UNIVERSIDADE FEDERAL DE MINAS GERAIS
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Biologia Vegetal

MATEUS FERNANDES DE OLIVEIRA

BRIÓFITAS, CIANOBACTÉRIAS E ALGAS EM CROSTAS BIOLÓGICAS DO SOLO: diversidade e padrões ecológicos em afloramentos rochosos brasileiros

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Dissertação apresentada ao Programa de Pós-Graduação em Biologia Vegetal da Universidade Federal de Minas Gerais, como requisito parcial à obtenção do título de Mestre em Biologia Vegetal.

Orientadora: Profa. Dra. Adaíses Simone Maciel da Silva

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“Sou singelo musgo
Cresço entre metidas flores
E prospero sem rusgos.”

RESUMO

As crostas biológicas do solo (CBSs ou biocrostas) são comunidades estruturadas pela interação entre bactérias, fungos, algas eucarióticas, cianobactérias, liquens, archea e briófitas que vivem interagindo intimamente com as partículas mais superficiais do solo. As biocrostas ocorrem predominantemente em terras áridas, onde fornecem importantes serviços ecológicos, como agregação do solo, retenção de umidade e fixação de nitrogênio. Infelizmente, muitas comunidades de CBSs permanecem pouco exploradas, especialmente nos trópicos. Neste estudo compilamos o conhecimento sobre as CBSs no Brasil, comparamos as comunidades de biocrostas brasileiras com outras ao redor do mundo, descrevemos porque as BSCs podem ser consideradas engenheiras de ecossistemas e propomos seu uso na colonização de outros mundos. Também exploramos pela primeira vez aspectos ecológicos de biocrostas em três dos tipos mais comuns de afloramentos rochosos no Brasil — ferruginoso, quartzítico e calcário. Apresentamos uma lista florística, uma caracterização de microhabitats e solos onde as biocrostas crescem, uma descrição de padrões positivos de co-ocorrência e a criação de uma estrutura relevante para futuras ações efetivas de conservação de biocrostas em afloramentos. Finalmente, exploramos as preferências de crescimento do musgo comum em biocrostas *Bryum atenense* em relação às concentrações de cálcio relatadas em afloramentos rochosos brasileiros. Os resultados desta dissertação mostram a importância e relevância das crostas biológicas do solo nos ecossistemas brasileiros e enfatizam os potenciais usos de biocrostas em processos voltados para a recuperação de áreas degradadas. Além disso, os afloramentos brasileiros são refúgios de crostas dominadas por musgos, que possuem adaptações para crescer em diferentes microhabitats, inclusive naqueles com condições ambientais mais severas. Incentivamos futuros inventários e esforços de conservação envolvendo afloramentos rochosos em todo o mundo, pois as biocrostas nesses ecossistemas são pouco estudadas e comumente ignoradas. Por fim, o experimento com *B. atenense* em um gradiente de concentrações de cálcio suscita questões sobre adaptabilidade e ecótipos dentro de táxons de biocrostas.

Palavras-chave: Biocrostas; Musgos; Hepáticas; Cianobactérias; Algas eucarióticas; Brasil, Tolerância ao cálcio.

ABSTRACT

Biological soil crusts (BSC or biocrust) are communities structured by the interaction between bacteria, fungi, eukaryotic algae, cyanobacteria, lichens and bryophytes that live interacting intimately with the most superficial particles of the soil. 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. In this study we summarize the knowledge about BSCs in Brazil, compare Brazilian BSCs communities to others around the world, describe why BSCs can be considered ecosystem engineers and propose their use in the colonization of other worlds. We also explore for the first time ecological aspects of biocrusts in three of the most common types of rocky outcrops in Brazil — ironstone, quartzite-sandstone and limestone. We present a floristic list, a characterization of microhabitats and soils where biocrusts grow, a description of positive co-occurrence patterns and a creation of a relevant framework for future effective conservation actions to biocrusts within outcrops. Finally, we explored the growth preferences of the common biocrusts moss *Bryum atenense* relative to calcium concentrations reported from Brazilian rocky outcrops. The findings of this study show the importance and relevance of biological soil crusts in Brazilian ecosystems and emphasized the potential uses of biocrusts in processes aimed at the recovery of degraded areas. Moreover, Brazilian outcrops are refuges for moss-dominated crusts, which have adaptations to grow in different microhabitats, including those with harsher environment conditions. We encourage future inventories and conservation efforts involving rocky outcrops throughout the world, as biocrusts in these ecosystems are poorly studied and commonly ignored. Lastly, the experiment with *B. atenense* in a gradient of calcium concentrations suggest issues about adaptability and ecotypes within biocrusts taxa.

Keywords: Biocrusts; Mosses; Liverworts; Cyanobacteria; Eukaryotic algae; Brazil; Calcium tolerance.

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LISTA DE ABREVIATURAS E SIGLAS

SIGLA	SIGNIFICADO
CBSs	Crostas biológicas do solo
BSC	Biological soil crusts
IRO	Ironstone rocky outcrop
QRO	Quartzite-sandstone rocky outcrop
LRO	Limestone rocky outcrop
GRO	Granite-gneiss rocky outcrop

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1. INTRODUÇÃO

As crostas biológicas de solo (biocrostas ou CBSs) são comunidades compostas por organismos poiquiloídricos como briófitas, algas, cianobactérias, fungos, bactérias, liquens e archea que vivem entre as partículas superficiais do solo (SOULE *et al.*, 2009; BÜDEL *et al.*, 2016; MAIER *et al.*, 2016; ROSENTRETER *et al.*, 2016; SEPPELT *et al.*, 2016). Com base na espécie dominante, as CBSs podem ser classificadas em três tipos diferentes: crosta de algas, crosta de líquen e crosta de musgos (ZHAO *et al.*, 2009). Entretanto, esta definição exclui certas comunidades de organismos, como as de algas e cianobactérias que vivem sobre a areia no litoral e não agregam suas partículas e as de tapetes de musgos e liquens que crescem sobre matéria orgânica em decomposição (BENALP, BÜDEL & LANGE, 2001).

Reconhecidas como engenheiras de ecossistemas devido aos diversos serviços ecológicos que prestam (JONES, LAWTON & SHACHAK, 1994; BOWKER, 2007), as biocrostas possuem um papel importante na agregação do solo (GUO *et al.*, 2008; CHAUDHARY *et al.*, 2009; BOWKER *et al.*, 2013; FAIST *et al.*, 2017), onde compostos orgânicos liberados pelos organismos e a rede de tramas formada pelos rizóides das briófitas, os filamentos das algas e cianobactérias e as hifas dos fungos, geram uma estabilização do solo (BENALP, 1995). Além disto, elas fixam nitrogênio e carbono (BARGER *et al.*, 2016; SANCHO *et al.*, 2016), auxiliam na infiltração e retenção de umidade no solo (CHAMIZO *et al.*, 2016; ELDRIDGE *et al.*, 2020) e ainda desempenham papel como berçário de sementes (ZHANG *et al.*, 2016; HAVRILLA *et al.*, 2019).

Ocorrendo geralmente em regiões áridas e semiáridas do planeta (BENALP, WEBER & BÜDEL, 2016), as biocrostas habitam predominantemente ecossistemas de vegetação esparsa, crescendo nos espaços terrestres livres de sombras excessivas e de outros organismos competidores, o que permite que as crostas biológicas tenham maior acesso à luz (THOMPSON, ELDRIDGE & BONSER, 2006; BELNAP, WEBER & BÜDEL, 2016). Elas também podem ser encontradas em florestas secas (e.g. MAYA & LÓPEZ-CORTÉS, 2002), estepes (e.g. BIAZROV, 2015), pradarias (e.g. CASTILLO-MONROY *et al.*, 2010) e savanas (e.g. JOSÉ & BRAVO, 1991; WILLIAMS *et al.*, 2014). Embora diversos estudos descrevam as biocrostas em diversas regiões do planeta, poucos esforços estão relacionados aos ecossistemas brasileiros.

Desta forma, procuramos com este estudo compreender um pouco mais sobre a organização e distribuição destas biocrostas no Brasil, bem como aspectos mais específicos de sua ecologia, diversidade e atributos fisiológicos. Assim, essa dissertação compila dados até a presente data sobre crostas biológicas do solo no Brasil, inova com a exploração desta comunidade de organismos em ecossistemas ameaçados e propõe seus usos em processos de recuperação de áreas degradadas. O texto é composto por uma breve fundamentação teórica onde se aborda os grupos taxonômicos focais das crostas biológicas de solo e também por três capítulos em forma de manuscrito.

O Capítulo I é uma revisão sobre CBSs no Brasil, um país tropical megadiverso, e mostra a importância de se investigar aspectos ecológicos, fisiológicos e taxonômicos de biocrostas. Nele também comparamos as comunidades brasileiras de CBSs com outras ao redor do mundo, descrevemos o porquê as biocrostas podem ser consideradas engenheiras de ecossistema e propomos seu uso na colonização de outros mundos.

No Capítulo II exploramos pela primeira vez aspectos ecológicos de biocrostas em três tipos de afloramentos rochosos no Brasil. Desta forma, nos propomos fornecer uma visão geral das briófitas, cianobactérias e algas eucarióticas que compõem as biocrostas nestes afloramentos, caracterizamos o solo e os microhabitats onde as biocrostas crescem, exploramos padrões de co-ocorrência ao nível da comunidade e avaliamos o estado de conservação dos afloramentos rochosos brasileiros que podem abrigar comunidades complexas de CBSs.

Por fim, no Capítulo III investigamos a resposta de um musgo comum em biocrostas a concentrações crescentes de cálcio e, consequentemente, ao pH associado. Por ser um musgo bem representativo em biocrostas de distintos afloramentos rochosos com solos bem distintos quanto às concentrações de cálcio e pH, entender como essa espécie se comporta sobre essas condições pode esclarecer como as populações evoluíram para lidar com locais tão distintos – levantando hipóteses sobre adaptabilidade e ecótipos em musgos.

2. REFERENCIAL TEÓRICO

2.1. BRIÓFITAS

As briófitas são plantas que apresentam uma gama de características semelhantes, tais como seu pequeno tamanho, a ausência de sistema de transporte de água lignificado, o gametófito como fase de vida dominante e o esporófito como fase nutricionalmente dependente (GLIME, 2017). Entretanto, apesar das muitas semelhanças, o termo briófitas abrange três linhagens distintas de organismos que formam um grupo monofilético:

Bryophyta, Marchantiophyta e Anthocerotophyta - representados respectivamente pelos musgos, pelas hepáticas e pelos antóceros (GLIME, 2017). Elas são o segundo grupo de plantas mais diverso, com cerca de 21.925 espécies descritas, dentre as quais 12.700 são musgos (COX *et al*., 2014), 9.000 são hepáticas (CRANDALL-STOTLER & STOTLER, 2000) e 225 são antóceros (VILLARREAL *et al*., 2010). Já no Brasil existem cerca de 1.524 espécies de briófitas registradas (COSTA & PERALTA, 2015).

As briófitas, em especial os musgos e as hepáticas, podem ser um componente conspícuo da biocrostas, particularmente nos estágios posteriores do desenvolvimento da CBSs (LANGE *et al*. 1997). Os musgos são caracterizados pelos gametófitos folhosos, que possuem rizóides multicelulares e coloridos (GLIME, 2017). Já as hepáticas, podem possuir o gametófito taloso ou folhoso, e seus rizóides são unicelulares e hialinos (GLIME, 2017). Uma diferença marcante entre hepáticas e musgos é que elas apresentam uma orientação dorsiventral do gametófito (GLIME, 2017).

Quando presentes nas biocrostas, as briófitas contribuem com a estabilização do solo por reterem umidade e facilitarem a infiltração de água (ZHANG *et al*., 2009), promovem a formação de solo por acelerarem o intemperismo químico e físico de rochas e aprisionarem as partículas geradas (DANIN & GANOR, 1991) e ainda podem prover habitats para invertebrados, algas, cianobactérias, fungos e liquens (DAVIDSON, HARBORNE, & LONGTON *et al*., 1990). Algumas briófitas são muito importantes para a fixação de nitrogênio, pois essas podem possuir associações com bactérias e outros organismos fixadores desse nutriente (TURETSKY, 2003).

O que permite que as briófitas sobrevivam nos ambientes áridos que as biocrostas geralmente ocorrem são suas adaptações morfológicas e fisiológicas (SEPPELT *et al*., 2016). Entre elas, destacam-se a poiquilohidria (capacidade de redução do metabolismo da planta quando não há água no ambiente), a presença de ápices hialinos nos filídios, lamelas, papilas e células alares, que ajudam na retenção e distribuição de água (SCHOFIELD, 1981; FRAHM, 1996; VANDERPOORTEN & GOFFINET, 2009), e múltiplas formas de propagação, seja por meios sexuados ou assexuados (GLIME, 2017).

2.2. CIANOBACTÉRIAS E ALGAS EUCARIÓTICAS

As cianobactérias são seres procariotos (não apresentam plastos e núcleo verdadeiro) e fotossintetizantes, possuindo como pigmento principal a clorofila a (LEE, 2018; REVIERS, 2006). A maioria das espécies apresenta uma morfologia simples, sendo cocóides, filamentosas ou coloniais (LEE, 2018; REVIERS, 2006). Em biocrostas, as cianobactérias filamentosas são as primeiras colonizadoras, nas quais seus filamentos e a matéria orgânica exsudada estabilizam o solo e proporcionam o microclima necessário para que outros organismos se estabeleçam (BARAN *et al.*, 2015; BÜDEL *et al.*, 2016). Algumas adaptações estão presentes em algumas cianobactérias de CBSs para lidar com ambientes xéricos, tais como a produção de bainha espessa associada com substâncias que servem como um filtro solar (DILLON & CASTENHOLZ, 1999) e a capacidade de suportar uma perda da água intracelular por longos períodos de tempo (LEE, 2018).

Dentre os serviços ecológicos que elas prestam, destaca-se a fixação de nitrogênio. De forma geral, a fixação de nitrogênio nas cianobactérias ocorre devido a um processo enzimático, onde o gás nitrogênio é convertido em amônio, uma forma na qual o nitrogênio se torna disponível para as reações biológicas (REVIERS, 2006; LEE, 2018). No caso das cianobactérias filamentosas, a fixação do nitrogênio frequentemente é realiza no interior de heterocistos, que são células especializadas (LEE, 2018).

Diferentemente das cianobactérias, as algas são organismos eucariotos, possuindo núcleo circundado por um envoltório nuclear e plastos (LEE, 2018). Entretanto, esta definição para o termo “alga” abrange muitos grupos de organismos, que não são necessariamente filogeneticamente relacionados (LEE, 2018). Nas CBSs, os filos Chlorophyta, Charophyta, Euglenophyta e Heterokontophyta são os mais representativos, sendo que no filo Heterokontophyta, apenas as algas das classes Tribophyceae e Bacillariophyceae foram reportadas para as crostas biológicas (BELNAP, BÜDEL & LANGE, 2001; BÜDEL *et al.*, 2016).

Assim como as cianobactérias, as algas encontradas nas crostas biológicas também prestam serviços ecológicos importantes nos ambientes terrestres. Dentre eles, pode-se citar a fixação de carbono, a diminuição da erosão do solo e o aumento da infiltração e retenção de umidade (BÜDEL *et al.*, 2016). Entretanto, apesar destes serviços ecológicos prestados pelas algas, elas possuem uma importância secundária na formação de crostas biológicas (BELNAP, BÜDEL & LANGE, 2001). Isto ocorre por elas possuírem uma biomassa limitada e por dependerem de uma colonização prévia do solo por cianobactérias filamentosas para poderem se estabelecer (EVANS & JOHANSEN, 1999).

3. CAPÍTULO I

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 BSCs communities to others around the world, describe why BSCs can be considered ecosystem engineers and propose their use in the colonization of other worlds.

Key words: 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 proportions (Benalp *et al.*, 2001; Büdel, 2002; Benalp *et al.*, 2016) 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 BSCs succession (Benalp *et al.*, 2001). However, mosses can also be primary colonizers as an intermediate state of succession following disturbances (Gall *et al.*, 2022).

Constituting up to 12% of the earth's terrestrial surface (Rodriguez-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; Elbert *et al.*, 2012; Benalp *et al.*, 2016). 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 ancestor (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; Benalp, 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), 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 underrepresented 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, like 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 vs. 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 vs. 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) and Trindade *et al.* (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, likely 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 to compile 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, in 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 thesis. Nonetheless, these unpublished data have the potential to contribute significantly to improving knowledge regarding the taxonomy, geographic distribution and applied ecology of Brazilian BSCs.

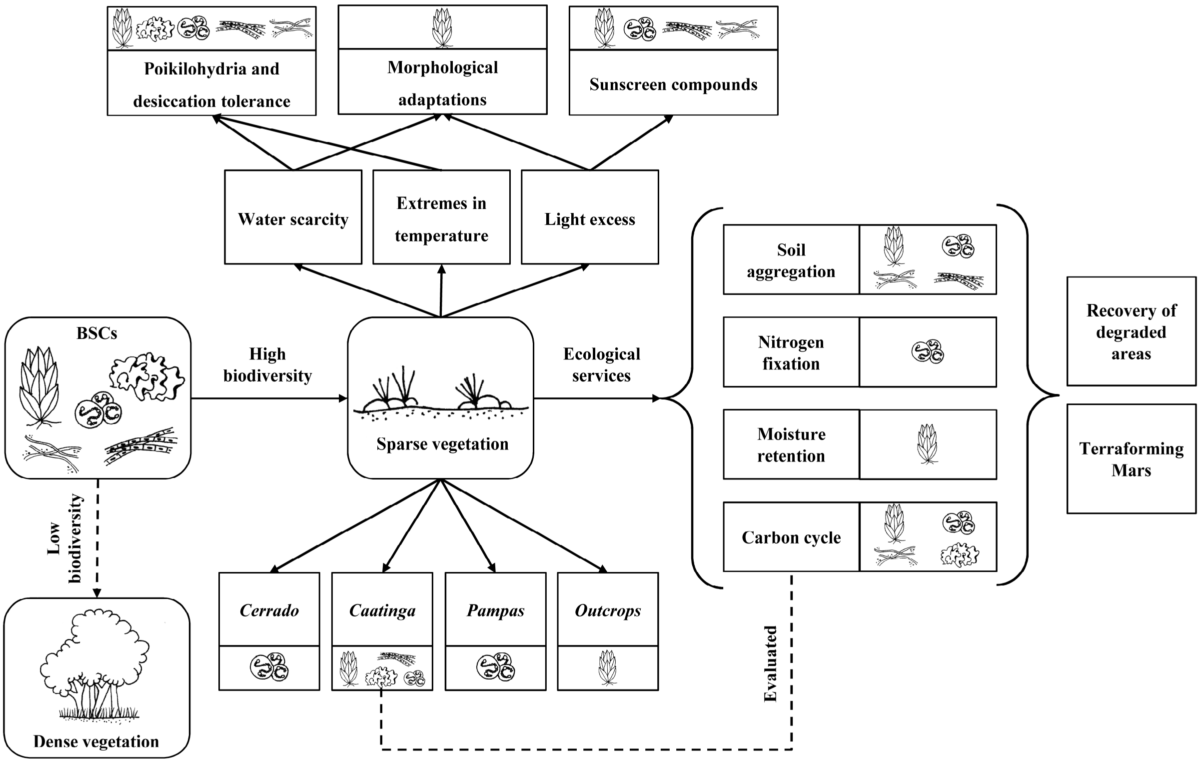

Fig. 1 - An overview of knowledge about biological soil crusts.

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 entire biodiversity of the *Caatinga*, including its community of BSCs. Despite encompassing 862,636 km^2 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 BSCs 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 km^2 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 km^2 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 km^2 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 5,876 km^2 protected by Conservation Units (CNUC, 2020).

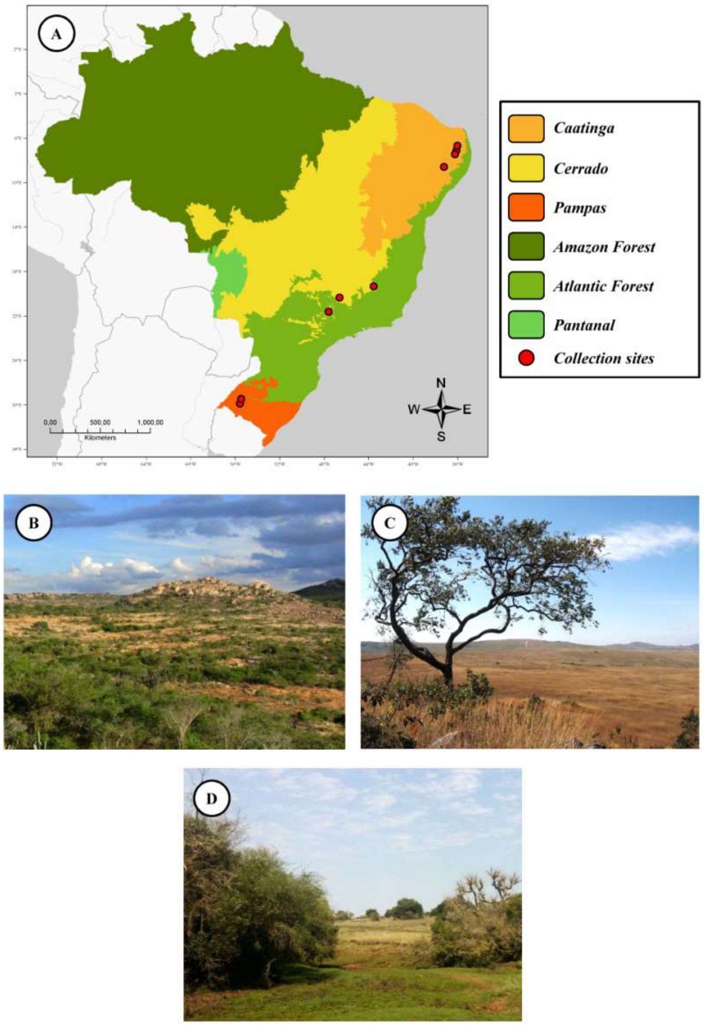

Fig. 2 - The homes of Brazilian BSCs. (A) Collection sites. (B) Caatinga. (C) Cerrado. (D) Pampas. Photos by Nivea Dias dos Santos (B) and Elisa Teixeira Aires (D).

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 outcrop) 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 can not 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) has 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.

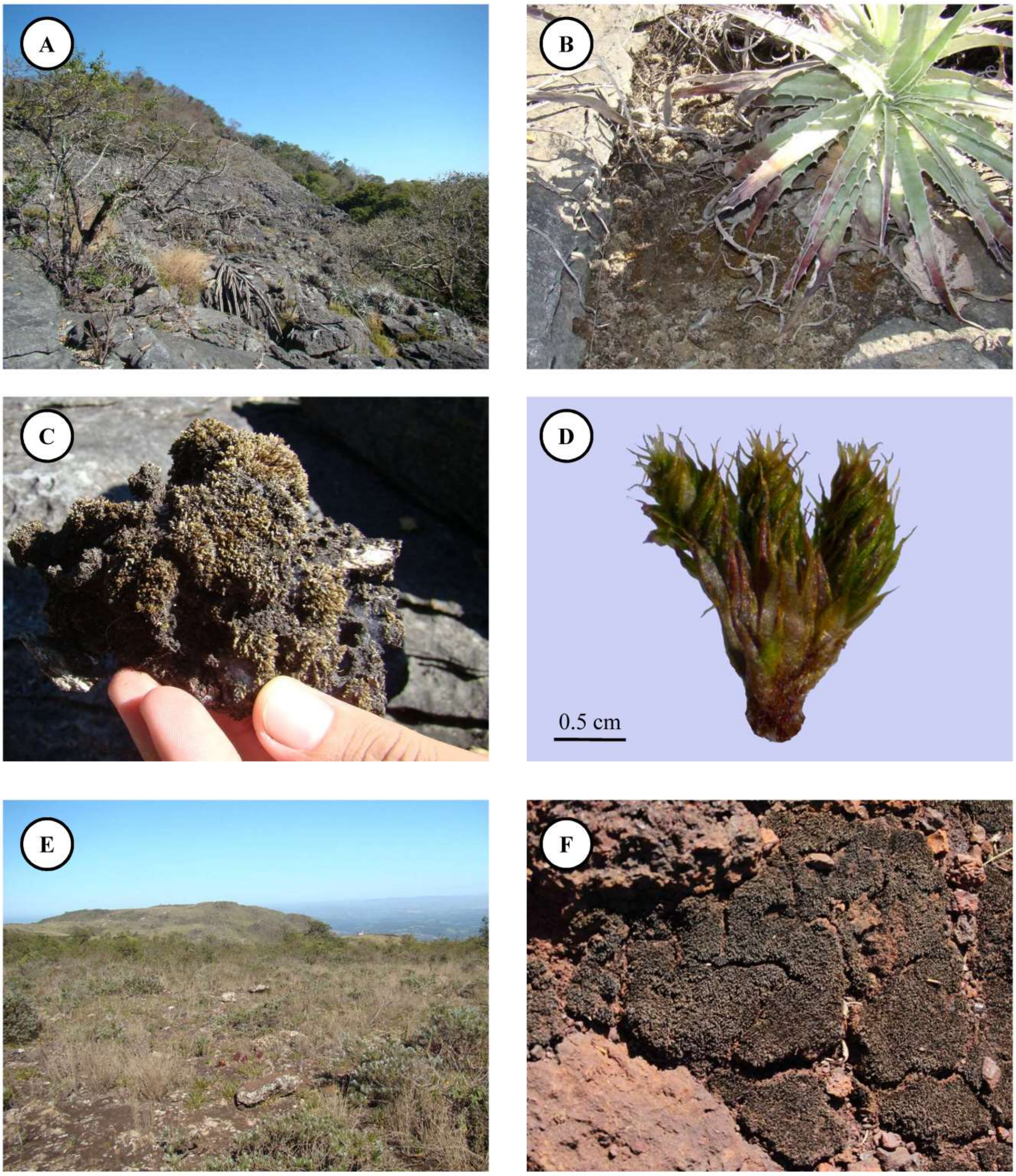

Fig. 3 - BSCs in smaller ecosystems of Brazil. (A) Karst area. (B) Biocrusts growing in a limestone rock crevice. (C) Moss dominated biocrust. (D) *Bryum atenense* R.S. Williams, a moss species common in biocrusts of karst areas. (E) Ironstone outcrop with sparse vegetation. (F) Biocrust (photo by Pablo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

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 published literature). Machado-de-Lima *et al.* (2019), Machado-de-Lima & Branco (2020) and Machado-de-Lima *et al.* (2021) 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 ca. 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; Szyja *et al.*, 2019; Machado-de-Lima and Branco, 2020; Machado-de-Lima *et al.*, 2021). The *Caatinga* has the greatest diversity of BSC cyanobacteria, with six new species being recently described for this ecosystem by Machado-de-Lima & Branco (2020), showing the importance of studying BSCs in environments of tropical countries.

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

Cyanobacteria	
Species	**References**
Aetokthonos S.B.Wilde & J.R.Johansen	Machado-de-Lima *et al*. (2019).
Aphanocapsa C. Nägeli	Szyja *et al*. (2019).
Brasilonema Fiore, Sant-Anna, de Paiva Azevedo, Komarek, Kastovsky, Sulek & Lorenzi	Machado-de-Lima *et al*. (2019).
Calothrix C. Agardh ex Bornet & Flahault	Szyja *et al*. (2019).
Chroococcidiopsis Geitler	Szyja *et al*. (2019); Machado-de-Lima *et al*. (2019).
Desmonostoc P. Hrouzek & S.Ventura	Machado-de-Lima *et al*. (2019).
Gloeocapsa Kützing	Szyja *et al*. (2019).
Gracilinea arenicola Machado de Lima & L.H.Z. Branco	Machado-de-Lima & Branco (2020).
Hassallia Berkeley ex Bornet & Flahault	Machado-de-Lima *et al*. (2019).
Komvophoron K .Anagnostidis & J. Komárek	Machado-de-Lima *et al*. (2019).
Koniacronema caatingensis Machado de Lima & L.H.Z. Branco	Machado-de-Lima & Branco (2020).
Leptolyngbya Anagnostidis & Komárek	Szyja *et al*. (2019); Machado-de-Lima *et al*. (2019); Machado-de-Lima *et al*. (2021).
Macrochaete lichenoides Berrendero, J.R. Johansen &Kastovsky	Szyja *et al*. (2019).
Marmoreocelis xerophila Machado de Lima & L.H.Z. Branco	Machado-de-Lima & Branco (2020).
Mastigocladus Cohn ex O.Kirchner	Machado-de-Lima et al. (2019).
Microcoleus vaginatus Gomont ex Gomont	Szyja et al. (2019); Machado-de-Lima et al. (2019).
Microcoleus steenstrupii J.B. Petersen	Machado-de-Lima et al. (2019); Machado-de-Lima et al. (2021).
Microcystis Lemmermann	Machado-de-Lima et al. (2019).

Table 1 – Cont.

Cyanobacteria	
Species	**References**
Nostoc Vaucher ex Bornet &Flahault	Szyja *et al*. (2019); Machado-de-Lima *et al*. (2019); Machado-de-Lima *et al*. (2021).
Nostoc edaphicum Kondrateva	Szyja *et al*. (2019).
Nostoc ellipsoideum N.L. Gardner	Szyja *et al*. (2019).
Nostochopsis H.C.Wood ex É. Bornet & C. Flahault	Machado-de-Lima *et al*. (2019).
Oculatella Zammit, Billi & Albertano	Machado-de-Lima *et al*. (2019).
Oscillatoria Vaucher ex Gomont	Szyja *et al*. (2019).
Pantanalinema Vieira Vaz *et al*.	Machado-de-Lima *et al*. (2019).
Phormidesmis Turicchia, Ventura, Komárková & Komárek	Machado-de-Lima *et al*. (2019).
Porphyrosiphon Kützing ex M. Gomont	Machado-de-Lima *et al*. (2019).
Porphyrosiphon notarisii Kützing ex Gomont	Machado-de-Lima *et al*. (2021).
Potamolinea M.D. Martins & L.H.Z. Branco	Machado-de-Lima *et al*. (2019).
Potamosiphon G.B. McGregor & B.C. Sendall	Machado-de-Lima *et al*. (2019).
Prochlorococcus Chisholm, Frankel, Goericke, Olson, Palenik, Waterbury, West-Johnsrud & Zettler	Machado-de-Lima *et al*. (2019).
Pseudophormidium (Forti) Anagnostidis & Komárek	Szyja *et al*. (2019); Machado-de-Lima *et al*. (2019).
Pycnacronema M.D. Martins & Branco	Machado-de-Lima *et al*. (2019).
Pycnacronema caatingensis Machado-de-Lima & L.H.Z. Branco	Machado-de-Lima & Branco (2020).
Pycnacronema edaphica Machado-de-Lima & L.H.Z. Branco	Machado-de-Lima & Branco (2020).
Schizothrix Kützing ex Gomont	Szyja *et al*. (2019).
Schizothrix acutíssima Drouet	Machado-de-Lima *et al*. (2021).
Schizothrix telephoroides Gomont	Machado-de-Lima *et al*. (2021).
Scytonema C.Agardh ex É. Bornet & C. Flahault	Szyja *et al*. (2019); Machado-de-Lima *et al*. (2019).
Scytonema hyalinum N.L. Gardner	Szyja *et al*. (2019).
Scytonema guyanense Bornet &Flahault	Machado-de-Lima *et al*. (2021).
Scytonema javanicum Bornet ex Bornet & Flahault	Machado-de-Lima *et al*. (2021).
Scytonema ocellatum Lyngbye ex Bornet & Flahault	Machado-de-Lima *et al*. (2021).
Stigonema C. Agardh ex Bornet &Flahault	Szyja *et al*. (2019); Machado-de-Lima *et al*. (2019).
Stigonema ocellatum Thuret ex Bornet &Flahault	Machado-de-Lima *et al*. (2021).
Tolypothrix Kützing ex Bornet &Flahault	Szyja *et al*. (2019).
Trichocoleus caatingensis Machado-de-Lima & L.H.Z. Branco	Machado-de-Lima & Branco (2020).
Trichormus (Ralfs ex Bornet &Flahault) Komárek & Anagnostidis	Machado-de-Lima *et al*. (2019).

Green algae	
Species	**References**
Chlorella Beij.	Szyja *et al*. (2019).
Cylindrocystis brebissonii Menegh.	Szyja *et al*. (2019).
Desmococcus F. Brand	Szyja *et al*. (2019).
Follicularia V.V. Miller	Szyja *et al*. (2019).
Heterococcus Chodat	Szyja *et al*. (2019).
Klebsormidium P.C. Silva, Mattox & W.H. Blackwell	Szyja *et al*. (2019).
Macrochloris multinucleata (Reisigl) Ettl & Gärtner	Szyja *et al*. (2019).
Neochloris Starr	Szyja *et al*. (2019).

Table 1 – Cont.

Green algae

Species	**References**
Scenedesmus Meyen	Szyja *et al*. (2019).
Scotiellopsis rubescens Vinatzer	Szyja *et al*. (2019).
Spongiochloris Star	Szyja *et al*. (2019).
Stichococcus Nägeli	Szyja *et al*. (2019).

Lichens

Species	**References**
Bibbya cf. *albomarginata* (H. Kilias&Gotth. Schneid.) Kistenich *et al.*	Szyja *et al*. (2019).
Buellia De Not.	Szyja *et al*. (2019).
Cladonia P. Browne	Trindade *et al*. (2005).
Cladonia foliacea (Huds.) Willd.	Szyja *et al*. (2019).
Cladonia verticillaris (Raddi) Fr.	Szyja *et al*. (2019).
Heppia conchiloba Zahlbr.	Szyja *et al*. (2019).
Lecidea Ach.	Szyja *et al*. (2019).
Peltula michoacanensis (B. de Lesd.) Wetmore	Szyja *et al*. (2019).

Liverworts

Species	**References**
Riccia L.	Szyja *et al*. (2019).
Riccia vitally Jovet-Ast	Szyja *et al*. (2019).

Mosses

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

Conversely 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 Brazilians 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.

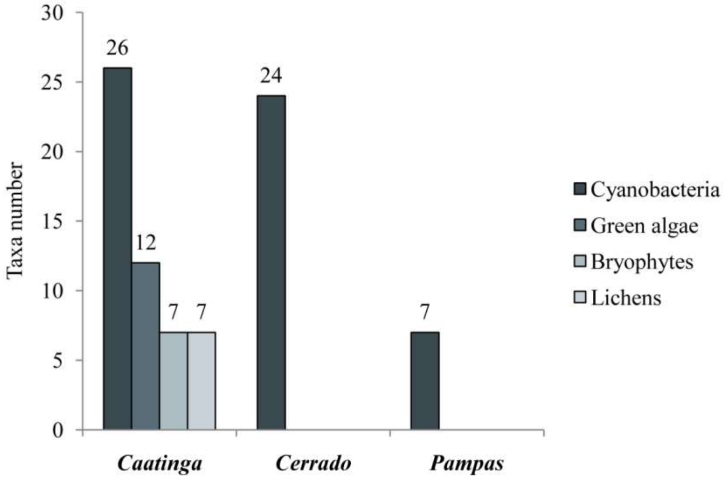

Fig. 4 -The number of taxa recorded for BSCs in each major Brazilian ecosystem.

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 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 cyanobacteria and eukaryotic algae composition in the Gurbantunggut Desert (China) to 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 site.

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 to 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**.

As 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 R Core Team software (2020), we calculated 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 of R Core Team (2020).

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

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

Our analysis found that the community composition of biocrusts in different Brazilian biomes were not similar to the composition of BSCs in comparable biomes worldwide (**Fig. 5**). We found that 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 vs. 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 nor mention the biome where biocrusts occur, thus complicating our data compilation.

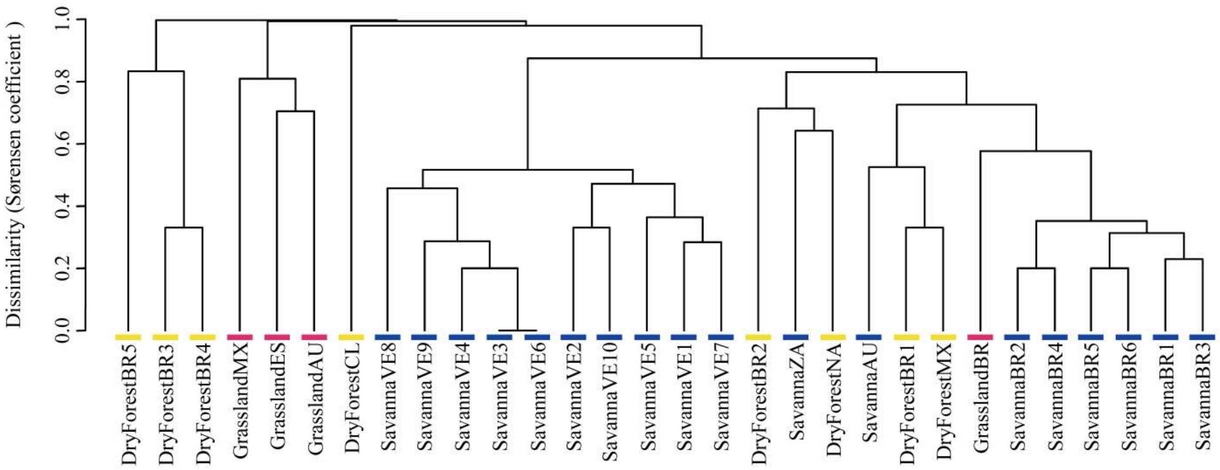

Fig. 5 - Dendrogram groupings based on dissimilarity for all biocrust communities in biomes worldwide (correlation coefficient = 0.91). Yellow: dry forests, pink: grasslands, blue: savannas. For details about site abbreviations, see **Table 2**.

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 poikilohydria 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 (Benalp *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; Smirnoff, 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 are 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).

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*.

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 Smirnoff, 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 fungus 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 (Garcia-Pichel and Wojciechowski, 2009; Benalp *et al*., 2001; 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 *Zygogonium*, 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* (Szyja *et al.*, 2019; Machado-de-Lima *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 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 (Colesie *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 biological soil crusts 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 (Garcia-Pichel and Wojciechowski, 2009; Benalp *et al.*, 2016; Eldridge and Rosentreter, 1999; Gundlapally and Garcia-Pichel, 2006), fixing nitrogen and carbon (Benalp *et al.*, 2001; Wu *et al.*, 2009; Zhao *et al.*, 2010), 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). In Brazil, an unprecedented method of BSC inoculation of disturbed *campos rupestres* has shown promising results for bryophyte and vascular plant establishment after one year (Scotti-Muzzi *et al.*, in prep).

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, Vera *et al.*, 2019; Huwe *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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4. CAPÍTULO II

Brazilian rocky outcrops as tropical refuges for biological soil crusts

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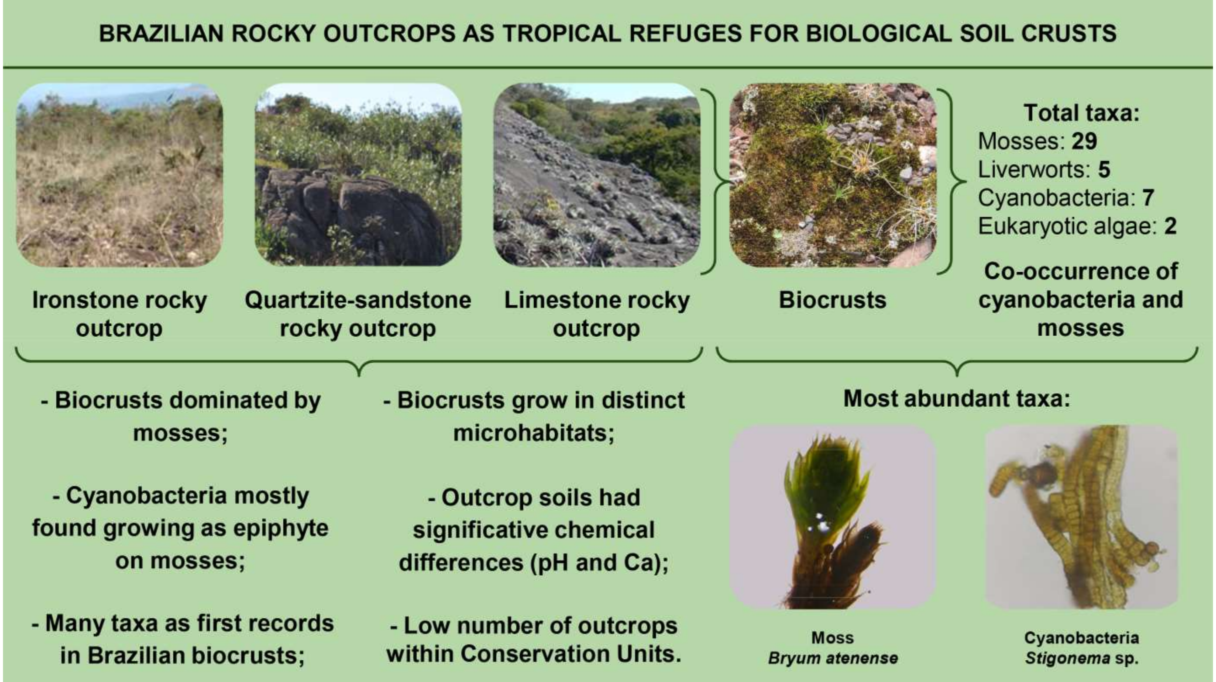
Highlights

- Brazilian outcrops are refuges for moss-dominated biocrusts.
- Co-occurrence of species may indicate a moss-cyanobacteria association.
- Outcrops microhabitats and their chemical features act filtering biocrust communities.
- Few outcrops are inserted in Brazilian Conservation Units.

Graphical abstract



- Biocrusts dominated by mosses;

- Cyanobacteria mostly found growing as epiphyte on mosses;

- Many taxa as first records in Brazilian biocrusts;

- Biocrusts grow in distinct microhabitats;

- Outcrop soils had significative chemical differences (pH and Ca);

- Low number of outcrops within Conservation Units.

Abstract

Biological soil crusts are communities structured by the interaction between bacteria, fungi, eukaryotic algae, cyanobacteria, lichens and bryophytes over the most superficial particles of the soil. These complex communities are mostly found in arid and semiarid regions, but they can also be conspicuous members of the vegetation in moist tropical ecosystems. This study explored for the first time ecological aspects of biocrusts in three of the most common types of rocky outcrops in Brazil — ironstone, quartzite-sandstone and limestone. Thirty-four bryophyte species (29 mosses and 5 liverworts), seven genera of cyanobacteria and one genus each of the algae groups Charophyta and Chlorophyta were identified. Twenty-four of the species (19 mosses and 5 liverworts) have never been previously reported in biocrusts associations in any ecosystem. Seven microhabitats were characterized where biocrusts were found and a single composition of microhabitats was noted for each study site. Soil composition of each studied rocky outcrop showed that pH, total acidity, and phosphorus, organic matter, calcium, and iron concentrations were the characteristics that best differentiated the analyzed soils. Positive co-occurrence patterns were determined in two of the studied outcrops (ironstone and limestone), indicating a possible ecological interaction between mosses and cyanobacteria. The three studied types of Brazilian rocky outcrops differ in their proportions that are within Conservations Unites (CUs). Ironstone and limestone rocky outcrops are the most threatened, with only 0.25% and 5.11% of sites within CUs, respectively. These findings corroborate the importance of preserving multiple rocky outcrops, as they harbor significant biodiversity, including very specific biocrust communities. We encourage future inventories and conservation efforts involving rocky outcrops throughout the world, as biocrusts in these ecosystems are poorly studied and commonly ignored.

Key words: biocrusts; conservation; cyanobacteria; microhabitats; mosses; outcrops.

Nomenclature: Gradstein et al. (2001) and references therein for mosses; Gradstein and Costa (2003) for liverworts and Guiry and Guiry (2023) for eukaryotic algae and cyanobacteria.

1. Introduction

Biological soil crusts (BSCs), also called biocrusts, are a complex community of photoautotrophic and heterotrophic poikilohydric organisms including eukaryotic algae, cyanobacteria, mosses, liverworts, lichens, fungi, bacteria and archaea (Soule et al., 2009; Büdel et al., 2016; Maier et al., 2016; Rosentreter et al., 2016; Seppelt et al., 2016). They provide important ecological services, such as nitrogen and carbon fixation (Barger et al., 2016; Sancho et al., 2016), aggregation and stabilization of soil particles (Bowker et al., 2013; Faist et al., 2017) and soil moisture retention (Chamizo et al., 2016; Eldridge et al., 2020). The dynamics of the ecological services provided by the BSC community as a whole can be impacted by the co-occurrence of different taxa, since they participate in distinct ecological interactions (Bowker et al., 2010; Maestre et al., 2008, 2009).

Biocrusts live on the topsoil layer in water-limited ecosystems with low vascular plant cover (Belnap et al., 2016; Weber et al., 2022), being a conspicuous component of vegetation in arid and semi-arid regions (West, 1990; Belnap et al., 2001). The occurrence of BSCs is therefore more common and relevant in hot and cold deserts (e.g., Rozenstein and Karnieli, 2015; Pushkareva et al., 2018), but they are also present in steppes (e.g., Biazrov, 2015), grassland regions (e.g., Castillo-Monroy et al., 2010), savannas (e.g., José and Bravo, 1991) and dry forests (e.g., Maya and López-Cortés, 2002). Furthermore, although biocrusts are usually not expected to be either abundant or ecologically relevant in tropical environments (Belnap et al., 2001), they are indeed present in rocky outcrops embedded in different moist tropical Brazilian ecosystems (Oliveira and Maciel-Silva, 2022).

By definition, rocky outcrops are geological formations comprised by exposed bedrock, and can be found on all continents (Fitzsimons and Michael, 2017). They have sandy, shallow and nutrient deficient soils (Messias et al., 2013) and, in some cases, the geology of each type of rock affects soil characteristics like depth and drainage (Messias et al., 2011). Thereby, different types of rocky outcrops are formed depending on the type of exposed matrix rock, such as sandstone escarpments, granite outcrops, limestone cliffs and gneissic tors (Larson et al., 2005; Migon, 2006). This study will focus on biocrusts potentially present in ironstone, quartzite-sandstone and limestone rocky outcrops of Brazil.

Ironstone rocky outcrops, locally known as *Cangas* (Jacobi and Carmo, 2008), are characterized by high concentrations of iron (Carmo and Kamino, 2015) and by mosaics of smooth surfaces, fissures, holes and boulders where the plant community establishes and develops (Jacobi et al., 2007). Quartzite-sandstone rocky outcrops present exposed rocks and recently-decomposed stony, sandy or colluvial soils that serve as substrates for the plant mosaic composed of shrubs and subshrubs (Messias et al., 2011). Finally, limestone rocky outcrops constitute the most superficial part of karst formations (Ford and Williams, 2007), where rupicolous xerophytic communities of plants grow directly or into crevices or fissures of rocks (Pérez-García and Meave, 2005; Zhu et al., 2017). Unfortunately, annual anthropogenic burnings, grazing, uncontrolled urbanization, tourism expansion, deforestation, non-native invasive species, land exploitation and mining threaten the conservation status of these rocky outcrops (Giulietti et al., 1997; Safford, 2000; Jacobi and Carmo, 2008; Kolbek and Alves, 2008; Barbosa et al. 2010; Auler and Piló, 2015a, b; Porembski et al., 2016; Salles et al., 2019).

On a global scale, BSC communities of rocky outcrops have been poorly investigated, with some exceptions of studies on limestone outcrops in China (e.g. Chen et al., 2014; Hu et al., 2019) and granite outcrops in Antarctica (e.g., Colesie et al., 2014) and Australia (e.g., Briggs and Morgan, 2008). Only recently have biocrusts been recognized as singular and conspicuous communities on rocky outcrops in Brazil (Oliveira and Maciel-Silva, 2022). To our knowledge, the present study is the first to investigate biocrust communities in rocky outcrops in Brazil. Thus, our aims were: (I) to provide an overview of the bryophytes, cyanobacteria and eukaryotic algae that compose the biocrusts in three different types of rocky outcrops — ironstone, quartzite-sandstone and limestone; (II) to characterize the soil and microhabitats where biocrusts grow in each outcrop type; (III) to explore co-occurrence patterns at the community level; and (IV) to evaluate the conservation status of Brazilian rocky outcrops where BSCs may occur.

2. Material and methods

2.1. *Study sites*

Field study took place at three distinct rocky outcrops embedded within transitional vegetation between *Cerrado* (Brazilian savannah) and Atlantic Forest in the state of Minas Gerais, Southeast Brazil (Brina, 2020; Jacobi et al., 2007, 2008). The sites of the ironstone rocky outcrop (IRO; **Fig. 1A**) and the quartzite-sandstone rocky outcrop (QRO**; Fig. 1B**) are located in the Natural Monument Serra da Calçada (20°05’43”S, 43°58’59”W and 20°06’08”S, 43°59’27”W, respectively), with minimum and maximum mean annual temperatures of 11.8°C and 23.9°C, respectively, and mean annual rainfall of 1,559 mm (WorldClim 2 data; Fick and Hijmans, 2017). The site of the limestone rocky outcrop (LRO; **Fig. 1C**) is located in the Environmental Protection Area of Lagoa Santa Karst (19°32'56"S,43°59'34"W), with minimum and maximum mean annual temperatures of 15.6°C and 27.7°C, respectively, and mean annual rainfall of 1,321 mm (WorldClim 2 data; Fick and Hijmans, 2017).

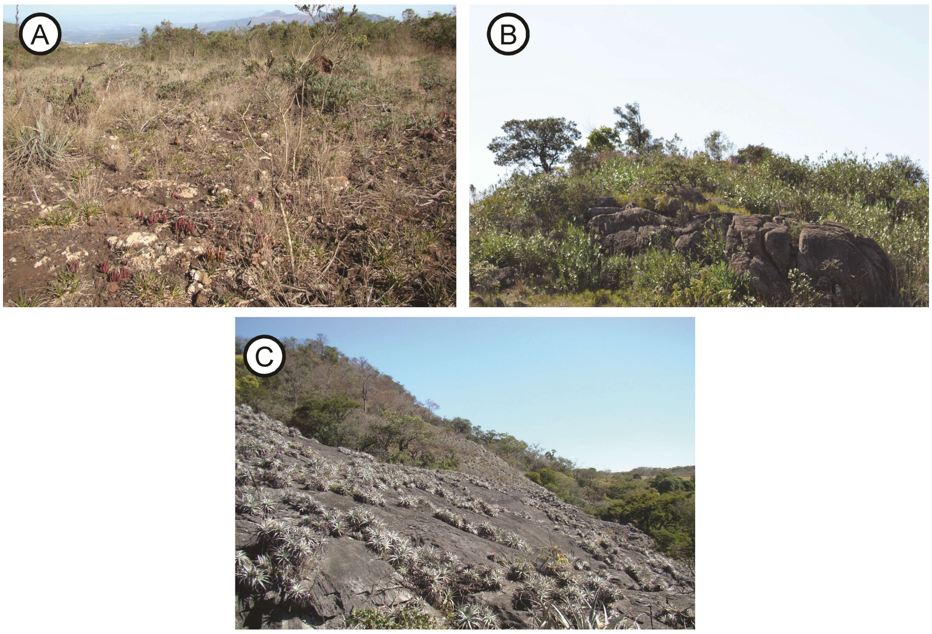


Fig. 1 – Brazilian rocky outcrops where biocrusts were sampled. A – Ironstone rocky outcrop in the Natural Monument Serra da Calçada. B – Quartzite-sandstone rocky outcrop in the Natural Monument Serra da Calçada. C – Limestone rocky outcrop in the Environmental Protection Area of Lagoa Santa Karst.

2.2. *Biocrust sampling and inventory*

Samples of BSCs were collected according to Schulz et al. (2016) during field campaigns to the three study rocky outcrops in March – June 2019. The collection campaigns lasted about four hours in each outcrop, with three researches actively searching for biocrusts. Samples (ca. 100 cm^2 and at least 1m apart) were taken from the topsoil layer by gently inserting a spatula into the substrate. Samples were carefully stored in small paper bags and were subsequently air dried. The taxonomical composition of the sampled BSCs was analyzed with a stereomicroscope and a light microscope. All bryophytes (e.g., mosses and liverworts) were identified to species level (following Frahm, 1991; Gradstein et al., 2001; Gradstein and

Costa, 2003; Costa, 2016; Canestraro and Peralta, 2022). Cyanobacteria and eukaryotic algae were identified to genus level (following Komárek and Anagnostidis, 1999, 2005; Hoppert et al., 2004; Komárek, 2013; Samolov et al., 2020; Hakkoum et al., 2021). Voucher specimens were deposited in the BHCB herbarium (Departamento de Botânica, Universidade Federal de Minas Gerais).

2.3. *BSC microhabitat description*

Rocky outcrop environments were classified into microhabitats for BSCs based on Peñaloza-Bojacá et al. (2018), Jacobi et al. (2007), Jacobi and Carmo (2012), Porembski et al. (1994) and Porembski and Barthlott (2000). Since these studies were not focused on BSCs, some adaptations were necessary to adjust the classification to BSC microhabitats. Thus, the microhabitats where BSCs were found were characterized according to soil depth (more or less than 10 cm), presence of superficial stones from the matrix rock (with a maximum diameter of 8 cm), presence of shadow (due to shrubs, grasses or self-shading) and association with vascular plants (shrubs or grasses) and insect nests over the soil.

Six soil samples (ca. 300g) were collected from each site according to Lemos and Santos (2002) for chemical characterization. These samples were taken at least 2m apart and from the topsoil (0–20 cm) below biocrust communities and packed in properly labeled plastic bags. The soil samples were dried in an oven for 72 hours at 40°C and then sent to the Soil Analysis Laboratory of the Universidade Federal de Lavras, Brazil. All chemical analyses were performed according to Embrapa (1997, 1999).

2.4. *Brazilian rocky outcrops in Conservation Units*

Even though BSCs were not studied as focal components of vegetation in Brazilian rocky outcrops, some components of biocrusts like bryophytes and lichens were found in the soil of some of these ecosystems by many authors (e.g. Silva and Germano, 2013; Carmo and Peralta, 2016; Cáceres et al., 2017; Oliveira-da-Silva and Ilkiu-Borges, 2018; Peñaloza-Bojacá *et al.*, 2018; Oliveira *et al.*, 2021). These reports suggest that Brazilian outcrops can be expected to harbor rich biocrust diversity (Oliveira and Maciel-Silva 2022). So, even biocrusts were not collected from granite-gneiss rocky outcrops (GRO) in our study, they were included, along with ironstone, quartzite-sandstone and limestone rocky outcrops, in the current conservation analysis due to their potential to harbor conspicuous biocrust communities. So, to evaluate the conservation status of the most common Brazilian rocky outcrops and to generate a relevant framework for future effective conservation actions, the geographical occurrence of these ecosystems was overlapped with that of Brazilian Conservation Units (CU). This process used the geographic coordinates of rocky outcrops from the AFLO data base providedby Geosciences System of the Geological Survey of Brazil - CPRM (https://geosgb.cprm.gov.br/). Since we were interested in four specific types of outcrops (ironstone, quartzite-sandstone, limestone and granite-gneiss), the available data were filtered according to the rock matrix of each outcrop (itabirite, quartzite, limestone and granite-gneiss, respectively). The locations of rocky outcrops were subsequently plotted along with those for the Brazilian Conservation Units (available on https://doi.org/10.55881/CEM.db.unc001) using ArcGIS 10.1 software (Esri, Redlands, California, USA).

2.5. *Statistical analysis*

We explored patterns of taxa co-occurrence in BSCs by Veech's method (Veech, 2013), which was performed with the 'cooccur' package (Griffith et al., 2016) in R 4.0.2 software (Team, 2020). We created a species coincidence matrix (presence/absence of taxa in each biocrust sample) for each studied rocky outcrop, in which the probabilistic approach removed expected co-occurrences < 1from the analysis. Finally, positive, negative or random co-occurrence patterns of pairs of taxa were determined.

To characterize the soil of each outcrop, chemical variables for the three studied rocky outcrops were compared by Multivariate Analysis of Variance (MANOVA), performed in R 4.0.2 software (Team, 2020). We grouped the variables into two categories (chemical features and concentrations of chemical elements) and performed the MANOVA for each of them. To meet the assumptions of a normal distribution of data residuals and homogeneity of variances, data were previously transformed into $\log_{10}(□ + 1)$. For some specific soil variables, we used R 4.0.2 software (Team, 2020) to perform a one-way analysis of variance (ANOVA) followed by Tukey's test to verify differences between the rocky outcrops.

3. Results

3.1. *Biocrust community composition*

The BSC surveys resulted in 128 samples: 73 from the ironstone outcrop (IRO), 29 from the quartzite-sandstone outcrop (QRO) and 27 from the limestone outcrop (LRO). A total of 317 specimens were identified, representing five phyla (in decreasing order of number of taxa: Bryophyta > Cyanobacteria > Marchantiophyta > Chlorophyta = Charophyta), 23 families, 29 genera and 43 species (**Table 1, Supplementary Table A**). Some of the species are notorious for being part of BSCs around the world, but many species were also registered as part of these complex communities for the first time (first records in BSCs are indicated by an * in **Table 1)**. The thalloid liverwort *Metzgeria lechleri* and the mosses *Holomitrium crispulum*, *Sematophyllum subpinnatum* and *Schlotheimia rugifolia*, for example, have not been previously reported as components of biocrusts from many ecosystems.

Table 1 - Species found in biological soil crusts and the number of colonies per area. IRO – Ironstone rocky outcrop, QRO- Quartzite-sandstone rocky outcrop, LRO – Limestone rocky outcrop. First records in BSCs are indicated by an ***.**

Bryophyta	Sampled areas		
	IRO	**QRO**	**LRO**
Bartramiaceae			
Philonotis hastata (Duby) Wijk & Margad.*	-	-	1
Bryaceae			
Bryum arachnoideum Müll. Hal.*	-	-	2
Bryum argenteum Hedw.	8	-	3
Bryum atenense R. S. Williams	29	3	15
Bryum chryseum Mitt*.	-	-	1
Bryum leptocladon Sull.*	-	3	-
Rosulabryum billardierei (Schwägr.) Spence	1	-	-
Rosulabryum capillare (Hedw.) J.R. Spence	1	-	-
Dicranaceae			
Dicranella hilariana (Mont.) Mitt	-	2	-
Holomitrium crispulum Mart.*	1	-	-
Erpodiaceae			
Erpodium coronatum (Hook. f. & Wilson) Mitt.*	-	-	1
Fissidentaceae			
Fissidens flaccidus Mitt.*	-	-	1
Helicophyllaceae			
Helicophyllum torquatum (Hook.) Brid.*	-	-	4
Leucobryaceae			
Campylopus arctocarpus (Hornsch.) Mitt.*	-	1	-
Campylopus carolinae Grout*	-	1	-
Campylopus heterostachys (Hampe) A. Jaeger*	-	5	-

Table 1. Cont.

Bryophyta		Sampled areas	
	IRO	**QRO**	**LRO**
Leucobryaceae			
Campylopus lamellinervis (Müll. Hal.) Mitt.*	3	-	-
Campylopus savannarum (Müll. Hal.) Mitt.*	27	-	-
Orthotrichaceae			
Schlotheimia rugifolia (Hook.) Schwägr.*	1	-	-
Polytrichaceae			
Pogonatum pensilvanicum (Hedw.) P. de Beauv*	-	1	-
Polytrichum commune Hedw.	-	1	-
Polytrichum juniperinum Hedw.	4	2	-
Pottiaceae			
Plaubelia sprengelli (Schwägr.) R.H. Zander*	-	-	1
Tortella humilis (Hedw.) Jenn.	5	-	14
Trichostomum arboreum (Mitt.) R.H. Zander*	1	-	-
Trichostomum tenuirostre (Hook. & Taylor) Lindb.*	-	-	2
Weissia controversa Hedw.	-	-	1
Sematophyllaceae			
Sematophyllum subpinnatum (Brid.) E. Britton*	1	-	-
Total	104	33	46

Charophyta		Sampled areas	
	IRO	**QRO**	**LRO**
Zygnemataceae			
Zygogonium sp. Kützing	7	13	-
Total	7	13	0

Chlorophyta		Sampled areas	
	IRO	**QRO**	**LRO**
Radiococcaceae			
Gloeocystis sp. Nägeli	13	1	-
Total	13	1	0

Cyanobacteria		Sampled areas	
	IRO	**QRO**	**LRO**
Aphanothecaceae			
Gloeothece sp. C. Nägeli	6	1	-
Microcoleaceae			
Microcoleus sp. Desmazières ex Gomont	4	4	1
Nostocaceae			
Nostoc sp. Vaucher ex Bornet & Flahault	-	-	9
Oscillatoriaceae			
Oscillatoria sp. Vaucher ex Gomont	3	3	4
Pseudanabaenaceae			
Jaaginema sp. Anagn. & Komárek	-	-	1
Scytonemataceae			
Scytonema sp. C.Agardh ex É.Bornet & C.Flahault	5	1	19
Stigonemataceae			
Stigonema sp. C.Agardh ex Bornet & Flahault	32	1	-
Total	50	10	34

Table 1. Cont.

Marchantiophyta	Sampled areas		
	IRO	**QRO**	**LRO**
Frullaniaceae			
Frullania brasiliensis Raddi*	1	-	-
Frullania dusenii Steph.*	1	-	-
Frullania kunzei (Lehm. & Lindenb.) Lehm. & Lindenb.*	1	-	-
Metzgeriaceae			
Metzgeria lecheri Steph.*	2	-	-
Plagiochilaceae			
Plagiochila corrugata (Nees) Nees & Mont.*	1	-	-
Total	6	0	0

The greatest number of taxa was for IRO (25 of 180 specimens), while QRO and LRO had the same number (17 of 57 and 80 specimens, respectively). Interestingly, each studied outcrop had a unique species composition. Some taxa were recorded for two or all three studied outcrops. Among the mosses, only *Bryum atenense* (**Fig. 2A**) was present in all three outcrops, while *Bryum argenteum* (in IRO and LRO), *Campylopus lamellatus* (in IRO and QRO, **Fig. 2B**), *Polytrichum juniperinum* (in IRO and QRO) and *Tortella humilis* (in IRO and LRO, **Fig. 2C**) were all present in two. The cyanobacteria *Microcoleus* sp., *Oscillatoria* sp. and *Scytonema* sp. (**Fig. 2D**) were present in all three outcrops, while *Gloeothece* sp. and *Stigonema* sp. (**Fig. 2E**) were only observed in IRO and QRO. The same pattern was observed for the two eukaryotic algae *Gloeocystis* sp. and *Zygogonium* sp. (**Fig. 2F**), being present in IRO and QRO.

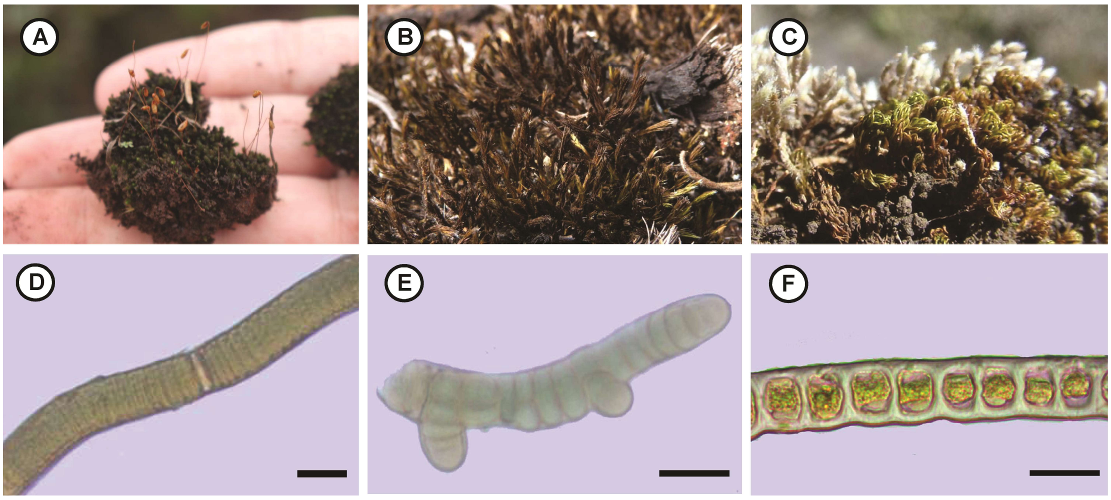


Fig. 2- Some biocrust taxa shared between the studied Brazilian rocky outcrops. A – *Bryum atenense*. B- *Campylopus lamellatus*. C- *Tortella humilis*. D- The filamentous cyanobacteria *Scytonema* sp., with heterocyst. E- *Stigonema* sp., the true-branched filamentous cyanobacterium. F- The filamentous green algae *Zygogonium* sp. Scale bars correspond to 20 µm.

Each of the three outcrops had exclusive species, with 13 species recorded only at IRO, seven only at QRO and 11 only at LRO. Only IRO had liverworts in biocrusts, while LRO had *Nostoc* sp. and *Jaaginema* sp. as exclusive cyanobacteria. Some examples of BSC taxa that were exclusive to one of the three studied Brazilian rocky outcrops are: *Campylopus lamellinervis* (**Fig, 3A**), *Rosulabryum billardierei* (**Fig. 3B**) and *Frullania brasiliensis* (**Fig. 3C**) for IRO; *Campylopus carolinae* and *Campylopus heterostachys* for QRO (**Fig.3D-F**); and *Bryum arachnoideum* (**Fig. 3G**), *Weissia controversa* (**Fig. 3H**) and *Helicophylum torquatum* (**Fig. 3I**) for LRO.

Very distinct relative abundances were observed among communities for non-exclusive species (**Fig. 3**). The moss *Bryum atenense*, for example, represented more than 15% of the BSCs records in IRO and LRO, while at QRO it corresponded to less than 6%. This was also observed for the cyanobacterium *Scytonema* sp., which was conspicuous at LRO (> 20%), but not at IRO and QRO (2.8% and 1.8%, respectively). The most abundant species (> 10%) at IRO were *Bryum atenense*, *Campylopus lamellatus*, *Campylopus savannarum* and *Stigonema* sp., while at QRO they were *Campylopus lamellatus* and *Zygogonium* sp. and at LRO they were *Bryum atenense*, *Nostoc* sp., *Scytonema* sp. and *T. humilis*.

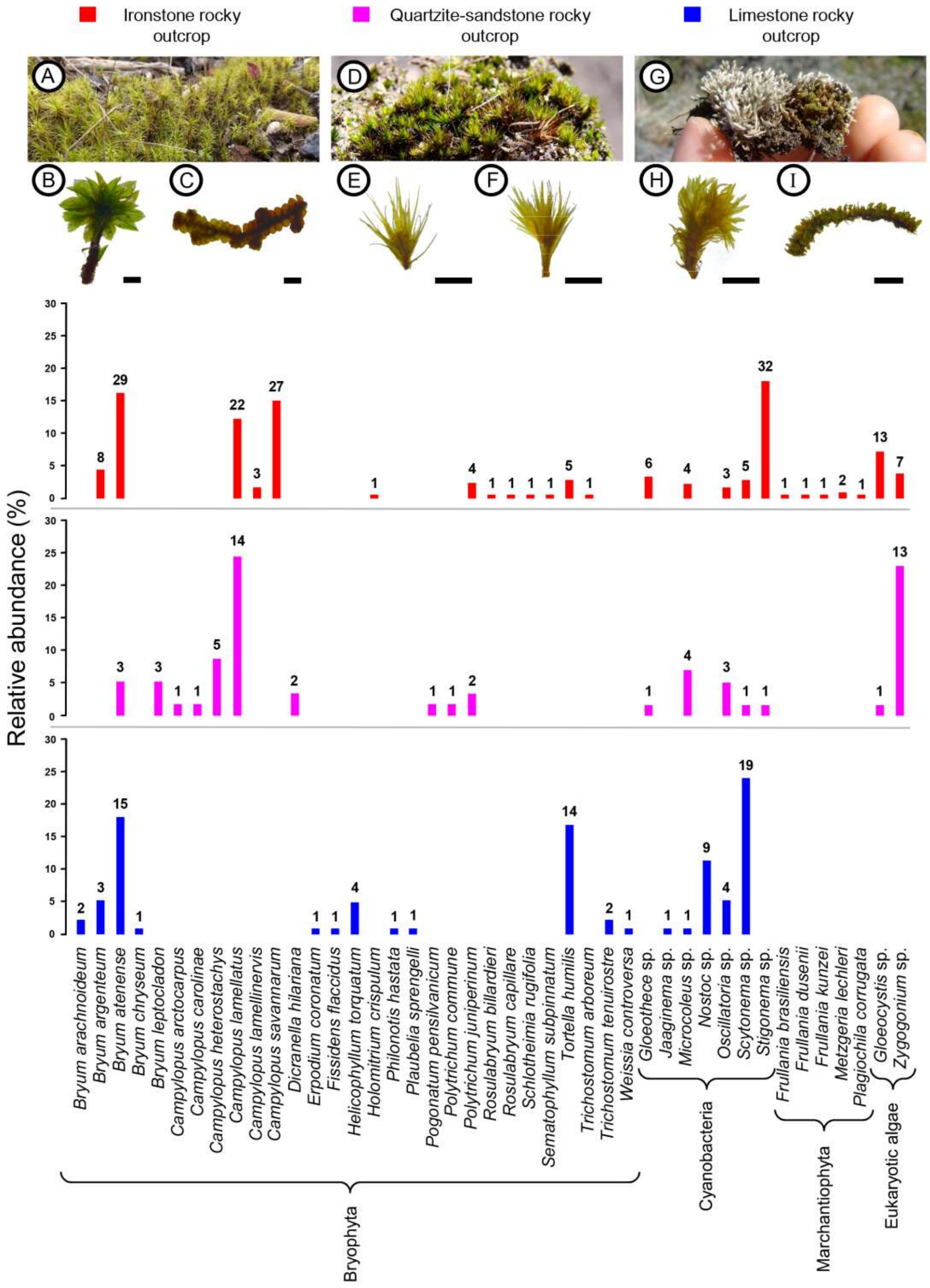


Fig. 3- Relative abundance (total number of samples per species/ total number of samples per outcrop) and number of specimens (over the bars) per study site for species found in biological soil crusts. A- *Campylopus lamellinervis*. B- *Rosulabryum billardierei*. C- *Frullania brasiliensis*. D – *Campylopus* dominated-crust. E- *Campylopus carolinae*. F- *Campylopus heterostachys*. G- *Bryum arachnoideum*. H- *Weissia controversa*. I- *Helicophylum torquatum*. Scale bars correspond to2 mm.

3.2. *Biocrust microhabitat description*

The BSC microhabitats of the rocky outcrops were classified into seven types (**Fig. 4**): (I) deep soil islands - soils stuffed with little stones, depth greater than 10 cm, may be associated with shrubs that cause shading over biocrust or be present on exposed sites; (II) superficial soil islands - embedded in large and irregular rock matrices, maximum soil depth 10 cm, soil surface directly exposed to intense solar radiation and strong winds, sl fragments of rock can be found in soil, no occurrence of vascular plants; (III) termite mounds and surroundings - in exposed areas or near shrubs, characterized by durable surface with high nutrient concentrations, self-shading on base at certain times of day, absence of little stones in substrate matrix; (IV) large sandy soil islands - characterized by very thin substrate matrix mixed with quartz fragments, really deep soil (more than 30 cm), can be very close to grasses and other herbaceous plants that cause shading over biocrust; (V) shallow crevice - maximum depth of 20 cm where nutrient-rich particulate matter accumulates (ca. 10 cm thick), no little stones, vascular plants can be present, central part of crevice more exposed to sun than edges, shading biocrust at certain times of the day; (VI) deep crevice - very similar to shallow crevice but deeper than 20 cm and with self-shading covering a greater extent of edges; (VII) proximity of bromeliads - particulate matter rich in nutrients accumulating at base of the endemic and endangered *Dyckia luxor* (L.B.Sm.&Read) Forzza, which also shades biocrusts on its own base at certain times of day.

All of these microhabitats were not found in all the studied rocky outcrops. Superficial soil islands and termite mounds and surroundings were found only at the ironstone rocky outcrop (IRO) and the quartzite-sandstone rocky outcrop (QRO). Deep soil islands were exclusive to IRO and large sandy soil islands were observed only at QRO. The limestone rocky outcrop (LRO) had a unique composition of microhabitats with proximity of bromeliads and shallow and deep crevices.

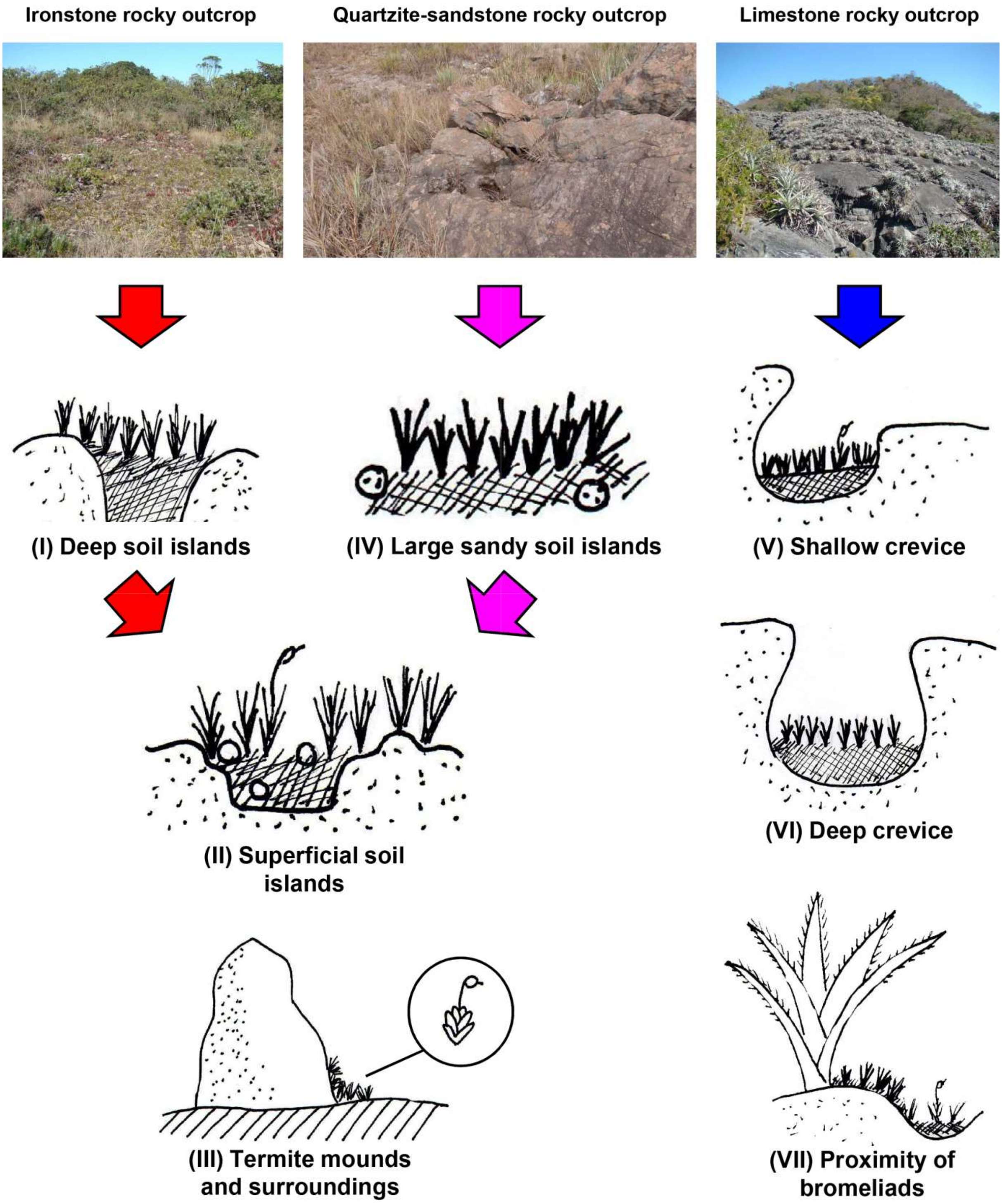


Fig. 4- Sites of the studied Brazilian rocky outcrops and their biological soil crust microhabitats.

MANOVA showed significant differences in the chemical features of the soil (pH, total acidity, organic matter and remaining phosphorus) among the three studied outcrops (**Table 2**). Only boron (B) and aluminum (Al) did not differ in concentration among the three types of rocky outcrops (**Table 2**). LRO soils were more alkaline and nutrient rich, with higher pH, calcium (Ca), phosphorus (P), potassium (K) and organic matter (OM) values while the soils of IRO and QRO were very similar (**Fig. 5, Supplementary Table B**). IRO also had higher concentrations of zinc (Zn) and copper (Cu) than QRO and LRO (**Fig. 5, Supplementary Table B**).

Table 2 - Summary of MANOVA of chemical features and concentrations of chemical elements of the soils of the three studied rocky outcrops. Significant P-values are in bold.

MANOVA	**Pillai's trace**	**F (d.f.$_{num}$, d.f.$_{den}$)**	**P**
Chemical features	1.804	29.90 (8, 26)	**< 0.0001**

Response	**Df**	**F (Sum$_{Sq}$, Mean$_{Sq}$)**	**P**
pH	2	72.05 (0.0832, 0.0416)	**< 0.0001**
Total acidity (H+Al)	2	60.72 (2.2781, 1.1391)	**< 0.0001**
Organic matter (OM)	2	42.62 (3.1744, 1.5872)	**< 0.0001**
Remaining phosphorus (PRem)	2	9.20 (0.4159, 0.2080)	**0.0025**

MANOVA	**Pillai's trace**	**F (d.f.$_{num}$, d.f.$_{den}$)**	**P**
Chemical elements concentrations	1.941	13.62 (24, 10)	**< 0.0001**

Response	**Df**	**F (Sum$_{Sq}$, Mean$_{Sq}$)**	**P**
Potassium (K)	2	30.26 (0.5765, 0.2883)	**< 0.0001**
Phosphorus (P)	2	21.95 (7.1809, 3.5904)	**< 0.0001**
Sodium (Na)	2	5.82 (0.2426, 0.1213)	**0.0135**
Calcium (Ca)	2	89.07 (6.2162, 3.1081)	**< 0.0001**
Magnesium (Mg)	2	4.41 (0.0911, 0.0456)	**0.0311**
Aluminum (Al)	2	3.40 (0.0320, 0.0160)	0.0607
Zinc (Zn)	2	15.51 (1.2602, 0.6301)	**< 0.0001**
Iron (Fe)	2	122.38 (14.5870, 7.2935)	**< 0.0001**
Manganese (Mn)	2	8.09 (3.0623, 1.5312)	**0.0041**
Cupper (Cu)	2	22.95 (0.2111, 0.1055)	**< 0.0001**
Boron (B)	2	1.53 (0.0005, 0.0002)	0.2484
Sulfur (S)	2	24.77 (2.4287, 1.2143)	**< 0.0001**

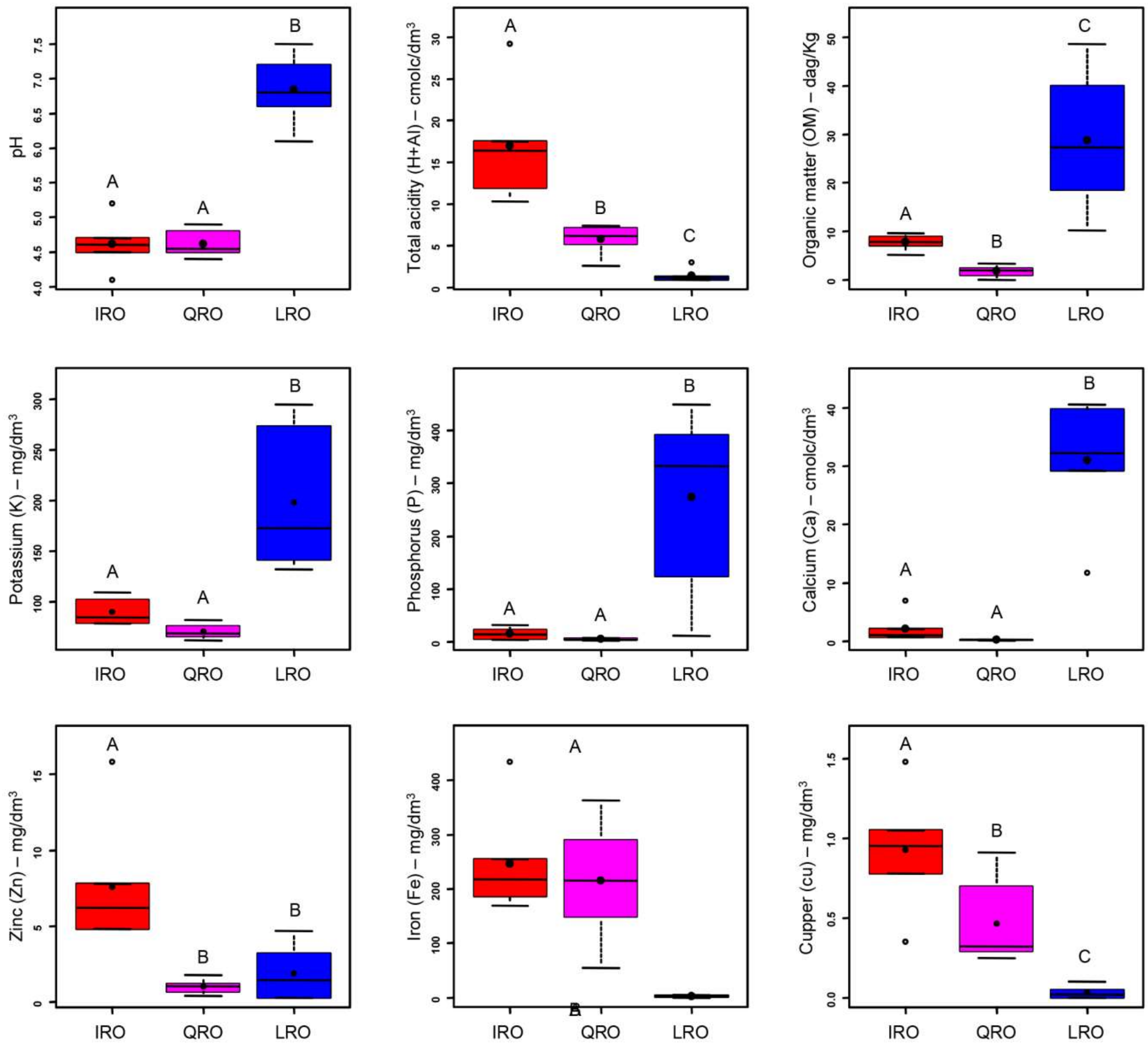


Fig. 5 –Box plots for soil variables for the three studied rocky outcrops. IRO: ironstone rocky outcrop; QRO: quartzite-sandstone rocky outcrop; LRO: limestone rocky outcrop. Lines in boxes are medians, ends of boxes show quartiles, whiskers show range, black dots are means and empty dots are outliers. Different letters represent a significant difference at P< 0.05 (Tukey's test).

3.3. *Co-occurrence patterns*

The co-occurrence patterns revealed interesting characteristics for each type of rocky outcrop. IRO showed more random co-occurrences (seven pairs) than negatively associated pairings (two pairs) or positive associations (one pair, moss *Bryum argenteum*/cyanobacteria *Stigonema* sp.; **Fig. 6A**). QRO showed the moss *Campylopus heterostachys* to be negatively associated with its congener *C. lamellatus* and the eukaryotic algae *Zygogonium* sp. (**Fig. 6B**). Finally, LRO was characterized by the highest number of positive co-occurrence associations (four pairs, moss *Tortella humilis*/cyanobacteria *Nostoc* sp.; moss *Bryum* *atenense*/cyanobacteria *Scytonema* sp.; moss *Tortella humilis*/ cyanobacteria *Scytonema* sp.; and cyanobacteria *Nostoc* sp./ cyanobacteria *Scytonema* sp.) and only two pairs of random associations (**Fig. 6C**). The most observed pattern was mosses with epiphytic filamentous cyanobacteria (**Fig. 6D**).

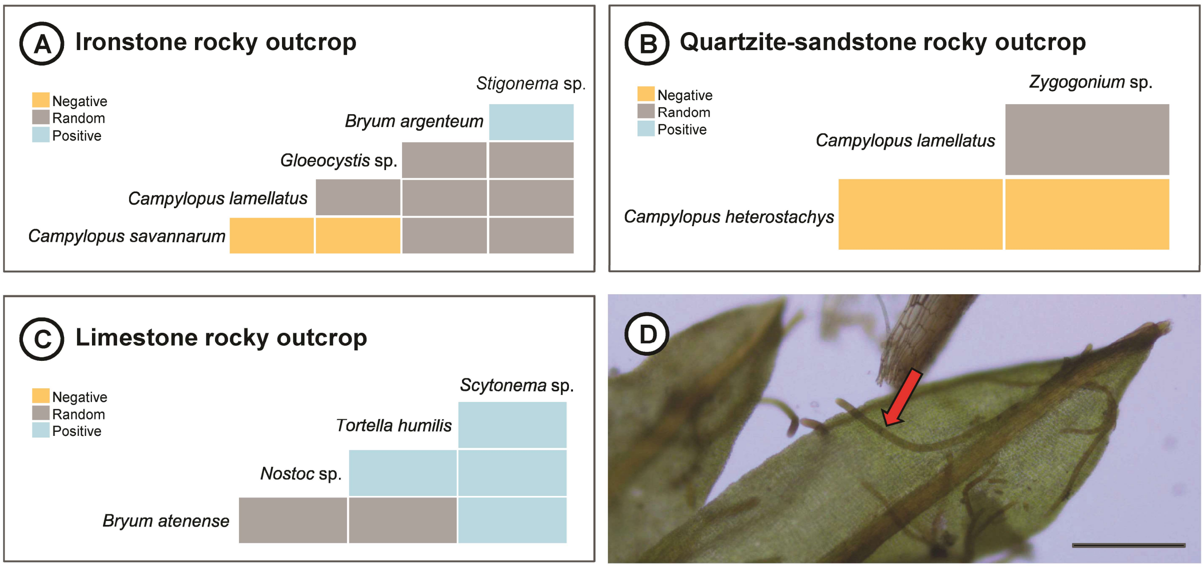


Fig. 6 – Co-occurrence patterns for biological soil crusts of the three studied rocky outcrops. Taxa co-occurrence matrix output: A - ironstone rocky outcrop (IRO), with 276 species pair combinations and only 38 pairs analyzed; B - quartzite-sandstone rocky outcrop (QRO), with 105 species pair combinations and only 11 pairs analyzed; and C - limestone rocky outcrop (LRO), with 136 species pair combinations and only 24 pairs analyzed. D - *Tortella humilis* and *Scytonema* sp. (red arrow). Scale bar corresponds to 0.5 mm. Positive patterns suggest a high likelihood of co-occurrence, while negative patterns have a low likelihood of co-occurrence, and random show no discernible pattern.

3.4. *Brazilian Conservation Units and rocky outcrops*

We created a framework for the conservation of Brazilian rocky outcrops. A total of 58,624 geographic points of rocky outcrops were detected in Brazil, with 147 IRO, 2,998 LRO, 15,918 QRO and 39,561 GRO. These ecosystems had a very irregular distribution within the Conservation Units (CUs) (**Fig. 7**), with some of them being more threatened than others. IRO and LRO had the lowest proportion of sites located within CUs (0.25% for IRO and 5.11% for LRO), while QRO and GRO had the highest (27.15% and 67.48%, respectively). High incidences of outcrops were detected for the *Cerrado* (savannah), Atlantic Forest and *Caatinga* (tropical dry forest) biomes and low incidences for the Amazon Forest, *Pantanal* (wetlands) and *Pampas* (grasslands). A high distribution of rocky outcrops in CUs was detected for the Atlantic Forest.

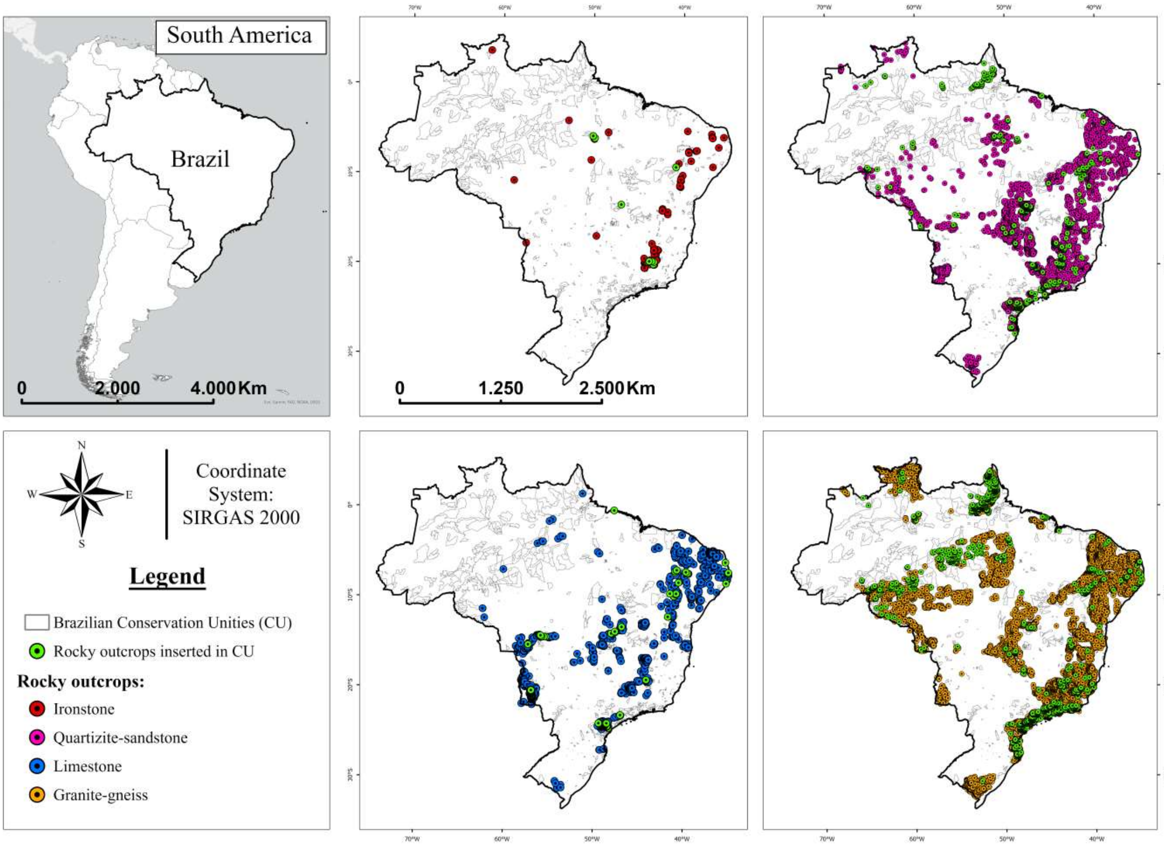


Fig. 7 - Distribution of rocky outcrops in Conservation Units in Brazil.

4. Discussion

4.1. *Biocrust diversity*

Brazilian rocky outcrops can harbor distinct biological soil crust communities. The present study found communities composed of eukaryotic algae, cyanobacteria, mosses and liverworts in differing proportions, as commonly recorded for other BSCs (Belnap et al., 2001, 2016; Büdel, 2002). Bryophytes, especially mosses, dominated all the studied biocrusts, with cyanobacteria and eukaryotic algae living on top of mosses or between their stems and leaves (e.g., Veluci et al., 2006; Colesie et al., 2016). According to Zhao et al. (2009), cyanobacteria, lichen or moss can be the dominant photosynthetic taxa in BSCs, whereas all the rocky outcrops studied here had moss-dominated BSCs. This finding may indicate a later stage of crust development (Lange et al., 1997). However, previous studies of biocrusts in different Brazilian ecosystems found greater diversity and abundance of cyanobacteria

(Machado-de-Lima et al., 2019; Szyja et al., 2019; Machado-de-Lima and Branco, 2020; Machado-de-Lima et al., 2021). Differences in sampling methods or even the occurrence of an ecological or biogeographic pattern may explain this divergence of dominate species for Brazilian BSCs.

The higher relative abundance of moss at the studied sites, with Bryaceae and Leucobryaceae (or ancient Dicranaceae for *Campylopus*) dominating biocrusts at IRO, Leucobryaceae at QRO, and Bryaceae and Pottiaceae at LRO, has been observed in other studies (Seppelt et al., 2016). In fact, the moss families Pottiaceae and Bryaceae usually dominate the bryoflora of BSCs (North America: Rosentreter et al., 2007; Seppelt et al., 2016; Australia: Eldridge and Tozer, 1997; and Asia: Zhang et al., 2007). More specifically in geographical terms, previous studies in Brazil have only reported the moss families Bryaceae, Leucobryaceae, Fissidentaceae and Pottiaceae in biocrusts (Szyja et al., 2019), all of which were recorded in the BSCs of the rocky outcrops studied here.

Although some taxa of thallose liverworts, especially the genera *Riccia* and *Asterella*, are abundant in different biocrusts (e.g., Downing and Selkirk, 1993; Eldridge and Tozer, 1997; Seppelt et al., 2016; Szyja et al., 2019), only *Metzgeria lecheri* was detected in the present study, and only from IRO biocrust. The genus *Metzgeria* has been previously recorded in rocky outcrops in Brazil (Silva et al., 2014; Peñaloza-Bojacá et al., 2018; Oliveira et al., 2021) but preferably developing as epiphytic on trunks and branches of living trees (Costa, 2008). Leafy liverworts are uncommon in BSCs, and were found only in IRO biocrusts, with many of them being recorded for the first time in these communities. Based on the literature, few taxa of leafy liverworts are usually found in BSCs around the world, such as *Cephaloziella* and *Fossombronia* (Rosentreter et al., 2007), but they were not found in the present study. The occurrence of liverworts as a component of outcrop BSCs maybe stochastic, which would explain their low abundance.

All the cyanobacteria registered in the studied rocky outcrops were already known to be components of BSCs. Furthermore, the genera *Microcoleus*, *Nostoc*, *Oscillatoria*, *Scytonema* and *Stigonema* have already be found in BSCs in Brazil (Machado-de-Lima et al., 2019; Szyja et al., 2019; Machado-de-Lima et al., 2021). The record of *Jaaginema* sp. at LRO was unusual, possibly originating from aquatic habitats, similar to the stochastic records of *Gleocapsa* sp. and *Cylindrospermum* sp. in biocrusts of other countries (Büdel et al., 2016). The main crust-forming cyanobacteria (e.g., *Microcoleus* sp., *Nostoc* sp., *Scytonema* sp., and *Stigonema* sp.) generally occur in exposed soils and so are not expected to be found in moss-dominated biocrusts (Büdel et al., 2016). However, *Nostoc* sp. and *Scytonema* sp. occurred at high frequency at LRO and *Stigonema* sp. at IRO, always occurring epiphytically on mosses. Conversely to cyanobacteria, the eukaryotic algae observed in the studied rocky outcrops (i.e., *Gloeocystis* sp. and *Zygogonium* sp.) were previously unknown from Brazilian BSCs (see Oliveira and Maciel-Silva, 2022).

4.2. *Biocrust microhabitats*

Microhabitats can be important local filters for moss-biocrust communities of rocky outcrops of Brazil, as detected by Peñaloza-Bojacá et al. (2018) for bryophytes in ironstone rocky outcrops. The sunny microhabitats in IRO and QRO, such as deep soil islands, superficial soil islands and large sandy soil islands, were dominated by the moss species *Campylopus lamellatus, Campylopus savannarum, Bryum atenense* and *Bryum argenteum*, which are highly tolerant of harsh environmental conditions (Frahm, 2007). On the other hand, species generally adapted to wetter microhabitats, such as *Polytrichum juniperinum*, *Helicophylum torquatum* and *Tortella humilis*, were found in the self-shaded microhabitats (e.g., shallow and deep crevices, termite mounds and surroundings).

The chemical features and concentrations of elements in the soil of microhabitats act as abiotic filters for moss-biocrusts. Deep and shallow crevices in LRO can accumulate all the leached basic and calcareous fine-textured substrate, rich in calcium and organic matter, which promote biocrust development (Eldridge and Tozer, 1997; Pietrasiak et al. 2011, 2014; Williams et al. 2012; Seppelt et al., 2016). In fact, mosses of the family Pottiaceae generally grow in alkaline conditions (see in Costa, 2016), and were proportionally more relevant at LRO (e.g., *Tortella humilis*, *Weissia controversa*, and *Plaubelia sprengelli*). Finally, despite environments with calcareous substrates supporting higher species richness than non-calcareous ecosystems (Downing and Selkirk, 1993), the present results suggested that IRO, a non-calcareous outcrop, could harbor a large number of BSC species.

4.3. *Ecological interactions between biocrust taxa*

The pattern found here of heterocystous cyanobacteria (e.g., *Scytonema*, *Nostoc* and *Stigonema*) growing epiphytically on mosses is already well known for other ecosystems, such as post-fire sites in Tasmania (Brasell et al., 1986), boreal forests (Renaudin, 2022), temperate grasslands (Calabria, 2020) and Antarctica (Alfinito et al., 1998). This occurrence could be advantageous for bryophytes, since many mosses regularly house epiphytic cyanobacterial colonies on their leaf surfaces, which could be accompanied by a large range of N_2 fixation rates (Liu and Rousk, 2021; Rousk, 2022). This ecological interaction, called moss-cyanobacteria association, occurs principally when nitrogen is scarce and limits the development of host bryophytes. Under this condition, the moss secretes chemical attractants for heterocystous cyanobacteria and provides carbon and sulfur to support them, receiving N fixation in return (Berg et al., 2013; Liu et al., 2020; Stuart et al., 2020). Even though co-occurrence is not evidence of ecological interactions (Blanchet et al., 2020), our present results highlight a specific epiphytic co-occurrence between some species of heterocystous cyanobacteria (e.g., *Scytonema*, *Nostoc* and *Stigonema*) and mosses (e.g., *Bryum argenteum, Tortella humilis* and *Bryum atenense*) that maybe represent an ecological interaction based on the principles of moss-cyanobacteria association.

4.4. *Implications for conservation of Brazilian rocky outcrops*

The results of the present study revealed that Brazilian rocky outcrops embedded in the Atlantic Forest are mostly located within Conservation Units (CUs). In fact, this biome was protected through Federal Law 11428/2006 (Vasconcelos, 2014) and most of Brazilian CUs comprise regions of the Atlantic Forest (Mattar et al., 2018). On the other hand, even with many rocky outcrops overlapping with CUs, the *Cerrado* remains the biome with the highest biodiversity conservation gap among the Brazilian protected area network (Fonseca and Venticinque, 2018).

Even if rocky outcrops are impacted by anthropic actions, techniques of recovery of degraded areas can be applied (e.g., Shen et al., 2020; Zanetti et al., 2020; Medeiros et al., 2023). In such cases, the use of biocrusts is strongly recommended as they aggregate and stabilize soil particles preventing soil degradation (Bowker et al., 2013; Faist et al., 2017), play an important role in carbon and nitrogen input in ecosystems (Barger et al., 2016; Sancho et al., 2016) and favor the establishment of native vascular plants (Li et al., 2005; Havrilla et al., 2019), which can accelerate, through facilitation, processes of ecological restoration (Bowker, 2007; Antoninka et al., 2020). Although the use of biocrusts in the restoration of degraded rocky outcrops is still incipient, the use of moss-dominated crusts in a Brazilian quartzite-sandstone outcrop appeared to facilitate natural vegetation succession around rocks two years after inoculation (Medeiros et al., 2023).

Distinct Brazilian rocky outcrops are exceptional tropical refuges for biocrusts and endemic flora and fauna, but they remain severely endangered (e.g., Burke, 2003; Gastauer et al., 2012; Skirycz et al., 2014; Geekiyanage et al., 2019). Efficient management of these areas is a key factor to promote biodiversity conservation, including BSCs and their ecological, physiological and taxonomic roles. The creation of Conservation Units (CUs), in association with educational practices, could be applied, such as the "Don't Bust the Crust" logo of US National Parks Service in Utah that increases the understanding of the importance and fragility of BSCs (Pointing and Belnap, 2012).

5. *Conclusions*

The findings of the present study show that biocrusts can be ecologically and taxonomically diverse and abundant at Brazilian rocky outcrops. The potential occurrence of BSCs in similar outcrops located in other Brazilian biogeographic regions was evaluated. The studied Brazilian outcrops are refuges for moss-dominated crusts, which have adaptations to grow in different microhabitats, including those with harsher environment conditions. In addition, the results revealed that these microhabitats and their chemical features act as filters for moss-biocrust communities. Experimental investigation needs to be further explored to better understand the mechanisms that drive moss-cyanobacteria associations. Finally, Conservation Units (CUs) need to be created or expanded, principally to protect sites of IRO and LRO that currently do not belong to any CUs. Concomitant educational practices are relevant and should be implemented for the conservation of biocrust communities on rocky outcrops in Brazil.

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Supplementary tables

Supplementary Table A -Species found in biological soil crusts and voucher number.

Bryophyta	**Voucher number**
Bartramiaceae	
Philonotis hastata (Duby) Wijk & Margad.	204024
Bryaceae	
Bryum arachnoideum Müll. Hal.	204041; 204042
Bryum argenteum Hedw.	203877; 203880; 203922; 203925; 203926; 203927; 203959; 203963204038, 204039; 204040
Bryum atenense R. S. Williams	203872; 203874; 203876; 203881; 203883; 203894; 203904; 203905; 203912; 203913; 203926; 203929; 203932; 203936; 203942; 203943; 203945; 203947; 203948; 203949; 203950; 203954; 203957; 203959; 203963; 203966; 203967; 203970; 203971; 203973; 203991; 203992; 204017; 204020; 204021; 204023; 204027; 204030; 204031; 204032; 204034; 204035; 204037; 204040; 204042; 204043; 204044
Bryum dichotomum Hedw.	204021
Bryum leptocladon Sull.	203986; 203993; 203995
Rosulabryum billardierei (Schwägr.) Spence	203890
Rosulabryum capillare (Hedw.) J.R. Spence	203888
Dicranaceae	
Dicranella hilariana (Mont.) Mitt	203987; 203995
Holomitrium crispulum Mart.	203892
Erpodiaceae	
Erpodium coronatum (Hook. f. & Wilson) Mitt.	204023
Fissidentaceae	
Fissidens flaccidus Mitt.	204024
Helicophyllaceae	
Helicophyllum torquatum (Hook.) Brid.	204013; 204015; 204023; 204025
Leucobryaceae	
Campylopus arctocarpus (Hornsch.) Mitt.	204010
Campylopus carolinae Grout*	203994
Campylopus heterostachys (Hampe) A. Jaeger	203976; 203982; 204001; 204009; 204011
Campylopus lamellatus Mont.	203884; 203891; 203911; 203913; 203922; 203923; 203933; 203936; 203941; 203943; 203944; 203945; 203946; 203947; 203948; 203951; 203953; 203956; 203962; 203963; 203964; 203965; 203974; 203975; 203977; 203978; 203981; 203983; 203984; 203985; 203986; 203988; 203989; 203990; 203996; 204002
Campylopus lamellinervis (Müll. Hal.) Mitt.	203886; 203895; 203902
Campylopus savannarum (Müll. Hal.) Mitt.	203870; 203871; 203873; 203876; 203877; 203881; 203882; 203883; 203885; 203902; 203903; 203925; 203926; 203927; 203932; 203933; 203934; 203935; 203938; 203939; 203952; 203934; 203966; 203967; 203968; 203969; 203971
Orthotrichaceae	
Schlotheimia rugifolia (Hook.) Schwägr.	203889
Polytrichaceae	
Pogonatum pensilvanicum (Hedw.) P. de Beauv	204012
Polytrichum commune Hedw.	204011

Supplementary Table A – Cont.

Bryophyta	**Voucher number**
Polytrichum juniperinum Hedw.	203878; 203879; 203880; 203924; 203975; 204012
Pottiaceae	
Plaubelia sprengelli (Schwägr.) R.H. Zander	204026
Tortella humilis (Hedw.) Jenn.	203887; 203889; 203891; 203907; 203965; 204021; 204022; 204023; 204028; 204031; 204032; 204033; 204034; 204035; 204036; 204037; 204041; 204042; 204043
Trichostomum arboreum (Mitt.) R.H. Zander	203907
Trichostomum tenuirostre (Hook. & Taylor) Lindb.	204038; 204040
Weissia controversa Hedw.	204039
Sematophyllaceae	
Sematophyllum subpinnatum (Brid.) E. Britton	203888
Charophyta	**Voucher number**
Zygnemataceae	
Zygogonium sp. Kützing	203872; 203874; 203883; 203904; 203907; 203942; 203949; 203975; 203978; 203981; 203983; 203986; 203987; 203989; 203990; 203991; 203992; 203995; 204002; 204010
Chlorophyta	**Voucher number**
Radiococcaceae	
Gloeocystis sp. Nägeli	203876; 203879; 203883; 203887; 203889; 203891; 203892; 203904; 203922; 203938;203951; 203962; 203988
Cyanobacteria	**Voucher number**
Aphanothecaceae	
Gloeothece sp. C. Nägeli	203884; 203923; 203946; 203947; 203953; 203968; 203995
Microcoleaceae	
Microcoleus sp. Desmazières ex Gomont	203881; 203907; 203911; 203956; 203976; 203993; 203994; 204002; 204022
Nostocaceae	
Nostoc sp. Vaucher ex Bornet & Flahault	204017; 204022; 204023; 204031; 204033; 204034; 204035; 204036; 204043
Oscillatoriaceae	
Oscillatoria sp. Vaucher ex Gomont	203881; 203887; 203907; 203982; 203995; 204010; 204020; 204024; 204030; 204031
Pseudanabaenaceae	
Jaaginema sp. Anagn. & Komárek	204020
Scytonemataceae	
Scytonema sp. C.Agardh ex É.Bornet & C.Flahault	203887; 203889; 203891; 203892; 203904; 203973; 204017; 204020; 204021; 204023; 204024; 204027; 204028; 204030; 204031; 204032; 204033; 204034; 204035; 204036; 204040; 204041; 204042; 204043
Stigonemataceae	
Stigonema sp. C.Agardh ex Bornet & Flahault	203874; 203876; 203881; 203882; 203883; 203884; 203885; 203888; 203895; 203905; 203911; 203922; 203923; 203924; 203924; 203926; 203927; 203936; 203938; 203939; 203941; 203943; 203944; 203947; 203952; 203953; 203954; 203959; 203962; 203963; 203965; 203968; 203981

Supplementary Table A – Cont.

Marchantiophyta	**Voucher number**
Frullaniaceae	
Frullania brasiliensis Raddi	203884
Frullania dusenii Steph.	203890
Frullania kunzei (Lehm. & Lindenb.) Lehm. & Lindenb.	203888
Metzgeriaceae	
Metzgeria lecheri Steph.	203887; 203889
Plagiochilaceae	
Plagiochila corrugata (Nees) Nees & Mont.	203887

Supplementary Table B -Descriptive statistics of chemical features and concentrations of chemical elements for each sampled area. IRO: ironstone rocky outcrop; QRO: quartzite-sandstone rocky outcrop; LRO: limestone rocky outcrop. SD = standard deviation.

Soil variables	**Sampled areas**		
	IRO	**QRO**	**LRO**
		Mean ± SD	
pH	4.62 ± 0.36	4.62 ± 0.19	6.83 ± 0.49
Potassium (K) – mg/dm^3	90.13 ± 12.78	71.08 ± 7.29	197.79 ± 71.31
Phosphorus (P) – mg/dm^3	15.67 ± 11.83	5.15 ± 1.75	273.30 ± 168.46
Sodium (Na) – mg/dm^3	4.83 ± 2.79	2.00 ± 0.63	4.17 ± 1.72
Calcium (Ca) – $cmolc/dm^3$	2.10 ± 2.46	0.27 ± 0.08	30.93 ± 10.45
Magnesium (Mg) – $cmolc/dm^3$	0.36 ± 0.24	0.10 ± 0.02	0.74 ± 0.69
Aluminum (Al) – $cmolc/dm^3$	0.38 ± 0.38	0.48 ± 0.16	0.17± 0.05
Total acidity (H+Al) – $cmolc/dm^3$	16.95 ± 6.64	5.77 ± 1.82	1.38 ± 0.81
Organic matter (OM) – dag/Kg	7.70 ± 1.55	1.75 ± 1.15	28.66 ± 13.98
Remaining phosphorus (PRem) – mg/L	23.60 ± 7.55	49.85 ± 6.16	26.02 ± 12.28
Zinc (Zn) – mg/dm^3	7.60 ± 4.26	1.03 ± 0.48	1.90 ± 1.82
Iron (Fe) – mg/dm^3	246.35 ± 97.01	214.52 ± 108.54	2.00 ± 1.69
Manganese (Mn) – mg/dm^3	56.73 ± 53.61	5.65 ± 5.42	80.03 ± 95.75
Cupper (Cu) – mg/dm^3	0.93 ± 0.37	0.47 ± 0.27	0.03 ± 0.04
Boron (B) – mg/dm^3	0.01 ± 0.004	0.04 ± 0.01	0.03 ± 0.05
Sulfur (S) – mg/dm^3	33.52 ± 12.23	3.90 ± 2.07	16.57 ± 7.23

5. CAPÍTULO III

Everything is not what it seems: testing calcium tolerance of an apparently generalist biocrust moss

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Abstract

Brazilian rocky outcrops possess biological soil crusts (biocrusts or BSCs) as a conspicuous component of the vegetation, where mosses, cyanobacteria and eukaryotic algae perform diverse ecological services. Moss-dominated crusts grow over distinct types of soils but calcium (Ca) content and pH directly affect their distribution, with some moss species differing in their calcium preference. Three types of rocky outcrops in Brazil represent a soil calcium gradient: quartzite-sandstone < ironstone < limestone. The present study explored the growth preferences of the common moss *Bryum atenense* relative to calcium concentrations reported from Brazilian rocky outcrops. Higher calcium concentrations (≥156.35 mmol/L) inhibited the establishment and asexual reproduction of the moss, suggesting a calcium evasive strategy. We hypothesize that populations of *B. atenense* from distinct outcrops differ in calcium adaptability.

Keywords: biological soil crusts; bryophytes, calcium, pH, establishment.

1. Introduction

Mosses are generally associated with moist ecosystems, but they can colonize xeric environments through specific adaptations (e.g., hyaline hairpoints and leaf lamellae to promote water absorption), especially when associated with biological soil crusts (also biocrusts or BSCs; Seppelt et al., 2016). Commonly found in arid and semiarid ecosystems, biocrusts are formed when mosses, eukaryotic algae, cyanobacteria, liverworts, lichens, fungi and bacteria live on the topsoil and interact directly with soil particles (Belnap et al., 2016). Moss-dominated BSCs perform diverse ecological services, such as soil stabilization, moisture retention, carbon fixation and seed germination promotion (Seppelt et al., 2016). Biocrusts have also been used in the ecological restoration of soils (Antoninka et al., 2020).

Conspicuous moss-dominated biocrusts are found on Brazilian outcrops, especially ironstone, quartzite-sandstone and limestone rocky outcrops (Oliveira and Maciel-Silva, 2022; Oliveira et al., 2023). However, Oliveira et al. (2023) found *Bryum atenense* R. S. Williams (family Bryaceae) to be the only moss to occur in all these distinct ecosystems, with higher abundance on ironstone outcrop. These authors also verified that soil calcium (Ca) concentration and associated pH differ significantly among types of outcrops. Indeed, soil Ca content and pH are important environmental factors that affect the distribution of moss-dominated biocrusts (Seppelt et al., 2016).

Many moss species are considered edaphic specialists, being found predominantly on a specific type of substrate. Thus, they can be classified as calcicoles (e.g., family Pottiaceae), with preference for establish on calcium rich substrates, or as calcifuges, with intolerance to high Ca concentrations (Palmer and Wilson, 2021). However, other species are edaphic generalists, being able to grow on a range of parent rock types (Palmer and Wilson, 2021). Within this framework, we hypothesized that *B. atenense* had tolerance to calcium due its presence in various BSC communities among outcrops with distinct soil calcium contents. Thus, we predicted that *B. atenense* will be able to produce rhizoids and asexual propagules regardless of soil calcium content.

2. Materials and methods

Six biocrust communities dominated by *B. atenense* (at least 2m apart) were chosen on ironstone rocky outcrop located in the Natural Monument Serra da Calçada (20°05’43”S, 43°58’59”W), due to the high abundance of the species in the ecosystem. Samples (ca. 100 cm^2) were taken from the topsoil layer by gently inserting a spatula into the substrate followed by careful placement in small plastic bags, which were subsequently stored in freezer at 7°C. The moss *B. atenense* is small (3–4 mm high), dioicous and can present rhizoidal tubers and axillary bulbils as asexual propagules (Canestraro and Peralta, 2022). Moss species identification was confirmed following Canestraro and Peralta (2022) using a stereomicroscope and a light microscope. Voucher specimens (211376 –211389) were deposited in the BHCB herbarium (Departamento de Botânica, Universidade Federal de Minas Gerais).

Soil analysis by Oliveira et al. (2023) revealed that Brazilian rocky outcrops present a gradient of mean calcium concentration (quartzite-sandstone < ironstone < limestone). Thus, an experiment was performed to determine whether *B. atenense* is a edaphic generalist by preparing five calcium solutions corresponding to a control, the outcrops (quartzite-sandstone < ironstone < limestone) and 2x the highest concentration: 0 mmol/L and pH = 7.0; 1.35 mmol/L and pH = 4.7; 12 mmol/L and pH = 4.7; 156.35 mmol/L and pH = 7.0; and 312.7mmol/L and pH = 8.5. The Ca^{2+} solutions were prepared using anhydrous $CaCl_2$, with pH adjustment using NaOH or HCl (consistent with the average pH of the soil at the sampling sites; Meng et al., 2023).

Moss gametophytes were separated from the substrate (mixed sample of 200 shoots) and cleaned with distillated water. Plants were cultivated in cell plates on clean cotton (c.a. 1 cm high) moistened with 5 mL of each calcium solution (treatments): 0 mmol/L; 1.35 mmol/L; 12 mmol/L; 156.35 mmol/L; and 312.7 mmol/L. The plates were placed in a growth room with a temperature of 16.2°C – 22.7°C, light at 24 µmol.m^{-2}.s^{-1} and a 12 h photoperiod, where the plants were cultivated for 98 days.

A stereomicroscope was used to determine the presence or absence of rhizoids on plants of the different treatments. We opted to use this variable as a proxy for successful establishment due the importance of rhizoids in fixing plants to the substrate. Since *B. atenense* can produce asexual propagules, we also quantified the final number of these structures per plant.

Rates of establishment in the treatments were compared by a Generalized Linear Mixed-Effect Model (GLMM) using the function *glmer* from the package “lme4” (Bates et al., 2015). Calcium concentration was considered a fixed factor and observation time a random factor. The proportion of presence-absence per treatment was modeled using a binomial distribution with a logit link function. The final number of asexual propagules was compared among treatments with a Generalized Linear Model (GLM; gaussian family and identity link function) using the function *glm* from the package "glm2" (Marschner, 2011). The analyses were performed with R 4.0.2 software (R Development Core Team 2013).

3. Results and discussion

The shoots of *B. atenense* of all treatments produced rhizoids and asexual propagules during the 98 days of cultivation, except for those under the highest calcium concentration. The propagules produced by *B. atenense* in this experiment have never been recorded by bryologists. Mosses of the family Bryaceae present spherical to ovoid rhizoidal tubers in the subterranean parts of the moss (Spence, 2015), whereas the gemmae present in the experimental shoots of *B. atenense* were axillary propagules with a predominantly ginger rhizome-like shape with some greenish edges (**Fig. 1A**). In fact, many bryophyte species produce unusual asexual propagules when cultivated under stressful conditions related to light, humidity, temperature and nutrient availability (Duckett et al., 2004).

Both plant establishment and asexual propagule production of *B. atenense* showed the same pattern across calcium concentrations and associated pH (**Fig. 1B-C**). The shoots cultivated in treatments of 0 mmol/L, 1.35 mmol/L and 12 mmol/L of Ca^{2+} produced 7x more rhizoids and asexual propagules than plants cultivated in treatments of 156.35 mmol/L and 312.7 mmol/L. Moreover, the gametophytes of the 312.7 mmol/L treatment did not develop and many shoots died. Experiments with calcicole mosses from China had similar results, with calcium concentrations below 100 mmol/L favoring the optimum growth of *Eurohypnum leptothallum* and *Didymodon constrictus* (Meng et al., 2023).

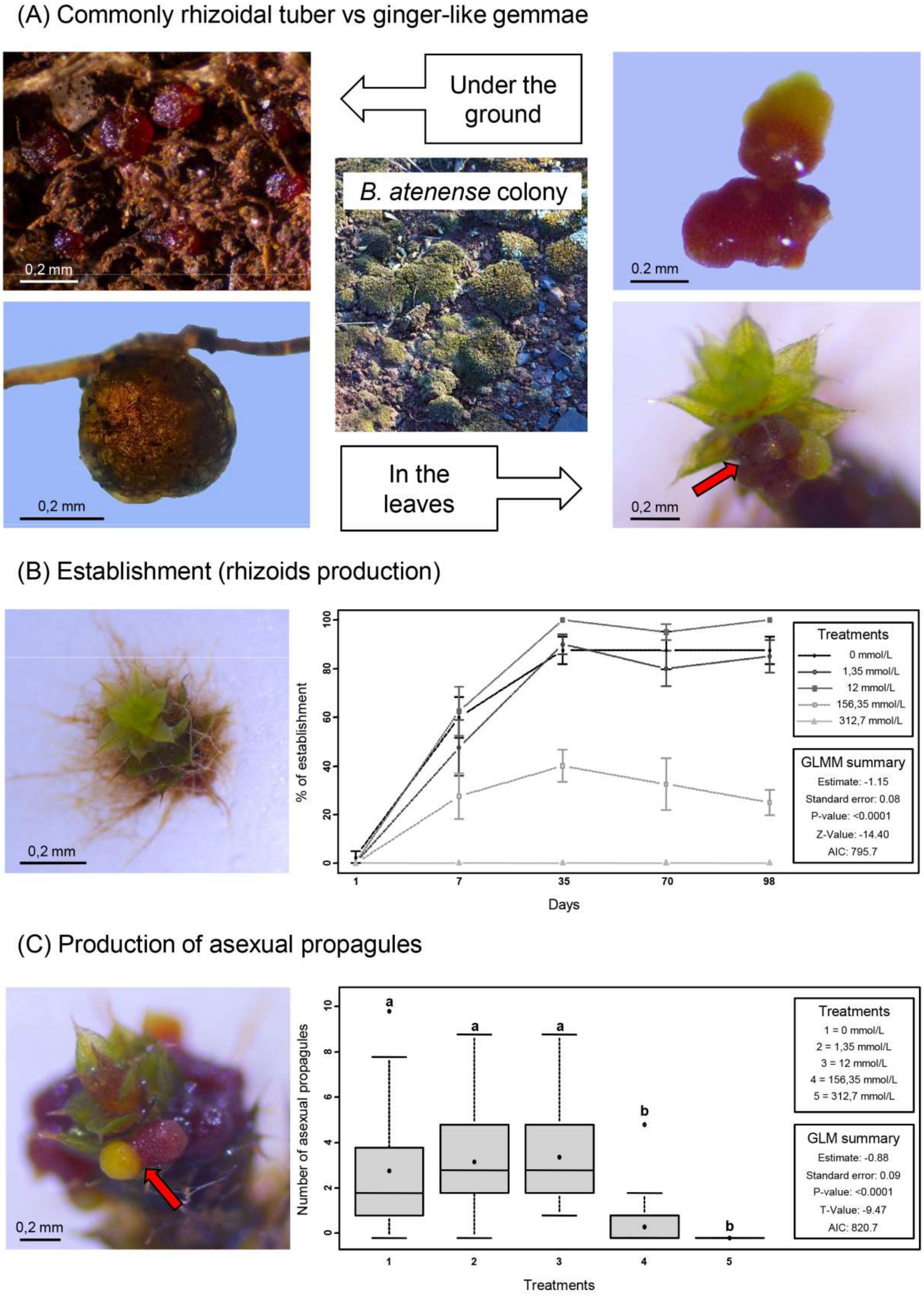

Fig. 1- Experiment with *Bryum atenense*. A-Comparison of regular tuber and unusual ginger rhizome-like gemmae. B- Establishment (%). C- Asexual propagule production. Bold indicates statistical significance and arrow indicates asexual propagules. AIC = Akaike Information Criterion.

On the other hand, some moss species, such as *Hyophila involuta*, have optimum growth with high Ca^{2+} concentrations (100 mmol/L–200 mmol/L) and present physiological adaptations to calcium stress (Meng et al., 2023). In fact, calcium maintains a low permeability of plant cells to intracellular solutes and drives the uptake of ions, but its excess in the moss organism results in a high degree of impermeability that decreases the absorption of essential nutrients for plant growth (Bates, 1982). However, some moss species can tolerate excess damage from calcium due to possessing a well-developed antioxidant enzyme system that protects cell membrane structure (Meng et al., 2023).

The results of both the present study and Meng et al. (2023) highlight the differential calcium adaptability of bryophytes at population scale. For instance, the liverwort *Aneura pinguis* (L.) Dumort. has high genetic diversity caused by the mineral composition of the growth medium and its pH resulting in populations with a preference for high calcium concentrations and others for low calcium concentrations (Bączkiewicz et al., 2021). It should be emphasized that the specimens used by Meng et al. (2023) were from Karst areas with naturally elevated calcium while the *B. atenense* of the present study came from a low calcium substrate.

The results of the present study suggest that *B. atenense* from the ironstone rocky outcrop were not tolerant to high calcium concentrations. We hypothesize that populations in each outcrop type have evolved to grow under the specific soil calcium concentration and associated pH of its ecosystem, which would characterize the populations of *B. atenense* present on limestone outcrops with tolerant to high calcium substrates, being potentially calcicoles. In fact, this pattern seems to be associated with adaptability and ecotypes, where natural selection operates at a local scale driving the evolution of populations (Matesanz et al., 2010). Future calcium tolerance experiments with *B. atenense* from the three outcrops are needed to confirm that the populations are differentiating in ecotypes.

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6. CONCLUSÕES

I. A revisão de dados realizada nesta dissertação possibilitou compilar a composição das espécies de crostas biológicas do solo brasileiras, os ecossistemas onde vivem, suas contribuições ecológicas, algumas das adaptações que possuem para sobreviver em ambientes adversos e suas aplicações (**Capítulo I**).

II. Embora as biocrostas ainda sejam consideradas escassas e de pouca relevância em ambientes tropicais, elas estão de fato dispersas em diferentes ecossistemas brasileiros, mas principalmente em habitats menores que favorecem seu crescimento e estabelecimento – como afloramentos rochosos (**Capítulos I e II**).

III. Pela primeira vez biocrostas foram estudadas em afloramentos rochosos brasileiros. Os musgos foram o grupo taxonômico mais abundante nas comunidades amostradas e apresentaram um padrão de co-ocorrência com cianobactérias fixadoras de nitrogênio (**Capítulo II**).

IV. Os microhabitats que são colonizados por biocrostas nos afloramentos rochosos foram caracterizados. Além disso, os resultados revelaram que esses microhabitats e suas características químicas, especialmente as concentrações de cálcio e o pH, atuam como filtros para biocrostas dominadas por musgos (**Capítulo II**).

V. Unidades de Conservação (UCs) precisam ser criadas ou ampliadas, principalmente para proteger afloramentos rochosos ferruginosos e calcários que atualmente não pertencem a nenhuma UC. Práticas educativas concomitantes são relevantes e devem ser implementadas para a conservação de comunidades de biocrostas em afloramentos rochosos no Brasil (**Capítulo II**).

VI. Devido à sua presença em todas as comunidades de biocrostas estudadas em afloramentos rochosos com teores distintos de cálcio no solo, *Bryum atenense* R.S. Williams aparenta ser uma espécie com potencial tolerância a altas concentrações de cálcio (**Capítulo II e Capítulo III**).

VII. Os gametófitos de *B. atenense* não produziram rizóides e propágulos assexuados nas concentrações mais altas de cálcio a que foram submetidos. Isso indica que as populações de *B. atenense* de diferentes afloramentos rochosos possivelmente apresentam graus de adaptabilidade distintos - um padrão que parece estar associado com evolução de ecótipos (**Capítulo III**).

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