Received: 15 July 2022 | Accepted: 12 October 2022

DOI: 10.1002/jpln.202200252

VIEWPOINT

Biocrusts: Overlooked hotspots of managed soils in mesic environments

Corinna Gall[1] | **Juliette Ohan**[2] | **Karin Glaser**[3] | **Ulf Karsten**[3] | **Michael Schloter**[2,4] | **Thomas Scholten**[1] | **Stefanie Schulz**[2] | **Steffen Seitz**[1] | **Julia Katharina Kurth**[2,4]

[1] Soil Science and Geomorphology, Department of Geoscience, University of Tübingen, Tübingen, Germany

[2] Research Unit Comparative Microbiome Analyses, Helmholtz Zentrum München, Neuherberg, Germany

[3] Department of Applied Ecology & Phycology, Institute of Biological Sciences, University of Rostock, Rostock, Germany

[4] Chair of Soil Science, Department for Life Science Systems, School of Life Science, Technical University of Munich, Freising, Germany

Correspondence
Corinna Gall and Julia Katharina Kurth, Soil Science and Geomorphology, Department of Geoscience, University of Tübingen, Rümelinstrasse 19–23, 72070 Tübingen, Germany.
Email: corinna.gall@uni-tuebingen.de; J.kurth@tum.de

Funding information
DFG; Leibniz ScienceCampus

Abstract

Biological soil crusts, or “biocrusts”, are biogeochemical hotspots that can significantly influence ecosystem processes in arid environments. Although they can cover large areas, particularly in managed sites with frequent anthropogenic disturbance, their importance in mesic environments is not well understood. As in arid regions, biocrusts in mesic environments can significantly influence nutrient cycling, soil stabilization, and water balance; however, their persistence may differ. We call for interdisciplinary physical, biological, microbiological, chemical, and applied soil science research with a special focus on biocrusts of managed soils from mesic environments, to better understand their impact on overall ecosystem health and resilience, particularly with regard to climate change.

KEYWORDS
biological soil crust, climate change, erosion, hotspot, managed sites, mesic environments, soil degradation

1 | OVERLOOKED BIOCRUST HABITATS

Biological soil crusts (hereafter referred to as biocrusts) are hotspots of microbial activity, characterized by large amounts of microbial biomass, high nutrient turnover rates, and intensive biotic interactions. This is due to the supply of numerous bioavailable organic compounds provided by plants and/or animals (Kuzyakov & Blagodatskaya, 2015). Biocrusts develop on and a few millimeters below the soil’s surface, and modify their surroundings with organismal metabolites to create new habitats. Typical biocrust biota include algae, cyanobacteria, fungi, bacteria, archaea, protists, lichens, bryophytes, and microarthropods (Belnap et al., 2001; Khanipour Roshan et al., 2021; Weber et al., 2016, 2022). Biocrusts play an important ecological role in the creation and maintenance of healthy soils, and can (1) improve nutrient availability and fertility (Evans & Ehleringer, 1993; Gao et al., 2010; Li et al., 2012), (2) influence plant germination (Godínez-Alvarez et al., 2012; Havrilla et al., 2019; Zhang & Belnap, 2015), (3) increase biogeochemical cycling (Miralles et al., 2012; Wang et al., 2017; Xu et al., 2013), (4) keep and enhance water availability at the soil surface (George et al., 2003; Li et al., 2022), (5) increase soil aggregate stability (Cania et al., 2020; Riveras-Muñoz et al., 2022; Zhang et al., 2006), and (6) protect the soil surface by counteracting soil erosion from water (Chamizo et al., 2017; Seitz et al., 2017) or wind (Bullard et al., 2022; Zhang et al., 2006). However, thus far, biocrusts have primarily been studied in arid and semiarid regions (Weber et al., 2016).

Most studies of biocrusts in temperate regions have concentrated on bare soils or on soils with minimal vascular plant cover. Similar to arid soils, these soils are often too poor for vascular plant establishment and growth, with high salinity and/or low nutrient and water availability (Corbin & Thiet, 2020). Some temperate regions that biocrusts have been investigated include coastal areas (Khanipour Roshan et al., 2021; Mikhailyuk et al., 2019; Schulz et al., 2016; Thiet et al., 2014), inland dunes (Fischer, Veste, Wiehe, et al., 2010; Thiet et al., 2005), sand plains and pine barrens (Gilbert & Corbin, 2019; Hawkes & Flechtner, 2002), reclaimed lignite open-cast mining sites (Fischer, Veste, Schaaf, et al., 2010; Gypser et al., 2015), and potash tailings piles (Pushkareva et al., 2021; Sommer et al., 2020). Corbin and Thiet (2020) focused their review on biocrusts in temperate environments with restricted vascular plant productivity due to challenging soil and/or climatic conditions. While low vascular plant cover is common in arid regions, that is not reflective of most temperate regions. These regions are largely characterized by adequate water availability and unrestricted vascular plant growth, which can also be colonized by biocrusts. Recent studies have also found biocrusts at mesic, managed sites, which are anthropogenically impacted, such as monospecific pine forests, broadleaf-mixed forests, and agricultural fields (Baumann et al., 2017; Gall et al., 2022; Glaser et al., 2018; Kurth et al., 2021; Nevins et al., 2020, 2021; Ngosong et al., 2020). As the study of biocrusts on managed soils in mesic environments is still in its infancy, herein, we will elaborate on their dynamics, distribution, and potential impacts on ecosystem services.

2 | BIOCRUST DEVELEOPMENT ON DISTURBED SILVI- AND AGRICULTURAL SOIL SURFACES IN MESIC ENVIRONMENTS

The essential requirements for biocrust development include bare soil and a minimum amount of light. These conditions act as a starting point for biocrust establishment and succession, and can be created in mesic environments by disturbing or removing layers of vegetation and/or litter. As a result, soil is directly exposed to sunlight and biocrusts can rapidly colonize within a few weeks (Seitz et al., 2017). Recent work has described biocrusts in forests (Baumann et al., 2017; Gall et al., 2022; Glaser et al., 2018; Kurth et al., 2021; Ngosong et al., 2020) and on agricultural fields (Nevins et al., 2020, 2021, 2022). In these environments, biocrusts are ephemeral and do not usually persist unless the disturbance is permanent (Szyja et al., 2018).

In forests, bare soil can be natural or human induced. The total area of natural (e.g., caused by pest insects, disease, heavy storms, drought stress) and anthropogenic (e.g., clearcutting, forest roads, or skid trails) disturbance amounts to 39 million hectares, or 17% of the total area of all European forests (Senf & Seidl, 2021). Biocrusts can be found in both coniferous and deciduous forests of mesic environments, and are visible in the field as green cover (Baumann et al., 2017; Glaser, Albrecht, et al., 2022; Kurth et al., 2021) (Figure 1). While they can quickly establish in disturbed areas such as skid trails, their biocrust characteristics rapidly disappear with succession of vascular vegetation (Gall et al., 2022). Other cryptogamic communities that host a large part of their biomass above the soil's surface (such as thick moss mats, which are common in coniferous forests) are not always classified as biocrusts. However, there is a smooth transition between these communities and biocrusts (Belnap et al., 2003; Weber et al., 2022).

Biocrusts have also been found on agricultural soils (Figure 1), often in conjunction with copiotrophic microorganisms (Nevins et al., 2020, 2021, 2022). Agricultural practices such as plowing or other methods of tillage create large amounts of bare soil. This bare soil provides niches for biocrust development until crops shade the ground (limiting the light required for biocrust development). Additionally, many crops, such as potatoes, sugar beet, and maize, are grown in rows that allow for solar radiation to reach the ground during the entire growing season. In Europe, this results in 12.4 million hectares of potential biocrust cover, or approximately 12.6% of total arable land (Eurostat, 2020).

As biocrusts have been documented in forests and agricultural fields, they have the potential to colonize very large areas in mesic environments. Considering this and the fact that biocrusts are biogeochemical hotspots that can increase nutrient pools and turnover rates (Glaser et al., 2018; Kurth et al., 2021; Nevins et al., 2020), we hypothesize that they play a significant role in nutrient cycling in agri- and silvicultural soils, but this perspective has not yet been addressed.

3 | BENEFICIAL EFFECTS OF BIOCRUSTS IN MESIC ENVIRONMENTS

A large number of beneficial ecosystem functions can be attributed to biocrust development (Weber et al., 2016). However, there are very few studies dealing with the beneficial effects of biocrusts in mesic environments, and even fewer address managed soils.

In disturbed areas, biocrusts have great potential to reduce soil erosion (Seitz et al., 2017), and in some cases are even more effective than vascular plant cover (Bu et al., 2015; Gall et al., 2022). In particular, pioneer biocrust cover can protect against erosion as early as a few weeks following timber harvest (Gall et al., 2022), a very vulnerable stage for soils. Three main erosion-reducing mechanisms in biocrusts have been described. First, the sticky filamentous structure of many pioneer microalgae and cyanobacteria can glue soil particles together (Glaser et al., 2018; Glaser, Albrecht, et al., 2022; Glaser, Van, et al., 2022). Second, biocrusts are able to store water and reduce the kinetic energy of raindrops relative to bare soil (Zhao et al., 2014), which can reduce overland runoff (Bu et al., 2015). Third, biocrusts can increase soil organic matter (Gao et al., 2017) and improve aggregate stability by bacterial metabolites such as exo- and lipopolysaccharides (Cania et al., 2020). However, these effects depend on climatic conditions (Kidron, Lichner, et al., 2022; Riveras-Muñoz et al., 2022) and species composition (Gypser et al., 2016) and have been poorly studied in mesic environments. As shown in Kidron, Lichner, et al. (2022), biocrust-related mechanisms of runoff generation are very complex, with significant variability documented in arid environments.

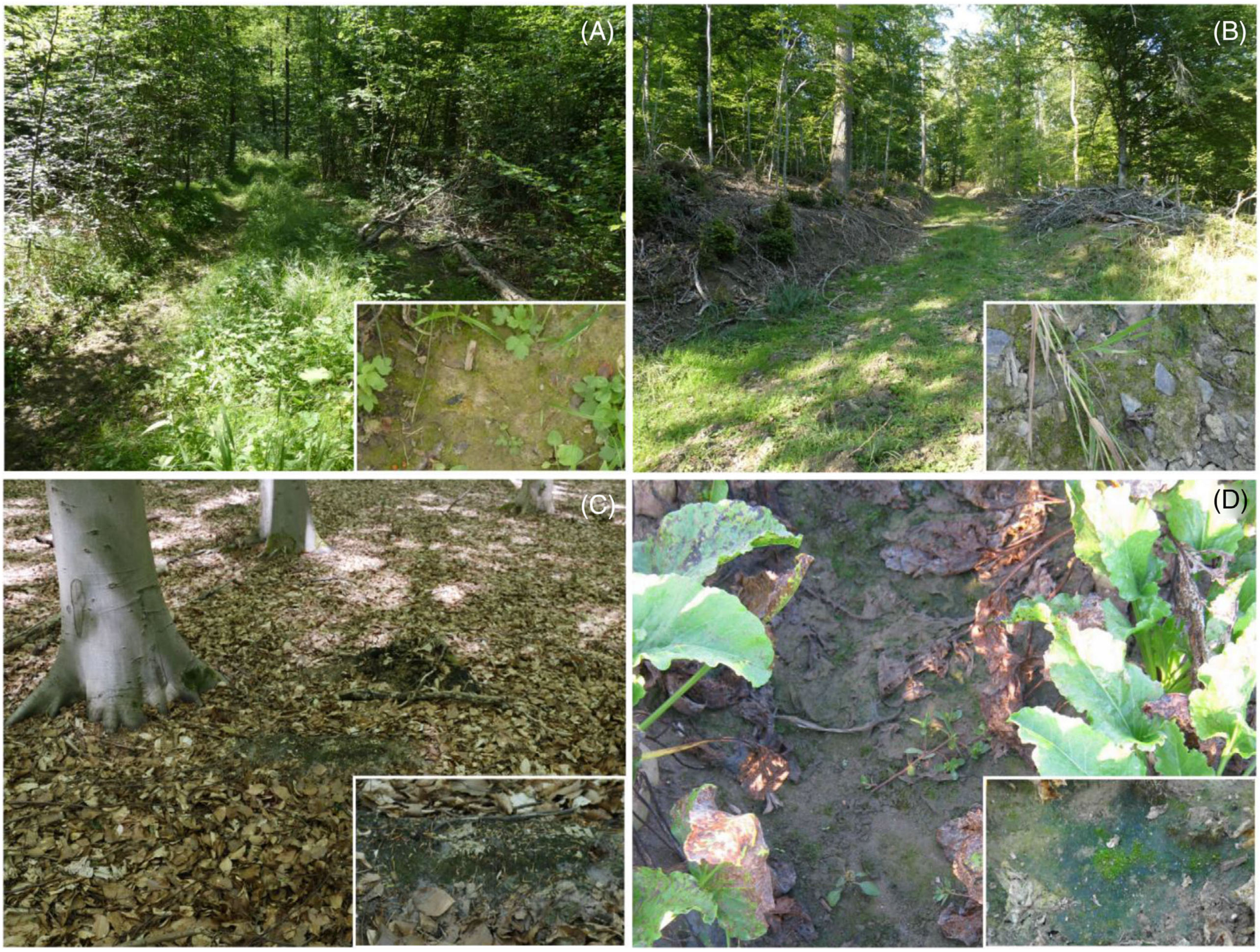

FIGURE 1 Overview of biocrusts on managed soils in mesic environments: (A, B) early successional bryophyte-dominated biocrusts on skid trail wheel tracks in a deciduous forest; (C) bryophyte-dominated biocrust under leaf litter; (D) bryophyte- and cyanobacteria-dominated biocrusts on arable land between sugar beet crops

Increased surface runoff from biocrusts, for example, could lead to more soil erosion downslope, assuming an uncovered soil there. For a better understanding of biocrust-related mechanisms of soil erosion and runoff generation in mesic environments, more field experiments are necessarily needed.

The impact of biocrusts on the soil water balance in arid environments has been contradictory (Kidron, Fischer, et al., 2022; Kidron, Lichner, et al., 2022). On one hand, they can improve infiltration into the soil and increase water content while reducing evaporation—although these effects can vary depending on rainfall intensity, temperature, and soil texture (Chamizo et al., 2016). On the other hand, biocrusts may have a negative effect on the soil water balance, due to pore clogging by exopolysaccharides and/or water repellence (Kidron, Lichner, et al., 2022; Xiao et al., 2019). Additionally, recent studies of biocrusts in temperate environments have primarily been conducted in challenging conditions for vascular plant growth (Gypser et al., 2016; Thiet et al., 2005), and cannot be generalized. Therefore, further studies in managed mesic environments are needed to fully characterize the potential beneficial effects of biocrusts on the soil water balance.

Biocrusts have been referred to as biogeochemical hotspots in mesic environments (Kuzyakov & Blagodatskaya, 2015). They host higher microbial biomass compared to surrounding bulk soil (Glaser, Albrecht, et al., 2022; Glaser, Van, et al., 2022; Kurth et al., 2021; Nevins et al., 2021), exhibit more nutrient turnover, and can consequently impact biogeochemical cycling (Glaser et al., 2018; Kurth et al., 2021). Recent work has found a carbon enrichment from microbial biomass and plant-available nitrogen beneath biocrusts in agricultural soils (Nevins et al., 2020), and that biocrusts play a key role in the biogeochemical phosphorus cycle in forests (Baumann et al., 2017, 2019; Kurth et al., 2021). Artificially cultivated biocrusts have also been found to increase carbon, nitrogen, and phosphorus contents at the soil's surface (Deng et al., 2020; Wu et al., 2013). Kheirfam (2020) observed an increase in carbon sequestration when soils were inoculated with bacteria, cyanobacteria, or both, resulting in an extrapolated removal of 3.11–3.93 t ha^{-1} y^{-1} of CO_2 from the atmosphere. Several other studies have primarily been concerned with the composition of biocrust soil microbial communities (Glaser, Albrecht, et al., 2022; Glaser, Van, et al., 2022; Kurth et al., 2021; Nevins et al., 2021), and their changes with elevation and microclimates (You et al., 2021). However, further work

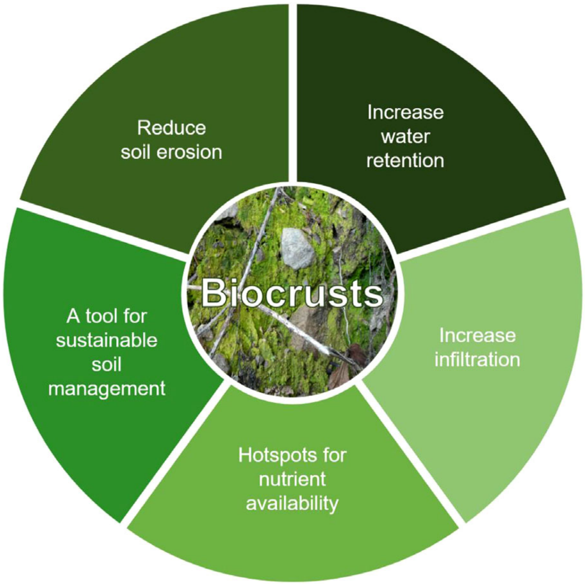

FIGURE 2 Summary of the potential beneficial effects of biocrusts in mesic environments (Illustration: Julia Dartsch)

will be required to determine which specific organisms or community profiles contribute to these changes in biogeochemical cycling. Additionally, future investigations could determine biocrusts' capability to store nitrogen or phosphorus temporally in their biomass, particularly over winter when microbial activity is reduced.

Based on these ecological functions, biocrusts bear the potential as novel tools for sustainable soil management. They have already been explored as possible avenues for the restoration of degraded soils, such as in the rehabilitation of salt heaps (Sommer et al., 2020) and felled/burned forests (Chamizo et al., 2020; Olarra, 2012). In addition to habitat restoration by loose soil particle stabilization (Grover et al., 2020), they can also serve as a "living" fertilizer in agriculture, as they biologically fix atmospheric nitrogen and retain nutrients and water (Sears & Prithiviraj, 2012; Vinoth et al., 2020). Methods to facilitate and accelerate biocrust establishment have primarily been applied in arid environments, and include the addition of chemical or physical soil stabilizers (Antoninka et al., 2020), improved light conditions (Zhao et al., 2021), irrigation (Wu et al., 2013; Zhou et al., 2020), and the inoculation of pioneer organisms with single or multispecies biocrusts to close gaps in natural biocrust cover (Bowker, 2007). In agriculture in particular, large-scale biocrust inoculation could be carried out by airplane in the future (Sears & Prithiviraj, 2012). We propose these approaches could also be applied for use in mesic environments after modification (Figure 2).

4 | OUTLOOK: BIOCRUSTS' POTENTIAL TO MITIGATE CLIMATE CHANGE IN MESIC ENVIRONMENTS

Global climate change is becoming increasingly visible in mesic environments, and will bring extreme weather events like heavy rain and extended drought (Olsson et al., 2019). As a result, soils will be more vulnerable and require new forms of management for their protection, as stipulated by the UN's "Sustainable Development Goals". Accordingly, biocrusts could make a significant contribution. Considering the large extent of biocrust colonization in managed mesic environments, and these areas' projected expansion due to climate change (Gejdoš & Michajlová, 2022; Senf & Seidl, 2021), further studies will be necessary to evaluate their contributions to ecosystem services and global relevance (Ferrenberg et al., 2017). Interdisciplinary physical, biological, microbiological, chemical, and applied soil research will be indispensable in understanding the development and influence of biocrusts in mesic and anthropogenically impacted environments. Their inoculation as an erosion control measure may be of particular importance (Cruz de Carvalho et al., 2018; Varela et al., 2021), especially as erosion rates are projected to increase due to climate change (Li & Fang, 2016). In addition, biocrusts' ability to store carbon could help in combating climate change in general (Kheirfam, 2020; Kheirfam et al., 2017), and applied in agriculture (Vinoth et al., 2020) or restoration (Román et al., 2018). We call for interdisciplinary research with a focus on biocrusts of managed soils in mesic environments, in order to better understand their multitrophic interactions, consequences on chemical and physical soil properties, and impact on overall ecosystem health.

ACKNOWLEDGMENTS

We acknowledge support from *DFG Project SE2767/2-1* "*MesiCrust*" and *DFG Priority Program 1803 "EarthShape"*, as well as help provided by *Julia Dartsch*, *Lena Grabherr*, *Sonja M. Thielen*, *Martin Nebel*, and *Michael Sauer*. Moreover, we are grateful for funding from *DFG Priority Program 1374 "Biodiversity—Exploratories"* (*GL909/2-3*, *KA899/28-1/2/3*, *SCHL446/31–2*, *SCHU2907/7-3*) and the inspiring scientific community within that program, as well as by the *Leibniz ScienceCampus "Phosphorus Research Rostock"*. We acknowledge support from the Open Access Publishing Fund of the University of Tübingen.

Open access funding enabled and organized by Projekt DEAL.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Corinna Gall https://orcid.org/0000-0002-6318-4113
Karin Glaser https://orcid.org/0000-0002-5962-3603
Ulf Karsten https://orcid.org/0000-0002-2955-0757
Michael Schloter https://orcid.org/0000-0003-1671-1125
Thomas Scholten https://orcid.org/0000-0002-4875-2602
Stefanie Schulz https://orcid.org/0000-0001-5520-8106
Steffen Seitz https://orcid.org/0000-0003-4911-3906
Julia Katharina Kurth https://orcid.org/0000-0002-4753-6166

REFERENCES

Antoninka, A., Faist, A., Rodriguez-Caballero, E., Young, K. E., Chaudhary, V. B., Condon, L. A., & Pyke, D. A. (2020). Biological soil crusts in ecological restoration: Emerging research and perspectives. *Restoration Ecology*, *28*, S3–S8.

Baumann, K., Siebers, M., Kruse, J., Eckhardt, K.-U., Hu, Y., Michalik, D., Siebers, N., Kar, G., Karsten, U., & Leinweber, P. (2019). Biological soil crusts as key player in biogeochemical P cycling during pedogenesis of sandy substrate. *Geoderma*, *338*, 145–158.

Baumann, K., Glaser, K., Mutz, J.-E., Karsten, U., MacLennan, A., Hu, Y., Michalik, D., Kruse, J., Eckhardt, K.-U., Schall, P., & Leinweber, P. (2017). Biological soil crusts of temperate forests: Their role in P cycling. *Soil Biology and Biochemistry*, *109*, 156–166.

Belnap, J., Büdel, B., & Lange, O. L. (2001). Biological soil crusts: Characteristics and distribution. In J. Belnap & O. L. Lange (Eds.), *Biological soil crusts: Structure, function, and management* (pp. 3–30). Springer.

Bowker, M. A. (2007). Biological soil crust rehabilitation in theory and practice: An underexploited opportunity. *Restoration Ecology*, *15*(1), 13–23.

Bu, C., Wu, S., Han, F., Yang, Y., & Meng, J. (2015). The combined effects of moss-dominated biocrusts and vegetation on erosion and soil moisture and implications for disturbance on the Loess Plateau, China. *PLoS ONE*, *10*(5), e0127394. https://doi.org/10.1371/journal.pone.0127394

Bullard, J. E., Strong, C. L., & Aubault, H. A. P. (2022). Cyanobacterial soil crust responses to rainfall and effects on wind erosion in a semiarid environment, Australia: Implications for landscape stability. *Journal of Geophysical Research: Biogeosciences*, *127*(2), e2021JG006652. https://doi.org/10.1029/2021JG006652

Cania, B., Vestergaard, G., Kublik, S., Kohne, J. M., Fischer, T., Albert, A., Winkler, B., Schloter, M., & Schulz, S. (2020). Biological soil crusts from different soil substrates harbor distinct bacterial groups with the potential to produce exopolysaccharides and lipopolysaccharides. *Microbial Ecology*, *79*(2), 326–341.

Chamizo, S., Adessi, A., Certini, G., & De Philippis, R. (2020). Cyanobacteria inoculation as a potential tool for stabilization of burned soils. *Restoration Ecology*, *28*, 106–114.

Chamizo, S., Cantón, Y., Rodríguez-Caballero, E., & Domingo, F. (2016). Biocrusts positively affect the soil water balance in semiarid ecosystems. *Ecohydrology*, *9*(7), 1208–1221.

Chamizo, S., Rodríguez-Caballero, E., Román, J. R., & Cantón, Y. (2017). Effects of biocrust on soil erosion and organic carbon losses under natural rainfall. *Catena*, *148*, 117–125.

Corbin, J. D., & Thiet, R. K. (2020). Temperate biocrusts: Mesic counterparts to their better-known dryland cousins. *Frontiers in Ecology and the Environment*, *18*(8), 456–464.

Cruz de Carvalho, R., dos Santos, P., & Branquinho, C. (2018). Production of moss-dominated biocrusts to enhance the stability and function of the margins of artificial water bodies. *Restoration Ecology*, *26*(3), 419–421.

Deng, S., Zhang, D., Wang, G., Zhou, X., Ye, C., Fu, T., Ke, T., Zhang, Y., Liu, Y., & Chen, L. (2020). Biological soil crust succession in deserts through a 59-year-long case study in China: How induced biological soil crust strategy accelerates desertification reversal from decades to years. *Soil Biology and Biochemistry*, *141*, 107665. https://doi.org/10.1016/j.soilbio.2019.107665

Eurostat. (2020). *Agriculture, forestry and fishery statistics—2020 edition*. Publications Office of the European Union.

Evans, R. D., & Ehleringer, J. R. (1993). A break in the nitrogen cycle in aridlands? Evidence from δ^{p15}N of soils. *Oecologia*, *94*(3), 314–317.

Ferrenberg, S., Tucker, C. L., & Reed, S. C. (2017). Biological soil crusts: Diminutive communities of potential global importance. *Frontiers in Ecology and the Environment*, *15*(3), 160–167.

Fischer, T., Veste, M., Wiehe, W., & Lange, P. (2010). Water repellency and pore clogging at early successional stages of microbiotic crusts on inland dunes, Brandenburg, NE Germany. *Catena*, *80*(1), 47–52.

Fischer, T., Veste, M., Schaaf, W., Dümig, A., Kögel-Knabner, I., Wiehe, W., Bens, O., & Hüttl, R. F. (2010). Initial pedogenesis in a topsoil crust 3 years after construction of an artificial catchment in Brandenburg, NE Germany. *Biogeochemistry*, *101*(1), 165–176.

Gall, C., Nebel, M., Quandt, D., Scholten, T., & Seitz, S. (2022). Pioneer biocrust communities prevent soil erosion in temperate forests after disturbances. *Biogeosciences*, *19*, 3225–3245.

Gao, L., Bowker, M. A., Xu, M., Sun, H., Tuo, D., & Zhao, Y. (2017). Biological soil crusts decrease erodibility by modifying inherent soil properties on the Loess Plateau, China. *Soil Biology and Biochemistry*, *105*, 49–58.

Gao, S., Ye, X., Chu, Y., & Dong, M. (2010). Effects of biological soil crusts on profile distribution of soil water, organic carbon and total nitrogen in Mu Us Sandland, China. *Journal of Plant Ecology*, *3*(4), 279–284.

Gejdoš, M., & Michajlová, K. (2022). Analysis of current and future forest disturbances dynamics in central Europe. *Forests*, *13*(4), 554. https://doi.org/10.3390/f13040554

George, D. B., Roundy, B. A., St Clair, L. L., Johansen, J. R., Schaalje, G. B., & Webb, B. L. (2003). The effects of microbiotic soil crusts on soil water loss. *Arid Land Research and Management*, *17*(2), 113–125.

Gilbert, J. A., & Corbin, J. D. (2019). Biological soil crusts inhibit seed germination in a temperate pine barren ecosystem. *PLoS ONE*, *14*(2), e0212466. https://doi.org/10.1371/journal.pone.0212466

Glaser, K., Albrecht, M., Baumann, K., Overmann, J., & Sikorski, J. (2022). Biological soil crust from mesic forests promote a specific bacteria community. *Frontiers in Microbiology*, *13*, 769767. https://doi.org/10.3389/fmicb.2022.769767

Glaser, K., Baumann, K., Leinweber, P., Mikhailyuk, T., & Karsten, U. (2018). Algal richness in BSCs in forests under different management intensity with some implications for P cycling. *Biogeosciences*, *15*(13), 4181–4192.

Glaser, K., Van, A. T., Pushkareva, E., Barrantes, I., & Karsten, U. (2022). Microbial communities in biocrusts are recruited from the neighboring sand at coastal dunes along the Baltic Sea. *Frontiers in Microbiology*, *13*, 859447. https://doi.org/10.3389/fmicb.2022.859447

Godínez-Alvarez, H., Morín, C., & Rivera-Aguilar, V. (2012). Germination, survival and growth of three vascular plants on biological soil crusts from a Mexican tropical desert. *Plant Biology*, *14*(1), 157–162.

Grover, H. S., Bowker, M. A., & Fulé, P. Z. (2020). Improved, scalable techniques to cultivate fire mosses for rehabilitation. *Restoration Ecology*, *28*, 17–24.

Gypser, S., Veste, M., Fischer, T., & Lange, P. (2015). Formation of soil lichen crusts at reclaimed post-mining sites, Lower Lusatia, North-east Germany. *Graphis Scripta*, *27*, 3–14.

Gypser, S., Veste, M., Fischer, T., & Lange, P. (2016). Infiltration and water retention of biological soil crusts on reclaimed soils of former opencast lignite mining sites in Brandenburg, north-east Germany. *Journal of Hydrology and Hydromechanics*, *64*(1), 1–11. https://doi.org/10.1515/johh-2016-0009

Havrilla, C. A., Chaudhary, V. B., Ferrenberg, S., Antoninka, A. J., Belnap, J., Bowker, M. A., Eldridge, D. J., Faist, A. M., Huber-Sannwald, E., Leslie, A. D., Rodriguez-Caballero, E., Zhang, Y., Barger, N. N., & Vries, F. (2019). Towards a predictive framework for biocrust mediation of plant performance: A meta-analysis. *Journal of Ecology*, *107*(6), 2789–2807.

Hawkes, C. V., & Flechtner, V. R. (2002). Biological soil crusts in a xeric Florida shrubland: Composition, abundance, and spatial heterogeneity of crusts with different disturbance histories. *Microbial Ecology*, *43*(1), 1–12.

Khanipour Roshan, S., Dumack, K., Bonkowski, M., Leinweber, P., Karsten, U., & Glaser, K. (2021). Taxonomic and functional diversity of heterotrophic protists (Cercozoa and Endomyxa) from biological soil crusts. *Microorganisms*, *9*(2), 205. https://doi.org/10.3390/microorganisms9020205

Kheirfam, H. (2020). Increasing soil potential for carbon sequestration using microbes from biological soil crusts. *Journal of Arid Environments*, *172*, 104022. https://doi.org/10.1016/j.jaridenv.2019.104022

Kheirfam, H., Sadeghi, S. H., Homaee, M., & Darki, B. Z. (2017). Quality improvement of an erosion-prone soil through microbial enrichment. *Soil and Tillage Research*, *165*, 230–238.

Kidron, G. J., Fischer, T., & Xiao, B. (2022). The ambivalent effect of biocrusts on evaporation: Can the contradictory conclusions be explained? A review. *Geoderma*, *416*, 115805. https://doi.org/10.1016/j.geoderma.2022.115805

Kidron, G. J., Lichner, L., Fischer, T., Starinsky, A., & Or, D. (2022). Mechanisms for biocrust-modulated runoff generation–A review. *Earth-Science Reviews*, *231*, 104100. https://doi.org/10.1016/j.earscirev.2022.104100

Kurth, J. K., Albrecht, M., Karsten, U., Glaser, K., Schloter, M., & Schulz, S. (2021). Correlation of the abundance of bacteria catalyzing phosphorus and nitrogen turnover in biological soil crusts of temperate forests of Germany. *Biology and Fertility of Soils*, *57*(2), 179–192.

Kuzyakov, Y., & Blagodatskaya, E. (2015). Microbial hotspots and hot moments in soil: Concept & review. *Soil Biology and Biochemistry*, *83*, 184–199.

Li, S., Bowker, M. A., Chamizo, S., & Xiao, B. (2022). Effects of moss biocrusts on near-surface soil moisture are underestimated in drylands: Insights from a heat-pulse soil moisture sensor. *Geoderma*, *413*, 115763. https://doi.org/10.1016/j.geoderma.2022.115763

Li, X. R., Zhang, P., Su, Y. G., & Jia, R. L. (2012). Carbon fixation by biological soil crusts following revegetation of sand dunes in arid desert regions of China: A four-year field study. *Catena*, *97*, 119–126.

Li, Z., & Fang, H. (2016). Impacts of climate change on water erosion: A review. *Earth-Science Reviews*, *163*, 94–117.

Mikhailyuk, T., Glaser, K., Tsarenko, P., Demchenko, E., & Karsten, U. (2019). Composition of biological soil crusts from sand dunes of the Baltic Sea coast in the context of an integrative approach to the taxonomy of microalgae and cyanobacteria. *European Journal of Phycology*, *54*(3), 263–290.

Miralles, I., Domingo, F., Cantón, Y., Trasar-Cepeda, C., Leirós, M. C., & Gil-Sotres, F. (2012). Hydrolase enzyme activities in a successional gradient of biological soil crusts in arid and semi-arid zones. *Soil Biology and Biochemistry*, *53*, 124–132.

Nevins, C. J., Inglett, P. W., & Strauss, S. L. (2021). Biological soil crusts structure the subsurface microbiome in a sandy agroecosystem. *Plant and Soil*, *462*(1), 311–329.

Nevins, C. J., Strauss, S. L., & Inglett, P. W. (2020). Biological soil crusts enhance moisture and nutrients in the upper rooting zone of sandy soil agroecosystems. *Journal of Plant Nutrition and Soil Science*, *183*(5), 615–626.

Nevins, C. J., Inglett, P. W., Reardon, C. L., & Strauss, S. L. (2022). Seasonality drives microbiome composition and nitrogen cycling in soil below biocrusts. *Soil Biology and Biochemistry*, *166*, 108551. https://doi.org/10.1016/j.soilbio.2022.108551

Ngosong, C., Buse, T., Ewald, M., Richter, A., Glaser, K., Schöning, I., & Ruess, L. (2020). Influence of management intensity and environmental conditions on microbiota in biological soil crust and crust-free soil habitats of temperate forests. *Soil Biology and Biochemistry*, *144*, 107761. https://doi.org/10.1016/j.soilbio.2020.107761

Olarra, J. (2012). *Biological soil crusts in forested ecosystems of southern Oregon: Presence, abundance and distribution across climate gradients* (Master thesis). Oregon State University.

Olsson, L. B., Barbosa, H., Bhadwal, S., Cowie, A., Delusca, K., Flores-Renteria, D., Hermans, K., Jobbagy, E., Kurz, W., Li, D., Sonwa, D. J., & Stringer, L. (2019). Land degradation. In P. R. Shukla, J. Skea, E. Calvo Buendia, V. Masson-Delmotte, H.-O. Pörtner, D. C. Roberts, P. Zhai, R. Slade, S. Connors, R. van Diemen, M. Ferrat, E. Haughey, S. Luz, S. Neogi, M. Pathak, J. Petzold, J. Portugal Pereira, P. Vyas, E. Huntley, … J. Malley (Ed.), *Climate Change and Land: An IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems* (pp. 345–436). IPCC.

Pushkareva, E., Sommer, V., Barrantes, I., & Karsten, U. (2021). Diversity of microorganisms in biocrusts surrounding highly saline potash tailing piles in Germany. *Microorganisms*, *9*(4), 714. https://doi.org/10.3390/microorganisms9040714

Riveras-Muñoz, N., Seitz, S., Witzgall, K., Rodríguez, V., Kühn, P., Mueller, C. W., Oses, R., Seguel, O., Wagner, D., & Scholten, T. (2022). Biocrust-linked changes in soil aggregate stability along a climatic gradient in the Chilean Coastal Range. *Soil Discussions*, . https://doi.org/10.5194/soil-2021-141

Román, J. R., Roncero-Ramos, B., Chamizo, S., Rodríguez-Caballero, E., & Cantón, Y. (2018). Restoring soil functions by means of cyanobacteria inoculation: Importance of soil conditions and species selection. *Land Degradation & Development*, *29*(9), 3184–3193.

Schulz, K., Mikhailyuk, T., Dreßler, M., Leinweber, P., & Karsten, U. (2016). Biological soil crusts from coastal dunes at the Baltic Sea: Cyanobacterial and algal biodiversity and related soil properties. *Microbial Ecology*, *71*(1), 178–193.

Sears, J. T., & Prithiviraj, B. (2012). *Seeding of large areas with biological soil crust starter culture formulations: Using an aircraft disbursable granulate to increase stability, fertility and CO2 sequestration on a landscape scale*. 2012 IEEE Green Technologies Conference, pp. 1–3.

Seitz, S., Nebel, M., Goebes, P., Käppeler, K., Schmidt, K., Shi, X., Song, Z., Webber, C. L., Weber, B., & Scholten, T. (2017). Bryophyte-dominated biological soil crusts mitigate soil erosion in an early successional Chinese subtropical forest. *Biogeosciences*, *14*(24), 5775–5788.

Senf, C., & Seidl, R. (2021). Mapping the forest disturbance regimes of Europe. *Nature Sustainability*, *4*(1), 63–70.

Sommer, V., Mikhailyuk, T., Glaser, K., & Karsten, U. (2020). Uncovering unique green algae and cyanobacteria isolated from biocrusts in highly saline potash tailing pile habitats, using an integrative approach. *Microorganisms*, *8*(11), 1667. https://doi.org/10.3390/microorganisms8111667

Szyja, M., Büdel, B., & Colesie, C. (2018). Ecophysiological characterization of early successional biological soil crusts in heavily human-impacted areas. *Biogeosciences*, *15*(7), 1919–1931.

Thiet, R. K., Doshas, A., & Smith, S. M. (2014). Effects of biocrusts and lichen-moss mats on plant productivity in a US sand dune ecosystem. *Plant and Soil*, *377*(1), 235–244.

Thiet, R. K., Boerner, R. E. J., Nagy, M., & Jardine, R. (2005). The effect of biological soil crusts on throughput of rainwater and N into Lake Michigan sand dune soils. *Plant and Soil*, *278*(1), 235–251.

Varela, Z., Real, C., Branquinho, C., do Paço, T. A., & Cruz de Carvalho, R. (2021). Optimising artificial moss growth for environmental studies in the Mediterranean area. *Plants*, *10*(11), 2523.

Vinoth, M., Sivasankari, S., Ahamed, A. K. K., Al-Arjani, A. B. F., Abd_Allah, E. F., & Baskar, K. (2020). Biological soil crust (BSC) is an effective biofertilizer on *Vigna mungo* (L.). *Saudi Journal of Biological Sciences*, *27*(9), 2325–2332.

Wang, Y.-F., Xiao, B., Wang, B., Ma, S., & Yao, X.-M. (2017). Effects of moss-dominated biological soil crusts on soil enzyme activities in water-wind erosion crisscross region on the Loess Plateau of China. *Chinese Journal of Applied Ecology*, *28*(11), 3553–3561.

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

Weber, B., Belnap, J., Büdel, B., Antoninka, A. J., Barger, N. N., Chaudhary, V. B., Darrouzet-Nardi, A., Eldridge, D. J., Faist, A. M., Ferrenberg, S., Havrilla, C. A., Huber-Sannwald, E., Malam Issa, O., Maestre, F. T., Reed, S. C., Rodriguez-Caballero, E., Tucker, C., Young, K. E., Zhang, Y., … Bowker, M. A. (2022). What is a biocrust? A refined, contemporary definition for a broadening research community. *Biological Reviews*, *97*(5), 1768–1785.

Wu, Y., Rao, B., Wu, P., Liu, Y., Li, G., & Li, D. (2013). Development of artificially induced biological soil crusts in fields and their effects on top soil. *Plant and Soil*, *370*(1), 115–124.

Xiao, B., Sun, F., Hu, K., & Kidron, G. J. (2019). Biocrusts reduce surface soil infiltrability and impede soil water infiltration under tension and ponding conditions in dryland ecosystem. *Journal of Hydrology*, *568*, 792–802.

Xu, Y., Rossi, F., Colica, G., Deng, S., De Philippis, R., & Chen, L. (2013). Use of cyanobacterial polysaccharides to promote shrub performances in desert soils: A potential approach for the restoration of desertified areas. *Biology and Fertility of Soils*, *49*(2), 143–152.

You, Y., Aho, K., Lohse, K. A., Schwabedissen, S. G., Ledbetter, R. N., & Magnuson, T. S. (2021). Biological soil crust bacterial communities vary along climatic and shrub cover gradients within a sagebrush steppe ecosystem. *Frontiers in Microbiology*, *12*, 569791. https://doi.org/10.3389/fmicb.2021.569791

Zhang, Y., & Belnap, J. (2015). Growth responses of five desert plants as influenced by biological soil crusts from a temperate desert, China. *Ecological Research*, *30*(6), 1037–1045.

Zhang, Y. M., Wang, H. L., Wang, X. Q., Yang, W. K., & Zhang, D. Y. (2006). The microstructure of microbiotic crust and its influence on wind erosion for a sandy soil surface in the Gurbantunggut Desert of Northwestern China. *Geoderma*, *132*(3–4), 441–449.

Zhao, Y., Qin, N., Weber, B., & Xu, M. (2014). Response of biological soil crusts to raindrop erosivity and underlying influences in the hilly Loess Plateau region, China. *Biodiversity and Conservation*, *23*(7), 1669–1686.

Zhao, Y., Wang, N., Zhang, Z., Pan, Y., & Jia, R. (2021). Accelerating the development of artificial biocrusts using covers for restoration of degraded land in dryland ecosystems. *Land Degradation & Development*, *32*(1), 285–295.

Zhou, X., Zhao, Y., Belnap, J., Zhang, B., Bu, C., & Zhang, Y. (2020). Practices of biological soil crust rehabilitation in China: Experiences and challenges. *Restoration Ecology*, *28*, 45–55.

How to cite this article: Gall, C., Ohan, J., Glaser, K., Karsten, U., Schloter, M., Scholten, T., Schulz, S., Seitz, S., & Kurth, J. K. (2022). Biocrusts: Overlooked hotspots of managed soils in mesic environments. *Journal of Plant Nutrition and Soil Science*, 1–7. https://doi.org/10.1002/jpln.202200252