

## The Organizing Principle in Dryland Ecosystems: Biological soil crusts

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By:

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*Illustration: Belnap and Lange (2013)*

**Abstract:**

Biological soil crusts (BSC) cover 70% of the earth's drylands, making them an integral part of dryland ecosystem functioning in the Colorado Plateau and beyond. As a diverse, ground-dwelling symbiotic community of lichen, mosses, fungi and bacteria, BSC directly impact soil hydrology, carbon and nitrogen cycling, and soil stabilization in the Colorado river shed. Late successional communities of BSC can decrease rates of soil evaporation and infiltration through their physical crust barrier, fix and store carbon and nitrogen, and decrease erosion and dust emissions from otherwise erodible soils. In this paper, I present case studies that demonstrate the threats of global climate change and physical disturbance to BSC in the U.S. Southwest. The results from a long-term experiment overwhelmingly suggests that both physical disturbance and projected changes in the U.S. Southwest's climate will cause a shift from late succession to early succession BSC communities. Furthermore, physical disturbances will also cause decreases in total BSC cover and BSC community richness. These effects will largely result in early successional BSC communities that are less fertile, less stable and more vulnerable than their late succession counterparts. I end the paper by proposing a simple yet challenging way to best protect BSC for generations to come – by leaving them alone.

**Goals of the paper:**

- Briefly review the structure of biocrusts and discuss their extent and ecosystem impact globally and in the Colorado Plateau.
- Present two pressing threats to biological soil crusts in the Colorado Plateau and beyond and discuss why these threats matter.
- Propose feasible ways to act and preserve biological soil crusts for generations to come.

**Literature review:***Structure of Biological Soil Crusts*

Biological soil crusts (BSC) are the “continuous living skin” of soil surfaces (top 2 cm) throughout the world (Weber et al., 2016). As a diverse and living community of lichens, mosses, algae, fungi, and cyanobacteria, biological soils crusts thrive in environments ranging from Alaska to the southwestern regions of Africa (Ullmann & Büdel, 2003; Root et al., 2020; Miller et al., 2017). As a community overall, BSC can fix substantial amounts of nitrogen and carbon (via photosynthesis) from the atmosphere (Rajeev et al., 2013). Cyanobacteria, the primitive cornerstone of early successional BSC communities, are thin, filamentous nitrogen-fixing bacteria that secrete sticky substances and provide carbon to their fungal partners via photosynthesis (Miller et al., 2017; Belnap and Eldridge, 2001). The most common cyanobacteria found in the Great Basin and Colorado Plateau is *Microcoleus vaginatus*. Fungi found in BSC can be symbionts of plant roots, algae or cyanobacteria, but can also be free-living decomposers (Miller et al., 2017). When participating in a symbiotic relationship with cyanobacteria, the fungus provides a hospitable environment for the cyanobacteria by regulating the amount and intensity of sunlight and water. Mosses and lichen, which comprise the late-successional BSC community (Miller et al., 2017), appear in BSC communities if the community is stable and soil moisture levels are adequate (Weber et al., 2016).

While BSC is a ground-dwelling community, its' propagules are readily carried in dust and are known to be able to survive long periods of desiccation (Rajeev et al., 2013). This ability

to withstand desiccation in large stems from the fact that members of BSC are poikilohydric – meaning they are unable to maintain cellular homeostasis and only become metabolically active when water is present (Weber et al., 2016; Ferrenberg et al., 2017). However, the previously mentioned cornerstone cyanobacteria species *Microcoleus vaginatus*, can migrate vertically in the soil strata to seek available soil water and escape harsh UV radiation (Rajeev et al., 2013). This in tandem with the ability to very rapidly (~ 3 minutes) resuscitate from a dormant state uniquely situates the microbe to take advantage of short water pulses, which are projected to become more prevalent in arid lands with impending climate change (Rajeev et al., 2013).

### *Extent and ecosystem impact of BSC*

Dryland ecosystems cover roughly 45% of the world surface (Právělie, 2016), with BSC alone comprising 70% of the ground cover in these fragile ecosystems (Ferrenberg et al., 2017). Given their extent and the fact that they exist in every desert in the world (Miller et al., 2017), it's not surprising that biological soil crusts are a defining feature of drylands– otherwise known as the “critical zone” of arid and semi-arid ecosystems (Weber et al. 2016). In cooler or wetter regions, the critical zone may occur within meters above or below the soil surface (Weber et al., 2016). The shallow rooted plants and sparse vegetative landscape characteristic of global desert ecosystems make only the top few centimeters of soil a hot spot for major inputs, outputs, translocations and transformations (Weber et al., 2016). In regions such as the Colorado River watershed, the shallow critical zone where biological soil crust community reside presumably have direct impacts on ecosystem processes and functions such as soil stabilization, soil hydrology, surface albedo, and nitrogen and carbon cycling (Ferrenberg et al., 2017).

BSC, and more specifically the lichen and cyanobacteria community members of BSC, weather rocks into soil particles that are then subsequently stabilized by the creation of soil aggregates (Weber et al., 2016). Aggregate formation via BSC is catalyzed through the exudation of polysaccharides from their cyanobacterial, lichen, or moss community members, or via the physical aggregation of soil microaggregates by interactions with fungal hyphae (Ferrenberg et al., 2017; Tisdall et al., 1994). Enhanced aggregation and the creation of a physical surface crust through exudation and fungal mechanisms can decrease soil erosion caused by wind and water (Belnap and Büdel et al., 2016). This crust also significantly slows rates of soil drying after precipitation events and creates microtopography in desert ecosystems, which has important implications for soil hydrology (Ferrenberg et al., 2017).

Biological soil crusts can affect soil hydrology both on the soil surface and areas immediately underneath the crust (Bowker et al., 2013) by controlling evaporation and infiltration rates. In regions that receive annual precipitation and experience freezing and thawing cycles such as the Colorado Plateau and Great Basin, these effects are amplified (Miller et al., 2017). This is in large due to the enhancement of microtopography via frost and heave processes that occur in the soil as well as the higher proportions of late succession BSC community members such as mosses and lichens (Miller et al., 2017). In a 1983 study conducted in the pinyon-juniper woodlands of the Colorado Plateau, researchers found that late succession BSC community members such as lichen and algae significantly slowed infiltrations rates of ponded water compared to BSC comprised of earlier successional community members such as cyanobacteria (Brotherson and Rushforth, 1983). This was corroborated by a 2013 study that found that total cover and community composition (i.e., late succession community members such as lichens or mosses) significantly decrease infiltration rates (Bowker et al., 2013). This function of decreased infiltration is important for dryland ecosystems, as decreasing the overall

infiltration rate will allow water to runoff to other areas, subsequently increasing total ecosystem productivity at the landscape scale (Bowker et al., 2013). Furthermore, upon infiltration, the decay of tall moss BSC community members could create long vertical macropores that serve as water conduit from the soil surface to the sub-surface soil microbial community (Bowker et al., 2013). Conceivably, BSC's ability to significantly alter hydrological processes could have implications for the Great Basin region as it could control the amount of water, nutrients, and sediment entering the Colorado River. In addition to controlling major hydrological processes, BSC communities directly affect the surface albedo of dryland ecosystems (Ferrenberg et al., 2017).

The absorptive and reflective properties of early and late successional community are intrinsically different (Rutherford et al., 2017). The early succession community members, cyanobacteria, are typically shiny and light pigmented which leads to an increased surface reflectance (albedo) and decreased surface energy absorbance (Rutherford et al., 2017). The late succession community members such as algae, lichens, and mosses, have darker pigments and thus a decreased albedo and increased surface energy absorbance (Rutherford et al., 2017). Even in regions where biocrust is dominated by only cyanobacteria communities, late-successional cyanobacterial species are dark due to UV-absorbing pigmentation developed for UV protection – similar to that of sunscreen (Jazi, 2017). The absorptive and reflective properties associated with BSC are important to consider, as the succession of BSC communities can significantly alter soil temperatures (Jazi, 2017) and the amount of light or radiation being reflected off of the earth's surface – both of which are crucial components of modeling projections for global climate change.

Biological soil crusts play a critical role in carbon fixation and nutrient acquisition – more specifically nitrogen and carbon cycling – in dryland ecosystems (Ferrenberg et al., 2017; Miller et al., 2017). Soil immediately below BSC are speculated to contain 200% more soil nitrogen and upwards of 300% more soil carbon than soils with no presence of biological soil crusts (Pointing and Belnap, 2013). On a global scale, models estimate that BSC could account for nearly 50% of terrestrial N fixation and 7% C fixation, though these estimates can vary widely in the literature (Elbert et al. 2012; Porada et al. 2014). In addition to the amount of C fixed globally, the overall biomass produced by BSC in select ecosystems can exceed that produced by vascular plants (Miller et al., 2017) – suggesting that they could play an integral role in soil C accumulation and subsequent stabilized organic matter. Furthermore, recent literature has shown that BSC presence can control vascular plant establishment by providing or limiting the number of microsites available for annual grass establishment (Root et al., 2020; Miller et al., 2017). This means that not only do they directly contribute a significant amount of carbon to the ecosystem, they can control the type and amount of carbon contributed to the system by controlling vascular plant establishment (Root et al., 2020). Once vascular plants are established in proximity to BSC, it's hypothesized that fungal bridges could be controlling nutrient exchanges between vascular plants and biocrusts (Zhang et al., 2016). Dark septate fungi from the BSC community have been found to translocate solubilized nutrients (i.e., phosphorus) to vascular plants as far as 1 meter away even in the absence of roots (Zhuang et al., 2014) by directly entering plant tissues, while the vascular plants in return provide carbon to their fungal partner that was assimilated during photosynthesis (Green et al., 2008). The last two ways that the BSC can control N and C cycling is through physical SOM protection via it's ability to enhance aggregation (Ferrenberg et al., 2017) and by exuding C and N compounds directly into

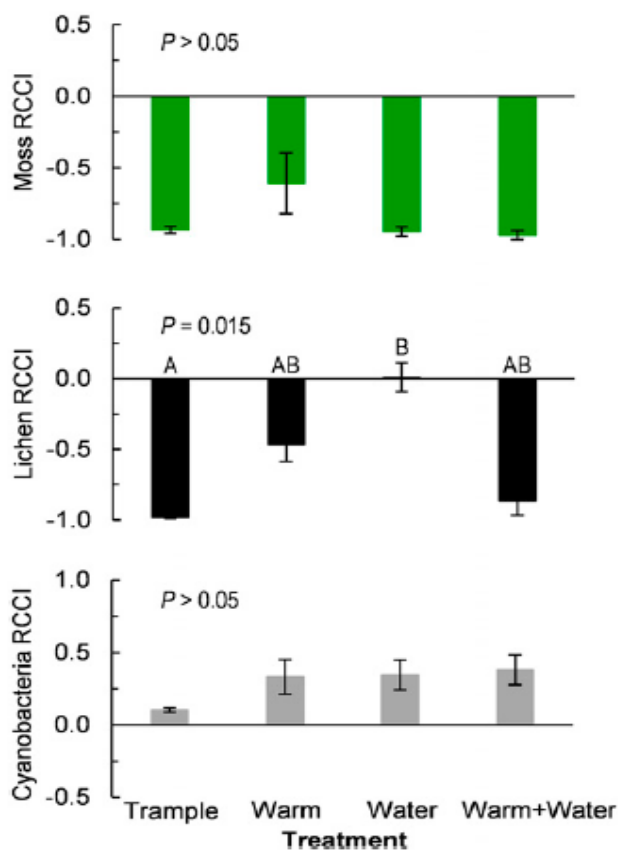
the soil – these compounds can be consumed by microbes and subsequently stabilized through biogeochemical reactions (Ferrenberg et al., 2017; Future of Soil Carbon Book).

## Recent Case Studies

*What are two serious threats to biological soil crusts currently?*

### Climate change

As with many fragile biological systems, BSC are extremely vulnerable to alterations in climatic conditions. Disturbances such as those associated with significant changes in ambient air temperature and shifts in precipitation patterns have recently been found to alter BSC cover and species and composition (Reed et al., 2016). To address the concerns associated with BSC community shifts in response to global climate change, a long-term (15 year) BSC field



**Fig. 1.** Relative Cover Change Index, RCCI for moss (Top), lichen (Middle), and cyanobacteria (Bottom) in biocrusts subjected to climate manipulations or physical disturbance from repeated human trampling. RCCI shows changes in biotic cover relative to controls (Methods). The RCCI value ranges from +1 (100% increase in cover in response to treatment) to -1 (100% decrease in cover in response to treatment). Bars are means  $\pm$  1 SE, P values are probability of type I error (Kruskal–Wallis tests), and lettering indicates significant differences via Steel–Dwass nonparametric pairwise comparisons. **Ferrenberg et al. (2015)**

experiment was established in the Colorado Plateau. Simulated climate change conditions closely followed those predicted for the US Southwest by the year 2100 – a four-degree Celsius increase in ambient air temperature and small (1.2 mm), frequent pulses of summer precipitation followed by drought. Researchers at this site examined the effects of 10 years of warming (Ferrenberg et al., 2015) and altered precipitation patterns in a full-factorial design with four treatments: control (no warming or water), watering, warming, and warming + watering. The three BSC community members that they were interested in were cyanobacteria, mosses, and lichens.

The results of this long term study overwhelmingly demonstrated three important trends that occur as a result of climate change in the Colorado Plateau: (i) biological soil crust communities experience more respiratory loss than photosynthetic gain (thus net loss in C) under smaller but more frequent precipitation scenarios (Reed et al., 2012); (ii) increased rates of nitrification and thus available soil nitrate under smaller but more frequent precipitation scenarios (Reed et al., 2012); (iii) transition from late successional BSC communities to early succession communities (Rutherford et al.,

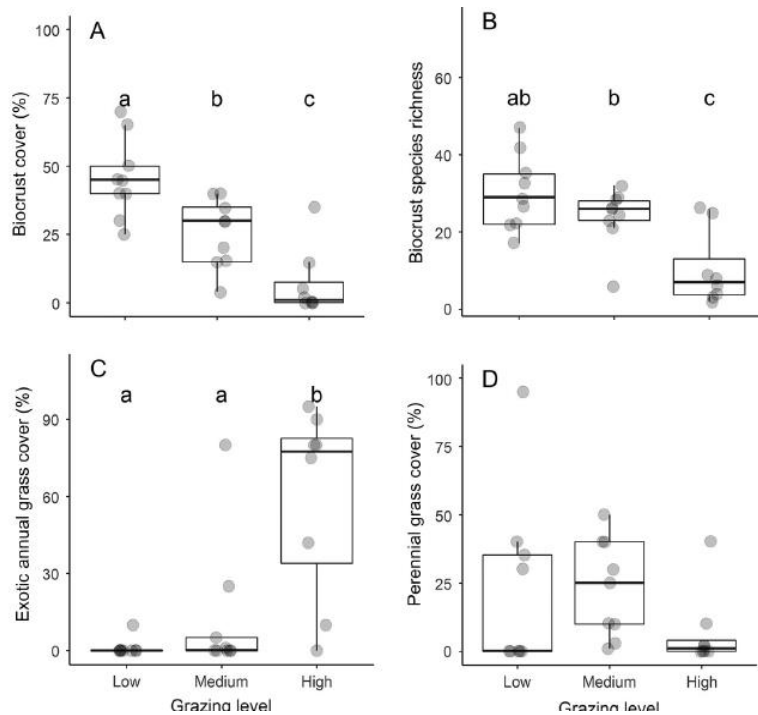
2017; Ferrenberg et al., 2015; **Fig. 1**). The transition from late to early succession of BSC communities is primarily characterized by a severe decrease in moss and lichen communities under watering and warming relative to the control (Ferrenberg et al., 2015; **Fig. 1**).

Contrastingly, cyanobacteria communities increase significantly over a ten-year period in response to warming and watering (Ferrenberg et al., 2015, **Fig. 1**).

Though not yet experimentally proven in this study, it is hypothesized that this community shift in large stems from the fact that moss's and lichen's ability to survive in harsh conditions ultimately lead to their demise under simulated climate change scenarios (Herrington, 2015). Photosynthesis is an energy intensive process, and when the moss and lichen are reactivated upon wetting (because they are poikilohydric), they rejuvenate from desiccation and begin fixing carbon. However, since the precipitation amount is so little (< 2mm) and evaporation rates are increased with warmer temperatures, the photosynthesis process is halted in such a way that the moss and lichen don't actually yield the end carbon benefit from the expensive photosynthetic process (Herrington, 2015). After this occurrence multiple times, the moss and lichen become resource exhausted and eventually starve to death (Herrington, 2015). It's thought that cyanobacteria may have an inverse relationship with this warming and watering trend because they are able to quickly (3 minutes) resuscitate from a dormant state and begin photosynthesizing within an hour of rehydration (Rajeev et al., 2013), while also being able to migrate vertically within the top soil layer. This permits cyanobacteria to take advantage of small water pulses and escape harmful UV radiation (Rajeev et al., 2013).

### **Physical Disturbance**

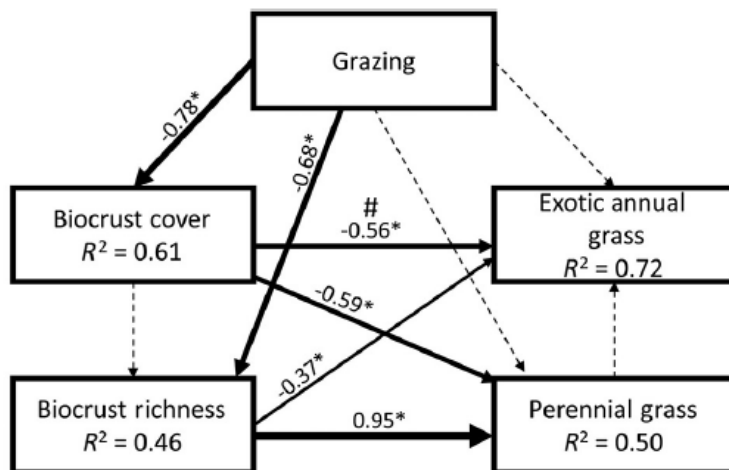
The two leading threats to BSC associated with physical disturbance in the Colorado Plateau and beyond are grazing and recreational activities. When vehicles, livestock, or human trampling occur atop biocrusts, the bonds holding biocrust together are broken and the pores where BSC community members reside are compacted (Ferrenberg et al., 2017). After these bonds are broken, BSC and the surrounding soil are more prone to erosion, which can physically remove BSC organisms – often moving them to water or under sediments (Ferrenberg et al., 2017). In the same long-term Colorado Plateau as described in the climate change case study, researchers found that human trampling (i.e., recreation) has the same effect on BSC community composition as climate change – moss and lichen BSC communities decrease while cyanobacteria increase (Ferrenberg et al., 2015, **Fig. 1**). As for grazing activities, emerging research from a dry, hot region in Idaho has shed light on how livestock pressure could affect BSC communities and subsequent exotic annual grass invasions (Root et al., 2020).



**Fig. 2.** Soil biocrust and vascular plants related to three levels of grazing intensity at 27 sites in Idaho, USA. Different lowercase letters indicate significantly different groups ( $P < 0.05$ ). Box plot components are midline, median; box edges, 25th and 75th percentiles; and whiskers, 1.5 times the inter-quartile range. **Root et al. (2020)**

Researchers have long known there to be an inverse relationship between exotic annual grass invasions and biological soil crusts, but the causal link between the two has remained unclear until this last year. It was unknown if exotic annual grass litter was suppressing BSC establishment or if BSC presence suppressed exotic annual grass establishment. In order to test their hypothesis, researchers had to impose a treatment that would be both: i) realistic in sensitive dryland ecosystems; ii) directly affect BSC communities and annual exotic annual grass growth. Root et al. (2020) selected grazing as the treatment, which resulted in a decrease in BSC cover (%) and BSC community richness when grazing intensity increased (Root et al., 2020, **Fig. 2**). In contrast,

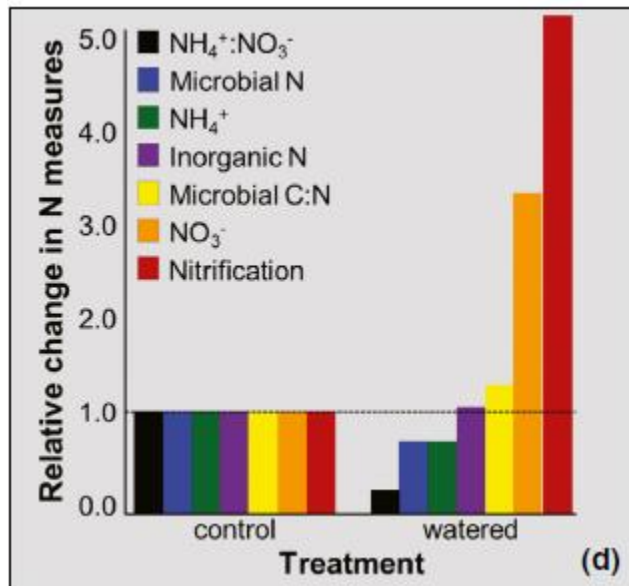
exotic annual grass cover (%) increased with increasing grazing intensity (**Fig. 2**). Using structural equation modeling, they discovered that there was a negative relationship between grazing and BSC cover and richness, but no significant relationship between grazing and annual exotic annual grass cover (**Fig. 3**). Furthermore, the authors found a negative relationship between BSC cover and exotic annual grass cover, suggesting that the deterioration of biocrusts via physical disturbance (i.e., grazing) promotes exotic annual grass invasions (Root et al., 2020; **Fig 3**).



**Fig. 3.** Structural equation models (SEMs) testing the effects of grazing intensity on soil biocrust and vascular plant communities. Numbers indicate standardized path coefficients and arrow thickness is weighted by the strength of the path with their associated sign. Paths with  $P < 0.05$  are labeled (\*) and hypothesized paths that were not significant ( $P > 0.1$ ) are shown as dashed black lines. (A) The first SEM examines the direct and indirect effects of grazing on exotic annual grass cover. A # marks a potential recursive path in which exotic annual grasses affect biocrust cover. **Root et al. (2020)**

### Why should we care about these threats?

Given the extent of BSC throughout the Colorado Plateau and beyond, the deleterious effects of climate change and physical disturbance on BSC could have serious global-scale environmental consequences. Regarding climate change, the Colorado Plateau study demonstrates that with shifts in precipitation patterns, there could be much higher levels of soil nitrate – a form of nitrogen that is readily lost to volatilization and leaching (Reed et al., 2012;



**Fig. 4.** N pools and fluxes in watered plots relative to control plots: watered plots maintained lower NH<sub>4</sub> C concentrations, NH<sub>4</sub> C=NO<sub>3</sub> ratios and microbial biomass N, and higher microbial biomass C/N ratios, soil NO<sub>3</sub> concentrations and potential nitrification rates. Values are means and asterisks depict significant differences among samples taken from the control plots and those taken from watered plots: \* P<0:05; \*\* P<0:01; \*\*\* P<0:001. Data suggest that increased frequency of small precipitation events led to rapid moss die off and a switch to a NO<sub>3</sub>-based soil N economy.

Reed et al. (2012).

increase. Additionally, if BSC communities decline globally and exotic annual grass invasions increase, it will likely lead to an increase in wildfire size and intensity (Root et al., 2020). When combined with projected increases in temperature and decreases in annual rainfall in the Colorado Plateau, the invasion of annual grasses could lead to ecologically catastrophic wildfire seasons.

## Going Forward

### How can we help biological soil crusts in the Colorado Plateau and beyond?

As with many other biotic components of ecosystems, the best thing humanity can do for biological soil crusts is to leave them alone. In a recent article by Warren et al. (2019), authors point out the downfalls of previous attempts to restore BSC in dryland ecosystems, such as transplanting BSC communities from one region to another (Cole et al., 2010) or inoculating a degraded region with BSC propagules, fertilizer and water (Maestre et al. 2006). These attempts

**Fig. 4).** This could have lasting effects on ground water quality and global N balances, which drive primary productivity. With increased respiration and decreased photosynthetic rates occurring with these shifts in precipitation, positive global feedback loops will likely occur – as more CO<sub>2</sub> enters the atmosphere from BSC respiratory losses, it will exacerbate warming which will then intensify respiration rates. Shifts from late to early succession will likely increase albedo on a global scale under warming and water trends projected in the U.S. Southwest, leading to shifts in dryland soil surface energy balance (Rutherford et al., 2017). All of these demonstrated effects should be considered in global climate model projections going forward.

As for physical disturbance, increased erosion and dust emissions as well as increased frequency of annual grass invasions are to be expected if BSC communities are compromised (Ferrenberg et al., 2015; Root et al., 2020). With increased soil erosion, human health could be threatened (Griffin et al., 2007) and sediment transport into fragile ecosystems such as the Colorado River could



have had moderate to limited success, with the cost of regeneration often exceeding what is practical for BSC rehabilitation on a global scale. Warren et al. (2019) urges that we adopt passive restoration, as it is the most viable method of catalyzing BSC recovery. This primarily entails removing disturbances that suppress BSC growth, as BSC propagules are in the air and will inoculate viable soil via aerobiology and passive dispersal (Warren et al., 2019).

BSC cover majority of the world's drylands and provide a plethora of ecosystem services. To maintain vital soil functioning in these fragile ecosystems, it's imperative that we fiercely protect them by implementing progressive climate and land management policies. Policies that reward and incentivize land stewards to combat global climate change and implement sustainable grazing practices will be a promising step towards conserving BSC. Additional steps include educating the general public on the importance of staying on trails and managing our parks in ways that balance human activity and BSC conservation. Any steps taken, both on an individual or policy level, will be a path forward in the preservation of this precious soil resource for generations to come

## Literature Cited

- 1) Belnap, J., and D. Eldridge. "Disturbance and Recovery of Biological Soil Crusts." *Biological Soil Crusts: Structure, Function, and Management*, edited by Jayne Belnap and Otto L. Lange, vol. 150, Springer Berlin Heidelberg, 2001, pp. 363–83. DOI.org (Crossref), doi:10.1007/978-3-642-56475-8\_27.
- 2) Belnap, Jayne, and Otto L. Lange. *Biological Soil Crusts: Structure, Function, and Management*. Springer Science & Business Media, 2013.
- 3) Belnap, Jayne, and Burkhard Büdel. "Biological Soil Crusts as Soil Stabilizers." *Biological Soil Crusts: An Organizing Principle in Drylands*, edited by Bettina Weber et al., Springer International Publishing, 2016, pp. 305–20. Springer Link, doi:10.1007/978-3-319-30214-0\_16.
- 4) Bowker, Matthew A., et al. "Hydrology in a Patterned Landscape Is Co-Engineered by Soil-Disturbing Animals and Biological Crusts." *Soil Biology and Biochemistry*, vol. 61, June 2013, pp. 14–22. ScienceDirect, doi:10.1016/j.soilbio.2013.02.002.
- 5) Brotherson, Jack D., and Samuel R. Rushforth. "INFLUENCE OF CRYPTOGAMIC CRUSTS ON MOISTURE RELATIONSHIPS OF SOILS IN NAVAJO NATIONAL MONUMENT, ARIZONA." *The Great Basin Naturalist*, vol. 43, no. 1, Monte L. Bean Life Science Museum, Brigham Young University, 1983, pp. 73–78. JSTOR.
- 6) Cole, Christina, et al. "Transplant Survivorship of Bryophyte Soil Crusts in the Mojave Desert." *Restoration Ecology*, vol. 18, no. 2, 2010, pp. 198–205. Wiley Online Library, doi:10.1111/j.1526-100X.2008.00445.x.
- 7) Elbert, Wolfgang, et al. "Contribution of Cryptogamic Covers to the Global Cycles of Carbon and Nitrogen." *Nature Geoscience*, vol. 5, no. 7, 7, Nature Publishing Group, July 2012, pp. 459–62. [www.nature.com](http://www.nature.com), doi:10.1038/ngeo1486.
- 8) Ferrenberg, Scott, et al. "Climate Change and Physical Disturbance Cause Similar Community Shifts in Biological Soil Crusts." *Proceedings of the National Academy of Sciences*, vol. 112, no. 39, Sept. 2015, pp. 12116–21. [www.pnas.org](http://www.pnas.org), doi:10.1073/pnas.1509150112.
- 9) Ferrenberg, Scott, et al. "Biological Soil Crusts: Diminutive Communities of Potential Global Importance." *Frontiers in Ecology and the Environment*, vol. 15, no. 3, 2017, pp. 160–67. Wiley Online Library, doi:10.1002/fee.1469.

- 10) Fick, Steve. Extent and Ecosystem Impacts of Biological Soil Crust in the Colorado River Basin. 2015.
- 11) Garcia, Carlos, et al. The Future of Soil Carbon: Its Conservation and Formation. Academic Press, 2018.
- 12) Green, Laura E., Andrea Porras-Alfaro, and Robert L. Sinsabaugh. "Translocation of nitrogen and carbon integrates biotic crust and grass production in desert grassland." *Journal of Ecology* 96.5 (2008): 1076-1085.
- 13) Griffin, Dale W. "Atmospheric Movement of Microorganisms in Clouds of Desert Dust and Implications for Human Health." *Clinical Microbiology Reviews*, vol. 20, no. 3, American Society for Microbiology Journals, July 2007, pp. 459–77. *cmr.asm.org*, doi:[10.1128/CMR.00039-06](https://doi.org/10.1128/CMR.00039-06).
- 14) Herrington, Lara. "Warming Trends, Increasing Precipitation Signal Biocrust Decline." *Colorado Arts and Sciences Magazine*, 3 Dec. 2015, <https://www.colorado.edu/asmagazine/2015/12/03/warming-trends-increasing-precipitation-signal-biocrust-decline>.
- 15) Jazi, Everly. Our Impact on Growth: Reducing Our Trace on Cryptobiotic Soils - Katmai National Park & Preserve (U.S. National Park Service). <https://www.nps.gov/katm/blogs/our-impact-on-growth-reducing-our-trace-on-cryptobiotic-soils.htm>. Aug. 2017. Accessed 25 Feb. 2020.
- 16) Maestre, Fernando T., et al. "Watering, Fertilization, and Slurry Inoculation Promote Recovery of Biological Crust Function in Degraded Soils." *Microbial Ecology*, vol. 52, no. 3, Oct. 2006, pp. 365–77. Springer Link, doi:10.1007/s00248-006-9017-0.
- 17) Miller, Sue, Steve Warren, and Larry St Clair. "Don't bust the biological soil crust: Preserving and restoring an important desert resource." *Science You Can Use Bulletin, Issue 23. Fort Collins, CO: Rocky Mountain Research Station. 10 p.* (2017).
- 18) Prăvălie, Remus. "Drylands Extent and Environmental Issues. A Global Approach." *Earth-Science Reviews*, vol. 161, Oct. 2016, pp. 259–78. ScienceDirect, doi:10.1016/j.earscirev.2016.08.003.
- 19) Pointing, Stephen B., and Jayne Belnap. "Microbial Colonization and Controls in Dryland Systems." *Nature Reviews Microbiology*, vol. 10, no. 8, 8, Nature Publishing Group, Aug. 2012, pp. 551–62. [www.nature.com](http://www.nature.com), doi:10.1038/nrmicro2831.
- 20) Porada, Philipp, et al. "Estimating Impacts of Lichens and Bryophytes on Global Biogeochemical Cycles." *Global Biogeochemical Cycles*, vol. 28, no. 2, 2014, pp. 71–85. Wiley Online Library, doi:10.1002/2013GB004705.
- 21) Rajeev, Lara, et al. "Dynamic Cyanobacterial Response to Hydration and Dehydration in a Desert Biological Soil Crust." *The ISME Journal*, vol. 7, no. 11, Nov. 2013, pp. 2178–91. [www.nature.com](http://www.nature.com), doi:10.1038/ismej.2013.83.
- 22) Reed, Sasha C., et al. "Changes to Dryland Rainfall Result in Rapid Moss Mortality and Altered Soil Fertility." *Nature Climate Change*, vol. 2, no. 10, Oct. 2012, pp. 752–55. [www.nature.com](http://www.nature.com), doi:10.1038/nclimate1596.
- 23) Reed, Sasha C., et al. "Biocrusts in the Context of Global Change." *Biological Soil Crusts: An Organizing Principle in Drylands*, edited by Bettina Weber et al., Springer International Publishing, 2016, pp. 451–76. Springer Link, doi:10.1007/978-3-319-30214-0\_22.
- 24) Root, Heather T., et al. "Grazing Disturbance Promotes Exotic Annual Grasses by Degrading Soil Biocrust Communities." *Ecological Applications*, vol. 30, no. 1, 2020, p. e02016. Wiley Online Library, doi:10.1002/eap.2016.

- 25) Rutherford, William A., et al. “Albedo Feedbacks to Future Climate via Climate Change Impacts on Dryland Biocrusts.” *Scientific Reports*, vol. 7, no. 1, Mar. 2017, pp. 1–9. [www.nature.com](http://www.nature.com), doi:10.1038/srep44188.
- 26) Tisdall, J. M. “Possible Role of Soil Microorganisms in Aggregation in Soils.” *Plant and Soil*, vol. 159, no. 1, Feb. 1994, pp. 115–21. Springer Link, doi:10.1007/BF00000100.
- 27) Ullmann, I., and B. Büdel. “Biological Soil Crusts of Africa.” *Biological Soil Crusts: Structure, Function, and Management*, edited by Jayne Belnap and Otto L. Lange, Springer, 2003, pp. 107–18. Springer Link, doi:[10.1007/978-3-642-56475-8\\_9](https://doi.org/10.1007/978-3-642-56475-8_9).
- 28) Warren, Steven D., et al. “Aerobiology and Passive Restoration of Biological Soil Crusts.” *Aerobiologia*, vol. 35, no. 1, Mar. 2019, pp. 45–56. Springer Link, doi:10.1007/s10453-018-9539-1.
- 29) Weber, Bettina, et al., editors. *Biological Soil Crusts: An Organizing Principle in Drylands*. Springer International Publishing, 2016. DOI.org (Crossref), doi:[10.1007/978-3-319-30214-0](https://doi.org/10.1007/978-3-319-30214-0).
- 30) Zhang, Yuanming, et al. “Interactions of Biological Soil Crusts with Vascular Plants.” *Biological Soil Crusts: An Organizing Principle in Drylands*, edited by Bettina Weber et al., Springer International Publishing, 2016, pp. 385–406. Springer Link, doi:10.1007/978-3-319-30214-0\_19.
- 31) Zhuang, WeiWei, et al. “The Influence of Biological Soil Crusts on <sup>15</sup>N Translocation in Soil and Vascular Plant in a Temperate Desert of Northwestern China.” *Journal of Plant Ecology*, vol. 8, no. 4, Oxford Academic, Aug. 2015, pp. 420–28. [academic.oup.com](http://academic.oup.com), doi:10.1093/jpe/rtu033.