



Proposed Relationships Between Climate, Biological Soil Crusts, Human Health, and in Arid Ecosystems

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Key Points:

- Biocrusts reduce dust emissions that may carry pathogens that impact human health by reducing pathogenic microbe load in the ambient air
- Biocrust could be used to stimulate nutrient cycling in agricultural fields

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Abstract Biological soil crusts (or biocrust) are diminutive soil communities with ecological functions disproportionate to their size. These communities are composed of lichens, bryophytes, cyanobacteria, fungi, liverworts, and other microorganisms. Creating stabilizing matrices, these microorganisms interact with soil surface minerals thereby enhancing soil quality by redistributing nutrients and reducing erosion by containment of soil particles. Climatic stressors and anthropogenic disturbances reduce the cover, abundance, and functions of these communities leading to an increase of aeolian dust, invasive plant establishment, reduction of water retention in the environment, and overall poor soil condition. Drylands are the most degraded terrestrial ecosystems on the globe and support a disproportionately large human population. Restoration of biocrust communities in semi-arid and arid ecosystems benefits ecosystem health while decreasing dust emissions. Dust abatement can improve human health directly but also indirectly by reducing pathogenic microbe load circulating in the ambient air. We hypothesize that biocrusts not only reduce pathogen load in the air column but also inhibit the proliferation of certain pathogenic microbes in the soil. We provide a review of mechanisms by which healthy biocrusts in dryland systems may reduce soil-borne pathogens that impact human health. Ecologically sustainable mitigation strategies of biocrust restoration will not only improve soil conditions but could also reduce human exposure to soil-borne pathogens.

Plain Language Summary Biocrust compacts soil and redistributes nutrients to neighboring vegetation that can be utilized in agricultural fields and natural ecosystems. These communities can restore degraded drylands from overgrazing, anthropogenic disturbances, and weathering events which contribute to an increase in dust emissions. The reduction of dust has a direct impact on human health but also has an indirect impact by reducing the number of pathogenic microbes that are circulating in the ambient air. Not only do biocrusts contribute to biological and chemical processes, but biocrusts aid in stabilizing the soil reducing dust emissions dramatically. We provide a hypothetical framework of how healthy biocrusts in dryland systems can lead to the reduction of soil-borne pathogens. It is predicted that with climate change, infectious diseases, especially fungal diseases, are going to increase in the future by altering virulence and/or expanding the defined habitat range. Ecologically sustainable mitigation strategies, such as biocrust restoration, are imperative to combat this increase.

1. Impact on Drylands From Climate Change/Land Use Change

Drylands make up 41% of the earth's terrain and support roughly 35% of the human population through provisioning services like agricultural production of crops (Právělie, 2016). These areas are characterized by an aridity index of less than 0.65 (mean annual precipitation/mean annual potential evapotranspiration) (Antoninka et al., 2022; Reynolds et al., 2007). They play a key role in regulating the global carbon, nitrogen, and water cycles, supporting 44% of global cropland (Davies et al., 2016). Drylands are one of the most important ecosystems that support human productivity and the most degraded worldwide due to activities like grazing, farming, and mineral extraction (Antoninka et al., 2022; Reynolds et al., 2007). Negative impacts from globalization have contributed to the erosion of dryland resources (Právělie, 2016; Reynolds et al., 2007). Additionally, changes in vegetation in drylands are predominantly caused by two factors (Právělie, 2016): anthropogenic climate change (ACC), which includes both changes in water availability driven by changes in precipitation and global temperature increases (Burrell et al., 2020; Tong et al., 2018); and increased water use efficiency (carbon gain per unit of water lost) in response to rising atmospheric CO₂ (Donohue et al., 2013). With a decrease in available resources, native plant and animal competition responses will be impacted by increasingly limited resources that

fluctuate through time and vary across space. Climate variability will further decrease biocrust cover and may increase various soil- and vector-borne zoonotic diseases associated with dryland ecosystems. Biocrust restoration is an attractive approach to mitigate the impact of climate and land use change on dryland ecosystems.

As mentioned previously, in drylands, dust is generated from both natural wind erosion and anthropogenic sources. Upon emission, dust may be transported over long distances before deposition. Dust particles may negatively influence human health through inhalation of fine dust particles or microbial pathogens (e.g., viruses, bacteria, and fungi) causing respiratory diseases. Several studies have shown a link between dust and pathogen deposition, which increases the risk of infection in animals and plants. For example, airborne *Staphylococcus aureus* was shown to be better able to produce biofilms and in turn better able to infect a host when aerosols contained a higher concentration of dust versus when the aerosols contained little dust (White et al., 2020). This makes dust mitigation essential for human health. In addition, evidence has been reported that the frequency of dust events (i.e., sandstorms) over American deserts has increased in the past decades (1988–2011) (Tong et al., 2017). A recent study estimated that biocrusts reduce global atmospheric dust emissions by around 60% and prevent the release of about 0.7 Pg of dust annually (Rodríguez-Caballero et al., 2022). Many pathogenic diseases are acquired through dust emissions aerosolized directly from the soil, which makes biocrusts an ideal candidate to reduce the transmission of aerosolized pathogens through the reduction of dust emissions.

2. Biocrusts

Biocrusts are composed of lichens, bryophytes, cyanobacteria, fungi, liverworts, and other microorganisms. They bind and live in the top layer of mineral soil predominantly in drylands (approximately 40% of terrestrial ecosystems). Often inhabiting interspaces between and under plant canopies, it is estimated that up to 70% of the soil surface within some dryland ecosystems is colonized by biocrusts (Rutherford et al., 2017). Biocrusts create a thin cohesive layer that interact with the soil surface minerals (Bowker, 2007) and enhances soil quality by (a) increasing fertility through N and C fixation (Antoninka et al., 2009; Davies et al., 2016), (b) reducing wind and water erosion through aggregating soil particles (Borrelli et al., 2017; Evans & Ehleringer, 1993; Mazor et al., 1996), and (c) redistribution and enhanced containment of soil water to benefit neighboring vegetation (Bowker et al., 2013; Chamizo et al., 2016).

Biocrusts can tolerate stressors that are common within dryland ecosystems due to the ability to suspend metabolic activity during drought and dry periods, and they can reactivate metabolism in response to minor rain events (Antoninka et al., 2022; Coe et al., 2012). However, biocrusts are vulnerable to global climate change stressors, such as greater evapotranspiration due to higher temperatures and lower precipitation. The decrease in the length of hydration events increases metabolic respiration compared to reactivating metabolic activity and net primary productivity. Recent studies have indicated that increased aridity associated with climate change will reduce the diversity of soil microorganisms causing a shift in community composition (Delgado-Baquerizo et al., 2018; Ferrenberg et al., 2015; Maestre et al., 2015). Climate manipulation treatments suggest that climate change may have dramatic effects on biocrust community composition by eliminating key species of mosses and lichens, which are large contributors to biogeochemical and hydrological functions in drylands (Delgado-Baquerizo et al., 2018; Ferrenberg et al., 2015; Maestre et al., 2015; Rutherford et al., 2017). This climate-induced loss of mosses and lichens in favor of early successional cyanobacteria-dominated biocrusts also reduces the characteristically dark, textured soil surface. Thus, a shift in biocrust community states could cause rapid alteration of dryland albedo and energy balance by returning energy to the atmosphere that was once absorbed by the dark biocrust surfaces (Antoninka et al., 2022; Belnap, 1995; Matthias et al., 2000; Nash, 1996; Rutherford et al., 2017).

In addition to climate change stressors, land use changes with physical disturbances (e.g., livestock grazing, damage from vehicles) have been shown to reduce the diversity and abundance of lichens and mosses in biocrust communities which play an important role in ecosystem function (Antoninka et al., 2022; Ferrenberg et al., 2015; Rutherford et al., 2017). This can lead to decreased water availability to neighboring vascular plants through decreased water infiltration into the soil (Belnap, 1995). In addition, the loss of biocrusts can disrupt the net primary productivity, and fertility of soil through soil erosion, as well as the loss of the biota that perform these functions (Antoninka et al., 2022; Ferrenberg et al., 2015; Rutherford et al., 2017). A shift in biocrust community successional states could cause rapid alteration of dryland albedo (Ferrenberg et al., 2015; Maestre et al., 2015; Rutherford et al., 2017) and increase soil loss from wind and water erosion (Delgado-Baquerizo et al., 2018).

Concerns about survival of biocrust communities have prompted many researchers to investigate how to recover communities and how long recovery may take. Studies have explored biocrust restoration through the inoculation of cyanobacteria (Román et al., 2018, 2021). Other approaches, such as organism translocation have been attempted, but this method does not show complete recovery of biocrust (Belnap, 1993; Bowker et al., 2010; Davidson et al., 2002) and may compromise the integrity of biocrust in other areas (Zhao et al., 2016). Given these challenges, studies on natural recovery processes are crucial. These studies not only help inform management of degraded ecosystems but also provide insights into how recovery might be accelerated by understanding the natural restoration process.

3. Dryland Soil and Airborne Pathogens

There are several pathogenic or potentially pathogenic taxa that are soil-borne and are a risk to both animals and plants. Soil-borne pathogens are both medically and agriculturally important and directly impact humans through infection and indirectly through impacts on food security. Viruses, bacteria, fungi, protozoans, and microarthropods are all soil-dwelling microbes that have species that can cause disease in plants and animals. These pathogenic species mainly get dispersed through dust via soil disturbance. It is estimated that 15% of the annual global crop production is lost to biological threats, such as soil pathogens, and that number is expected to increase due to climate change (Barford, 2013; Delgado-Baquerizo et al., 2020a, 2020b; Newbery et al., 2016). This poses a major threat to global food security. Two examples of common soil-borne plant pathogens that cause leaf rot on various hosts are *Alternaria alternata* and *Fusarium oxysporum*, both of which are becoming increasingly resistant to chemical fungicides (Delgado-Baquerizo et al., 2020a, 2020b; Nguyen et al., 2016). Soil is also a reservoir for many pathogens that cause disease in animals, including humans. These pathogens can be residents of the soil community, or the soil may get contaminated by other sources such as animal manure leading to the establishment of the pathogen (Vivant et al., 2013a, 2013b; Wallwork, 1972). Permanent soil pathogens can complete their entire life cycle within the soil. Examples include the bacteria *Clostridium tetani* (Tetanus), and *Listeria monocytogenes* (Listeriosis), and the fungal pathogens *Coccidioides posadasii* and *Coccidioides immitis* (Valley fever) (Pappagianis, 1988; Smith, 1975; Weis & Seeliger, 1975). Some pathogens complete only a part of their life cycle within the soil, such as the bacteria *Bacillus anthracis* (Anthrax) and *Rickettsia rickettsii* (Rocky Mountain spotted fever) (Burgdorfer, 1963, 1975; Hugh-Jones & Blackburn, 2009). Transient or incidental soil microbes can survive in the soil but the soil environment is not necessary to complete their life cycle such as the protozoan parasite *Giardia lamblia* (giardiasis), viruses in the genus *hantavirus* and *poliovirus*, and the bacteria *Leptospira* (Leptospirosis) (Bultman et al., 2013). The complex life cycles of these microbes make it hard to predict where “hot spots” or areas of high pathogen burden occur and with the development of antimicrobial resistance, thus controlling or eliminating these organisms in the environment is an extremely difficult task.

Soil is a dynamic ecosystem that changes through time and the microbes that inhabit the soil in turn respond to these fluctuations (Lauber et al., 2013). Changes in moisture, temperature, pH, and other variables can influence the population dynamics of the entire soil microbial community. Pathogens are usually rare members of the community, existing in low numbers relative to other microbial members. Changes in the soil environment can cause a pathogen population to become a more dominant member of the community potentially leading to more disease (Lauber et al., 2013). A stable biocrust community can potentially combat the temporal expansion of pathogens in the soil due to changes in the soil habitat. Biocrusts could be used as a noninvasive bioremediation mechanism to be deployed at pathogen “hot spots.” Restoring biocrusts at these locations will reduce aeolian dust and therefore direct exposure to pathogens from the soil and dust. Additionally, biocrusts may outcompete pathogens for available nutrients within the soil and reduce pathogen biomass.

One specific disease of interest, common in arid drylands, is coccidioidomycosis, otherwise known as Valley Fever. This fungal disease is caused by both *Coccidioides immitis* and *C. posadasii*. Both species are soil-dwelling fungi that are endemic to the arid and semi-arid deserts of the western United States, Mexico, and parts of Central and South America (Baptista-Rosas et al., 2012; Barker et al., 2007, 2012; Fisher et al., 2007; Maddy, 1958, 1965). Genetically distinct populations of *C. immitis* have been detected in Central and Southern California, and Northern Mexico. For *C. posadasii*, genetically isolated populations are found in Arizona, parts of Mexico, New Mexico, Texas, Central, and South America (Barker et al., 2007, 2012; Teixeira & Barker, 2016). Valley fever has gained attention in the United States due to a recent increase in cases primarily in southern Arizona and California and a newly discovered novel genotype identified in the state of Washington, which was

significantly outside the previously defined endemic area in 2016 (Barker et al., 2019; Benedict et al., 2019; Litvintseva et al., 2015; McCotter et al., 2019).

Valley fever is an exclusively environmentally acquired disease (not communicable) and infection dynamics are inherently influenced by environmental changes such as climate and land use. *Coccidioides* is a dimorphic fungus found growing in the soil as mycelia with alternating spore-containing cells known as arthroconidia. *Coccidioides* spp. growth and abundance are influenced by environmental conditions, proliferating during wet periods. When water is limited and soils are dry, environmental disturbances (e.g., livestock grazing, damage from vehicles, extreme weathering) allow spores to be discharged into the atmosphere. These spores cause infection when inhaled. Although there is much debate, Valley fever is linked to dust emissions where higher airborne particulate matter is linked to a higher incidence of disease. PM₁₀ has been shown to be positively correlated with increased Valley fever cases and there is evidence that dust events and soil-disturbing activities lead to an infection increase (Freedman et al., 2018; Kollath et al., 2022; Laws et al., 2018; Tong et al., 2017, 2022). The same soil-disturbing activities implicated to disperse infectious spores into the air are also shown to disturb biocrust communities.

Biocrusts have also been shown to alter the microbial communities of the soil which could inhibit the proliferation of pathogens, such as *Coccidioides* (Maier et al., 2014). This begs the question if mature biocrust communities in areas endemic to *Coccidioides* spp. can reduce the abundance of pathogen in the environment via direct effects (out-competing *Coccidioides* for soil niche) or indirect effects (reduced dust emissions through soil stabilization, and reduction of animal burrows).

Coccidioides spp. has also been shown to be associated with desert rodents and their burrows. Multiple studies have shown that the probability of detecting the fungus in the environment is greatly increased when collecting soil from within rodent burrows as opposed to outside of the burrow (Kollath et al., 2019; Lacy & Swatek, 1974; Wagner et al., 2023). This evidence suggests that animal burrows are an important reservoir for the pathogen in the environment.

The link between biocrusts and soil-borne pathogens has not been explored thoroughly. The ecology and distribution of *Coccidioides* makes it a model disease system to investigate the role of biocrusts on soil-borne pathogens in dryland environments. Here we review a hypothetical framework of how the importance of healthy biocrust in dryland systems can lead to the reduction of soil-borne pathogens, impacting human health.

4. Human/Environment Interface

Valley fever is on the rise, particularly in southern Arizona and California (Benedict et al., 2019). In the Southwest, areas with high incidences of Valley fever correspond with areas where biocrusts are major contributors to ecosystem function (Lau & Lennon, 2012; Rodriguez-Caballero et al., 2018). To date, no one has attempted to address Valley fever through environmental remediation and restoration of natural soil communities. Restoration of biocrusts in areas of high *Coccidioides* endemism could reduce Valley fever incidence via several pathways (Figure 1). First, stabilizing the soil surface with biocrusts should reduce the potential of *Coccidioides* spores to aerosolize. Second, the increase in biocrust cover contributes to the fertility and water-holding capacity of soils, which could decrease the abundance of *Coccidioides* directly by reducing favorable habitat, or indirectly by creating competition from a more diverse and active soil microbial community. Our overarching objective in this review is to propose soil remediation efforts with biocrust to reduce the occurrence of environmental pathogens like *Coccidioides* spp. in the soil and air by stabilizing the soil surface, reducing soil erosion and associated dust, and increasing below-ground microbial competition. Although there have not been inhibition studies on biocrust microbial communities and human environmentally acquired pathogens, a study utilizing native biocrust cyanobacteria strains with antagonistic properties showed to inhibit the growth of *Phytophthora capsici* in vitro (Águila-Carricondo et al., 2024). Additional research is necessary to understand antagonistic properties of biocrust microbial communities.

5. Effects of Fossorial Animals

Fossorial animals are considered ecosystem engineers as they directly modify ecosystems and shift the availability of resources (Jones et al., 1994, 1997; Lawton & Jones, 1995). This direct modification of habitat impacts geomorphic processes, nutrient turnover, and influences soil hydrology (Eldridge et al., 2012). Interestingly, studies have examined the link between established biocrust communities and a reduction in the amount of animal

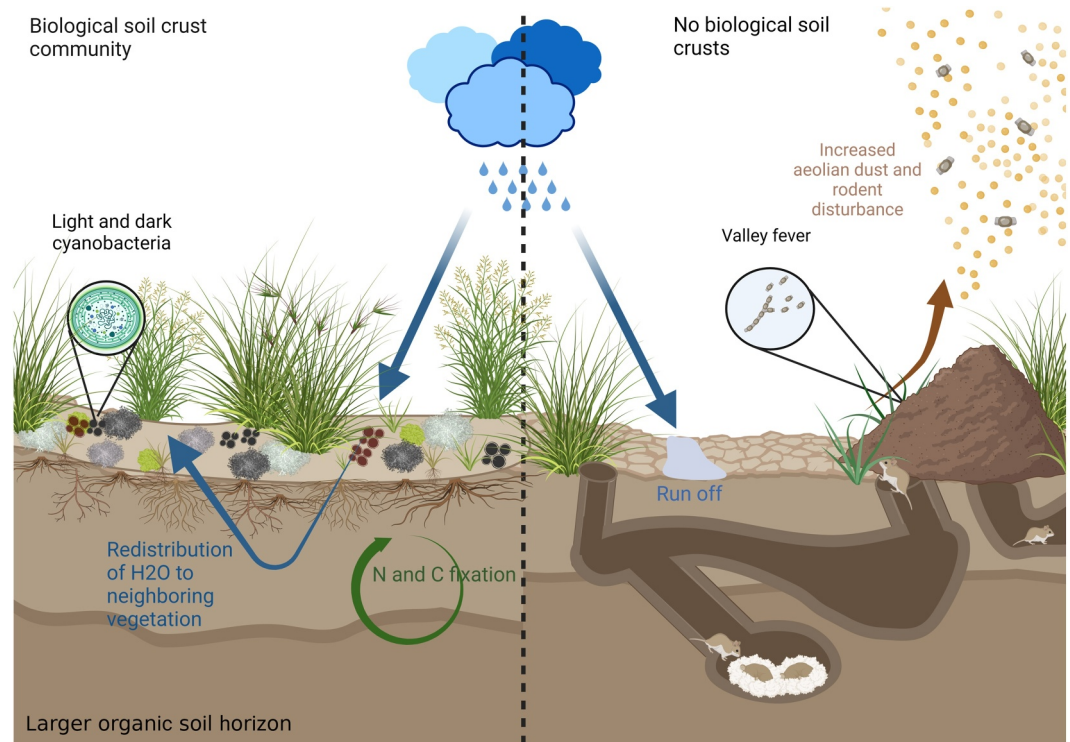


Figure 1. Benefits of biocrust in arid ecosystems versus heavily disturbed and climatically impacted drylands. Biocrust actively redistributes water to neighboring vegetation while also aggregating soil particles and increasing nitrogen and carbon fixation creating a larger organic layer of soil. Heavily disturbed and climatically challenged soils have decreased water infiltration and increased aeolian dust due to erosion leading to a decrease in available resources causing native vegetation and animal competition responses. These areas may also harbor an increase in soil pathogens due to soil biota shifts. Created with [BioRender.com](https://www.biorender.com).

burrows present (Rengifo & Arana, 2017; Zaady & Bouskila, 2002). A study in the Arava desert (eastern Negev desert) monitored the association between burrowing geckos (*Stenodactylus doriae*) and diurnal lizards (*Acanthodactylus* spp.) on preferred soils for burrows. It was found that both geckos and diurnal lizards strongly preferred the fragile crust, where they dug 80% and 94% of their burrows, respectively, instead of more established crust communities (Zaady & Bouskila, 2002). Another study examined fossorial birds impact on biocrust communities in the Lomas of the Sechura-Atacama Desert in Peru. It was noted that bioperturbations made by the fossorial birds increase seed germination promoting vascular plant growth; however, biocrust communities would be disturbed and buried with a soil layer from the burrowing activities of the birds (Rengifo & Arana, 2017). When these burrows are abandoned, biocrust can recolonize the topsoil and a new layer is added to the soil profile. The establishment of biocrust communities could be an important deterrent to keratin-degrading pathogens like *Coccidioides* or hantavirus in the environment by reducing the number of burrowing animals in an area and therefore reducing the amount of the pathogen load. Surveying the environment to determine the association between native dryland burrowing organisms and biocrust would be beneficial in understanding arid ecological associations, and therefore, may be used as a means of pest control in agricultural settings.

6. Climate Induced Land Degradation

As droughts become more frequent, the need for water management and conservation will impact agricultural lands. In the arid environment of the Southwest United States, the Colorado River Basin provides water to seven US states and Mexico. The Basin is divided into two regions; the Upper Basin includes Colorado, New Mexico, Utah, and Wyoming; and the Lower Basin includes Arizona, California, and Nevada. 80% of the Colorado River water supports agricultural purposes and 15% of the United States total agriculture output. This area of the river is experiencing a severe drought, and contributing to the increase in wildfires across the Western United States (Abatzoglou & Williams, 2016). With drastic changes to the environment from drought stressors, studies have

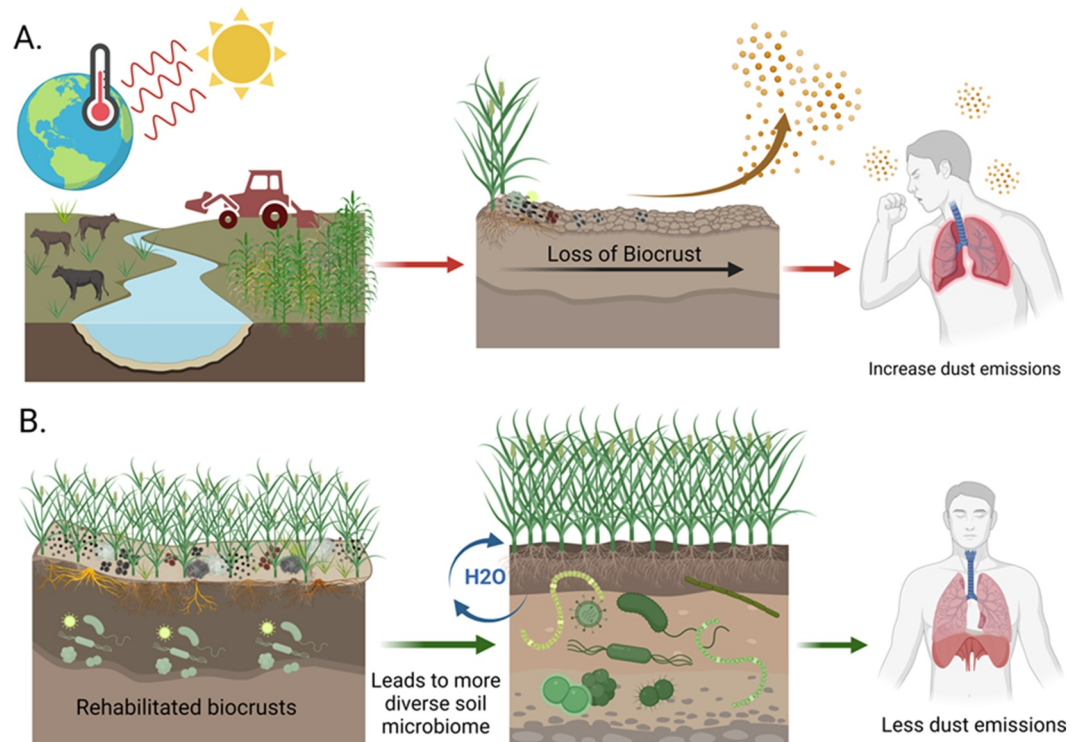


Figure 2. Depiction of effects of disrupted drylands on the ecosystem and health (a) versus biocrust restoration benefits (b). Created with BioRender.com.

identified an increase in respiratory disease related to extreme drought events (Gwon et al., 2023; Li et al., 2020). This can be attributed to unhealthy native plant communities, disturbed soils, and increase dust emissions from wildfires or aeolian dust. Reintroducing biocrust in impacted areas could be used to aid in the redistribution of water to crops as drought conditions impact available water reserves while also creating a natural biofilm compacting soil (Figure 2).

7. Fallow Fields

Croplands that are left vacant for seasons (fallow fields) allow soils to regenerate nutrients that were stripped from the soil during repetitive agricultural use. These 1–5 years of dormancy can allow the recolonization of beneficial microorganisms into the soil, rejuvenating the cycle of nutrients and fertility of the soil. There is a growing interest in utilizing soil microorganisms in agriculture to improve crop turnout. Soil microbes have been studied to enhance plant tolerance to abiotic stresses, such as drought (Ludwig-Müller, 2015) and biotic stresses, such as pathogens and herbivores. Microorganisms can affect plants' resistance to pathogens and herbivores by altering secondary metabolite production, as well as inducing plant defense responses (Grunseich et al., 2019; Harun-Or-Rashid & Chung, 2017).

Agricultural cultivation alters soil conditions, which can have long-term negative consequences for plant performance. These disturbances can be caused by multiple conventional practices such as tillage and fertilizer application (Howard et al., 2020) which have been associated with lower levels of beneficial soil microbes. 44% of croplands are located in drylands where water limitations are high due to drought and climate change leading to fertility loss (Davies et al., 2016). Had these areas not been converted to croplands, soil nutrients and communities would be healthy and mature, allowing native vegetation to flourish, and prevent the development of degraded lands, increased dust emissions that may benefit environmental pathogens like Valley fever. Implementing biocrust restoration would provide beneficial microorganisms to these areas and may counteract the transmission of particulate matter via erosion from water and wind. Large-scale restoration methods of crust has surged in the last decade. One process includes using specific cyanobacteria inoculums like *Tolypothrix distorta* (heterocystous strains), which can be produced with agricultural fertilizers (Roncero-Ramos et al., 2022). Utilizing agricultural

fertilizers to promote the growth of biocrust could be a cost-effective strategy for farmers, requiring little to no additional labor while enhancing soil health and reducing erosion.

8. No-Till Agriculture Impacts on Foliar Pathogens

A copious amount of research has been conducted on agricultural pathogens that threaten crop health and human health, leading to severe economic losses. The importance of soil health has also become a major focus in agricultural systems because chemical, physical, and biological properties may impact plant growth and health. Common practices like tillage, and mechanical disruption of soil, are used for row crops, like cotton and corn, to prepare the soil for seed planting and weed control (Tyler, 2019). This practice has been found to disrupt soil structure and cause erosion (Prasuhn, 2012) and nutrient loss (Jackson et al., 2003; Shipitalo et al., 2013). Two studies found that tillage also negatively influences soil quality variables, such as decreasing organic carbon content, water holding capacity, and mineralizable nitrogen, all of which biocrusts influence positively (Antoninka et al., 2022; Bowker, 2007; Bowker et al., 2013; Davies et al., 2016; Karlen et al., 2013; Kumar et al., 2012, 2013; Mazor et al., 1996).

No-till agriculture (or minimal soil disturbance) has been introduced to decrease repetitive soil disturbances that have detrimental effects and improve soil structure. In Arizona, most crops grown are alfalfa, hay, corn, cotton, and wheat where tillage is often used. These extreme soil disturbances in dryland ecosystems can lead to increased dust aerosolization. This generation of increased dust could carry and disperse infectious particles to neighboring communities. The increasing use of these practices in dryland agriculture is concerning due to the possible presence of endemic soil pathogens, like *Coccidioides* (Valley fever) and *Cephalosporium* (Wilt Rot) (Águila-Carricondo et al., 2024; Barker et al., 2019).

Reducing the use of tillage practices is also beneficial to biocrusts. It can lead to the natural remediation of dryland soil communities without the use of chemicals such as pesticides and fungicides that may impact soil health. Educating farmers in no-tillage areas on enhancing the redistribution of water to vegetation through the cultivation of biocrust as well as the benefits of decreased dust aerosolization that can harbor pathogens, could be beneficial to combat long-term and short-term effects on agriculture due to drought while also preventing disease (Figure 2). Águila-Carricondo (2024) showed native biocrust cyanobacteria strains that inhibit three soil-borne fungal phytopathogen growth via mycelial growth inhibition assays (Águila-Carricondo et al., 2024). Although there is much research on cyanobacteria antifungal production (Manjunath et al., 2010; Roncero-Ramos et al., 2022), further research is needed to explore the potential of biocrust cyanobacteria in antifungal production, particularly in relation to agricultural applications, to better understand their effectiveness and potential for crop protection.

9. Grazing Impacts

Grasslands managed for grazing are the largest land-use category globally, with a significant proportion of these grasslands occurring in semiarid and arid regions that biocrusts inhabit. In such dryland systems, the effect of grazing on native plant diversity has been uncertain with some studies suggesting that grazing reduces native plant diversity while others identify moderate to small-scale grazing has nearly little effect on native communities (Souther et al., 2020). Livestock grazing often alters aboveground and belowground communities of grasslands and their mediated carbon (C) and nitrogen (N) cycling processes at the local scale (Wang et al., 2020). Studies have also found that community compositions that have undergone intense grazing that exceeds community tolerance coupled with climate change factors, like drought, over relatively long timescales can increase invasiveness of nonnative species (Souther et al., 2020).

Agricultural expansion and overgrazing are globally recognized as key contributors to accelerated soil degradation and surface erosion (Donovan & Monaghan, 2021; Trimble & Mendel, 1995). The degree of grazing and intensity of use can create a soil compaction problem and contribute to increased surface runoff. Extreme grazing can damage biocrusts that prevent the effects of erosion, support soil hydrology, and possibly increase dust emissions that could harbor pathogens.

Trade-mediated dispersal of organisms beyond their natural range leads to the introduction and spread of invasive species that harm native biodiversity and impair different functions of socio-biological systems (Qu et al., 2021; Sala et al., 2000; Walsh et al., 2016). The definite consequence of increasing rates and volumes of such biotic

exchange is the co-occurrence of multiple invasive species across different habitats (Kuebbing et al., 2013). Invasive plants modify soil conditions either directly by depositing leaf litter of different quality and quantity (Ehrenfeld, 2001) or indirectly by affecting microbial communities and their activity (Kourtev et al., 2003; Qu et al., 2021; Vujanović et al., 2022). Non-native species introduction skew soil nutrients and can promote the propagation of soil pathogens by shifting microbial communities, stressing plants, and making them more susceptible to infection.

9.1. Mining

Global annual mineral production (AMP) in arid and semiarid regions has increased by $\sim 120 \times 10^8$ t from 19,901 to 2018 (British Geological Survey). Increasing global demands for mineral resources have exploited environments causing groundwater and air pollution, depletion of groundwater, and deforestation. Drylands rely on groundwater storage for vegetation sustainability due to intermittent precipitation which greatly affects the physical damage caused by mining. In extractive processes such as open-cut and strip mining, it is common practice to remove topsoil that harbors seeds, nutrients, and microorganisms. Large-scale mining activities break and bury biocrust organisms, resulting in changed biocrust communities (Gabay et al., 2023). Additionally, these activities result in intense dust emissions that can lead to pathogen exposure, like Valley fever. Construction, mining, and agricultural occupations are at high risk of Valley fever exposure in endemic areas. Despite the biocrust ability to restore degraded lands by kick-starting soil carbon sequestration (Duran et al., 2021) it has yet to be harnessed as a tool during mining recovery.

9.2. Fire

In recent decades, uncontrolled sporadic wildfires have become more of a concern in arid and semi-arid ecosystems due to extreme droughts. Outcomes of this are soil loss to wind and water erosion, increased exotic grass cover, and loss of native species. As with other disturbances, wildfire degradation leads to more dust production as well as rodents that can be environmental vectors of Valley fever and other pathogens. To minimize long-term damage to the ecosystem, active rehabilitation of fire-affected areas is often quickly initiated. However, restoration is challenging due to low and variable moisture conditions in these regions (Jiménez-Morillo et al., 2020). Fire moss biocrust restoration has been proposed as a method to restore ecosystem health in dryland forests (Grover et al., 2020). It is unclear the effects of pathogen dispersal during and after wildfires to new areas although the conditions during a wildfire (high winds and soil disturbance) have the potential to increase the pathogen load into the air column causing more infections. There have been reports of wildland fire fighters and state prison inmates employed to fight fires having an increased risk of respiratory infections, such as Valley fever (Betchley et al., 1997; Donnelly et al., 2022; Laws et al., 2021).

10. Conclusion

Biocrusts are an essential component of dryland soil ecosystems. Not only do they contribute to biological and chemical processes, but biocrusts aid in stabilizing the soil reducing dust emissions dramatically (Antoninka et al., 2022; Burrell et al., 2020; Davies et al., 2016; Maier et al., 2014). These complex communities are also very susceptible to disturbance. The reduction of dust has a direct impact on human health but also has an indirect impact by reducing the number of pathogenic microbes that are circulating in the ambient air. We hypothesize that biocrusts are not only reducing the pathogen load in the air column, they are inhibiting the proliferation of certain pathogenic microbes in the soil. A healthy biocrust community will lead to fewer soil-borne pathogens. Examining this dynamic in the Valley fever disease system is a great model for other dryland soil pathogens.

We argue that the destruction of biocrust systems will lead to an increase in Valley fever cases in humans. There is strong evidence that suggests a link between dust emissions and the increase in Valley fever cases in the endemic region (Tong et al., 2017, 2022). Many studies have shown that healthy biocrust communities limit the amount of dust that is emitted into the atmosphere, in some cases by 60% (Rodríguez-Caballero et al., 2018, 2022). The reduction of dust emissions in the endemic region for Valley fever will reduce the number of infectious spores present in air.

There is also evidence linking the presence of the fungus that causes Valley fever to animal burrows in the environment (Kollath et al., 2019; Lacy & Swatek, 1974; Taylor & Barker, 2019; Wagner et al., 2023). Previous studies have suggested that established biocrust communities reduce the number of animal burrows by deterring

the animals from constructing their burrows at that location (Zaady & Bouskila, 2002). Reducing the amount of animal burrows at locations near heavenly inhabited by humans, by establishing healthy biocrusts, may reduce the transmission of the fungus by eliminating environmental point sources.

Another hypothesis that we propose is that healthy biocrust communities will reduce the amount of Valley fever in the soil by directly outcompeting the fungus. Biocrusts alter the microbial communities in soil by changing the physio-chemical properties of the soil at a microscale increasing the amount of microbial diversity underneath established soils (Maier et al., 2014). These alterations can apply selection pressures to the microbial communities that select for certain microbes over others. These alterations in the community can lead to an abundance of microbial antagonists that may outcompete the fungal pathogen reducing the load and therefore reducing the transmission risk.

We provide a hypothetical framework of how the importance of healthy biocrusts in dryland systems can lead to the reduction of soil-borne pathogens, directly improving human health. It is predicted that with climate change, infectious diseases, especially fungal diseases, are going to increase in the future by adapting to become more virulent and/or by range expansion. Ecologically sustainable mitigation strategies, such as biocrust restoration, are imperative to combat this increase.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

No data were generated or analyzed for this review.

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