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BIOCRUST FOR ENVIRONMENTAL SUSTAINABILITY: A REVIEW

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ABSTRACT

A noticeable and significant biotic component of many terrestrial ecosystems around the world are soil surface communities, which are made up of cyanobacteria, mosses, liverworts, fungus, eukaryotic algae and lichens (also known as biological soil crusts or biocrusts). Biocrusts demonstrate the adaptability and tenacity of life in harsh environments as well as perplexing resistance to the interplay of several environmental factors. Artificially induced biocrusts can thrive and significantly improve the soil environment through their biochemical activities. By secreting plant growth regulators and activating nitrogenase, cyanobacteria in biological soil crusts enhance the absorption of organic carbon and nitrogen, thereby increasing nutrient availability and maintaining soil fertility. Biocrusts are common, but they are threatened by global change-related causes, especially the interplay between intensifying land use and changing climate. The quantity of biocrust that is present locally, regionally and globally may be greatly decreased by these factors. As biocrusts are vital to the health of ecosystems and are in risk of vanishing, their influence on ecosystems and the consequences of their loss should be considered in studies and models of global change.

Key words : Biocrust, Nutrient cycling, Soil functions, Carbon sequestration.

Introduction

Over 45% of the world's geographical area is made up of dry lands (Hijmans *et al.*, 2005), which are also home to over 40% of the global population. In arid regions, soil quality declines as a result of decades-long climatic change. In light of these constrictive climatic circumstances, biodiversity which, despite common assumption, is abundant in many dry lands-plays, a crucial role in preserving the many ecosystem services and functions, or the ecosystem's multi-functionality (Maestre *et al.*, 2012). In dry lands biological soil crust (BSC) has crucial role in soil quality, it takes years to heal when we lost completely. Biocrusts are present in nearly all terrestrial environments where vegetation does not cover the entire soil surface, but they are especially common in arid, semi-arid, and dry-subhumid environments (referred

to as drylands from now on) (Safirel and Adeel, 2005). Throughout the world, biocrusts, or biological soil crusts, create a "living skin" at the soil's surface in a variety of low-productivity habitats, such as those with restricted access to water or cold, as well as early successional series (Belnap *et al.*, 2003). They can consist of any arrangement of cyanobacteria, eukaryotic algae, lichens, mosses, or liverworts that grow on the soil's surface. They also serve as a food source for animals and assemblages of decomposers. Given that these soil surface communities are thought to presently make up around 12% of the terrestrial surface, they are globally significant (Rodriguez-Caballero *et al.*, 2018). The thin layer at the soil's surface that is well-aggregated and known as a biocrust is created by the organisms' activities. Due to the fact that biocrusts are naturally soil aggregating

and erosion-resistant, there has been a great deal of interest in the contributions that biocrusts provide to ecosystem function. Under natural circumstances, the biocrusts release chemicals known as plant growth regulators (PGRs), which include vitamins, amino acids, and carbohydrates, as well as hormones that promote plant development (Paul and Nair, 2008). The most crucial elements required to promote plant development are these polymorphic compounds (Rastogi and Sinha, 2009). A large number of macro and micronutrients are stored in dried form in this biological soil crust. According to Román-Fernández *et al.* (2018), the dry matter of BSC adds to organic matter, which enhances soil fertility, keeps NPK levels at optimal levels and increases water-holding capacity. The member of the BSC transforms complicated nutrients so that plants may easily absorb them. One effective strategy for restoring soil is the BSC inoculum present in the soil (Rossi *et al.*, 2017). As of late, biocrusts have been recognized as a multifunctional, globally-significant ecosystem component that plays a key role in constructing or modifying soil nutrient stocks via N-fixation (Elbert *et al.*, 2012); influencing soil hydrological properties like the water balance (Chamizo *et al.*, 2016) and the ecosystem's thermal energy balance (Coradeau *et al.*, 2016; Rutherford *et al.*, 2017).

Modern times have seen a widespread usage of chemical pesticides and fertilizers, which has polluted the soil. The increased expense of these chemical fertilizers has a negative financial impact on farmers. Therefore, it has been discovered that these biological soil crusts improve soil fertility by raising crop output in the absence of contamination from the environment, water, or soil (Rossi *et al.*, 2017). Despite being widespread, biocrusts are in danger due to factors related to global change, particularly the interaction between land-use intensification and climate change. These factors have the potential to significantly reduce the amount of biocrust that is present at the local, regional and global levels (Reed *et al.*, 2012). Biocrusts are essential to the health of ecosystems and are in danger of disappearing, so studies and models of global change should take into account their impact on ecosystems and the repercussions of their

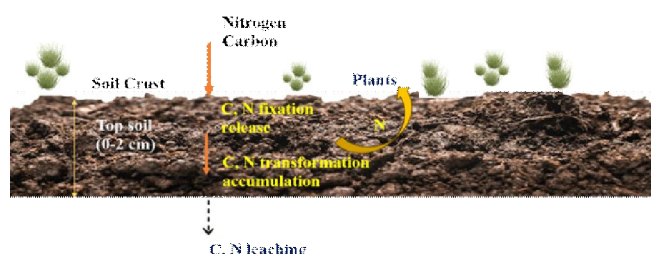


Fig. 1: A Schematic diagram showing the presence of biocrusts modified from Belnap *et al.* (2003).

disappearance (Rodríguez-Caballero *et al.*, 2018). This review will highlight the function of biocrust in soil and plant management in light of these gaps in existing biocrust research and as a means of igniting interest in biocrusts from a scientific and practical standpoint.

Elements of biocrust

Characteristics of habitat, function, physical structure and taxonomy can be used to characterize biocrusts. When these qualities are together:

- i) **Habitat characteristics :** A colony of organisms living on the soil's surface is first defined as a biocrust. In addition, soils on the sides and under transparent rocks are home to hypo lithic biocrusts (Pointing, 2016). We note that there may be circumstances where it is useful to investigate all such groups together, but we omit species that mostly grow in or on rocks, leaves, and wood. A soil's topmost surface, known as the organo-mineral A horizon, or, in some severely deteriorated conditions, the exposed underlying mineral horizon, are where the majority of biocrust instances found in literature may be found (Gretarsdottir *et al.*, 2004). Further, most biocrusts occupy terrestrial soils that desiccate regularly, and are dry often.
- ii) **Physical structural characteristics :** A discernible structural shift—that is, the formation of a physically cohesive, thin and slightly hardened top surface layer—occurs at the soil surface as a result of the soil aggregation carried out by biocrust organisms and its exclusive position at the soil surface. This structural arrangement is in line with how the word “crust” is generally used, which refers to an outer layer that has solidified (like the crust of bread or the Earth). Dust entrapment and soil weathering processes frequently increase the number of fine soil particles inside the biocrust or just below it, which further distinguishes the biocrust from underlying soil (Chen *et al.*, 2009; Garcia-Pichel *et al.*, 2016). According to Felde *et al.* (2014), Gao *et al.* (2017), biocrusts can occasionally have many hardened layers layered on top of one another as a result of repeated biocrust burial.
- iii) **Functional characteristics :** The fact that the constituent organisms and their exudates agglomerate surface soil particles, raising the stability of the soil surface above that of the underlying soil, may be the primary functional component in the concept of a biocrust (Chaudhary *et al.*, 2009; Belnap *et al.*, 2014). Because the aggregation is at least partially and frequently predominantly designed by living (*i.e.*,

biocrust) organisms, a biocrust differs from a physical soil crust. This aggregation is mostly produced by the secretion of extracellular polymeric substances and filamentous biological structures, such as cyanobacterial filaments, lichen rhizines and moss rhizoids (Mager and Thomas, 2011; Rossiet *et al.*, 2018). Photosynthesizing organisms can be found in biocrusts. It is necessary for these photoautotrophs to be present at the soil's surface because they fix carbon dioxide from the air. Extremotolerance: due to their resistance to desiccation, biocrusts can tolerate high temperatures and little precipitation (Karsten *et al.*, 2016). The physiological stage of biocrust organisms, which is characterized by a broad resistance to harsh environmental circumstances, is essentially inactive once they become dry.

iv) Taxonomic composition : Since biocrusts are made up of a variety of photoautotrophic and heterotrophic species from different domains, kingdoms, and phyla, defining them taxonomically is challenging. The photoautotrophic component does not contain ferns, fern allies, or vascular seed plants (West, 1990). Instead, it comprises several lineages, including cyanobacteria, algae, lichens and bryophytes. All members of the ancient class of “cryptogams,” or “hidden reproduction,” which are organisms that reproduce by spores rather than seeds, including cyanobacteria, algae, lichens and bryophytes, lack highly developed vascular tissue and many, if not most, are capable of desiccating on a regular basis. Thus, non-vascular cryptogams make up the photoautotrophic portion of biocrusts (Weber *et al.*, 2022).

Biological Soil Crusts (BSCs) : Types and classification

About 12% of the earth's terrestrial surface is made

up of biological soil crusts, or “bio-crusts” (BSCs) (Rodriguez-Caballero *et al.*, 2018). These highly specialized organisms are made up of (i) heterotrophic microorganisms like bacteria, actinomycetes, fungi, and microfauna and (ii) photoautotrophic microorganisms like cyanobacteria, algae, lichens and mosses (Weber *et al.*, 2016). Depending on microbial metabolic activities, reproductive methods, species diversity and soil–climate–microorganism interactions, the creation of BSCs can take anywhere from 10 to 1000 years (Kidron *et al.*, 2008). Under ideal circumstances, smooth cyanobacterial–algal crusts form the first step in the development of BSCs. Short moss–lichen crusts next form and finally tall moss–lichen pinnacled crusts (Williams *et al.*, 2012). High variety of microorganisms is a characteristic of soil bio-crusts. They create a living, protective film by combining with soil particles.

BSCs have been shown to be widespread in the top 0–1 cm of soil (Weber *et al.*, 2016; Bowker *et al.*, 2018) and they are especially prevalent in dry and semi-arid locations (Maestre *et al.*, 2021), where they can account for up to 80% of the total area (Chen *et al.*, 2020). Within the upper few millimeters of soil, loose soil particles are adhered to one another by cyanobacterial and microfungi filaments, lichen rhizinae and rhizomorphs and bryophyte rhizinae and protonemata.

According to Williams *et al.* (2012), three morphotypes of BSCs may be identified based on the percentage of species found in bio-crusts: (1) A smooth, 1.5 mm thick bio-rich zone made up of filamentous cyanobacteria is the cyanobacteria-dominated crust; (2) A short, 11 mm thick bio-rich zone consisting of approximately 50% lichen and 50% mosses; (3) A tall, 22 mm thick bio-rich zone consisting pinnacle-shaped crust of approximately 50% lichen and 50% cyanobacteria and some cyanobacteria is the moss-lichen pinnacle crust.

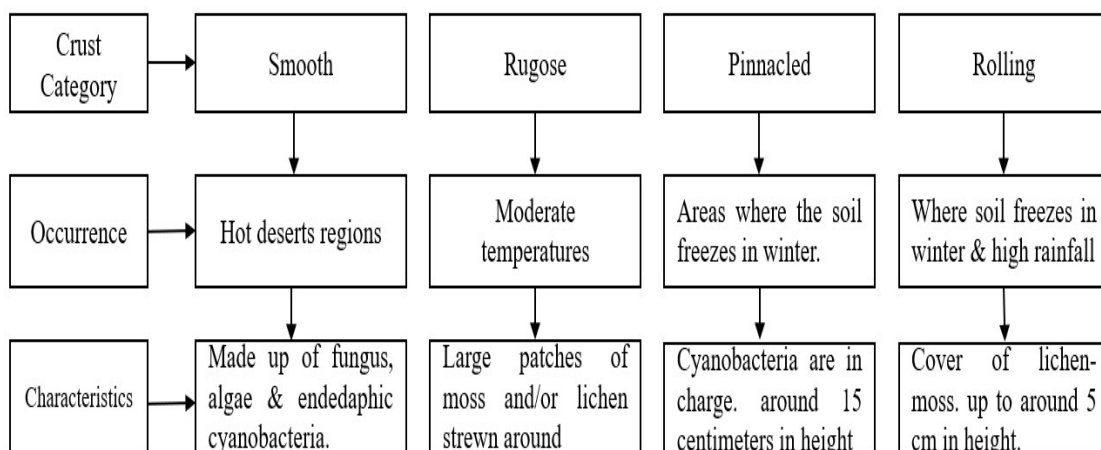


Fig. 2 : Classification of biological soil crust. Modified from Belnap *et al.* (2003), Bhattacharyya and Furtak (2022).

BSCs can also be categorized as follows, according to Belnap and Lange (2017): (1) Physical crusts (rain/desiccation): radicles, bacteria and fungi flourish before cyanobacteria and algae; (2) Cyanobacterial/algal crusts: primarily composed of lichens and cyanobacteria (*e.g.*, *Microcoleus* and *Scytonema* sp.); (3) Lichen crust: composed of lichens and various saprotrophic fungi; (4) Bryophyte crusts: predominantly composed of bryophytes (*e.g.*, *Microcoleus* sp.), developing in the presence of substantial amounts of organic matter deposited by wind and precipitation; (5) Mixed biotic crusts: a complex structure of communities: bryophytes, lichens, algae, cyanobacteria and associated decomposing microorganisms (humicolous, lignicolous fungi).

Bio-Crusts function in elemental cycling of nutrients

Biocrusts, also known as biological soil crusts, serve as a bridge between the rhizosphere, soil bacteria and nutrient cycling (Bhattacharyya and Furtak, 2023). The rhizosphere controls soil functions and processes that are aided by microbes, including as nutrient metabolism and fixation, as well as nutrient cycling. Microorganisms found in the rhizosphere play a crucial role in environmentally friendly agriculture and sustainable development (Adedeji *et al.*, 2020; Basu *et al.*, 2021). This biological ability of soil helps in maintaining and improve the physical and chemical characteristics of soil while providing plants, people, and animals with the necessary quantity of nutrients to complete their life cycles (Bhattacharyya and Furtak, 2023). One of the main participants in the worldwide sequestration of C and N in soils is biocrusts. Because of their crucial roles related to physiological or chemical properties, an improved understanding of the structures, composition, and functions of biocrust microbiomes and their geological implications (geomicrobiology) enables changes in soil ecosystem structures to be forecasted for long-term restoration (Duran *et al.*, 2021). Rhizosphere and nutrient cycling, rhizosphere and soil microorganisms, and biocrusts and nutrient cycling are some important variables linked to soil biological fertility. Depending on rhizosphere ventilation (Xiao *et al.*, 2015), the rhizosphere may have a significant impact on soil nutrient status (Finzi *et al.*, 2015). In temperate forest soils, rhizosphere activities and root priming can accelerate the rates of carbon (C) and nitrogen (N) mineralization, as demonstrated by a meta-analysis by Finzi *et al.* (2015). Rhizosphere ventilation has the potential to improve soil N and P availability (Xiao *et al.*, 2016). Through nitrification and N fixing; BSCs from dry habitats have an impact on N cycling (Nevins *et al.*, 2022).

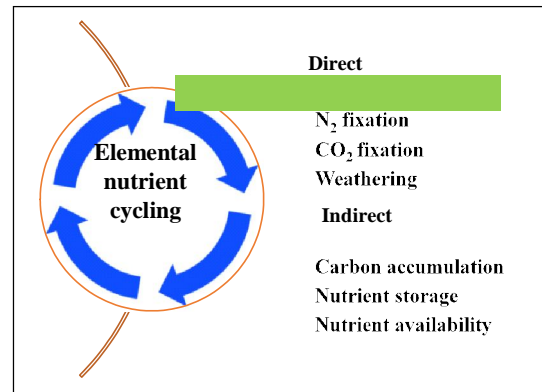


Fig. 3 : Bio-Crusts function in elemental cycling of nutrients modified from Duran *et al.* (2021).

Cyanobacteria and cyanolichens (such as *Collema*, *Microcoleus* and *Nostoc*) are among the species that create BSCs; these organisms fix nitrogen, which is then released into the soil environment. The soil receives up to 70% of the nitrogen that is bound by these microbes. Research has demonstrated that BSCs considerably raise the N content of soil (Beraldi-Campesi *et al.*, 2009). Elbert *et al.* (2012), estimate of the annual nitrogen intake by cryptogamic covers is around 49 Tg, indicating that nitrogen fixation by covers may be essential for plants to sequester carbon. Research has demonstrated that the biogeochemical cycling of P is significantly influenced by the populations of organisms in BSCs, particularly by the conversion of stable P into labile, easily accessible P (Baumann *et al.*, 2019; Qi *et al.*, 2021). According to Beraldi-Campesi *et al.* (2009), bio-crusts have more overall P concentrations compared to nearby soils. In particular, P-containing mineral concentrations dropped and organic P concentrations rose in BSCs as compared to volumetric soil in a temperate German forest, as demonstrated by Baumann *et al.* (2019). Metals can be chelated by cyanobacteria, such as *Anabaena*, *Anacystis*, *Lyngbya* and *Nostoc*, as well as by lichens, fungi, and some bacteria (Gehlot *et al.*, 2022; Magan *et al.*, 2022). This enhances Cu, Zn, Ni, Fe and other elements' availability to plants (Beraldi-Campesi *et al.*, 2009).

Bio-Crusts' function in physicochemical properties of soils

The soil mineral particles and microorganisms that comprise free-living, lichenized and mycorrhizal fungi, chemoheterotrophic bacteria, cyanobacteria, diazotrophic bacteria, archaea, eukaryotic algae and bryophytes come together to produce biocrusts. Exopolysaccharides (EPSs), glycoproteins and the formation of filament networks are ways in which biocrusts can clump soil particles together (Warren *et al.*, 2019). However, the environment, the characteristics of the soil, and the degree

of disturbance all affect the species composition and physical characteristics of biocrusts. For instance, on more acidic and less salted soils, green algae predominate in biocrusts. On alkaline soils, however, cyanobacteria are more prevalent (Baumann *et al.*, 2018). The physicochemical characteristics of soil can be changed by BSCs (Bu *et al.*, 2015; Zhang *et al.*, 2022) (Fig. 2). They primarily serve to defend against erosive pressures and maintain the soil surface (Weber *et al.*, 2016). In forest contexts (southeastern China), Seitz *et al.* (2017), demonstrated that bryophyte-dominated BSCs are more efficient than abiotic soil surface cover at reducing soil erosion. Furthermore, it was demonstrated by Bowker *et al.* (2018), that cyanobacteria's extracellular polysaccharides improve soil stability and lessen soil erosion. In semi-arid regions, BSCs can have an impact on soil fertility, stability, and water availability (Chamizo *et al.*, 2012). Crust-covered soils usually include more silt or clay, which enhances the soil's fertility and facilitates plant macronutrient absorption.

BSCs can improve water availability (bind surface water) and aid in the morphology, ecosystem services, and buildup of silt in arid (desert) environments (Williams *et al.*, 2012; Chamizo *et al.*, 2012). By affecting the detachment and movement of soil particles, BSCs also inhibit soil desertification, as demonstrated by Miralles-Mellado *et al.* (2011). Research conducted in cold deserts has demonstrated that BSCs may alter the pH of soil (Harper and Belnap, 2001) and raise the nutritional content (*i.e.*, N, K, Ca, Mg, P, Fe and Mn) of soil (Beraldi-Campesi *et al.* (2009). Particularly in soils with a pH greater than 7 (such as deserts), where some elements form insoluble oxides/hydroxides, the chelation of metals by microbes is crucial (Olaniran *et al.*, 2013), furthermore, BSCs have the capacity to absorb large concentrations of accessible metallic elements (Cu, Fe, K, Mg, Mn, Na and Zn) and are crucial in preserving and shielding these nutrients from erosion and leaching in dry soils (Moreno-Jiménez *et al.*, 2020).

Bio-Crusts' function in carbon (CO₂) sequestration

Accurately quantifying and predicting the C balance through monitoring C fluxes in terrestrial ecosystems is one of the top research goals worldwide (Musche *et al.*, 2019). Making these projections is crucial to locating and measuring the sources and sinks of greenhouse gas (GHG, such as CO₂) emissions. A fundamental comprehension of the C cycling of these ecosystems, which occupy 45% of the Earth's surface area, depends on quantifying the C stocks and fluxes in these biomes and identifying the mechanisms that govern them (Pravalié *et al.*, 2016). Considering that soil carbon intake is expected to be

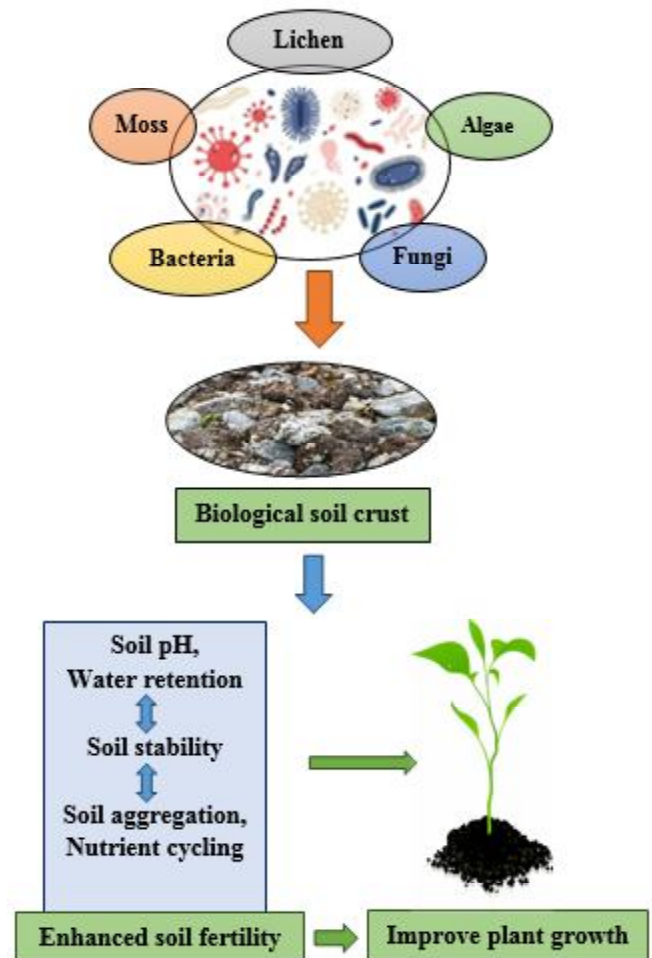


Fig. 4: Schematic illustration of BSC roles in soil (Modified from Chamizo, 2018).

between 3.5 and 5.2 Gt year⁻¹ (Batjes, 1996), it is projected that raising soil C reserves in these low-productive ecosystems might significantly lower atmospheric CO₂ levels (Ahlström *et al.*, 2015). According to estimates, cryptogamic communities, which comprise crusts, absorb around 3.9 Pg of carbon annually, or roughly 7% of the net primary output produced by terrestrial plants (Elbert *et al.*, 2012). The application of a biocrust can raise the C budgets in these ecosystems related to agriculture and forests.

A biocrust can play different roles in the storage of carbon: (a) it can aggregate soil particles by secreting exopolysaccharides, which create networks of filaments that strengthen the soil's stability against erosion and other degradation factors (Colica *et al.*, 2014; Kheirfam *et al.*, 2017); (b) it can increase porosity (Miralles-Mellado *et al.*, 2011); (c) it can retain water and/or infiltrate it (Chamizo *et al.*, 2011; Sadeghiet *et al.*, 2017); (d) it can increase soil fertility by accumulating nutrients (Kheirfam *et al.*, 2017) and (e) it can aid in the establishment of other organisms like mosses, lichens, cyanobacterias,

microfungi, and plants, which increases the soil's capacity to store carbon (Molina-Montenegro *et al.*, 2016). The soil biota, which includes nematodes, tardigrades, rotifers, mites, collembola, arthropods and mollusks, also finds a home in BSCs (Belnap *et al.*, 2006; Rutherford *et al.*, 2017; Couradeau *et al.*, 2016). Furthermore, the existence of BSCs raises the polysaccharide and total carbon content of soil (Nevins *et al.*, 2022; Sancho *et al.*, 2016). This is due to the fact that organisms that produce crusts release extracellular carbon shortly after acquiring it. In cyanobacteria, this can reach up to 50% of the carbon that they have taken in. Higher soil carbon levels are linked to higher numbers of heterotrophic microorganisms and accelerated decomposition. Because of their capabilities, biocrusts play a significant role in the global sequestration of carbon in soils (Duran *et al.*, 2021). These tasks carried out by a biocrust are significant because it is one of the main soil coverings, accounting for as much as 70% of the surface in certain regions (such as drylands) and because it is frequently the main source of soil organic carbon (SOC). Biocrusts are thought to account for around 15% of the world's terrestrial carbon stock and 40–85% of nitrogen fixation globally (Rodríguez-Caballero *et al.*, 2018; Samolov *et al.*, 2020). Thus, measuring C fluxes and nutrients through biocrust community assembly in field settings would greatly improve our knowledge and forecast, via mathematical models, of how particular pressures resulting from global change could modify the biocrust community's structure. This would then direct our efforts to improve C sequestration and nutrient availability in soils (Dettweiler-Robinson *et al.*, 2018; Heindel *et al.*, 2018).

Over 2 billion tons of CO₂ might be removed annually by the process of enhanced mineral weathering, a method of sequestering carbon. The strength of the atmospheric greenhouse effects can be lessened by sequestering atmospheric CO₂ and converting it into HCO₃⁻ using silicate minerals that are exposed to the weathering surface. An essential factor to take into account for geological carbon sinks is rock weathering. The two main processes behind rock weathering carbon sinks are carbon sinks resulting from silicate weathering and carbonate weathering (Zhang *et al.*, 2021). The anthropogenic activity caused by human activity takes too long for this process to offset the CO₂ flow. Inoculation of biocrust can be used to improve weathering rates in order to make up for this constraint. Because the biocrust initiates the Urey reaction, a chemical reaction, when it comes into touch with the rock. By removing CO₂ from the environment and combining it with calcium or magnesium silicates and water, this process traps CO₂ in

these carbonates, which remain in the soil. The enhanced chemical weathering process of C capture has the potential to remove over 2 billion tons of CO₂ annually (Samolov *et al.*, 2020). Additionally, as a result of weathering, additional Mg, Fe and Ca silicates are exposed in the rock pieces, increasing porosity and permeability (Beraldi-Campesi *et al.*, 2009; Celle *et al.*, 2000). Further suggestions for a C sequestration method to lessen climate change include the reactive mineral component (Fe and Mn) establishing connections with the organic materials (Sommer and Sommer, 2005; Zamanian *et al.*, 2016). This is so because silicate minerals—composed mostly of silicon and oxygen compounds—make up around 95% of the Earth's crust.

While individual biocrust organisms will react differently to changing climatic conditions, rising temperatures and altered precipitation patterns, along with strong interactions between the two are significantly altering the structure, function, and resilience of biocrust communities. Biocrusts appear to be particularly resilient to climate change. Therefore, further consequences for mineralization and organic C storage may arise based on the changes in microbial community compositions (Samolov *et al.*, 2020). The prediction, scaling, restoration, and C sequestration options at the forefront of modern biocrust science are advanced by this scientific interest in understanding how biocrusts contribute to global climate change.

Conclusion

Chemical fertilizers and pesticides are widely used in modern times, which have contaminated the soil. For farmers, the higher cost of these chemical fertilizers is a financial burden. As a result, it has been shown that these biological soil crusts increase agricultural production by improving soil fertility when soil, water, or the environment is not contaminated. The rhizosphere, soil microorganisms and nutrient cycling are all connected via biocrusts, also referred to as biological soil crusts. Biocrusts are a major player in nutrient cycling and the global sequestration of C and N in soils. The biological (such as species composition/ function and organism condition) and physical (such as activity rates and timings as dictated by climatic variables, soils) elements that affect C fixation and loss need to be properly documented in biocrusts. These species' innate ability to tolerate harsh environments makes them useful model organisms for research on systems related to photoprotection or desiccation tolerance. More research is being done on how climate change affects the components of the biocrust and the ecological processes that are connected to them.

Understanding the structures, composition and functions of biocrust microbiomes is important because of their critical roles related to physiological or chemical properties. This understanding allows changes in soil ecosystem structures to be predicted for long-term restoration.

References

- Adedeji, A.A., Häggblom M.M. and Babalola O.O. (2020). Sustainable agriculture in Africa: Plant growth-promoting rhizobacteria (PGPR) to the rescue. *Sci. African*, **9**, e00492.
- Ahlström, A., Raupach M.R., Schurgers G., Smith B., Arnett A., Jung M., Reichstein M., Canadell J.G., Friedlingstein P. and Jain A.K. (2015). The dominant role of semi-arid ecosystems in the trend and variability of the land CO₂ sink. *Science*, **348**, 895–899.
- Basu, A., Prasad P., Das S.N., Kalam S., Sayyed R.Z., Reddy M.S. and Enshasy H. El (2021). Plant growth promoting rhizobacteria (Pgpr) as green bioinoculants: Recent developments, constraints and prospects. *Sustainability*, **13**, 1140.
- Batjes, N.H. (1996). Total carbon and nitrogen in the soils of the world. *Eur. J. Soil Sci.*, **47**, 151–163.
- Baumann, K., Jung P., Samolov E., Lehnert L.W., Büdel B., Karsten U., Bendix J., Achilles S., Schermer M. and Matus F. (2018). Biological soil crusts along a climatic gradient in Chile: Richness and imprints of phototrophic microorganisms in phosphorus biogeochemical cycling. *Soil Biol. Biochem.*, **127**, 286–300.
- Baumann, K., Siebers M., Kruse J., Eckhardt K.U., Hu Y., Michalik D., Siebers N., Kar G., Karsten U. and Leinweber P. (2019). Biological soil crusts as key player in biogeochemical P cycling during pedogenesis of sandy substrate. *Geoderma*, **338**, 145–158.
- Belnap, J., Büdel B. and Lange O.L. (2003). Biological soil crusts: characteristics and distribution. In: Belnap, J. and Lange O.L. (eds). *Biological soil crusts: structure, function, and management*. Ecological Studies 150, Springer, Berlin, pp 3–30.
- Belnap, J. (2006). The potential roles of biological soil crusts in dryland hydrologic cycles. *Hydrol. Process*, **20**, 3159–3178.
- Belnap, J., Walker B.J., Munson S.M. and Gill R.A. (2014). Controls on sediment production in two US deserts. *Aeolian Res.*, **14**, 15–24.
- Belnap, J. and Lange O.L. (2017). Lichens and microfungi in biological soil crusts. In: *The Fungal Community. Its Organization and Role in the Ecosystem*. 4th ed.; Dighton, J. and White J.F. (Eds.). CRC Press: Boca Raton, FL, USA, 2017; pp. 137–158. ISBN 9781315119496.
- Beraldi-Campesi, H., Hartnett H.E., Anbar A., Gordon G.W. and Garcia-Pichel F. (2009). Effect of biological soil crusts on soil elemental concentrations: Implications for biogeochemistry and as traceable biosignatures of ancient life on land. *Geobiology*, **7**, 348–359.
- Bhattacharyya, S.S. and Furtak K. (2023). Soil–Plant–Microbe Interactions Determine Soil Biological Fertility by altering Rhizospheric Nutrient Cycling and Biocrust Formation. *Sustainability*, **15**, 625. <https://doi.org/10.3390/su15010625>.
- Bowker, M.A., Reed S.C., Maestre F.T. and Eldridge D.J. (2018). Biocrusts: The living skin of the earth. *Plant Soil*, **429**, 1–7.
- Bu, C., Wu S., Zhang K., Yang Y. and Gao G. (2015). Biological soil crusts: An eco-adaptive biological conservative mechanism and implications for ecological restoration. *Plant Biosyst.*, **149**, 364–373.
- Celle, H. (2000). Caractérisation des Précipitations sur le Pourtour de la Méditerranée Occidentale: Approche Isotopique et Chimique. *Ph.D. Thesis*, Université d'Avignon et des, Pays de Vaucluse, France, 2000.
- Chamizo, S., Cantón Y., Rodríguez-Caballero E. and Domingo F. (2016). Biocrusts positively affect the soil water balance in semiarid ecosystems. *Ecohydrology*, **9**, 1208–1221.
- Chamizo, S. (2018). Soil Inoculation with Cyanobacteria: Reviewing Its' Potential for Agriculture Sustainability in Drylands. *Agric. Res. Technol. Open Access J.*, **18**, 1–5.
- Chamizo, S., Cantón Y., Domingo F. and Belnap J. (2011). Evaporative losses from soils covered by physical and different types of biological soil crusts. *Hydrol. Process*, **27**, 324–332.
- Chamizo, S., Cantón Y., Miralles I. and Domingo F. (2012). Biological soil crust development affects physicochemical characteristics of soil surface in semiarid ecosystems. *Soil Biol. Biochem.*, **49**, 96–105.
- Chaudhary, V.B., Bowker M.A., O'Dell T.E., Grace J.B., Redman A.E., Rillig M.C. and Johnson N.C. (2009). Untangling the biological contributions to soil stability in semiarid shrublands. *Ecological Applications*, **19**, 110–122.
- Chen, N., Yu K., Jia R., Teng J. and Zhao C. (2020). Biocrust as one of multiple stable states in global drylands. *Sci. Adv.*, **6**, eaay3763.
- Chen, R.Y., Zhang Y.M., Li Y., Wei W.S., Zhang J. and Wu N. (2009). The variation of morphological features and mineralogical components of biological soil crusts in the Gurbantunggut Desert of Northwestern China. *Environ. Geol.*, **57**, 1135–1143.
- Colica, G., Li H., Rossi F., Li D., Liu Y. and De Philippis R. (2014). Microbial secreted exopolysaccharides affect the hydrological behavior of induced biological soil crusts in desert sandy soils. *Soil Biol. Biochem.*, **68**, 62–70.
- Couradeau, E., Karaoz U., Lim H.C., Nunes da Rocha U., Northen T., Brodie E. and Garcia-Pichel F. (2016). Bacteria increase arid-land soil surface temperature through the production of sunscreens. *Nat. Commun.*, **7**, 10373.
- Dettweiler-Robinson, E., Nuñez M. and Litvak M.E. (2018). Biocrust contribution to ecosystem carbon fluxes varies along an elevational gradient. *Ecosphere*, **9**, e02315.
- Duran, P., Mora M.D.L.L., Matus F., Barra P.J., Jofré I., Kuzuyakov

- Y. and Merino C. (2021) Biological Crusts to Increase Soil Carbon Sequestration: New Challenges in a New Environment. *Biology*, **10**, 1190. <https://doi.org/10.3390/biology10111190>.
- Elbert, W., Weber B., Burrows S., Steinkamp J., Budel B., Andreae M.O. and Pöschl U. (2012). Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nat. Geosci.*, **5**, 459–462.
- Felde, V.J.M.N.L., Peth S., Uteau-Puschmann D., Drahorad S. and Felix-Henningsen P. (2014). Soil microstructure as an under-explored feature of biological soil crust hydrological properties: Case study from the NW Negev Desert. *Biodiver. Conser.*, **23**, 1687–1708.
- Finzi, A.C., Abramoff R.Z., Spiller K.S., Brzostek E.R., Darby B.A., Kramer M.A. and Phillips R.P. (2015). Rhizosphere processes are quantitatively important components of terrestrial carbon and nutrient cycles. *Glob. Change Biol.*, **21**, 2082–2094.
- Gao, L., Bowker M.A., Xu M., Sun H., Tuo D. and Zhao Y. (2017). Biological soil crusts decrease erodibility by modifying inherent soil properties on the Loess Plateau, China. *Soil Biol. Biochem.*, **105**, 49–58.
- Garcia-Pichel, F., Felde V.J.M.N.L., Drahorad S.L. and Weber B. (2016). Microstructure and weathering processes within biological soil crusts. In *Biological Soil Crusts: An Organizing Principle in Drylands* (eds Weber, B., Budel B. and Belnap J.), pp. 237–255. Springer, Cham.
- Gehlot, P., Vivekanand V. and Pareek N. (2022). Cyanobacterial and microalgal bioremediation: An efficient and eco-friendly approach toward industrial wastewater treatment and value-addition. In *Microbial Biodegradation and Bioremediation*; Elsevier: Amsterdam, The Netherlands, pp. 343–362.
- Gretarsdottir, J., Aradottir A.L., Vandvik V., Heegaard E. and Birks H.J.B. (2004). Long-term effects of reclamation treatments on plant succession in Iceland. *Restoration Ecology*, **12**, 268–278.
- Harper, K.T. and Belnap J. (2001). The influence of biological soil crusts on mineral uptake by associated vascular plants. *J. Arid Environ.*, **47**, 347–357.
- Heindel, R.C., Governali F.C., Spickard A.M. and Virginia R.A. (2018). The Role of Biological Soil Crusts in Nitrogen Cycling and Soil Stabilization in Kangerlussuaq, West Greenland. *Ecosystems*, **22**, 243–256.
- Hijmans, R.J., Cameron S.E., Parra J.L., Jones P.G. and Jarvis A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.*, **25**(15), 1965–1978. <https://doi.org/10.1002/joc.1276>.
- Karsten, U., Herburger K. and Holzinger A. (2016). Living in biological soil crust communities of African deserts – physiological traits of green algal Klebsormidium species (Streptophyta) to cope with desiccation, light and temperature gradients. *J. Plant Physiol.*, **194**, 2–12.
- Kheirfam, H., Sadeghi S.H., Homae M. and Darki B.Z. (2017). Quality improvement of an erosion-prone soil through microbial enrichment. *Soil Tillage Res.*, **165**, 230–238.
- Kidron, G.J., Vonshak A. and Abeliovich A. (2008). Recovery rates of microbiotic crusts within a dune ecosystem in the Negev Desert. *Geomorphology*, **100**, 444–452.
- Maestre, F.T., Benito B.M., Berdugo M., Concostrina-Zubiri L., Delgado-Baquerizo M., Eldridge D.J., Guirado E., Gross N., Kéfi S. and Le Bagousse-Pinguet Y. (2021). Biogeography of global drylands. *New Phytol.*, **231**, 540–558.
- Magan, N., Gouma S., Fragoeiro S., Shuaib M.E. and Bastos A.C. (2022). Bacterial and fungal bioremediation strategies. In *Microbial Biodegradation and Bioremediation*. Elsevier: Amsterdam, The Netherlands, 2022; pp. 193–212.
- Mager, D.M. and Thomas A.D. (2011). Extracellular polysaccharides from cyanobacterial soil crusts: a review of their role in dryland soil processes. *J. Arid Environ.*, **75**, 91–97.
- Miralles-Mellado, I., Cantón Y. and Solé-Benet A. (2011). Two-dimensional porosity of crusted silty soils: Indicators of soil quality in semiarid rangelands? *Soil Sci. Soc. Am. J.*, **75**, 1330–1342.
- Molina-Montenegro, M.A., Osés R., Torres-Díaz C., Atala C., Zurita-Silva A. and Ruiz-Lara S. (2016). Root-endophytes improve the ecophysiological performance and production of an agricultural species under drought condition. *AoB Plants*, **8**, plw062.
- Moreno-Jiménez, E., Ochoa-Hueso R., Plaza C., Aceña-Heras S., Flagmeier M., Elouali F.Z., Ochoa V., Gozalo B., Lázaro R. and Maestre F.T. (2020). Biocrusts buffer against the accumulation of soil metallic nutrients induced by warming and rainfall reduction. *Commun. Biol.*, **3**, 1–8.
- Musche, M., Adamescu M., Angelstam P., Bacher S., Bäck J., Buss H.L., Duffy C., Flaim G., Gaillardet J. and Giannakis G.V. (2019). Research questions to facilitate the future development of European long-term ecosystem research infrastructures: A horizon scanning exercise. *J. Environ. Manage.*, **250**, 109479.
- Nevins, C., Strauss S.L. and Inglett P. (2022). Contrasting effects of agroecosystem biocrusts on seedling growth and nitrogen accumulation in a greenhouse environment. *Agrosystems Geosci. Environ.*, **5**, e20295.
- Olaniran, A., Balgobind A. and Pillay B. (2013). Bioavailability of Heavy Metals in Soil: Impact on Microbial Biodegradation of Organic Compounds and possible improvement Strategies. *Int. J. Mol. Sci.*, **14**, 10197–10228.
- Paul, D. and Nair S. (2008). Stress adaptations in a plant growth promoting rhizobacterium (PGPR) with increasing salinity in the coastal agricultural soils. *J. Basic Microbiol.*, **48**, 378–384.
- Pointing, S.B. (2016). Hypolithic communities. In *Biological Soil Crusts: An Organizing Principle in Drylands* (eds Weber, B., Budel B. and Belnap J.), pp. 199–213. Springer, Cham.
- Pravalie, R. (2016). Drylands extent and environmental issues. A global approach. *Earth-Sci. Rev.*, **161**, 259–278.
- Qi, J., Liu Y., Wang Z., Zhao L., Zhang W., Wang Y. and Li X.

- (2021). Variations in microbial functional potential associated with phosphorus and sulfur cycling in biological soil crusts of different ages at the Tengger Desert, China. *Appl. Soil Ecol.*, **165**, 104022.
- Rastogi, R.P. and Sinha R.P. (2009). Biotechnological and industrial significance of cyanobacterial secondary metabolites. *Biotechnol. Adv.*, **27**, 521–539.
- Reed, S.C., Coe K.K., Sparks J.P., Housman D.C., Zelikova T.J. and Belnap J. (2012). Changes to dryland rainfall result in rapid moss mortality and altered soil fertility. *Nature Climate Change*, **2**, 752–755.
- Rodriguez-Caballero, E., Castro A.J., Chamizo S., Quintas-Soriano C., Garcia-Llorente M., Canton Y. and Weber B. (2018). Ecosystem services provided by biocrusts: from ecosystem functions to social values. *J. Arid Environ.*, **159**, 45–53.
- Rodriguez-Caballero, E., Belnap J., Büdel B., Crutzen P.J., Andreae M.O., Pöschl U. and Weber B. (2018). Dryland photoautotrophic soil surface communities endangered by global change. *Nat. Geosci.*, **11**, 185–189.
- Rodríguez-Caballero, E., Chamizo S., Roncero-Ramos B., Roman R. and Canton Y. (2018). Runoff from biocrust: A vital resource for vegetation performance on Mediterranean steppes. *Ecohydrology*, **11**, e1977.
- Román-Fernández, R., Roncero-Ramos B., Chamizo S., RodríguezCaballero E. and Cantón Y. (2018). Restoring soil functions by means of cyanobacteria inoculation: importance of soil conditions and species selection. *Land Degrad. Develop.*, **29** (9). <https://doi.org/10.1002/ldr.3064>.
- Rossi, F., Li H., Liu Y. and De Philippis R. (2017). Cyanobacterial inoculation (cyanobacterisation): Perspectives for the development of a standardized multifunctional technology for soil fertilization and desertification reversal. *Earth-Sci. Rev.*, **171**, 28–43.
- Rossi, F., Mugnai G. and Philippis R.D. (2018). Complex role of the polymeric matrix in biological soil crusts. *Plant and Soil*, **429**, 19–34.
- Rutherford, W.A., Painter T.H., Ferrenberg S., Belnap J., Okin G.S., Flagg C. and Reed S.C. (2017). Albedo feedbacks to future climate via climate change impacts on dryland biocrusts. *Sci. Rep.*, **7**, 1–9.
- Sadeghi, S.H., Kheirfam H., Homaei M., Darki B.Z. and Vafakhah M. (2017). Improving runoff behavior resulting from direct inoculation of soil micro-organisms. *Soil Tillage Res.*, **171**, 35–41.
- Safirel, U. and Adeel Z. (2005). Dryland systems. In: Hassan, R., Scholes R. and Neville A. (eds) *Ecosystems and human well-being: current state and trends*, vol 1. Island Press, Washington, DC, pp 623–662.
- Samolov, E., Baumann K., Büdel B., Jung P., Leinweber P., Mikhailyuk T., Karsten U. and Glaser K. (2020). Biodiversity of Algae and Cyanobacteria in Biological Soil Crusts Collected Along a Climatic Gradient in Chile using an Integrative Approach. *Microorganisms*, **8**, 1047.
- Sancho, L.G., Belnap J., Colesie C., Raggio J. and Weber B. (2016). Carbon Budgets of Biological Soil Crusts at Micro-, Meso- and Global Scales; Springer: Berlin/Heidelberg, Germany, 2016; pp. 287–304.
- Seitz, S., Nebel M., Goebes P., Käppeler K., Schmidt K., Shi X., Song Z., Webber C.L., Weber B. and Scholten T. (2017). Bryophytedominated biological soil crusts mitigate soil erosion in an early successional Chinese subtropical forest. *Biogeosciences*, **14**, 5775–5788.
- Sommer, U. and Sommer F. (2005). Cladocerans versus copepods: The cause of contrasting top-down controls on freshwater and marine phytoplankton. *Oecologia*, **147**, 183–194.
- Warren, S.D., Clair L.L.S., Stark L.R., Lewis L., Pombubpa N., Kurbessoian T., Stajich J.E. and Aanderud Z.T. (2019). Reproduction and Dispersal of Biological Soil Crust Organisms. *Front. Ecol. Evol.*, **7**.
- Weber, B., Belnap J., Büdel B., Antoninka A., Barger N.N., Chaudhary V.B., Darrouzet Nardi A., Eldridge D.J., Faist A.M., Ferrenberg S., Havrilla C.A., Huber Sannwald E., Issa O.M., Maestre F.T., Reed S.C., Rodríguez Caballero E., Tucker C., Young K.E., Zhang Y. and Bowker M.A. (2022). What is a biocrust? A refined, contemporary definition for a broadening research community. *Biological Reviews*, **97**(5), 1768–1785. <https://doi.org/10.1111/brv.12862>.
- Weber, B., Büdel B. and Belnap J. (Eds.) *Biological Soil Crusts: An Organizing Principle in Drylands; Ecological Studies*. Springer International Publishing: Cham, Switzerland, 2016; Volume 226, ISBN 978-3-319-30212-6.
- West, N.E. (1990). Structure and function of microphytic soil crusts in wildland ecosystems of arid to semi-arid ecosystems. *Adv. Ecol. Res.*, **20**, 179–223.
- Williams, A.J., Buck B.J. and Beyene M.A. (2012). Biological Soil Crusts in the Mojave Desert, USA: Micromorphology and Pedogenesis. *Soil Sci. Soc. Am. J.*, **76**, 1685–1695.
- Xiao, C., Yang L., Zhang L., Liu C. and Han M. (2016). Effects of cultivation ages and modes on microbial diversity in the rhizosphere soil of panax ginseng. *J. Ginseng Res.*, **40**, 28–37.
- Xiao, Y., Peng F., Dang Z., Jiang X., Zhang J., Zhang Y. and Shu H. (2015). Influence of rhizosphere ventilation on soil nutrient status, root architecture and the growth of young peach trees. *Soil Sci. Plant Nutr.*, **61**, 775–787.
- Zamanian, K., Pustovoytov K. and Kuzyakov Y. (2016). Pedogenic carbonates: Forms and formation processes. *Earth-Sci. Rev.*, **157**, 1–17.
- Zhang, J., Xu M. and Xu M.X. (2022). Characterising the diversity and functionality of the microbial community within biocrusts associated with different vegetation communities and soil habitats. *Appl. Soil Ecol.*, **175**, 104458.
- Zhang, S., Bai X., Zhao C., Tan Q., Luo G., Wang J., Li Q., Wu L., Chen F. and Li C (2021). Global CO₂ Consumption by Silicate Rock Chemical Weathering: Its Past and Future. *Earth's Futur.* **9**, e2020EF001938.