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REVIEW ARTICLE

Biological soil crusts in ecological restoration: emerging research and perspectives

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Drylands encompass over 40% of terrestrial ecosystems and face significant anthropogenic degradation causing a loss of ecosystem integrity, services, and deterioration of social-ecological systems. To combat this degradation, some dryland restoration efforts have focused on the use of biological soil crusts (biocrusts): complex communities of cyanobacteria, algae, lichens, bryophytes, and other organisms living in association with the top millimeters of soil. Biocrusts are common in many ecosystems and especially drylands. They perform a suite of ecosystem functions: stabilizing soil surfaces to prevent erosion, contributing carbon through photosynthesis, fixing nitrogen, and mediating the hydrological cycle in drylands. Biocrusts have emerged as a potential tool in restoration; developing methods to implement effective biocrust restoration has the potential to return many ecosystem functions and services. Although culture-based approaches have allowed researchers to learn about the biology, physiology, and cultivation of biocrusts, transferring this knowledge to field implementation has been more challenging. A large amount of research has amassed to improve our understanding of biocrust restoration, leaving us at an opportune time to learn from one another and to join approaches for maximum efficacy. The articles in this special issue improve the state of our current knowledge in biocrust restoration, highlighting efforts to effectively restore biocrusts through a variety of different ecosystems, across scales and utilizing a variety of lab and field methods. This collective work provides a useful resource for the scientific community as well as land managers.

Key words: biocrust, biocrust cultivation, drylands, inoculation, rehabilitation, soil stabilization

Implications for Practice

- Effective restoration techniques exist to reestablish some biocrust taxa while methods are still in development for others.
- Emerging research from a rapidly expanding discipline, with advances on all phases of restoration, including interactions with managers, culturing, field application, and their overarching guiding principles can guide practitioners in effective restoration with biocrust.
- The next frontiers for biocrust restoration are in cultivation, scaling up to areas relevant to land managers and bridging the gap between science and practice.

Biocrusts, Their Functions and Utility in Restoration

Biological soil crusts (biocrusts) are a community of interacting organisms, including cyanobacteria, algae, lichens, and bryophytes that live in and bind the top millimeters of mineral soil (Belnap et al. 2016). Biocrusts are miniature ecosystems, performing all the vital functions of larger ecosystems, but at a smaller scale (Bowker et al. 2014). Relative to their biomass, biocrusts provide disproportionately greater ecosystem services across scales (Ferrenberg et al. 2017). Biocrusts enhance soil aggregation (compared to other dryland biota), which reduces soil loss to wind and water erosion (Chaudhary et al. 2009). Primary producers in biocrusts collectively fix 0.58 Pg C/year and the nitrogen fixers in biocrusts fix 24 Tg of N (40–85% of global terrestrial biologically fixed N; Rodriguez-Caballero et al. 2018). Climate interacts with soil type to influence how biocrusts affect hydrology, in some

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cases increasing run-off (but not sediment loading), and in other cases increasing infiltration (Chamizo et al. 2016; Faist et al. 2017). Biocrusts also interact with plant establishment and growth in both negative and positive ways (Condon & Pyke 2018a; Havrilla et al. 2019; Chaudhary et al. 2020); biocrusts may serve as an armor, preventing seed penetration, but, if seeds can break through, biocrusts can promote seedling establishment and growth (Ferrenberg et al. 2018; Slate et al. 2019). Condon and Pyke (2018a, 2018b) as well as Slate et al. (2019) observed decreases in exotic plant cover with biocrusts, but Ferrenberg et al. (2018) found that when exotic plants did germinate under a biocrust, they grew larger than in bare soil. Biocrusts also have positive effects on soil food webs, providing food and habitat for bacteria and fungi as well as micro-, meso-, and macrofauna (Darby et al. 2007; Maestre et al. 2012), which further contribute to ecosystem productivity, fertility, and function.

The Scope of the Problem

Biocrusts are more prominent in ecosystems across the globe that are limiting to plant growth because of water, temperature, growing season, soil chemistry, and other abiotic constraints. The majority of these ecosystems are drylands, but biocrusts are also common in more humid ecosystems, in some cases as an early successional element that is later replaced by vascular plants. Drylands make up more than 40% of the terrestrial biome and it is estimated that at least 23% of dryland areas are degraded due to human population expansion, energy and mineral extraction, and agriculture (Reynolds et al. 2007; Zika & Erb 2009). Biocrusts are susceptible to climate and physical disturbances, and thus with continued land degradation and negative impacts from climate change in all ecosystems where biocrusts are present, estimates of biocrust cover are expected to further decrease globally by 24–40% (Rodriguez-Caballero et al. 2018). This has major implications for the functioning of dryland ecosystems (Rodriguez-Caballero et al. 2018). Dryland restoration has been targeted by the United Nations Sustainable Development Goal Number 15: Life on Land (United Nations Sustainable Development Goals 2019). The inclusion of biocrusts in dryland restoration has the potential to improve restoration practices and outcomes (Bowker 2007). Including biocrusts in restoration has utility for two main reasons. First, biocrusts provide a suite of ecosystem functions. In this context, biocrusts can be a means to introduce or restore important ecosystem functions. Second, biocrusts increase biodiversity and ecosystem resilience. Biocrust taxa are diverse in life form and support a vast microbiome and soil food web. They build the foundation for a vast number of other organisms, from microbes to plants, and thus restored biocrusts can bolster ecosystem biodiversity. Within this special issue, both of these important aspects of biocrust restoration are discussed.

Developing effective methods to restore biocrusts to degraded drylands is critical to the restoration of ecosystem function and resilience. One reason why biocrust restoration has not received as much attention compared to other practices is the assumption that biocrusts are slow growing, meaning that their establishment, and thus their utility in facilitating improved ecosystem function would be futile. However, recent synthesis has demonstrated that natural recovery generally happens faster than previously reported, on the scale of years to decades, largely dependent on the type of disturbance, soil type, and climate (Weber et al. 2016; Condon et al. 2020). Moreover, many labs have developed methods to successfully cultivate biocrusts (e.g. Giraldo-Silva et al. 2020; Velasco-Ayuso et al. 2020; Zhou et al. 2020), which allow inoculum to be rapidly produced and applied to the field to increase recovery rates. Land managers are also becoming increasingly interested in the utility of biocrusts in rehabilitation and restoration. Managers are working with scientists (e.g. Chua et al. 2019; Lorite et al. 2019) to test methods and requirements for the use of biocrusts, including requiring salvage work to happen before disturbance (Tucker et al. 2020).

A Framework for Using Biocrusts in Restoration

Because biocrusts are diverse with respect to ecosystem assemblage and function and because restoration goals differ among projects, no single approach is appropriate for biocrust restoration (Fig. 1). Bowker (2007) provides the foundation for a hierarchy of barriers to restoration success, where success is only achieved if the highest barrier is addressed in the restoration plan. For instance, if soils are actively eroding, no other activity will help. This framework is useful in guiding restoration actions for stabilizing soils, addressing nutrient or habitat deficiencies, determining if inoculation is necessary or if simply removing the disturbance is sufficient. The literature leading up to this special issue (reviewed in Zhao et al. 2016), a recent manual for biocrust restoration (https://anitaantoninka.wixsite.com/biocrustrestoration) and the articles compiled here offer insights that will help guide practitioners, managers, and scientists in their work. The compilation of 21 articles included in this special issue represents an approximately 23% increase in the total number of articles addressing biocrust restoration and advances our understanding of how to use biocrusts in restoration (Fig. 2). We offer below some common themes in these papers that can guide decision-making for restoration and rehabilitation using biocrusts.

Ecoclimatic Context Determines Biocrust Restoration Success

A framework for restoration begins with assessing the nature and scale of the disturbance as well as the ecoclimatic context. Large or more severe disturbances will require different approaches than small or minor disturbances. Similarly, the type and timing of precipitation in relation to temperature will determine how slowly or quickly biocrusts might recover alone and with intervention. We saw that passive restoration was possible in Condon et al. (2019), but not in Lorite et al. (2019). This suggests that the context of climate and disturbance type are important (Weber et al. 2016). This is further supported by Faist et al. (2019) who found that soil texture and climate regime were the strongest predictors of biocrust establishment.

Promising Technologies Stabilize Soil With Biocrusts In Situ

In this special issue, several articles offer potential solutions to stabilizing soils that also promote biocrust colonization.

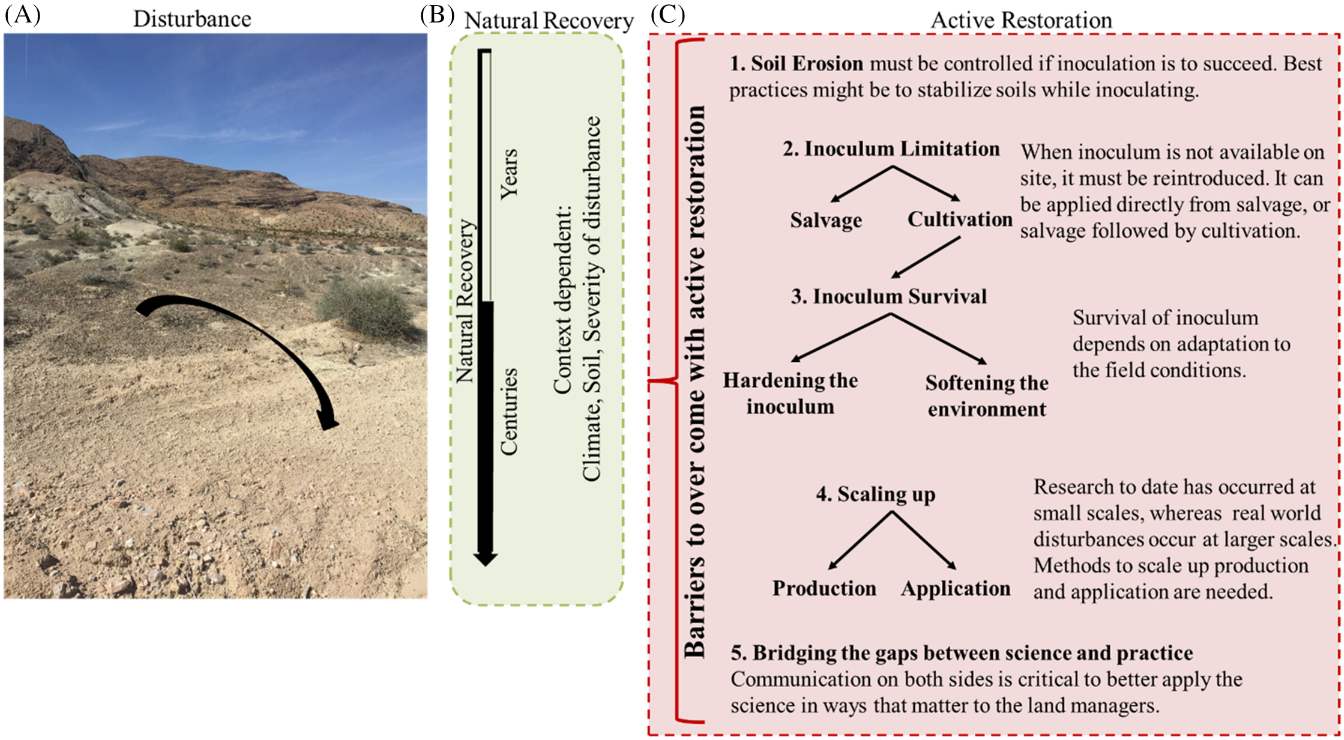

Figure 1 Biocrusts perform ecosystem functions that are lost when disturbance occurs (A). Natural recovery depends on the context in which it occurred and can takes years to centuries (B). Active restoration with biocrusts can speed up recovery substantially. It is important to consider the barriers to success before prescribing treatment (C). Photo credit: A. Antoninka.

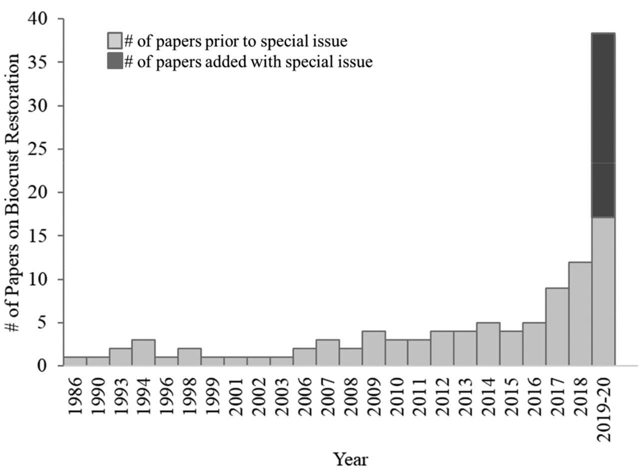

Figure 2 The number of articles found in a targeted search on the topic of biocrust restoration each year to date (light gray), highlighting the contribution of this special issue with 21 new articles (dark gray). Search terms and curation methods provided in Supplement S1.

Stabilizing soils is often a critical need for any restoration success (Bowker 2007). Chamizo et al. (2020) investigated a novel application of cyanobacteria post-fire that also stabilized soil. Similarly, Chaudhary et al. (2020) tested inoculation with salvaged biocrust in the greenhouse and field, both finding that application rapidly promoted soil stability. Blankenship et al. (2019) demonstrate that polyacrylamide (PAM) and psyllium, tackifiers used in soil stabilization, have neutral to positive effects respectively on mosses in the lab. Fick et al. (2019) also found that psyllium in combination with biocrust inoculum most strongly promotes soil aggregate stability in field trials. Antoninka et al. (2019) tested three PAM products and straw borders, finding that polymers were not a hindrance to biocrust development, but straw borders were. Faist et al. (2019) found that straw borders did stabilize soil and did not inhibit biocrust development, perhaps because of the larger perimeter of plots used in this study. As previously employed by Condon and Pyke (2016), Slate et al. (2020) and Bowker et al. (2019) all found jute to be effective at facilitating biocrust growth while stabilizing soils. Mallen-Cooper et al. (2019) provide a guide for the types of measurements that one can use to assess the success of the treatments.

Advances in Biocrust Inoculum Production Methods

Perhaps the most rapid advances in biocrust restoration have occurred in the area of cultivation. Past efforts have focused on identifying how to rapidly grow biocrust in greenhouse or lab scenarios using single species, targeted mixed taxa, or mixed communities with a variety of novel cultivation systems (Doherty et al. 2015; Antoninka et al. 2016; Bowker et al. 2017; Velasco Ayuso et al. 2017; Giraldo-Silva et al. 2019). This issue builds on this research with three articles directly addressing new or enhancing biocrust culture methods (Giraldo-Silva et al. 2020; Grover et al. 2020; Velasco-Ayuso et al. 2020), demonstrating that the methods are scalable, and can include whole communities or individual isolates. Zhou et al. (2020) also highlight the work across China with cyanobacteria and moss culture methods. We also are given some necessary guidance on how gametophytes of desiccation-tolerant mosses can be stored for up to 197 days prior to their use as inoculation material (Guo et al. 2020) and salvaging biocrust for field inoculation or culture from Tucker et al. (2020).

Insights Into Promoting Biocrust Establishment in the Field

Giraldo-Silva et al. (2020) demonstrate that preconditioning methods such as stepwise increases in light exposure and recurrent wet–dry cycles aid inoculated cyanobacteria in surviving field conditions. This is the first hardening experiment to date to show a real benefit and suggests that hardening to UV or hydration alone are inadequate to promote survival in the field (e.g. Antoninka et al. 2018; Bowker et al. 2019). What has been effective is to modify the habitat to "soften" the conditions for inoculum. Shade (Antoninka et al. 2019; Fick et al. 2019), jute (Condon & Pyke 2016; Bowker et al. 2019; Slate et al. 2020), and water (Fick et al. 2019; Antoninka et al. 2019; Lorite et al. 2019; Zhou et al. 2020; but not Condon & Pyke 2016) can improve water residence time, reduce UV, and increase relative humidity, which led to better establishment of biocrust across a variety of ecosystems.

This issue also provides a comprehensive guide for inoculation methods from trials conducted at many scales and a variety of taxa in China (Zhou et al. 2020). We are also given a guide to some biocrust species traits that can be used in considering and planning biocrust restoration by Rosentreter (2019) and how these traits can be measured (Mallen-Cooper et al. 2019). Chiquoine et al. (2019), Rosentreter (2019), and Condon et al. (2019) all demonstrate the need to consider restoration goals in planning activities. In Lorite et al. (2019), as in Zhou et al. (2020), hydroseeding biocrust was found to be useful for establishing biocrusts in larger areas. Doherty et al. (2020) tested tools commonly used in rangeland restoration and agriculture, using seed drilling and imprinting to inoculate fields. They found that imprinting was promising, likely by promoting microhabitats, but seed drilling likely buried inoculum too deeply to recover. Other research addresses methods to keep the inoculum on site to prevent it from washing or blowing away before it can establish. For example, Chua et al. (2019) and Slate et al. (2020) created pellets to keep biocrust propagules in place.

Biotic and Abiotic Interactions With Biocrusts Influence Restoration Success

Studying interactions between biocrusts and the biotic and abiotic environment, including vascular plants, are essential to understanding restoration success. In this issue, we find that seed biopriming with cyanobacteria can facilitate seedling establishment (Chua et al. 2019). Furthermore, interactions between biocrusts and other soil communities, such as arbuscular mycorrhizal fungi, have the potential to affect dryland restoration success; biocrust inoculation can enhance drought tolerance, but reduce biomass of some plant and associated mycorrhizal symbioses (Chaudhary et al. 2020). Chiquoine et al. (2019) demonstrate that efforts to aid native plant communities using sucrose addition can be detrimental to existing biocrust.

Frontiers in Biocrust Restoration Research

The field of biocrust restoration has advanced tremendously over the last decade (Fig. 2), and in this special issue we continue that trend, with 21 contributions from four continents. In determining how to proceed with a restoration effort, one needs to consider the type and nature of the disturbance, the barriers to inoculation success, and the desired outcomes. All these topics are addressed in this special issue. While we have made considerable advances as a field there is still substantial work to be done. We offer three areas below that we believe are most in need of increased research (Fig. 1).

Translating Cultivation to Field Success

Although cultivation has received much research attention in recent years, and rapid yet effective cultivation techniques have been identified, there is still poor success when applying the cultivated inoculum to the field (e.g. Bowker et al. 2019; Faist et al. 2019; Zhou et al. 2020). Determining the causes for failure and success needs to be addressed by studying the biology and ecology of these organisms. We need more cultivation studies looking at interactions among biocrust taxa, with soil microbes and with vascular plants to maximize restoration success. Work has been done addressing biocrust species interactions, finding facilitation and competition (e.g. Antoninka et al. 2016; Bowker et al. 2017), and some research has looked at relevant ecological traits (e.g. Mallen-Cooper & Eldridge 2016; Rosentreter 2019). Similarly, biocrust by plant or by microbial interactions has been studied (e.g. Maestre et al. 2011; Havrilla et al. 2019; Condon & Pyke 2020; Chaudhary et al. 2020; Chiquoine et al. 2019; Condon et al. 2019), but the number of ecologically important questions that will inform restoration success remains high.

Scaling Up Biocrust Restoration

Most research on biocrust inoculation has been conducted at the plot scale, which is a necessary starting point; however, we need methods that can scale up production, reduce costs, treat areas of ecological and management relevance, and utilize equipment already developed for other purposes. For example, hydroseeders (Blankenship et al. 2019; Lorite et al. 2019; Zhou et al. 2020) and rangeland restoration/farm equipment (Doherty et al. 2020) work at large scales and require large amounts of biocrust. Working with land managers (see below) will be essential to scale up biocrust restoration. In addition, research into novel applications of biocrust is needed across scales. For example, Grover et al. (2020) have developed methods to cultivate biocrust moss for use in post-fire recovery, and Chamizo et al. (2020) have tested the viability of using biocrust organisms in post-fire recovery. Fire disturbance can require rapid action to stabilize soils if biocrusts were lost following fire (Warren et al. 2015; Condon & Pyke 2018a, 2018b).

Bridging Science and Practice

Because biocrusts remain dormant when dry and can be safely stored (Guo et al. 2020) and rates of land development continue to accelerate (Tucker et al. 2020), we are in need of: (1) working relationships with land managers and developers to salvage ahead of known soil surface disturbance, and (2) methods to improve the speed and efficiency of salvage. To date, there has been no inoculation with cultured biocrust that has done better than inoculation from a field source. This suggests that salvaged biocrust is our best resource in restoration because it relieves the cultivation requirement and can be locally sourced. As evidenced in this issue, land managers are finding utility in reclamation with biocrust, and are funding research in this area (e. g. Blankenship et al. 2019; Chaudhary et al. 2020; Chua et al. 2019; Condon et al. 2019; Faist et al. 2019). Building these relationships is of utmost importance to continue to bridge the gaps between science and practice and could provide the foundation to building technology to address management needs at relevant scales with manageable costs.

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Supporting Information

The following information may be found in the online version of this article:

Supplement S1. Search terms and curation methods.

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