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Biocrusts: Engineers and architects of surface soil properties, functions, and processes in dryland ecosystems

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ABSTRACT

Biocrusts are photosynthetic biotic communities of cryptogams and microbes that aggregate minerals at the soil surface in many ecosystems. Due to their high tolerance to harsh environments, biocrusts are present in a wide range of habitats, but are especially representative ground covers in regions with restricted vegetation growth, such as drylands (hyperarid, arid, semiarid, and dry subhumid regions) where water is a limiting factor, or high latitude or altitude regions where cold is a limiting factor. Since biocrusts fulfill a large range of ecological roles particularly in modifying soil properties and regulating functions, their rehabilitation and management is believed to be a promising measure for combating land degradation. We organized this article collection to further highlight the importance of biocrusts and their fundamental roles in reshaping soil properties and multifunctionality in drylands and other ecosystems, and to elucidate the ways in which global change factors are influencing biocrust-soil systems. The special issue brings together 27 research articles pertinent to soil-biocrust interactions or biocrust response to global change and disturbance from 12 countries worldwide (10 papers from China, 6 papers from the USA, 2 papers from Spain, 2 papers from Australia, in addition to studies from Antarctica, Argentina, Brazil, Iceland, Iran, Mexico, Norway, South Africa, and Sweden). The discussed topics include biocrust roles in regulating soil hydrology (6 papers), reducing soil erosion (4 papers), affecting soil carbon fixation and respiration (2 papers), and influencing soil microbial biodiversity (5 papers). The responses of biocrusts themselves and their functions to trampling disturbance (2 papers), land use shifts (2 papers), and climate change (5 papers) are also emphasized. On the whole, we highlight the capability of biocrusts in reshaping most properties of surface soil, acting as engineers and architects of surface soil properties, functions, and processes in dryland or other harsh environments, and we recognize the necessity of their protection and consideration as valuable nature-based measures to combat soil and land degradation.

1. Introduction

Drylands, including hyperarid, arid, semiarid, and dry subhumid climate regions, cover 47% of the world land surface and are inhabited by 39% of the world's population (Koutroulis, 2019). Most drylands suffer from considerable vegetation degradation due to global warming and intensive human activities (Huang et al., 2020). The interspaces between sparse vegetation in drylands are supposed to be "bare" and exposed to soil erosion, but a large proportion of these areas are actually covered and protected by biocrusts (a contracted expression of the term "biological soil crusts") (Weber et al., 2022). These biocrusts "result from an intimate association between soil particles and differing proportions of photoautotrophic (e.g., cyanobacteria, algae, lichens, bryophytes) and heterotrophic (e.g., bacteria, fungi, archaea) organisms, which live within, or immediately on top of, the uppermost millimeters of soil" (Weber et al., 2022). Further, "soil particles are aggregated through the presence and activity of these often extremotolerant biota that desiccate regularly, and the resultant living crust covers the surface of the ground as a coherent layer" (Weber et al., 2022).

Thus, biocrusts are thin surface layers, sometimes compared to a soil "skin" with highly organized structure and high rates of biological activity, which make the biocrust layer easily distinguishable from the underlying soil (Bowker et al., 2018). Over the last few decades, we have increasingly recognized that biocrusts are capable of reshaping and sustaining surface soil properties and multifunctionality in drylands. For this reason, biocrusts show promise as a nature-based measure to combat soil and land degradation in dryland and similarly fragile ecosystems (Zhao et al., 2019).

We view biocrusts as engineers and architects of surface soil properties, functions, and related processes in drylands. To document and stimulate research on their pervasive shaping of the soil environment in drylands and other environments around the world, we organized this soil-centered special issue. The special issue brings together 27 research articles (from 12 countries) related to various topics. These topics are divided into two categories: biocrust influences on the soil environment (i.e., soil properties and functions), and environmental threats (i.e., disturbance and climate change) to biocrusts and their recovery and conservation.

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2. Spatial distribution of biocrusts

Although biocrusts are distributed in a wide range of habitats throughout the world (especially drylands), studies are numerically concentrated in the USA (e.g., the Colorado Plateau, the Great Basin, and the Mojave, Sonoran, Chihuahuan Deserts), China (e.g., the Loess Plateau, and Tengger, Gurbantunggut, and Mu Us Deserts), Israel (the Negev Desert), Spain (e.g., semi-arid steppes and the Tabernas Desert, in the Central and Southeast of Spain), and Australia (e.g., semi-arid eucalypt woodlands). This special issue covers articles from most of the above mentioned regions (10 papers from China, 6 papers from the USA, 2 papers from Spain, and 2 papers from Australia), but it also includes contributions from emerging research hotspots or less documented ecosystems in Argentina (Aranibar et al., 2022), Brazil (Machado de Lima et al., 2021), Iceland (Pushkareva et al., 2021), Iran (Kakeh et al., 2021), Mexico (Sosa-Quintero et al., 2022), South Africa (Rodríguez-Caballero et al., 2022), and Norway, Sweden, and Antarctica (Agnelli et al., 2021). All of these biocrust studies increase our knowledge of global biocrust distribution and also our understanding of their functional diversities among different climates, soil types, and levels of aridity.

Notably, scientists in China have become more active in biocrust research in recent years, and they are contributing an increasing number of biocrust articles to the general literature and also in this special issue, revealing that a greater level of attention is being paid to biocrusts in China, where drylands account for more than half of the land.

3. Biocrust influences on soil properties and functions

3.1. Biocrust effects on soil properties

The modification of surface soil properties induced by biocrusts are mediated through the physical structure and biotic components of the biocrust layer. These two features fundamentally explained the specific biocrust functions in affecting soil physical (Caster et al., 2021), hydraulic (Kakeh et al., 2021; Li et al., 2021; Sun et al., 2021), erosional (Yang et al., 2022), chemical (Agnelli et al., 2021; Pushkareva et al., 2021; Young et al., 2022), and biological (Jiménez-González et al., 2022; Thomas et al., 2022; Xu et al., 2021) processes in dryland or polar ecosystems in the special issue.

The physical structure of biocrusts is distinct in that the soil particles and biotic components are tightly integrated and form a clearly discernible, but thin horizontal layer on the soil surface. This physical structure means that the biocrust layer behaves mechanically differently compared to the underlying soil. This is the reason why biocrusts can mostly protect soil from water and wind erosion as well as provide some level of resistance to mechanical penetration and shear forces (Yang et al., 2022). Equally importantly, the higher content of fine soil particles in biocrusts contribute to the distinctive behaviors and structural stability of biocrusts; these fine particles possibly come from both dust capture and enhanced mineral weathering (Agnelli et al., 2021; Sun et al., 2021). As a consequence, for example, the finer texture of soil in biocrusts make them more effective in holding soil water after rainfall (Sun et al., 2021) and adsorbing water vapor during evaporation or dew formation (Li et al., 2021).

Another key feature of biocrusts derives from the high cover and biomass of mosses, lichens, cyanobacteria or algae (Yang et al., 2022), and the abundant and diverse microbes inhabiting biocrusts (Machado de Lima et al., 2021; Pushkareva et al., 2021; Xu et al., 2021; Zhao et al., 2021) owing to the more favorable microhabitat conditions that biocrusts provide in harsh environments (Xiao et al., 2016). These microbial and microfaunal communities in biocrusts are also affected by biocrust type and season (Omari et al., 2022). The biocrust biota fix and cycle carbon and nitrogen under appropriate microenvironmental conditions (Chamizo et al., 2022; Wang et al., 2022b), and these biological activities are of the greatest importance for dryland ecosystem functioning.

As biocrusts mostly grow in patches and the variability in biocrust composition and coverage is scale-dependent, all of their effects on soil properties should be assessed based on a representative elementary area, as discussed by Wang et al. (2022a) in this special issue.

3.2. Biocrust roles in soil hydrology

Biocrust effects on water dynamics, including soil moisture, infiltrability, the infiltration-runoff partition, evaporation, and non-rainfall water (fog, dew, and water vapor sorption) are pervasive and could be highly impactful for ecosystems. While biocrusts may increase surface water availability and have a positive effect for some annual and even perennial plants (especially shallow-rooted ones), in other cases they can intercept limited soil water resources before the sparse vegetation can access it, thus increasing the risks of vegetation and land degradation in drylands (Xiao and Hu, 2017). On this topic, many studies have been conducted in different regions around the world, yielding many contradictory findings, especially for the primary water input (infiltration) (Kakeh et al., 2021) and water output (evaporation) (Li and Xiao, 2022), as well as the water balance which dictates soil water content and distribution (Xiao et al., 2016).

Generally, biocrust influences on soil hydrology are primarily modulated by soil properties, such as texture. For example, biocrusts possibly have opposite effects on the infiltration-runoff relationship between sandy soil and loamy soil (Xiao et al., 2019c). In this special issue, the case study by shows that biocrusts enhance infiltration and reduce runoff on a heavily salinized dryland loamy soil (reduced salinity and sodicity are also very important in this case, in addition to soil texture). Biocrusts grown on loamy soil may decrease infiltration and increase runoff compared to uncrusted loamy soils during large and intense rainfall events, owing to the much lower infiltrability of loamy soil in contrast to sandy soil (Xiao et al., 2019c). Cases of biocrust-increased infiltration may be explained by the increased soil surface roughness induced by biocrusts, as measured by a mm-resolution terrestrial LiDAR (Caster et al., 2021) in this special issue. In some regions, within the same site, water runoff and runon zones may occur, creating patchiness in the distribution of water and other mobile resources, concentrating them in productive patches. In the special issue, Eldridge et al. (2021) document distinct traits among biocrust organisms growing in these different zones, potentially reinforcing patchiness in water distribution.

Similar to infiltration and runoff, biocrust influences on soil evaporation are also quite complex, with studies showing decreased evaporation in biocrusts compared to bare soils, owing to the higher water-holding capacity of the biocrust layer (Sun et al., 2021) and the pore clogging effect on vapor flux, or alternatively, increased evaporation in biocrusts through increasing surface temperature and the available water for evaporation after rainfall (Li and Xiao, 2022). However, there is a consensus that biocrusts enhance water retention at the soil surface (Sun et al., 2021), thus increasing surface moisture content and also exerting an important effect on non-rainfall water uptake (Li et al., 2021). In our special issue, a study including soil water retention curve analysis and modeling confirms that biocrusts greatly increase surface soil water holding capacity and water availability (Sun et al., 2021). Similarly, another study finds that biocrusts enhance water vapor sorption capacity of surface soil and increase non-rainfall water deposition (Li et al., 2021). The increased non-rainfall water may partially offset some negative effects of biocrusts on soil water such as increased evaporation. Biocrust effects on evaporation and non-rainfall water deposition are also controlled by soil surface and profile temperatures, which are further determined by surface soil thermal properties (Xiao et al., 2019b), albedo, and land-surface energy balance changed by biocrusts (Xiao and Bowker, 2020).

3.3. Biocrust roles in reducing soil erosion

Unlike their influence on soil hydrology, biocrusts have consistent effects leading to reduction of soil erosion (Yang et al., 2022). As runoff is the driving force underlying water erosion, a reduction in runoff caused by biocrusts will generally result in decreasing sediment yield, which is exactly the case demonstrated by in this special issue. However, even though biocrusts sometimes increase runoff as we discussed above, they simultaneously reduce water erosion, because the well-aggregated biocrust layer provides a protective cover on the soil surface against raindrop splash-erosion and runoff scouring-erosion (Gao et al., 2020). Remarkably, in some cases, a high cover of biocrusts can bring down soil water erosion to a negligible or unmeasurable rate; however, lower or patchy biocrust development would be expected to have a lesser suppressive effect on water erosion.

In this special issue, a study from the Chinese Loess Plateau shows that runoff rates and sediment yield decrease with increasing biocrust cover following logarithmic and exponential functions (Yang et al., 2022). These results suggest that the effectiveness of biocrusts in reducing runoff and erosion should be included into soil erosion models such as RUSLE, through revising the cover-management factor (Gao et al., 2020).

Although biocrusts are mostly studied at plot or slope scales, they are actually expected to be prominent landscape components in some rangelands (Stovall et al., 2022) and have geomorphological consequences at the landscape scale such as reinforcing catchment asymmetry (Lázaro et al., 2022), after their long-term impacts on soil erosion.

3.4. Biocrust roles in soil carbon cycling

Biocrust effects on soil carbon is another hot topic owing to the fundamental importance of accumulated soil organic matter (Baumann et al., 2021) in reshaping soil properties and multifunctionality, and the potential contribution of soil carbon sequestration in reducing greenhouse gas emissions and thus slowing global warming (Yao et al., 2020). Our current evidence implies that biocrusts can strongly influence dryland soil carbon cycling, by (1) directly increasing carbon inputs though photosynthesis (Miralles et al., 2018), (2) accelerating soil respiration (Chamizo et al., 2021), and (3) boosting carbon decomposition and mineralization (Baumann et al., 2021), as well as (4) through indirectly changing environmental factors that regulate the above processes (Xiao et al., 2016).

It is clear that biocrusts accumulate and stock more carbon than bare soil through photosynthesis. The carbon input through photosynthesis is preponderant in the trade-off between carbon fixation and release in biocrusts (Yao et al., 2020), and this is the major carbon resource supporting microbial reproduction and respiratory activities within the biocrust. Although biocrusts also greatly increase carbon release through soil respiration (Chamizo et al., 2022), biocrusts behave mainly as carbon sinks rather than carbon sources, as supported by the fact that thickness, biomass, and organic matter content all increase through time and through developmental stages. Although carbon fixation and accumulation mostly occur in the biocrust layer, the soluble carbon (as well as other nutrients and clay) can move vertically with infiltrated water from biocrusts to deeper subsurface soils, as indicated by in this special issue. This means that biocrust influences on carbon are concentrated in but not restricted to the biocrust itself.

At present, one remaining research gap is that we still have high uncertainty in measuring and estimating the rates of carbon fixation and efflux from different types of biocrusts in different climates, particularly at larger spatial and temporal scales (Yao et al., 2020). This problem is mostly caused by the absence of comparable measures of biocrust photosynthesis and respiration using standard methodologies applicable to different biocrust types, as well as the lack of high temporal resolution measures able to characterize rapid dynamics in CO_2 fluxes from biocrusts. In the special issue, the high-frequency measurements of soil CO_2 efflux using non-dispersive infrared absorption sensors were able to characterize temporal dynamics of CO_2 efflux in response to changing environmental conditions, and provide an alternative means to measure the annual CO_2 efflux of biocrusts (Chamizo et al., 2022). Another study discusses how biocrust hydration and illumination affect soil CO_2 flux and photosynthesis in dryland dune soils, and finds that biocrust respiration and photosynthesis respond differently to hydration and shading (Thomas et al., 2022), further increasing the complexity of predicting biocrust carbon stocks and CO_2 exchanges. We expect that an advanced CO_2 analyzer with more biocrust-specific design would be beneficial for measuring biocrust influx and efflux in the future. Nevertheless, the contribution of biocrusts to soil carbon, as an important reserve of soil nutrients and the global carbon sink, will still be of great concern in coming decades.

4. Impacts of disturbance and climate change and biocrust recovery dynamics

4.1. Impacts of land use shifts and disturbance on biocrusts

Biocrusts are quite fragile and their biological component is highly sensitive to soil surface physical disturbances (Xiao et al., 2019a), especially surface soil trampling (including unintentional trampling such as grazing and human foot traffic, and intentional trampling to avoid impeded infiltration and enhanced runoff). Therefore, the shifts of microbial communities in biocrusts and their multifunctionality after disturbances are also a focus in this special issue.

For example, the surface roughness of biocrust is significantly decreased after a mechanical disturbance, and biocrust recovery within two years after disturbance coincides with an up to three-fold increase in roughness (Caster et al., 2021). The long-term effects of moderate disturbance on the dynamics and sustainability of microbial community structure in biocrusts are also reported (Bao et al., 2022). While low and high intensity disturbances had negative effects, moderate disturbance increased microbial abundance and changed community structure (e.g., the ratios of fungi to bacteria and gram-negative to gram-positive bacteria) in biocrusts (Bao et al., 2022). The interaction between soil heating (simulation of fire effects) and biocrust presence on plant growth and biocrust-fire interactions are compared across five North American deserts, including the Chihuahuan, Colorado Plateau, Great Basin, Mojave, and Sonoran (McCann et al., 2021), showing that biocrusts and soil heating positively influenced plant growth. Distinct land uses lead to different types of disturbance. Accordingly, rainfed agriculture has negative influences on the taxonomic and functional structure of biocrusts in Central Mexico, but firewood extraction has less detrimental effects on biocrusts (Sosa-Quintero et al., 2022).

Natural and assisted recovery of biocrusts after disturbance is another hot topic. In drylands, the natural recovery rates of biocrusts after trampling disturbance are highly variable from <5 years in semi-arid or dry subhumid climates to >250 years in hyperarid or arid climates (Xiao et al., 2019a); other sources report even wider ranges but similar dependence on climate. Therefore, it is highly recommended to protect biocrust resources from severe disturbance, especially in hyperarid and arid drylands. For this reason, researchers have been working to develop methods to artificially inoculate and culture biocrusts in controlled environments to enhance biocrust recovery in the field, with occasional success and many instructive failures. Consistent with this theme in the special issue, an inoculation of biocrust cyanobacteria is also conducted to biomineralize gypsum and preserve indigenous bacterial communities in dryland topsoil in a microcosm experiment (Jiménez-González et al., 2022). Attaining wider success of inoculation in the field is still a major research focal area.

4.2. Biocrust feedbacks to climate changes

Warmer temperatures and changing patterns of precipitation around the world exert an uncertain influence on every aspect of our environment and all organisms on Earth, especially in drylands and other harsh environments. Biocrusts are affected in varying ways by climate change and in turn, their development can influence local climates and microclimates (Xiao and Bowker, 2020); thus feedbacks may exist.

In this special issue, five papers originating from 4 continents simulate or model diverse climate changes to track ways that biocrusts respond to or are altered by climate change: reports that rain addition of 5–40 mm affects biocrust respiration through changing bacterial community composition and soil properties in Northwestern China; examines the functional responses of biocrusts to simulated small precipitation pulses (1–10 mm) in the Monte Desert of Argentina; Hui et al. (2022) investigates the importance of snow depth in winter on water content, carbon and nutrient availability, and microbial biomass of biocrusts in the Gurbantunggut Desert of China; Ferrenberg et al. (2022) quantifies the influences of different biocrust community states and their responses to warming temperatures on soil biogeochemistry in field and mesocosm studies using the soils and biocrusts from the Colorado Plateau of the USA; and studies the effects of climate change (dryer or wetter combined with increased temperatures) and land use intensification (livestock density) on regional biocrust cover and composition in the Succulent Karoo of South Africa. As presented in this special issue, all of the above scenarios of climate change produce remarkable influences on biocrust composition and functions in drylands.

This concentrated emphasis on biocrust response to climate change (5 papers) in this special issue reveals our great concern about the instability of biocrust structure and functions in drylands under a changing climate. Although much uncertainty is expected, climate change will certainly generate large influences on biocrusts and their effects on surface soil properties, functions, and processes in drylands and other ecosystems where they occur.

5. Summary

This special issue is a collection of 27 articles, which highlights the importance of biocrusts in drylands and other ecosystems and concentrates on biocrust effects on soil properties, processes and functions, particularly in regulating soil hydrology, decreasing soil erosion, affecting soil carbon fixation and respiration, and influencing microbial biodiversity. The responses of biocrusts themselves and their functions to trampling disturbance and global climate change are also points of emphasis. We should fully understand that biocrusts are capable of reshaping all physical, chemical, and biological properties of surface soil, because they are engineers and architects of surface soil properties, functions, and processes in dryland and other ecosystems. Yet, these strong and pervasive influences on the environment are poised to change as land uses shift and the climate changes. Amidst this change, biocrusts hold potential to be a nature-based agent used to combat soil and land degradation, and must be incorporated into our land use decisions in the future.

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