

REVIEW PAPER

Biological soil crusts and how they might colonize other worlds: insights from these Brazilian ecosystem engineers

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Abstract

When bryophytes, lichens, eukaryotic algae, cyanobacteria, bacteria, and fungi live interacting intimately with the most superficial particles of the soil, they form a complex community of organisms called the biological soil crust (BSC or biocrust). These biocrusts occur predominantly in drylands, where they provide important ecological services such as soil aggregation, moisture retention, and nitrogen fixation. Unfortunately, many BSC communities remain poorly explored, especially in the tropics. This review summarizes studies about BSCs in Brazil, a tropical megadiverse country, and shows the importance of ecological, physiological, and taxonomic knowledge of biocrusts. We also compare Brazilian BSC communities with others around the world, describe why BSCs can be considered ecosystem engineers, and propose their use in the colonization of other worlds.

Keywords: Biological soil crusts, bryophytes, cyanobacteria, ecosystem engineers, eukaryotic algae, lichens.

Introduction

Biological soil crusts (BSCs), also called biocrusts, are communities of organisms that are abundant in arid and semi-arid regions of the planet, colonizing the topsoil layer in ecosystems with sparse vegetation and the absence of excessive shadows and other competing organisms (Benalp *et al.*, 2001; Thompson *et al.*, 2006). These regions where BSCs occur encompass not only hot and cold deserts around the world, but also other biomes (Bowker *et al.*, 2016). Well-developed biocrusts occur in steppes (e.g. Biazrov, 2015), grassland regions (e.g. Delgado-Baquerizo *et al.*, 2013), savannas (e.g. Neher *et al.*, 2003), and dry forests (e.g. Maya and López-Cortés, 2002).

Eukaryotic algae, cyanobacteria, bacteria, fungi, mosses, liverworts, and lichens occur in biocrusts in differing propor-

tions (Benalp *et al.*, 2001, 2016; Büdel, 2002) and, based on the dominant taxon, biocrusts can be classified into three different types: cyanobacteria, lichen, and moss biocrusts (Zhao *et al.*, 2009; Colesie *et al.*, 2016). Commonly, the first colonizers are large filamentous cyanobacteria, followed by smaller cyanobacteria and green algae (Benalp *et al.*, 2001). After these organisms have prepared and stabilized soil surfaces, bryophytes and lichens tend to appear, representing the final stage BSC succession (Benalp *et al.*, 2001). However, mosses can also be primary colonizers as an intermediate state of succession following disturbances (Gall *et al.*, 2022, Preprint).

Constituting up to 12% of the earth's terrestrial surface (Rodríguez-Caballero *et al.*, 2018), these communities of

organisms comprise an important part of the biogeochemistry and biodiversity of the ecosystems where they live (Benalp *et al.*, 2001, 2016; Elbert *et al.*, 2012). In fact, biocrusts were important in the conquest of land by plants. Many studies support the hypothesis that a green algae ancestor of land plants (e.g. streptophyte algae) probably lived in communities very similar to those of BSCs (Wellman and Strother, 2015; Del-Bem, 2018; Fürst-Jansen *et al.*, 2020). Moreover, Del-Bem (2018) proposed that xyloglucan, a potent soil aggregator (Galloway *et al.*, 2018), evolved in organisms that lived on primitive BSCs during land colonization.

Furthermore, BSCs can be characterized as ecosystem engineers since they provide important ecological services (Jones *et al.*, 1994; Bowker *et al.*, 2006; Bowker, 2007; Starkenburg *et al.*, 2011). Examples of such services include soil aggregation (Guo *et al.*, 2008; Bowker *et al.*, 2013; Baran *et al.*, 2015), nitrogen and carbon fixation (Benalp, 2001, 2002; Mager, 2010; Miralles *et al.*, 2013; Barger *et al.*, 2016; Zhang *et al.*, 2018; Hu *et al.*, 2019; Kheirfam, 2020; Zhou *et al.*, 2020), capacity to affect the P-cycle (Baumann *et al.*, 2017), contribution to organic matter composition (Baumann *et al.*, 2021), and water infiltration and soil moisture retention (Benalp, 2006; Li *et al.*, 2018; Shi *et al.*, 2018). They also interact directly with seed establishment (Li *et al.*, 2005; Langhans *et al.*, 2009) and provide food and habitats for many animals, such as some nematodes (Darby *et al.*, 2007) and microarthropods (Neher *et al.*, 2009).

The ecology, physiology, and taxonomy of biocrusts have been the subjects of studies in recent years, encompassing ecosystems from throughout the world, including in North America (Rivera-Aguilar *et al.*, 2006; Breen and Lévesque, 2008; Soule *et al.*, 2009; Torres-Cruz *et al.*, 2018), Africa (Büdel *et al.*, 2009; Dojani *et al.*, 2014; Rozenstein and Karnieli, 2015), Asia (Tirkey and Adhikary, 2005; Feng *et al.*, 2021; Mikhailyuk *et al.*, 2021), Oceania (Read *et al.*, 2011; Büdel *et al.*, 2018), Antarctica (Pushkareva *et al.*, 2018; Canini *et al.*, 2020), and South America (Arana *et al.*, 2016; Baumann *et al.*, 2018; Romero *et al.*, 2020).

Some regions of the planet are still under-represented among studies on BSCs, with a significant knowledge gap for South America (Bowker *et al.*, 2016). Since biocrusts are generally not expected to be either abundant or ecologically relevant in tropical ecosystems (Benalp *et al.*, 2001; Maestre and Cortina, 2002; Seitz *et al.*, 2017), countries considered megadiverse, such as Brazil (Mittermeier *et al.*, 1999), remain poorly explored. In this review, we summarize studies on BSCs in different Brazilian ecosystems. We hypothesized that the distribution of BSCs among biomes in Brazil would resemble that of BSCs communities worldwide. We highlight the ecological relevance of BSCs and their importance as ecosystem engineers, and propose the use of biocrusts to colonize other worlds.

Brazilian biological soil crusts: what is really known?

There is little known about BCSs in Brazil to date. The revision of Büdel (2001a) indicated the occurrence of BSCs in

Brazil, although references therein do not clarify their exclusive aspects. Also, Bowker *et al.* (2016) mentioned that data on the species composition of biocrusts in South America are rare and represent a large taxonomic knowledge gap for the continent. Thus, we used the study of Büdel (2001a) as a starting point for our review, only evaluating data published in 2001 and later. We performed a literature-based assessment using records obtained from Google Scholar by searching, from 2001 to 2021, with the terms 'biological soil crusts' * 'biocrusts' * 'Brazil', and '*crostas biológicas*' * '*Brasil*'. Only studies published as scientific articles and those focusing on BSCs in Brazilian ecosystems were considered, resulting in a total of eight studies.

The majority of the studies found about BSCs in Brazil focused only on cyanobacteria and added knowledge regarding the ecology, physiology, and taxonomy of these biocrust components. Machado-de-Lima *et al.* (2019) performed a floristic study and compared the biodiversity of the cyanobacterial assemblages of biocrusts from different biomes (Brazilian savannas versus North American deserts), and found that the biodiversity of Brazilian BSCs seems to be distinct from that of North American deserts. Machado-de-Lima and Branco (2020) focused on exploring taxonomically the species complex formed by the biocrust cyanobacteria *Microcoleus Desmazières ex Gomont* and *Phormidium Kützing ex Gomont*, and described six new species. Lastly, Machado-de-Lima *et al.* (2021) investigated and compared the cyanobacterial composition of biocrusts from contrasting Brazilian biomes (dry forest versus grassland) and evaluated abiotic factors to explain the spatial distribution of cyanobacterial communities in these ecosystems. As a result, these authors revealed differences in the biocrust cyanobacteria communities of the two studied biomes and showed that soil temperature and pH were the main environmental drivers of BSC structures at the study sites.

Szyja *et al.* (2019) evaluated the occurrence, diversity, and ecological role of biocrusts inhabiting a human-modified landscape of a Brazilian dry forest. The study was the only one in our review to encompass bryophytes, lichens, cyanobacteria, and eukaryotic algae together in BSCs. Szyja *et al.* (2019) also determined that biocrusts play an important role in the sequestering of soil organic carbon in the studied biome, although anthropogenic disturbances have decreased this ecosystem service.

In contrast to the studies cited above, Trindade *et al.* (2001, 2005) evaluated the biogeochemistry aspects of BSCs. Trindade *et al.* (2001) observed the nutrient cycling performed by biocrusts and found an association between the presence of these complex communities of organisms and chemical elements in the most superficial layer of the soil (e.g. BSCs promoted inputs of K, Ca, Mg, Al, and N). Also, Trindade *et al.* (2005) found that BSCs in nutrient-poor soil improved nutrient cycling, probably providing essential nutrients for vascular plant establishment. Both studies emphasized the potential uses of biocrusts in processes aimed at the recovery of degraded areas.

Finally, [Giraldo-Silva et al. \(2020\)](#) and [Fernandes et al. \(2021\)](#) performed extensive meta-analyses based on molecular data of BSCs, which included Brazilian reports from [Machado-de-Lima et al. \(2019\)](#). [Giraldo-Silva et al. \(2020\)](#) explored segregation patterns among BSCs in natural ecosystems, and showed that cyanobacteria crusts had a consistent world-wide distribution. On the other hand, [Fernandes et al. \(2021\)](#) focused on exploring taxonomically the species complex formed by the biocrust cyanobacterium *Microcoleus steenstrupii* J.B.Petersen and allied taxa, redescribing the family Coleofasciculaceae and describing new genera.

Our data review made possible the compilation of the occurrence of species in Brazilian BSCs, the ecosystems where they live, their ecological contributions, some of the adaptations they possess for surviving in adverse and harsh environments, and their applications ([Fig. 1](#)). Thus, within the following topics, we discuss in more detail the biodiversity of Brazilian BSCs, where they occur in Brazil, their ecological relevance, and their importance as ecosystem engineers. We emphasize that our review focused only on published articles, thus excluding data from dissertations and theses. Nonetheless, these unpublished data have the potential to contribute significantly to improving knowledge regarding the taxonomy, geographic distribution, and applied ecology of Brazilian BSCs.

Homes of Brazilian BSCs: why protect them?

South America has been entirely overlooked concerning studies on BSCs ([Büdel, 2001a](#)). For Brazil, [Büdel \(2001a\)](#) referenced two studies about the components of BSCs, which reported bryophyte species in the *Caatinga* ([Bastos et al., 1998](#)) and cyanobacteria in the *Cerrado* ([Sant'Anna and Azevedo, 1995](#)), although the latter authors did not directly mention these species as part of BSCs. The present revision, however, demonstrated that Brazilian BSCs do indeed occur in sites embedded within ecosystems of the *Cerrado*, *Caatinga*, and *Pampas* ([Fig. 2A](#)).

The *Caatinga* ([Fig. 2B](#)), located in Northeast Brazil, is the largest and most species-rich seasonally dry tropical forest of the world ([Silva et al., 2017](#)). The regional climate is semi-arid ([Sampaio et al., 1995](#)) and the vegetation is dominated by xeric shrublands ([Pennington et al., 2009](#)) that are adapted to long periods of drought conditions ([Silva et al., 2017](#)). [Szyja et al. \(2019\)](#) mentioned that the *Caatinga* supports a relatively diverse community of BSCs at the landscape scale. Unfortunately, this ecosystem is highly affected by anthropogenic disturbance, such as firewood and forage collection, timber exploitation, and livestock grazing ([Arnan et al., 2018](#); [Souza et al., 2019](#)). All these activities generate negative effects on the

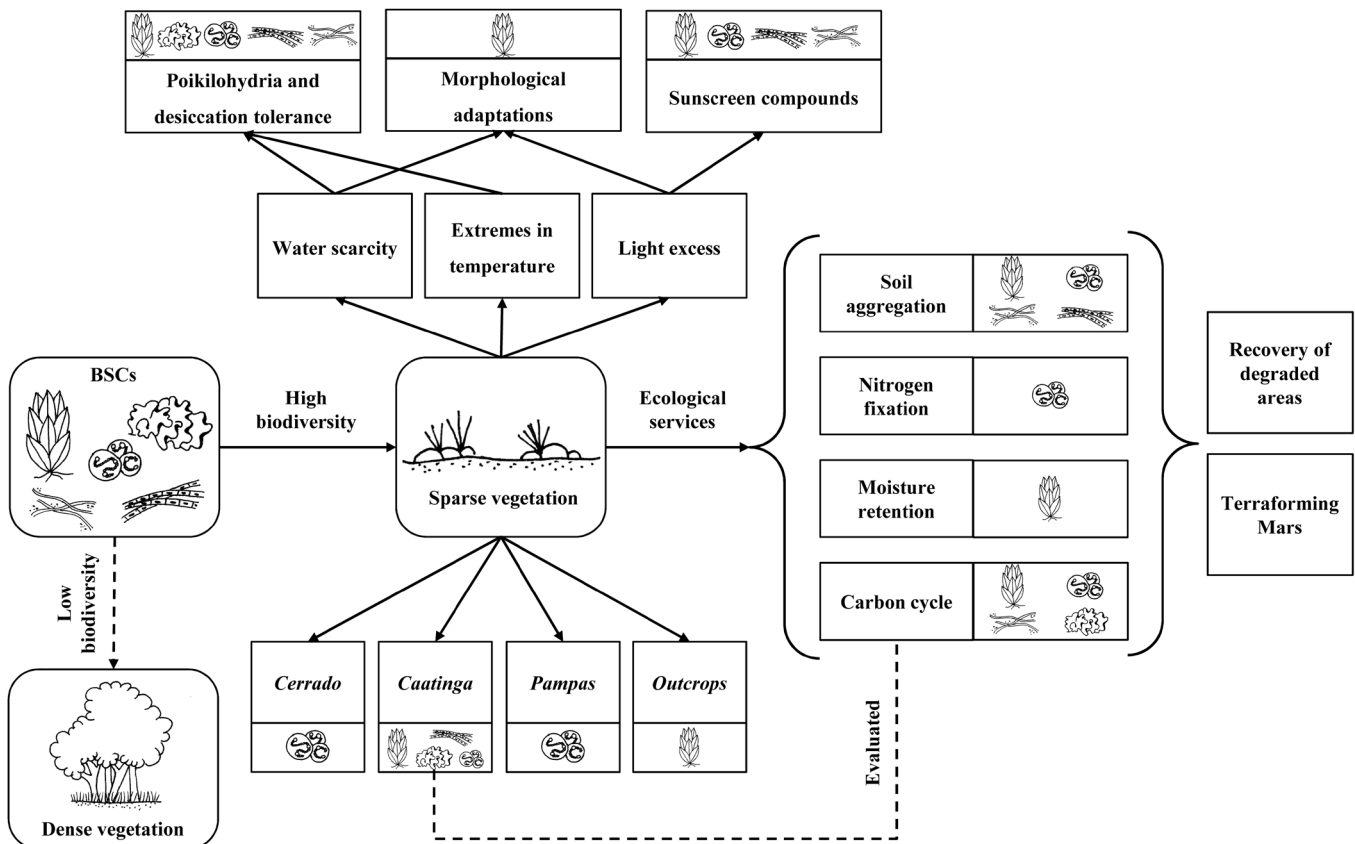


Fig. 1. An overview of knowledge about biological soil crusts.

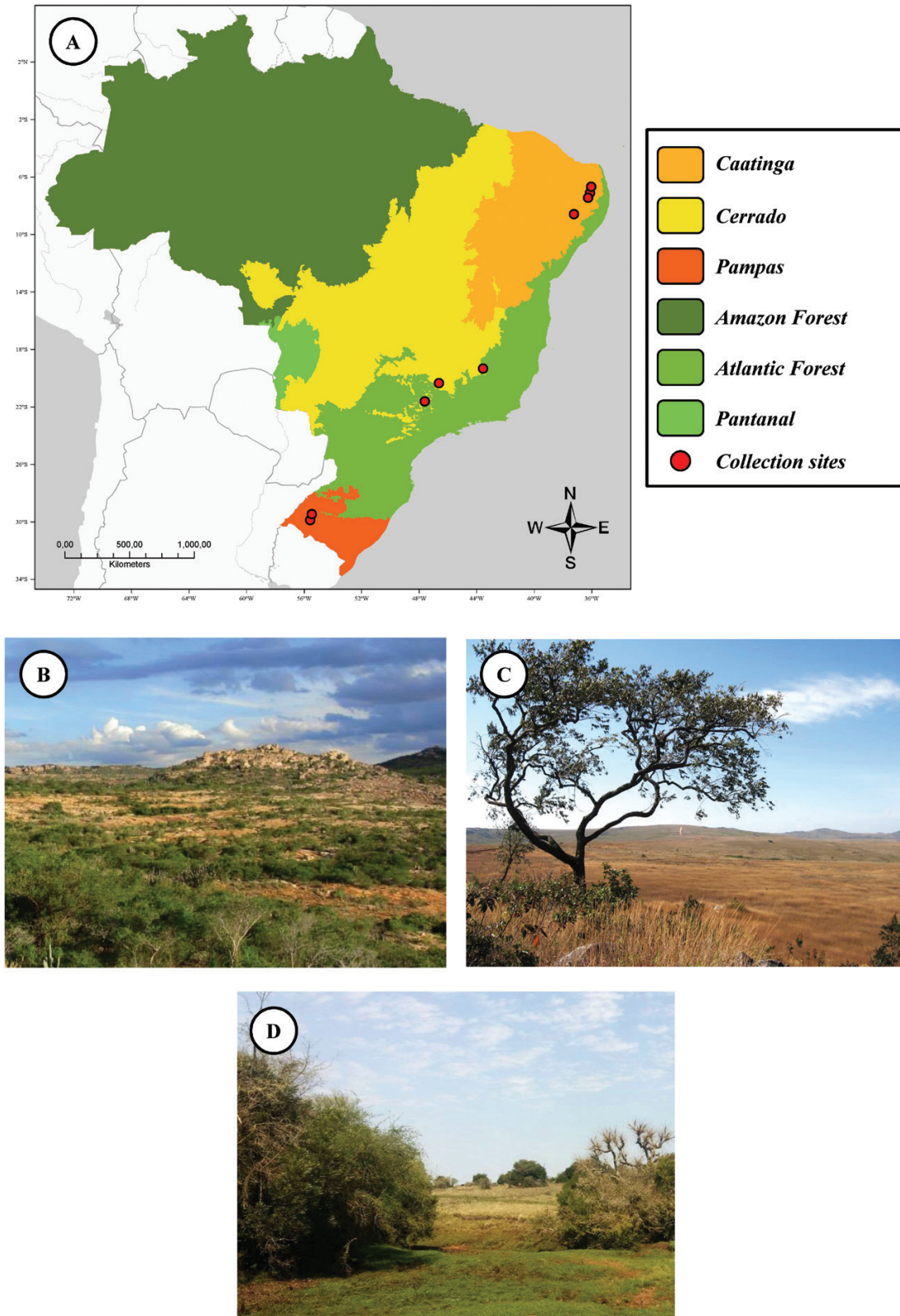


Fig. 2. The homes of Brazilian BSCs. (A) Collection sites. (B) *Caatinga*. (C) *Cerrado*. (D) *Pampas*. Photos by Nivea Dias dos Santos (B) and Elisa Teixeira Aires (D).

entire biodiversity of the *Caatinga*, including its community of BSCs. Despite encompassing 862 636 km² of the Brazilian territory, only 9% of the *Caatinga* is protected by Conservation Units (CNUC, 2020). Biodiversity conservation has been neglected for this ecosystem and has received little investment, since human poverty is the priority for politicians of the region (Leal *et al.*, 2005).

The *Cerrado* (Fig. 2C), a typical savanna formation in central Brazil (Zimbres *et al.*, 2020), is considered a hotspot for global biodiversity conservation (Ratter *et al.*, 1997; Mittermeier *et al.*, 2000). The climate is semi-humid tropical (Eiten, 1982), and the vegetation is characterized by a gradient of phytophysiognomies (Goodland and Pollard, 1973), with some being more favorable to biocrust establishment (Machado-de-Lima *et al.*, 2019). An example is the *Campo Sujo* formation, which can host a relevant biodiversity of BSC communities since this phytophysiognomy possesses herbaceous vegetation in association with very scattered small trees (Goodland and Pollard, 1973). Even though the *Cerrado* is considered the most humid savanna in the world, a severe dry season occurs during April–September (Eiten, 1982). The *Cerrado* encompasses 1 984 659 km² of the Brazilian territory (CNUC, 2020) and suffers severe environmental pressures due to human occupation, such as habitat fragmentation, soil erosion, aquifer pollution, and fire regime changes. However, 173 548 km² of the *Cerrado* is protected by Conservation Units (CNUC, 2020), and trade-offs between land use and conservation are being encouraged to improve biodiversity conservation efforts (Klink and Machado, 2005).

Finally, BCSs are also found in the *Pampas* (Fig. 2D) of South Brazil (Machado-de-Lima *et al.*, 2021). This ecosystem encompasses 193 948 km² with mainly subtropical and temperate climates (Roesch *et al.*, 2009), sandy soils with low fertility, and high temperatures (Freitas *et al.*, 2010). The vegetation is composed of native grasslands, sparse shrubs, and tree formations (Verdum *et al.*, 2019). Even though it is one of the most species-rich grasslands in the world (Overbeck *et al.*, 2007), the *Pampas* is the ecosystem with the least conservation of biodiversity by the Brazilian protected area network (Fonseca and Venticinque, 2018), with only 5876 km² protected by Conservation Units (CNUC, 2020).

Furthermore, smaller ecosystems can be found in association with the large biogeographic units of Brazil, such as *campos de altitude* of the Atlantic Forest, inselbergs of the Amazon and Atlantic Forest, *campos rupestres* of the *Cerrado* and rocky outcrops of the *Caatinga* (Scarano, 2007), in addition to karst areas (limestone outcrops) that are distributed throughout these ecosystems (Auler and Farrant, 1996). Although some studies have reported the presence of bryophytes in the soil of some of these ecosystems (Silva and Germano, 2013; Carmo and Peralta, 2016; Oliveira-da-Silva and Ilkiu-Borges, 2018; Peñaloza-Bojacá *et al.*, 2018; Oliveira *et al.*, 2021), there have been no studies focusing exclusively on BSCs in these environments. Similar habitats around the world have biocrusts as relevant components of their biodiversity.

Studies related to the biodiversity and ecology of biocrusts have been performed in different types of outcrops throughout the world, such as granite outcrops in Austria and Italy (Mikhailyuk *et al.*, 2015), gypsum outcrops in Spain (Maestre *et al.*, 2011), and granite outcrops in continental Antarctica (Colesie *et al.*, 2014). Also, BSCs in granite and quartz outcrops of South Africa were mapped with hyperspectral images (Weber *et al.*, 2008). Thus, the existence and ecological relevance of BSCs in *campos rupestres*, *campos de altitude*, inselbergs, and rocky outcrops of Brazil cannot be ignored (Fig. 3). Furthermore, since the biodiversity and ecophysiology of biocrusts of karst areas in China reveal exciting results (Chen *et al.*, 2014; Hu *et al.*, 2019; Cheng *et al.*, 2021), Brazilian karsts can also be expected to harbor rich biocrust diversity.

Biocrusts are very vulnerable to anthropogenic disturbance and take a long time to recover naturally (Benalp *et al.*, 2001). The species composition, cover, and physiological functioning of these complex communities of organisms are directly affected by human actions (Benalp *et al.*, 2001). The habitats of BSCs in Brazil currently suffer from several anthropogenic disturbances, yet the taxonomy, physiology, and ecology of most BSCs have yet to be studied. To our knowledge, only Szyja *et al.* (2019) have studied the effects of anthropogenic disturbances on Brazilian BSCs, finding a considerable decrease in the ecosystem services (e.g. contributing to soil organic carbon sequestering) provided by biocrusts in the *Caatinga*. We highlight the relevance of studying holistic aspects of biocrusts because such data are key to mitigating species extinctions and supporting conservation and restoration projects for BSCs in Brazil and elsewhere.

Biodiversity of BSCs in Brazil: what still needs to be studied?

Although all the components of BSCs have been inventoried throughout the world, fungi and bacteria taxonomic diversity have yet to be evaluated in Brazil (at least not reported in the published literature). Machado-de-Lima *et al.* (2019, 2021) and Machado-de-Lima and Branco (2020) exclusively evaluated cyanobacteria of BSCs, and only Szyja *et al.* (2019) studied the combined biodiversity of cyanobacteria, lichens, eukaryotic algae, and bryophytes. Trindade *et al.* (2005) identified lichens and bryophytes to genus and species levels, but also mentioned the presence of cyanobacteria and fungi filaments (with no taxonomic identification).

Cyanobacteria have been relatively well investigated in BSCs around the world, with ~320 species known to be crust components (Büdel *et al.*, 2016). In Brazil, cyanobacteria have been recorded in the *Caatinga*, *Cerrado*, and *Pampas*, with a total of 49 taxa (Table 1) distributed among 35 genera (Machado-de-Lima *et al.*, 2019, 2021; Szyja *et al.*, 2019; Machado-de-Lima and Branco, 2020). The *Caatinga* has the greatest diversity of BSC cyanobacteria, with six new species being recently described

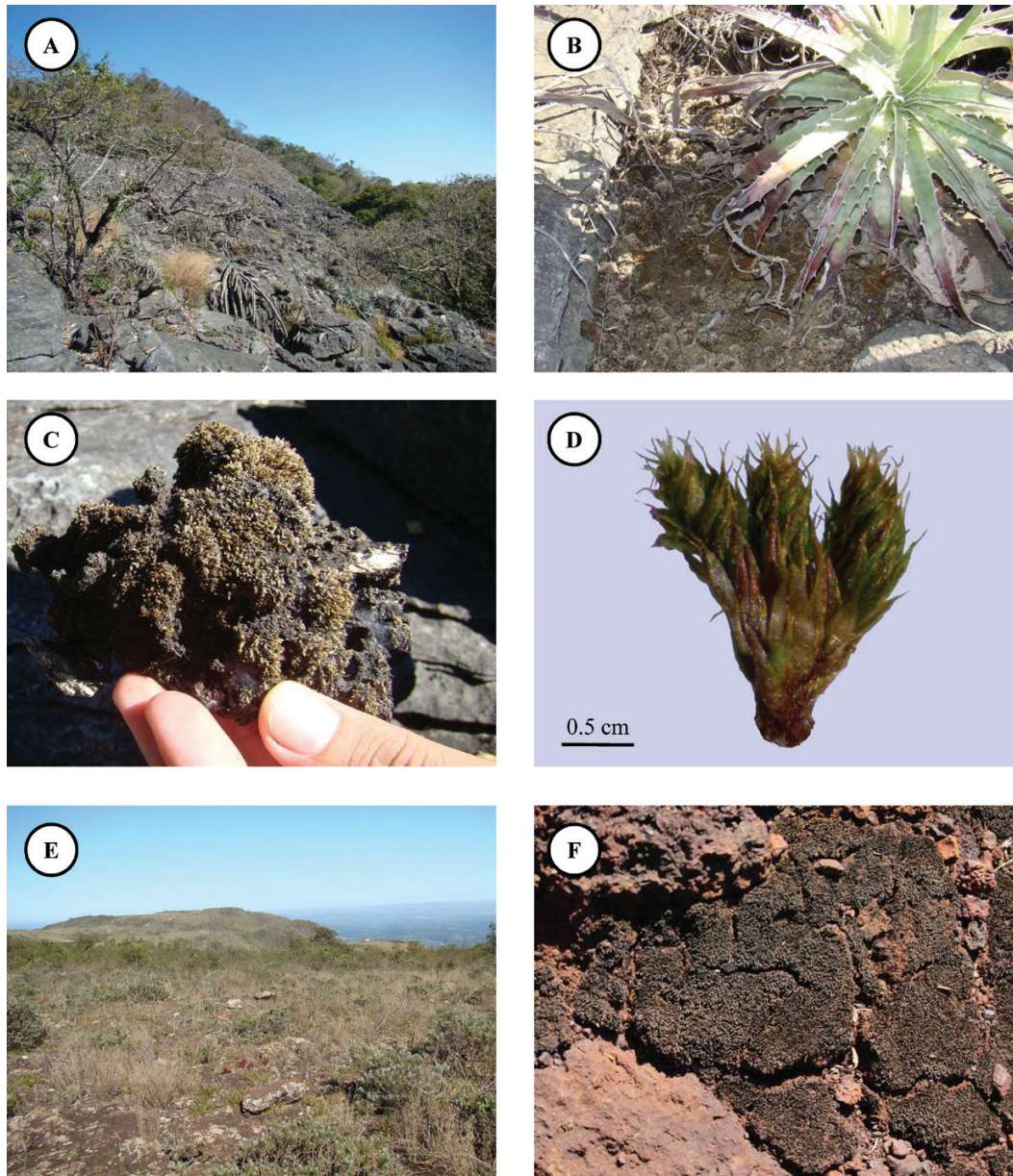


Fig. 3. BSCs in smaller ecosystems of Brazil. (A) Karst area. (B) Biocrusts growing in a limestone rock crevice. (C) Moss-dominated biocrust. (D) *Bryum atenense* R.S. Williams, a moss species common in biocrusts of karst areas. (E) Ironstone outcrop with sparse vegetation. (F) Biocrust (photo by Pablo Oliveira Santos).

for this ecosystem by Machado-de-Lima and Branco (2020), showing the importance of studying BSCs in environments of tropical countries.

In contrast to cyanobacteria, other BSC components remain poorly studied in Brazil (Fig. 4). These components have only been evaluated in the *Caatinga* (Szyja *et al.*, 2019), where 12 taxa of eukaryotic algae, seven of bryophytes (five mosses and two liverworts), and seven of lichens were recorded (Table 1), and in the Atlantic Forest (Trindade *et al.*, 2005), where five taxa of mosses and one lichen were recorded from slopes along roads. Bowker *et al.* (2016) noted that these taxonomic gaps

exist in many localities around the world and that just a few researchers are struggling to identify all the diverse groups of the biota comprising biocrusts. Investigations in Brazilian ecosystems would reveal a large diversity of native organisms in BSCs, which could serve as an incentive to investigate biocrusts in similar environments throughout the world.

Despite all the efforts to assess the biodiversity of bryophytes, lichens, eukaryotic algae, cyanobacteria, bacteria, and fungi of BSCs, the worldwide number of taxa described for this community must be higher. Since some specimens of BSCs are morphologically very similar and difficult to distinguish

Table 1. Diversity of biological soil crusts in Brazil from a literature-based synthesis

Cyanobacteria	
Species	References
<i>Aetokthonos</i> S.B.Wilde & J.R.Johansen	Machado-de-Lima <i>et al.</i> (2019)
<i>Aphanocapsa</i> C. Nägeli	Szyja <i>et al.</i> (2019)
<i>Brasilonema</i> Fiore, Sant-Anna, de Paiva Azevedo, Komarek, Kastovsky, Sulek & Lorenzi	Machado-de-Lima <i>et al.</i> (2019)
<i>Calothrix</i> C. Agardh ex Bornet & Flahault	Szyja <i>et al.</i> (2019)
<i>Chroococcidiopsis</i> Geitler	Machado-de-Lima <i>et al.</i> (2019); Szyja <i>et al.</i> (2019)
<i>Desmonostoc</i> P. Hrouzek & S.Ventura	Machado-de-Lima <i>et al.</i> (2019)
<i>Gloeocapsa</i> Kützing	Szyja <i>et al.</i> (2019)
<i>Gracilinea arenicola</i> Machado de Lima & L.H.Z. Branco	Machado-de-Lima and Branco (2020)
<i>Hassallia</i> Berkeley ex Bornet & Flahault	Machado-de-Lima <i>et al.</i> (2019)
<i>Komvophon</i> K.Anagnostidis & J. Komárek	Machado-de-Lima <i>et al.</i> (2019)
<i>Koniacronema caatingensis</i> Machado de Lima & L.H.Z. Branco	Machado-de-Lima and Branco (2020)
<i>Leptolyngbya</i> Anagnostidis & Komárek	Machado-de-Lima <i>et al.</i> (2019); Szyja <i>et al.</i> (2019); Machado-de-Lima <i>et al.</i> (2021)
<i>Macrochaete lichenoides</i> Berrendero, J.R. Johansen &Kastovsky	Szyja <i>et al.</i> (2019)
<i>Marmoreocelis xerophila</i> Machado de Lima & L.H.Z. Branco	Machado-de-Lima and Branco (2020)
<i>Mastigocladus</i> Cohn ex O.Kirchner	Machado-de-Lima <i>et al.</i> (2019)
<i>Microcoleus vaginatus</i> Gomont ex Gomont	Machado-de-Lima <i>et al.</i> (2019); Szyja <i>et al.</i> (2019)
<i>Microcoleus steenstrupii</i> J.B. Petersen	Machado-de-Lima <i>et al.</i> (2019, 2021)
<i>Microcystis</i> Lemmermann	Machado-de-Lima <i>et al.</i> (2019)
<i>Nostoc</i> Vaucher ex Bornet &Flahault	Machado-de-Lima <i>et al.</i> (2019, 2021); Szyja <i>et al.</i> (2019)
<i>Nostoc edaphicum</i> Kondratava	Szyja <i>et al.</i> (2019)
<i>Nostoc ellipsoideum</i> N.L. Gardner	Szyja <i>et al.</i> (2019)
<i>Nostochopsis</i> H.C.Wood ex É. Bornet & C. Flahault	Machado-de-Lima <i>et al.</i> (2019)
<i>Oculatella</i> Zammit, Billi & Albertano	Machado-de-Lima <i>et al.</i> (2019)
<i>Oscillatoria</i> Vaucher ex Gomont	Szyja <i>et al.</i> (2019)
<i>Pantanalinema</i> Vieira Vaz <i>et al.</i>	Machado-de-Lima <i>et al.</i> (2019)
<i>Phormidesmis</i> Turicchia, Ventura, Komárková & Komárek	Machado-de-Lima <i>et al.</i> (2019)
<i>Porphyrosiphon</i> Kützing ex M. Gomont	Machado-de-Lima <i>et al.</i> (2019)
<i>Porphyrosiphon notarisii</i> Kützing ex Gomont	Machado-de-Lima <i>et al.</i> (2021)
<i>Potamolinea</i> M.D. Martins & L.H.Z. Branco	Machado-de-Lima <i>et al.</i> (2019)
<i>Potamosiphon</i> G.B. McGregor & B.C. Sendall	Machado-de-Lima <i>et al.</i> (2019)
<i>Prochlorococcus</i> Chisholm, Frankel, Goericke, Olson, Palenik, Waterbury, West-Johnsrud & Zettler	Machado-de-Lima <i>et al.</i> (2019)
<i>Pseudophormidium</i> (Forti) Anagnostidis & Komárek	Machado-de-Lima <i>et al.</i> (2019); Szyja <i>et al.</i> (2019)
<i>Pycnacronema</i> M.D. Martins & Branco	Machado-de-Lima <i>et al.</i> (2019)
<i>Pycnacronema caatingensis</i> Machado-de-Lima & L.H.Z. Branco	Machado-de-Lima and Branco (2020)

Table 1. Continued

Cyanobacteria	
Species	References
<i>Pycnacronema edaphica</i> Machado-de-Lima & L.H.Z. Branco	Machado-de-Lima and Branco (2020)
<i>Schizothrix</i> Kützing ex Gomont	Szyja <i>et al.</i> (2019)
<i>Schizothrix acutissima</i> Drouet	Machado-de-Lima <i>et al.</i> (2021)
<i>Schizothrix telephoroides</i> Gomont	Machado-de-Lima <i>et al.</i> (2021)
<i>Scytonema</i> C.Agardh ex É. Bornet & C. Flahault	Machado-de-Lima <i>et al.</i> (2019); Szyja <i>et al.</i> (2019)
<i>Scytonema hyalinum</i> N.L. Gardner	Szyja <i>et al.</i> (2019)
<i>Scytonema guyanense</i> Bornet &Flahault	Machado-de-Lima <i>et al.</i> (2021)
<i>Scytonema javanicum</i> Bornet ex Bornet & Flahault	Machado-de-Lima <i>et al.</i> (2021)
<i>Scytonema ocellatum</i> Lyngbye ex Bornet & Flahault	Machado-de-Lima <i>et al.</i> (2021)
<i>Stigonema</i> C. Agardh ex Bornet &Flahault	Machado-de-Lima <i>et al.</i> (2019); Szyja <i>et al.</i> (2019)
<i>Stigonemaocellatum</i> Thuret ex Bornet &Flahault	Machado-de-Lima <i>et al.</i> (2021)
<i>Tolypothrix</i> Kützing ex Bornet &Flahault	Szyja <i>et al.</i> (2019)
<i>Trichocoleus caatingensis</i> Machado-de-Lima & L.H.Z. Branco	Machado-de-Lima and Branco (2020)
<i>Trichormus</i> (Ralfs ex Bornet &Flahault) Komárek & Anagnostidis	Machado-de-Lima <i>et al.</i> (2019)
Green algae	
Species	References
<i>Chlorella</i> Beij.	Szyja <i>et al.</i> (2019)
<i>Cylindrocystis brebissonii</i> Menegh.	Szyja <i>et al.</i> (2019)
<i>Desmoccoccus</i> F. Brand	Szyja <i>et al.</i> (2019)
<i>Follicularia</i> V.V. Miller	Szyja <i>et al.</i> (2019)
<i>Heterococcus</i> Chodat	Szyja <i>et al.</i> (2019)
<i>Klebsormidium</i> P.C. Silva, Mattox & W.H. Blackwell	Szyja <i>et al.</i> (2019)
<i>Macrochloris multinucleata</i> (Reisigl) Ettl & Gärtner	Szyja <i>et al.</i> (2019)
<i>Neochloris</i> Starr	Szyja <i>et al.</i> (2019)
<i>Scenedesmus</i> Meyen	Szyja <i>et al.</i> (2019)
<i>Scotiellopsis rubescens</i> Vinatzer	Szyja <i>et al.</i> (2019)
<i>Spongiochloris</i> Star	Szyja <i>et al.</i> (2019)
<i>Stichococcus</i> Nägeli	Szyja <i>et al.</i> (2019)
Lichens	
Species	References
<i>Bibbya</i> cf. <i>albomarginata</i> (H. Kiliass&Gotth. Schneid.) Kistenich <i>et al.</i>	Szyja <i>et al.</i> (2019)
<i>Buellia</i> De Not.	Szyja <i>et al.</i> (2019)
<i>Cladonia</i> P. Browne	Trindade <i>et al.</i> (2005)
<i>Cladonia foliacea</i> (Huds.) Willd.	Szyja <i>et al.</i> (2019)
<i>Cladonia verticillaris</i> (Raddi) Fr.	Szyja <i>et al.</i> (2019)
<i>Heppia conchiloba</i> Zahlbr.	Szyja <i>et al.</i> (2019)
<i>Lecidea</i> Ach.	Szyja <i>et al.</i> (2019)
<i>Peltula michoacanensis</i> (B. de Lesd.) Wetmore	Szyja <i>et al.</i> (2019)
Liverworts	
Species	References
<i>Riccia</i> L.	Szyja <i>et al.</i> (2019)
<i>Riccia vitalis</i> Jovet-Ast	Szyja <i>et al.</i> (2019)

Table 1. Continued

Cyanobacteria	
Species	References
Mosses	
Species	References
<i>Bryum</i> Hedw.	Trindade <i>et al.</i> (2005)
<i>Bryum argenteum</i> Hedw.	Szyja <i>et al.</i> (2019)
<i>Campylopus</i> Brid.	Trindade <i>et al.</i> (2005)
<i>Campylopus lamellatus</i> Mont.	Szyja <i>et al.</i> (2019)
<i>Dicranella hilariana</i> (Mont.) Mitt.	Trindade <i>et al.</i> (2005)
<i>Fissidens submarginatus</i> Bruch	Szyja <i>et al.</i> (2019)
<i>Funaria hygrometrica</i> Hedw.	Trindade <i>et al.</i> (2005)
<i>Gemmabryum exile</i> (Dozy & Molk.) J.R. Spence & H.P. Ramsay	Szyja <i>et al.</i> (2019)
<i>Polytrichum juniperinum</i> Hedw.	Trindade <i>et al.</i> (2005)
<i>Tortella humilis</i> (Hedw.) Jenn.	Szyja <i>et al.</i> (2019)

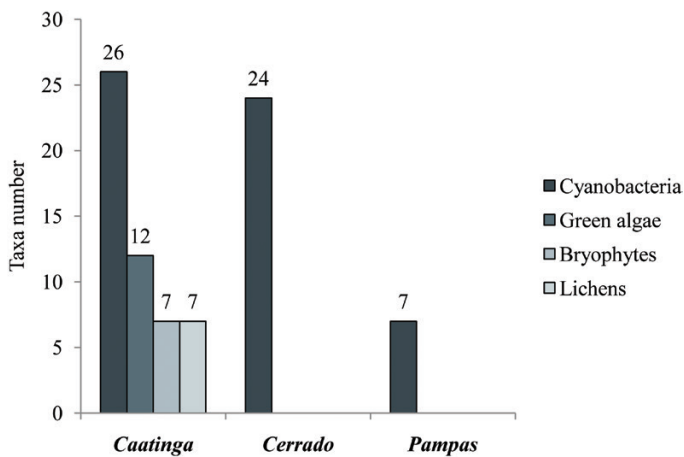


Fig. 4. The number of taxa recorded for BSCs in each major Brazilian ecosystem.

taxonomically (i.e. cryptic species, Lewis and Flechtner, 2004; Becerra-Absalón *et al.*, 2020; Irisarri *et al.*, 2021), we can assume a large hidden diversity for BSCs. For instance, Machado-de-Lima and Branco (2020) recently described new cyanobacteria taxa from cryptic genera of *Microcoleus* Desmazières ex Gomont and *Phormidium* Kützing ex Gomont in Brazil.

Brazilian and worldwide BSCs: is there any similarity?

Biocrusts seem to be spatially variable regarding their diversity (Bowker *et al.*, 2016), and many researchers have explored their biogeography. Zhang *et al.* (2011), for example, compared the composition of cyanobacteria and eukaryotic algae in the Gurbantunggut Desert (China) with those of other deserts of the world, and found spatial heterogeneity for these biocrust components. Zedda *et al.* (2011) investigated distribution patterns of lichen biocrusts among the principal biomes of Namibia

and western South Africa, and showed that climate, soil characteristics, and altitude modulate species composition at different study sites.

In Brazil, Machado-de-Lima *et al.* (2019) found the composition of cyanobacterial biocrusts of *Cerrado* to be distinct from those from North American deserts and emphasized the compositional uniqueness of *Cerrado* biocrust. Machado-de-Lima *et al.* (2021) revealed differences in biocrust cyanobacteria communities between the Brazilian biomes of *Caatinga* and *Pampas*, reinforcing the occurrence of biocrust spatial variation.

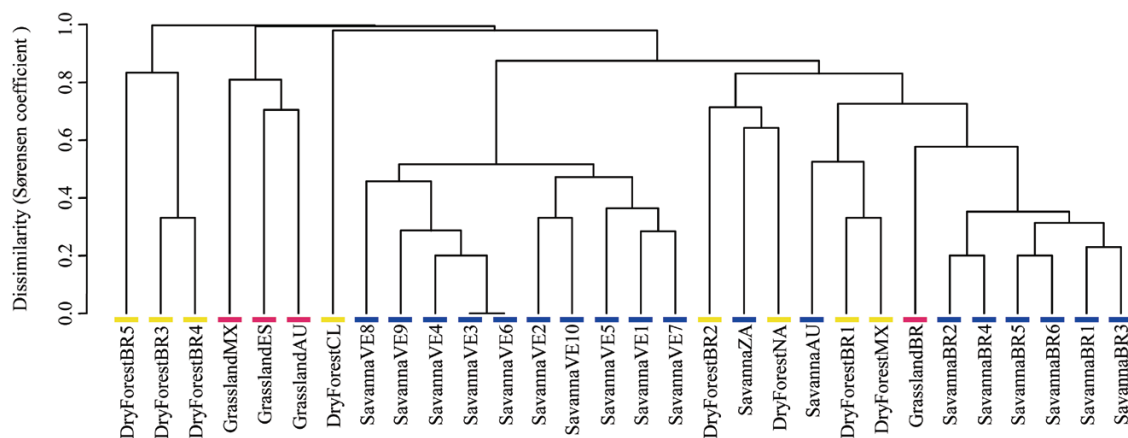
In an attempt to better understand patterns of biocrust biodiversity among different biomes, we compared the species composition of Brazilian biocrusts with BSCs in comparable biomes throughout the world. We performed a literature-based assessment using records obtained from Google Scholar by searching for the terms ‘biological soil crusts’ associated with ‘savanna’, ‘dry forest’, or ‘grassland’ (corresponding to the Brazilian biomes *Cerrado*, *Caatinga*, and *Pampas*, respectively). We selected studies with floristic data for each of the above combinations, which are listed in Table 2.

Like Büdel (2001b), we restricted comparisons of biome similarity to the genus level, thus eliminating some of the problems involving different species concepts, different protocols for isolation and identification, and the selective focusing on certain organisms of BSCs. Finally, using the vegan package (Oksanen, 2013) of the R software (R Core Team, 2020), we calculated the Sørensen coefficient based on presence/absence data as: $2A/(2A+B+C)$, where A=number of species common to two sites, B=number of species exclusive to site 1, and C=number of species exclusive to site 2. Dendrograms from the dissimilarity matrix were also derived using the vegan package (R Core Team, 2020).

Our analysis found that the community compositions of biocrusts in different Brazilian biomes were not similar to the composition of BSCs in comparable biomes worldwide (Fig. 5). We found the BSC communities of Venezuelan savanna and Brazilian savanna to be distinct from each other, although the sites in each country formed a group on the dendrogram. Also, three Brazilian dry forest sites form the outermost group of the dendrogram, since they share recently described taxa (e.g. Machado-de-Lima and Branco, 2020). Finally, grasslands from throughout the world formed a group with the exclusion of the Brazilian *Pampas* due to the focal taxa in each study (lichen and mosses worldwide versus cyanobacteria in Brazil). As noted by Büdel (2001b), our floristic knowledge of BSCs is incomplete and even unknown in many regions, which may have interfered with our analysis. Although some studies only cover a group of focal organisms, other components of BSCs are probably present in the same study areas. We also noticed that many ecological studies of BSCs do not publish a species list or mention the biome where biocrusts occur, thus complicating our data compilation.

Table 2. Summary of studies compiled for the comparison of BSC communities of biomes

Reference	Organisms evaluated	Biome	Country	Sampling site
Machado-de-Lima <i>et al.</i> (2019)	Cyanobacteria	Savanna	Brazil	SavannaBR1 to SavannaBR6
José and Bravo (1991)	Cyanobacteria	Savanna	Venezuela	SavannaVE1 to Savanna VE10
Büdel <i>et al.</i> (2009)	Cyanobacteria and eukaryotic algae	Savanna	South Africa	SavannaZA
Williams <i>et al.</i> (2014)	Cyanobacteria	Savanna	Australia	SavannaAU
Szyja <i>et al.</i> (2019)	Cyanobacteria	Dry Forest	Brazil	DryForestBR2
Machado-de-Lima and Branco (2020)	Cyanobacteria	Dry Forest	Brazil	DryForestBR3 to DryForestBR5
Machado-de-Lima <i>et al.</i> (2021)	Cyanobacteria	Dry Forest	Brazil	DryForestBR1
Maya and López-Cortés, 2002	Cyanobacteria	Dry Forest	Mexico	DryForestMX
Büdel <i>et al.</i> (2009)	Cyanobacteria and eukaryotic algae	Dry Forest	Namibia	DryForestNA
Samolov <i>et al.</i> (2020)	Cyanobacteria and eukaryotic algae	Dry Forest	Chile	DryForestCL
Machado-de-Lima <i>et al.</i> (2021)	Cyanobacteria	Grassland	Brazil	GrasslandBR
Eldridge <i>et al.</i> (2000)	Lichens, mosses and liverworts	Grassland	Australia	GrasslandAU
Castillo-Monroy <i>et al.</i> (2010)	Lichens and mosses	Grassland	Spain	GrasslandES
Concostrina-Zubiri <i>et al.</i> (2013)	Lichens and mosses	Grassland	Mexico	GrasslandMX

**Fig. 5.** Dendrogram groupings based on dissimilarity for all biocrust communities in biomes worldwide (correlation coefficient=0.91). Yellow, dry forests; pink, grasslands; blue, savannas. For details about site abbreviations, see Table 2.

Adaptations of BSC taxa to harsh environments: why consider them?

Biological soil crusts occur in arid and semi-arid regions of the planet under harsh conditions, such as water scarcity, extreme temperatures, and excess light (Büdel, 2001b). Some BSC species possess a diversity of morphological and physiological adaptations that permit them to survive and proliferate in these adverse ecosystems. Some of these adaptations are similar to those in distantly related taxa, and thus imply convergent evolutionary trends (Büdel, 2001a). One example is poikilohydia associated with desiccation tolerance of photoautotrophic species of biocrusts. The internal water content of these organisms depends on external moisture, but physiological mechanisms allow them to remain alive during desiccation and revive after rehydration (Green and Proctor, 2016). Many species of cyanobacteria, eukaryotic algae, lichens, and mosses of BSCs tolerate desiccation for long periods (Bewley and Krochko, 1982). For instance, the moss *Bryum argenteum*, found in BSCs in the

Brazilian *Caatinga* (Szyja *et al.*, 2019), can survive a year of desiccation with rapid recovery of the photosynthetic apparatus (Li *et al.*, 2014).

Biocrust heterotrophs, such as free-living fungi, can also tolerate desiccation stress (Maier *et al.*, 2016). One mechanism that confers desiccation tolerance is the production of melanin, which is synthesized by dark septate fungi and accumulated in their cell walls (Gostinčar *et al.*, 2009; Reed *et al.*, 2016). Melanin could also enhance tolerance of stress from UV irradiation (Gostinčar *et al.*, 2009).

Filamentous cyanobacteria are adapted to live in the harsh environments where BSCs occur, since some species can produce a thick sheath associated with substances that serve as a sunscreen (Dillon and Castenholz, 1999). Additionally, some species can tolerate intracellular water loss for extended periods of time (Lee, 2018). Furthermore, some species live in layers below where the species that produce sunscreen compounds live on the surface, and species with no protection move to the surface only when soils are wet (Benal *et al.*, 2001).

As with cyanobacteria, eukaryotic algae have also evolved mechanisms to support harsh and strongly fluctuating environmental conditions, such as photoprotection by sunscreen pigments (Bandaranayake, 1998; Aigner *et al.*, 2013) or self-shading (Karsten *et al.*, 2010). Some groups have flexible secondary cell walls and maintain cell turgor even in situations of water scarcity (Holzinger *et al.*, 2011).

Lichens are a colorful component of BSCs (Rosentreter *et al.*, 2016), and they produce pigments that provide tolerance to excess light, such as the carotenoid zeaxanthin (Kappen, 1973; Demmig-Adams *et al.*, 1990). Another mechanism interpreted as photoprotective in lichens is hygroscopic thallus movements (Büdel and Wessels, 1986), which involves the curling of thallus lobes when they are dry, thus protecting the photobionts from insolation (Barták *et al.*, 2006).

When bryophytes go through periods of drought, they suspend their metabolism and minimize the strain of drought stress (Vitt *et al.*, 2014; Zhang *et al.*, 2017). Desiccation tolerance in bryophytes is provided through cellular protection from desiccation-induced damage. During the wet–dry cycle, cellular components become protected by polysaccharides and proteins (Oliver, 1991; Smirnov, 1992; Buitink *et al.*, 2002; Gao *et al.*, 2017). Some proteins that play important roles in desiccation tolerance by biocrust mosses are early light-inducible proteins (ELIPs) and late embryogenesis abundant (LEA) proteins (Zeng *et al.*, 2002; Oliver *et al.*, 2004; Wood and Oliver, 2004). ELIPs provide photoprotection since they can bind to free chlorophyll and prevent photo-oxidative damage (Montané and Kloppstech, 2000). On the other hand, LEA proteins bind to small lipid vesicles, thus changing their own secondary structure and stabilizing these cell components (Koag *et al.*, 2003).

Bryophytes also possess morphological adaptations such as hyaline hairpoints, lamellae, papillae, and alar cells in the leaves, which help in the retention and distribution of water (Frahm, 1996; Vanderpoorten and Goffinet, 2009). Some of these morphological adaptations have been recorded for bryophytes in BSCs of the Brazilian *Caatinga*. The moss *Campylopus lamellatus* Mont. has a hyaline hairpoint (Fig. 6A) and lamellae in the leaves, while the moss *Bryum argenteum* Hedw. has tightly overlapping leaves (Fig. 6B) that maximize water absorption, retain moisture, and retard water loss (Wu *et al.*, 2013; Seppelt *et al.*, 2016).

Bryophytes of BSCs have many mechanisms to avoid the stress of living under the high radiation of dry areas, such as leaf orientation, self-shading within the canopy, chloroplast movement, and specific screening compounds (Robinson and Waterman, 2014). Other mechanisms include the activation of pathways that consume excess light energy, such as cyclic electron flow and photorespiration (Heber *et al.*, 2006; Takahashi and Badger, 2011; Perera-Castro *et al.*, 2021). Also, light stress leads to the accumulation of reactive oxygen species (ROS), but some mosses perform non-photochemical quenching (NPQ), which dissipates excess light energy as heat and thus

prevents ROS formation (Müller *et al.*, 2001; Nabe *et al.*, 2007, Proctor and Smirnov, 2011; Serpe *et al.*, 2013).

All components of BCSs are diminutive in size (Green and Proctor, 2016). Nonetheless, they have several adaptive mechanisms for surviving in harsh environments. These adaptations to aridity, however, cannot guarantee the resilience of BSCs to climate change (Reed *et al.*, 2016). Increasing temperatures and alterations to precipitation patterns are modifying the structure and function of biocrust communities (Escolar *et al.*, 2012; Ferrenberg *et al.*, 2015). It is important to understand the adaptive aspects of BSCs, such as their life habit, niche specificity, physiological and morphological adaptations, and longevity or shortness of life spans, since these traits drive the survival and colonization of biocrust species.

Ecological functions of BSCs: why care about them?

The naked soil of dry areas is highly vulnerable to wind and water erosion (Benalp *et al.*, 2001). However, when a complex community of BSC organisms is present, soil aggregation and stabilization prevent soil degradation (Benalp *et al.*, 2001). Several mechanisms generate this resistance to soil erosion, including the production and extravasation of organic compounds and the formation of webs of bryophyte rhizoids, filaments of algae and cyanobacteria, and fungal hyphae (Benalp *et al.*, 2016).

Filamentous cyanobacteria, such as those of the genera *Microcoleus*, *Porphyrosiphon*, and *Schizothrix* (Benalp *et al.*, 2001; Lee, 2018), produce a mucilaginous extracellular matrix that adheres to and aggregates soil particles (Benalp *et al.*, 2001; Garcia-Pichel and Wojciechowski, 2009; Rossi *et al.*, 2018). Some species of eukaryotic algae may also play important roles in soil stabilization due to their filamentous nature and mucilage secretion, such as those of the genera *Klebsormidium* and *Zygonium*, for example (Benalp *et al.*, 2016). Some of these organisms are important components of BSCs in Brazil and can provide significant ecological services where they occur, such as species of *Microcoleus* in the *Cerrado* and *Caatinga* (Machado-de-Lima *et al.*, 2019; Szyja *et al.*, 2019), and those of *Schizothrix* in the *Pampas* and *Caatinga* (Szyja *et al.*, 2019; Machado-de-Lima *et al.*, 2021).

Heterotrophic organisms of biocrusts can also produce compounds that contribute to soil aggregation. Fungal hyphae of lichen-dominated crusts are able to penetrate deeper into substrates while producing soil-aggregating compounds that increase resistance to wind and water erosion (Eldridge and Rosentreter, 1999). Bacteria of the clades Proteobacteria and Bacteroidetes produce exopolysaccharides, which can also play a role in soil stabilization (Gundlapally and Garcia-Pichel, 2006).

The autotrophic components of BCSs play an important role in carbon input in the ecosystems where they live, mainly



Fig. 6. Adaptations of some moss species that occur in BSCs of the Brazilian *Caatinga*. (A) Hair point of the moss *Campylopus lamellatus*. (B) Tightly overlapping leaves of the moss *Bryum argenteum*.

when vascular plants are restricted by harsh environmental conditions (Benalp *et al.*, 2001), making them relevant at both local and regional scales (Beymer and Klopatek, 1991). Lichen- and moss-dominated crusts have high carbon fixation rates. Pietrasiak *et al.* (2013) suggest that such rates are driven by carbon-concentrating mechanisms of the autotrophic organisms of BSCs. Fungi also play an important role in the cycling of nutrients in BSCs (Green *et al.*, 2008). In Brazil, Szyja *et al.* (2019) observed that soil organic carbon content is doubled in crusts dominated by cyanobacteria.

Nitrogen fixation is provided by some species of cyanobacteria and cyanobacterial symbionts in lichens of BSCs. These organisms perform an enzymatic process that converts nitrogen gas into ammonium, which makes nitrogen available for biological reactions (Lee, 2018). Nitrogen fixation by filamentous cyanobacteria is often performed inside specialized cells called heterocysts (Lee, 2018). Many nitrogen-fixing cyanobacteria are often associated with mosses in moss-dominated crusts, growing in their leaves and increasing the nitrogen fixation of these crusts (Wu *et al.*, 2009; Zhao *et al.*, 2010).

Different from cyanobacteria-dominated biocrusts, indicators of early-stage biocrusts and drier conditions (Issa *et al.*, 1999), bryophyte-dominated biocrusts indicate a later successional stage of BSCs and conditions of greater moisture (Cole-sie *et al.*, 2016; Seppelt *et al.*, 2016). This can be explained by the dense growth form of moss gametophytes, which increases water transfer and absorption among capillary spaces and shoots, thereby minimizing water loss to the surrounding environment (Proctor, 1982).

Although more ecological aspects of biocrusts are being unveiled, local studies on these organisms need to be encouraged,

mostly in megadiverse tropical ecosystems such as those in Brazil. Local variations in temperature, humidity, and solar incidence affect the diversity of BSC components (Concostrina-Zubiri *et al.*, 2014; Bowker *et al.*, 2016). This has the potential of changing the rates of ecological services provided by BSCs. Thus, studies on the local relevance of BSCs and their ecotypic functioning, as well as the discovery of potential model systems, need to be encouraged.

Preparing new habitats and colonizing other worlds: how can BSCs help?

The homes of biocrusts are threatened worldwide for several reasons, and many disturbances directly affect the cover, species composition, and physiological functioning of BSC communities (Benalp and Eldridge, 2001). Zaady *et al.* (2016) classified these disturbances as those caused by direct human activities and natural disturbances. Some examples are livestock grazing (Thomas, 2012), human recreation disturbances (e.g. tracks, Benalp and Warren, 2002), fire (Bowker *et al.*, 2004), and sand deposition (Rao *et al.*, 2012).

Similar disturbances affect the ecosystems where BSCs occur in Brazil. The *Caatinga* is affected by firewood and forage collection, timber exploitation, and livestock grazing by goats (Arnan *et al.*, 2018; Souza *et al.*, 2019), whereas the most substantial human threats in the *Cerrado* are burning and ranching operations (Silva and Bates, 2002). Agricultural land use changes are the major factor impacting the *Pampas* (Oliveira *et al.*, 2017). Smaller ecosystems embedded in large biogeographic units of Brazil (e.g. *campos rupestres*, rocky outcrops, *campos de altitude*, inselbergs, karst areas), where biocrusts remain poorly

explored, experience disturbances from motorcycling (Lopes *et al.*, 2009; Neto *et al.*, 2013) and mining (Skirycz *et al.*, 2014; Salles *et al.*, 2019; Carmo *et al.*, 2020; Kamino *et al.*, 2020).

In fact, minimizing or preventing disturbance means protecting all the biodiversity and ecological services that BSCs provide (Zaady *et al.*, 2016). Nonetheless, BSCs can be recovered even in disturbed environments. They can act by aggregating soil particles (Eldridge and Rosentreter, 1999; Gundlapally and Garcia-Pichel, 2006; Garcia-Pichel and Wojciechowski, 2009; Benalp *et al.*, 2016), fixing nitrogen and carbon (Benalp *et al.*, 2001; Wu *et al.*, 2009; Zhao *et al.*, 2010), and filtering water and retaining moisture (Proctor, 1982; Benalp, 2006; Li *et al.*, 2018; Shi *et al.*, 2018)—all of which would be very useful in processes of ecological restoration (Bowker, 2007; Antoninka *et al.*, 2020).

Many researchers are focusing on developing effective methods to restore biocrusts to degraded drylands so as to promote the restoration of ecosystem functions (Antoninka *et al.*, 2020). For instance, Chiquoine *et al.* (2016) demonstrated that inoculation with salvaged biocrust accelerates surface soil recovery in the Mojave Desert, USA. In the laboratory, Chamizo *et al.* (2020) tested the capacity of cyanobacteria biocrusts to stabilize burned soils. Furthermore, some studies have tested initial rehabilitation of areas disturbed by mining using biocrusts (Stewart and Siciliano, 2015), and found that BSCs promote soil and ecosystem development and establish a basis for further vegetation growth (Gypser *et al.*, 2016).

As discussed above, biocrusts have the ability to regenerate their own homes by the different ecological services they perform. Furthermore, they can restore extremely human-modified environments, such as mining areas. Would it not be reasonable, from the same perspective, to consider using biocrusts to create new homes in environments beyond Earth?

We are experiencing huge advances in space technology that will eventually allow us to reach Mars (Musk, 2017). However, a terraforming plan for this planet needs to be developed to contribute to making the environment suitable for life forms from Earth (Fogg, 1998). The concept of terraforming can be defined as a process of planetary engineering with the aim of transforming an inhospitable extra-terrestrial environment into a habitable place for terrestrial life (Fogg, 1995).

In this sense, one of the biggest challenges has been the formation of a soil where plants can thrive—and thus produce food for future colonizers (Kanazawa *et al.*, 2008). This is due to the environment on Mars being hostile to terrestrial life in terms of high radiation and low temperature and pressure. Some studies suggest the use of individual cyanobacteria (Arai, 2009; Vasileva *et al.*, 2019), bacteria (Kanazawa *et al.*, 2008), and mosses (Huwe *et al.*, 2019) in processes of transforming the lifeless Martian soil into one that is nutrient-rich and self-sustainable.

Since the ultimate goal is the creation of soil in which food plants can start to grow in a short period of time, BSCs have great potential as they are considered ecosystem engineers

(Jones *et al.*, 1994; Bowker *et al.*, 2006; Bowker, 2007; Starkenburg *et al.*, 2011). BSCs provide critical ecological services to the ecosystems where they grow (Fig. 1), which can be leveraged for future use in preparing soils on Mars. Graham (2003) proposes stages for the transformation of Mars whereby eukaryotic algae, cyanobacteria, mosses, and lichens prepare Mars for the establishment of flowering plants. However, the methodology proposed by Graham (2003) does not mention a holistic knowledge of these organisms as components of BSCs, including their capacity to survive together in harsh environments and provide desirable ecosystem services.

Thus, we emphasize the importance of a more complete understanding of this community of organisms and their roles in the environment since they provide crucial ecological services on Earth. Furthermore, how these organisms would behave in environments similar to that of Mars needs to be tested (see BIOMEX results, although for isolated organisms, Huwe *et al.*, 2019; Vera *et al.*, 2019), in order to produce increasingly effective methodologies for creating an ideal soil for agricultural cultivation beyond Earth.

Conclusions

Although biological soil crusts are still considered as scarce and of little relevance in tropical environments, they are indeed dispersed in different Brazilian ecosystems, but mostly in smaller habitats that favor their growth and establishment. We note a bias in the sampling of these complex communities of organisms in Brazil, in favor of the *Caatinga*, *Cerrado*, and *Pampas*, since other environments embedded in Brazilian tropical forests may also harbor BSCs. Furthermore, biocrust species have important adaptations that allow them to deal with water scarcity, extreme temperature, and excess solar radiation. Biocrusts also play fundamental ecological roles where they occur. Soil aggregation and stabilization, nitrogen fixation, maintenance of the carbon cycle, and moisture retention are examples of the ecological services they provide. Finally, the components of BSCs in Brazil, such as cyanobacteria, eukaryotic algae, and mosses, are candidate models for use in studies of biotechnology and the colonization of bare soils.

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Conflict of interest

The authors declare no conflict of interest.

Data availability

No new data were created or analyzed in this study.

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