggleston 1989; Sharma et al. 2007; Genitsaris et al. 2011; Després et al. 2012; Tesson et al. 2016; Lewandowska et al. 2017). Recent studies have reported the presence of hundreds of BSC taxa and thousands of individual organisms in dust samples collected from the external surfaces of homes around the USA (Barberán et al. 2015). It has been recently suggested that some organisms may go through multiple generations while in the atmosphere, such that the atmosphere becomes a truly aerial habitat (Womack et al. 2010).

Organisms that achieve airborne status may come from a variety of potential sources including plant surfaces, animals, water, and soil (Pearce et al. 2009). Unsurprisingly, many of the species documented in the atmosphere are also common in BSC communities. Airborne BSC organisms suspended by wind storms or other factors may be transported and deposited almost anywhere. Bioaerosols have been reported as being transported by dust storms in the western USA (Hallar et al. 2011). Fungi may be transported long distance by wind (Marshall 1997; Golan and Pringle 2017). Algae and cyanobacteria have been reported to occur on high latitude and high elevation glaciers from the Arctic to the Antarctic (Marshall and Chalmers 1997; Harding et al. 2011; Kvíderová 2012; Takeuchi 2013; Vonnahme et al. 2016). They have also been collected from building facades (Samad and Adhikary 2008; Sethi et al. 2012), stone monuments and statues (Lamenti et al. 2000; Tomaselli et al. 2000; Macedo et al. 2009; Verma et al. 2014), cave and catacomb walls (Castellani 2005), exposed rocks (Danin 1999), and plant surfaces (Sethi et al. 2012; McGorum et al. 2015). In addition to algae and cyanobacteria, other

BSC components can also be dispersed by wind. These include asexual reproductive lichen fragments, isidia, soredia, and/or lichen-forming fungal spores (Bailey 1966; Büdel and Wessels 1986; Heinken 1999; Tormo et al. 2001; Bannister and Blanchon 2003; Hugonnot and Celle 2012; Leavitt and Lumbsch 2016). In addition, spores, gametophyte fragments, and specialized asexual diaspores of bryophytes (Marshall and Convey 1997; Stark 2003; Laaka-Lindberg et al. 2003; Pohjamo et al. 2006; Lönnell et al. 2012) have been reported. Airborne bacteria and fungi have even been found in the atmosphere of salt mines 400 m below the surface (Gębarowska et al. 2017). The pattern of airborne dispersal of BSC propagules has resulted in many species occurring in both the northern and southern Polar regions in Iceland, and extreme southern Chile (Piñeiro et al. 2012).

5 Atmospheric mixing and dispersion

A logical question may arise as to how BSC organisms are able to achieve airborne status. Many people living in arid and hyper-arid regions of the world have, at one time or another, heard stories of, or personally witnessed, dust storms that develop when strong non-convective horizontal winds blowing over unconsolidated or even intact soil surfaces pick up large quantities of soil (Fig. 1b; Kok et al. 2012). Although not at all limited to the Dust Bowl era, such conditions prevailed in the 1930's in the North America (McLeman et al. 2014). Similarly, strong dust storms have been recorded in Alaska (Nickling 1978), China (Qian et al. 2002; Wang et al. 2004), Australia (McTainsh et al. 1998; Ekström et al. 2004), Africa (Prospero and Mayor-Bracero 2013), and the Middle East (Orlovsky et al. 2005; Almuhanna 2015; Sissakian et al. 2013). On a smaller, but much more common scale, dust may be lifted into the atmosphere by strong vertical vortices or 'dust devils' (Fig. 1c) (Metzger et al. 2011; Kok et al. 2012; Horton et al. 2016). The maximum wind speeds of dust devils have been recorded as 22 ms^{-1} (45 mph) (Schwiesow and Cupp 1976).

Once airborne (Fig. 1d), dust particles and the BSC organisms that accompany them are subject to a variety of forces that carry them between hemispheres, continents, and climatic zones (Griffin et al. 2002; Prospero and Lamb 2003; Kellogg and Griffin 2006; Uno et al. 2009; Pointing and Belnap 2014). Near the Earth's surface, airborne particles are carried predominantly by trade winds, which were given their name because of the effect they had on global oceanic trade prior to the advent of fossil fuel powered transport. Trade winds exist in six major belts which circle the globe. Between the equator and 30° north or south latitude, the trade winds generally blow from east to west; between 30° and 60° latitude, the winds then shift to from west to east; between 60° north or south latitude and the respective poles, easterly winds again prevail. The major jet streams exist at about 9–15 km above the Earth's surface and blow from west to east (Lewis 2003). They meander north or south, and may cross between the northern and southern hemispheres (Rangarajan and Eapen 2012). Other than the trade winds and jet streams, a primary force mixing the atmosphere within the northern and southern hemispheres is the global Hadley, Ferrel, and polar cells (Kjellsson and Döös 2012; Huang and McElroy 2014) which correspond latitudinally to the trade wind belts. Hadley cells begin where warm air rises near the equator, generally resulting in heavy rainfall. After reaching the upper atmosphere, the Hadley cells carry the flow of air poleward. At approximately 30° north and south latitude, the Hadley cells diverge earthward, converging with the downward flow of the Ferrel cells bringing air masses from greater latitudes. The result in both hemispheres is a very large body of descending dry air and high pressure. As descending air masses typically offer little precipitation, the zones of convergence correspond with some of the world's most recognized arid zones. The dry air moves poleward after reaching the Earth's surface. As the Ferrel cells pass over the Earth's surface, they collect moisture until they reach approximately 60° north and south latitude, where the air masses ascend after converging with the polar cells. In order to continue the ascent, the air masses lose moisture, and precipitation increases. The polar cells descend earthward near the poles, a region also widely known for aridity.

Given the forces mixing the atmosphere, and the likelihood for BSC propagules to be airborne, there can be little doubt that organisms originating from almost any given location have the potential to be deposited anywhere on Earth (Jungblut et al. 2010; Barberán et al. 2014; Herbold et al. 2014). Carson and Brown (1976) found little correlation between the diversity of airborne algae, and soil algae at corresponding altitudes on the Island of Hawaii, suggesting atmospheric mixing of airborne organisms. Evidence of mixing can also be seen on a global scale by the bipolar similarity of BSC species in the Arctic and Antarctic (Galloway and Aptroot 1995; Søchting and Olech 1995; Jungblut et al. 2012; Fernández-Mendoza and Pritzen 2013). Dust deposited in Antarctica originates in Patagonia, Australia, and the Northern Hemisphere (Li et al. 2008). Dust originating during dust storms in China and the Middle East has been documented as arriving in Japan within just a few days (Lee et al. 2006). Dust from the Middle East has been recorded in the Caribbean (Doherty et al. 2008; Swarf et al. 2014) and the southeastern USA (Prospero 1999). Many BSC propagules carried with dust can survive long periods of desiccation (Potts 1994; Holzinger and Karsten 2013; Rajeev et al. 2013), thus becoming immigrants deposited in distant BSC communities globally (Rosselli et al. 2015; Rahav et al. 2016). For example, lichen species of South African origin are now present in Australia and South America (Amo de Paz et al. 2012). Similarity of BSC communities is better predicted by the so-called dust highways than by the proximity of potential source species (Muñoz et al. 2004). Dust and microbial deposition are both seasonal (Sharma et al. 2006a, b; Dubey et al. 2010; Sahu and Tangutur 2015) and cyclical over time (Rousseau et al. 2007).

The apparent airborne and global distribution of BSC propagules should not be construed to imply that BSC species composition will be the same worldwide, nor that natural recovery of BSC's will be necessarily rapid. The distribution of BSC propagules is shaped by the dynamic interplay of a range of factors operating across multiple temporal scales. That many propagules are distributed globally is apparently true. However, whether they will develop and thrive in a new location is still dependent on being deposited on a suitable substrate determined by chemistry, texture, fertility, particle and pore size analysis, moisture content and seasonality, and temperature, among other factors that determine the suitability of habitat for the BSC taxa in question (Miller and McDaniel 2004; Nagy et al. 2005; Kharkongor and Ramanujam 2014; Johansson et al. 2015). For example, it is hardly realistic to expect most BSC species adapted to the frigid conditions of polar regions to survive and persist in hot deserts, and vice versa.

6 The nexus of aerobiology and land reclamation

The use of corn stalk fences and wheat straw checkerboard sand barriers to stabilize dune sands have been successfully used for years in China (Qiu et al. 2004; Zhang et al. 2004; Li et al. 2006). These barriers create turbulence in the flow of wind across the dune surfaces, and cause the deposition of sand and soil, and associated BSC organisms. Researchers have discovered that biological soil crust organisms precipitated in this fashion can successfully colonize stabilized dunes (Li et al. 2003; Guo et al. 2008; Zhang et al. 2014). Li et al. (2016) reported the results of projects in a severely disturbed sandy habitat of the Qinghai–Tibet Plateau near the Yellow River in China. Grass and woody species were planted to increase wind turbulence and promote the deposition of eolian sediments. Within as little as 10 years, the clay and humus content of the soil had increased by 15%, and a BSC community, comprised primarily of lichens, mosses, and algae, had become established.

One must bear in mind that while airborne BSC propagules may provide an answer to the restoration of BSCs in many situations, their presence and composition depends on climatic conditions in locations that may be very far away. As discussed, BSC propagules may originate from distant continents and hemispheres. BSC organisms from a specific soil type, chemistry, and alkalinity may not always be suitable for other locations. The arrival of appropriate propagules is likely episodic, seasonal, and less frequent than desired (Favero-Longo et al. 2014; Gosselin et al. 2016; Weber et al. 2016a). However, there can be little doubt that airborne propagules are found in the atmosphere circling the globe. Whether they will be deposited in sufficient quantities, in the right species composition, and at the right season for any specific area remains unknown.

7 Conclusions

Over the years, millions of dollars have been expended on various approaches to soil crust establishment and restoration, often culminating in the production and application of large quantities of inoculants. Many of these approaches have been less than successful to one degree or another. Those approaches that did not fail outright have been so dependent on large quantities of water for production, application, and maintenance that they have not been practical for broad-scale application to arid and semiarid environments. Several approaches to restoration have depended on the destruction of the soil crust community in one area in order to restore another. A review of the field of aerobiology seems to indicate that there may be good reasons for considering and incorporating passive restoration more seriously as a viable method to support BSC recovery. Propagules of many, if not most BSC organisms are already present and circulating the globe in the atmosphere. Perhaps, now we should carefully examine the possibilities of a more natural approach to crust restoration. Whether we artificially produce and apply inoculants, or rely on natural, passive dispersal, the overall success depends on coordination of inoculation with appropriate environmental conditions. At any given location, regardless of the mode of inoculation, success depends on receiving adequate moisture at the right time of year, the availability of appropriate substrata, a host of other environmental factors, and some measure of better controlling anthropogenic disturbance to BSC communities. We anticipate that incorporating principles of aerobiology and passive dispersal into the BSC restoration paradigm will facilitate more effective and less costly management and recovery of BSCs.

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References

Almuhanna, E. A. (2015). Dustfall associated with dust storms in the Al-Ahsa Oasis of Saudi Arabia. *Open Journal of Air Pollution, 4,* 65–75.

Amo de Paz, G., Cubas, P., Crespo, A., Elix, J. A., & Lumbsch, H. T. (2012). Transoceanic dispersal and subsequent diversification on separate continents shaped diversity of the *Xanthoparmelia pulla* group (Ascomycota). *PLoS ONE, 7,* e39683.

Anderson, D. C., Harper, K. T., & Rushforth, S. R. (1982). Recovery of cryptogamic soil crusts from grazing on Utah winter ranges. *Journal of Range Management, 35,* 355–359.

Antoninka, A., Bowker, M. A., Reed, S. C., & Doherty, K. (2016). Production of greenhouse-grown biocrust mosses and associated cyanobacteria to rehabilitate dryland soil function. *Restoration Ecology, 24,* 324–335.

Bailey, R. H. (1966). Studies on the dispersal of lichen soredia. *Journal of the Linnean Society of London, Botany, 59,* 479–490.

Bannister, J. M., & Blanchon, D. J. (2003). The lichen genus *Ramalina* Ach. (*Ramalinaceae*) on the outlying islands of the New Zealand geographic area. *Lichenologist, 3,* 137–146.

Barberán, A., Henley, J., Fierer, N., & Casamayor, E. O. (2014). Structure, inter-annual recurrence, and global-scale connectivity of airborne microbial communities. *Science of the Total Environment, 487,* 187–195.

Barberán, A., Ladau, J., Leff, J. W., Pollard, K. S., Menninger, H. L., Dunn, R. R., et al. (2015). Continental-scale distributions of dust-associated bacteria and fungi. *Proceedings of the National Academy of Science, 112,* 5756–5761.

Belnap, J. (1993). Recovery rates of cryptobiotic crusts: Inoculant use and assessment methods. *Great Basin Naturalist, 53,* 89–95.

Belnap, J., & Eldridge, D. (2001). Disturbance and recovery of biological soil crusts. In J. Belnap & O. L. Lange (Eds.), *Biological soil crusts: Structure, function and management* (pp. 363–383). Berlin: Springer.

Belnap, J., & Lange, O. L. (Eds.). (2001). *Biological soil crusts: Structure, function and management*. Berlin: Springer.

Belnap, J., & Warren, S. D. (2002). Patton's tracks in the Mojave Desert, USA: An ecological legacy. *Arid Land Research and Management, 16,* 245–258.

Benninghoff, W. J. (1991). Aerobiology and its significance in biogeography and ecology. *Grana, 30,* 9–15.

Bowker, M. A. (2007). Biological soil crust rehabilitation in theory and practice: An underexploited opportunity. *Restoration Ecology, 15,* 13–23.

Bowker, M. A., & Antoninka, A. J. (2016). Rapid ex situ culture of N-fixing soil lichens and biocrusts is enhanced by complementarity. *Plant and Soil*. https://doi.org/10.1007/s11104-016-2929-7.

Bu, C., Wu, S., Yang, Y., & Zheng, M. (2014). Identification of factors influencing the restoration of cyanobacteria-dominated biological soil crusts. *PLoS ONE, 9,* e90049.

Büdel, B., & Wessels, D. C. J. (1986). *Parmelia hueana* Gyeln., a vagrant lichen from the Namib Desert, SWA/Namibia. I Anatomical and reproductive adaptation. *Dinteria, 12,* 3–16.

Buttars, S. M., St. Clair, L. L., Johansen, J. R., Sray, J. C., Payne, M. C., Webb, B. L., et al. (1998). Pelletized cyanobacterial soil amendment: Laboratory testing for survival, escapability, and nitrogen fixation. *Arid Soil Research and Rehabilitation, 12,* 165–178.

Callison, J., Brotherson, J. D., & Bowns, J. E. (1985). The effects of fire on the blackbrush [*Coleogyne ramosissima*] community of southwestern Utah. *Journal of Range Management, 38,* 535–538.

Carson, J. L., & Brown, R. M. (1976). The correlation of soil algae, airborne algae, and fern spores with meteorological conditions on the Island of Hawaii. *Pacific Science, 30,* 197–205.

Castellani, F. (2005). Historical monuments: The film. *Nature, 43,* 100–101.

Castenholz, R. W., & Garcia-Pichel, F. (2012). Cyanobacterial responses to UV radiation. In B. A. Whitton (Ed.), *Ecology of Cyanobacteria II* (pp. 481–499). Dordrecht: Springer.

Chen, R., Zhang, Y., Li, Y., Wei, W., Zhang, J., & Wu, Nan. (2009). The variation of morphological features and mineralogical components of biological soil crusts in the

Gurbantunggut Desert of Northwestern China. *Environmental Geology, 57*(5), 1135–1143.
Chiquoine, L. P., Arbella, S. R., & Bowker, M. A. (2016). Rapidly restoring biological soil crusts and ecosystem functions in a severely disturbed desert ecosystem. *Ecological Applications, 26,* 1260–1272.
Cole, D. N. (1990). Trampling disturbance and recovery of cryptogamic soil crusts in Grand Canyon National Park. *The Great Basin Naturalist, 50,* 321–325.
Cole, C., Stark, L. R., Bonine, M. L., & McLetchie, D. N. (2010). Transplant survivorship of bryophyte soil crusts in the Mojave Desert. *Restoration Ecology, 18,* 198–205.
Danin, A. (1999). Desert rocks as plant refugia in the Near East. *The Botanical Review, 65*(2), 93–170.
Darwin, C. (1846). An account of the fine dust which often falls on vessels in the Atlantic Ocean. *Quarterly Journal of the Geological Society of London, 2,* 26–30.
Després, V. R., Huffman, J. A., Burrows, S. M., Hoose, C., Safatov, A. S., Buryak, G., et al. (2012). Primary biological aerosol particles in the atmosphere: A review. *Tellus, 64,* 11598.
Doherty, O. M., Riemer, N., & Hameed, S. (2008). Saharan mineral dust transport into the Caribbean: Observed atmospheric controls and trends. *Journal of Geophysical Research, 113,* D07211.
Dojani, S., Büdel, S., Deutschewitz, K., & Weber, B. (2011). Rapid succession of biological soil crusts after experimental disturbance in the Succulent Karoo, South Africa. *Applied Soil Ecology, 48,* 263–269.
Dor, I., & Danin, D. (2001). Life strategies of *Microcoleus vaginatus*: A crust forming cyanophyte on desert soils. *Nova Hedwigia, 123,* 317–339.
Dubey, S., Dixit, A., & Boswal, M. V. (2010). Seasonal distribution of aero algal allergens in the wetlands of Kanpur. *The Bioscan, 3,* 673–680.
Dümig, A., Veste, M., Hagedorn, F., Fischer, T., Lange, P., Spröte, R., et al. (2013). Biological soil crusts on initial soils: Organic dynamics and chemistry under temperate climatic conditions. *Biogeosciences, 10,* 851–894.
Durrell, L. W. (1962). Algae of death valley. *Transactions of the American Microscopical Society, 81,* 267–273.
Ekström, M., McTainsh, G. H., & Chappell, A. (2004). Australian dust storms: Temporal trends and relationships with synoptic pressure distributions (1960–00). *International Journal of Climatology, 24,* 1581–1599.
Eldridge, D. J., & Ferris, J. M. (1999). Recovery of populations of the soil lichen *Psora crenata* after disturbance in arid South Australia. *The Rangeland Journal, 21,* 194–198.
Favero-Longo, S. E., Sandrone, S., Matteucci, E., Appolonia, L., & Piervittori, R. (2014). Spores of lichen-forming fungi in the mycoaerosol and their relationships with climate factors. *Science of the Total Environment, 466–467,* 26–33.
Fernández-Mendoza, F., & Pritzen, C. (2013). Pleistocene expansion of the bipolar lichen *Cetraria aculeata* into Southern hemisphere. *Molecular Ecology, 22,* 1961–1983.
Galloway, D. J., & Aptroot, A. (1995). Bipolar lichens: A review. *Cryptogamic Botany, 5,* 184–191.
Gębarowska, E., Pusz, W., Kucińska, J., & Wita, W. (2017). Comparative analysis of airborne bacteria and fungi in two salt mines in Poland. *Aerobiologia*. https://doi.org/10.1007/s10453-017-9502-6.
Genitsaris, S., Kormas, K. A., & Moustaka-Gouni, M. (2011). Airborne algae and cyanobacteria: Occurrence and related health effects. *Frontiers in Bioscience, 3,* 772–787.
Golan, J. J., & Pringle, A. (2017). Long-distance dispersal of fungi. *Microbiology Spectrum*. https://doi.org/10.1128/microbiolspec.funk-0047-2016.
Gosselin, M. I., Rathnayake, C. M., Crawford, I., Pöhlker, C., Fröhlich-Nowolsky, J., Schmer, B., et al. (2016). Fluoresent bioaerosol particle, molecular tracer, and fungal spore concentrate.ons during dry and rainy periods in a semiarid forest. *Atmospheric Chemistry and Physics, 16,* 15165–15184.
Green, T. G., & Broady, P. A. (2001). Biological soil crusts of Antarctica. In J. Belnap & O. L. Lange (Eds.), *Biological soil crusts: Structure, function, and management* (pp. 133–139). Berlin: Springer.
Griffin, D. W., Kellogg, C. A., Garrison, V. H., & Shinn, E. A. (2002). The global transport of dust: An intercontinental river of dust, microorganisms and toxic chemicals flows through the Earth's atmosphere. *American Scientist, 90,* 228–235.
Guo, Y., Zhao, H., Zuo, X., Drake, S., & Zhao, X. (2008). Biological soil crust development and its topsoil properties in the process of dune stabilization, Inner Mongolia, China. *Environmental Geology, 54,* 653–662.
Hallar, A. G., Chirokova, G., McCubbin, I., Painter, T. H., Wydinmyer, C., & Dodson, C. (2011). Atmospheric bioaerosols transported by dust storms in the western United States. *Geophysical Research Letters, 38,* L17801.
Harding, T., Jungblut, A. D., Lovejoy, C., & Vincent, W. F. (2011). Microbes in high arctic snow and implications for the cold biosphere. *Applied and Environmental Microbiology, 77,* 3234–3243.
Harmata, K., & Olech, M. (1991). Transect for aerobiological studies from Antarctica to Poland. *Grana, 30,* 458–463.
Heinken, T. (1999). Dispersal patterns of terricolous lichens by thallus fragments. *The Lichenologist, 31,* 603–612.
Herbold, C. W., Lee, C. K., McDonald, I. R., & Cary, S. C. (2014). Evidence of global-scale aeolian dispersal and endemism in isolated geothermal microbial communities of Antarctica. *Nature Communications, 5,* 3875.
Holzinger, A., & Karsten, U. (2013) Desiccation stress and tolerance in green algae: Consequences for ultrastructure, physiological, and molecular mechanisms. *Frontiers in Plant Science, 4*, article 327
Horton, W., Miura, H., Onishchenko, O., Couede, L., Arnas, C., Escarguel, A., et al. (2016). Dust devil dynamics. *Journal of Geophysical Research: Atmospheres, 121,* 7197–7214. https://doi.org/10.1002/2016JD024832.
Howard, G. L., & Warren, S. D. (1998). The incorporation of cyanobacteria into starch pellets and determination of escapability rates for use in land rehabilitation. US Army Construction Engineering Research Laboratory Special Report 98/56
Huang, J., & McElroy, M. B. (2014). Contributions of the Hadley and Ferrel circulation to the energetics of the atmosphere over the past 32 years. *Journal of Climate, 17,* 2656–2666.
Hugonnot, V., & Celle, J. (2012). Asexual reproduction by leaf fragmentation in *Mnium stellare* Hedw. *Journal of Bryology, 39,* 67–70.

Jeffries, D. L., & Klopatek, J. M. (1987). Effects of grazing on the vegetation of the blackbrush association. *Journal of Range Management, 40,* 390–392.

Johansen, J. R. (2001). Impacts of fire on biological soil crusts. In J. Belnap & O. L. Lange (Eds.), *Biological soil crusts: Structure, function, and management* (pp. 386–397). Berlin: Springer.

Johansson, V., Lönnell, N., Rannik, Ü., Sundberg, S., & Hylander, K. (2015). Air humidity thresholds trigger moss spore release to extend dispersal in space and time. *Functional Ecology, 30,* 1196–1204.

Jungblut, A. D., Lovejoy, C., & Vincent, W. F. (2010). Global distribution of cyanobacterial ecotypes in the cold biospherere. *The ISME Journal, 4,* 191–202.

Jungblut, A. D., Vincent, W. F., & Lovejoy, C. (2012). Eukaryotes in Arctic and Antarctic cyanobacterial mats. *FEMS Microbial Ecology, 82,* 416–428.

Kade, A., & Warren, S. D. (2002). Soil and plant recovery after historic military disturbances in the Sonoran Desert, USA. *Arid Land Research and Management, 16,* 231–243.

Kellogg, C. A., & Griffin, D. W. (2006). Aerobiology and the global transport of desert dust. *Trends in Ecology & Evolution, 21,* 638–644.

Kharkongor, D., & Ramanujam, P. (2014). Diversity and species composition of subaerial algal communities in forested areas of Meghalaya, India. *International Journal of Biodiversity, 2014,* 456202.

Kjellsson, J., & Döös, K. (2012). Lagrangian decomposition of the Hadley and Ferrel cells. *Geophysical Research Letters, 39,* L15807.

Kok, J. F., Parteli, E. J. R., Michaels, T. I., & Karam, D. B. (2012). The physics of wind-blown sand and dust. *Reports on Progress in Physics, 75,* 106901.

Kubečková, K., Johansen, J. R., Warren, S. D., & Sparks, R. (2003). Development of immobilized cyanobacterial amendments for reclamation of microbiotic soil crusts. *Algological Studies, 109,* 341–362.

Kvíderová, J. (2012). Research on cryosestic communities in Svalbard: The snow algae of temporary snowfields in Petuniabukta, Central Svalbard. *Czech Polar Reports, 2,* 8–19.

Laaka-Lindberg, S., Korpelainen, H., & Pohjamo, M. (2003). Dispersal of asexual propagules in bryophytes. *The Journal of Hattori Botanical Laboratories, 93,* 319–330.

Lalley, J. S., & Viles, H. A. (2008). Recovery of lichen-dominated soil crusts in a hyperarid desert. *Biodiversity and Conservation, 17,* 1–20.

Lamenti, G., Tiano, P., & Tomaselli, L. (2000). Biodeterioration of ornamental marble statues in Boboli Gardens (Florence, Italy). *Journal of Applied Phycology, 12,* 427–433.

Leavitt, S. D., & Lumbsch, H. T. (2016). Ecological biogeography of lichen-forming fungi. In I. S. Druzhinina & C. P. Kubicek (Eds.), *Environmental and microbial relationships* (pp. 15–37). Cham: Springer International Publishing.

Lee, T. F., & Eggleston, P. M. (1989). Airborne algae and cyanobacteria. *Grana, 28,* 63–66.

Lee, H. N., Igarashi, Y., Chiba, M., Aoyama, M., Hirose, K., & Tanaka, T. (2006). Global model simulation of the transport of Asian and Saharan dust: Total deposition of dust mass in Japan. *Water, Air, and Soil pollution, 169,* 137–166.

Lewandowska, A. U., Śliwińska-Wilczewska, S., & Woźniczka, D. (2017). Identification of cyanobacteria and microalgae of various sizes in the air over the Southern Baltic Sea. *Marine Pollution Bulletin, 125,* 30–38.

Lewis, J. M. (2003). Ooishi's observation viewed in the context of jet stream discovery. *Bulletin of the American Meteorological Society, 84*(3), 357–369. https://doi.org/10.1175/BAMS-84-3-357369.

Li, F., Ginoux, P., & Ramaswamy, V. (2008). Distribution, transport, and deposition of mineral dust in the Southern Ocean and Antarctica: Contribution of major sources. *Journal of Geophysical Research, 113,* D10207.

Li, Y. F., Li, Z. W., Jia, Y. H., & Zhang, K. (2016). Biological soil crust formation under artificial vegetation effect and its properties in the Mugetan sandy land, northeastern Qinghai-Tibet Plateau. *Earth and Environmental Science, 39,* 012070.

Li, X. R., Xiao, H. L., He, M. Z., & Zhang, J. G. (2006). Sand barriers of straw checkerboards for habitat restoration in extremely arid desert regions. *Ecological Engineering, 28,* 149–157.

Li, X.-R., Zhao, H.-Y., Wang, X.-P., Zhu, Y.-G., & O'Conner, P. J. (2003). The effects of sand stabilization and revegetation on cryptogam species diversity and soil fertility in the Tengger Desert, Northern China. *Plant and Soil, 251,* 237–245.

Lönnell, N., Hylander, K., Jonsson, B. G., & Sundberg, S. (2012). The fate of the missing spores—Patterns of realized dispersal beyond the closest vicinity of a sporulating moss. *PLoS ONE, 7*(7), e41987.

Macedo, M. F., Miller, A. Z., Dionísio, A., & Saiz-Jimenez, C. (2009). Biodiversity of cyanobacteria and green algae on monuments in the Mediterranean Basin: An overview. *Microbiology, 155,* 3476–3490.

Maestre, F. T., Martín, N., Díez, B., López-Poma, R., Santos, F., Luque, I., et al. (2006). Watering, fertilization, and slurry inoculation promote recovery of biological crust function in degraded soils. *Microbial Ecology, 52,* 365–377.

Marshall, W. A. (1997). Seasonality in Antarctic airborne fungal spores. *Applied and Environmental Microbiology, 63,* 220–2245.

Marshall, W. A., & Chalmers, M. O. (1997). Airborne dispersal of antarctic terrestrial algae and cyanobacteria. *Ecography, 20,* 585–594.

Marshall, W. A., & Convey, P. (1997). Dispersal of moss propagules on Signy Island, maritime Antarctic. *Polar Biology, 18,* 376–383.

McGorum, B. C., Pirie, R. S., Glendinning, L., McLachlan, G., Metcalf, J. S., Banack, S. A., et al. (2015). Grazing livestock are exposed to terrestrial cyanobacteria. *Veterinary Research, 46,* 16. https://doi.org/10.1186/s13567-015-0143-x.

McLeman, R. A., Dupre, J., Berrang Ford, L., Ford, J., Gajewski, K., & Marchildon, G. (2014). What we learned from the Dust Bowl: Lessons in science, policy, and adaptation. *Population and Environment, 35,* 417–440.

McTainsh, G. H., Lynch, A. W., & Tews, E. K. (1998). Climatic controls upon dust storm occurrence in eastern Australia. *Journal of Arid Environments, 39,* 457–466.

Meier, F. C., & Lindbergh, C. A. (1935). Collecting microorganisms from the Arctic atmosphere: With field notes and material. *The Scientific Monthly, 40,* 5–20.

Metzger, S. M., Balme, M. R., Towner, M. C., Bos, B. J., Ringrose, T. J., & Patel, M. R. (2011). *In situ* measurements of particle load and transport in dust devils. *Icarus, 214,* 766–772.

Miller, N. G., & McDaniel, S. F. (2004). Bryophyte disperal inferred from colonization of an introduced substrate on Whiteface Mountain, New York. *American Journal of Botany, 91,* 1173–1182.

Muñoz, J., Felicísimo, Á. M., Cabezas, F., Burgaz, A. R., & Martínez, I. (2004). Wind as a long-distance dispersal vehicle in the Southern Hemisphere. *Science, 304,* 1144–1147.

Nagy, M. L., Pérez, A., & Garcia-Pichel, F. (2005). The prokaryotic diversity of biological soil crusts in the Sonoran Desert (Organ Pipe Cactus National Monument, AZ). *FEMS Microbiology Ecology, 54,* 233–245.

Nickling, W. G. (1978). Eolian sediment transport during dust storms: Slims River Valley, Yukon Territory. *Canadian Journal of Earth Sciences, 15,* 1069–1084.

Orlovsky, L., Orlovsky, N., & Durdyev, A. (2005). Dust storms in Turkmenistan. *Journal of Arid Environments, 60,* 83–97.

Park, C. H., Li, X.-R., Jia, R. L., & Hur, J. S. (2017). Combined application of cyanobacteria with soil fixing chemicals for rapid induction of biological soil crust formation. *Arid Land Research and Management, 31,* 81–93.

Patzelt, D. J., Hodac, L., Friedl, T., Pietrasiak, N., & Johansen, J. R. (2014). Biodiversity of soil cyanobacteria in the hyperarid Atacama Desert, Chile. *Journal of Phycology, 50,* 698–710.

Pearce, D. A., Bridge, P. D., Hughes, K. A., Sattler, B., Psenner, R., & Russell, N. J. (2009). Microorganisms in the atmosphere over Antarctica. *FEMS Microbiology Ecology, 69,* 143–157.

Piñeiro, R., Popp, M., Hassel, K., Listl, D., Westergaard, K. B., Flatberg, K. I., et al. (2012). Circumarctic dispersal and long-distance colonization of South America: The moss genus *Cinclidium*. *Journal of Biogeography, 39,* 2041–2051.

Pohjamo, M., Laaka-Lindberg, S., Ovaskainen, O., & Korpelainen, H. (2006). Dispersal potential of spores and asexual propagules in the epixylic hepatic *Anastrophyllum hellerianum*. *Evolutionary Ecology, 20,* 415–430.

Pointing, S. B., & Belnap, J. (2014). Disturbance to desert soil ecosystems contributes to dust-mediated impacts at regional scales. *Biodiversity Conservation, 23,* 1659–1667.

Potts, M. (1994). Desiccation tolerance of prokaryotes. *Microbiological Reviews, 58,* 755–805.

Prospero, J. M. (1999). Long-range transport of mineral dust in the global atmosphere: Impact of African dust on the environment of the southeastern United States. *Proceedings of the National Academy of Science, 96,* 3396–3403.

Prospero, J. M., & Lamb, P. J. (2003). African droughts and dust transport to the Caribbean: Climate change implications. *Science, 302,* 1024–1027.

Prospero, J. M., & Mayor-Bracero, O. L. (2013). Understanding the transport and impact of African dust on the Caribbean Basin. *Bulletin of the American Meteorological Society, 94*(9), 1329–1337. https://doi.org/10.1175/BAMS-D-12-00142.1.

Qian, W., Quan, L., & Shi, S. (2002). Variations of the dust storms in China and its climatic control. *Journal of Climate, 15,* 1216–1229.

Qiu, G. Y., Lee, I.-B., Shimizu, H., Gao, Y., & Ding, G. (2004). Principles of sand dune fixation with straw checkerboard technology and its effect on the environment. *Journal of Arid Environments, 56,* 449–464.

Rahav, E., Paytan, A., Chien, C.-T., Ovadia, G., Katz, T., & Herut, B. (2016). The impact of atmospheric dry deposition associated microbes on southeastern Mediterranean Sea surface water following an intense dust storm. *Frontiers in Marine Science, 3,* 127. https://doi.org/10.3389/fmars.2016.00127.

Rajeev, L., Nunes da Rocha, U., Klitgord, N., Luning, E. G., Fortney, J., Axen, S. D., et al. (2013). Dynamic cyanobacterial response to hydration and dehydration in a desert biological soil crust. *International Society for Microbial Ecology Journal, 7,* 2178–2191.

Rangarajan, C., & Eapen, C. D. (2012). Estimates of interhemispheric transport of radioactive debris by the east African low level jet stream. *Journal of Geophysical Research: Oceans, 1978–2012*(86), 12153–12154.

Read, C. F., Duncan, D. H., Vesk, P. A., & Elith, J. (2011). Surprisingly fast recovery of biological soil crusts following livestock removal in southern Australia. *Journal of Vegetation Science, 42*(5), 905–916. https://doi.org/10.1111/j.1654-1103.2011.01296.x.

Rosselli, R., Fiamma, M., Deligios, M., Pintus, G., Pellizzaro, G., Canu, A., et al. (2015). Microbial immigration across the Mediterranean via airborne dust. *Scientific Reports, 5,* 16306.

Rousseau, D.-D., Antoine, P., Kunesch, S., Hatté, C., Rossignol, J., Packman, S., et al. (2007). Evidence of cyclic dust deposition in the US Great Plains during the last deglaciation from the high-resolution analysis of the Peoria Loess in the Eustis sequence (Nebraska, USA). *Earth and Planetary Science Letters, 262,* 159–174.

Sahu, N., & Tangutur, A. D. (2015). Airborne algae: Overview of the current status and its implications on the environment. *Aerobiology, 31,* 89–97.

Samad, L. K., & Adhikary, S. P. (2008). Diversity of microalgae and cyanobacteria on building facades and monuments in India. *Algae, 23*(2), 91–114.

Schlichting, H. E. (1969). The importance of airborne algae and protozoa. *Journal of the Air Pollution Control Association, 19,* 946–951.

Schwiesow, R. L., & Cupp, R. E. (1976). Remote Doppler velocity measurements of atmospheric dust devil vortices. *Applied Optics, 15,* 1–2.

Sethi, S. K., Samad, L. K., & Adhikary, S. P. (2012). Cyanobacteria and micro-algae in biological crusts on soil and sub-aerial habitats of eastern and north eastern region of India. *Phycos, 42,* 1–9.

Sharma, N. K., Rai, A. K., & Singh, S. (2006a). Meteorological factors affecting the diversity of airborne algae in an urban atmosphere. *Ecography, 29,* 766–772.

Sharma, N. K., Rai, A. K., Singh, S., & Brown, R. M. (2007). Airborne algae: Their present status and relevance. *Journal of Phycology, 43,* 615–627.

Sharma, N. K., Singh, S., & Rai, A. K. (2006b). Diversity and seasonal variation of viable algal particles in the atmosphere of a subtropical city in India. *Environmental Research, 102,* 252–259.

Sissakian, V. K., Al-Asari, N., & Knutsson, S. (2013). Sand and dust storm events in Iraq. *Natural Science, 5,* 1084–1094.

Søchting, U., & Olech, M. (1995). The lichen genus *Caloplaca* in polar regions. *Lichenologist, 27*(6), 463–471.

Spröte, R., Fischer, T., Veste, M., Raab, T., Wiehe, W., Lange, P., et al. (2010). Biological topsoil crusts at early successional stages on Quaternary substrates dumped by mining in Brandenburg, NE Germany. *Géomorphologie, 16*(4), 359–370.

St. Clair, L. L., Johansen, J. R., & Webb, B. L. (1986). Rapid stabilization of fire-disturbed sites using a soil crust slurry: Inoculation studies. *Reclamation and Rehabilitation Research, 4,* 261–269.

Stark, L. R. (2003). Mosses in the desert. *Fremontia, 31,* 26–33.

Swarf, P. K., Oehlert, A. M., Mackenzie, G. J., Eberli, G. P., & Reijmer, J. J. G. (2014). The fertilization of the Bahamas by Saharan dust: A trigger for carbonate precipitation? *Geology, 42,* 671–674.

Takeuchi, N. (2013). Seasonal and altitudinal variations in snow algal communities on an Alaskan glacier (Gulkana glacier in the Alaska range). *Environmental Research Letters, 8*(3), 035002.

Tesson, S. V., Skjøth, C. A., Šanti-Temkiv, T., & Löndahl, J. (2016). Airborne microalgae: Insights, opportunities, and challenges. *Applied and Environmental Microbiology, 82,* 1978–1991.

Tomaselli, L., Lamenti, G., Bosco, M., & Tiano, P. (2000). Biodiversity of photosynthetic micro-organisms dwelling on stone monuments. *International Biodeterioration and Biodegradation, 46,* 251–258.

Tormo, R., Recio, D., Silva, I., & Muñoz, A. F. (2001). A quantitative investigation of airborne algae and lichen soredia obtained from pollen traps in south-west Spain. *European Journal of Phycology, 36,* 385–390.

Uno, I., Eguchi, K., Yumimoto, K., Takemura, T., Shimizu, A., Uematsu, M., et al. (2009). Asian dust transported one full circuit around the globe. *Nature Geoscience, 2,* 557–560.

Verma, P. K., Kumar, N., Kaushik, P. K., & Yadav, A. (2014). Bryophyte invasion on famous archaeological site of Ahom Dynasty 'Talatal Ghar' of Sibsagar, Assam (India). *Proceedings of the National Academy of Sciences, India Section B, Biological Sciences, 84*(1), 71–74.

Vonnahme, T. R., Devetter, M., Źárský, J. D., Šabacká, M., & Elster, J. (2016). Controls on microalgal community structures in cryoconite holes upon high-Arctic glaciers, Svalbard. *Biogeosciences, 13,* 659–674.

Wang, X., Dong, Z., Zhang, J., & Liu, L. (2004). Modern dust storms in China: An overview. *Journal of Arid Environments, 58,* 559–574.

Warren, S. D. (1995). Ecological role of microphytic soil crusts in arid environments. In D. Allsopp, R. R. Caldwell, & D. L. Hawksworth (Eds.), *Microbial diversity and function* (pp. 199–209). Wellingford: CAB International.

Warren, S. D. (2014). Role of biological soil crusts in desert hydrology and geomorphology: Implications for military training operations. *Reviews in Engineering Geology, 22,* 177–186.

Warren, S. D., & Eldridge, D. J. (2001). Biological soil crusts and livestock in arid ecosystems: Are they compatible? In J. Belnap & O. L. Lange (Eds.), *Biological soil crusts: Structure, function and management* (pp. 401–415). Berlin: Springer.

Webb, R. H., Steiger, J. W., & Newman, E. B. (1988) The response of vegetation to disturbance in Death Valley National Monument, California. US Geological Survey Bulletin 1793

Weber, B., Bowker, M., Zhang, Y., & Belnap, J. (2016a). Natural recovery of biological soil crusts after disturbance. In B. Weber, B. Büdel, & J. Belnap (Eds.), *Biological soil crusts: An organizing principle in drylands* (pp. 479–498). Cham: Springer.

Weber, B., Büdel, B., & Belnap, J. (Eds.). (2016b). *Biological soil crusts: An organizing principal in drylands*. Cham: Springer.

Wilshire, H. G. (1983). The impact of vehicles on desert stabilizers. In R. H. Webb & H. G. Wilshire (Eds.), *Environmental effects of off-road vehicles* (pp. 31–50). New York: Springer.

Womack, A. M., Bohannan, B. J. M., & Green, J. L. (2010). Biodiversity and biogeography of the atmosphere. *Transactions of the Royal Society, 365,* 3645–3653.

Xu, S., Yin, C., He, M., & Wang, Y. (2008). A technology for rapid reconstruction of moss-dominated soil crusts. *Environmental Engineering Science, 25,* 1129–1137.

Zhang, J., Zhang, C., Ma, X., Zhou, N., Wang, H., & Rissler, P. S. (2014). Dust fall and biological soil crust distribution as indicators of the aeolian environment in China's Shapatou railway protective system. *CATENA, 114,* 107–118.

Zhang, T.-H., Zhao, H.-L., Li, S.-G., Li, L.-R., Shirato, Y., & Ohkuro, T. (2004). A comparison of different measures for stabilizing moving sand dunes in the Horqin Sandy Land of Inner Mongolia, China. *Journal of Arid Environments, 58,* 203–214.

Zhao, Y., Bowker, M. A., Zhang, Y., & Zaady, E. (2016). Enhanced recovery of biological soil crusts after disturbance. In B. Weber, B. Büdel, & J. Belnap (Eds.), *Biological soil crusts: An organizing principle in drylands* (pp. 499–523). Cham: Springer.