Earth-Science Reviews 243 (2023) 104516

Contents lists available at ScienceDirect

Earth-Science Reviews

journal homepage: www.elsevier.com/locate/earscirev

A review on effects of biological soil crusts on hydrological processes

Gaetano Guida [a,*], Alessio Nicosia [a], Luca Settanni [a], Vito Ferro [a,b]

[a] Department of Agricultural, Food and Forest Sciences, University of Palermo, Viale delle Scienze, Building 4, 90128 Palermo, Italy
[b] NBFC, National Biodiversity Future Center, 90133 Palermo, Italy

ARTICLE INFO

Keywords:
Biocrusts
Soil hydrology
Soil erosion
Microbiological composition
Microbiological indicators
Microbiological inoculum

ABSTRACT

Biological soil crusts (BSCs) are complex consortia of microorganisms able to modify soil physical, chemical, and hydrological characteristics and influence soil erosion resistance. Given their importance, this paper analyses the current knowledge about BSCs reporting the findings of 163 papers about different BSC aspects published from 1990 to 2023. At first, a review of the BSC main detection methods (visual inspection, remote sensing, and morphological characterization) is presented as they represent valuable tools in BSC identification and mapping, revealing some issues related to the adopted classification criteria and the BSC microbial composition. Then, the literature results about their influence on soil characteristics, hydrology, and erosion processes are reported. Although their positive effects on soil characteristics (e.g., stability and fertility) and resistance to soil erosion are widely recognized, conflicting results are reported on their influence on soil hydrology. The analysis of the available literature allowed for providing indications about the choice of which microorganisms are the most suitable to form BSCs, following the required objectives (soil physic-chemical improvements, soil hydrology, erosion processes resistance, cost, and time to produce their effects). In particular, the results showed that i) the BSC effects on the soil physic-chemical characteristics improve along their successional series; ii) bacteria and cyanobacteria can be considered the most valuable BSC in limiting and degraded conditions (sediment concentration in the runoff reduced by 87% in comparison to bare soils, cost of 350 USD ha^{-1}, and a recovery time of 5–10 years); iii) the intrinsic heterogeneity of BSCs does not allow for explaining the divergence of the literature results on soil hydrology; and iv) mosses are the best BSC anti-erosive type as they produce the most similar effects as compared to vegetation. Finally, the main steps required to obtain microbial inoculums, the effects of their application to induce BSC formation, and future prospects of research are reported.

1. Introduction

Biocrust (BSCs) communities have been recently redefined by Weber et al. (2022) as "*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 millimetres of soil*". Weber et al. (2022) also reported that "*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*". BSCs colonize very different habitats throughout the world, such as desert, glacial, woodland, dryland soils, temperate inland, and road slopes; where they represent one of the most conspicuous and important biotic components of these habitats (Cantón et al., 2011, 2020; Chamizo et al., 2012a, 2016; Concostrina-Zubiri et al., 2019; Eldridge et al., 2020).

BSC microbial composition is various and includes eukaryotic algae, cyanobacteria, microfungi, lichens, mosses, and liverworts (Cantón et al., 2011; Castillo-Monroy et al., 2010; Li et al., 2021; Reed et al., 2019). Eukaryotic algae are a group of primitive, single-cell organisms. Algae are ubiquitous and can be found in freshwater lakes, ponds, and streams as well as in soil, dunes, rocks, ice, snow, plants, and animals (Pluis, 1994; Robinson et al., 2015). Cyanobacteria are primitive filamentous bacteria that photosynthesize and fix atmospheric Nitrogen under anaerobic conditions. Cyanobacteria can be distinguished into heterocystous and non-heterocystous, and this difference derives from the presence or the absence of some specialized cells, called heterocysts, in which Nitrogen fixation (N-fix) occurs (Cantón et al., 2020; Garcia-Pichel et al., 2001; Roncero-Ramos et al., 2019). Heterocystous species are eligible for the status of pioneer organisms, contributing about 30% of total N-fix, and increasing soil fertility via Carbon sequestration. Moreover, some cyanobacteria show thermo-tolerant physiology in

* Corresponding author.
E-mail address: gaetano.guida@unipa.it (G. Guida).

https://doi.org/10.1016/j.earscirev.2023.104516
Received 24 January 2023; Received in revised form 3 July 2023; Accepted 19 July 2023
Available online 26 July 2023

response to stressing environmental conditions and allow the development of BSCs even in hot degraded areas (Roncero-Ramos et al., 2019). Microfungi can be found either as free-living organisms, as substance decomposers, or in mycorrhizal associations with plant roots. Fungal filaments (hyphae) bind soil particles together, improve soil porosity and increase soil water-holding capacity (Belnap, 2006; Cosentino et al., 2006; Grishkan et al., 2019; Rodríguez-Caballero et al., 2012, 2014). Lichens are the result of a symbiotic association between a filamentous fungus, a mycobiont, and a photosynthetic organism, a photobiont, that can be a microalga or a cyanobacterium (Ladrón de Guevara et al., 2014; Robinson et al., 2015; Rodríguez-Caballero et al., 2019). Mosses and liverworts belong to bryophytes, which are tiny non-vascular plants. They reproduce by spore capsules that rise above the leaves. In arid environments, mosses can lack reproductive structures and reproduce asexually by simple or specialized fragmentation (Bu et al., 2015; García-Carmona et al., 2020; Slate et al., 2020).

BSC morphology and appearance are affected by their microbiological composition, in terms of the number and diversity of species that form the microbial consortium (Chilton et al., 2018; Garcia-Pichel et al., 2001). Morphology-based classifications permit to distinguish BCSs in (i) *green algal* BSCs, (ii) *cyanobacterial* BSCs, (iii) *lichen* BSCs which are further distinguished (Belnap and Lange, 2003) into a) *crustose lichen* BSCs, b) *gelatinous lichen* BSCs, c) *squamulose lichen* BSCs, d) *foliose lichen* BSCs, e) *fruticose lichen* BSCs, (iv) *moss* BSCs, and (v) *liverwort* BSCs.

BSCs grow by developmental and successional stages (Bowker, 2007; Maestre et al., 2006). The developmental stages are due to the interaction between BSCs and the environmental biotic and abiotic factors (Bowker, 2007). Successional stages are defined as steps of biological changes in which the species composition of a given community or environment varies in response to biotic and abiotic factors (Deng et al., 2020; Redford and Fierer, 2009). The sequence of successional stages shows the evolution of an ecosystem, and the climax stage represents the final and most complex successional stage that better fits the environmental conditions of a given ecosystem. The successional stages are classified as a function of the dominant taxa that compose the BSC community.

The dominant populations of the microbial consortia allow classifying the BSCs as early successional stage BSCs (ESS-BSCs) and late successional stage BSCs (LSS-BSCs). ESS-BSCs are the simplest BSC communities, majorly represented by cyanobacterial species, and form a thin, dark, low-biomass layer on the soil surface, having the role of pioneer communities (Cantón et al., 2020; Lázaro et al., 2008; Román et al., 2021). LSS-BSCs, composed of lichens and mosses, represent the most developed type of BSCs, able to form a thick, high-biomass layer on the soil surface. LSS-BSCs can constitute a resistant "living mulch" on the soil surface and might show hydrophobic characteristics (Cosentino et al., 2006; García-Carmona et al., 2020; Kidron et al., 2020b). Table 1 reports a list of the most common species which constitute each BSC class, including the respective morphologic properties and successional stage. Intermediate successional stages can be found between these two extreme types of BSC successional stages. Intermediate successional stages show different microbial composition, amount of biomass, color, and surface roughness and influence the hydrological response of interplant areas (Bullard et al., 2018; Cantón et al., 2011; Chamizo et al., 2017; Chilton et al., 2018; Gao et al., 2020a; García-Carmona et al., 2020; Rodríguez-Caballero et al., 2012). Deng et al. (2020) described the successional stages that constitute the BSC ecological succession distinguishing between human induced BSCs (aged 7, 8, 10, 11, and 13 years) and naturally developed BSCs (aged 34, 54, and 59 years) and registered different microbial compositions. In that work, the ecological succession began with the youngest and simplest BSC, dominated by cyanobacteria and eukaryotic algae, followed by BSC dominated by lichen (*Athelia pyriformis*) and then BSC characterized by lichens and mosses and representing a transitional stage. The ecological succession continues with BSC dominated by mosses and finally by a vascular plant (*Camelina sativa*), which represents the climax stage of BSC succession. The definition of successional stages implies that a given successional stage can be replaced by a more developed one when the environmental conditions permit the establishment of a more complex community or a less developed one if environmental conditions are limiting (Belnap et al., 2013; Bowker, 2007; van der Heijden et al., 2008). Indeed LSS-BSCs, under limiting environmental conditions, can induce a shift towards ESS-BSCs with a loss of biodiversity and ecosystem functionality (Barger et al., 2006; Cantón et al., 2020; Faist et al., 2017; Ferrenberg et al., 2015). Furthermore, various Authors (De Winder, 1990; Pluis and De Winder, 1990; Pluis, 1994) focusing on the ecological succession of the coastal dunes of Netherlands, reported that green algae crusts substituted the initial cyanobacteria crust.

BSCs are influenced by available water content, rainfall event intensity, seasonal precipitation patterns, soil texture and cohesiveness, calcium carbonate and gypsum content, nutrient availability, slope steepness, and slope aspect (Belnap et al., 2005; Carson et al., 2010; Chamizo et al., 2018; Garcia-Pichel et al., 2001; Grishkan et al., 2019; Reed et al., 2019; Rodríguez-Caballero et al., 2019; Zhou et al., 2020a). Intensity and type of environmental disturbances factors, such as erosion processes or fire, affect the species composition of BSCs (Cantón et al., 2020; Chamizo et al., 2012a; Faist et al., 2017; Ferrenberg et al., 2015; Li et al., 2021; Rossi et al., 2017). Indeed, if erosion processes occur with high intensity, the replacement of well-developed LSS-BSC with simple and less developed ESS-BSC happens and limits their impact on ecosystem dynamics reducing the positive effects carried out by BSCs, composed of only a few species (Belnap and Eldridge, 2003). Changes in land use and increased grazing pressure represent highly impacting BSC disturbance factors inducing reduction of Carbon fixation, soil capacity to regulate water availability, and increasing soil erosion (Ferrenberg et al., 2015; López-Rodríguez et al., 2020). A reduction in BSC cover and microbial composition reduces soil biodiversity and resilience of dryland landscapes (Ladrón de Guevara et al., 2014; Maestre et al., 2013; Reed et al., 2019).

During growth, BSCs can modify soil characteristics to increase their development and allow the establishment of a more complex BSC community. BSCs affect the physical and chemical characteristics of soils influencing soil particle aggregation, soil porosity, pore size, soil surface albedo, soil temperature, organic matter content, Nitrogen content, nutrient localization in soil, soil resistance to splash erosion resistance and soil surface roughness (Bullard et al., 2018; Cantón et al., 2020; Chamizo et al., 2018; Gao et al., 2017; Kidron et al., 2020b; Lázaro et al., 2008; Li et al., 2021; Rodríguez-Caballero et al., 2012, 2013; Rutherford et al., 2017).

BSCs influence soil infiltration and runoff modifying water dynamics in soils with their secondary metabolites, cellular morphologies, crust morphologies, and soil characteristic modifications (Cantón et al., 2020; Chamizo et al., 2018). While organic matter produced by BSCs increases soil porosity and, consequently, infiltration, other extracellular substances, such as exopolysaccharides (EPS) and hydrophobic compounds, reduce soil infiltration by inducing soil pore-clogging or by forming an impermeable layer on the soil surface (Cantón et al., 2020; Chamizo et al., 2012a; Eldridge et al., 2020; Kidron et al., 2022; Rodríguez-Caballero et al., 2013).

Soil hydrology is influenced by BSC morphology and microbial composition (Fick et al., 2019) and by the successional stage of BSCs (Bu et al., 2015). The occurring BSC successional stage affects the local hydrological response. Numerous metabolic processes depend on the microbiological composition of BSCs and their successional stage, with different impacts on the environment in which BSCs inhabit (Barger et al., 2006; Cantón et al., 2004; Rossi et al., 2017; van der Heijden et al., 2008). For instance, LSS-BSCs produce a higher amount of organic matter than ESS-BSCs and the higher organic matter induces higher soil porosity and infiltration. On the other hand, some lichen and moss species that form LSS-BSCs secrete hydrophobic substances, thus reducing soil infiltration (Chamizo et al., 2012a; Rodríguez-Caballero et al., 2013). ESS-BSCs increase infiltration enhancing soil roughness,

Table 1
BSC most common species, morphologic properties, and successional stages (Belnap and Lange, 2003; Bowker et al., 2016; Büdel et al., 2009; Dojani et al., 2014; Grishkan and Kidron, 2013; Mallen-Cooper and Eldridge, 2016; Rosentreter, 2020; Young et al., 2019).

BSC classification	Most common BSC species		BSC morphology and appearance	Successional stage
Green algae	*Bracteacoccus minor* *Bracteacoccus giganteus* *Chlorella* cf. *sorokiniana* *Chlorolobion lunulatum* *Chlorosarcinopsis* cf. *variabilis* *Chlorosarcinopsis bastropiensis* *Chlorosarcinopsis minor* *Desmococcus olivaceus* *Diplosphaera* cf. *chodatii* *Eustigmatos magnus* *Klebsormidium crenulatum*	*Klebsormidium flaccidum* *Klebsormidium montanum* *Neospongiococcum* cf. *punctatum* *Neospongiococcum granatum* *Pseudochlorococcum typicum* *Scenedesmus* cf. *rotundus* *Spongiochloris excentrica* *Spongiochloris minor* *Stichococcus bacillaris* *Trebouxia* cf. *arboricola*	Not visible when dry, but if moistened appear as a green crust on the soil surface	Early successional stage
Cyanobacteria	*Calothrix* spp. *Chroococcidiopsis* spp. *Hormoscilla pringsheimii* *Leptolyngbya compacta* *Leptolyngbya subtilissima* *Leptolyngbya crispata* *Leptolyngbya frigida* *Leptolyngbya schmidlei* *Leptolyngbya byascottii* *Leptolyngbya foveolarum* *Lyngbya* cf. *semiplena* *Microcoleus chthonoplastes* *Microcoleus paludosus* *Microcoleus paludosus* *Microcoleus steenstrupii* *Microcoleus vaginatus* *Nostoc commune* *Nostoc* cf. *calcicola* *Nostoc* cf. *punctiforme* *Oculatella kazantipica* *Oscillatoria limosa* *Oscillatoria subbrevis* *Oscillatoria tenuis* *Phormidium ambiguum* *Phormidium* cf. *aerugineo-caeruleum* *Phormidium* cf. *caerulescens*	*Phormidium* cf. *nigrum* *Phormidium chlorinum* *Phormidium murrayii* *Phormidium vulgare* *Pseudanabaena* cf. *frigida* *Pseudanabaena* cf. *starmachii* *Pseudanabaena* cf. *tenuis* *Pseudanabaena minima* *Pseudophormidium hollerbachianum* *Schizothrix* cf. *arenaria* *Schizothrix calcicola* *Schizothrix lardacea* *Scytonema* cf. *millei* *Scytonema hofmanni* *Scytonema hyalinum* *Scytonema javanicum* *Scytonema ocellatum* *Stigonema ocellatum* *Symplocastrum* cf. *friesii* *Tolypothrix bouteillei* *Tolypothrix distorta* *Trichocoleus* cf. *cavanillesii* *Trichocoleus* cf. *delicatulus* *Trichocoleus desertorum* *Trichocoleus sociatus*	Appear like black or dark-colored filaments on soil surface when moistened	Early successional stage
Microfungi	**Anamorphic Ascomycota** *Alternaria alternata* *Aphanocladium album* *Aspergillus fumigatus* *Aspergillus niger* *Botryotrichum piluliferum* *Cladosporium cladosporioides* *Drechslera australiensis* *Embellisia chlamydospore* *Embellisia phragmospora* *Fusarium oxysporum* *Fusarium equiseti* *Geotrichum candidum* *Lecanicillium psalliota* *Papulaspora pannosa* *Penicillium aurantiogriseum* *Phoma exigua* *Pyrenochaeta cava* *Stachybotrys chartarum* *Ulocladium atrum*	**Teleomorphic Ascomycota** *Canaryomyces notabilis* *Chaetomium cochlioidese* *Chaetomium globosum* *Chaetomium nigricolor* *Chaetomium strumarium* *Chaetomium succineum* *Sporormiella minima* *Thielavia terricolae* **Basidiomycota** *Sporotrichum* spp. *Mycelia sterilia* **Mucoromycotina** *Mortierella humilis*	Not visible when dry. When soil surface is moistened, they are barely visible as dark-colored patches Their filaments are visible under microscope and appear as dark septate fungi	Early successional stage
Lichens	*Acarospora schleicheri* *Acarospora terricola* *Arthonia glebosa* *Aspicilia aspera* *Aspicilia filiformis* *Aspicilia hispida* *Aspicilia mansourii* *Aspicilia reptans*	*Lecidea laboriosa* *Lepraria* spp. *Leptochidium albociliatum* *Leptogium lichenoides* *Massalongia carnosa* *Pannaria cyanolepra* *Peltigera rufescens* *Peltula patellata*	Occur with different morphologies. They are further distinguished into: a) **crustose lichen BSCs**, flat and different colored crusts b) **gelatinous lichen BSCs**, 3D, gelatinous, black crusts that increase in dimension if moistened c) **squamulose lichen BSCs**, flakes or scales and generally grow in clusters d) **foliose lichen BSCs**, little leaves near to soil surface varying in color from dark green to light green to whitish	Late successional stage

(*continued on next page*)

Table 1 (*continued*)

BSC classification	Most common BSC species		BSC morphology and appearance	Successional stage
	Aspicilia rogeri	*Peltula richardsii*	e) **fruticose lichen BSCs**, green to yellow or orange 3D-shaped lichens similarly to tree roots or tree framework	
	Buellia elegans	*Peltula* spp.		
	Buellia punctata (syn = *Amandinea*)	*Physconia enteroxantha*		
		Physconia muscigena		
	Caloplaca atroalba	*Placidium lachneum*		
	Caloplaca jungermanniae	*Placidium squamulosum*		
	Caloplaca lacteal	*Placynthiella icmalea*		
	Caloplaca tominii	*Psora cerebriformis*		
	Candelariella aggregate	*Psora decipiens*		
	Candelariella rosulans	*Psora icterica*		
	Cladonia fimbriata	*Psora montana*		
	Cladonia pocillum	*Psora tuckermanii*		
	Clavascidium lacinulatum	*Sarcogyne mitziae*		
	Collema coccophorum	*Squamarina lentigera*		
	Collema tenax	*Trapeliopsis wallrothii*		
	Diploschistes muscorum	*Texosporium sancti-jacobi*		
	Endocarpon loscosii	*Thelenella muscorum* var. *octospora*		
	Endocarpon pusillum	*Thrombium epigaeum*		
	Heppia lutosa	*Toninia sedifolia*		
	Heteroplacidium congestum	*Trapeliopsis bisorediata*		
	Lecanora epibryon	*Trapeliopsis steppica*		
	Lecanora flowersiana	*Xanthoparmelia* spp.		
	Lecanora muralis			
	Aloina bifrons			
	Bryoerythrophyllum columbianum	*Didymodon vinealis*		
		Encalypta vulgaris		
	Bryum argenteum	*Funaria hygrometrica*		
Mosses	*Bryum lanatum*	*Grimmia tenerrima*	Easy to detect and appearing as green, brown or black hairy patches on soil surface	Late successional stage
	Bryum caespiticium	*Pterygoneurum ovatum*		
	Bryum kunzei	*Syntrichia caninervis*		
	Cephaloziella divaricate	*Syntrichia ruralis*		
	Ceratodon purpureus	*Tortula brevipes*		
	Didymodon brachyphyllus			
	Asterella drummondii	*Riccia nigrella*		
Liverworts	*Athalamia hyaline*	*Riccia sorocarpa*	Not easy to detect, if moistened and observed with a hand lens appear as black ribbons	Late successional stage
	Fossombronia spp.	*Riccia spongiosula*		
	Riccia limbata			

particle aggregation, porosity, and pore size.

The presence, absence, and abundance of one or more cyanobacterial, lichen or moss species are important indicators of the intensity of erosion processes and can give hints on a site's healthiness and BSC and ecosystem evolution (Belnap et al., 2013; Deng et al., 2020; Maestre et al., 2006). For instance, moss cover represents a good indicator of soil erosion protection and when the coverage is above 35–36%, moss BSCs almost totally protect soil from water erosion (Gao et al., 2020a, 2020b). When moss cover is below 35–36%, cyanobacterial BSC cover represents an important indicator of erosion processes providing important information on BSC health state and ecosystem functionality (Gao et al., 2020a). Furthermore, some lichen species, such as *Acarospora schleicheri*, *Massalongia carnosa*, *Pannaria cyanolepra*, *Trapeliopsis wallrothii*, and *Texosporium sancti-jacobi*, can be also considered as good healthiness indicators of arid and semiarid environments. These lichen species develop only in particular environmental conditions. If the ecosystem is in a degraded condition (e.g., intensive erosion processes, high grazing pressure), these species are not present and their absence is related to the reduced environmental health state of the ecosystem (Belnap and Lange, 2003). In these areas, lichens represent one of the late-successional communities and are highly responsive to the environmental conditions. If environmental conditions are similar to growing optimum conditions for lichens, lichen BSCs develop and the BSC community can evolve into a more complex lichen-moss BSC community (Maestre et al., 2006). On the contrary, when environmental conditions vary greatly, going beyond lichen's optimum growing range, or if a new disturbance factor occurs (such as grazing, soil tillage, and fire), lichen species are not able to develop, and their absence represents an important indicator of loss of healthiness and functionality of the ecosystem (Bowker, 2007; Bu et al., 2015; Chamizo et al., 2012a; Jafari et al., 2004; Maestre et al., 2006). The BSC capacity to return to the pre-disturbance conditions, defined recovery time, should be considered selecting the microorganism to be inoculated for environmental restoration. The results obtained in the literature report BSC recovery times varying from decades to centuries depending on the BSC composition and the entity and lasting of disturbances. Liu et al. (2017) found that the recovery time for bacteria was >15 years, whereas that for fungi ranged from decades to centuries. Moreover, Kidron et al. (2020a) stated that the short-time and the extrapolation which characterize the literature works may result in misinterpretation of the recovery time and reported that cyanobacteria recover in 5–10 years, while lichens and mosses in 10–20 years. Belnap and Eldridge (2003) stated that BSCs are very sensitive to disturbances, and their recovery times under natural conditions in arid and semiarid areas typically are in the range of decades to millennia. However, the recovery times can be boosted by in situ inoculation of soils with biological crust components, such as cyanobacteria, in degraded arid and semiarid ecosystems (Belnap, 1993).

The environmental influences of BSCs can be retrieved from the identification of their microbial composition and their specific metabolisms. Some studies differentiated BSCs into main groups (green algae, cyanobacteria, lichens, and mosses) and analyzed their environmental influences. A list of the main factor that can influence BSCs, the main BSCs properties and the influence that they carried out on soil properties are listed in Table 2.

One of the main issues dealing with BSCs is to consider it as a unique organism, although it is composed of various microorganisms with

Table 2
Lists of environmental factors that influence BSCs, BSC characteristics, and BSC effects on soil characteristics, soil hydrology, and erosion processes.

Influence of environmental factors on BSCs	BSC characteristics	BSC influences on soil characteristics
Precipitation	**Microbial composition**	**Physical**
Water availability	Number of species	Soil particle aggregation
Rainfall intensity	Diversity of species	Soil porosity
Seasonal precipitation patterns		Pore size
Soil albedo	**Successional stage**	Pore connectivity
Soil texture	ESS-BSCs	
Soil cohesion	Green algae	**Chemical**
	Cyanobacteria	Organic matter content
Chemical	Microfungi	Nitrogen content
Calcium carbonate content	LSS-BSCs	Nutrient localization
Gypsum content	Lichens	Solute mobilization
Nutrients availability	Mosses	
		Hydrological
Topographic	**Morphology**	Infiltration
Slope	Crust color	Runoff
Aspect	Crust roughness	Soil moisture
Soil temperature	Crust thickness	
	Crust biomass	**Erosion resistance**
	Crusts cover	Rain splash erosion resistance
	Penetrative structures	Penetration resistance
	Cellular shapes	Soil roughness
		Soil loss
	Metabolism	Sediment concentration
	UV-absorbing pigments	
	Carbon fixation	
	Carbon respiration	
	Organic compound production	
	EPS production	
	Nitrogen fixation	

different metabolisms influencing differently the erosion processes (Belnap, 2006; Belnap and Lange, 2003; Chamizo et al., 2013; Garcia-Pichel et al., 2001; Rodríguez-Caballero et al., 2012, 2014). However, species identification approach allows to explain microorganism-soil interactions (Belnap et al., 2013; Carson et al., 2010; Chamizo et al., 2012a; Dahal et al., 2017; Dojani et al., 2014). Specific microorganism ecology and metabolism provide useful information on soil characteristics, soil hydrology, and erosion processes (Belnap and Lange, 2003; Chamizo et al., 2016; Cosentino et al., 2006). Recently, some studies focused on the development of microbial inoculums to induce BSC formation and enabled the study of their influences on soil chemical, physical and hydrological characteristics (Chamizo et al., 2020a; Kheirfam et al., 2017a, 2017b, 2020). Discovering the microbial composition and ecology of a BSC community that inhabits a given environment allows for identifying what is the role played by BSCs within the ecosystem.

Despite the increasing number of works published in the literature about BSCs, contrasting results have been obtained regarding some aspects (e.g., soil hydrology) and several gaps still need to be filled. Moreover, determining the most suitable microorganisms or communities of microorganisms, depending on their characteristics (i.e., climate adaptation, recovery time, effects on soil hydrology, cost), to use in restoration of degraded areas is one of the main objectives to be pursued by the scientific community in this field of study. At the state of the art, an exhaustive synthesis of the BSC effects on soil characteristics, hydrology, and erosion processes and the choice of the most suitable microorganisms to form BSCs to reach the required objectives is needed to fully understand the possible applications of BSCs in management of degraded and arid areas. For this reason, the main aim of this paper, developed examining 163 papers about different BSC aspects published from 1990 to 2023 (Fig. 1) reporting measurements and results obtained in different sites distributed all over the world (Fig. 2), is to give indications on their applicability. In particular, this paper analyses the current knowledge on BSCs and reviews the BSC detection methods, the microbiological analysis aimed to explore BSC composition, as well as the influence of BSCs on soil characteristics, soil hydrology, and erosive processes. Finally, the selection and application of microbial inoculums on BSC formation are reported.

2. BSC detection methods

Different methods can describe the microbial composition of BSCs and their microbial diversity (Belnap et al., 2008; Dojani et al., 2014; Eldridge and Rosentreter, 1999; Muñoz-Martín et al., 2019; Rodríguez-Caballero et al., 2017; Weber et al., 2018). The mostly applied methods are:

a) *visual inspection* (Belnap et al., 2008, 2013; Bowker et al., 2008; Chamizo et al., 2018; Muñoz-Martín et al., 2019; Read et al., 2014);

b) *morphological characterization* (Dojani et al., 2014; Eldridge and Rosentreter, 1999; Muñoz-Martín et al., 2019; Read et al., 2014; Weber et al., 2018);

c) *remote sensing* (Allen, 2010; Chamizo et al., 2012b; Chen et al., 2005; Karnieli, 1997; Rodríguez-Caballero et al., 2017; Weber et al., 2008, 2018).

These methods show a different level of precision which have to been related to the aims of the investigation. BSCs can be classified per classes or main groups constituting the microbial consortia or described with a high level of identification of the species.

The *visual inspection* of the soil surface represents the first step of preliminary studies for the initial recognition of BSCs. BSCs appear as small crusts, darker than the soil surface, and in the case of lichens and mosses, they may occur with outgrowths. Several authors used this approach to determine prevalent BSC composition (Belnap et al., 2013; Bowker et al., 2008; Chamizo et al., 2018; Muñoz-Martín et al., 2019; Read et al., 2014).

The BSC *morphological classification* represents a fast on-field method. The classification of BSCs into morphological groups (groups sharing a high similarity of appearance) is based on the macroscopic characteristics observable with the naked eye or a hand lens. BSC main classes are reported in Table 1.

BSC morphology reflects BSC microbial composition and allows for recognizing the influences of BSCs on ecological processes (Eldridge and Rosentreter, 1999). Indeed, morphological groups are useful for assessing shifts in BSC composition in response to ecological

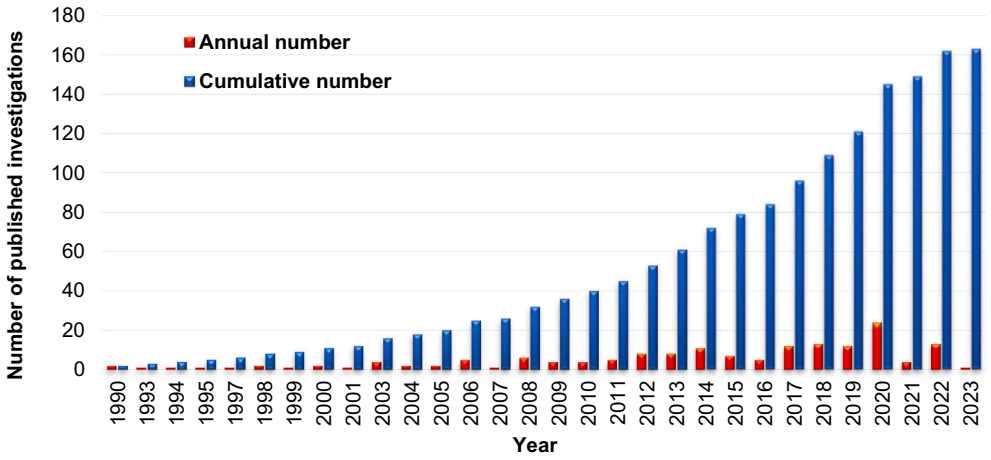

Fig. 1. Rate of publication on BSCs in the period 1990–2023.

Fig. 2. Global distribution map of the experimental studies on BSC.

degradation (Read et al., 2014). The applicability of the morphogroup classification is limited to BSCs that are visible to the naked eye (especially lichens and mosses) and cannot be applied to cyanobacteria and algae due to their small dimensions requiring a microscopic visualization. Another limitation of this method is that different microbial compositions might share similar morphologies.

The identification of the dominant microorganisms of a BSC community can be evaluated by classifying them into a taxonomic level, which can range from a low inclusion level to a high one (Domain, Kingdom, Phylum, Class, Order, Family, Genus, Species, and Strain). Some authors recognized low detail identification, such as morphological group identification or classification in successional stages, as being able to provide information about the ecological functions performed by BSCs, although they are classified only in the most inclusive levels (Eldridge and Rosentreter, 1999; Read et al., 2014).

Remote sensing based on the use of multispectral or hyperspectral cameras provides a higher level of precision and reproducibility of results than visual inspection. Several authors focused on the main spectral characteristics of BSCs and highlighted the relation between variation in absorption and reflectivity at different spectral wavelength and soil coverage (bare soil, vegetation, and different types of BSCs) (Rodríguez-Caballero et al., 2017; Weber and Hill, 2016). These authors used airborne or spaceborne images methods for identifying and mapping the distribution of BSCs using the following BSC mapping indexes: the Crust Index (CI) (Karnieli, 1997); the Biological Soil Crust Index (BSCI) (Chen et al., 2005); the Continuum Removal Crust Identification Algorithm (CRCIA) (Weber et al., 2008); and the Crust Development Index (CDI) (Chamizo et al., 2012b). The first two indexes are obtained from multispectral optical information, while the CRCIA and CDI from optical hyperspectral information.

The CI was designed by Karnieli (1997) to map BSCs with a cyanobacteria coverage of about 90% in Negev Desert (Israel-Egypt border). This index utilizes the cyanobacterial BSC high reflectivity in the blue region of the visible spectrum and is calculated as follows:

$$CI = \frac{1 - (R_{RED} - R_{BLUE})}{R_{RED} + R_{BLUE}} \quad (1)$$

where R_{RED} and R_{BLUE} are the mean reflectances in the red and blue band of the Landsat Thematic Mapper sensor.

The BSCI was built by Chen et al. (2005) to map areas with >30% lichen BSCs in the Gurbantünggüt Desert (China) using Landsat Enhanced Thematic Mapper Plus (ETM+) images, and it is calculated as follows:

$$BSCI = \frac{1 - L(\,|R_{RED} - R_{GREEN}|\,)}{R_{GREENREDNIR}} \quad (2)$$

where R_{RED} and R_{GREEN} are the reflectances in the red and green bands, $R_{GREENREDNIR}$ is the mean value calculated by reflectances in the red, green and near infrared bands of the Enhanced Thematic Mapper Plus sensor and L is a parameter to amplify the absolute difference between R_{RED} and R_{GREEN}.

The CRCIA proposed by Weber et al. (2008) mapped cyanobacterial BSCs in the Soebatsfontein region by using Compact Airborne Spectrographic Imager 2 (CASI 2) hyperspectral images. In the Soebatsfontein region, the BSC Continuum Removal spectrum permits the development of the following algorithm:

$$CRCIA = 0.75 < CR_{516\ nm} < 0.88; \quad (3a)$$

$$0.9 < CR_{667\ nm} < 0.988; \quad (3b)$$

$$CR_{637\ nm} > CR_{552\ nm} > CR_{667\ nm}; \quad (3c)$$

$$CR_{683\ nm} < CR_{698\ nm}; \quad (3d)$$

$$CR_{606\ nm}\ or\ CR_{622\ nm} = 1; \quad (3e)$$

$$(CR_{652\ nm} - CR_{667\ nm})\langle(CR_{698\ nm} - CR_{682\ nm}) \quad (3f)$$

where $CR_{x\ nm}$ are the absorption values, respectively at x = 516, 667, 637, 552, 683, 689, 606, 622, 652, 698, 682 nm wavelength. BSC areas are identified according to their spectral response. If the spectral

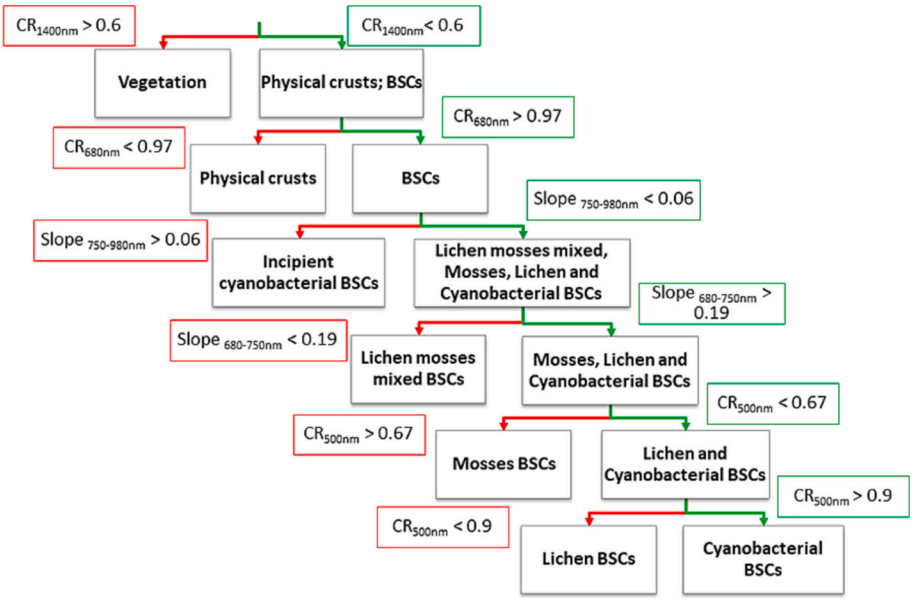

Fig. 3. Crust Development Index modified from Chamizo et al. (2012b).

response of a given area fits all the conditions of the algorithm, then that area is covered by BSCs otherwise, other types of cover (vegetation, rocks, or bare soil) are present.

The CDI, proposed by Chamizo et al. (2012b), allowed for distinguishing BSCs from bare soil and vegetation in El Cautivo and Las Amoladeras areas (SE Spain) and recognizing BSC successional stage. It consists of a decision tree (Fig. 3) based on the main characteristics of the BSC spectral signature at different wavelengths.

Rodríguez-Caballero et al. (2017) tested the four abovementioned indexes and compared the accuracy of multispectral and hyperspectral indexes. Multispectral cameras and indexes are useful to map and classify the BSC distribution and hyperspectral cameras and indexes showed higher accuracy in detecting and distinguishing among different types of BSCs. Indeed, hyperspectral sensors can detect absorption features related to BSC pigments such as carotenoids and chlorophyll α. On the other hand, due to the high cost of hyperspectral information and its limited availability, the use of multispectral information represents a cost-saving choice to obtain the identification of BSC-covered areas. In this case, the application of BSCI, jointly with multispectral information, represents an efficient tool in BSC mapping (Rodríguez-Caballero et al., 2017; Weber et al., 2018).

One critical point of the remote sensing methods is that the BSC spectral response varies in response to the precipitation, leading to possible misinterpretation (Allen, 2010). This problem can be counteracted by remote sensing observation of small areas at low altitudes or on the ground by using pole cameras or drones equipped with hyperspectral cameras. This approach permits to differ among the spectral responses of BSCs and that obtained from the other ground covers and evaluate the spectral BSC variations caused by precipitation. Finally, Collier et al. (2022) reported that the combination of RGB images acquired at low altitudes and on the ground permits the distinction of BSCs from the other ground covers and between different types of BSCs.

3. Culture-dependent and culture-independent microbiological methods

Bacterial diversity can be analyzed by two different microbiological approaches: a culture-dependent and a culture-independent approach.

The *culture-dependent approach* consists of a polyphasic method that combines phenotypic and genetic techniques (Dojani et al., 2014; Muñoz-Martín et al., 2019; Weber et al., 2018). This approach can only be applied to pure cultures of microorganisms isolated from soil (Muñoz-Martín et al., 2019; Weber et al., 2018). The phenotypic techniques allow the identification of the morphological characteristics (mainly shape and occurrence of special structures, such as spores and appendixes), the physiological needs (temperature, pH, and O_2 exposure), and biochemical features (metabolism type, metabolic products, and cell secretions of pure cultures of microorganisms). To investigate cellular morphology, BSC microorganisms are routinely observed under optical microscopes. In general, the optical microscopes used for bacterial cell visualization are equipped with a 100× magnifier immersed in mineral oil. The *culture-dependent* genetic techniques permit the genetic identification of the strains obtained from the pure cultures. Generally, the bacterial DNA is extracted from the pure cultures after overnight growth. The diversity of the strains is evaluated by a fingerprint analysis based on the random amplification of polymorphic DNA (RAPD)-PCR analysis and agarose gel electrophoresis (De La Puente-Redondo et al., 2000; Settanni et al., 2012). The strains' DNA fingerprints are evaluated for similarity by examining the band patterns generated by electrophoresis on agarose gel. Different RAPD-PCR fingerprints are associated with different strains and clustering methods as similarity dendrograms can be used to assess the similarity among the strains. The 16S rRNA gene sequencing is applied for the genotypic identification of strains with various RAPD-PCR profiles. A detailed protocol of 16S rRNA sequencing analysis is reported by Weisburg et al. (1991). The obtained sequences are then compared to those in the online databases (Greengenes (http://greengenes.secondgenome.com), Silva (https://www.arb-silva.de), EzBioCloud (https://www.ezbiocloud.net)), which only matches a particular 16S rRNA gene sequence to strains that are the type for that specie (Park and Won, 2018), permitting the genetic identification of the strains.

Several studies coupled the genetic methods (using 16S rRNA gene or 23S rRNA gene) to the morphological ones (Büdel et al., 2009; Dojani et al., 2014; Muñoz-Martín et al., 2019) to explore the bacterial diversity of BSCs. Büdel et al. (2009) and Dojani et al. (2014) sequenced 16S rRNA extracted from cyanobacterial cultures after their cultivation and morphological identification. One limit of the culture-dependent approach is represented by the fact that the microbial composition is determined only on cultured microorganisms, without considering the ones present in soil and BSC communities but not cultivable.

The *culture-independent approach* permits a genetic characterization of the whole microbial community, providing a deep and accurate

description of microbial diversity, without the limitation of pure cultures isolation and including also non-cultivable microorganisms. Starting from a soil sample four main phases can be distinguished: a) DNA extraction from the soil sample; b) construction of a genomic library, constituted by all DNA fragments extracted; c) sequencing and d) sequence processing. Finally, an analysis of the sequence dataset is carried out to determine community composition.

The success of DNA-based culture-independent methods is directly related to the yield and quality of DNA extracted from a given environmental sample, and the complexity of the sample affects DNA extraction (Kunin et al., 2008). Numerous DNA extraction kits are available to extract DNA from different environmental samples. An issue related to DNA is the low content of the sample, and extraction does not provide sufficient DNA requested for analysis. To overcome this issue, environmental DNA can be subjected to whole genome amplification (Kunin et al., 2008). Whole Genome Amplification (WGA) allows for replicating the entire genome of a bacterium, thus forming a genomic library.

A genomic library is a collection of the total genomic DNA fragments from a single organism. Libraries are usually constituted by merging cloned DNA of three different average sizes (3, 8, and 40 kbp). Once cloned DNA is merged, libraries are subjected to sequencing.

Sequencing is the process of determining the exact position of nucleotides to retrieve information from a given DNA sequence (Tringe and Rubin, 2005). Various technologies of Next-Generation Sequencing (NGS) are available (Illumina, Roche, 454) and allow for studying more DNAs at once. Depending on the objectives of the research, one region of RNA may be chosen over another to be sequenced. Ribosomal RNA (rRNA) is a highly conservable molecule that occurs in all bacteria and is used as microbial fingerprints for species identification. For instance, the sequencing of rRNA subunits 16S rRNA and 23S rRNA allows the identification of BSC microorganisms (Ahmadian et al., 2006; Kunin et al., 2008). The subunit 16 s rRNA is the world's most widely used marker gene for the identification of bacterial and archaeal communities (DeSantis et al., 2006). Similarly, 18S rRNA and 28S rRNA are sequenced to explore fungal diversity (Wijayawardene et al., 2020).

The steps after sequencing are the read preprocessing, assembly, gene prediction, and annotation. The *read preprocessing* phase includes base-calling of the raw data obtained from the sequencing machines, and vector screening to remove cloning vector sequences (Chou and Holmes, 2001; Ewing et al., 1998).

Assembly permits to join DNA fragments. Merging overlapping sequences permits obtaining a larger sequence formed by continuous, but not contiguous, DNA fragments, called contig. Complete removal of cloning vector sequences during assembly is particularly important to avoid erroneous merging of sequences. Jointly, the sequences are subjected to a sequence quality control, thus eliminating sequences with a low-quality score associated with reads or contigs. Finally, datasets need to be screened for the detection of sequence contamination. Some microorganisms are used as cloning vector hosts (e.g., *Escherichia coli*). Screening for host contamination should be considered carefully because *Escherichia coli* may be present in the environment under study. Elimination of this vector sequence may result in the elimination of *Escherichia coli*-related sequences and the representation of species present in the sample would therefore be biased.

During assembly, sequence reads are combined into contigs by similarity of the reads. Several criteria can be applied to form contigs such as selecting the best quality nucleotide for each position or choosing the most commonly encountered nucleotide for each position (Jaffe et al., 2003). Sequencing is typically performed on both sides of a sequence resulting in paired reads. The presence of paired reads in two separate contigs allows their joining into a non-contiguous DNA sequence called scaffold. Scaffolds and contigs are then published in public databases as flat text files. All the information about the procedures that led to their obtainment is included with the sequences.

Gene prediction is the identification of protein and RNA sequences encoded in the sample DNA.

Functional *gene annotation* is the comparison of predicted genes to existing ones, annotated in a reference sequence database. Sequence reads are reread to detect possible errors that occurred during one of the previous phases. Then, sequences are matched to homologs in reference sequence databases, using sequence similarity tools such as BLAST (Kunin et al., 2008). This last phase allows the assessment of the identity of the microorganisms and their weight within the microbiological community of the sample.

Sequences can be grouped by DNA sequence similarity into clusters of microorganisms, defined as Operational Taxonomic Unit (OTU) or in a phylogenetic tree-like Neighbor-Joining Tree (McHardy et al., 2007). Neighbor-Joining is one of the most used clustering methods of sequence data. This algorithm considers similarities and distances between each sequence and species and thus, forms the phylogenetic tree.

The widespread use of the 16S rRNA subunit has resulted in a large number of deposited sequences corresponding to this subunit and the creation of very large and reliable databases (Tringe and Hugenholtz, 2008).

The culture-independent approach allows the identification of bacterial taxa which constitute the BSC community and permits the correlation of the detected species with ecosystem functions. On the other hand, their use is often limited by costs, the need for appropriate laboratory tools and the high skills required in protocols applying. Moreover, all DNA present in the soil sample is extracted without considering whether the microorganism from which the DNA was extracted is alive or dead. This brings to an overestimation of BSC microbial composition due to the inclusion of dead microorganisms.

Recently Guida et al. (2022) combined culture-dependent and culture-independent approach. Authors isolated and cultivated BSC microorganisms, determining the number of microorganisms present in different degraded soils, and coupled it with the sequencing of 16S rRNA extracted from a soil sample, to examine the microbial diversity. Despite the lack of determination of the microbial composition of isolated microorganisms, this work suggests the possibility of combining genetic identification by both a cultivable method (DNA extracted from microbial cultures) and a non-cultivable method (DNA extracted from soil samples). These coupled approaches allow for defining which microorganisms are present in the soil and recognizing which are alive and viable. However, cultivable methods permit obtaining pure cultures of microorganisms. Coupling cultivation methods with genetic analysis allows for identifying which microorganism constitutes the pure cultures also evaluating their potential application in restoration techniques for degraded areas.

4. BSCs influence on soil characteristics

BSCs influence soil physical (soil particle aggregation, porosity, pore size and connectivity, albedo, surface roughness, resistance to rainfall impact, and crust resistance to penetration) and chemical characteristics (organic Carbon content, Nitrogen content, EPS content, and spatial distribution of nutrients).

BSCs improve soil particle aggregation by increasing soil organic matter content, which is higher for LSS-BSCs than ESS-BSCs (Gao et al., 2017). ESS-BSCs, with their gluing cyanobacterial EPS, are responsible for the chemical aggregation of soil particles (Cosentino et al., 2006; Gao et al., 2017; Kidron et al., 2020b, 2022). In addition, in LSS-BSCs, lichen and moss penetrative structures (hyphae and rhizines) are also responsible for the physical bonding of soil particles, creating a net that brings soil particles together (Bowker et al., 2008; Cosentino et al., 2006). Type and quantity of EPSs, which depend on the BSC microbial composition and amount of nutrients available in soil (Gao et al., 2020a, 2020b; Rodríguez-Caballero et al., 2018; Rossi et al., 2017), influence soil particle aggregation (Chamizo et al., 2020b). LSS-BSCs show higher EPS production than ESS-BSCs (Gao et al., 2017, 2020a, 2020b). The amount and chemical composition of EPSs are strongly related to metabolisms of

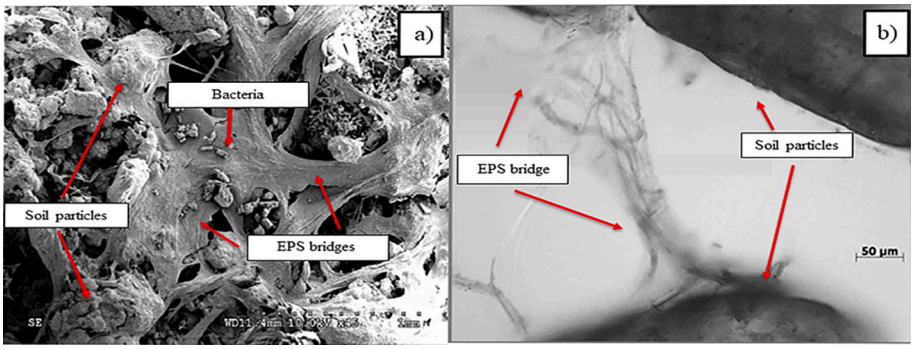

Fig. 4. Soil particles, bacteria, and EPS bridges induced by different microorganisms (*Nostoc commune* in a), and *Schizothrix* cf. *delicatissima* in b) observed under SEM microscope.

the species constituting a BSC community. Chamizo et al. (2020b) compared the EPSs produced by three different cyanobacteria (*Nostoc commune*, *Scytonema javanicum*, and *Phormidium ambiguum*) in terms of volumes secreted and chemical composition. The cyanobacterium *Phormidium ambiguum* showed a higher EPS production with a lower binding capacity than the other two cyanobacteria. EPSs produced by *Phormidium ambiguum* and *Scytonema javanicum* are polymers with high molecular weight. Both species form larger and more stable polysaccharide matrices than that generated by *Nostoc commune*. The same authors (Chamizo et al., 2020b) observed better BSC microbial growth on sandy soil when high molecular weight EPSs are secreted. In addition, when environmental and nutritional conditions are limiting (oligotrophic environments), BSCs are induced to produce fewer and simpler organic compounds, resulting in less soil particle aggregation (Chamizo et al., 2020b) (Fig. 4).

BSCs modify soil porosity, pore size, and pore connectivity. Porosity and pore size increased moving from bare soil towards ESS-BSCs and, even more, towards LSS-BSCs (Felde et al., 2014; Rodríguez-Caballero et al., 2013; Whitney et al., 2017). Indeed, filamentous structures can lead to channel formation in soils, enhancing porosity. In opposition, EPSs can induce partial pore-clogging in soil (Kidron, 2015; Kidron et al., 2020b, 2022), interrupting the water path and, consequently, reducing pore connectivity, infiltration, and evaporation. ESS-BSCs also bring the formation of vesicular pores, a discontinuous pore system with capillarity barrier effects, negatively affecting infiltration (Cantón et al., 2020) and extending the delay for infiltration of water above BSCs (Xiao et al., 2019). Combined effects of pore-clogging and interrupted water pathways lead to a reduction in evaporation and an increase in water retention capacity and soil water content (Chamizo et al., 2020b; Román et al., 2021).

Cyanobacterial BSCs produce UV-absorbing pigments that darken microbial cells and soil surface (Belnap et al., 2008; Ferrenberg et al., 2015; Rutherford et al., 2017). These pigments, reduce soil albedo and, consequently, increase soil temperature that affects microbial metabolism. These effects are amplified for LSS-BSCs, which form darker crusts and produce more UV-absorbing pigments than ESS-BSCs (Chilton et al., 2018; Rutherford et al., 2017).

BSCs modify soil surface roughness and the degree of this modification is related to BSC morphology. The dominant species of the microbial community affect BSC morphology which can vary from smooth crusts to rugose (Belnap, 2006; Belnap et al., 2008). ESS-BSCs create smooth crusts and their roughness is lower than bare soil; conversely, lichen and especially moss BSCs create 3D-shaped structures on the soil surface whose roughness is higher than bare soil (Felde et al., 2014; Rodríguez-Caballero et al., 2012, 2013; Wei et al., 2015). Soil Carbon cycle and CO_2 exchange are under BSC influence. BSCs fix Carbon into a wide range of organic compounds, but they also use soil organic matter to complete their metabolisms and produce CO_2 emissions. The variability of these effects is related to soil water content (Ladrón de Guevara et al., 2014). A positive correlation between BSC Carbon fixation, BSC biomass, Carbon losses, and soil water content exists (Pen-Mouratov et al., 2011), and a water treatment threshold (2 mm for cyanobacterial BSCs and 2–5 mm for moss BSCs) can be identified to define differences in BSC metabolic behaviors due to water content in soil (Coe et al., 2012; Zhang et al., 2018b). When the water content is below these thresholds, poikilohydric organisms of BSCs stop their organic Carbon compound production and begin Carbon respiration, using organic matter in soil and producing CO_2 (Miralles et al., 2018; Rodríguez-Caballero et al., 2018). When barely moistened, poikilohydric organisms of BSC reactivate their metabolic functions but continue to use soil organic compounds and produce CO_2 with the consequent losses for C respiration (Miralles et al., 2018; Rodríguez-Caballero et al., 2018). Some authors reported BSC ability to maintain metabolic functions also with rainfall <1 mm, providing water from dew or fog (Miralles et al., 2018). Above that threshold, BSCs are sufficiently moistened and poikilohydric organisms increase the Carbon fixation rate. In this way, BSCs produce enough organic compounds to overcome losses by Carbon respiration (Chamizo et al., 2018; Rodríguez-Caballero et al., 2018) and to supply to organic matter degradation (Zhang et al., 2018b). Similarly, Bullard et al. (2022) observed that the cyanobacterial BSCs rapidly recover the photosynthetic activity and EPS production within few hours of rainfall. BSC successional stage also influences soil organic matter content with ESS-BSCs that have lower Carbon fixation rates than LSS-BSCs (Gao et al., 2017, 2020a, 2020b; Li et al., 2021). Furthermore, BSCs reduce soil organic Carbon losses compared to bare soils. Organic Carbon losses represent one of the main drivers of global changes in arid and semiarid environments (Cantón et al., 2014) and are influenced by BSC successional stages. Indeed, LSS-BSCs are the most effective type of BSCs in reducing organic Carbon losses (Cantón et al., 2014). Despite their limited Carbon fixation rates, cyanobacterial BSCs show an increase in soil Carbon content up to 83% compared to bare soils (Chamizo et al., 2018; Kheirfam, 2020; Sepehr et al., 2019). However, the enrichment in organic matter is limited to the upper soil layer (Cantón et al., 2020).

Similar to Carbon, also Nitrogen content in soil is affected by BSCs and it increases following BSC successional stage sequence (Bowker et al., 2018; Cantón et al., 2020). Cyanobacteria fix atmospheric Nitrogen into nitrate and ammonia (Billings et al., 2003; Elbert et al., 2012). Although ESS-BSCs exhibit a predominantly cyanobacterial composition, lichen, and moss BSCs show higher N content in soil than ESS-BSCs (García-Carmona et al., 2020; Li et al., 2021). Cyanobacteria are present both in ESS-BSCs and in LSS-BSCs, but in LSS-BSCs they are helped into Nitrogen fixation by mosses and lichens that contribute to higher organic matter content and higher soil stability, and consequently to higher N content in soil (Chamizo et al., 2018; Kheirfam, 2020).

BSC microorganisms can accelerate the rate of mineral weathering to obtain nutrients. These microorganisms can produce nutrient-mineralizing enzymes (e.g., deaminases, phosphatases, and

sulphatases) or secrete organic and inorganic acids, thus favoring mineral solubilization (Killham, 1994; Zhang et al., 2018a). Also, the BSC secretions can expand and contract in response to the wetting and drying of the BSCs, thus exerting a physical weathering process (Chen et al., 2000, 2014; Garcia-Pichel et al., 2016). As a result, BSCs increase soil fertility by favoring the accumulation of macro- (C, N, and P) and micronutrients (Ca, Cr, Mn, Zn, As, and Zr) (Beraldi-Campesi et al., 2009; Garcia-Pichel et al., 2016).

Carbonate rocks and sediments are largely colonized and weathered by BSCs, while silicates are more resistant to solubilization (Garcia-Pichel et al., 2016). However, silicate substrates (micas, phlogopite, muscovite, olivine, and plagioclase) are sensitive to the weathering by BSCs, which also include lichens and mosses (Serstevens et al., 1978; Garcia-Pichel et al., 2016; Dorn, 2021). On the contrary, some scholars reported no solubilization of silicate by cyanobacteria (Beraldi-Campesi and Garcia-Pichel, 2011; Fischer et al., 2010). BSCs also protect soil from sulphate and carbonate loss. The BSC composition affects solute mobilization in areas with ESS-BSCs higher runoff volume occurs, generating higher values of carbonates and solutes in runoff; instead, in areas with LSS-BSCs, characterized by higher infiltration rates, lower values of runoff volume occur also generating lower carbonates in runoff (Lázaro and Mora, 2014).

To detect and quantify the beneficial effects of the different BSCs on soil characteristics some tests of inoculation have been performed on soil plots (Chamizo et al., 2018, 2020a; Kheirfam et al., 2017a, 2017b, 2020). Kheirfam et al. (2017a) inoculated *Nostoc*, *Oscillatoria,* and *Lyngbya* as representative native cyanobacteria and *Azotobacter* and *Bacillus* as soil bacteria on erosion-prone, bare, and degraded soils. The bacteria inoculated exerted benefits to soil fertility since both bacterial inoculums increased Nitrogen and Carbon fixation and organic matter content. Individual inoculation of cyanobacteria increased organic Carbon and Nitrogen content more than *Azotobacter* and *Bacillus* alone or in combination. Indeed, BSCs induced by cyanobacteria inoculums can partially restock Carbon and Nitrogen losses due to disturbance effects such as fire (Chamizo et al., 2020a). Román et al. (2021) inoculated other native cyanobacteria (*Microcoleus vaginatus*, *Nostoc commune*, *Scytonema hyalinum*, and *Tolypothrix distorta*) on different textured soils and under different caprwatering regimes. All inoculation trials increased organic Carbon content and EPS production. *Nostoc commune* showed the highest capacity to form BSCs, the highest soil organic carbon content, and the highest EPS production, also in fine textured and less fertile soils. Regardless water regime, *Nostoc commune* showed higher drought resistance and stronger protective effects against soil erosion processes than other microorganisms. For this reason, this specie is suitable to restore microbial activity in arid environments (Román et al., 2021).

BSCs affect soil resistance to rainfall impact by improving soil physicochemical characteristics. Several studies provided evidence that BSCs increase resistance to rainfall impact (Bowker et al., 2008; Bullard et al., 2018; Kheirfam, 2020; Lázaro and Mora, 2014; Zhao et al., 2014). Some authors (Rodríguez-Caballero et al., 2013; Zhao et al., 2014) reported that cyanobacterial BSC resistance to rain splash erosion is higher than that of bare soil. Gao et al. (2020a) and Zhao et al. (2014) observed that protection provided by moss BSCs against rain splash erosion was 21-fold higher than that provided by cyanobacterial BSCs. BSC resistance to rainfall impact also depends on soil texture. Cyanobacterial BSCs grown on silt and loam soils shows higher resistance to rainfall impact than the same on sandy soil (Zhao et al., 2014). Cyanobacterial EPSs form more bonds among the finer particles rather than coarser particles. On the contrary, mosses of BSCs show a higher resistance to rainfall impact on sand than silt and loams (Zhao et al., 2014). Moss BSCs with their penetrative structures create a filamentous network able to trap soil particles, also providing high protection against the detachment of soil particles. This network is particularly effective in trapping coarse particles, determining the higher resistance to rainfall impact recorded on sand than that recorded on silt and loams.

Moreover, some authors (Kheirfam et al., 2020; Sadeghi et al., 2020b) observed that, in the first minutes of rainfall, water is absorbed by cyanobacteria, increasing their cellular volume, and creating a more resistant physical barrier against raindrops. However, cyanobacteria are characterized by different cellular shapes and soil-cell interactions. For example, *Scytonema javanicum*'s thick cellular filaments are organized as branches and bind together soil particles, similarly to the roots of plants, while *Phormidium ambiguum* covers all the surfaces with thin filaments, such as a web that enhances crust resistance to penetration (Chamizo et al., 2018). In addition, LSS-BSCs, due to their higher biomass and their hyphae and rhizines, form a thicker layer (~10 mm) on the soil surface that better resists rain splash erosion and penetration in comparison to thinner (~1–3 mm) ESS-BSC crusts (Bullard et al., 2018; Felde et al., 2018; Kidron, 2015).

Some Authors (Chamizo et al., 2019, 2020a; DeJong et al., 2006) reported that induction of BSC formation by cyanobacterial and bacterial inoculum lead to improvement of soil stability, also in degraded environments. Inoculation of different cyanobacteria (*Scytonema javanicum* and *Phormidium ambiguum*) in single or dual combination, improved soil characteristics of two burned forest soils, one loam soil and one sandy loam soil (Chamizo et al., 2019, 2020a). Despite the short duration of those laboratory studies (45 days), cyanobacteria inoculum induced a reduction in soil hydrophobicity and increased soil particle aggregation in both highly degraded soil. Similarly, the addition of *Bacillus pasteurii* to soil improved soil particle aggregation and contributed to sand particle cementation due to microbial-induced calcium carbonate and gypsum sedimentation (DeJong et al., 2006).

5. Role of BSC on soil surface hydrology

Understanding BSC influences on soil surface hydrology is one of the hot topics of the last years. The works carried out in different countries to elucidate the BSC role showed contradictory results. Some studies reported that BSCs increase infiltration (Barger et al., 2006; Belnap, 2006; Belnap et al., 2013; Chamizo et al., 2012a; Faist et al., 2017; Gao et al., 2017; Wei et al., 2015; Xiao et al., 2011), others showed opposite results, since BSCs hindered infiltration (Belnap, 2006; Eldridge et al., 2020; Faist et al., 2017; Felde et al., 2014; Kidron et al., 2020b; Xiao et al., 2019), and other simply found that BSCs showed no influence on water infiltration (Chamizo et al., 2016; Faist et al., 2017; Fick et al., 2019).

As a matter of fact, soil hydrology is affected by several aspects of BSCs such as successional stage, degree of cover, biomass, thickness, surface roughness, production of organic matter, EPSs, and hydrophobic substances, by BSC spatial distribution, but also by soil characteristics including texture, porosity, and micro-depression formed by BSCs, by moisture and rainfall characteristics (intensity and volume). The influence of each factor related to BSCs and soil on soil hydrology are reported in Table 3 and will be examined individually to facilitate their comprehension.

In general, infiltration (mm) increases with the successional stage and cover increase (Belnap et al., 2013; Román et al., 2021). Indeed, many characteristics of BSCs, such as biomass, thickness, surface roughness, and organic matter production, increase as BSCs move along with the successional stage series, also affecting soil hydrologic response. For instance, LSS-BSCs, with their protruding structures, determine higher soil surface roughness, and, with their leaves and leaf hair points, absorb and store a larger amount of water in comparison to ESS-BSCs and bare soil. These combined effects also lead to higher infiltration of LSS-BSCs compared with ESS-BSCs and bare soil (Román et al., 2021). On the other hand, LSS-BSC higher biomass can induce pore clogging, while the hydrophobic substances secreted by lichens and mosses can seal the soil surface impeding water infiltration (Belnap et al., 2013; Chamizo et al., 2016; Xiao et al., 2011). Time to runoff, defined as the time from the beginning of the rainfall to the beginning of runoff, is strictly related to BSC successional stage and cover (Eldridge

Table 3
Types of BSC and relative influences on soil properties and hydrology.

Type of BSC	Phenomenon	Influences	References
Green algae	Carbohydrates production	Increase water holding capacity	Fischer et al. (2013)Lichner et al. (2013)
		On sandy soils:	
		Increase water drop penetration	
		Decrease water sorptivity	
		Decrease hydraulic conductivity	Zhang et al. (2015)
		Induce superficial pore clogging	
		Decrease evaporation (dry periods)	
		Increase overland flow (wet periods)	
	Photosynthetic assimilation of CO_2	Increase pH	Zhang and Koehler (2022)
Cyanobacteria	EPS production	*On sandy soils*:	
		Induce soil pore clogging	
		Reduce soil porosity	
		Reduce hydraulic conductivity	Cantón et al. (2020)
		Reduce infiltration	Chamizo et al. (2012a)
		Reduce time to runoff	Chamizo et al. (2016)
		Increase runoff	Eldridge et al. (2020)
		Increase time to runoff	Kidron et al. (2020b)
		Reduce runoff	Rodríguez-Caballero et al. (2013)
		On silty soils:	Xiao et al. (2011)
		Increase hydraulic connectivity	Xiao et al. (2019)
		Increase soil microporosity	Jafarpoor et al. (2022)
		Increase infiltration	Sadeghi et al. (2020b)
		Increase time to ponding	
		Increase time to runoff	
		Reduce runoff	
	Organic matter production	Increase soil particle aggregation	Cantón et al. (2020)
		Increase soil stability	Chamizo et al. (2012a)
		Increase soil porosity	Chamizo et al. (2016)
		Increase infiltration	
	Smooth crusts	Reduce surface roughness	Rodríguez-Caballero et al. (2012)
		Increase runoff pathway connection,	
	Occurrence of protruding structures	Water absorption in BSC tissue	Cantón et al. (2020)
		Increase surface roughness	Faist et al. (2017)
		Increase infiltration	Kidron (2015)
		Reduce runoff	Rodríguez-Caballero et al. (2013)
		Reduce runoff velocity	Román et al. (2021)
			Wei et al. (2015)
	Occurrence of penetrative structures	Increase soil porosity	Felde et al. (2014)
		Increase soil hydraulic connectivity	
		Increase soil infiltration	
	Occurrence of swelling sheaths	Increase soil porosity	Chamizo et al. (2016)
		Increase infiltration	Rodríguez-Caballero et al. (2012)
		Increase surface roughness	Rodríguez-Caballero et al. (2013)
		Reduce runoff	
Lichen	Hydrophobic substances secretion (higher than mosses)	Induce soil surface sealing	Eldridge et al. (2020)
		Reduce infiltration	Rodríguez-Caballero et al. (2012)
		Increase runoff	
	Organic matter production (higher than cyanobacteria BSCs)	Increase soil particle aggregation	Cantón et al. (2020)
		Increase soil stability	Chamizo et al. (2016)
		Increase soil porosity	Rodríguez-Caballero et al. (2013)
		Increase infiltration	
	Biomass and thickness (higher than cyanobacteria BSCs)		Belnap et al. (2013)
		Induce soil pore clogging	Chamizo et al. (2016)
		Reduce infiltration reduction	Felde et al. (2014)
		Induce faster runoff generation	Kidron (2015)
			Xiao et al. (2011)
	Biomass and thickness (higher than cyanobacteria and lichen BSCs)		Belnap et al. (2013)
		Induce soil pore clogging	Chamizo et al. (2016)
		Reduce infiltration reduction	Felde et al. (2014)
		Induce faster runoff generation	Kidron (2015)
			Xiao et al. (2011)
Moss	Occurrence of protruding structures		Cantón et al. (2020)
		Water absorption in BSC tissue	Eldridge et al. (2020)
		Increase surface roughness	Faist et al. (2017)
		Increase infiltration	Kidron (2015)
		Reduce runoff	Román et al. (2021)
		Reduce runoff velocity	Rodríguez-Caballero et al. (2013)
			Wei et al. (2015)

(*continued on next page*)

Table 3 (*continued*)

Type of BSC	Phenomenon	Influences	References
	Occurrence of penetrative structures	Increase soil porosity	Felde et al. (2014)
		Increase soil hydraulic connectivity	
		Increase soil infiltration	
	Organic matter production (higher than cyanobacteria and lichen BSCs)	Increase soil particle aggregation	Cantón et al. (2020)
		Increase soil stability	Chamizo et al. (2016)
		Increase soil porosity	Rodríguez-Caballero et al. (2013)
		Increase infiltration	
	Hydrophobic substances secretion	Induce soil surface sealing	Eldridge et al. (2020)
		Reduce infiltration	Rodríguez-Caballero et al. (2012)
		Increase runoff	Rodríguez-Caballero et al. (2013)

et al., 2020). Time to runoff declines with increasing cover of ESS-BSCs, while it increases as the cover of LSS-BSCs increases. These different behaviors may be explained by different metabolisms of the species of the BSC community. ESS-BSCs by secreting EPSs induce the clogging of soil pores, block water infiltration pathways and generate runoff earlier. On the contrary, LSS-BSCs increase infiltration and reduce runoff and runoff generation time by absorbing water due to the swelling sheaths of BSCs, increasing soil porosity and enhancing soil roughness (Chamizo et al., 2016; Rodríguez-Caballero et al., 2013). Moving from ESS-BSCs to LSS-BSCs, BSC biomass and thickness increase and this affects surface runoff rates.

Felde et al. (2014) focused only on BSC thickness and reported that the thicker BSCs can absorb higher amounts of water during rainfall events than thinner BSCs. The last BSC types are saturated more rapidly than thicker BSCs and generate runoff earlier. Kidron (2015) observed that older cyanobacterial BSCs with a thickness in the range 1–3 mm showed higher runoff than the youth and thinner (~1 mm) ones, while moss BSCs thick ~10 mm showed similar runoff to thinner cyanobacterial BSCs. These results showed that BSC influence on runoff cannot be explained exclusively by crust thickness, because this behavior depends on pore clogging and roughness. Indeed, a high amount of EPSs secreted by cyanobacterial BSCs determines pore clogging, reduces infiltration, and triggers runoff. On the other hand, moss BSCs are characterized by a rougher and more complex 3-D morphology than cyanobacterial BSCs, causing an increase in soil surface roughness and leading to a reduction of runoff velocity (Kidron, 2015).

In general, surface roughness increases with BSC successional stage (Felde et al., 2014; Rodríguez-Caballero et al., 2012). ESS-BSCs create smooth crusts on soil surfaces, characterized by a lower surface roughness than bare soil, and which highly connect runoff paths (Rodríguez-Caballero et al., 2012). On the contrary, lichen thalli and moss leaves of LSS-BSCs highly increase surface roughness in comparison to bare soil. Water infiltration in soil increases with BSC surface roughness, especially in fine-textured soils (Cantón et al., 2020) and this reduces runoff (Faist et al., 2017). The influences of BSC roughness on runoff also depend on rainfall amount and rainfall intensity (Chamizo et al., 2016; Rodríguez-Caballero et al., 2013). BSCs reduce runoff generated by rainfall events characterized by low rainfall heights and intensities but do not affect it for rainfall events characterized by high rainfall heights and intensities (Chamizo et al., 2016; Rodríguez-Caballero et al., 2013). BSC roughness effect on soil hydrology is mainly due to the increased roughness in micro-depressions (small hollows formed by BSCs in the soil) thus reducing the flow velocity of the overland flow and increasing infiltration. When high-magnitude or high-intensity rainfall events occur, micro-depressions are filled by water, thus mitigating the effect of roughness on surface runoff.

Some authors (Cantón et al., 2020; Chamizo et al., 2012a, 2016) suggested that increased infiltration is due to BSC's higher organic matter content and the related soil stability and physical structure improvements. Other authors suggested that EPSs secreted by cyanobacteria, which induce pore-clogging (Chamizo et al., 2012a; Xiao et al., 2011, 2019), and the hydrophobic substances secreted by lichen and moss BSCs, which seal soil surface (Rodríguez-Caballero et al., 2013), decrease infiltration.

BSCs increase soil organic matter content, thereby, increasing soil porosity and soil particle aggregation. Organic matter content is related to BSC successional stage and cover (Cantón et al., 2020; Chamizo et al., 2016). Indeed, ESS-BSCs and even more LSS-BSCs increase organic matter content and soil porosity, enhancing infiltration (Rodríguez-Caballero et al., 2013). EPSs produced by ESS-BSCs increase hydraulic conductivity on silty soils by improving macroporosity (Cantón et al., 2020). At the same time, on sandy soils EPS may induce pore-clogging, and cyanobacteria generate earlier and more runoff than those registered for bare soils (Cantón et al., 2020). Moreover, the differences between runoff generated in bare soils and ESS-BSCs are emphasized by increasing BSC cover (Eldridge et al., 2020). EPSs swell when wet, resulting in an increased thickness of BSCs, and can block soil pores. Recently, Kidron et al. (2022) reviewed the role of EPSs and their swelling properties distinguishing two different behaviors in function of soil dry or wet. When the soil is dry, the EPSs strongly contribute to improve soil particle aggregation and consequently to the soil infiltration. On the other hand, when wet, EPSs may increase in volume, similarly to swelling clays, inducing soil pore clogging and limiting infiltration. EPSs are strictly related to BSC composition and determine different viscoelastic properties in BSCs, such as elasticity, rigidity, and viscosity.

Furthermore, the secretion of hydrophobic substances induces soil hydrophobicity and creates an impermeable layer on the soil surface (Eldridge et al., 2020). The ability to produce these substances is particularly relevant in lichen BSCs, followed by moss BSCs, while it does not occur in cyanobacterial BSCs. The waterproof layer created on the soil surface by lichen BSCs blocks water movement to lower soil layers with the consequence that infiltration is reduced while runoff is increased (Rodríguez-Caballero et al., 2012). Kidron et al. (2012) evaluated the hydrophobicity of BSCs by applying the Water Drop Infiltration Time (WDPT) method and measured the surface runoff generated on plots with and without BSCs. The plots were subjected to natural rainfall events for approximately two years, and no influence of hydrophobicity on surface runoff was observed at the annual time scale. On the contrary, Chamizo et al. (2016) recorded similar results under high-intensity rainfall events (rainfall intensity in 5 min, $I_5 > 20$ mm h^{-1}) comparing annual infiltration of lichen BSCs, ESS-BSCs, and bare soils. A different behavior was shown by lichen BSCs that caused the highest infiltration under low-intensity events ($I_5 < 20$ mm h^{-1}). Despite lichen BSCs induce the formation of an impermeable layer on the soil surface, infiltration is not affected by hydrophobicity under high-intensity events. However, the higher infiltration recorded by Chamizo et al. (2016) for LSS-BSCs under low-intensity events is justified by the improved porosity, mainly due to the increased organic matter content and by penetrative structures of these biological structures. Higher soil porosity allows higher water infiltration into the soil. Alternatively, hydrophobicity is limited only to the LSS-BSC surface. In relation to the water drop pathway, when a raindrop impacts the hydrophobic surface of the BSC, it remains on the BSC surface or moves over it until the water drop reaches the edge of the BSC. At this point, the increased porosity of soil promotes infiltration, and this hides the BSC hydrophobic effect on

soil infiltration.

Runoff is also influenced by the spatial distribution and the specific position of BSCs. Wei et al. (2015) compared runoff generated on plots fully covered by BSCs, plots with the upper half covered by BSCs and lower half bare soil, and plots with the upper half bare soil and lower half covered by BSCs. Surfaces totally covered by LSS-BSCs generated less runoff than those partially covered by BSCs or with no BSCs coverage (Wei et al., 2015). Due to increased surface roughness and reduced overland flow velocity, BSCs can be considered runoff sink, and their influence increases as the area covered by BSCs increases. The plots totally covered by BSCs showed the lowest runoff, followed by the plots with the upper half bare soil and lower half covered by BSCs, while the highest runoff was recorded in the plots with the upper half covered by BSC and lower half bare soil. BSC spatial distribution influences runoff. When located in the lower part of the plot BSCs are particularly effective in converting surface runoff generated in the upper part of the plot into infiltration, also reducing overland flow velocity upstream generated.

Soil texture modulates the influence exerted by BSCs on the hydrological processes (Cantón et al., 2020; Eldridge et al., 2020). In fine-textured soils, BSCs reduce runoff but increase the time to ponding, time to runoff, and infiltration (Eldridge et al., 2020; Rodríguez-Caballero et al., 2013). On the contrary, BSC cover reduces infiltration and increases runoff in coarse-textured soils, and this is due to the reduction of soil porosity and the interruption of hydraulic conductivity (Eldridge et al., 2020). The typical high porosity of coarse-textured soils can be reduced by EPSs and BSC anchoring structures leading to a reduction of infiltration and an increase in runoff. Indeed, BSC runoff increases on sand and loams, while time to ponding, time to runoff, and infiltration reduce with BSC coverage (Cantón et al., 2020; Eldridge et al., 2020). However, some authors (Jafarpoor et al., 2022; Sadeghi et al., 2020b) reported that the presence of cyanobacterial BSCs on coarse-textured soil reduces runoff volume, and runoff is generated later than bare soil. These discrepancies may be due to the microbial composition of the BSCs tested in the different studies. Different types of BSCs induce different surface roughness and porosity, and result in different soil hydrologic responses, such as a reduction of surface runoff.

Some scholars (Sadeghi et al., 2020a, 2020b) tested the applicability of microbial inoculum to induce BSCs formation and studied the influence of the induced BSCs on the soil hydrology. Sadeghi et al. (2020a) inoculating strains of *Nostoc* spp. and *Oscillatoria* spp. under natural rainfall events obtained a runoff reduction ranging from 25 to 57% compared to bare soil plots. Sadeghi et al. (2020b) tested the effect of bacteria ad cyanobacteria inoculation on runoff generation reporting a reduction of runoff yield (from ~30 to 77%) in comparison to the control conditions.

Regarding soil porosity, Felde et al. (2014) applied mercury intrusion porosimetry and X-ray computed microtopography to BSC soil samples and observed that total porosity and range of pore size increase with the BSC successional stage. Lichen and moss BSCs showed higher total soil porosity in comparison with cyanobacterial BSCs. In addition, BSCs induce vesicular pore formation in soil. Vesicular pores are spherical single voids with no connection to one another. The presence of these pores is induced by BSCs, and it decreases along the successional stages (Felde et al., 2014). Vesicular pores are formed by air trapped in the soil between BSC crusts and water in soil pores. When soil water content increases, the air is trapped in limited areas of soil and is subjected to an increased pressure that leads to the creation of voids in the soil matrix (Felde et al., 2014). However, the penetrative structures of lichens and mosses can further improve soil porosity and pore connection, connecting these discontinuous pores.

Soil moisture also determines different BSC influences on runoff and infiltration. When soil is dry, BSCs are characterized by cracks on their surface that increase infiltration. When soil is wet these cracks disappear because they are filled up by cyanobacterial BSCs inducing an increase of runoff (Rodríguez-Caballero et al., 2012). In addition, an increase of BSC cover increases soil moisture on loam and sand (Eldridge et al., 2020). Higher soil moisture can be justified by the BSC's ability to intercept moisture and limit water movement to deeper soil layers, keeping water close to the surface. LSS-BSC crusts occur on the soil surface with cucullate leaves (hood-like shape) and leaf hair points allowing BSCs to capture and store water. The volume of water absorbed by moss structures results in lower volumes of infiltration (Eldridge et al., 2020).

Lichen BSCs induce micro-depression formation on soil surfaces more than ESS-BSCs (Cantón et al., 2020; Rodríguez-Caballero et al., 2012, 2013). In these micro-depressions water easily infiltrates into soil pores, justifying the higher infiltration recorded for low-intensity rainfall events. Micro-depressions can be considered as runoff sinks, increasing infiltration, and reducing runoff connectivity (Rodríguez-Caballero et al., 2012). Furthermore, a higher infiltration is observed in BSC micro-depressions than in bare soils, with increasing effect moving from plot scale towards hillslope scale (Cantón et al., 2020; Chamizo et al., 2016; Rodríguez-Caballero et al., 2013). While at the plot scale ESS-BSCs determine higher runoff than vegetation, they reduce runoff at the hillslope scale, due to the increase in vegetation productivity, water availability, and the ability of plants to partially convert runoff into infiltration (Cantón et al., 2020). LSS-BSCs reduce runoff and increase moisture retention more than ESS-BSCs, both at the plot and hillslope scale (Cantón et al., 2020). However, contrasting results are reported by some authors (Chamizo et al., 2016; Rodríguez-Caballero et al., 2013) on lichen BSC influences on infiltration. Chamizo et al. (2016) and Rodríguez-Caballero et al. (2013) reported lower infiltration in soils covered by lichen BSCs compared to cyanobacterial or moss BSCs, especially during high-intensity rainfall events. Reduction in infiltration may be explained by hydrophobic substances produced by lichen BSCs that create an impermeable layer on the soil surface and hinder water infiltration (Chamizo et al., 2016; Rodríguez-Caballero et al., 2012, 2013).

The divergence of the literature results may be due to the adopted classification of the BSCs, as in the same categories, are included microorganisms causing different hydrological effects, such as occluding pores or favoring infiltration. Therefore, the intrinsic heterogeneity of BSCs does not lead to a general conclusion regarding their effects on soil hydrology.

6. BSCs and soil erosion processes

In arid and semi-arid regions, BSCs contribute to protecting soil from water erosion, especially when vegetation cover is low (Belnap and Lange, 2003; Gao et al., 2017). Numerous studies carried out throughout the world confirmed the BSC protection against water erosion even though some contradictory results have been registered (Belnap, 2006; Belnap and Lange, 2003; Bowker et al., 2008; Chamizo et al., 2017; Gao et al., 2017, 2020a, 2020b; Kheirfam et al., 2017a, 2020; Rodríguez-Caballero et al., 2012, 2013; Sadeghi et al., 2020a).

Soil erosion is affected by BSC successional stage and cover as demonstrated by several studies focused on soil loss (Chamizo et al., 2012a; Gao et al., 2020a, 2020b; Rodríguez-Caballero et al., 2012; Sadeghi et al., 2021; Zhao et al., 2014). BSCs create increasingly rough crusts and soil stability as the successional stage evolves. Indeed, LSS-BSCs, and in particular mosses, are able to protect more effectively soil against soil erosion than ESS-BSCs.

Gao et al. (2020a) found negative correlations between cyanobacterial BSCs and sediment concentration and between moss BSC features (cover and biomass) and sediment concentration. Gao et al. (2020a, 2020b) identified a moss cover threshold of 35% at which sediment production is annulled and soils hosting this kind of LSS-BSCs with at least 35% of cover are totally protected from erosion. High biomass and high cover of mosses also lead to higher soil particle stability against water erosion. This reduction is less effective in ESS-BSCs. Belnap et al. (2013) registered a sediment loss of 400 g m^{-2} in presence of ESS-BSCs, while the loss displayed by soils with LSS-BSCs was about 0

g m^{-2}. Similarly, Chamizo et al. (2017) reported 465 ± 314, 75 ± 46, and 24 ± 14 g m^{-2} sediment loss in bare soil, soil with ESS-BSCs, and soil with LSS-BSCs, respectively, clearly showing the positive effect of LSS-BSCs on soil erosion. However, it is important to notice that ESS-BSCs reduce sediment production considerably in comparison to bare soils, despite at a lower level than LSS-BSCs.

The development time of BSCs also plays a crucial role in the benefits given to soil by BSCs. Soil erosion protection given by cyanobacterial BSCs is positively related to BSC age. When cyanobacterial BSCs are grown for at least 60 days, soil erosion splash loss is reduced from 95% (Bullard et al., 2018) to 98–99% (Kheirfam et al., 2017a, 2017b), and reduce sediment concentration in the runoff by 87% in comparison to that registered for bare soils (Gao et al., 2020a).

Benefits provided by the various BSC successional stages are indeed the cumulative results of multiple modifications of soil properties, surface roughness, and soil hydrology. BSCs improve soil stability and resistance to water erosion by various mechanisms. BSC influences can be summarized as follows: (i) interception of the raindrops, reduction of kinetic energy, and increase of soil resistance to rainfall impact; (ii) reduction of runoff volume and runoff velocity by increasing surface roughness and soil porosity; (iii) and soil aggregate stabilization. These mechanisms can be also categorized in accordance with the *K* and *C* terms of the Revised Universal Soil Loss Equation (RUSLE) (Bowker et al., 2008; Gao et al., 2017). The *K* factor indicates soil erodibility and is affected by various soil properties, such as texture and organic matter content and the factor *C* represents the effect of vegetation cover on the intensity of erosion processes and, more extensively, the effect of BSCs. BSCs modify the physicochemical characteristics of the soil, such as organic matter content, soil particle size distribution, and bulk density with a high impact on soil erosion. Soil erodibility (K factor) declines considerably with ESS-BSCs and further with LSS-BSCs (Gao et al., 2017). Nonetheless, Bowker et al. (2008) stated that the BSC influences on erosion are primarily due to a change in the *C* factor than in the *K* factor. Davenport et al. (1998) recognized the importance of the BSCs (microphytic soil crusts) in the reduction of the soil loss. These Authors highlighted that the role of BSCs is particularly important in low erosion state, while in high erosion rates the rope of physical processes is prominent.

BSCs represent a physical barrier that intercepts raindrops and dampens raindrop kinetic energy (Kheirfam et al., 2020; Lázaro and Mora, 2014; Sadeghi et al., 2020b). Crust thickness and above-ground structures strongly increase the BSC resistance to rainfall impact. These BSC characteristics are more pronounced in the LSS-BSCs than in the ESS-BSCs, thus accounting for the higher erosion resistance provided by the LSS-BSSs. As the erosion resistance increases, the amount of detached soil particles and soil particles transported away from the surface runoff decrease.

The influence of BSCs on soil erosion is also related to surface runoff. As above explained, BSCs reduce surface runoff in some cases, while in others they even increase it. Despite these contrasting behaviors, in both cases, BSCs reduce soil erosion. BSCs limit the volume of surface runoff and runoff erosivity and, consequently, the losses generated by soil erosion. Even with high runoff, BSCs increase surface roughness in comparison to bare soil, reducing the velocity of surface runoff and its erosive force (Belnap, 2006; Chamizo et al., 2016; Rodríguez-Caballero et al., 2012, 2013). Due to the increased roughness, flow transport capacity is reduced and BSCs can retain soil particles transported by surface runoff. Indeed, some studies (Chamizo et al., 2019; Gao et al., 2017; Xiao et al., 2019) found differences between BSCs and bare soils concerning soil particle distribution. An increase in fine particles, such as silt and clay, was recorded in BSC-covered soils due to the trapping action exerted by the BSCs increased surface roughness. However, Rodríguez-Caballero et al. (2013) suggested joining the effects of surface roughness to rainfall erosion resistance, because increased surface roughness also affects the raindrop impact angle and the force exerted by the raindrop when it reaches the soil surface.

The increased soil stabilization induced by BSCs is mainly imputable to the improved physical and chemical bonds between soil particles due to the organic matter and EPSs. Some studies (Sadeghi et al., 2017, 2020a, 2020b) recognized that ESS-BSCs, connecting soil particles together and forming soil particle aggregates, better face the erosion processes. Furthermore, the network of filamentous cyanobacteria (Fig. 5) as well as the anchoring structures of mosses and lichens highly improve soil erosion resistance. The different microbial filaments create a grid that retains and blocks soil particles together. Resistance to water erosion increases as the number and extension of cyanobacterial filaments and LSS-BSC anchoring structures increase (Belnap, 2006; Li et al., 2021). Recently, Riveras-Muñoz et al. (2022) reported that effect of BSCs on soil aggregate stability is higher in arid climate and decreases moving to humid climate conditions. However, the Authors also reported that the effects of BSCs on humid climate can be hindered by the vascular plant stabilization.

Several experiments subjected BSCs to the erosive action of natural rainfall (Bu et al., 2015; Cantón et al., 2020; Chamizo et al., 2016, 2017; Kheirfam et al., 2020; Lázaro et al., 2008; Rodríguez-Caballero et al., 2012, 2013; Sadeghi et al., 2020a, 2020b) or simulated rainfall (Belnap et al., 2013; Cantón et al., 2020; Chamizo et al., 2012a, 2016; Faist et al., 2017; Fick et al., 2019; Gao et al., 2017, 2020a; Kheirfam et al., 2017a; Lázaro and Mora, 2014; Sadeghi et al., 2021; Wei et al., 2015; Yang et al., 2022) and measured the associated soil loss by surface runoff. Different rainfall intensities and volumes, slope steepness, plot lengths, types of BSCs, and degree of BSC cover were tested in laboratory and

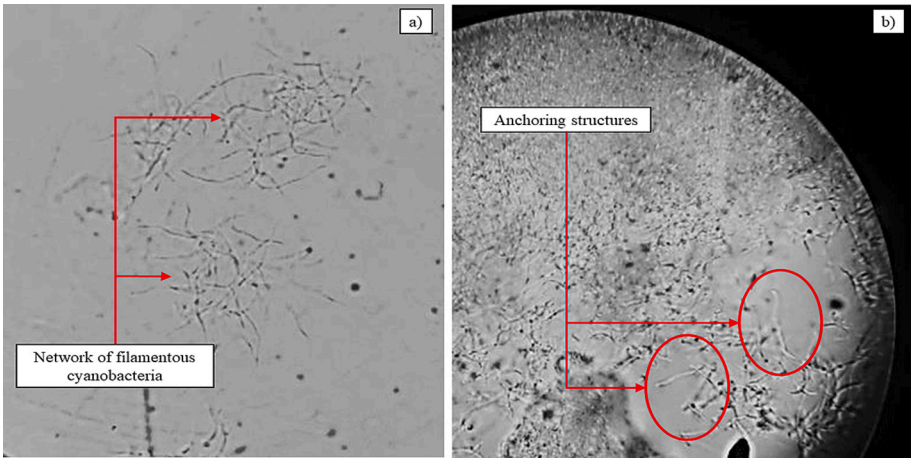

Fig. 5. Network of filamentous cyanobacteria (a) and anchoring structures of mosses and lichens (b) observed under optical microscope.

Table 4
Experimental conditions of rill and interrill literature erosion investigations.

Authors	Year	Rainfall or runoff type	Rainfall or flow characteristics	Erosion type	Plot area [m^2]	Plot length [m]	Plot width [m]	Soil texture	Slope	Type of BSCs
Yair et al.	1995	Natural rainfall	Average annual rainfall: 93 mm	Interrill	510–1520	–	–	Desert brown loessian serozem	12–29%	Mycrophytic crusts (lichens and algae).
Lázaro et al.	2008	Natural rainfall	maximum rainfall in 24 h = 76 mm; rainfall intensity exceeds 100 mm h^{-1} only when considered for an interval of 5 min, or 150 mm h^{-1} for intervals shorter than 1 min.	Interrill	0.25	0.5	0.5	–	–	Cyanobacteria and lichens.
Kidron et al.	2009	Natural rainfall	30 rainfall events (0.2–24.2 mm)	Interrill	1.2–6.6	–	–	Active and stabilized dunes, interdunes	1° – 23°	Cyanobacteria
Rodríguez-Caballero et al.	2012	Natural rainfall	–	Interrill	~ 1	–	–	–	–	Cyanobacteria and lichens.
Rodríguez-Caballero et al.	2013	Natural rainfall	High-intensity rainfall events (4 events): I_5 = 27–34.38 mm h^{-1}. Low-intensity rainfall events (13 events): I_5 = 5.78–19 mm h^{-1}.	Interrill	1	1	1	29.2 ± 5.4% sand, 58.6 ± 5.8% silt, 12.2 ± 4.2% clay	5–24.9%	Cyanobacteria and lichens.
Bu et al.	2015	Natural rainfall	Nine rainfall events (cumulative rainfall = 224.5 mm).	Interrill	8	4	2	22.11% silt, 6.33% clay, 71.57% sand.	26.8%	Mosses alone or associated with *Stipa bungeana* or *Caragana korshinkii*.
Chamizo et al.	2016	Natural rainfall	Five rainfall events: 8.9 mm h^{-1} (19.4 mm), 15.5 mm h^{-1} (37.2 mm), 12.4 mm h^{-1} (57.8 min), 27.9 mm h^{-1} (19.8 mm), 29.7 mm h^{-1} (11.9 mm).	Interrill	~ 1	–	–	El Cautivo 30% sand, 59% silt 1% clay. Las Amoladeras 61% sand, 29% silt 10% clay.	17.6–26.8%	Dark cyanobacteria and lichens.
Chamizo et al.	2017	Natural rainfall	Four rainfall events: 47 mm h^{-1} (29 mm), 13 mm h^{-1} (72 mm), 5 mm h^{-1} (31 mm), 8 mm h^{-1} (10 mm).	Interrill	~ 1	–	–	Silty loam (silt ~60%)	26.8%	Cyanobacteria and lichens.
Cantón et al.	2020	Natural rainfall	Five rainfall events: 7.1 mm h^{-1} (46 mm), 4.5 mm h^{-1} (50 mm), 5.6 mm h^{-1} (37 min), 3.4 mm h^{-1} (19 mm), 1.7 mm h^{-1} (24 mm).	Interrill	1, 10, 20	1, n.d., n.d.	1, n.d., n.d.	El Cautivo silty loam (~ 60% silt); Las Almoderas s sandy loam (~ 60% sand)	gentle slopes (~30°) and steep slopes (~50°)	Incipient cyanobacteria and well-developed cyanobacteria.
Kheirfam et al.	2020	Natural rainfall	1.18 mm h^{-1} (660 min), 1.77 mm h^{-1} (710 min), 100.20 mm h^{-1} (10 min), 35.10 mm h^{-1} (20 min), 3.80 mm h^{-1} (270), 8.91 mm h^{-1} (70 min), 6.14 mm h^{-1} (170 min).	Interril	40.44	22.1	1.83	Clay loam	25%	Cyanobacteria inoculation (*Nostoc* spp. and *Oscillatoria* spp.).
Sadeghi et al.	2020a	Natural rainfall	1.18 mm h^{-1} (660 min), 1.77 mm h^{-1} (710 min), 100.20 mm h^{-1} (10 min), 35.10 mm h^{-1} (20 min), 3.80 mm h^{-1} (270), 8.91 mm h^{-1} (70 min),	Interrill	40.44	22.1	1.83	–	25–30%	Cyanobacteria (*Nostoc* spp. and *Oscillatoria* spp.).

(*continued on next page*)

Table 4 (*continued*)

Authors	Year	Rainfall or runoff type	Rainfall or flow characteristics	Erosion type	Plot area [m^2]	Plot length [m]	Plot width [m]	Soil texture	Slope	Type of BSCs
			6.14 mm h^{-1} (170 min).							
Sadeghi et al.	2020b	Natural rainfall	55.3 mm h^{-1} (114 min), 26.3 mm h^{-1} (16 min), 20.0 mm h^{-1} (24 min), 48.9 mm h^{-1} (54 min), 44.0 mm h^{-1} (75 min).	Interrill	0.25	0.5	0.5	46% silt, 40% clay, 14% sand	25%	Bacteria, cyanobacteria and bacteria + cyanobacteria.
Chamizo et al.	2012a	Rainfall simulation	50 mm h^{-1} (1 h).	Interrill	0.25	–	–	El Cautivo 29.2 ± 5.4 sand, 58.6 ± 5.8 silt, 12.2 ± 4.2, clay. Las Almoderas 61.5 ± 5.1 sand, 28.4 ± 4.8 silt, 10.1 ± 2.1 clay.	–	El Cautivo: incipient-cyanobacterial crust, cyanobacterial crust and lichen crust. Las Amoladeras: cyanobacterial crust, lichen crust and cyanobacterial crust with abundant moss.
Belnap et al.	2013	Rainfall simulation	115 mm h^{-1}	Interrill	0.5	0.71	0.71	sandy loams	2–20%	crusts divided into 6 LOD classes.
Lázaro et al.	2014	Rainfall simulation	42 mm h^{-1}(20 min), 63 mm h^{-1}(20 min), 77 mm h^{-1}(20 min).		0.4, 0.8, 1.2, 1.6.	1, 2, 3, 4.	0.4, 0.4, 0.4, 0.4.	> 60% silt, 20–35% sand, 5–10% clay	–	Cyanobacteria and lichens.
Wei et al.	2015	Rainfall simulation	0.50 mm h^{-1} ($\langle 1h$)	Interrill	0.5	1	0.5	clay 33–42%	14%	Mosses and lichens.
Chamizo et al.	2016	Rainfall simulation	50 mm h^{-1} (1 h)	Interrill	0.25 (circular)	–	–	El Cautivo 30% sand, 59% silt, 1% clay. Las Amoladeras 61% sand, 29% silt, 10% clay.	17.6–26.8%	El Cautivo: light cyanobacteria, dark cyanobacteria and lichen. Las Amoladeras: dark cyanobacteria, lichen and moss.
Faist et al.	2017	Rainfall simulation	227 mm h^{-1} (30 min) for dark BSCs; 222 mm h^{-1} (30 min) light BSCs.	Interrill	~ 0.50	0.71	0.71	16–10.91% silt, 7.82–6.2% clay, 81.3–77.6% sand	3.6%	Light BSCs, dark BSCs.
Gao et al.	2017	Rainfall simulation	2 mm min^{-1} (30 min).	Interrill	0.2	1	0.2	–	36.3%	Cyanobacteria and mosses.
Kheirfam et al.	2017a	Rainfall simulation	50 ± 2 mm h^{-1} (100 min).	Interrill	0.25	–	–	46% silt, 40% clay, 14% sand	25%	Cyanobacteria, bacteria and cyanobacteria + bacteria inoculation.
Fick et al.	2019	Rainfall simulation	75 mm h^{-1} (30 min).	Interrill	~ 0.65	0.81	0.81	50–65% sand, 30–44% silt, 4–6% clay	9.9–10.5%	Well-developed dark BSCs rich in lichen and more disturbed crusts BSCs rich in mosses and cyanobacteria
Cantón et al.	2020	Rainfall simulation	50 mm h^{-1} (1 h).	Interrill	0.25	0.5	0.5	El Cautivo silty loam (~ 60% silt); Las Almoderas sandy loam (~ 60% sand)	gentle slopes (~30°) and steep slopes (~50°)	Incipient cyanobacteria, well-developed cyanobacteria.
Gao et al.	2020a	Rainfall simulation	120 mm h^{-1} (30 min).	Interrill	0.06	0.3	0.2	loess soil	46.6%	Cyanobacteria, mosses, and mixed.
Sadeghi et al.	2021	Rainfall simulation	72 mm h^{-1} (30 min)	Interrill	0.25	0.5	0.5	48% silt, 28% clay, 24% sand	20%	Bacteria (*Azotobacter* spp. and *Bacillus subtilis*) and cyanobacteria (*Nostoc* spp., *Oscillatoria* spp. and *Microcoleus* spp.).
Jafarpoor et al.	2022	Rainfall simulation	50 ± 7 mm h^{-1} (30 min).	Interrill	6	6	1	64.71% sand, 16.86% silt, 18.43% clay	30%	Cyanobacteria (70% of *Nostoc* spp. and *Lyngbya* spp., and 30% of *Oscillatoria* spp.).
Yang et al.	2022	Rainfall simulation	1.50 mm h^{-1} (1 h)	Interrill	21	10	2.1	47% silt, 46.01% clay, 13.52% sand	30%	Mosses and cyanobacteria mixed with mosses.

(*continued on next page*)

Table 4 (*continued*)

Authors	Year	Rainfall or runoff type	Rainfall or flow characteristics	Erosion type	Plot area [m^2]	Plot length [m]	Plot width [m]	Soil texture	Slope	Type of BSCs
Gao et al.	2020b	Runoff	4.0 L min^{-1} (30 min).	Interrill	0.02	0.2	0.1	35% sand, 55% silt, 10% clay	46.6%	Cyanobacteria and mosses.
Zhang et al.	2020	Runoff	0.502 L s^{-1}, 0.493 L s^{-1}, 0.755 L s^{-1}, 0.980 L s^{-1}, 1.258 L s^{-1}, 1.498 L s^{-1}.	Interrill	–	diameter 0.5	–	22.04–26.90% silt, 11.72–14.92% clay, 59.60–64.87% sand	17.4%, 25.9%, 34.2%, 42.3%.	Moss cover (0–20; 20–40; 40–60; 60–80; 80–100%).
Jafarpoor et al.	2022	Runoff	2.0 ± 0.32 L min^{-1} (30 min).	Rill	6	6	1	64.71% sand, 16.86% silt, 18.43% clay	30%	Cyanobacteria (70% of *Nostoc* spp. and *Lyngbya* spp., and 30% of *Oscillatoria* spp.).

field conditions. A list reporting the experimental conditions and the plot dimensions of several literature studies is reported in Table 4.

Various Authors studied the influence of microbial inoculum to induce BSCs on the soil erosion. Sadeghi et al. (2020b) inoculated bacteria, cyanobacteria and combined inoculum reporting a reduction of soil loss (2.56–64.64 g m^{-2}) and sediment concentration (1.01–3.61 g L^{-1}) in inoculated compared to soil loss (21.12–274.56 g m^{-2}) and sediment concentration (2.4–9 g L^{-1}) for the control one. Sadeghi et al. (2021) inoculating native bacteria and cyanobacteria showed a reduction of soil loss by 3 to 7 times and of mean sediment concentrations by 2 and 2.90 times compared to control conditions. Kheirfam et al. (2017a) compared the effect of the development of different microbial inoculum on and soil loss. The effect of bacteria inoculum on soil loss reduction is more relevant on short-time scales, reducing soil loss by 89% at 15 days after the inoculation and by 96% at 30 days, while cyanobacteria reduce soil loss by 73% at 15 days after the inoculation and by 92% at 30 days after inoculation. On the contrary, cyanobacteria are more effective on long-time scales (60 days after inoculum), reducing soil loss by 98%, while bacteria reduce soil loss by 93%. The combination of cyanobacteria with bacteria inoculum decreases soil loss by 92%, 97%, and 98% showing that their combination brings better results despite the solo-microorganism inoculation, also affecting raindrop splash erosion on a short time scale (Kheirfam et al., 2017a). These results highlight the high applicability of the native microbial inoculum to induce BSC formation because their innate adaptation to the environmental factors encountered ensures their attachment to the soil. The observed effects on soil characteristics and hydrological processes due to different bacteria and cyanobacteria inoculums represent a promising tool in the restoration of degraded areas (Chamizo et al., 2020a). Due to the rapid benefits that bacteria bring to the soil and the long-term effects of cyanobacteria, the dual bacteria-cyanobacteria inoculum is a highly successful inoculum combination (Sadeghi et al., 2017). The combined cyanobacteria-bacteria inoculum determines an increase in soil particle aggregation, nutrient availability, and reduction of soil and sediment loss compared to non-inoculated control soils (Chamizo et al., 2018, 2019; Kheirfam et al., 2017a, 2020).

All these experiments considered as erosion losses the soil resulting from interrill erosion generated by overland flow. Differently, some authors placed a portion of soil covered by BSCs downstream of a flume with a known inflow, and soil loss is measured (Gao et al., 2020b; Zhang et al., 2020). Although attempting to create channelized erosion and induce rill erosion, the small plot sizes with BSCs do not permit rill formation (Loch, 1996). Despite the different characteristics of these studies, also in these cases, soil erosion is to be considered as interrill erosion due to overland flow.

Only one study investigated the impact of BSCs on rill erosion. Jafarpoor et al. (2022) observed that BSCs reduce soil loss by reducing runoff velocity and influencing rill formation. Specifically, comparing plots (6 × 1 × 0.5 m) with bare soil and cyanobacterial BSCs subjected to rainfall simulation (50 ± 7 mm h^{-1}), rills began to form 3.23 min and 37.05 min after the beginning of the rainfall simulation, respectively (Jafarpoor et al., 2022). In addition, rills formed on plots with cyanobacterial BSCs are shorter, narrower, and shallower than those formed on bare soil (Jafarpoor et al., 2022). Since rill formation itself leads to soil loss and enhances sediment production, the effects provided by cyanobacterial BSCs on the formation and properties of rills also help to mitigate water erosion. Although the evidence provided by Jafarpoor et al. (2022) indicate that cyanobacterial BSCs are effective in reducing soil losses due to rill erosion, even by limiting their formation and sizes, the paucity of rill erosion studies represents a gap that must be filled to evaluate deeply the role of BSCs in soil erosion processes.

Several studies investigated the influence of BSCs on soil erosion at plot size scale involving plots with a maximum size of 1 m^2. However, the analysis of soil erosion at higher dimensional scales may include phenomena and variables that are not detectable at smaller scales. From this perspective, some authors have simulated rainfall or runoff on plots larger than 1 m^2 but <10 m^2 (Bu et al., 2015; Jafarpoor et al., 2022; Lázaro and Mora, 2014), while others have analyzed plots larger than 10 m^2 (Kheirfam et al., 2020; Sadeghi et al., 2020a; Yang et al., 2022).

Studies carried out at scales larger than 1 m^2 have shown a reduction in soil loss due to the effects of BSCs, but the number of works is limited to fully understand the role of BSCs on erosive processes at hillslope or catchment scale.

The BSC effect on soil erosion processes is unambiguous, as all microorganisms, creating patches on soil surface, can reduce the erosive process. Moreover, the capacity of protecting the soil surface follows the gradient of the successional series and reaches its maximum at the most evolved successional stage, which is the closest to the vegetation.

7. Microbial inoculums to induce BSC formation

The application of bacterial inoculums to induce BSC formation in soils represents a powerful tool to protect soil from water erosion and face desertification processes (Chamizo et al., 2018; Kheirfam et al., 2017a; Sadeghi et al., 2017, 2020a).

The detection of suitable bacteria, including cyanobacteria, useful for soil and water conservation strategies consists of the following steps (Rossi et al., 2017, 2022): (i) extraction and isolation of microorganisms from a given soil sample; (ii) purification and identification of microorganisms; (iii) selection of the most suitable microorganisms for inoculation; (iv) propagation and inoculation of selected bacteria on the soil.

Soil microorganisms are extracted from soil sample and isolated in a Petri dish filled with culture medium obtaining non pure colonies of alive microorganisms The isolated colonies are then purified to obtain pure cultures (i.e., composed by a single strain). Extraction, isolation, and purification phases permit to obtain a strain collection of soil

Table 5
Phases, instruments and time required to obtain inoculum starting from a soil sample.

Phases	Procedure	Instruments	Time required	References
1) Soil sample preparation	**1.1)** In sterility, crushing soil samples with a mortar to break up soil aggregates. **1.2)** Sieving soil samples with a 2 mm mesh sieve. **1.3)** Air drying for 24 h.	Mortar, mesh sieve, laminar hood.	24 h	Kheirfam et al. (2017a) Sadeghi et al. (2017, 2020b, 2021)
2) Extraction and Isolation	**2.1)** Preparation of the serial dilutions of the soil sample. The first dilution is made adding 10–25 g of soil samples in pyrophosphate solution (0.16% *w/v*) to break up soil aggregates that can trap microorganisms. The following serial dilutions will be prepared in Ringer's solution (NaCl 0.9% *w/v*), **2.2)** Plating in cultivation medium. For liquid culture media procedure provides for pipetting aliquots (1 mL) of each dilution into one or more tubes containing the culture medium. For agarized culture media, two main procedures can be used: plating by inclusion (or diffusion), superficial plating. **2.3)** Microbiological media and incubation conditions. **2.3.1)** Bacteria **Soil Extract Medium (SEM)** incubated aerobically at 30 °C for 48 h. **Nutrient Agar (NA)** incubated aerobically at 30 °C for 48 h. **Bacteria Medium (BM)** incubated aerobically at 30 °C for 72 h. **2.3.2)** Cyanobacteria **Blue Green Medium (BG-11)** incubated aerobically at 30 °C for 48 h. AMA (enriched sea water) incubated aerobically at 30 °C for 48 h. ASNIII incubated aerobically at 30 °C for 48 h. **2.3.3)** Actinomycetes **Actinomycetes Isolation Agar (AIA)** incubated aerobically at 30 °C for 48 h. **2.3.4)** Fungi **Fungi Culture Media (FCM)** incubated at 30 °C for 7 days.	Tubes, pyrophosphate solution (0.16% *w/v*), Ringer's solution (NaCl 0.9% w/v), Petri dishes, thermostated incubator, culture media.	1 h + incubation time (48 h – 7 days)	Chamizo et al. (2012a, 2018) Kheirfam et al. (2017a, 2020) Rossi et al. (2022) Whitton and Potts (2012)
3) Purification	The isolated bacteria are removed with a microbiological loop and streaked on a Petri dish containing the same agar medium used for the growing of the isolated colonies. A purification streak method is performed to obtain pure cultures. These cultures consist of a single type of cell and are subsequently placed to grow in a liquid medium, generally corresponding to the growing agar medium or another optimal medium for growth. This process is repeated until bacterial strains are purified.	microbiological loop, petri dishes, culture media.	1–2 min for streaking for each strain; then incubation time (48 h - 7 days)	Chamizo et al. (2012a, 2018) Kheirfam et al. (2017a, 2020) Rossi et al. (2022) Whitton and Potts (2012)
4) Morphological and biochemical identification	The phenotypic characterization permits the differentiation of various isolates into groups. Microscopic observation of cellular morphologies, Gram test with KOH (3%) and the catalase enzyme with H_2O_2 (5%) are performed. The preliminary identification based on morphological and biochemical characteristics conducted according to Bergey's bacteriological guidelines can indicate the most probable genus.	optical microscope, slides, coverslides, mineral oil, distilled water, KOH (3%), H_2O_2 (5%)	3–5 min for each strain	Bergey (1994)
5) Genetic identification	**5.1)** DNA extraction after overnight growth, **5.2)** DNA amplification by the Randomly Amplified of Polymorphic DNA (RAPD) - PCR technique, **5.3)** Analysis of the DNA polymorphic profile, **5.4)** Analysis of the gene sequence of the 16S or 23S RNA ribosomal subunit, **5.5)** Isolate identification by comparison of the isolate sequences with the sequences stored in online databases.	culture medium broth, centrifuge, extraction kit, primers, PCR kit.	Dependent by protocol applied (~5 h for each phase)	Dojani et al. (2014) Garcia-Pichel et al. (2001)
6) Selection of microorganism suitable to inoculation	Microorganisms are selected based on potential viability (evaluated as growth rate) and microbial activity at different soil temperatures, pH, and humidity. The production of EPSs, the Nitrogen and Carbon fixation, water retention, the ability to aggregate soil particles, easy isolation, and	–	–	Chamizo et al. (2012a, 2018) Kheirfam et al. (2020) Kheirfam et al. (2017a)

(*continued on next page*)

Table 5 (*continued*)

Phases	Procedure	Instruments	Time required	References
	propagation, and non-pathogenicity represents other selection criteria.			Sadeghi et al. (2021)
7) Propagation and inoculation	The microorganisms are propagated until the reach of the required concentration and centrifuged in order to separate microorganisms from the culture medium. Finally, inoculation is performed adding distilled water and spraying the inoculum on the soil surface.	conical tubes 50 mL, various volume sterile flask (100–2000 mL), sterile distilled water, centrifuge, sprayer.	Dependent by microorganism growing velocity (~5 days)	Kheirfam et al. (2020) Kheirfam et al. (2017a) Sadeghi et al. (2017, 2021)

microorganisms that can be potentially inoculated. The identification phase includes phenotypic and genotypic tests and permits to evaluate the physiological characteristics of the collected microorganisms. Strain selection is a screening phase in which the microorganisms are selected considering the inoculation aims. The propagation is necessary to increase microbial cell densities in terms of the Colony Forming Unit (CFU). A CFU is a unit of microorganisms able to produce a single colony on a given agar culture medium (Ujváry, 2010). Finally, the microorganisms at the appropriate level (expressed as CFU/mL) are inoculated in soil. Different inoculum concentrations can be applied (e.g., 5 g of dry weight m^{-2} (Chamizo et al., 2020b); 0.232–0.294 g m^{-2} (Kheirfam, 2020); 30 mg cell dry weight in 92 mm Petri dishes (Mugnai et al., 2018); 1.5 g L^{-1} (Sadeghi et al., 2020b) and 2 g L^{-1} of fresh biomass concentration (Román et al., 2021)). A description of phases, instruments and time required to obtain inoculum starting from a soil sample is summarized in Table 5.

Inoculation of cyanobacteria (*Nostoc* spp., *Oscillatoria* spp., and *Lyngbya* spp.) and bacteria (mainly *Bacillus subtilis* strain and *Azotobacter* spp.) and the combination of both can significantly modify soil hydrological response. Sadeghi et al. (2017) demonstrated that cyanobacteria inoculation increases the time to start runoff (38–205%), and time to reach runoff peak (48–52%) and decreases runoff volume (48–86%) in comparison to that registered for bare soils.

Unlike in vitro (laboratory) conditions, the inoculum application in the open field can be characterized by limited BSC growth due to the diversity of BSCs employed and, especially, to the environmental conditions encountered and the growing conditions requested by the microorganisms (Chamizo et al., 2018; Román et al., 2021). Performing the inoculation with microorganisms isolated from the same site might allow, to a certain extent, the adaptation of the inoculum and their natural overcoming of the physicochemical and biological barriers (Chamizo et al., 2018; Sadeghi et al., 2021). The choice of the microorganisms to be inoculated is just one of several variables (e.g., seasonality of inoculum, precipitation pattern, and addition of supplements) that affect whether the inoculation process is successful or not.

The seasonality of inoculum can determine the success or failure of microbial inoculum techniques. Late autumn or early winter must be considered, theoretically, the best time to apply inoculum, but choosing of winter season does not permit the inoculum to develop due to freeze-thaw dynamics (Young et al., 2019). Otherwise, applying inoculum in summer does not permit BSC growth due to lack of water and high temperature, and light stress (Pen-Mouratov et al., 2011; Young et al., 2019). In addition, an increase in vegetation cover on inoculated plots during the spring season suggested a synergic relationship between plants and microbial communities (Kheirfam et al., 2020; Sadeghi et al., 2020a). Despite this overall information, the seasonality of inoculum should be defined according to growing conditions needed by chosen microorganisms and to the environmental conditions of the site subjected to inoculum.

Rainfall precipitation pattern and water availability influence microbial growth of inoculum, and a reduction in BSC growth is observed in areas with low precipitation and low water content (Zhou et al., 2020b). When low precipitation occurs and soil water content is limiting, the weekly addition of water on inoculated soil plots allows for filling up the water lack and to obtain higher BSC growth than BSCs without water addition (Young et al., 2019). Some authors (Bu et al., 2014; Román et al., 2021) tested different watering regimes and found that BSCs are limited by water deficit and that watering can enhance their development. However, at the same time, BSCs are not fostered by more frequent watering regimes. Treatments, such as irrigation and soil stabilization, increase the recovery and development of BSCs. Under laboratory conditions, BSC growth was positively affected by irrigation and the addition of organic sources such as straw (Cosentino et al., 2006). A treatment with amendments combined with cyanobacteria and vascular seedlings in China has shown to be a successful restoration procedure (Zhou et al., 2020b).

Microbial inoculation represents an economical alternative to the application of classical soil stabilizers (application cost of 350 USD ha^{-1} (cyanobacteria inoculum) vs 8000 USD ha^{-1} (biochar), 750 USD ha^{-1} (straw mulch), 150 USD ha^{-1} (manure), and 1000 USD ha^{-1} (polyacrylamide) (Sadeghi et al., 2020a) considering that BSCs can last in fields for at least 18 months (Bowker et al., 2020). However, Kidron et al. (2020a) suggested that, in case of light-moderate disturbance, it may be more financially convenient only reducing the disturbance than inducing BSC restoration by inoculation.

To improve the success of inoculation techniques several authors (Fick et al., 2019; Kheirfam, 2020; Kheirfam et al., 2017a, 2017b) tested the addition of nutritive supplements and soil stabilizers to the microbial inoculum. The addition of nutrient supplements, such as supplement B4, to bacteria and cyanobacteria inoculum, improves microbial growth and Carbon sequestration (by 23-folds) compared to control conditions (Kheirfam, 2020; Kheirfam et al., 2017a, 2017b). Soil stabilizers are organic or inorganic substances that increase soil stability when applied on soil surfaces and can also be used jointly with microbial inoculum (Fick et al., 2019; Jafarpoor et al., 2022). For instance, psyllium-based soil stabilizer enhances soil particle aggregation and reduces runoff and sediment yield only on plots where soil stabilizer is combined with microbial inoculum (Fick et al., 2019). Soil stabilizers are effective immediately after application, while BSCs need time to establish and also more time to exert their ecological functions. The application of soil stabilizers improves BSC development and growth and reduces the time required for BSCs to exert their functions. The application of soil stabilizers combined with microbial inoculum guarantees soil erosion protection at short and long-time spans (Fick et al., 2019). The combination of various supplements (water, nutritive supplements, soil stabilizers) with cyanobacteria and bacteria inoculums further enhances BSC inoculum effectiveness. The addition of optimal supplements seems to be defining the success rates and improve soil erosion protection.

8. Research needs

The detection and identification of BSCs have evolved in recent years, and this topic is still arising. Understanding how BSCs respond to the climate gradient is crucial. Parallelly, an in-depth analysis of the BSC's tolerance and recovery to environmental or anthropic stresses would permit a clearer evaluation of the BSC's suitability as a component of restoration techniques. Genotypic analyses applied on BSC communities must be intended as a required step for defining the species composition and to discriminate the behavior of the different

microorganisms and their influence on the ecosystem. The microbial image in a given moment is important to retrieve information on the health status of the ecosystem object of investigation. The monitoring of the site over time allows for evaluating the evolution of the microbial community under study, and the characterization of BSC in large areas and different geographical regions is important to understand how these communities react to different ecosystems and different disturbance factors. In particular, the absence of one or more species that fulfill an ecological function can suggest the disappearance of the ecological function associated with that microbial group, and globally how this affects the health status of the ecosystem. The isolation of BSC microorganisms is preliminary to obtain strain libraries for future applications in soil restoration strategies.

The wide range of metabolic processes carried out by BSCs and the cross-interactions between these processes and the soil physical, chemical, and hydrological characteristics make further investigation necessary to clarify the role of these microorganisms in natural ecosystems and how this knowledge can be used to design rehabilitation techniques of degraded areas. Finally, further studies are needed to recognize the microorganisms appropriate to restore degraded areas.

9. Conclusions

BSCs constitute a very complex community of microorganisms able to influence in various ways the processes of the ecosystem in which they live. Their environmental importance has led to a growing number of studies on BSC characterization, their influence on soil physical and chemical characteristics, hydrology and erosion processes, their importance as bioindicators and, finally, their applicability to restore degraded areas.

The detection methods allow a fast identification and classification of BSC into main group or classes, while hindering the heterogeneity of their composition. In particular, remote sensing represents a useful approach which permits the identification and mapping of different BSCs on ecosystem scale. However, the loss of information about the microbial composition of BSC, as result of their classification, lead to consider the BSCs as homogeneous despite their intrinsic heterogeneity. These classification approaches lead to the incapacity of discriminate the different behavior reported in the literature.

BSCs improve the soil physic-chemical characteristics (e.g., soil stability, fertility) and better results are related to the BSC evolution along the successional series (from ESS-BSC to LSS-BSC). Under limiting environmental conditions, in which only ESS-BSCs can settle, an increase of soil stability and fertility is also guaranteed. Consequently, bacteria and cyanobacteria can be considered the most valuable BSC able to provide benefits in limiting and degraded conditions. Moreover, they represent a valuable BSC for their short recovery times (5–10 years) and their high economic efficiency.

Notwithstanding numerous investigations have been made to ascertain how BSCs affect soil hydrology, there is still no consensus on the role they provide. In fact, many factors do not allow for explaining the divergence of the literature results on soil hydrology. For sure, the intrinsic heterogeneity of BSCs influences the interaction between soil and water. Moreover, the measurement scale and the experimental setup and apparatus (patches of vegetation, surface roughness imposed by vascular plants, or channelized flow that influences runoff more at larger spatial scales) affect the hydrological results. These differences could have determined the failure of past research finding a uniform outcome and could represent a limit determining the best choice to guarantee optimal results in terms of soil hydrology.

Also, it is widely recognized that BSCs have an anti-erosive effect. The BSC anti-erosive behavior is common to all microorganisms and the intensity of the soil protection follows the successional series. In that sense, mosses represent the best BSC type as they produce the most similar effects as compared to those given by the vegetation.

At the current state, the analysis of the available literature does not provide answers on the connection between the bioindicator functions and the intensity of the examined phenomenon.

Microbial inoculation might be a successful technique to control and counteract soil degradation processes. Bacteria, and cyanobacteria showed high capability to improve soil erosion resistance, as well as soil chemical and physical characteristics. Most of the microbial inoculation investigations were done using re-inoculated microorganisms that were isolated from the same site as they are already adapted to the investigated conditions and have already biological interactions with the soil biotic community.

Notwithstanding the numerous studies available in the literature, various knowledge gaps still exist, as the environmental, and anti-erosive roles played by the various microorganisms of BSCs should be completely clarified. However, the existing literature supports the idea that BSCs represent a valid tool to be used in degraded areas restoration. In particular, the main literature findings are that i) their effects on the soil physic-chemical characteristics improve along their successional series; ii) bacteria and cyanobacteria can be considered the most valuable BSC in limiting and degraded conditions (sediment concentration in the runoff reduced by 87% in comparison to bare soils, cost of 350 USD ha^{-1}, and a recovery time of 5–10 years); iii) the intrinsic heterogeneity of BSCs does not allow for explaining the divergence of the literature results on soil hydrology; and iv) mosses are the best BSC anti-erosive type as they produce the most similar effects as compared to vegetation. Consequently, these research results should be considered in field practical applications to mitigate erosion processes and improve soil characteristics.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgements

All authors set up the research, analyzed and interpreted the results and contributed to write the paper. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

References

Ahmadian, A., Ehn, M., Hober, S., 2006. Pyrosequencing: history, biochemistry and future. Clin. Chim. Acta 363, 83–94. https://doi.org/10.1016/j.cccn.2005.04.038.
Allen, C.D., 2010. Biogeomorphology and biological soil crusts: a symbiotic research relationship. Géomorphol. Relief Processus Environ. 16, 347–358.
Barger, N.N., Herrick, J.E., Van Zee, J., Belnap, J., 2006. Impacts of biological soil crust disturbance and composition of C and N loss from water erosion. Biogeochem. 77, 247–263. https://doi.org/10.1007/s10533-005-1424-7.
Belnap, J., 1993. Recovery rates of cryptobiotic crusts: inoculant use and assessment methods. The Great Basin Naturalist 53, 89–95.
Belnap, J., 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. Hydrol. Process. 20, 3159–3178. https://doi.org/10.1002/hyp.6325.
Belnap, J., Eldridge, D.J., 2003. Disturbance and recovery of biological soil crusts. In: Belnap, J., Lange, O.L. (Eds.), Biological Soil Crusts: Structure, Function and Management. Springer, Berlin, pp. 363–383. https://doi.org/10.1007/978-3-642-56475-8_27.
Belnap, J., Lange, O.L., 2003. Biological Soil Crusts: Structure, Function, and Management. Springer, Berlin. https://doi.org/10.1007/978-3-642-56475-8.
Belnap, J., Welter, J.R., Grimm, N.B., Barger, N., Ludwig, J.A., 2005. Linkages between microbial and hydrologic processes in arid and semiarid watershed. Ecol. 86, 298–307. https://doi.org/10.1890/03-0567.
Belnap, J., Phillips, S.L., Witwicki, D.L., Miller, M.E., 2008. Visually assessing the level of development and soil surface stability of cyanobacterially dominated biological soil crusts. J. Arid Environ. 72, 1257–1264. https://doi.org/10.1016/j.jaridenv.2008.02.019.

Belnap, J., Wilcox, B., Van Scoyoc, M.W., Phillips, S.L., 2013. Successional stage of biological soil crusts: an accurate indicator of ecohydrological conditions. Ecohydrol. 6, 474–482. https://doi.org/10.1002/eco.1281.

Beraldi-Campesi, H., Garcia-Pichel, F., 2011. The biogenicity of modern terrestrial roll-up structures and its significance for ancient life on land. Geobiol. 9, 10–23. https://doi.org/10.1111/j.1472-4669.2010.00258.x.

Beraldi-Campesi, H., Hartnett, H.E., Anbar, A., Gordon, G.W., 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. Geobiol. 7, 348–359. https://doi.org/10.1111/j.1472-4669.2009.00204.x.

Bergey, D.H., 1994. Bergey's Manual of Determinative Bacteriology, ninth ed. Lippincott Williams & Wilkins, Philadelphia.

Billings, S.A., Schaeffer, S.M., Evans, R.D., 2003. Nitrogen fixation by biological soil crusts and heterotrophic bacteria in an intact Mojave Desert ecosystem with elevated CO2 and added soil carbon. Soil Biol. Biochem. 35, 643–649. https://doi.org/10.1016/S0038-0717(03)00011-7.

Bowker, M.A., 2007. Biological soil crust rehabilitation in theory and practice: an underexploited opportunity. Restor. Ecol. 15, 13–23. https://doi.org/10.1111/j.1526-100X.2006.00185.x.

Bowker, M.A., Belnap, J., Chaudhary, V.B., Johnson, N.C., 2008. Revisiting classic water erosion models in drylands: the strong impact of biological soil crusts. S. Biol. Biochem. 40, 2309–2316. https://doi.org/10.1016/j.soilbio.2008.05.008.

Bowker, M.A., Belnap, J., Büdel, B., Sannier, C., Pietrasiak, N., Eldridge, D.J., Rivera-Aguilar, V., 2016. Controls on distribution patterns of biological soil crusts at micro- to global scales. In: Weber, B., Büdel, B., Belnap, J. (Eds.), Biological Soil Crusts: An Organizing Principle in Drylands. Springer, Cham, pp. 173–197. https://doi.org/10.1007/978-3-319-30214-0_10.

Bowker, M.A., Reed, S.C., Maestre, F.T., Eldridge, D.J., 2018. Biocrusts: the living skin of the earth. Plant Soil 429, 1–7. https://doi.org/10.1007/s11104-018-3735-1.

Bowker, M.A., Antoninka, A.J., Chuckran, P.F., 2020. Improving field success of biocrust rehabilitation materials: hardening the organisms or softening the environment? Restor. Ecol. 28, S177–S186. https://doi.org/10.1111/rec.12965.

Bu, C., Wu, S., Yang, Y., Zheng, M., 2014. Identification of factors influencing the restoration of cyanobacteria-dominated biological soil crusts. PLoS One 9, e90049. https://doi.org/10.1371/journal.pone.0090049.

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

Büdel, B., Darienko, T., Deutschewitz, K., Dojani, S., Friedl, T., Mohr, K.I., Salisch, M., Reisser, W., Weber, B., 2009. Southern african biological soil crusts are ubiquitous and highly diverse in drylands, being restricted by rainfall frequency. Microb. Ecol. 57, 229–247. https://doi.org/10.1007/s00248-008-9449-9.

Bullard, J.E., Ockelford, A., Strong, C., Aubault, H., 2018. Effects of cyanobacterial soil crusts on surface roughness and splash erosion. J. Geophys. Res.: Biogeosci. 123, 3697–3712. https://doi.org/10.1029/2018JG004726.

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. J. Geophys. Res.: Biogeosci. 127 https://doi.org/10.1029/2021JG006652 e2021JG006652.

Cantón, Y., Solé-Benet, A., Domingo, F., 2004. Temporal and spatial patterns of soil moisture in semiarid badlands of SE Spain. J. Hydrol. 285, 199–214. https://doi.org/10.1016/j.jhydrol.2003.08.018.

Cantón, Y., Solé-Benet, A., de Vente, J., Boix-Fayos, C., Calvo-Cases, A., Asensio, C., Puigdefábregas, J., 2011. A review of runoff generation and soil erosion across scales in semi-arid South-Eastern Spain. J. Arid Environ. 75, 1254–1261. https://doi.org/10.1016/j.jaridenv.2011.03.004.

Cantón, Y., Román, J.R., Chamizo, S., Rodríguez-Caballero, E., Moro, M.J., 2014. Dynamics of organic carbon losses by water erosion after BSCs removal. J. Hydrol. Hydromech. 62, 258–268. https://doi.org/10.2478/johh-2014-0033.

Cantón, Y., Chamizo, S., Rodriguez-Caballero, E., Lázaro, R., Roncero-Ramos, B., Román, J.R., Solé-Benet, A., 2020. Water regulation in cyanobacterial BSCs from drylands: negative impacts of anthropogenic disturbance. Water 12, 720. https://doi.org/10.3390/w12030720.

Carson, J.K., Gonzalez-Quiñones, V., Murphy, D.V., Hinz, C., Shaw, J.A., Gleeson, D.B., 2010. Low pore connectivity increases bacterial diversity in soil. Appl. Environ. Microbiol. 76, 3936–3942. https://doi.org/10.1128/AEM.03085-09.

Castillo-Monroy, A.P., Maestre, F.T., Delgado-Baquerizo, M., Gallardo, A., 2010. Biological soil crusts modulate nitrogen availability in semi-arid ecosystems: insights from a Mediterranean grassland. Plant Soil 333, 21–34. https://doi.org/10.1007/s11104-009-0276-7.

Chamizo, S., Cantón, Y., Lázaro, R., Solè-Benet, A., Domingo, F., 2012a. Crust composition and disturbance drive infiltration through biological soil crusts in semiarid ecosystems. Ecosyst. 15, 148–161. https://doi.org/10.1007/s10021-011-9499-6.

Chamizo, S., Stevens, A., Cantón, Y., Miralles, I., Domingo, F., Van Wesemael, B., 2012b. Discriminating soil crust type, development stage and degree of disturbance in semiarid environments from their spectral characteristics. Eur. J. Soil Sci. 63, 42–53. https://doi.org/10.1111/j.1365-2389.2011.01406.x.

Chamizo, S., Cantón, Y., Domingo, F., Belnap, J., 2013. Evaporative losses from soils covered by physical, and different types of biological soil crusts. Hydrol. Process. 27, 324–332. https://doi.org/10.1002/hyp.8421.

Chamizo, S., Cantón, Y., Rodrìguez-Caballero, E., Domingo, F., 2016. BSCs positively affect the soil water balance in semiarid ecosystems. Ecohydrol. 9, 1208–1221. https://doi.org/10.1002/eco.1719.

Chamizo, S., Rodríguez-Caballero, E., Román, J.R., Cantón, Y., 2017. Effects of BSCs on soil erosion and organic carbon losses under natural rainfall. Catena 148, 117–125. https://doi.org/10.1016/j.catena.2016.06.017.

Chamizo, S., Mugnai, G., Rossi, F., Certini, G., De Philippis, R., 2018. Cyanobacteria inoculation improves soil stability and fertility on different textured soils: gaining insights for applicability in soil restoration. Front. Environ. Sci. 6, 49. https://doi.org/10.3389/fenvs.2018.00049.

Chamizo, S., Adessi, A., Mugnai, G., Simiani, A., De Philippis, R., 2019. Soil type and cyanobacteria species influence the macromolecular and chemical characteristics of the polysaccharidic matrix in induced BSCs. Microb. Ecol. 78, 482–493. https://doi.org/10.1007/s00248-018-1305-y.

Chamizo, S., Adessi, A., Certini, G., De Philippis, R., 2020a. Cyanobacteria inoculation as a potential tool for stabilization of burned soils. Restor. Ecol. 28, S106–S114. https://doi.org/10.1111/rec.13092.

Chamizo, S., Adessi, A., Torzillo, G., De Philippis, R., 2020b. Exopolysaccharide features influence growth success in BSCs-forming cyanobacteria, moving from liquid culture to sand microcosms. Front. Microbiol. 11, 568224 https://doi.org/10.3389/fmicb.2020.568224.

Chen, J., Blume, H.P., Beyer, L., 2000. Weathering of rocks induced by lichen colonization—a review. Catena 39, 121–146. https://doi.org/10.1016/S0341-8162(99)00085-5.

Chen, J., Zhang, M.Y., Wang, L., Shimazaki, H., Tamura, M., 2005. A new index for mapping lichen-dominated biological soil crusts in desert areas. Remote Sens. Environ. 96, 165–175. https://doi.org/10.1016/j.rse.2005.02.011.

Chen, Y., Lian, B., Yin, Z., Tang, Y., 2014. Weathering of carbonate rocks by biological soil crusts in karst areas. J. Earth Sci. 25, 662–667. https://doi.org/10.1007/s12583-014-0455-1.

Chilton, A.M., Neilan, B.A., Eldridge, D.J., 2018. BSCs morphology is linked to marked differences in microbial community composition. Plant Soil 429, 65–75. https://doi.org/10.1007/s11104-017-3442-3.

Chou, H.H., Holmes, M.H., 2001. DNA sequence quality trimming and vector removal. Bioinform. 17, 1093–1104. https://doi.org/10.1093/bioinformatics/17.12.1093.

Coe, K.K., Belnap, J., Sparks, J.P., 2012. Precipitation-driven carbon balance controls survivorship of desert biocrust mosses. Ecol. 93, 1626–1636. https://doi.org/10.1890/11-2247.1.

Collier, E.A., Perroy, R.L., Reed, S.C., Price, J.P., 2022. Mapping biological soil crusts in a hawaiian dryland. Int. J. Remote Sens. 43, 484–509. https://doi.org/10.1080/01431161.2021.2003904.

Concostrina-Zubiri, L., Arenas, J.M., Martínez, I., Escudero, A., 2019. Unassisted establishment of biological soil crusts on dryland road slopes. Web Ecol. 19, 39–51. https://doi.org/10.5194/we-19-39-2019.

Cosentino, D., Chenu, C., Le Bissonnais, Y., 2006. Aggregate stability and microbial community dynamics under drying–wetting cycles in a silt loam soil. Soil Biol. Biochem. 38, 2053–2062. https://doi.org/10.1016/j.soilbio.2005.12.022.

Dahal, B., Nanda Kafle, G., Perkins, L., Brözel, V.S., 2017. Diversity of free-living nitrogen fixing Streptomyces in soils of the badlands of South Dakota. Microbiol. Res. 195, 31–39. https://doi.org/10.1016/j.micres.2016.11.004.

Davenport, D.W., Breshears, D.D., Wilcox, B.P., Allen, C.D., 1998. Sustainability of pinon-juniper ecosystems–a unifying perspective of soil erosion thresholds. Rangel. Ecol. Manag. / J. Range Manag. Archives 51, 231–240.

De la Puente-Redondo, V.D., Del Blanco, N.G., Gutierrez-Martin, C.B., Garcia-Pena, F.J., Ferri, E.R., 2000. Comparison of different PCR approaches for typing of Francisella tularensis strains. J. Clin. Microbiol. 38, 1016–1022. https://doi.org/10.1128/JCM.38.3.1016-1022.2000.

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 Biol. Biochem. 141, 107665 https://doi.org/10.1016/j.soilbio.2019.107665.

DeJong, J.T., Fritzges, M.B., Nüsslein, K., 2006. Microbially induced cementation to control sand response to undrained shear. J. Geotech. Geoenviron. Eng. 132, 1381–1392. https://doi.org/10.1061/(ASCE)1090-0241(2006)132:11(1381).

DeSantis, T.Z., Hugenholtz, P., Larsen, N., Rojas, M., Brodie, E.L., Keller, K., Huber, T., Dalevi, D., Hu, P., Andersen, G.L., 2006. Greengenes, a chimera-checked 16S rRNA gene database and workbench compatible with ARB. Appl. Environ. Microbiol. 72, 5069–5072. https://doi.org/10.1128/AEM.03006-05.

Dojani, S., Kauff, F., Weber, B., Büdel, B., 2014. Genotypic and phenotypic diversity of cyanobacteria in biological soil crusts of the Succulent Karoo and Nama Karoo of southern Africa. Microb. Ecol. 67, 286–301. https://doi.org/10.1007/s00248-013-0301-5.

Dorn, R.I., 2021. Assessing biological soil crusts as agents of Ca–Mg silicate dissolution and CO2 sequestration. Phys. Geogr. 42, 529–541. https://doi.org/10.1080/02723646.2021.1919379.

Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Budel, B., Andreae, M.O., Poschl, U., 2012. Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. Nat. Geosci. 5, 459–462. https://doi.org/10.1038/ngeo1486.

Eldridge, D.J., Rosentreter, R., 1999. Morphological groups: a framework for monitoring microphytic crusts in arid landscapes. J. Arid Environ. 41, 11–25. https://doi.org/10.1006/jare.1998.0468.

Eldridge, D.J., Reed, S., Travers, S.K., Bowker, M.A., Maestre, F.T., Ding, J., Havrilla, C., Rodriguez-Caballero, E., Barger, N., Weber, B., Antoninka, A., Belnap, J., Chaudhary, B., Faist, A., Ferrenberg, S., Huber-Sannwald, E., Malam Issa, O., Zhao, Y., 2020. The pervasive and multifaceted influence of BSCs on water in the world's drylands. Glob. Chang. Boil. 26, 6003–6014. https://doi.org/10.1111/gcb.15232.

Ewing, B., Hillier, L., Wendl, M.C., Green, P., 1998. Base-calling of automated sequencer traces usingPhredI. Accuracy assessment. Genome Res. 8, 175–185. https://doi.org/10.1101/gr.8.3.175.
Faist, A.M., Herrick, J.E., Belnap, J., Van Zee, J.W., Barger, N.N., 2017. Biological soil crusts and disturbance controls on surface hydrology in a semi-arid ecosystem. Ecosphere 8, e01691. https://doi.org/10.1002/ecs2.1691.
Felde, V.J., Peth, S., Uteau-Puschmann, D., Drahorad, S., Felix-Henningsen, D., 2014. Soil microstructure as an under-explored feature of biological soil crust hydrological properties: case study from NW Negev Desert. Biodivers. Conserv. 23, 1687–1708. https://doi.org/10.1007/s10531-014-0693-7.
Felde, V.J., Drahorad, S.L., Felix-Henningsen, P., Hoon, S.R., 2018. Ongoing oversanding induces biological soil crust layering–A new approach for biological soil crust structure elucidation determined from high resolution penetration resistance data. Geoderma 313, 250–264. https://doi.org/10.1016/j.geoderma.2017.11.022.
Ferrenberg, S., Reed, S.C., Belnap, J., 2015. Climate change and physical disturbance cause similar community shifts in biological soil crusts. Proc. Natl. Acad. Sci. 112, 12116–12121. https://doi.org/10.1073/pnas.1509150112.
Fick, S.E., Barger, N.N., Duniway, M.C., 2019. Hydrological function of rapidly induced BSCs. Ecohydrol. 12, e2089 https://doi.org/10.1002/eco.2089.
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. Biogeochem. 101, 165–176. https://doi.org/10.1007/s10533-010-9464-z.
Fischer, T., Yair, A., Veste, M., Geppert, H., 2013. Hydraulic properties of biological soil crusts on sand dunes studied by 13C-CP/MAS-NMR: a comparison between an arid and a temperate site. Catena 110, 155–160. https://doi.org/10.1016/j.catena.2013.06.002.
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 Biol. Biochem. 105, 49–58. https://doi.org/10.1016/j.soilbio.2016.11.009.
Gao, L., Bowker, M.A., Sun, H., Zhao, J., Zhao, Y., 2020a. Linkages between BSCs development and water erosion and implications for erosion model implementation. Geoderma 357, 113973. https://doi.org/10.1016/j.geoderma.2019.113973.
Gao, L., Sun, H., Xu, M., Zhao, Y., 2020b. Biocrusts resist runoff erosion through direct physical protection and direct modification of soil properties. J. Soils Sediments 20, 133–142. https://doi.org/10.1007/s11368-019-02372-w.
García-Carmona, M., Arcenegui, V., García-Orenes, F., Mataix-Solera, J., 2020. The role of mosses in soil stability, fertility and microbiology six years after a post-fire salvage logging management. J. Environ. Manag. 262, 110287 https://doi.org/10.1016/j.jenvman.2020.110287.
Garcia-Pichel, F., López-Cortés, A., Nubel, U., 2001. Phylogenetic and morphological diversity of cyanobacteria in soil desert crusts from the Colorado Plateau. Appl. Environ. Microbiol. 67, 1902–1910. https://doi.org/10.1128/AEM.67.4.1902-1910.2001.
Garcia-Pichel, F., Felde, V.J.M.N.L., Drahorad, S.L., Weber, B., 2016. Microstructure and weathering processes within biological soil crusts. In: Weber, B., Büdel, B., Belnap, J. (Eds.), Biological Soil Crusts: An Organizing Principle in Drylands. Springer, Cham., Berlin, pp. 237–255. https://doi.org/10.1007/978-3-319-30214-0_13.
Grishkan, I., Kidron, G.J., 2013. Biocrust-inhabiting cultured microfungi along a dune catena in the western Negev Desert,Israel. Eur. J. Soil Biol. 56, 107–114. https://doi.org/10.1016/j.ejsobi.2013.03.005.
Grishkan, I., Lázaro, R., Kidron, G.J., 2019. Cultured microfungal communities in biological soil crusts and bare soils at the Tabernas Desert,Spain. Soil Syst. 3, 36. https://doi.org/10.3390/soilsystems3020036.
Guida, G., Palmeri, V., Settanni, L., Gaglio, R., Tolone, M., Ferro, V., 2022. Ability of soil bacterial composition as an indicator of levels of soil erosion in a badland. Int. J. Sediment Res. 37, 493–504. https://doi.org/10.1016/j.ijsrc.2022.02.001.
Jafari, M., Tavili, A., Zargham, N., Heshmati, G.A., Chahouki, M.Z., Shirzadian, S., Azarnuvand, H., Zehtabian, Gh.R., Sohrabi, M., 2004. Comparing some properties of crusted and uncrusted soils in Alagol Region of Iran. Pak. J. Nutr. 3, 273–277.
Jafarpoor, A., Sadeghi, S.H., Darki, B.Z., Homaee, M., 2022. Changes in morphologic, hydraulic, and hydrodynamic properties of rill erosion due to surface inoculation of endemic soil cyanobacteria. Catena 208, 105782. https://doi.org/10.1016/j.catena.2021.105782.
Jaffe, D.B., Butler, J., Gnerre, S., Mauceli, E., Lindblad-Toh, K., Mesirov, J.P., Zody, M.C., Lander, E.S., 2003. Whole-genome sequence assembly for mammalian genomes: Arachne 2. Genome Res. 13, 91–96. https://doi.org/10.1101/gr.828403.
Karnieli, A., 1997. Development and implementation of spectral crust index over dune sands. Int. J. Remote Sens. 18, 1207–1220. https://doi.org/10.1080/014311697218368.
Kheirfam, H., 2020. Increasing soil potential for carbon sequestration using microbes from biological soil crusts. J. Arid Environ. 172, 104022 https://doi.org/10.1016/j.jaridenv.2019.104022.
Kheirfam, H., Sadeghi, S.H.R., Darki, B.Z., Honaee, M., 2017a. Controlling rainfall-induced soil loss from small experimental plots through inoculation of bacteria and cyanobacteria. Catena 152, 40–46. https://doi.org/10.1016/j.catena.2017.01.006.
Kheirfam, H., Sadeghi, S.H.R., Homaee, M., Zarei-Darki, B., 2017b. Quality improvement of an erosion-prone soil through microbial enrichment. Soil Tillage Res. 165, 230–238. https://doi.org/10.1016/j.still.2016.08.021.
Kheirfam, H., Sadeghi, S.H.R., Zarei-Darki, B., 2020. Soil conservation in an abandoned agricultural rain-fed land through inoculation of cyanobacteria. Catena 187, 104341. https://doi.org/10.1016/j.catena.2019.104341.
Kidron, G.J., 2015. The role of crust thickness in runoff generation from microbiotic crusts. Hydrol. Process. 29, 1783–1792. https://doi.org/10.1002/hyp.10243.
Kidron, G.J., Monger, H.C., Vonshak, A., Conrod, W., 2012. Contrasting effects of microbiotic crusts on runoff in desert surfaces. Geomorphol. 139, 484–494. https://doi.org/10.1016/j.geomorph.2011.11.013.
Kidron, G.J., Xiao, B., Benenson, I., 2020a. Data variability or paradigm shift? Slow versus fast recovery of biological soil crusts-a review. Sci. Tot. Environ. 721, 137683 https://doi.org/10.1016/j.scitotenv.2020.137683.
Kidron, G.J., Wang, Y., Herzberg, M., 2020b. Exopolysaccharides may increase BSCs rigidity and induce runoff generation. J. Hydrol. 588, 125081 https://doi.org/10.1016/j.jhydrol.2020.125081.
Kidron, G.J., Lichner, L., Fischer, T., Starinsky, A., Or, D., 2022. Mechanisms for biocrust-modulated runoff generation–a review. Earth Sci. Rev. 231, 104100 https://doi.org/10.1016/j.earscirev.2022.104100.
Killham, K., 1994. Soil Ecology. Cambridge University Press.
Kunin, V., Copeland, A., Lapidus, A., Mavromatis, K., Hugenholtz, P., 2008. A bioinformatician's guide to metagenomics. Microbiol. Mol. Boil. Rev. 72, 557–578. https://doi.org/10.1128/MMBR.00009-08.
Ladrón de Guevara, M., Lázaro, R., Quero, J.L., Ochoa, V., Gozalo, B., Berdugo, M., Uclés, O., Escolar, C., Maestre, F.T., 2014. Simulated climate change reduced the capacity of lichen dominated BSCs to act as carbon sinks in two semi-arid Mediterranean ecosystems. Biodivers. Conserv. 23, 1787–1807. https://doi.org/10.1007/s10531-014-0681-y.
Lázaro, R., Cantón, Y., Solé-Benet, A., Bevan, J., Alexander, R., Sancho, L.G., Puigdefábregas, J., 2008. The influence of competition between lichen colonization, and erosion on the evolution of soil surfaces in the Tabernas badlands (SE Spain), and its landscape effects. Geomorphol. 102, 252–266. https://doi.org/10.1016/j.geomorph.2008.05.005.
Lázaro, R., Mora, J.L., 2014. Sediment content and chemical properties of water runoff on BSCs in drylands. Biol. 69, 1539–1544. https://doi.org/10.2478/s11756-014-0466-5.
Li, X., Hui, R., Tan, H., Zhao, Y., Liu, R., Song, N., 2021. Biocrust research in China: recent progress and application in land degradation control. Front. Plant Sci. 12, 751521 https://doi.org/10.3389/fpls.2021.751521.
Lichner, L., Hallett, P.D., Drongová, Z., Czachor, H., Kovacik, L., Mataix-Solera, J., Homolák, M., 2013. Algae influence the hydrophysical parameters of a sandy soil. Catena 108, 58–68. https://doi.org/10.1016/j.catena.2012.02.016.
Liu, L., Liu, Y., Hui, R., Xie, M., 2017. Recovery of microbial community structure of biological soil crusts in successional stages of Shapotou desert revegetation, Northwest China. Soil Biol. Biochem. 107, 125–128. https://doi.org/10.1016/j.soilbio.2016.12.030.
Loch, R.J., 1996. Using rill/interrill comparisons to infer likely responses of erosion to slope length: implications for land management. Soil Res. 34, 489–502. https://doi.org/10.1071/SR9960489.
López-Rodríguez, M.D., Chamizo, S., Cantón, Y., Rodriguez-Caballero, E., 2020. Identifying social–ecological gaps to promote BSCs conservation actions. Web Ecol. 20, 117–132. https://doi.org/10.5194/we-20-117-2020.
Maestre, F.T., Martín, N., Díez, B., Lopez-Poma, R., Santos, F., Luque, I., Cortina, J., 2006. Watering, fertilization, and slurry inoculation promote recovery of biological crust function in degraded soils. Microb. Ecol. 52, 365–377. https://doi.org/10.1007/s00248-006-9017-0.
Maestre, F.T., Escolar, C., de Guevara, M.L., Quero, J.L., Lázaro, R., Delgado-Baquerizo, M., Ochoa, V., Berdugo, M., Gozalo, B., Gallardo, A., 2013. Changes in BSCs cover drive carbon cycle responses to climate change in drylands. Glob. Chang. Biol. 19, 3835–3847. https://doi.org/10.1111/gcb.12306.
Mallen-Cooper, M., Eldridge, D.J., 2016. Laboratory-based techniques for assessing the functional traits of biocrusts. Plant Soil 406, 131–143. https://doi.org/10.1007/s11104-016-2870-9.
McHardy, A.C., Martín, H.G., Tsirigos, A., Hugenholtz, P., Rigoutsos, I., 2007. Accurate phylogenetic classification of variable-length DNA fragments. Nat. Method. 4, 63–72. https://doi.org/10.1038/nmeth976.
Miralles, I., Ladrón de Guevara, M., Chamizo, S., Rodríguez-Caballero, E., Ortega, R., van Wesemael, B., Cantón, Y., 2018. Soil CO2 exchange controlled by the interaction of BSCs successional stage, and environmental variables in two semiarid ecosystems. Soil BiolBiochemist 124, 11–23. https://doi.org/10.1016/j.soilbio.2018.05.020.
Mugnai, G., Rossi, F., Felde, V.J.M.N.L., Colesie, C., Büdel, B., Peth, S., Kaplan, A., De Philippis, R., 2018. Development of the polysaccharidic matrix in biocrusts induced by a cyanobacterium inoculated in sand microcosms. Biol. Fertil. Soil. 51, 27–40. https://doi.org/10.1007/s00374-017-1234-9.
Muñoz-Martín, M.Á., Becerra-Absalón, I., Perona, E., Fernández-Valbuena, L., Garcia-Pichel, F., Mateo, P., 2019. Cyanobacterial biocrust diversity in Mediterranean ecosystems along a latitudinal and climatic gradient. New Phytol. 221, 123–141. https://doi.org/10.1111/nph.15355.
Park, S.C., Won, S., 2018. Evaluation of 16S rRNA databases for taxonomic assignments using a mock community. Genom. Inform. 16, e24 https://doi.org/10.5808/GI.2018.16.4.e24.
Pen-Mouratov, S., Hu, C., Hindin, E., Steinberger, Y., 2011. Soil microbial activity and a free-living nematode community in the playa and in the sandy biological crust of the Negev Desert. Biol. Fert. Soil. 47, 363–375. https://doi.org/10.1007/s00374-011-0540-x.
Pluis, J.L.A., de Winder, B., 1990. Natural stabilization. Catena Suppl. 18, 195–208.
Pluis, J.L.A., 1994. Algal crust formation in the inland dune area, Laarder Wasmeer, the Netherlands. Vegetatio 113, 41–51.
Read, C.F., Duncan, D.H., Vesk, P.A., Elith, J., 2014. Biocrust morphogroups provide an effective and rapid assessment tool for drylands. J. Appl. Ecol. 51, 1740–1749. https://doi.org/10.1111/1365-2664.12336.

Redford, A.J., Fierer, N., 2009. Bacterial succession on the leaf surface: a novel system for studying successional dynamics. Microb. Ecol. 58, 189–198. https://doi.org/10.1007/s00248-009-9495-y.
Reed, S.C., Delgado-Baquerizo, M., Ferrenberg, S., 2019. BSCs science, and global change. New Phytol. 223, 1047–1051. https://doi.org/10.1111/nph.15992.
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 8, 717–731. https://doi.org/10.5194/soil-8-717-2022.
Robinson, C.K., Wierzchos, J., Black, C., Crits-Christoph, A., Ma, B., Ravel, J., Ascaso, C., Artieda, O., Valea, S., Roldán, M., Gómez-Silva, B., Di Ruggiero, J., 2015. Microbial diversity and the presence of algae in halite endolithic communities are correlated to atmospheric moisture in the hyper-arid zone of the Atacama Desert. Environ. Microbiol. 17, 299–315. https://doi.org/10.1111/1462-2920.12364.
Rodríguez-Caballero, E., Cantón, Y., Chamizo, S., Afana, A., Solé-Benet, A., 2012. Effects of biological soil crusts on surface roughness and implications for runoff and erosion. Geomorphol. 145, 81–89. https://doi.org/10.1016/j.geomorph.2011.12.042.
Rodríguez-Caballero, E., Cantón, Y., Chamizo, S., Lázaro, R., Escudero, A., 2013. Soil loss and runoff in semiarid ecosystems: a complex interaction between biological soil crusts, micro-topography, and hydrological drivers. Ecosyst. 16, 529–546. https://doi.org/10.1007/s10021-012-9626-z.
Rodríguez-Caballero, E., Cantón, Y., Lazaro, R., Solé-Benet, A., 2014. Cross-scale interactions between surface components and rainfall properties. Non-linearities in the hydrological and erosive behavior of semiarid catchments. J. Hydrol. 517, 815–825. https://doi.org/10.1016/j.jhydrol.2014.06.018.
Rodríguez-Caballero, E., Escribano, P., Olehowski, C., Chamizo, S., Hill, J., Cantón, Y., Weber, B., 2017. Transferability of multi-and hyperspectral optical biocrust indices. ISPRS J. Photogram. Remote Sens. 126, 94–107. https://doi.org/10.1016/j.isprsjprs.2017.02.007.
Rodríguez-Caballero, E., Castro, A.J., Chamizo, S., Quintas-Soriano, C., Garcia-Llorente, M., Cantón, Y., Weber, B., 2018. Ecosystem services provided by BSCs: from ecosystem functions to social values. J. Arid Environ. 159, 45–53. https://doi.org/10.1016/j.jaridenv.2017.09.005.
Rodríguez-Caballero, E., Román, J.R., Chamizo, S., Roncero Ramos, B., Cantón, Y., 2019. BSCs landscape-scale spatial distribution is strongly controlled by terrain attributes: topographic thresholds for colonization in a semiarid badland system. Earth Surf. Process. Landf. 44, 2771–2779. https://doi.org/10.1002/esp.4706.
Román, J.R., Roncero-Ramos, B., Rodríguez-Caballero, E., Chamizo, S., Cantón, Y., 2021. Effect of water availability on induced cyanobacterial BSCs development. Catena 197, 104988. https://doi.org/10.1016/j.catena.2020.104988.
Roncero-Ramos, B., Muñoz-Martín, M.Á., Chamizo, S., Fernández-Valbuena, L., Mendoza, D., Perona, E., Cantón, Y., Mateo, P., 2019. Polyphasic evaluation of key cyanobacteria in BSCs from the most arid region in Europe. PeerJ 7, e6169. https://doi.org/10.7717/peerj.6169.
Rosentreter, R., 2020. Biocrust lichen and moss species most suitable for restoration projects. Restor. Ecol. 28, S67–S74. https://doi.org/10.1111/rec.13082.
Rossi, F., Li, H., Liu, Y., 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. https://doi.org/10.1016/j.earscirev.2017.05.006.
Rossi, F., Mugnai, G.De, Philippis, R., 2022. Cyanobacterial biocrust induction: a comprehensive review on a soil rehabilitation-effective biotechnology. Geoderma 415, 115766. https://doi.org/10.1016/j.geoderma.2022.115766.
Rutherford, W.A., Painter, T.H., Ferrenberg, S., Belnap, J., Okin, G.S., Flagg, C., Reed, C. S., 2017. Albedo feedbacks to future climate via climate change impacts on drylands BSCs. Sci. Rep. 7, 44188. https://doi.org/10.1038/srep44188.
Sadeghi, S.H.R., Kheirfam, H., Homaee, M., Zarei-Darki, B., Vafakhah, M., 2017. Improving runoff behavior resulting from direct inoculation of soil micro-organisms. Soil Till. Res. 171, 35–41. https://doi.org/10.1016/j.still.2017.04.007.
Sadeghi, S.H.R., Kheirfam, H., Zarei-Darki, B., 2020a. Controlling runoff generation and soil loss from field experimental plots through inoculating cyanobacteria. J. Hydrol. 585, 124814 https://doi.org/10.1016/j.jhydrol.2020.124814.
Sadeghi, S.H.R., Sadeghi-Satri, M., Kheirfam, H., Darki, B.Z., 2020b. Runoff and soil loss from small plots of erosion-prone marl soil inoculated with bacteria and cyanobacteria under real conditions. Eur. J. Soil Biol. 101, 103214 https://doi.org/10.1016/j.ejsobi.2020.103214.
Sadeghi, S.H.R., Najafinejad, A., Gharemahmudli, S., Darki, B.Z., Behbahani, A.M., Kheirfam, H., 2021. Reduction in soil loss caused by a freeze-thaw cycle through inoculation of endemic soil microorganisms. Appl. Soil Ecol. 157, 103770 https://doi.org/10.1016/j.apsoil.2020.103770.
Sepehr, A., Hassanzadeh, M., Rodriguez-Caballero, E., 2019. The protective role of cyanobacteria on soil stability in two Aridisols in northeastern Iran. Geoderma Reg. 16, 1–10. https://doi.org/10.1016/j.geodrs.2018.e00201.
Serstevens, A.T., Rouxhet, P.G., Herbillon, A.J., 1978. Alteration of mica surfaces by water and solutions. Clay Miner. 13, 401–410. https://doi.org/10.1180/claymin.1978.013.4.05.
Settanni, L., Miceli, A., Francesca, N., Moschetti, G., 2012. Investigation of the hygienic safety of aromatic plants cultivated in soil contaminated with Listeria monocytogenes. Food Control 26, 213–219. https://doi.org/10.1016/j.foodcont.2012.01.037.
Slate, M.L., Durham, R.A., Pearson, D.E., 2020. Strategies for restoring the structure and function of lichen-moss BSCs communities. Restor. Ecol. 28, S160–S167. https://doi.org/10.1111/rec.12996.
Tringe, S.G., Rubin, E.M., 2005. Metagenomics: DNA sequencing of environmental samples. Nat. Rev. Genetics 6, 805–814. https://doi.org/10.1038/nrg1709.
Tringe, S.G., Hugenholtz, P., 2008. A renaissance for the pioneering 16S rRNA gene. Curr. Opin. Microbiol. 11, 442–446. https://doi.org/10.1016/j.mib.2008.09.011.
Ujváry, I., 2010. Pest control agents from natural products. In: Krieger, R.I., Krieger, W.C. (Eds.), Hayes' Handbook of Pesticide Toxicology. Academic Press, San Diego, pp. 119–229. https://doi.org/10.1016/B978-0-12-374367-1.00003-3.
van der Heijden, M.G., Bardgett, R.D., van Straalen, N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol. Lett. 11, 296–310. https://doi.org/10.1111/j.1461-0248.2007.01139.x.
Weber, B., Olehowski, C., Knerr, T., Hill, J., Deutschewitz, K., Wessels, D.C.J., Eitel, B., Büdel, B., 2008. A new approach for mapping of biological soil crusts in semidesert areas with hyperspectral imagery. Remote Sens. Environ. 112, 2187–2201. https://doi.org/10.1016/j.rse.2007.09.014.
Weber, B., Hill, J., 2016. Remote sensing of biological soil crusts at different scales. In: Weber, B., Büdel, B., Belnap, J. (Eds.), Biological Soil Crusts: An Organizing Principle in Drylands. Springer, Cham, pp. 215–234. https://doi.org/10.1007/978-3-319-30214-0_12.
Weber, B., Tamm, A., Maier, S., Rodríguez-Caballero, E., 2018. Biological soil crusts of the Succulent Karoo: a review. Afr. J. Range Forage Sci. 35, 335–350. https://doi.org/10.2989/10220119.2018.1527782.
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., Bowker, M.A., 2022. What is a biocrust? A refined, contemporary definition for a broadening research community. Biol. Reviews 97, 1768–1785. https://doi.org/10.1111/brv.12862.
Wei, W., Yu, Y., Chen, L., 2015. Response of surface soil hydrology to the micro-pattern of bio-crust in a dry-land loess environment,China. PLoS ONE 10, e0133565. https://doi.org/10.1371/journal.pone.0133565.
Weisburg, W.G., Barns, S.M., Pelletier, D.A., Lane, D.J., 1991. 16S ribosomal DNA amplification for phylogenetic study. J. Bacteriol. 173, 697–703. https://doi.org/10.1128/jb.173.2.697-703.1991.
Wijayawardene, N.N., Hyde, K.D., Al-Ani, L.K.T., Tedersoo, L., Haelewaters, D., Rajeshkumar, K.C., Zhao, R.L., Aptroot, A., Leontyev, D.V., Saxena, R.K., Tokarev, Y. S., Dai, D.Q., Letcher, P.M., Stephenson, S.L., Ertz, D., Lumbsch, H.T., Kukwa, M., Issi, I., Madrid, H., Phillips, A.J.L., Selbmann, L., Pfliegler, W.P., Horváth, E., Bensch, K., Kirk, P.M., Kolařík, K., Raja, H.A., Radek, R., Papp, V., Dima, B., Ma, J., Malosso, E., Takamatsu, S., Rambold, G., Gannibal, P.B., Triebel, D., Gautam, A.K., Avasthi, S., Suetrong, S., Timdal, E., Fryar, S.C., Delgado, G., Réblová, M., Doilom, M., Dolatabadi, S., Pawłowska, J.Z., Humber, R.A., Kodsueb, R., Sánchez-Castro, I., Goto, B.T., Silva, D.K.A., de Souza, F.A., Oehl, F., da Silva, G.A., Silva, I.R., Błaszkowski, J., Jobim, K., Maia, L.C., Barbosa, F.R., Fiuza, P. O., Divakar, P.K., Shenoy, B.D., Castañeda-Ruiz, R.F., Somrithipol, S., Lateef, A.A., Karunarathna, S.C., Tibpromma, S., Mortimer, P.E., Wanasinghe, D.N., Phookamsak, R., Xu, J., Wang, Y., Tian, F., Alvarado, P., Li, D.W., Kušan, I., Matočec, N., Mešić, A., Tkalčec, Z., Maharachchikumbura, S.S.N., Papizadeh, M., Heredia, G., Wartchow, F., Bakhshi, M., Boehm, E., Youssef, N., Hustad, V.P., Lawrey, J.D., Santiago, A.L.C.M.A., Bezerra, J.D.P., Souza-Motta, C.M., Firmino, A. L., Tian, Q., Houbraken, J., Hongsanan, S., Tanaka, K., Dissanayake, A.J., Monteiro, J.S., Grossart, H.P., Suija, A., Weerakoon, G., Etayo, J., Tsurykau, A., Vázquez, V., Mungai, P., Damm, U., Li, Q.R., Zhang, H., Boonmee, S., Lu, Y.Z., Becerra, A.G., Kendrick, B., Brearley, F.Q., Motiejūnaitė, J., Sharma, B., Khare, R., Gaikwad, S., Wijesundara, D.S.A., Tang, L.Z., He, M.Q., Flakus, A., Rodriguez-Flakus, P., Zhurbenko, M.P., McKenzie, E.H.C., Stadler, M., Bhatm, D.J., Liu, J.K., Raza, M., Jeewon, R., Nassonova, E.S., Prieto, M., Jayalal, R.G.U., Erdoğdu, M., Yurkov, A., Schnittler, M., Shchepin, O.N., Novozhilov, Y.K., Silva-Filho, A.G.S., Gentekaki, E., Liu, P., Cavender, J.C., Kang, Y., Mohammad, S., Zhang, L.F., Xu, R.F., Li, Y.M., Dayarathne, M.C., Ekanayaka, A.H., Wen, T.C., Deng, C.Y., Pereira, O.L., Navathe, S., Hawksworth, D.L., Fan, X.L., Dissanayake, L.S., Kuhnert, E., Grossart, H. P., Thines, M., 2020. Outline of Fungi and fungus-like taxa. Mycosphere Online: J. Fungal Biol. 11, 1060–1456. https://doi.org/10.5943/mycosphere/11/1/8.
Whitney, K.M., Vivoni, E.R., Duniway, M.C., Bradford, J.B., Reed, S.C., Belnap, J., 2017. Ecohydrological role of biological soil crusts across a gradient in levels of development. Ecohydrol. 10, e1875 https://doi.org/10.1002/eco.1875.
Whitton, B.A., Potts, M., 2012. Introduction to the Cyanobacteria. In: Whitton, B.A. (Ed.), Ecology of Cyanobacteria II. Springer, Dordrecht, pp. 1–13. https://doi.org/10.1007/978-94-007-3855-3_1.
Xiao, B., Wang, Q., Zhao, Y., Shao, M., 2011. Artificial culture of biological soil crusts and its effects on overland flow and infiltration under simulated rainfall. Appl. Soil Ecol. 48, 11–17. https://doi.org/10.1016/j.apsoil.2011.02.006.
Xiao, B., Sun, F., Hu, K., Kidron, G.J., 2019. BSCs reduce surface soil infiltrability and impede soil water infiltration under tension and ponding conditions in dryland ecosystem. J. Hydrol. 568, 792–802. https://doi.org/10.1016/j.jhydrol.2018.11.051.
Yang, K., Zhao, Y., Gao, L., Sun, H., Gu, K., 2022. Nonlinear response of hydrodynamic and soil erosive behaviors to biocrust coverage in drylands. Geoderma 405, 115457. https://doi.org/10.1016/j.geoderma.2021.115457.
Young, K.E., Bowker, M.A., Reed, S.C., Duniway, M.C., Belnap, J., 2019. Temporal and abiotic fluctuations may be preventing successful rehabilitation of soil-stabilizing BSCs communities. Ecol. Appl. 29, e01908 https://doi.org/10.1002/eap.1908.
Zhang, Z., Chen, Y., Xu, B., Huang, L., Tan, H., Dong, X., 2015. Topographic differentiations of biological soil crusts and hydraulic properties in fixed sand dunes, Tengger Desert. J. Arid Land 7, 205–215. https://doi.org/10.1007/s40333-014-0048-y.
Zhang, B., Zhang, Y., Li, X., Zhang, Y., 2018a. Successional changes of fungal communities along the biocrust development stages. Biol. Fert. Soils 54, 285–294. https://doi.org/10.1007/s00374-017-1259-0.
Zhang, C., Niu, D., Song, M., Elser, J.J., Okie, J.G., Fu, H., 2018b. Effects of rainfall manipulations on carbon exchange of cyanobacteria and moss-dominated biological

soil crusts. Soil Biol. Biochem. 124, 24–31. https://doi.org/10.1016/j.soilbio.2018.05.021.
Zhang, G.H., Ding, W.F., Pu, J., Li, J.M., Qian, F., Sun, B.Y., 2020. Effects of moss-dominated biocrusts on soil detachment by overland flow in the three Gorges Reservoir Area of China. J. Mt. Sci. 17, 2418–2431. https://doi.org/10.1007/s11629-020-6200-6.
Zhang, X., Koehler, H., 2022. Soil algae for combating soil degradation–greenhouse experiment with different soil amendments. Soil Res. 61, 70–82. https://doi.org/10.1071/SR22074.
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. Biodivers. Conserv. 23, 1669–1686. https://doi.org/10.1007/s10531-014-0680-z.
Zhou, X., Ke, T., Li, S., Deng, S., An, X., Ma, X., Philippis, R.D., Chen, L., 2020a. Induced biological soil crusts and soil properties varied between slope aspect, slope gradient and plant canopy in the Hobq desert of China. Catena 190, 104559. https://doi.org/10.1016/j.catena.2020.104559.
Zhou, X., Zhao, Y., Belnap, J., Zhang, B., Bu, C., Zhang, Y., 2020b. Practices of biological soil crust rehabilitation in China: experiences and challenges. Restor. Ecol. 28, S45–S55. https://doi.org/10.1111/rec.13148.