UNIVERSIDADE FEDERAL DE MINAS GERAIS
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
Departamento de Botânica
Programa de Pós-Graduação em Biologia Vegetal

GABRIEL FELIPE PEÑALOZA BOJACÁ

PEQUENAS PLANTAS COM GRANDES ADAPTAÇÕES: BRIÓFITAS EM AFLORAMENTOS ROCHOSOS FERRUGINOSOS EM MINAS GERAIS, BRASIL

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

Área de Concentração Morfologia, Sistemática e Diversidade Vegetal.

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Sumário

RESUMO

Os afloramentos rochosos ferruginosos ou “Cangas”, no Brasil, estão localizados principalmente na região do Quadrilátero Ferrífero (QF) em Minas Gerais (MG). São reconhecidos por apresentam características ambientais únicas, como altas variações nas temperaturas diárias, exposição UV elevada, ventos constantes, solos impermeáveis com baixa capacidade de retenção de água, e principalmente seus elevados níveis de minério de ferro no solo. Este conjunto de características ambientais favorece a colonização de plantas xericas, bem como proporcionam uma alta frequência de espécies vegetais raras e/ou endêmicas. No entanto, infelizmente, estas áreas são fortemente ameaçadas pela alta exploração de minérios, pelo desmatamento e pela urbanização descontrolada. As briófitas são um grupo de plantas presentes nas Cangas, muito mal compreendidas e pouco estudadas. Estas têm papéis importantes na manutenção da umidade do solo e níveis de nutrientes, facilitando o estabelecimento de plantas de maior porte. Desta forma, os principais objetivos deste trabalho foram 1) Investigar e caracterizar como as briófitas se reproduzem sob as condições adversas encontradas nas Cangas (**Capítulo I**); 2) Descrever as comunidades de briófitas associadas a afloramentos rochosos ferruginosos, e avaliar a influência da filtragem ambiental em escala local e regional (**Capítulo II**); e 3) Reconhecer a brioflora presente nas Cangas do Parque Estadual da Serra do Rola-Moça (RM), relacionando os padrões de distribuição geográfica com características reprodutivas das briófitas (**Capítulo III**). Assim, no primeiro capítulo foram registrados os modos reprodutivos, estruturas de propagação assexual, sistemas sexuais, expressão sexual, sucesso reprodutivo e a razão sexual das briófitas. Ressaltamos o papel de importantes espécies de musgos dioicas, que contribuem com abundantes propágulos assexuados nas Cangas. No segundo capítulo, caracterizamos a comunidade de briófitas nas Cangas, em termos de seus diferentes microhabitats/substratos, e níveis de perturbação antrópica. Verificamos que as Cangas estudadas abrigam uma alta diversidade de briófitas, quando comparadas a afloramentos rochosos de outra natureza, embora a composição de musgos e hepáticas varie especialmente em resposta às perturbações antrópicas. Finalmente, no terceiro capítulo, observamos que o RM abriga considerável brioflora (70 spp.) cuja maior parte das espécies apresenta ampa distribuição geográfica nos Neotropicos e em mais de 10 estados brasileiros. Possivelmente, os padrões de distribuição das espécies são justificados pela efetividade da dispersão e do estabelecimento de seus diásporos. Os dados reunidos neste trabalho evidenciam a importância de continuar com os esforços de conservação das áreas naturais com afloramentos rochosos ferruginosos no país. Este estudo foi pioneiro em preencher importantes lacunas sobre o conhecimento das comunidades de briófitas em Cangas, destacando a importância do levantamento de dados florísticos e de história de vida das espécies para a conservação de táxons e do ecossistema como um todo.

Palavras claves: Cangas, Comunidades vegetais, Distribuição geográfica, Diversidade, Hepáticas, Musgos, Perturbação antrópica, Propágulos vegetativos, Reprodução assexuada, Reprodução sexuada.

ABSTRACT

Ironstone outcrops or "Cangas", in Brazil, are located mainly in the Quadrilátero Ferrífero (QF) region of Minas Gerais (MG). They are recognized as having unique environmental traits, such as high variations in daily temperatures, high UV exposure, constant winds, impermeable soils with low water retention capacity, and especially their high levels of iron in the soil. This set of environmental characteristics favors the colonization of xelotolerant plants, as well as provide a high frequency of rare and / or endemic plant species. Unfortunately, however, these areas are heavily threatened by high mineral exploitation, deforestation and uncontrolled urbanization. Bryophytes are a group of plants present in the Cangas, very poorly understood and little studied. These plants have important roles in maintaining soil moisture and nutrient levels, facilitating the establishment of larger plants. In this way, the main goals of this study were 1) To investigate and characterize how bryophytes reproduce under the adverse conditions found in Cangas (**Chapter I**); 2) To describe the bryophyte communities associated with ironstone outcrops, and to evaluate the influence of environmental filtration at local and regional scales (**Chapter II**); And 3) To recognize the bryoflora present in the Cangas of the State Park of Serra do Rola-Moça (RM), relating the patterns of geographical distribution with reproductive traits of bryophytes (**Chapter III**). Thus, in the first chapter we recorded reproductive modes, asexual propagation structures, sexual systems, sexual expression, reproductive success and the sex ratio of bryophytes. We emphasize the role of important species of dioecious mosses, which contribute with abundant asexual propagules in the Cangas. In the second chapter, we characterize the bryophyte community in the Cangas, in terms of their different microhabitats / substrates, and levels of anthropogenic disturbance. We found that the Cangas harbor a high diversity of bryophytes when compared to rocky outcrops of another nature, although the composition of mosses and liverworts varies especially in response to anthropogenic disturbances. Finally, in the third chapter, we observed that the RM houses a large bryoflora (70 spp.). Most of the species presented a large geographical distribution in the Neotropics and in more than 10 Brazilian states. Possibly, species distribution patterns are justified by the effectiveness of dispersal and establishment of their diaspores. The data gathered in this study show the importance of continuing the conservation efforts of the natural areas with ironstone outcrops in the country. This study was a pioneer in filling important gaps in the knowledge of the bryophyte communities in Cangas, highlighting the importance of floristic surveys and species life history data for the conservation of taxa and the ecosystem as a whole.

Key words: Cangas, Plant communities, Geographical distribution, Diversity, Liverworts, Mosses, Anthropogenic disturbance, Vegetative propagules, Asexual reproduction, Sexual reproduction.

INTRODUÇÃO GERAL

As Cangas foram formadas há milhões de anos, resultantes do intemperismo de rochas ferríferas subjacentes - tais como os itabiritos e diamictitos ferruginosos - e posterior enriquecimento de ferro, resultando em couraças que podem atingir dezenas de metros de espessura e se estender por milhares de hectares (Jacobi e Carmo 2012; Carmo e Jacobi 2013). Esses afloramentos rochosos podem ser reconhecidos por dois tipos de Canga: couraçada e nodular. A primeira forma uma laje sobre o substrato com cavidades, e pode abrigar uma fisionomia de campo sujo com muitos componentes lenhosos subarbustivos, ao lado de espécies herbáceas epilíticas. Já a segunda é uma área com um substrato bastante desagregado, apresentando uma fisionomia de campo sujo com muitos subarbustos (Jacobi e Carmo 2012; Schaefer *et al*. 2015). Esses habitats estão distribuídos em altitudes superiores a 800 m acima do nível do mar, de forma insular, possuindo solos rasos, ácidos e oligotróficos, além de alta limitação hídrica e forte exposição à ação dos ventos (Jacobi *et al*. 2007; Porembski 2007; Scarano 2007). Outra característica peculiar dessas áreas é a grande amplitude térmica diária, relativa ao intenso aquecimento da rocha durante o dia e seu resfriamento noturno (Vincent *et al*. 2002).

O Quadrilátero Ferrífero (QF) em Minas Gerais compreende uma área de aproximadamente 7.200 km² (Jacobi e Carmo 2012; Souza e Carmo 2015). Este geralmente apresenta Cangas nos topos dos morros, com uma área aproximada de 100 km² (Jacobi *et al*. 2007). Atualmente, as Cangas estão fortemente ameaçadas pela exploração de minérios, sendo este um dos principais problemas para sua preservação e conservação de suas espécies (Jacobi *et al*. 2007; Jacobi e Carmo 2012). Segundo Carmo (2010), cerca de 40% das áreas de Canga foi perdida em menos de 40 anos no Quadrilátero Ferrífero (QF), o que resultou na extinção de pelo menos 100 afloramentos ferruginosos.

A vegetação nas formações de Canga apresenta adaptações fisiológicas, morfológicas e reprodutivas típicas de plantas que vivem em afloramentos rochosos *lato sensu*, como esclerofilia, reprodução clonal e poiquiloidria, ou seja, capacidade de resistir a ciclos de completa dessecação e reidratação (Giulietti *et al*. 1987). Além disso, as plantas associadas às Cangas precisam lidar com um substrato rico em metais pesados (Jacobi *et al*. 2007; Messias *et al*. 2012). Devido às altas concentrações de metais pesados no solo, as Cangas são consideradas centros de endemismo e especiação de plantas conhecidas como metalófitas (Whiting *et al*. 2004; Jacobi e Carmo 2012).

Um exemplo de plantas abundantemente presentes nas Cangas são as briófitas, que compõem o segundo maior grupo de plantas terrestres no mundo (Goffinet e Shaw 2009). São plantas normalmente pequenas (a maioria até 10 cm de comprimento) e atraqueófitas (sem lignina, não chegam a apresentar traqueídeos ou elementos de vaso) (Goffinet *et al*. 2009; Glime 2013a). Briófitas são plantas poiquiloídricas, capazes de ganhar e perder água rapidamente, oscilando seu conteúdo hídrico de acordo com a disponibilidade de água no ambiente (Proctor *et al*. 2007). Devido a essa natureza poiquiloídrica, uma característica possivelmente compartilhada com as primeiras plantas que invadiram o ambiente terrestre, algumas espécies podem viver mesmo em ambientes com forte sazonalidade da precipitação (Gradstein *et al*. 2001; Proctor *et al*. 2007). Algumas espécies, especialmente de musgos e hepáticas, apresentam estratégias de tolerância à dessecação ou fuga de períodos de seca (Proctor 2000). Essas espécies podem ser encontradas em afloramentos rochosos e apresentam mecanismos de sobrevivência e reprodução moldados pelas condições climáticas desses ambientes (Frahm 1991).

O ciclo de vida nas briófitas é marcado pela alternância de gerações, com a geração gametofítica (haploide) dominante e a esporofítica (diploide) comparativamente mais curta e nutricionalmente dependente da gametofítica (Goffinet *et al*. 2009; Glime 2013b). Com relação ao sistema sexual das briófitas, espécies dioicas (i.e., sexos separados em plantas distintas) superam em número as espécies monoicas (i.e., dois sexos na mesma planta), com cerca de 70% de espécies dioicas em hepáticas e 55 – 60% em musgos (Wyatt 1982; Goffinet *et al*. 2009). Porém, além da reprodução sexuada, essas plantas também podem se propagar asexualmente por diferentes estruturas especializadas (*e.g.*, gemas, tubers e bulbilhos) e estruturas pouco especializadas (i.e., fragmentos do próprio corpo) (Kürschner e Frey 2012; Maciel-Silva e Pôrto 2014).

A reprodução sexuada nas briófitas, assim como em outros organismos, envolve gastos energéticos relacionados ao sexo (Stark *et al*. 2000; Goffinet e Shaw 2009). Particularmente nas briófitas, devido à produção de gametas e todos os custos relacionados à manutenção e crescimento da fase esporofítica, reproduzir-se sexuadamente envolve riscos e pode comprometer o desempenho do gametófito na próxima estação de reprodução (Longton e Schuster 1983; Glime 2013b; Maciel-Silva e Pôrto 2014). Somado a isso, muitas espécies dioicas não completam o ciclo sexuado, simplesmente porque indivíduos de sexos distintos permanecem distantes durante toda a vida. A necessidade de água, para que haja fertilização nas briófitas, é um componente chave nesse processo (Longton e Schuster 1983; Ortiz *et al*. 2002; Stark 2002). Por outro lado, essas plantas podem manter suas populações clonais e colonizar novos microhabitats por meio de propágulos vegetativos e/ou ramificações de plantas pré-existentes. Similarmente à propagação vegetativa em outras espécies vegetais (Matallana *et al*. 2005), essa forma de reprodução vegetal sem a fusão de gametas e consequente formação e dispersão de esporos é menos dispendiosa energeticamente e geralmente está associada a habitats com menos disponibilidade de recursos e/ou sob estresse fisiológico (Longton e Schuster 1983; Goffinet *et al*. 2009).

Os processos de dispersão de esporos e propágulos vegetativos estão diretamente relacionados ao tamanho e à longevidade dessas estruturas. Espécies de briófitas com esporos pequenos (*e.g.*, < 25 µm) e resistentes (sobretudo à dessecação, incidência de UV e oscilações da temperatura) tendem a apresentar alta capacidade de dispersão a longas distâncias pelo vento. Essas características parecem explicar os padrões fitogeográficos amplos de muitas espécies de briófitas quando comparadas a espécies de angiospermas (Söderström 1989; Frahm 2008; Heinrichs *et al*. 2009).

Diferentes estudos desenvolvidos em Cangas do QF reportam altos níveis de endemismo de plantas vasculares com mais de 1.100 espécies (Jacobi *et al*. 2007; Jacobi e Carmo 2008; Jacobi e Carmo 2012; Carmo e Jacobi 2013; Carmo e Kamino 2015; Carmo e Jacobi 2016). Por outro lado, com relação às briófitas das Cangas do QF, poucos estudos apenas citam a presença dessas plantas e a sua exploração via coleta e venda ilegais (Jacobi *et al*. 2007; Carmo 2010). Em suma, não há informações sobre a identidade das espécies de briófitas que vivem nesses ecossistemas, sua distribuição nos microhabitats de Canga, sua raridade, e formas de reprodução nesses ambientes adversos. Desta forma, nossos principais objetivos foram 1) Investigar e caracterizar como as briófitas se reproduzem sob as condições adversas encontradas nas Cangas (CAPÍTULO I); 2) Descrever as comunidades de briófitas associadas a afloramentos rochosos ferruginosos, e avaliar a influência da filtragem ambiental em escala local e regional (CAPÍTULO II); 3) Reconhecer a brioflora presente nas Cangas do Parque Estadual da Serra do Rola-Moça (RM), analisando a riqueza e a abundância de espécies, os padrões de distribuição geográfica, e as estruturas de dispersão das briófitas (CAPÍTULO III).

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CAPITULO I

Artigo Submetido ao Periódico *Flora - Morphology, Distribution, Functional Ecology of Plants.*

Bryophyte reproduction on ironstone outcrops: delicate plants in harsh environments

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Abstract

Ironstone outcrops are environments characterized by adverse environmental conditions, with high variations in daily temperatures, elevated UV exposure, constant winds, impermeable soils with low water retention capacities, and high levels of iron minerals. These conditions have selected for a very rich and endemic community of xerophilic plants, including many desiccation-adapted species, and we highlight here the importance of the bryophytes, a very poorly understood group that inhabits rocky outcrops. Our main aim was to investigate the reproductive strategies of bryophyte species growing on Brazilian ironstone outcrops (locally called "Cangas"). We studied the bryophytes in ten Cangas formations in two conservation areas in Minas Gerais State, Brazil, recording their reproductive modes (sexual vs. asexual), the types of asexual propagation structures produced, sexual systems, sexual expression, reproductive success, and their sex ratios. We encountered 108 species of bryophytes (42 liverworts and 66 mosses) with remarkable reproductive rates (ca. 50% of the specimens were observed to be reproducing sexually or asexually). Seventy percent of the bryophyte species were found reproducing, but with contrasting strategies in mosses (mostly asexually) and liverworts (mainly sexually). Among the asexually reproducing species, we recorded 31% having gemmae, in contrast to 69% with deciduous propagules. Sexual expression and reproductive success were mostly influenced by the sexual systems of the bryophyte species, reflecting the relevant role of dioecious mosses. The majority of dioecious species of bryophytes were female-biased. We emphasize the role of several key dioecious species of mosses that contribute large amounts of spores and asexual propagules in Cangas sites. These diaspores are very informative about how bryophytes growing on ironstone outcrops disperse and colonize new microhabitats at local and regional scales.

Key-words: Asexual propagation, cangas, gemmae, liverworts, mosses, spores,.

Introduction

Brazilian ironstone outcrops, locally called "Cangas", are located in the Iron Quadrangle (IQ) region of Minas Gerais State (MG), Brazil, between the Atlantic Rainforest and the Cerrado (neotropical savanna) – two of the 25 global biodiversity hotspots, with high levels of rare and endemic species (Jacobi et al., 2007; Jacobi and Carmo, 2008; Medina et al., 2006). The Cangas environment is characterized by a set of stressful factors, such as extreme daily thermal variations, high UV exposure, high evapotranspiration rates, constant winds, impermeable soils with low water-retention capacities, and high levels of iron minerals in the soil (Jacobi and Carmo, 2008; Jacobi et al., 2007; Porembski and Barthlott, 2000). These are highly threatened environments, especially due to iron ore mining, constant fires, and deforestation (Carmo and Jacobi, 2013; Carmo and Kamino, 2015; Jacobi and Carmo, 2008; Jacobi et al., 2007).

Cangas plants have developed specific traits that allow their survival under hostile environmental conditions (Porembski et al., 1998), including adaptations such as succulence, sclerophylly, desiccation-tolerance (i.e., poikilohydry) (Carmo and Jacobi, 2013; Jacobi and Carmo, 2012; Lüttge and Scarano, 2004; Porembski and Barthlott, 2000; Scarano, 2007), the establishment of seed/seedlings banks after the fruiting season, and conspicuous clonal growth (Jacobi et al., 2007; Kluge and Brulfer, 2000; Porembski and Barthlott, 2000). This latter trait is more frequently encountered among monocots, which seem to be able to establish themselves readily in stressful environments (Kluge and Brulfer, 2000).

An interesting plant group with numerous adaptive strategies to colonize adverse environments are the bryophytes, which comprise liverworts, mosses, and hornworts, with ca. 1,524 currently recognized species in Brazil (Costa and Peralta, 2015). Bryophytes are known to have conserved ancestral traits that first allowed plants to survive on land, such as poikilohydry and desiccation-tolerance (Stark et al., 2000, 2007). Additionally, sexual and asexual reproductive strategies allow bryophytes to successfully colonize hash environments (Longton, 1992; Nath and Asthana, 2004). Bryophyte diaspores are of two types, sexual (spores which are produced by sporophytes after fertilization) and asexual (such as gemmae and caducous propagules

(Crawford et al., 2009; Kürschner e Frey, 2012; Longton, 2006; Maciel-Silva e Pôrto, 2014).

Sexual systems in bryophytes (ca. 40% monoecious vs. 60% dioecious species (Maciel-Silva and Pôrto, 2014; Wyatt, 1982) promote different ecological patterns and evolutionary consequences for those species. While out-crossing processes and high levels of genetic variation are expected among dioecious species, self-fertilization and low genetic variation tend to occur most commonly among monoecious taxa (Longton and Schuster, 1983; Stark and Brinda, 2013). Dioecious bryophytes have to deal with the spatial segregation of sexes and male (or mate) limitation (Bisang and Hedenäs, 2005; Bowker et al., 2000; Longton and Schuster, 1983; Maciel-Silva et al., 2016; Pôrto et al., 2016; Stark et al., 2005a) that generally result in low spore outputs as compared to monoecious species. The causes of female dominance in bryophytes have been investigated in the last decades, with some studies suggesting that females can have high tolerances to adverse environmental conditions (Benassi et al., 2011; Marks et al., 2016; McLetchie, 1992; Newton, 1972) and low energy consumptions for sexual reproduction in stressful environments as compared to males (McLetchie, 1992; Stark et al., 2000).

In order to balance this rarity of spore production, dioecious species use asexual reproduction principally for local and short-distance propagation (Laenen et al., 2015; Longton and Schuster, 1983; Pohjamo et al., 2006). This propagation occurs through gametophyte branching and ramet detachment, or through regeneration from specialized structures. The latter can be miniature plants with differentiated leaves, stems and rhizoids (as in caducous propagules), or more specialized structures that must germinate before growing into a new plant (such as aerial and subterraneous gemmae) (Frey and Kürschner, 2010; Glime, 2007; Maciel-Silva and Pôrto, 2014; Pohjamo and Laaka-Lindberg, 2003).

Our principal aim was to determine how bryophytes are able to reproduce under the harsh conditions encountered on ironstone outcrops. As only scarce information is available concerning bryophyte communities associated with Cangas outcrops in Brazil, we proposed the following questions: 1) Which reproductive mode (sexual or asexual) predominates among those bryophyte communities? 2) Which reproductive structures are most used by bryophytes? 3) How frequent are sexual expression and reproductive success (sporophyte output) among monoecious and dioecious species? 4) What are the sex ratios expressed by the dioecious species growing on Cangas formations?

Based on the reproductive strategies commonly found in plant communities living in environments with severe water restrictions, and the patterns of plant reproductive strategies in those environments, we predicted that 1) Bryophytes growing on ironstone outcrops will show predominantly asexual reproductive mode; 2) The production of specialized structures such as propagules as opposed to gemmae, will be the main forms of propagation in Cangas ecosystems; 3) Sexual expression and reproductive success will be underrepresented among dioecious species as compared to monoecious taxa on ironstone outcrops; 4) Because female plants tend to present high performances under large variations in environmental conditions (Marks et al., 2016; McLetchie, 1992; Stark et al., 2000, 2005b), high female-bias and male rarity would be expected among dioecious Cangas species.

Methods

Study área

We carried out a bryophyte survey on ironstone outcrops in two different conservation areas in the Iron Quadrangle (IQ) mining zone of Minas Gerais State, Brazil: the Rola-Moça State Park (RM) in the northwestern region of the IQ (20° 03'04.49"S x 44° 00'29.65"W), which occupies 3.941,1 hectares at elevations of from 900 to 1,550 m, with mean annual temperatures of 18–21 ºC and annual rainfalls of 1,300–2,100 mm; and the Gandarela National Park (GA) in the central northeastern region of the IQ (20°03'28.38"S x 43°41'16.28"W), which occupies 31.270,8 hectares at 1,660 m, with mean annual temperatures of 17–24 ºC and a mean annual rainfall of 1,616 mm (Brandão et al., 1997; Brito et al., 2010; Guarçoni et al., 2010; Meyer et al., 2004; Silva and Salgado, 2009). The vegetation in the two study sites is characterized as a transition zone from savanna (Cerrado) to Atlantic Forest. Quartzitic and ironstone outcrops overlap in this landscape, and these geosystems are characterized by high numbers of drought tolerant vascular plants of the families Asteraceae, Orchidaceae, Poaceae, Melastomataceae, Bromeliaceae, Solanaceae, and Velloziaceae (Carmo and Jacobi, 2013; Jacobi and Carmo, 2008; Jacobi et al., 2007; Porembski et al., 1997, 1998; Scarano, 2002).

Species sampling

We selected three ironstone outcrops in RM and seven in GA where we carried out excursions between February/2015 and May/2016. We randomly collected bryophytes, from ca. 161 ha (65 ha in RM and 95 ha GA). In order to cover the largest possible amounts of species and reproductive strategies among bryophytes, we sampled plants from different microhabitats (e.g. monocotyledonous mats, rock pools, rock fissures, tree associations, exposed rock, crust edges and cave entrances (Jacobi et al., 2007), and substrates (tree bark, rocks, and soil). Samples of at least 5 cm^2 of mosses and liverworts were collected, placed in paper bags, and then taken to the laboratory. Plant material was air dried and examined under dissecting and optical microscopes for species identifications and for the presence of reproductive structures. Species determinations followed Gradstein et al. (2001), and references therein. The classification system was based on Crandall-Stotler et al. (2009) for liverworts, and Goffinet et al. (2009) for mosses, with updates (Santos and Stech, 2016). Vouchers were deposited in the BHCB herbarium (Departamento de Botânica, Universidade Federal de Minas Gerais).

Reproductive traits

We examined all bryophyte specimens (Total = 1,508; RM = 1,130; GA = 378) for sexual and asexual reproductive structures (Frey and Kürschner, 2010; Maciel-Silva and Pôrto, 2014). Each colony sample was classified in terms of the presence of reproductive structures: none- with no reproductive structures; sexual- with intact gametangia or remnant sporophytes; asexual- with gemmae and deciduous propagules; and sexual and asexual- species with both sexual and asexual structures.

We studied the asexual structures using both light and scanning electron microscopy. Several plants were dissected to look for reproductive structures such as gemmae and deciduous propagules. Images were taken using a Zeiss Axio Lab A1 light microscope equipped with an Axion Erc5s digital camera and a FEG - Quanta 200 FEI

Scanning Electron Microscope housed at the Microscopy Center of the Federal University of Minas Gerais.

Plant sexual expression and reproductive success were evaluated through general examinations of colony samples using a dissecting microscope, and by observing three to six dissected ramets under an optical microscope. Male and female gametangia and sporophytes were used to determine sexual expression; only sporophytes (or their remnants) were considered for counts of sexual reproductive success (Alvarenga et al., 2013; Bowker et al., 2000; Maciel-Silva et al., 2012; Pôrto et al., 2016; Stark et al., 2001, 2005b). Sexual systems were always verified (when possible) by examining the plant material and literature searches (Gradstein et al. 2001 and references therein).

Data analysis

We estimated the prevalence of reproductive modes in the overall bryophyte community (RM and GA) by developing a reproductive index (Ri) with two categories: 1. *asexual reproduction*, and 2. *sexual reproduction*. $Ri = (\Sigma n.1) + (\Sigma m.2)/(\Sigma n+m)$, where n is the number of specimens with asexual structures (gemmae and propagules), m is the number of specimens with sporophytes (as liverworts generally have fragile and fugacious sporophytes, the perianth was also used as a proxy in those plants), and $\Sigma n+m$ is the total number of specimens with both sexual and asexual structures. This index represents a variation from one (1) to two (2), where values next to 1 indicate a tendency of the community to reproduce asexually, and whereas values next to 2 show a tendency for sexual reproduction. We use the term "specimen" here to designate each bryophyte colony sample. We compared the proportions of the index values between mosses and liverworts using a G-test contingency table analysis using Bioestat 5.0 software (Ayres et al., 2007).

We investigated the influence of the sexual systems (monoecious and dioecious) of the liverworts and mosses (phylum) on their sexual expression and reproductive success (sporophyte output) at two different sites (RM and GA). Presence/absence counts of the response variables among the bryophyte species colonies were used to perform a Generalized Linear Model (GLZ) with a binomial distribution and a logit link function. We tested the model applying the factors: “sexual system”, “phylum”, “site”, and "sexual system vs. phylum" using Statistica 8.0 program (StatSoft, 2007).

To calculate the sex ratios, we used proportion of females/(numbers of females+numbers of males); we prefer to use proportion of females because the bryophytes commonly have female-biased ratios (Bisang and Hedenäs, 2005; Maciel-Silva et al., 2016). To analyze the sex ratios of bryophytes growing on Cangas, we studied only species with at least four colonies showing sexual reproductive structures. Four colonies are, in fact, a low number to infer the sex-ratio of a species. However, our aim was to detect a general reproductive pattern of the bryophyte community in the ironstone outcrops. Additionally, the majority of dioecious species in Table 3 have more than ten colonies. Thus, the ratios ranged from 0 (no females) to 1 (females only), with a value of 0.5 representing a 1♀:1♂. Binomial tests were performed to detect the presence of bias in the gender distributions of each species, using Bioestat 5.0 software (Ayres et al., 2007).

Results

We encountered 26 families, 54 genera, and 108 species of bryophytes on Cangas sites, with 51 moss species (16 monoecious, 35 dioecious) and 17 liverworts (10 mo; 7 di) in RM; and 33 moss species (9 mo, 24 di) and 33 liverworts (11 mo; 22 di) in GA (Fig. 1). Overall, 34% of the species were monoecious and 66% dioecious (Fig. 2).

Seven hundred and six specimens showed no reproductive structures, 294 were sexually reproducing, 345 were asexually reproducing, and 103 specimens had both sexual and asexual reproductive structures (Appendix Table 1A). The reproductive index for GA was 1.26 for mosses and 1.70 for liverworts; these indices in RM were 1.43 for mosses and 1.95 for liverworts. Asexual structures were proportionally over-represented in moss colonies as compared to liverworts in both GA ($G = 64.8$, d.f. = 1, $P < 0.001$) and RM ($G = 28.2$, d.f. = 1, $P < 0.001$). When the reproductive mode is considered by species, the number of taxa showing sexual mode was higher than those showing asexual mode at both sites and in both phyla (Table 1).

Among the set of species showing asexual reproductive structures in RM and GA, aerial gemmae and propagules were the most abundant structures. Gemmae were recorded in 31% of the asexually reproducing species (5% of the specimens), whereas deciduous propagules were recorded in 69% of the species (95% of the specimens). Gemmae, for example, were found in leaf axils (e.g., *Rosulabryum* sp. and *Didymodon* rigidulus), on the leaf/thallus blade (e.g., *Metzgeria lechleri* and *Syrrhopodon parasiticus*), on leaf tips (e.g., *Octoblepharum albidum*), and on the thallus margin (*M. albinea*) (Fig. 3A-D; Appendix. Table 1A). Deciduous propagules were frequently recorded in *Lejeunea laetevirens*, *Campylopus pilifer*, *C. julaceus*, *C. savannarum*, *Philonotis sphaerocarpa*, and *Bryum argenteum* (Fig. 3E-H; Appendix. Table 1A).

Sex expression and colony reproductive success were influenced by the sexual systems of the bryophyte species, especially because of the contributions of dioecious mosses. Bryophyte communities in RM were found to have more sexually expressing colonies as compared to GA (Table 2). The most frequent bryophyte species in the Cangas areas studied were strongly female-biased (Table 3).

Discussion

Reproduction among bryophytes on Cangas sites is very high, with ca. 50% of the community showing asexual or sexual reproductive structures. This data is surprising due to the recognized stressful conditions on rock outcrops (Carmo and Jacobi, 2016; Jacobi and Carmo, 2008; Jacobi et al., 2007; Medina et al., 2006; Porembski, 2007; Porembski and Barthlott, 2000) and the strict dependence of bryophytes on abundant water for growth and reproduction (Bates, 1998; Goffinet and Shaw, 2009; Proctor et al., 2007; Schofield, 1985).

In terms of the reproductive specimens, our predictions were partially fulfilled, as the mosses showed a high frequency of asexual reproduction mode as compared to liverworts. This tendency is largely related to moss colonies with high incidences of asexual structures (such as *Campylopus* spp. and *Bryum* spp.). These dioecious genera are frequently found without sporophytes, and their main reproduction strategy is likely linked to the production of propagules and gemmae (Frahm, 1991; Kürschner and Frey, 2012). Regarding the liverworts, a sexual mode is their most frequent strategy, especially among colonies of the monoecious *Cheilolejeunea* spp. and *Frullania* spp. This agrees with the observation that monoecious bryophytes tend to have high frequencies of sporophytes (Frey and Kürschner, 2010; Longton and Schuster, 1983; Maciel-Silva et al., 2012; Nath and Asthana, 2004).

In contrast, the contribution of a sexual mode at the species level is apparently more important than an asexual mode for both mosses and liverworts in our study areas. We suggest that bryophytes growing on Cangas sites have different reproductive strategies, with the most abundant species of mosses producing large asexual structures and different liverworts producing sporophytes and spores. Trade-offs involving the dispersal capacity and the establishment success of diaspores are recorded in bryophytes (Löbel and Rydin, 2010). Small spores and gemmae are commonly dispersed by wind for long distances (During, 1979; Kimmerer, 1991; Laaka-Lindberg et al., 2000; Longton, 1992, 2006; Lönnell et al., 2012; Pohjamo et al., 2006; please, see Stieha et al. (2014) for large gemmae being dispersed for long distance by water, and Laenen et al. (2015) for the important role of asexual propagules at long distance events), while the largest diaspores (e.g., > 100 µm gemmae and propagules in our samples) mostly stay within the colonies (Hedenås et al., 2003; Kimmerer, 1991; Kürschner and Frey, 2012; Longton, 2006).

As expected, propagules (caducous shoots) were the most abundant asexual structures in bryophytes. These structures are assumed to contribute to fast colonization of new niches on Cangas exposures as: they are readily detached from the mother plants, especially when moist; the primordia of essential organs (such as leaves, stems, and rhizoids) are already present; they likely show high desiccation tolerance (Proctor et al., 2007; Stark et al., 2016a, 2016b); and they may contribute to gene flow through long-distance dispersal (Laenen et al., 2015; Pohjamo et al., 2006; Virtanen, 2013).

Contrary to our prediction that monoecious species would have high rates of sexual expression and reproductive success, we detected an over-representation of both sexual and asexual modes among colonies of dioecious mosses, which appears to be associated with the high abundances of *Bryum argenteum*, *Rosulabryum capillare*, *Tortela humilis*, and *Schlotheimia tecta*. Although dioecy may promote spatial segregation of the sexes, female-bias, and sporophyte rarity (Bisang and Hedenäs, 2005; Longton and Schuster, 1983; Stark, 2002), these species show alternative strategies for the propagation of new individuals. Bryaceae and Pottiaceae are known to display many asexual reproduction modes (Gradstein et al., 2001; Zander, 1993), and *Schlotheimia* species are pseudoautoicous, with dwarf males, which apparently increases the likelihood of fertilizing any surrounding females (Hedenäs and Bisang, 2011, 2012, Rosengren and Cronberg, 2014, 2015).

A female bias pattern was also confirmed for bryophyte species in Cangas sites, in agreement with data usually reported for mosses and liverworts (Bisang and Hedenäs, 2005; Bowker et al., 2000; Longton, 1992). Female individuals of bryophyte species may be favored under water restriction conditions typical of arid environments (Stark et al., 2004, 2005a) and Cangas formations (see Bisang et al., 2015 for a different pattern).

Conclusions

Moss communities in Cangas sites tend to have high contribution to the asexual reproductive mode than liverworts (which produce mostly sporophytes and spores), and we identified several key species of mosses, especially dioecious ones, which contributed to the high numbers of both sexual and asexual reproductive structures (Fig. 4). These structures, and the abundance of those species, could be very informative about how bryophytes growing on ironstone outcrops, disperse, and colonize new microhabitats at local and regional scales.

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Tables

Table 1. Bryophyte species with reproductive structures from ironstone outcrops in two conservation units in Minas Gerais, Brazil. Marchantiophyta: liverworts, and Bryophyta: mosses; Mo. monoecious; Di. dioecious. % values in brackets.

Reproductive structures	Rola Moça Park				Gandarela Park			
	Marchantiophyta		Bryophyta		Marchantiophyta		Bryophyta	
	Mo	Di	Mo	Di	Mo	Di	Mo	Di
None	6 (40.0)	5 (41.7)	11 (44.0)	27 (43.5)	4 (30.8)	13 (41.9)	1 (11.1)	14 (28.6)
Sexual	9 (60.0)	5 (41.7)	13 (52.0)	20 (32.3)	7 (53.8)	13 (41.9)	8 (88.9)	19 (38.8)
Asexual	0	2 (16.7)	0	11 (17.7)	1 (7.7)	2 (6.5)	0	10 (20.4)
Both sexual and asexual	0	0	1 (4.0)	4 (6.5)	1 (7.7)	3 (9.7)	0	6 (12.2)
Total	15	12	25	62	13	31	9	0

Table 2. Summary of the generalized linear model, with binomial distribution and logit link function, of the sexual expression and reproductive success in liverworts and mosses in ironstone outcrops from two different sites, Minas Gerais, Brazil.

Source	Degree of freedom (d.f.)	Sexual Expression		Reproductive Success	
		Wald test	P	Wald test	P
Site	1	7.350	**0.007**	1.340	0.247
Phylum	1	4.773	**0.029**	0.013	0.907
Sexual System	1	52.371	**<0.001**	103.598	**<0.001**
Phylum vs. Sexual System	1	2.240	0.134	10.888	**<0.001**
Scaled Deviance		1388		1374	
d.f.		1382		1365	
Scaled Deviance / *d.f.*		1.004		1.000	

Table 3. Sex ratios among colonies (sample collections) in dioecious bryophyte species of ironstone outcrops in Minas Gerais, Brazil.

Species	No of colonies	Female colonies (♀)	Male colonies (♂)	Sex ratio ♀ / (♀+♂)	Sex characterization
Bryophyta					
Campylopus julaceus A.Jaeger	77	77	0	1.00	Female
Rosulabryum capillare (Hedw.) Pedersen	57	56	1	0.98	Female biased
Campylopus pilifer Brid.	49	46	3	0.94	Female biased
Schlotheimia tecta Hook. f. & Wilson	46	34	12	0.74	Unbiased
Bryum argenteum Broth	36	34	2	0.94	Female biased
Campylopus savannarum (Müll.Hal.) Mitt.	32	28	4	0.88	Female biased
Tortella humilis (Hedw.) Jenn	29	26	3	0.90	Female biased
Polytrichum juniperinum Willd. ex Hedw	27	20	7	0.74	Unbiased
Campylopus carolinae Grout	13	12	1	0.92	Female biased
Rosulabryum billarderi (Schwägr.) Spence	13	11	2	0.85	Female biased
Schlotheimia rugifolia (Hook.) Schwägr.	11	8	3	0.73	Unbiased
Campylopus lamellinervis (Müll.Hal.) Mitt.	8	7	1	0.88	Female biased
Campylopus arctocarpus (Hornsch.) Mitt.	4	4	0	1.00	Female
Philonotis sphaerocarpa (Hedw.) Brid.	4	4	0	1.00	Female
Schlotheimia fuscoviridis Hornsch.	4	3	1	0.75	Unbiased
Total Bryophyta	410	370	40	0.90	Female biased
Marchantiophyta					
Chonecolea doellingeri (Nees) Grolle	17	17	0	1.00	Female
Frullania ericoides (Nees) Mont.	4	4	0	1.00	Female
Plagiochila corrugata (Nees) Nees et Mont.	4	2	2	0.50	Unbiased
Total Marchantiophyta	25	23	2	0.92	Female biased
Community (Σ)	435	393	42	-	-
Community ($\overline{X}$)	24.2	21.8	2.3	0.90	Female biased

Figure legends

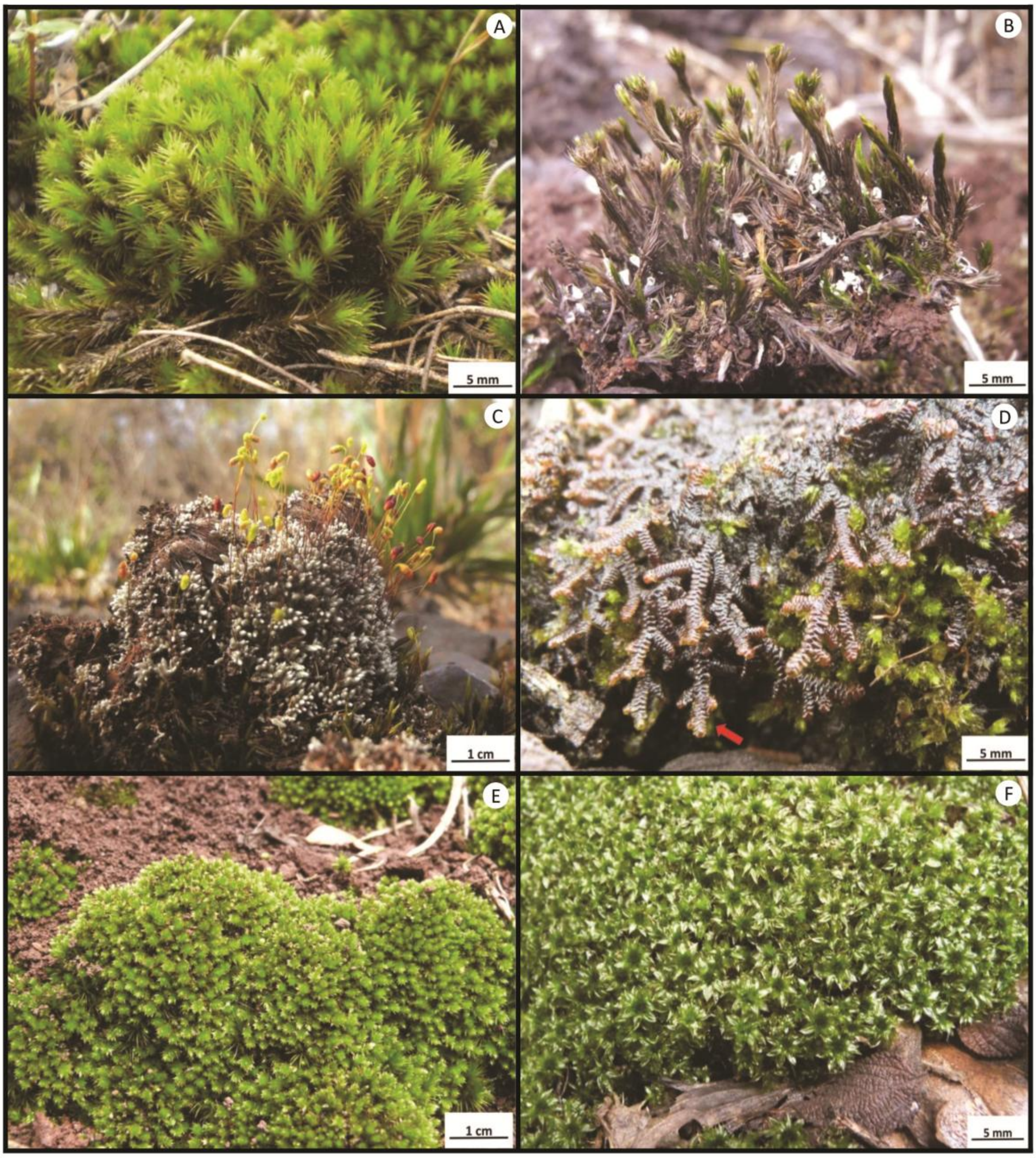

Figure 1. Key bryophyte species present in ironstone outcrops of Minas Gerais, Brazil. A. *Campylopus pilifer*; B. *Campylopus julaceus*; C. *Bryum argenteum*; D. *Frullania brasiliensis*; D. *Rosulabryum capillare*; E. *Rosulabryum huillense*.

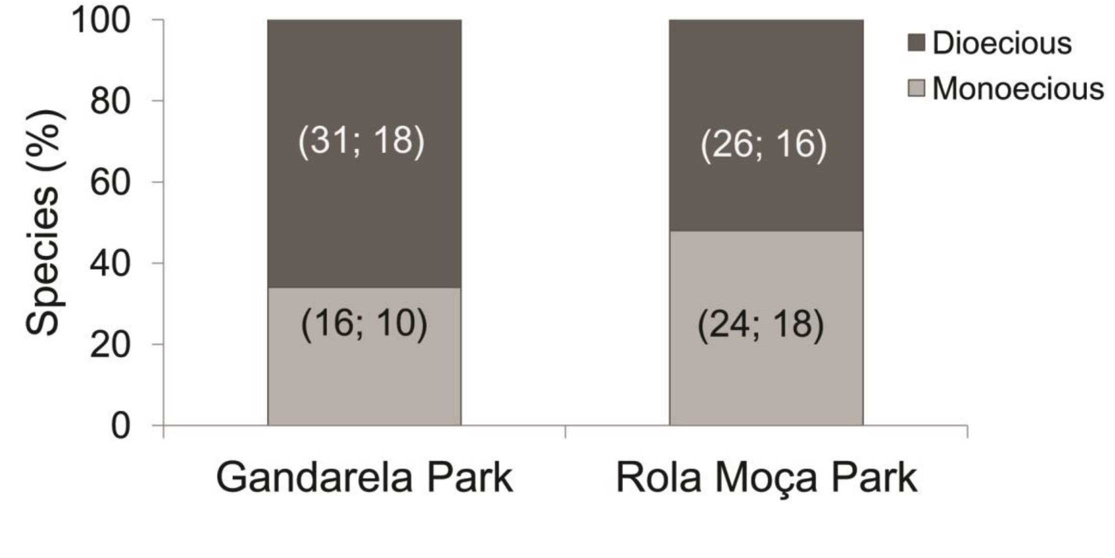

Figure 2. Bryophyte species (%) with sexual reproduction in Cangas of Minas Gerais, Brazil; values in brackets are absolute numbers of dioecious and monoecious species with sexual expression and reproductive success (sporophytes), respectively.

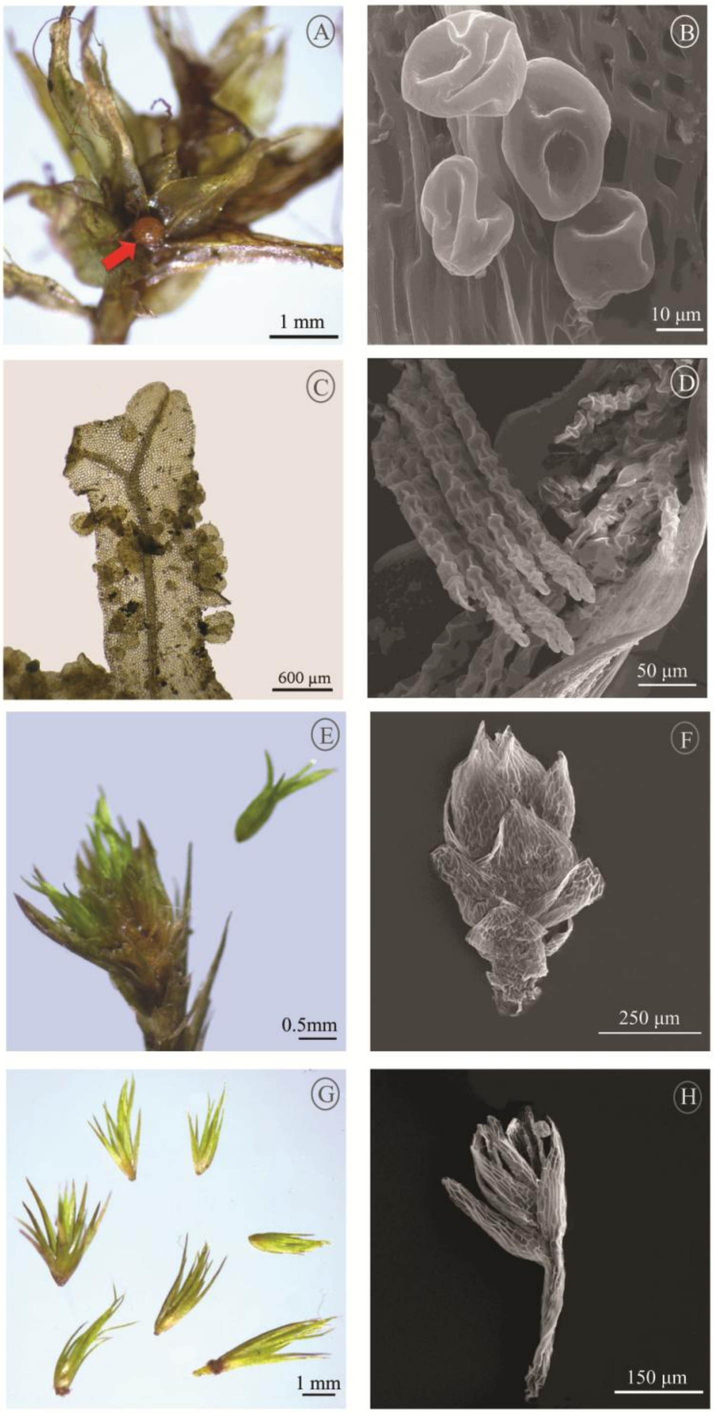

Figure 3. Types of asexual reproductive structures of bryophytes in Cangas. A-D. gemmae: in the leaf axil, A- *Rosulabryum sp*, B- *Didymodon rigidulus*; on the leaf/thallus blade, C- *Metzgeria lechleri*, D- *Syrrhopodon parasiticus*. E-H. Deciduous propagules: E- *Campylopus julaceus*, F- *Bryum argenteum*, G- *Campylopus pilifer* and H- *Philonotis sphaerocarpa*.

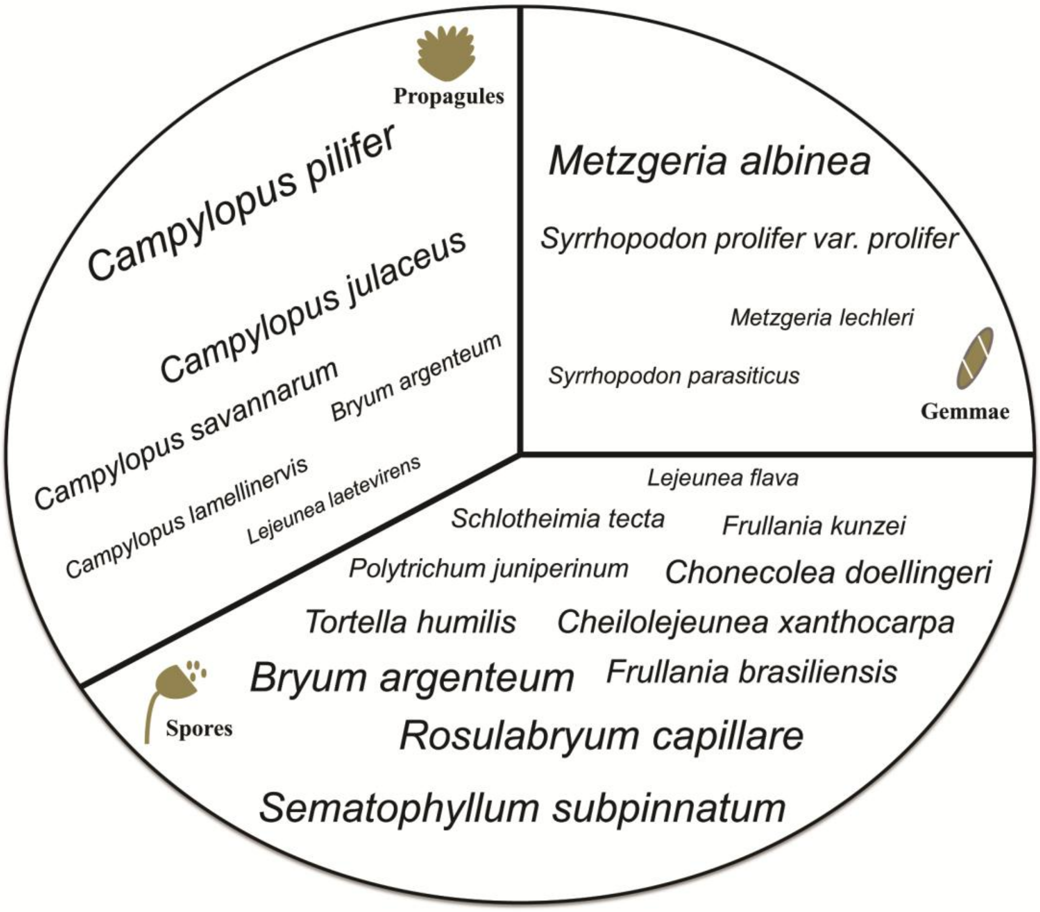

Figure 4. Conceptual model of the reproductive strategies of mosses and liverworts in ironstone outcrops, Minas Gerais, Brazil. Size of the species names varies according to the species abundance.

Appendix

Table 1A. Species of bryophytes in ironstone outcrops of Serra do Gandarela National Park (GA) and Serra do Rola-Moça State Park (RM); SEX – with sexual structures, sporophyte, perianth, archegonia and/or antheridia; ASX – with asexual structures, gemmae and/or propagules; SEX/ASX - with sexual and asexual structures; NONE- without sexual or asexual structures.

Taxons	**Ironstone Outcrops**	**Sexual System**	**Reproductive Structures**
MARCHANTIOPHYTA			
CEPHALOZIELLACEAE			
Cylindrocolea rhizantha (Mont.) R.M. Schust.	RM	Monoecious	SEX
CHONEOCOLEACEAE			
Chonecolea doellingeri (Nees) Grolle	RM	Dioecious	SEX
FRULLANIACEAE			
Frullania brasiliensis Raddi	GA; RM	Monoecious	SEX
Frullania caulisequa (Nees) Nees	GA	Monoecious	SEX
Frullania ericoides (Nees) Mont.	GA; RM	Dioecious	SEX
Frullania gibbosa Nees	RM	Monoecious	SEX
Frullania kunzei (Lehm. & Lindenb.) Lehm. & Lindenb.	GA; RM	Monoecious	SEX
Frullania setigera Steph.	GA	Dioecious	SEX/ASX
LEJEUNEACEAE			
Anoplolejeunea conferta (C.F.W.Meissn.) A. Evans	GA	Dioecious	SEX
Archilejeunea fuscescens (Hampe ex Lehm.) Fulford	GA	Monoecious	NONE
Brachiolejeunea laxifolia (Taylor) Schiffn.	GA	Monoecious	SEX
Cheilolejeunea acutangula (Nees) Grolle	RM	Monoecious	SEX
Cheilolejeunea holostipa (Spruce) Grolle & R.-L.Zhu	GA	Dioecious	SEX
Cheilolejeunea oncophylla (Aongström) Grolle & E.Reiner	GA	Monoecious	SEX
Cheilolejeunea revoluta (Herzog) Gradst. & Grolle	GA	Dioecious	NONE
Cheilolejeunea rigidula (Nees ex Mont.) R.M. Schust.	GA	Dioecious	SEX
Cheilolejeunea xanthocarpa (Lehm. & Lindenb.) Malombe	GA	Monoecious	SEX/ASX
Drepanolejeunea araucariae Steph.	GA	Dioecious	NONE
Drepanolejeunea bidens (Steph.) A.Evans	GA	Dioecious	NONE
Drepanolejeunea granatensis (J.B.Jack & Steph.) Bischl.	GA	Dioecious	NONE
Frullanoides tristis (Steph.) van Slageren	GA	Dioecious	NONE
Harpalejeunea stricta (Lindenb. & Gottsche) Steph.	GA	Dioecious	SEX
Lejeunea cristulata (Steph.) E.Reiner & Goda	GA	Monoecious	SEX
Lejeunea flava (Sw.) Nees	GA; RM	Dioecious	SEX
Lejeunea laetevirens Nees & Mont.	GA; RM	Dioecious	SEX
Lejeunea puiggariana Steph.	RM	Monoecious	SEX
Lopholejeunea nigricans (Lindenb.) Schiffn.	RM	Monoecious	SEX
Lopholejeunea subfusca (Nees) Schiffn.	RM	Monoecious	SEX
Mastigolejeunea innovans (Spruce) Steph.	RM	Monoecious	SEX
Metalejeunea cucullata (Reinw. et al.) Grolle	GA; RM	Monoecious	NONE
Microlejeunea bullata (Taylor) Steph.	RM	Dioecious	NONE
Omphalanthus filiformis (Sw.) Nees	GA	Dioecious	SEX
METZGERIACEAE			
Metzgeria albinea Spruce	GA	Dioecious	SEX/ASX
Metzgeria furcata (L.) Dumort.	GA	Dioecious	SEX/ASX
Metzgeria lechleri Steph.	RM	Dioecious	ASX

Table 1A. Cont.

Taxons	**Ironstone Outcrops**	**Sexual System**	**Reproductive Structures**
PLAGIOCHILACEAE			
Plagiochila bifaria (Sw.) Lindenb.	GA	Dioecious	NONE
Plagiochila corrugata (Nees) Nees & Mont.	GA	Dioecious	SEX
Plagiochila micropteryx Gottsche	GA	Dioecious	ASX
Plagiochila patula (Sw.) Lindenb.	GA	Dioecious	NONE
RADULACEAE			
Radula fendleri Gottsche ex Steph.	GA	Dioecious	SEX
BRYOPHYTA			
ARCHIDIACEAE			
Archidium tenerrimum Mitt.	GA	Monoecious	SEX
BARTRAMIACEAE			
Bartramia mathewsii Mitt.	GA	Dioecious	NONE
Philonotis sphaerocarpa (Hedw.) Brid.	GA; RM	Dioecious	SEX/ASX
Philonotis sp 1	RM	Dioecious	NONE
BRACHYTHECIACEAE			
Helicodontium capillare (Hedw.) A. Jaeger	RM	Dioecious	SEX
BRYACEAE			
Brachymenium systylium (Müll. Hal.) A. Jaeger	GA	Dioecious	SEX
Bryum apiculatum Schwägr.	RM	Dioecious	SEX
Bryum arachnoideum Müll. Hal.	GA; RM	Dioecious	SEX/ASX
Bryum argenteum Broth.	GA; RM	Dioecious	SEX/ASX
Bryum subapiculatum Hampe	RM	Dioecious	NONE
Bryum sp1	RM	Dioecious	NONE
Bryum sp2	RM	Dioecious	NONE
Ptychostomum cf *wrightii* (Sull.) J.R.Spence & H.P.Ramsay	RM	Dioecious	SEX
Rosulabryum billarderi (Schwägr.) Spence	GA; RM	Dioecious	SEX
Rosulabryum capillare (Hedw.) Pedersen	GA; RM	Dioecious	SEX
Rosulabryum huillense (Welw. & Duby) Ochyra	GA; RM	Dioecious	SEX
Rosulabryum sp1	RM	Dioecious	ASX
CALYMPERACEAE			
Syrrhopodon gardneri (Hook.) Schwägr.	RM	Dioecious	ASX
Syrrhopodon parasiticus (Brid.) Besch.	RM	Dioecious	ASX
Syrrhopodon prolifer Schwägr. var. *prolifer*	GA; RM	Dioecious	SEX/ASX
DICRANACEAE			
Holomitrium crispulum Mart.	GA	Dioecious	SEX
FABRONIACEAE			
Fabronia ciliaris (Brid.) Brid. subsp. *ciliaris*	RM	Monoecious	SEX
Fabronia ciliaris var. *polycarpa* (Hook.) W.R. Buck	RM	Monoecious	SEX
FISSIDENTACEAE			
Fissidens crispus Mont.	RM	Monoecious	SEX
Fissidens leptophyllus Mont.	RM	Monoecious	SEX
HYPNACEAE			
Chryso-hypnum diminutivum (Hampe) W.R.Buck	RM	Monoecious	SEX

Table 1A. Cont.

Taxons	**Ironstone Outcrops**	**Sexual System**	**Reproductive Structures**
LEUCOBRYACEAE			
Campylopus arctocarpus (Hornsch.) Mitt.	GA	Dioecious	SEX/ASX
Campylopus carolinae Grout	GA; RM	Dioecious	SEX/ASX
Campylopus heterostachys (Hampe) A. Jaeger	GA	Dioecious	ASX
Campylopus julaceus A. Jaeger	GA; RM	Dioecious	SEX/ASX
Campylopus julicaulis Broth.	RM	Dioecious	NONE
Campylopus lamellinervis (Müll. Hal.) Mitt.	GA; RM	Dioecious	SEX/ASX
Campylopus occultus Mitt.	RM	Dioecious	ASX
Campylopus pilifer Brid.	GA; RM	Dioecious	SEX/ASX
Campylopus savannarum (Müll. Hal.) Mitt.	GA; RM	Dioecious	SEX/ASX
Campylopus trachyblepharon (Müll. Hal.) Mitt.	GA	Dioecious	ASX
Leucobryum clavatum Hampe	RM	Dioecious	NONE
Pilopogon peruvianus (R.S. Williams) J.-P. Frahm	RM	Dioecious	SEX/ASX
OCTOBLEPHARACEAE			
Octoblepharum albidum Hedw.	RM	Monoecious	SEX/ASX
ORTHOTRICACAE			
Groutiella tomentosa (Hornsch.) Wijk & Margad.	RM	Dioecious	NONE
Macrocoma orthotrichoides (Raddi) Wijk & Margad.	GA; RM	Monoecious	SEX
Macromitrium microstomum (Hook. & Grev.) Schwägr.	GA	Monoecious	SEX
Macromitrium punctatum (Hook. & Grev.) Brid.	RM	Dioecious	SEX
Schlotheimia fuscoviridis Hornsch.	RM	Dioecious	NONE
Schlotheimia rugifolia (Hook.) Schwägr.	GA; RM	Dioecious	SEX
Schlotheimia sp 1	RM	Dioecious	NONE
Schlotheimia sp 2	GA	Dioecious	SEX
Schlotheimia tecta Hook. f. & Wilson	GA	Dioecious	SEX
*Zygodon reinwardtii (*Hornsch.) A.Braun var. *reinwardtii*	RM	Monoecious	NONE
POLYTRICHACEAE			
Polytrichum juniperinum Willd. ex Hedw.	GA; RM	Dioecious	SEX
POTTIACEAE			
Didymodon rigidulus Hedw.	RM	Dioecious	ASX
Hyophila involuta (Hook.) A. Jaeger	RM	Dioecious	SEX
Tortella humilis (Hedw.) Jenn.	GA; RM	Dioecious	SEX
Trichostomum sp 1	RM	Dioecious	SEX
Weissia controversa Hedw.	GA; RM	Monoecious	SEX
PYLAISIADELPHACEAE			
Isopterygium tenerum (Sw.) Mitt.	RM	Monoecious	NONE
RACOPILACEAE			
Racopilum tomentosum (Hedw.) Brid.	RM	Monoecious	SEX
SEMATOPHYLLACEAE			
Acroporium exiguum (Broth.) W.R.Buck & Schäf.-Verw.	GA	Monoecious	SEX
Donnellia commutata (Müll. Hal.) W.R.Buck	GA; RM	Monoecious	SEX
Donnellia lagenifera (Mitt.) W.R. Buck	GA	Monoecious	SEX
Sematophyllum galipense (Müll. Hal.) Mitt.	GA; RM	Monoecious	SEX

Table 1A. Cont.

Taxons	**Ironstone Outcrops**	**Sexual System**	**Reproductive Structures**
Sematophyllum sp 1	RM	Monoecious	SEX
Sematophyllum subpinnatum (Brid.) E. Britton	RM	Monoecious	SEX
Sematophyllum subsimplex (Hedw.) Mitt.	GA	Monoecious	SEX
STEREOPHYLACEAE			
Entodontopsis nitens (Mitt.) W.R.Buck & Ireland	RM	Monoecious	SEX

CAPITULO II

Artigo Submetido ao Periódico *Flora - Morphology, Distribution, Functional Ecology of Plants*.

Bryophytes on Brazilian ironstone outcrops: diversity, environmental filtering, and conservation implications

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Abstract

Brazilian ironstone outcrops ("*Cangas*") are characterized by high soil iron concentrations, high ambient temperatures, strong water restrictions, and occupation by vascular plants showing high levels of rarity and/or endemism. Another group of plants commonly inhabiting *Cangas* are bryophytes, which have important roles in maintaining soil moisture and nutrient levels, but are only infrequently investigated. *Cangas* sites are currently threatened by mining, uncontrolled urbanization, and deforestation. We therefore addressed the questions of: 1) What is the beta diversity of bryophyte communities on ironstone outcrops in two different Environmental Protection Areas – EPAs? 2) Does environmental filtering drive bryophyte community diversity? 3) What are the influences of microhabitats and substrate availability on bryophyte assemblages? We analyzed the bryophytes in eight *Cangas* sites in two EPAs in Minas Gerais State, Brazil, and characterized their communities in terms of their different microhabitats/substrates, elevation, and disturbance levels. Ninety-seven bryophyte species were identified (57 mosses, 40 liverworts), distributed mainly among Tree-Associated microhabitats (68 spp.) and Tree Bark substrates (67 spp.). In terms of environmental filtering, the EPAs were found to be separated into two specific floristic groups (GA and RM) that differed in relation to their elevations and levels of anthropogenic disturbance. We also identified compartmentalization of the bryophyte assemblages among the different microhabitats/substrates on ironstone outcrops, especially in GA sites. Compared to other plant communities encountered growing on different types of rocky outcrops, the ironstone outcrops in southeastern Brazil were found to harbor high bryophyte diversity. These findings highlight the importance of conserving diverse *Cangas* sites, as they accommodate specific bryophyte communities.

Key-words: Cangas; Community; Disturbance; Microhabitats; Mosses; Liverworts

Introduction

Rocky outcrops are considered biodiversity hotspots of global importance as they can support plant communities composed mostly of rare and/or endemic species (Carmo and Jacobi, 2016; Jacobi and Carmo, 2008; Medina et al., 2006; Scarano, 2007). Three important centers are recognized in the world: (I) southwestern Australia, (II) Madagascar, and (III) southeastern Brazil, and these diverse types of rocky outcrops (granitic, gneiss, and ironstone) can be easily distinguished by their geomorphologies (Fernandes, 2016; Porembski, 2007; Porembski and Barthlott, 2000; Scarano, 2007). Rocky outcrops experience adverse environmental conditions, including high evapotranspiration rates, high UV exposures, wide daily thermal variations, constant winds, low water retention, and impermeable soils (Jacobi et al., 2007; Jacobi and Carmo, 2008; Medina et al., 2006; Porembski and Barthlott, 2000).

Minas Gerais State in southeastern Brazil contains a region known as the Iron Quadrangle (IQ) with an extension of 158.022,38 hectares and with many ironstone outcrops ("*Cangas*"). This type of rocky outcrop differs from granitic and gneiss exposures as it forms soils with high concentrations of iron, which become a strong selective factor for plant establishment (Carmo and Kamino, 2015; Jacobi and Carmo, 2012, 2008). Ironstone outcrops show mosaics of microhabitats that can be classified (Jacobi et al. 2007) in terms of their micro-topography and vegetation types (*e.g.*, monocotyledonous mats, rock pools, rock fissures, tree associations, exposed rock, crust edges, and cave entrances). These different microhabitats host different types of plant communities, but their vascular plant populations have been better studied than the bryophytes (Carmo and Kamino, 2015; Jacobi and Carmo, 2008; Porembski et al., 1998; Porembski and Barthlott, 2000; Scarano, 2002).

The ironstone outcrop vegetation in the Iron Quadrangle (Minas Gerais, Brazil) is represented by ca. 1100 species of vascular plants; the families with the highest numbers of species are Asteraceae, Orchidaceae, Poaceae, Melastomataceae, Fabaceae, Bromeliaceae, Solanaceae, and Velloziaceae, and all of them show high numbers of rare and endemic species (Carmo and Jacobi, 2013, 2012; Jacobi et al., 2007; Jacobi and Carmo, 2008). These plant communities are highly threatened, and some are in danger of disappearing completely – largely due to iron ore strip mining. Approximately

300,000 km² of Brazilian territory was granted to mining companies in recent years, with more than 99% located in the areas with ironstone outcrops (Carmo and Kamino, 2015). These mines have generated strong alterations of the landscape and resulted in local and regional extinctions of plant species restricted to those formations (Carmo and Kamino, 2015; Jacobi and Carmo, 2012; Silveira et al., 2015).

Another factor that threatens ironstone outcrops is poorly controlled urban development, disorderly land use, and unregulated tourism (without conservation measures) – which have all promoted deforestation and facilitated the establishment of invasive species (Drummond et al., 2005; Marent et al., 2011). In addition to direct anthropogenic impacts, fires generate severe disturbances of ironstone outcrop vegetation. While wildfires are natural factors in this geosystem, fire frequencies have increased due to increased human presence in neighboring areas, promoting landscape alterations (Carmo and Kamino, 2015; Marent et al., 2011; Silveira et al., 2015).

Bryophytes are very abundant on ironstone outcrops, but there have been very few detailed investigations of their communities (Jacobi et al., 2007). These plants show multiple adaptations to harsh environments, such as poikilohydry, desiccation-tolerance, and the production of diverse types of asexual reproductive structures (Frey and Kürschner, 2010; Maciel-Silva and Pôrto, 2014; Proctor et al., 2007; Stark et al., 2007, 2000) that facilitate their rapid establishment and colonization of rocky outcrops (Frahm and Porembski, 1998; Silva et al., 2014; Silva and Germano, 2013; Valente and Pôrto, 2006). In the Serra dos Carajás Mountains (Pará State in northern Brazil), for example, a bryophyte survey on ironstone outcrops recorded 87 moss species, 14 of which were classified as rare (Moraes and Lisboa, 2006), and possible indicator-species for heavy metals (Lisboa and Ilkiu-Borges, 1996). After those early studies, however, additional research focusing on bryophytes on ironstone outcrops was not carried out until relatively recently – exemplifying the lack of detailed information about ironstone outcrops as well as the need for increased understanding of how bryophytes occupy ironstone outcrops and their numerous microhabitats.

The present work was designed to contribute to our knowledge of bryophyte communities growing on ironstone outcrops and to evaluate the influence of environmental filtering at both regional and local levels. The following questions were therefore proposed within a regional context: 1) What is the beta diversity of bryophyte communities growing on ironstone outcrops within two different Environmental Protection Areas (EPAs)? 2) Does environmental filtering drive bryophyte community structures? 3) What are the influences of microhabitats and substrate availability on bryophyte assemblages? Based on the premise that bryophytes are poikilohydric plants (Proctor, 2000) whose distributions are shaped by environmental filters (Oliveira et al., 2009; Santos et al., 2014, 2011), we expected higher similarities of species in ironstone outcrops located in the same EPA than between outcrops in the two different EPAs, as those areas would be expected to experience different anthropogenic disturbance levels and to occur at different elevations. On the other hand, since the microhabitats/substrates on ironstone outcrops may drive the establishment of bryophyte species and thus operate as important local filters (Batista and Santos, 2016; Oliveira and Steege, 2015; Silva et al., 2014), we would expect to detect a compartmentalization of the communities, with bryophyte assemblages colonizing the same types of microhabitats having higher species similarities.

Methods

Study area

We carried out bryophyte inventories on ironstone outcrops (Cangas) in two different Environmental Protection Areas (EPAs) located in the central region of the Iron Quadrangle (IQ), in Minas Gerais State, southeastern Brazil, having transitional vegetations between Neotropical Savanna (Cerrado) and Atlantic Forest (Jacobi et al., 2008, 2007). The Gandarela National Park (GA) (Fig. 1a) is located in the northeastern portion of the IQ (20°03'28"S x 43°41'16"W), with elevations up to 1660 m; with average annual temperatures of 17–24 ºC, and an average annual rainfall rate of 1616 mm. The second site was the Rola-Moça State Park (RM) (Fig. 1b), also located in the IQ (20°03'04"S x 44°00'29"W), in the metropolitan region of the state capital of Belo Horizonte, with elevations up to 1550 m, average annual temperatures of 18–21 ºC, and an average annual rainfall rate of 1509 mm (Brito et al., 2010; Carmo and Kamino, 2015; Drummond et al., 2005; Marent et al., 2011; Silva and Salgado, 2009).

Species sampling

We collected bryophytes from February/2015 to May/2016 on eight different ironstone outcrops, five in GA and three in RM; random bryophyte samples were collected in the study areas, together with data of site elevations and latitude and longitude (Tab. 1). Bryophytes samples at least 5 cm^2 were collected and stored temporarily in paper bags before being removed to the laboratory. The plant material was subsequently air dried and analyzed using dissecting and optical microscopes. Species determinations followed Gradstein et al. (2001) and references therein. The classification system used was based on Crandall-Stotler et al. (2009) for liverworts and Goffinet and Shaw (2009) for mosses (with updates). Voucher specimens were deposited in the BHCB herbarium (Departamento de Botânica, Universidade Federal de Minas Gerais).

Bryophyte species were collected from three very common substrates on ironstone outcrops: *terricolous* (those growing on the soil surface); *saxicolous* (directly on rock surfaces); and *epiphytic*/*epixylics* (on live bark or on dead trees and shrubs; we chose to group these substrates together in this study as epixylic bryophytes are very rare on ironstone outcrops). We classified Cangas environments into five microhabitats based on Jacobi et al. (2007) and Jacobi and Carmo (2012) for ironstone outcrops, and based on Porembski et al. (1994) and Porembski and Barthlott (2000) for other types of rocky outcrops. However, as those studies focused on vascular vegetation, we adapted our classification according to those microhabitats where bryophytes were best represented.

We recorded bryophytes in: 1) *Insect Nests* (IN), soil gathered and processed by termites or ants into temporary nests, with bryophytes growing on them and present in open areas and/or near the edges of Tree-Associations; 2) *Shrub-Associations* (SA), small to medium shrubs and/or herbs located in open Cangas areas, occasionally generating small shaded areas at their bases that aid in retaining small amounts of organic matter and moisture; 3) *Tree-Associations* (TA), vegetation islands in open areas and depressions composed of medium to large trees, shrubs, lianas, and ferns, creating shady and relatively humid sites; 4) *Soil Islands* (SI), on exposed sites and on the edges of Tree-Associations, which are small islands of land with the common presence of bryophytes, so that the species growing in these microhabitats are usually exposed directly to environmental variations; 5) *Exposed Rock* (ER), these microhabitats have some of the most adverse conditions, as they represent completely smooth surfaces on ironstone outcrops that are directly exposed to intense solar radiation and strong winds;

Additionally, we estimated the degrees of human disturbance on the different ironstone outcrops by measuring their center-point distances (in meters) from cities, constructions, roads, and mining sites – based on satellite images available using Google Earth software (https://google-earth.softonic.com.br).

Data analysis

Two frameworks were used to evaluate the beta diversity of bryophyte communities on ironstone outcrops: (1) similarities between the ironstone outcrops - using a floristic matrix was prepared from incidence data (presence/absence) of the species in the eight sampling areas (five in GA and three in RM). This analysis was performed with, and then without, rare species (those with less than three records in the community). As no differences were noted between the two results, we present here the results for all of the species encountered. (2) To examine the influence of local filters on bryophytes we analyzed the similarities between microhabitats; as preliminary analyzes indicated that the substrates demonstrated the same patterns as the microhabitats (Fig. S1), we present here data only for the latter variable. A second floristic matrix was prepared using the incidence data (presence/absence) of the species in the different microhabitats colonized by bryophytes in both EPAs. The Jaccard index was used with the two frameworks to calculate floristic similarities, and classification and ordination analyses were subsequently performed using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) method (data not shown) and Correspondence Analysis, both run on Fitopac 2.1 software (Shepherd, 2010). Additionally, we used Multiresponse Permutation Procedures (MRPP) in the PCO program (McCune and Mefford, 1999) to test whether a priori defined groups (the Environmental Protection Areas, GA x RM) differed from those expected by chance for (1) ironstone outcrops and for (2) the four microhabitat types. MRPP generates an index (index A) indicating the degree of cohesion between the samples, where higher values of A indicate greater similarity between the species in the different samples analyzed (McCune and Grace, 2002).

Proxy data for human activities was used to evaluate our assumption that the two Environmental Protection Areas were exposed to different levels of anthropogenic disturbances. The disturbance matrix was subsequently used in Principal Component Analysis (PCA) and for the Mantel Test. We used PCA to determine how these disturbance proxies vary among the ironstone outcrops examined and to select the variables most correlated with axes 1 and 2. Those variables were subsequently used in Canonical Correspondence Analysis (CCA), performed using a covariance matrix with Fitopac 2.1 software (Shepherd, 2010).

In order to better understand the influence of elevation and anthropogenic disturbances on bryophyte communities, we evaluated the correlations between the floristic matrix (based on species incidence data) and environmental gradients (anthropogenic disturbance and elevation data) using Canonical Correspondence Analysis (CCA), using Fitopac 2.1 software (Shepherd, 2010). CCA is a canonic ordination technique based on correspondence analysis that restricts the ordination of a species matrix through multiple linear regressions performed on the variables within a given environment (McCune and Grace, 2002). Monte Carlo tests with 1000 permutations were used to confirm the significance of the first ordination axis.

Mantel tests were used to assess if the geographical or environmental distances between ironstone outcrops influenced bryophyte composition. Mantel statistics test the correlations between two triangular matrices (Legendre and Legendre, 1988), which, in our case, were: floristics x geographic distances, and floristics x environmental distances (based on anthropogenic disturbance data), calculating the distances between the sampling pairs of the floristic (species dissimilarity = 1 - Jaccard similarity), geographic (geographical distance index), and environmental (Euclidean distance index) matrices. The Mantel statistics were tested using 10,000 permutations with Fitopac 2.1 software (Shepherd, 2010). According to our working hypothesis, bryophytes will demonstrate distributions shaped by environmental filters, thus generating predictions of: (1) a positive correlation between the floristic and environmental matrices; and (2) the absence of any correlation between the floristic and geographic matrices.

Results

Bryophytes in ironstone outcrop ecosystems

We recorded 1,495 bryophyte specimens distributed among 25 families, 54 genera, and 97 species (57 mosses, 40 liverworts) in the two EPAs, with 62 species (45 mosses, 17 liverworts) in the RM and 60 species (31 mosses, 29 liverworts) in the GA conservation areas. The most representative families in the Cangas were Lejeunaceae (24 spp.), Bryaceae (12 spp.), and Leucobryaceae (10 spp.). The moss species *Campylopus pilifer*, *C. savanarum*, *Rosulabryum capillare*, and *Bryum argenteum*, and the liverwort species *Chonecolea doellingeri* and *Frullania brasiliensis* were the most representative species in the bryophyte communities (Tab. 2).

At the microhabitat level, bryophytes were more diverse in Tree-Associations (68 spp.), followed by Shrub-Associations (58 spp.), Exposed Rocks (45 spp.), Soil Islands (35 spp.), and Insect Nests (10 spp.). In terms of the substrates occupied by bryophytes, tree bark harbored the greatest species diversity (67 spp.), followed by soils (59 spp.) and rocks (57 spp.; Tab. 3).

Beta diversity of bryophyte communities on ironstone outcrops

The floristic similarities of the bryophytes populations on the eight ironstone outcrops examined were low, varying between 0.12 (GA2 and RM3) and 0.46 (RM2 and RM3). The Jaccard index was highest among RM outcrops (Tab. S1). The cluster and ordination analyses formed similar groups – so we will report here only the ordination results. Correspondence analysis showed the bryophyte communities differentiated along axis 1 (Fig. 2), revealing distinct assemblages in the GA and RM EPAs. However, one GA outcrop (GA 5) showed higher floristic affinity with the RM outcrops. The percentage of accumulated inertia in the first two CA axes was 43.8%.

The Jaccard indices for the microhabitats varied between 0.02 (GA Insect Nests and RM Tree-Associations) to 0.48 (RM Shrub-Associations and Tree-Associations; Tab. S2). Similarly, the highest Jaccard indices were found among RM microhabitats, indicating a taxonomic homogenization of the bryophyte communities in this protected area – data that corroborates the correspondence analysis diagram (Fig. 3). The percentage of accumulated inertia in the first two CA axes was 34.5%.

MRPP tests confirmed significant differences in the identities of the bryophyte species in the two EPAs studied (A = 0.33, p = 0.009 for ironstone outcrops and A = 0.15, p = 0.003 for the microhabitats), indicating that heterogeneity (differences in species compositions) was greater between samples located in different Environmental Protection Areas.

Environmental filtering in ironstone outcrops

The PCA of the anthropogenic disturbance matrix yielded a heterogeneous diagram, with the presence of three groups (Fig. 4). The percentage of accumulated variance in the first two axes was 89.8%. The first axis was most strongly correlated with the distances to cities (0.61), roads (0.59), and constructions (0.49), isolating areas with lower disturbances (GA 2 and GA3). The second axis was most strongly correlated with larger distances to mining sites (-0.92), with areas GA1, GA4 and GA5 being grouped. The three areas of RM (in the upper left quadrant) showed higher levels of anthropogenic disturbance, confirming our initial assumption.

In the direct gradient analysis (CCA), only the first axis of the ordination diagram was significant (p = 0.038). This axis shows the separation of two floristic groups (GA x RM), with this floristic dissimilarity being related to elevation and anthropogenic disturbances (Fig. 5). The canonical eigenvalue (CE) obtained for the first axis was 0.57, being responsible for 23.5% of the total cumulative variance of the data. The environmental variables that most strongly correlated with the first environmental axis (LC scores) were elevation (-0.94), distances to mining sites (-0.86), and distances to cities (-0.85).

Bryophytes apparently demonstrate environmentally determined distributions. We found a positive correlation between the floristic and environmental matrices (rM = 0.47; p = 0.008), with the relationships between the floristic and geographic matrices not being significant (rM = -0.18; p = 0.25).

Discussion

Bryophyte Communities on ironstone outcrops

Compared to other rock outcrop environments in Brazil, we found that the ironstone outcrops in the Iron Quadrangle in Minas Gerais State harbored a high diversity of bryophyte species (57 mosses and 40 liverworts). Previous surveys of bryophytes in similar environments recorded diversities varying from 21 to 87 species (Frahm and Porembski, 1998; Moraes and Lisboa, 2006; Silva et al., 2014; Silva and Germano, 2013; Silva et al., 2014; Valente and Pôrto, 2006). Bryophyte populations appeared to be well-established on ironstone outcrops, with some colonies covering relatively large areas (mostly species of *Campylopus*). These plants are obviously well-adapted to life on ironstone outcrops and can tolerate extreme variations in abiotic conditions (e.g., moisture, temperature, and winds) and use a variety of asexual structures to reproduce and survive (Pôrto et al., 2016; Proctor et al., 2007; Silva et al., 2014; Stark et al., 2016, 2007). Bryophytes can have important roles in structuring and maintaining geosystems, and contribute to aggregating vascular plants (Hespanhol et al., 2011; Jacobi et al., 2007).

Bryophyte species on ironstone outcrops were mostly distributed in exposed and shaded microhabitats (Fig. 6). Exposed communities were observed in the Insect Nests, Soil Islands and Exposed Rock sites, demonstrating a strong dominance by mosses of the genera *Bryum*, *Rosulabryum* and *Campylopus*. These mosses show high production rates of vegetative propagules and sporophytes (spore sources), as well as hyaline apices that contribute to water uptake and protection against excessive UV radiation – allowing successful colonization of those microenvironments (Frahm, 1996; Kürschner and Frey, 2012; Stark et al., 2016; Vitt et al., 2014). The shaded micro-habitat group was observed in Shrub-Associations and Tree-Associations, which contained moss and liverwort species in similar proportions. Among the species in those shaded microhabitats, *Schlotheimia tecta* is pseudoautoecious (with dwarf males on female plants), while *Sematophyllum subpinnatum*, *Cheilolejeunea xanthocarpa*, *Frullania brasiliensis*, and *Lopholejeunea subfusca* are monoecious species that show prolific productions of sporophytes (Gradstein et al., 2001, and references therein). Additionally, the dioecious species *Metzgeria albinea* produces many gemmae as a propagation strategy (Costa, 2008). Other morpho-physiological adaptations in the above species include saccate lobules and dark pigmentation (*F. brasiliensis*), or white coloration (*C. xanthocarpa*) – which allow them to tolerate high evapotranspiration rates, UV exposure and daily thermal variations, as well as low water availability (Glime, 2013; Gradstein and Costa, 2003; Jacobi et al., 2007; Silva et al., 2014; Silva and Germano, 2013).

Regional diversity of bryophytes in ironstone outcrops

As was expected, the bryophyte assemblages within each of the two environmental Protection Areas were very similar as compared to the communities in the two different EPAs, and factors such as elevation and anthropogenic disturbances influence the species compositions on different ironstone outcrops. The RM ironstone outcrops occur at lower altitudes (*e.g.*, with consequently higher environmental temperatures and desiccation rates) and show the highest levels of anthropogenic disturbance – factors that act as important environmental filters on their bryophyte communities (Alvarenga et al., 2010, 2009; Gradstein et al., 2008; Wolf, 2005). Environmentally demanding species are most strongly affected by factors such as proximity to mining sites, cities and roads (Jacobi and Carmo, 2008; Silveira et al., 2015). Considered the most sensitive bryophyte species, liverworts were less diverse in RM than in GA, as very few of them can tolerate high disturbance levels (Goffinet et al., 2009; Silva et al., 2014).

Lower levels of disturbance were expected in GA due to local conditions (higher elevations and less human interference; Fig. 5). Higher frequencies of species living in shaded microhabitats (*e.g.*, SA and TA) were also observed in GA as opposed to RM, especially epiphytic/epyxilic species. These data allow us to confirm the smaller influence of disturbances in the GA area.

Our data agrees with previous studies carried out in different ecosystems that suggested a strong influence of environment variables (elevation and anthropogenic disturbances, in the present study) on the establishment of bryophyte communities. Batista and Santos (2016), for example, reported that environmental determinism (local filters, such as bark pH and its rugosity) influenced epiphytic bryophyte compositions; Oliveira and Steege (2015), in their study of bryophytes in the Amazonian Forest, likewise concluded that community compositions are mainly regulated by environmental conditions (*e.g.*, elevation and temperature); Kraichak (2014), in a study in a tropical rainforest in Polynesia, argued that fluctuations of vapor pressure deficits influence regional bryophyte diversity; Alvarenga et al. (2009) observed that abrupt losses of habitat negatively affect bryophyte community compositions. Silva et al. (2014), in their regional-scale study of bryophytes on rocky outcrops in Brazil, found that geographical distance was a key factor affecting bryophyte community compositions. Those authors emphasized, however, that stochastic and deterministic processes are not necessarily mutually exclusive, as they observed influences of temperature seasonality, precipitation, and continentality, as well as processes related to dispersal limitations on community assemblages.

Ver

Local diversity and environmental filtering

We observed a compartmentalization of the bryophyte assemblages among the different microhabitats on ironstone outcrops, especially in the GA site. There was low beta diversity among bryophyte communities in the different microhabitats and substrates in RM (Fig 3; Fig. S1), indicating taxonomic homogenization (Olden et al., 2004; Olden and Rooney, 2006), which suggests the undifferentiated establishment of moss and liverwort species that were able to overcome the regional filters (Frahm, 2008; Silva et al., 2014; Virtanen, 2013). Low elevations and high levels of disturbance are therefore the main environmental drivers of bryophyte assemblies on ironstone outcrops.

The compartmentalization of bryophyte communities among the different microhabitats and substrates was very high in the GA site as compared to RM. Moss and liverwort colonies were mostly epiphytic and terricolous and inhabited shaded microhabitats (*e.g.*, SA and TA; Tab. 3). Shrub- and tree-associated microhabitats apparently represent important habitats for bryophyte communities on ironstone outcrops, as their canopies attenuate direct exposition to UV and help control daily extreme temperature variations (Carmo and Jacobi, 2016; Jacobi et al., 2007). Additionally, the GA site showed 36 exclusive species (12 mosses and 24 liverworts; Tab. 2), indicating a more heterogeneous community as compared to RM.

Implications for conservation

We identified a high diversity of bryophytes on the ironstone outcrops in the IQ (Minas Gerais, Brazil) – a richness that is threatened by the potential degradation of those areas.

Negative effects are mostly caused by proximity to urban centers, deforestation, land exploitation, and mining activities – which increase the risk of losing this important geosystem and its component species. This situation is of great concern because the above factors can decrease the vegetation cover on ironstone outcrops and promote the local or total extinction of species (Jacobi and Carmo, 2008; Vincent and Meguro, 2008). Environmental degradation, anthropogenic processes (including urbanization), invasive species, and extinctions are the key drivers of biotic homogenization throughout the world (Olden, 2006). These processes are quite evident in the RM site as it is surrounded by large urban centers and iron mining areas that are now beginning to affect the even more distant GA site (unpublished results). Bryophytes contribute to the delicate web of maintenance and protection of this geosystem, contributing to nitrogen and water cycles, erosion control, and biomass generation, and providing habitat for other organisms (Goffinet and Shaw, 2009; Gradstein et al., 2001), so their loss or degradation will resonate throughout the ecosystem.

Ironstone outcrops are quite vulnerable to direct and indirect impacts caused by strip mining, and those activities will influence both internal and external areas in different EPAs. Only 1,96% of the Cangas areas in the IQ region are fully legally protected (Carmo and Kamino, 2015; Jacobi et al., 2007). The strong economic interests of mining companies in this region generate real constraints to the conservation of the peculiar biodiversity found on Brazilian ironstone outcrops. The recent “Bento Rodrigues” dam disaster (Minas Gerais, Brazil) is a case example, as it generated tons of toxic sludge that spread for 700 kilometers along the Rio Doce River and destroyed water resources, villages, and regional biodiversity all the way to the Atlantic Ocean (Costa, 2015; Garcia et al., 2016). This tragedy demonstrates the overwhelming need to strengthen mining controls to preserve the biodiversity associated with ironstone outcrops in Brazil.

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Tables

Table 1. Ironstone outcrop areas surveyed in Gandarela National Park (GA) and Rola-Moça State Park (RM).

Ironstone outcrops	**Latitude**	**Longitude**	**Elevation (m)**
GA1	20°05'28.41"	43°41'04.80"	1633
GA2	20°01'35.85"	43°40'41.14"	1585
GA3	20°02'37.65"	43°41'21.97"	1575
GA4	20°05'08.64"	43°41'15.63"	1648
GA5	20°05'16.30"	43°41'23.94"	1580
RM1	20°03'31.66"	44°00'35.05"	1432
RM2	20°03'36.93"	44°01'51.51"	1469
RM3	20°04'24.31"	44°03'22.81"	1302

Table 2. Bryophyte community in ironstone outcrops of the Gandarela National Park (GA) and Rola-Moça State Park (RM); ER - Exposed Rocks, IN - Insect Nests, TA - Tree Associations, SA - Shrub Associations, and SI- Soil Islands.

Taxons	N° colony	Ironstone outcrops	Substrates	Microh
MARCHANTIOPHYTA				
CEPHALOZIELLACEAE				
Cylindrocolea rhizantha (Mont.) R.M. Schust.	5	RM - 3	Rocks, Soil	ER, TA
CHONEOCOLEACEAE				
Chonecolea doellingeri (Nees) Grolle	46	RM - 1, 2, 3	Tree Bark, Rocks, Soil	SA, ER,
FRULLANIACEAE				
Frullania brasiliensis Raddi	35	GA - 1, 3, 4 RM - 1, 2, 3	Tree Bark, Rocks, Soil	SA, ER,
Frullania caulisequea (Nees) Mont.	2	GA - 1, 3	Tree Bark	TA
Frullania ericoides (Nees) Mont.	6	GA - 4 RM - 2, 3	Tree Bark, Rocks, Soil	TA, ER,
Frullania gibbosa Nees	2	RM - 2	Tree Bark, Rocks	SA, TA
Frullania kunzei (Lehm. & Lindenb.) Lehm. & Lindenb.	19	GA - 1, 2 RM - 2, 3	Tree Bark, Soil, Rocks	SA, ER,
Frullania setigera Steph.	5	GA - 1, 2, 3	Tree Bark, Soil	SA, TA
LEJEUNEACEAE				
Anoplolejeunea conferta (C.F.W.Meissn. ex Spreng.) A. Evans	1	GA - 1	Tree Bark	SA
Archilejeunea fuscescens (Hampe ex Lehm.) Fulford	1	GA - 1	Tree Bark	TA
Brachiolejeunea laxifolia (Taylor) Schiffn.	1	GA - 5	Tree Bark	TA
Cheilolejeunea acutangula (Nees) Grolle	1	RM - 3	Tree Bark	ER
Cheilolejeunea holostipa (Spruce) Grolle & R.L. Zhu	1	GA - 3	Tree Bark	TA
Cheilolejeunea oncophylla (Aongström) Grolle & E.Reiner	1	GA - 4	Tree Bark	SA
Cheilolejeunea revoluta (Herzog) Gradst. & Grolle	1	GA - 1	Rocks	SA
Cheilolejeunea xanthocarpa (Lehm. & Lindenb.) Malombe	15	GA - 1, 3, 4, 5	Tree Bark, Soil	SA, SI,
Drepanolejeunea araucariae Steph.	3	GA - 1, 4	Tree Bark	TA
Drepanolejeunea bidens (Steph.) A.Evans	2	GA - 1, 3	Tree Bark	SA
Drepanolejeunea granatensis (J.B.Jack & Steph.) Bischl.	1	GA - 4	Tree Bark	SA
Frullanoides tristis (Steph.) van Slageren	2	GA - 2,4	Tree Bark, Soil	SI, TA
Harpalejeunea stricta (Lindenb. & Gottsche) Steph.	1	GA -4	Tree Bark	TA

Tab. 2 Continuation …

Taxons	**N^o colony**	**Ironstone outcrops**	**Substrates**	**Microh**
Lejeunea cristulata (Steph.) E.Reiner & Goda	1	GA - 1	Tree Bark	TA
Lejeunea flava (Sw.) Nees	14	GA - 4 RM - 2, 3	Tree Bark, Rocks, Soil	SA, TA
Lejeunea laetevirens Nees & Mont.	6	GA - 1, 3 RM - 2	Tree Bark, Rocks, Soil	SA, ER,
Lejeunea puiggariana Steph.	1	RM - 3	Tree Bark	SA
Lopholejeunea nigricans (Lindenb.) Schiffn.	2	RM - 3	Rocks, Soil	ER, TA
Lopholejeunea subfusca (Nees) Schiffn.	21	RM - 2, 3	Tree Bark, Rocks, Soil	SA, ER,
Mastigolejeunea innovans (Spruce) Steph.	3	RM - 3	Tree Bark, Rocks	ER, TA
Metalejeunea cucullata (Reinw. et al.) Grolle	5	GA - 4 RM - 3	Tree Bark, Rocks, Soil	SA, TA
Microlejeunea bullata (Taylor) Steph.	11	RM - 2, 3	Tree Bark, Rocks, Soil	SA, TA
Omphalanthus filiformis (Sw.) Nees	2	GA - 4	Tree Bark	SA, TA
METZGERIACEAE				
Metzgeria albinea Spruce	12	GA - 1, 2, 4	Tree Bark, Rocks	SA, TA
Metzgeria lechleri Steph.	1	RM - 2	Tree Bark	SA
MYRINIACEAE				
Helicodontium capillare (Hedw.) A. Jaeger	1	RM - 3	Rocks	TA
PLAGIOCHILACEAE				
Plagiochila bifaria (Sw.) Lindenb.	1	GA-4	Rocks	SA
Plagiochila corrugata (Nees) Nees & Mont.	2	GA - 1	Tree Bark, Soil	ER, TA
Plagiochila micropteryx Gottsche	2	GA - 4	Rocks	SA
Plagiochila patula (Sw.) Lindenb.	2	GA - 4	Rocks	SA, TA
RADULACEAE				
Radula fendleri Gottsche ex Steph.	1	GA - 4	Tree Bark	TA
BRYOPHYTA				
ARCHIDIACEAE				
Archidium tenerrimum Mitt	1	GA - 4	Soil	ER
BARTRAMIACEAE				
Bartramia mathewsii Mitt.	2	GA - 4		SI
Philonotis sphaerocarpa (Hedw.) Brid.	18	GA - 5 RM - 1, 2, 3	Rocks, Soil	SA, SI
Philonotis sp 1	1	RM - 2	Soil	SA
BRYACEAE				
Bryum apiculatum Schwägr.	9	RM - 1, 2, 3	Rocks, Soil	SA, IN

Tab. 2 Continuation …

Taxons	N^o colony	Ironstone outcrops	Substrates	Microh
Bryum arachnoideum Müll. Hal.	9	GA - 5 RM - 2, 3	Tree Bark, Rocks, Soil	SA, ER,
Bryum argenteum Broth.	92	GA - 1, 2, 4 RM - 1, 2, 3	Tree Bark, Rocks, Soil	SA, IN,
Bryum subapiculatum Hampe	2	RM - 1, 3	Soil	ER, SI
Bryum sp 1	2	RM - 3	Soil	ER
Bryum sp 2	1	RM - 2	Soil	SI
Bryum sp 3	1	RM - 1	Soil	SI
Leptostomopsis systylia (Müll. Hal.) J.R. Spence & H.P. Ramsay	2	GA - 4	Soil	IN, ER
Ptychostomum cf *wrightii* (Sull. & Lesq.) J.R. Spence	1	RM - 2	Soil	IN
Rosulabryum billarderi (Schwägr.) Spence	22	GA - 1, 3, 4, 5 RM - 2, 3	Tree Bark, Soil, Rocks	SA, ER,
Rosulabryum capillare (Hedw.) Pedersen	109	GA - 1, 2, 3, 4 RM - 1, 2, 3	Tree Bark, Soil, Rocks	SA, IN, TA
Rosulabryum huillense (Welw. & Duby) Ochyra	12	GA - 1, 4, 5 RM - 1, 2	Soil, Rocks	SA, ER,
CALYMPERACEAE				
Syrrhopodon gardneri (Hook.) Schwägr.	3	RM - 2, 3	Soil, Rocks	SA, ER
Syrrhopodon parasiticus (Brid.) Besch.	1	RM-3	Tree Bark	SA
Syrrhopodon prolifer Schwägr. var. *prolifer*	8	GA - 1 RM - 1, 2, 3	Soil, Rocks	SA, ER,
DICRANACEAE				
Holomitrium crispulum Mart.	2	GA - 1	Rocks	SA
FABRONIACEAE				
Fabronia ciliaris (Brid.) Brid. subsp. *ciliaris*	6	RM - 2, 3	Tree Bark, Rocks	TA
Fabronia ciliaris var. *polycarpa* (Hook.) W.R. Buck	13	RM - 2, 3	Tree Bark, Rocks, Soil	SA, ER,
FISSIDENTACEAE				
Fissidens crispus Mont.	2	RM - 2	Tree Bark, Rocks	ER
Fissidens leptophyllus Mont.	3	RM - 2, 3	Rocks, Soil	ER
HYPNACEAE				
Chryso-hypnum diminutivum (Hampe) W.R. Buck	6	RM - 2, 3	Tree Bark, Rocks, Soil	SA, ER,
LEUCOBRYACEAE				
Campylopus arctocarpus (Hornsch.) Mitt.	8	GA-1, 3, 4	Tree Bark, Rocks, Soil,	SA, SI,
Campylopus carolinae Grout	9	GA - 5 RM - 2	Tree Bark, Rocks, Soil	SA, SI,
Campylopus heterostachys (Hampe) A. Jaeger	1	GA - 1	Soil	SI
Campylopus julaceus A. Jaeger	92	GA - 1, 2, 3, 4 5 RM - 1, 2, 3	Rocks, Soil	SA, ER,
Campylopus julicaulis Broth.	4	RM - 3	Soil	IN, ER

Tab. 2 Continuation …

Taxons	N^{o} colony	Ironstone outcrops	Substrates	Microh
Campylopus lamellinervis (Müll. Hal.) Mitt.	35	GA - 1, 2, 3, 4, 5 RM - 1, 2	Rocks, Soil	SA, IN, TA
Campylopus occultus Mitt.	5	RM - 1, 2, 3	Soil	SA, ER,
Campylopus pilifer Brid.	388	GA - 1, 2, 3, 4, 5 RM - 1, 2, 3	Tree Bark, Rocks, Soil	SA, IN E TA
Campylopus savannarum (Müll. Hal.) Mitt.	128	GA - 1, 2, 4 RM - 1, 2, 3	Tree Bark, Rocks, Soil	SA, IN E TA
Campylopus trachyblepharon (Müll. Hal.) Mitt.	1	GA - 3	Soil	SI
Leucobryum clavatum Hampe	1	RM - 2	Rocks	ER
Pilopogon peruvianus (R.S. Williams) J.-P. Frahm	2	RM - 3	Soil, Rocks	ER
OCTOBLEPHARACEAE				
Octoblepharum albidum Hedw.	1	RM - 2	Tree Bark	TA
ORTHOTRICACAE				
Groutiella tomentosa (Hornsch.) Wijk & Margad.	1	RM - 2	Rocks	TA
Macrocoma orthotrichoides (Raddi) Wijk & Margad.	5	GA - 5 RM - 2, 3	Tree Bark, Rocks, Soil	SA, TA
Macromitrium microstomum (Hook. & Grev.) Schwägr.	1	GA - 3	Tree Bark	SA
Macromitrium punctatum (Hook. & Grev.) Brid.	2	RM - 2	Tree Bark, Rocks	TA
Schlotheimia fuscoviridis Hornsch.	2	RM - 2	Rocks	TA
Schlotheimia rugifolia (Hook.) Schwägr.	13	GA - 3, 4 RM - 2, 3	Tree Bark, Rocks, Soil	SA, ER,
Schlotheimia sp 1	2	GA - 3 RM - 2	Tree Bark	TA
Schlotheimia sp 2	1	GA - 4	Tree Bark	TA
Schlotheimia tecta Hook. f. & Wilson	23	GA - 1, 2, 3, 4	Tree Bark, Soil	SA, ER,
*Zygodon reinwardtii (*Hornsch.) A.Braun var. *reinwardtii*	1	RM - 2	Soil	SA
POLYTRICHACEAE				
Polytrichum juniperinum Willd. ex Hedw.	62	GA - 1, 4, 5 RM - 1, 2, 3	Rocks, Soil	SA, IN, TA
POTTIACEAE				
Didymodon rigidulus Hedw.	1	RM - 2	Soil	ER
Hyophila involuta (Hook.) A. Jaeger	2	RM - 2	Soil	ER, SI
Tortella humilis (Hedw.) Jenn.	25	GA - 1 RM - 2, 3	Tree Bark, Rocks, Soil	SA, ER,
Trichostomum sp 1	9	RM - 1, 2, 3	Rocks, Soil	SA, SI
Weissia controversa Hedw.	3	GA - 1, 4 RM - 2	Rocks, Soil	ER, SI
PYLAISIADELPHACEAE				
Isopterygium tenerum (Sw.) Mitt.	3	RM - 1, 2	Tree Bark, Rocks, Soil	SI, TA
RACOPILACEAE				
Racopilum tomentosum (Hedw.) Brid.	5	RM - 3	Rocks	TA

Tab. 2 Continuation …

Taxons	N^o colony	Ironstone outcrops	Substrates	Microh
SEMATOPHYLLACEAE				
Acroporium exiguum (Broth.) W.R.Buck & Schäf.-Verw.	1	GA - 1	Tree Bark	TA
Donnellia commutata (Müll. Hal.) W.R.Buck	8	GA - 4, 5 RM - 3	Tree Bark	SA, TA
Donnellia lagenifera (Mitt.) W.R. Buck	1	GA - 1	Tree Bark	TA
Sematophyllum galipense (Müll. Hal.) Mitt.	18	GA - 1 RM - 2, 3	Tree Bark, Rocks, Soil	SA, ER,
Sematophyllum sp 1	3	RM - 2, 3	Tree Bark, Rocks	SA, TA
Sematophyllum subpinnatum (Brid.) E. Britton	56	RM - 1, 2, 3	Tree Bark, Rocks, Soil	SA, ER,
Sematophyllum subsimplex (Hedw.) Mitt.	1	GA - 1	Tree Bark	TA
STEREOPHYLACEAE				
Entodontopsis nitens (Mitt.) W.R. Buck & Ireland	2	RM - 3	Rocks	TA

Table 3. Species richness per microhabitat and substrate in ironstone outcrops in the Gandarela National Park (GA) and Rola-Moça State Park (RM); ER - Exposed Rocks, IN - Insect Nests, TA - Tree Associations, SA - Shrub Associations, and SI - Soil Islands.

		Microhabitats					**Substrate**		
Ironstone outcrops	**Species richness**	IN	SA	TA	SI	ER	Tree bark	Soil	Rocks
GA1	34	1	19	24	14	10	20	20	13
GA2	11	1	8	9	7	4	6	10	5
GA4	20	1	13	16	9	7	14	11	8
GA5	33	2	21	22	12	9	20	15	13
GA7	13	0	11	8	9	4	6	8	6
RM1	20	1	10	6	7	5	2	11	7
RM2	52	1	14	15	12	8	11	17	8
RM3	46	1	12	14	8	5	10	13	6
Total	**97**	**10**	**57**	**68**	**35**	**45**	**63**	**59**	**57**

Figures

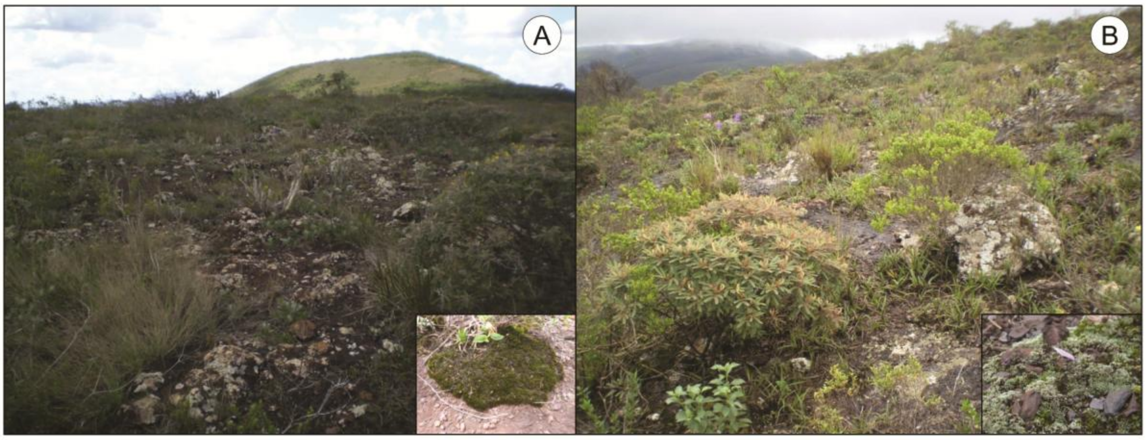

Figure 1. Overview of the Cangas: A - Gandarela National Park (GA), note in detail is a *Campylopus* colony on a Soil Island; B - Rola-Moça State Park (RM), in detail is a *Bryum* colony on Exposed Rock.

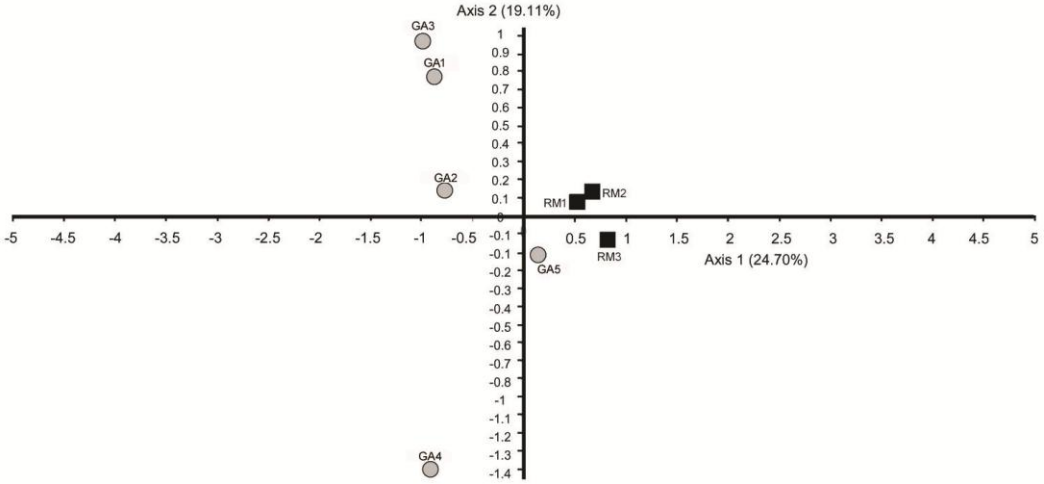

Figure 2. Correspondence analysis (CA) of bryophyte communities in the ironstone outcrops of the Gandarela National Park (GA) and Rola-Moça State Park (RM).

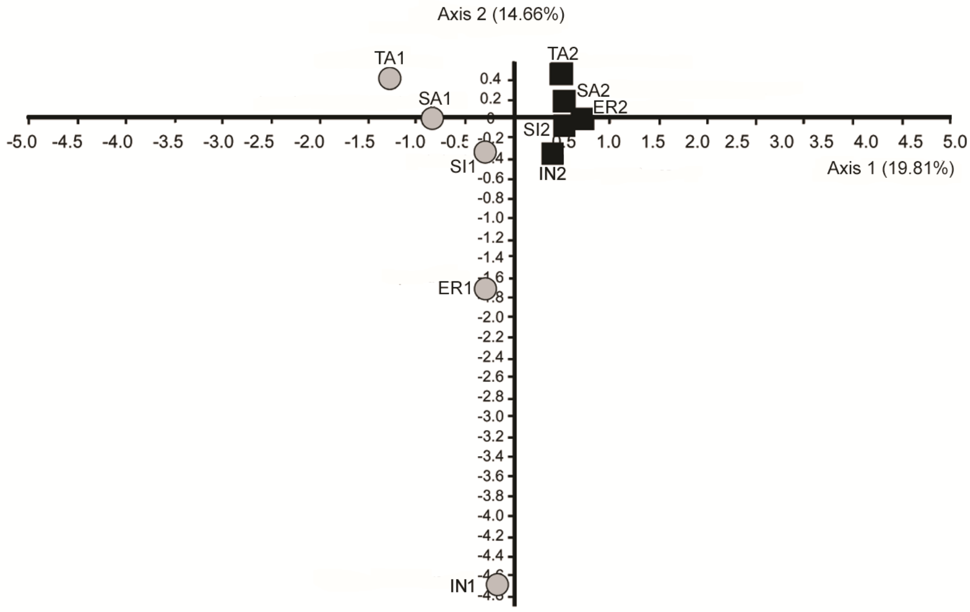

Figure 3. Correspondence analysis (CA) of bryophyte communities in different microhabitats of ironstone outcrops of Gandarela National Park – 1; and Rola-Moça State Park – 2; ER - Exposed Rocks, IN - Insect Nests, TA - Tree Associations, SA - Shrub Associations, and SI - Soil Islands.

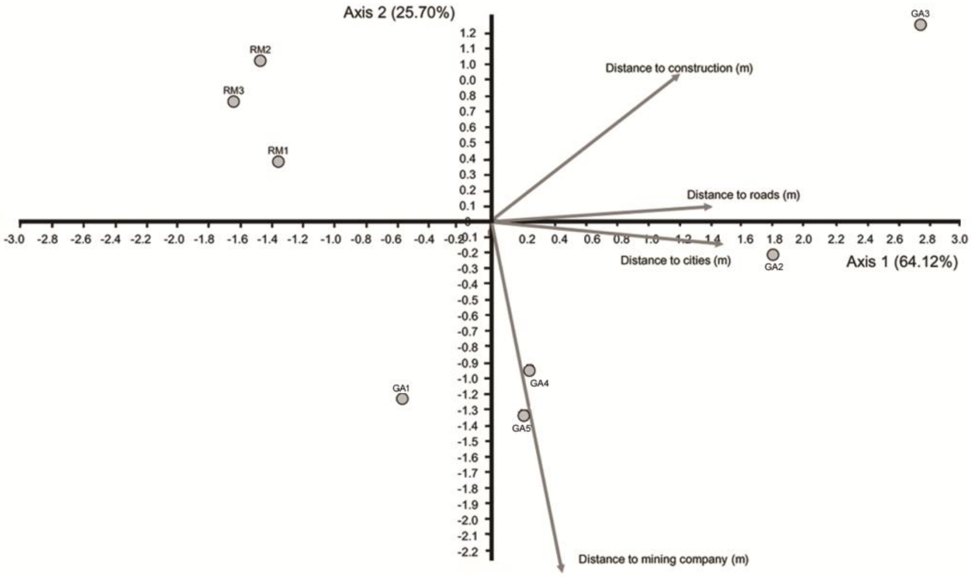

Figure 4. Principal Components Analysis (PCA) of the anthropogenic disturbances on the bryophyte communities in the ironstone outcrops of the Gandarela National Park (GA) and Rola-Moça State Park (RM).

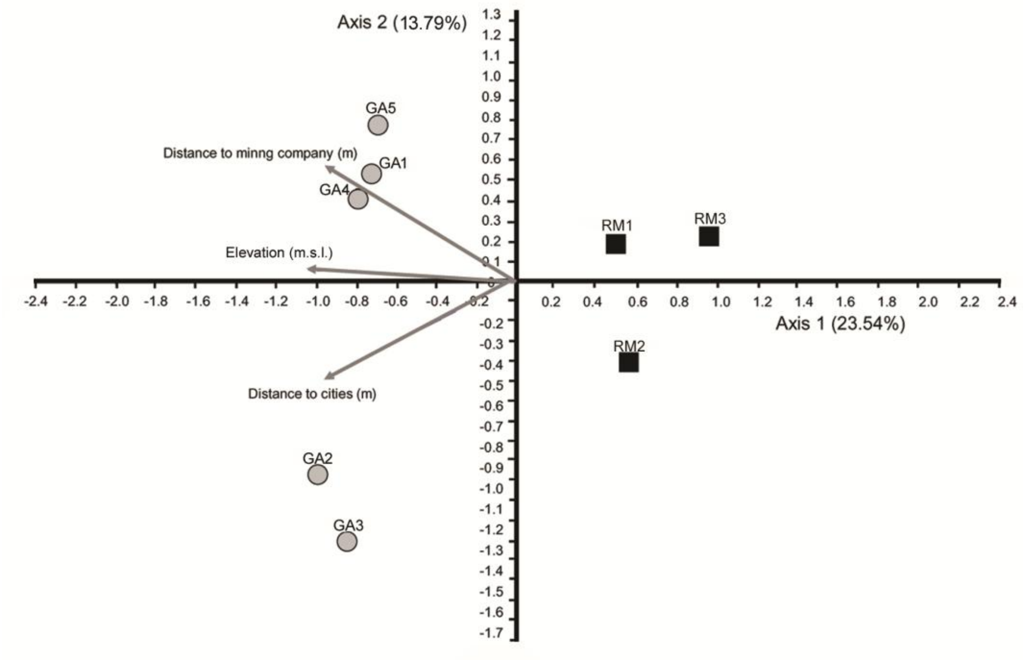

Figure 5. Canonical Correspondence Analysis (CCA) of different environmental gradients on the bryophyte community in ironstone outcrops of the Gandarela National Park (GA) and Rola-Moça State Park (RM).

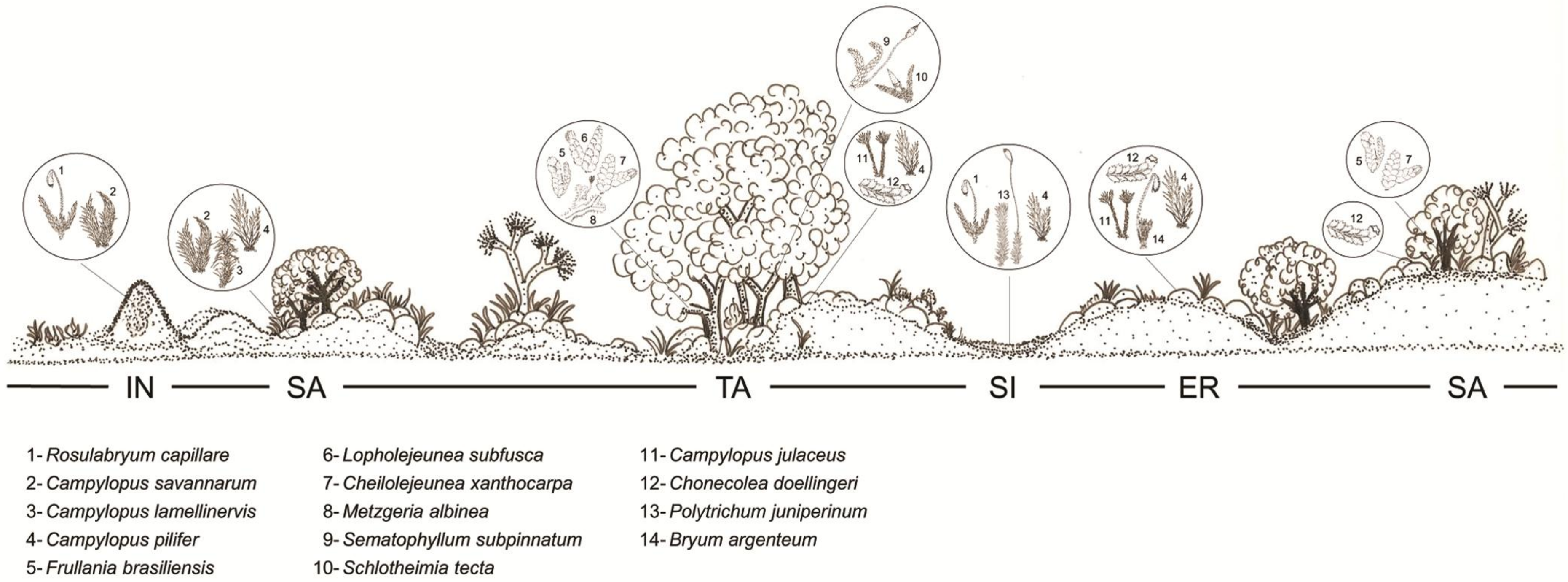

Figure 6. Conceptual model of the bryophyte community in the ironstone outcrops (based on Gandarela National Park and Rola-Moça State Park), illustrating the most abundant species of mosses and liverworts in the microhabitats; IN - Insect Nests, SA - Shrub Associations, TA - Tree Associations, SI - Soil Islands, and ER - Exposed Rocks.

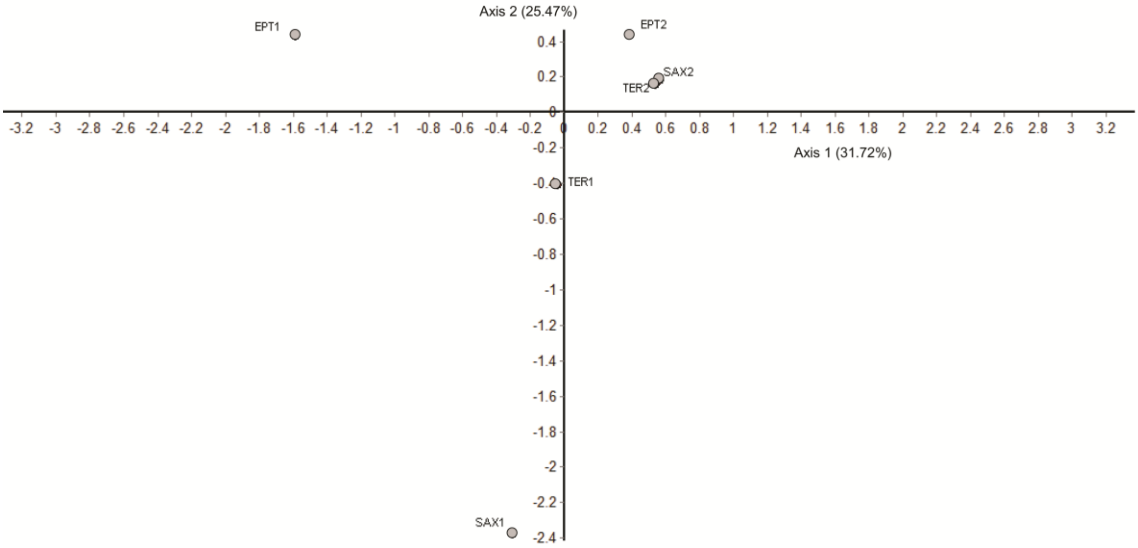

Figura S1. Correspondence analysis (CA) of the bryophyte communities in different substrate of ironstone outcrops of Gandarela National Park – 1; and Rola-Moça State Park – 2; EPT- Epiphytic, TER- Terricolous and SAX- Saxicolous.

CAPÍTULO III

Diversidade das briófitas em afloramentos rochosos ferruginosos do Parque Estadual da Serra do Rola-Moça, Minas Gerais, Brasil

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Resumo

Os afloramentos rochosos ferruginosos ou “Cangas” são importantes depósitos de minério de ferro no Brasil, localizados principalmente na região do Quadrilátero Ferrífero (QF) em Minas Gerais (MG). Estas áreas são ameaçadas pela forte exploração de minérios, desmatamento e urbanização descontrolados, que geralmente resultam na perda das áreas naturais de Cangas e de sua vegetação, que é caracterizada pelos altos índices de espécies vasculares raras e endêmicas. O Parque Estadual da Serra do Rola-Maça (RM), apesar de ser uma das mais importantes áreas verdes em Minas Gerais, convive com grandes conflitos ambientais envolvendo (rodovias atravessando o parque, urbanização e ocupação desordenada de áreas marginais, e processos de mineração nas margens do parque). Entre as plantas presentes nas Cangas, um grupo pouco investigado é as briófitas, que apresentam tolerância à dessecação e possuem diversas estruturas de propagação (esporos e estruturas assexuadas). Assim, nosso principal objetivo foi reconhecer a brioflora presente nas Cangas do RM, analisando a riqueza e a abundância de espécies, os padrões de distribuição geográfica, e as estruturas de dispersão utilizadas pelas briófitas. Foram selecionadas seis Cangas, totatilzando área de ca. 170 ha. Amostras (ca. 6 cm^2) foram coletadas entre 2015 e 2016, através de coletas extensivas. Em laboratório, cada espécime foi determinado taxonomicamente com auxílio de literatura específica. As estruturas de dispersão produzidas pelas espécies foram classificadas em esporos, gemas e propágulos vegetativos. As espécies foram classificadas quanto à distribuição geográfica (em escalas mundial, regional e local). Foram analisados 1.914 espécimes, registrados em 23 famílias, 45 gêneros e 70 espécies, sendo 47 espécies de musgos e 23 de hepáticas. O substrato com maior colonização, especialmente de musgos, foi o solo. Hepáticas foram mais frequentes em cascas de árvores. As briófitas no RM apresentaram padrões de distribuição mundial predominantemente neotropical; sendo também amplamente distribuídas no país. Localmente, destacaram-se as espécies com distribuição restrita. De forma geral, espécies de briófitas com padrões de distribuição amplos (mundial e nacionalmente) parecem se dispersar especialmente por esporos. Já em escala local, propágulos vegetativos foram aparentemente mais importantes paras as espécies abundantes. As Cangas do Parque Estadual da Serra do Rola-Moça contêm uma alta diversidade de espécies de briófitas, com distribuição geográfica ampla, que se dispersam principalmente por esporos e propágulos caducos. Esses dados ressaltam a relevância de estudos florísticos como importantes ferramentas a favor da conservação das áreas naturais com afloramentos rochosos ferruginosos no país.

Palavras-chave: Cangas, Dispersão, Distribuição Geográfica, Esporos, Propágulos vegetativos.

Introdução

Os afloramentos rochosos ferruginosos (localmente chamados de Cangas) estão distribuição em áreas restritas, associadas a importantes depósitos de minério de ferro no Brasil, localizados principalmente na região do Quadrilátero Ferrífero (QF) em Minas Gerais (Jacobi *et al*. 2007). Sendo o Brasil o segundo produtor de minério de ferro no mundo, as áreas de Canga enfrentam fortes ameaças devido à intensa exploração de minérios, resultando em perda e degradação das áreas naturais de afloramentos ferruginosos e de sua vegetação nativa (Jacobi *et al*. 2007; Madeira *et al*. 2015). Infelizmente, menos de 45% das áreas de Cangas do QF são atualmente protegidas por lei (Jacobi e Carmo 2008a; Carmo 2010).

Entre as áreas de Cangas protegidas, destaca-se o Parque Estadual da Serra do Rola-Moça (RM), como uma das mais importantes áreas verdes do estado de Minas Gerais, localizado no centro-sul da região metropolitana de Belo Horizonte. Esta unidade de conservação possui ca. 3.940 ha e está situado em área de transição entre Cerrado e Mata Atlântica, abrigando diversos campos ferruginosos. O Parque foi estabelecido em 1994 e é importante por sua biodiversidade e por mananciais que abastecem Belo Horizonte e região metropolitana (Brandão *et al*. 1997; Meyer *et al*. 2004; Oliveira 2008; Guarçoni *et al*. 2010). Apesar de tudo isto, esta unidade apresenta grandes conflitos ambientais como rodovias atravessando o parque, urbanização e ocupação desordenada de áreas marginais, desmatamento, fogo, presença de espécies invasoras e como principal fator, a mineração predatória presentes nas margens do parque, ameaças que impactam fortemente a diversidade vegetal presente no RM (Jacobi e Carmo 2008a; Oliveira 2008; Carmo 2010; Jacobi e Carmo 2012; Madeira *et al*. 2015).

A vegetação nos afloramentos rochosos ferruginosos no QF é constituída por ca. 1.100 espécies de plantas vasculares, das quais as famílias mais representativas são Asteraceae, Orchidaceae, Poaceae, Melastomataceae, Fabaceae e Bromeliaceae, registrando-se altos índices de espécies raras e endêmicas (Scarano 2002; Jacobi *et al*. 2008). Estas plantas apresentam diferentes adaptações anatômicas, morfológicas, fisiológicas e reprodutivas, que permitem sua sobrevivência neste ambiente adverso, caracterizado por alta exposição à radiação UV, variações extremas das temperaturas diárias, alta evapotranspiração, ventos constantes, baixa retenção de água, e solos impermeáveis (Porembski e Barthlott 2000; Medina *et al*. 2006; Jacobi *et al*. 2007; Jacobi e Carmo 2008b; Souza e Carmo 2015).

O Parque Estadual da Serra do Rola-Moça abriga uma elevada diversidade de espécies e famílias de plantas vasculares (*e.g*., Asteraceae, Bromeliaceae, Myrtaceae, Orchidaceae e Poaceae) sobre suas Cangas, abordada em diferentes estudos florísticos, fitossociológicos, ecológicos e de conservação (Meyer *et al*. 2004; Peixoto 2004; Jacobi *et al*. 2008; Jacobi e Carmo 2008a; Vincent e Meguro 2008; Carmo 2010; Guarçoni *et al*. 2010; Carmo e Jacobi 2016). Um grupo de plantas presente nestas formações, mas pouco investigado, são as briófitas. Essas plantas compreendem as hepáticas, os musgos e os antóceros, com ca. 1.524 espécies registradas no Brasil (Costa e Peralta 2015). Essas plantas apresentam elevada capacidade de suportar as condições ambientais adversas como as presentes nas Cangas, apresentando forte tolerância aos ciclos de dessecação e possuindo diversos mecanismos de propagação (Stark *et al*. 2000; Proctor *et al*. 2007; Stark *et al*. 2007; Frey e Kürschner 2010; Maciel-Silva e Pôrto 2014). Esses mecanismos de propagação contribuem para uma efetiva dispersão e rápido estabelecimento das espécies de briófitas em afloramentos rochosos (Frahm e Porembski 1998; Valente e Pôrto 2006; Silva e Germano 2013; Silva *et al*. 2014b, Pôrto *et al*. 2016).

Nas briófitas os processos de dispersão de esporos e propágulos vegetativos estão associados a características dos diásporos, como tamanho, ornamentação e longevidade dessas estruturas (Longton e Schuster 1983; Laaka-Lindberg *et al*. 2000; Longton 2006; Lönnell *et al*. 2012; Stieha *et al*. 2014; Stark *et al*. 2016). Esses diásporos podem variar desde ca. 10 µm (*e.g*., esporos e alguns propágulos vegetativos) até >200 µm (principalmente propágulos), com longevidade de poucos dias até mais de 50 anos (During 1979; Glime 2014). De forma geral, espécies que produzem abundantemente diásporos pequenos tendem a se dispersar por maiores distâncias; enquanto espécies que produzem menos frequentemente diásporos, e estes são maiores, podem ficar restritas em distribuição (Söderström 1989; Hedenås e Ericson 2000; Hedenås *et al*. 2003; Longton 2006; Pohjamo *et al*. 2006). Espécies de briófitas endêmicas parecem ter baixas produções de diásporos, geralmente menos tolerantes à dessecação, diferenciando-se de espécies amplamente distribuídas, cujos diásporos tendem a ser mais abundantes e resistentes às condições encontradas durante sua dispersão pelo ar, água ou animais. Tais características auxiliam na interpretação dos diferentes padrões fitogeográficos de muitas espécies de briófitas (van Zanten e Gradstein 1988; Miller e McDaniel 2004; Longton 2006; Pohjamo *et al*. 2006; Frahm 2008; Virtanen 2013; Medina e Banez 2014; Stieha *et al*. 2014; Laenen *et al*. 2015; Barbé *et al*. 2016).

Nosso principal objetivo foi reconhecer a brioflora presente nos afloramentos rochosos ferruginosos do Parque Estadual da Serra do Rola-Moça (RM), analisando a riqueza e a abundância de espécies, os padrões de distribuição geográfica, e as estruturas de dispersão das briófitas. São propostas as seguintes questões: 1) Qual é a diversidade e a composição das briófitas em Cangas do RM? 2) Quão abundantes e distribuídas são as espécies nos diferentes afloramentos do parque? 3) Quais são os padrões de distribuição geográfica e as estruturas de dispersão utilizados pelas espécies de briófitas do RM?

Material *& Métodos*

Área de estudo

O Parque Estadual da Serra do Rola-Moça está situado a noroeste do Quadrilátero Ferrífero em Minas Gerais (20° 03' 04,49" S e 44° 00' 29,65" O), em altitude de 900 a 1.550 m (IBGE 1976; IBGE 1977; Peixoto 2004; Carmo 2010). Também apresenta invernos secos e verões chuvosos, com temperaturas médias anuais que variam de 18ºC a 21ºC, e um regime pluviométrico de 1.300 a 2.100 mm de precipitação anual (Guarçoni *et al*. 2010). Os meses de novembro até janeiro são os mais chuvosos, e junho até agosto são os meses mais secos (Meyer *et al*. 2004; Guarçoni *et al*. 2010). Nestes meses mais secos, o fogo (natural ou antrópico) passa a governar a dinâmica da vegetação, limitando o estabelecimento de espécies vegetais pouco resistentes e selecionando espécies mais tolerantes, assim tornando-se um componente importante na dinâmica das Cangas (Schaefer *et al*. 2015).

Amostragem de espécies

Foram selecionados seis afloramentos ferruginosos inseridos no RM, distantes pelo menos 1,8 km um do outro (Tab. 1). Coletas extensivas foram realizadas entre 2015 e 2016, percorrendo-se toda área de cada afloramento. Espécies de briófitas foram coletadas a partir de quatro substratos presentes nas Cangas: solo, rochas, cascas de arbustos/árvores vivas, e madeira em decomposição. Amostras com pelos menos 5 cm² de briófitas, juntamente ao substrato adjacente, foram coletadas com ajuda de canivetes ou espátulas. Cada amostra foi acondicionada em saco de papel e levada ao laboratório para determinação taxonômica e análise de estruturas reprodutivas. Os espécimes foram dissecados e investigados sob esteromicroscópio e microscópio óptico. A identificação taxonômica seguiu Frahm (1991), Reese (1993), Zander (1993), Gradstein *et al*. (2001), Gradstein e Costa (2003), Costa (2008), e suas referências. O sistema de classificação seguiu Crandall-Stotler *et al*. (2009) para hepáticas e Goffinet *et al*. (2009) para musgos, com atualizações (Santos e Stech 2016). O materal foi depositado no herbário BHCB da Universidade Federal de Minas Gerais.

Tabela 1. Área (ha), coordenadas geográficas, abundância e riqueza de espécies de briófitas em seis localidades de Canga do Parque Estadual da Serra do Rola-Moça, Minas Gerais.

Canga	**Área (ha)**	**Latitude**	**Longitude**	**Altitude (m)**	**Abundância**	**Riqueza**
RM1	40.7	20° 03'33,33"S	44° 00'31,88"O	1374 a 1475	268	36
RM2	18.4	20° 03'34,39"S	44° 01'45,29"O	1430 a 1506	613	47
RM3	5.39	20° 04'28,01"S	44° 03'27,37"O	1284 a 1340	336	46
RM4	24.14	20° 04'12,13"S	43°59'34,01"O	1316 a 1433	235	44
RM5	17.6	20° 00'45,50"S	43°58'44,76"O	1314 a 1422	200	37
RM6	64	20° 02'24,57"S	43°59'48,38"O	1379 a 1511	262	44
Total	170.23				1914	70

Estruturas de dispersão

Estruturas de dispersão utilizadas pelas briófitas foram investigadas nos diferentes espécimes, e classificadas em três grandes categorias: 1) *esporos*: quando as espécies apresentaram esporófitos ou resquícios destes, e consequentemente produziram esporos; 2) *gemas*: presença de estruturas assexuadas especializadas dos gametófitos, que não apresentam primórdios de filídios e rizóides; e 3) *propágulos caducos*: presença de estruturas assexuadas caducas, que já apresentam primórdios de filídios e rizóides (Pohjamo e Laaka-Lindberg 2003; Glime 2007; Frey e Kürschner 2010; Maciel-Silva e Pôrto 2014).

Padrões de distribuição

A distribuição geográfica das espécies de briófitas, no Brasil e no mundo, foi baseada em Gradstein *et al*. (2001), Gradstein e Costa (2003), Costa e Peralta (2015), Carmo e Peralta (2016), e bases de dados *online* (Flora do Brasil 2017; GBIF 2017; SpeciesLink 2017). Três categorias de distribuição no Brasil foram usadas, de acordo com Valente e Pôrto (2006) e Carmo e Peralta (2016): *rara*- espécies conhecidas em menos de quatro estados brasileiros; de distribuição *moderada*- reportadas em cinco a nove estados; e *ampla*- ocorrendo em mais de dez estados. Para a distribuição local, a abundância das espécies (número de ocorrências na área de estudo) foi utilizada gerando três categorias: *restrita*- 1 a 22 registros; *moderada*- 26 a 41; *ampla*- > 58 registros.

Resultados & Discussão

Foram analisados 1.914 espécimes de briófitas nas Cangas do Parque Estadual da Serra do Rola-Moça, registrados em 23 famílias, 45 gêneros e 70 espécies, sendo 47 espécies de musgos e 23 de hepáticas (Tab. 2). As famílias mais representativas de musgos no parque foram Leucobryaceae (8 spp.), Bryaceae (7 spp.), Orthotricaceae e Pottiaceae (6 spp. cada). Quantos às hepáticas destacaram-se Lejeunaceae (12 spp.) e Frullaniaceae (5 spp.). As espécies de musgos mais abundantes no RM foram *Campylopus pilifer* (393 registros), *Campylopus savannarum* (193) e *Bryum argenteum* (122). Já as espécies de hepáticas mais abundantes foram *Frullania brasiliensis* (69), *Chonecolea doellingeri* (62) e *Frullania kunzei* (40). As espécies *Rhodobryum grandifolium*, *Fissidens leptophyllus*, e *Lejeunea puiggariana*, são registros inéditos para o estado de Minas Gerais, e as espécies *Pilopogon peruvianus*, *Mastigolejeunea innovans* e *Metalejeunea cucullata* são registradas pela segunda vez no estado (Tab. 2).

Podemos observar uma alta diversidade de briófitas nas Cangas do RM, comparada com outros trabalhos em ambientes similares. Por exemplo: 21 espécies em afloramentos na Serra da Jibóia, Bahia (Valente e Pôrto 2006); 31 e 25 espécies em afloramentos rochosos na Costa do Marfim e Zimbabwe na África (Frahm 1996); 43 espécies em afloramentos na região ocidental da África (Frahm e Porembski 1998); 49 espécies em afloramentos em Pernambuco (Silva *et al*. 2014b); 57 espécies na Chapada de Canga em Minas Gerais (Fantecelle *et al*. 2017); 87 espécies em Cangas de Carajás

(Moraes e Lisboa 2006); 90 espécies envolvendo afloramentos rochosos na Paraíba, Pernambuco e Bahia (Silva *et al*. 2014a).

Nossos dados ressaltam a importância de investigar a diversidade vegetal para a conservação das áreas de Cangas presentes no RM, que mesmo sob forte pressão antrópica, gerada pela presença de rodovias, urbanização descontrolada, desmatamento, fogo e proximidade de mineradoras (Oliveira 2008; Ruchkys 2015), ainda abrigam relevante diversidade biológica. A diversidade de musgos e hepáticas nas Cangas contribuem para a boa manutenção das Cangas, diminuindo os processos erosivos, gerando biomassa, facilitando o balanço hídrico, o ciclo do nitrogênio e facilitando a sobrevivência de outros organismos (Dale *et al*. 2009).

As espécies de briófitas das Cangas do RM foram observadas colonizando principalmente solo (52% dos espécimes), seguido de rochas (30%), cascas de árvores (15%) e madeira em decomposição (3%). Os musgos foram registrados principalmente sobre solo, e as hepáticas foram mais frequentes sobre cascas de árvores (Fig. 1). As espécies *Racopilum tomentosum*, *Wijkia flagellifera*, *Cheilolejeunea acutangula* e *Leucobryum clavatum* foram exclusivas de rocha. Já os musgos *Campylopus julicaulis* e *Rhodobryum grandifolium* foram encontrados apenas sobre solo (Tab. 2).

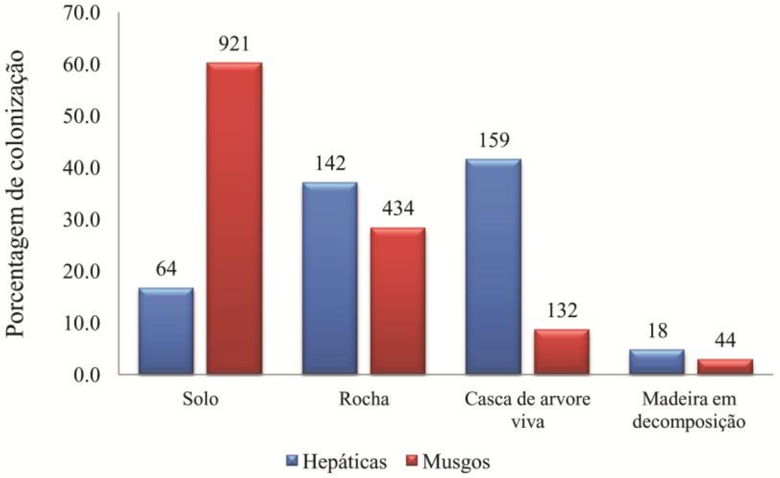

Figura 1. Porcentagem de espécies de briófitas presentes em diferentes substratos nas Cangas do Parque Estadual da Serra do Rola-Moça, Minas Gerais. Valores sobre as colunas representam a incidência de espécimes de briófitas.

A maior incidência de briófitas sobre solo nas Cangas do RM concorda com Silva *et al*. (2014b) e Fantecelle *et al*. (2017), onde mais de 60% da comunidade de briófitas foram encontrados neste substrato, com especial predominância de musgos acrocárpicos (*Campylopus* spp., *Bryum* spp. e *Rosulabryum* spp; Fig. 2 A-D). Muitas das espécies de musgos presentes em solo são espécies xerotolerantes e generalistas, típicas de ambientes abertos, perturbados e com restrições hídricas (Frahm 1996; Valente e Pôrto 2006; Silva e Germano 2013; Silva *et al*. 2014a; Silva *et al*. 2014b). No entanto, essas espécies podem apresentar grande relevância quando formam extensos tapetes que retêm umidade e nutrientes para outras plantas nas Cangas. Já as espécies de hepáticas presentes sobre casca de árvore viva, também foram encontradas em outros substratos (*e.g.*, *Chonecolea doellingeri*, *Frullania brasiliensis*, *Frullania kunzeí*, *Lejeunea flava*, *Microlejeunea bullata*; Tab. 2). Estas espécies normalmente são classificadas como generalistas ou especialistas de sol (Gradstein *et al*. 2001; Santos *et al*. 2011; Silva e Germano 2013; Brito e Ilkiu-Borges 2014), concordando com o ambiente encontrado no RM.

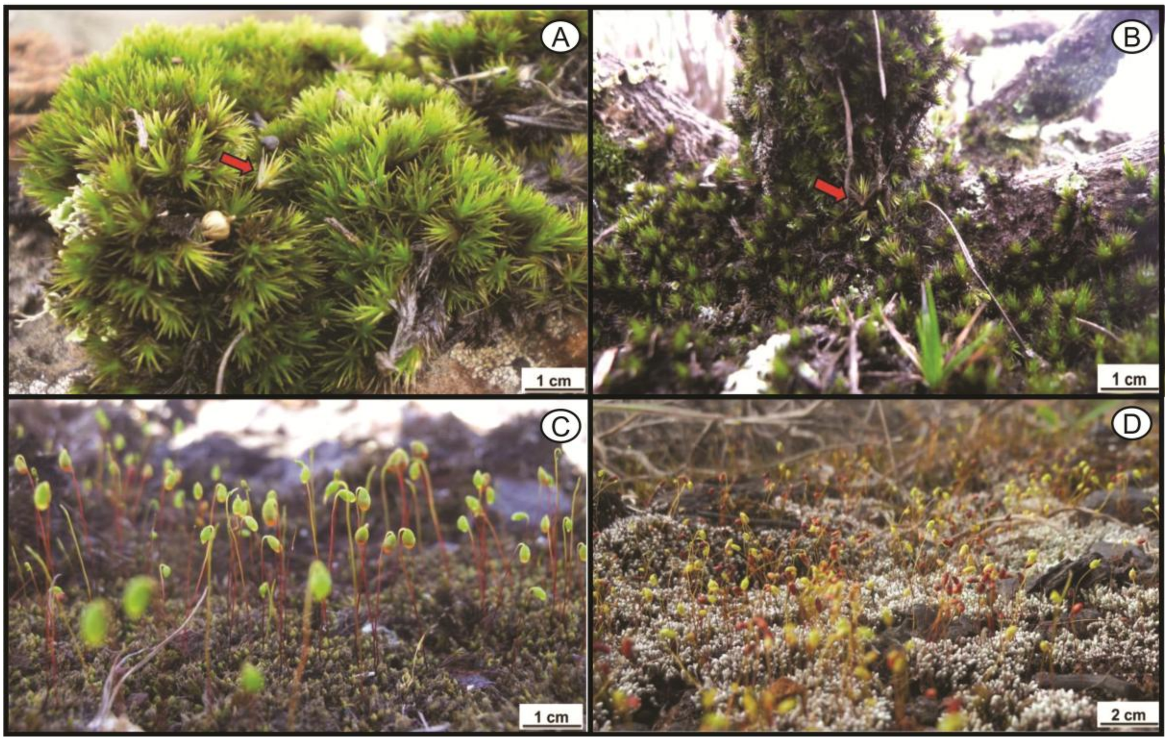

Figura 2. Briófitas em Cangas do Parque Estadual da Serra do Rola-Moça, MG, Brasil., A- *Campylopus savannarum*; B- *Campylopus pilifer*; C- *Rosulabryum capillare*; D- *Bryum argentum*. Setas indicam propágulos vegetativos caducos.

Tabela 2. Bioflora presente nos afloramentos rochosos ferruginosos do Parque Estadual da Serra do Rola-Moça, Minas Gerais. Espécies organizadas alfabeticamente por família; M- musgo, H- hepática; Ca- Casca de árvore viva, Ma- Madeira em decomposição; So- Solo, Ro- Rocha; Es- Esporos, Ge- Gemas, Pro- Propágulos, N- Nenhuma estrutura de dispersão registrada.

Espécies	**Filo**	**RM1**	**RM2**	**RM 3**	**RM4**	**RM5**	**RM6**	**Substrato**	**Estrutura de dispersão**	**Distribuição no Brasil**	**Distribuição mundial**
Bartraminaceae											
Philonotis sphaerocarpa (Hedw.) Brid.	M	4	6	7	4		1	Ca, Ma, So, Ro	Ge, Pro	Moderada	Américas
Bryaceae											
Bryum apiculatum Schwägr.	M	1	2	5		1		Ca, Ma, So, Ro	Es	Ampla	Cosmopolita
Bryum arachnoideum Müll. Hal.	M	1	5	2				Ca, So, Ro	Es, Pro	Rara	Pantropical
Bryum argenteum Broth.	M	43	41	18	3	14	3	Ca, Ma, So, Ro	Es, Pro	Ampla	Cosmopolita
Rosulabryum huillense (Welw. & Duby) Ochyra	M	3	5		8	4	7	So, Ro	N	Rara	Cosmopolita
Rhodobryum grandifolium (J.Taylor) Schimp.	M					3		So, Ro	Ge	Moderada	Neotropical
Rosulabryum billarderii (Schwägr.) Spence	M		6	2	3		1	Ca, Ma, So, Ro	Pro	Ampla	Cosmopolita
Rosulabryum capillare (Hedw.) Pedersen	M	29	57	14	1	2		Ca, Ma, So, Ro	Es, Ge	Ampla	Neotropical
Calymperaceae											
Syrrhopodon gardneri (Hook.) Schwägr.	M		1	2			4	Ca, So, Ro	Ge	Moderada	Pantropical
Syrrhopodon parasiticus (Brid.) Besch.	M			1			1	Ca, Ma	Ge	Ampla	Pantropical
Syrrhopodon prolifer Schwägr. *var. prolifer*	M	3	2	1	9	2	14	Ca, Ma, So, Ro	Ge	Ampla	Pantropical
Cephaloziellaceae											
Cylindrocolea rhizantha (Mont.) R.M.Schust.	H			5	1	4	2	Ca, So, Ro	Es	Moderada	Américas
Chonecoleaceae											
Chonecolea doellingeri (Nees) Grolle	H	2	23	21	11	2	4	Ca, Ma, So, Ro	Es	Ampla	Pantropical
Fabroniaceae											
Fabronia ciliaris (Brid.) Brid.	M		1	5	3			Ca, Ro	Es	Ampla	Américas
Fabronia ciliaris var policarpa (Hook.) W.R. Buck	M		3	10	1		3	Ca, So, Ro	Es	Ampla	Américas

Tabela 2 Continuação...

Espécies	**Filo**	**RM1**	**RM2**	**RM 3**	**RM4**	**RM5**	**RM6**	**Substrato**	**Estrutura de dispersão**	**Distribuição no Brasil**	**Distribuição mundial**
Fissidentaceae											
Fissidens cripus Mont.	M		2					Ca, Ro	N	Ampla	Cosmopolita
Fissidens leptophyllus Mont.	M		1	2			1	So, Ro	Es	Moderada	Américas
Frullaniaceae											
Frullania brasiliensis Raddi	H	2	19	8	11	7	22	Ca, Ma, So, Ro	Es	Ampla	Neotropical
Frullania ericoides (Nees) Mont.	H	1	2	6	3	2	1	Ca, Ma, So, Ro	Es	Ampla	Pantropical
Frullania gibbosa Nees	H		2			1		Ca, Ro	Es	Ampla	Neotropical
Frullania kunzeí (Lehm. & Lindenb.) Lehm. & Lindenb.	H	7	7	8	4	8	6	Ca, Ma, So, Ro	Es	Ampla	Neotropical
Frullania neurota Taylor	H			1		1		Ca, So	Es	Rara	Pantropical
Hypnaceae											
Chryso-hypnum diminutivum (Hampe) W.R. Buck	M	1	2	4	5		1	Ca, Ma, So, Ro	Es	Ampla	Cosmopolita
Lejeuneaceae											
Cheilolejeunea acutangula (Nees) Grolle	H			1	2		1	Ro	Es	Ampla	Neotropical
*Cheilolejeunea discoidea (*Lehm. & Lindenb.) Kachr. & R.M. Schust.	H					3		Ca, Ro	Es	Moderada	Neotropical
Drepanolejeunea fragilis Bischl.	H					1		Ca	Es	Ampla	Neotropical
Lejeunea flava (Sw.) Nees	H	3	10	3	6	4	3	Ca, So, Ro	Es	Ampla	Pantropical
Lejeunea laetevirens Nees & Mont.	H	2	4		3	2	7	Ca, Ma, So, Ro	Es, Pro	Ampla	Neotropical
Lejeunea puiggariana Steph.	H			1	1	1	1	Ca, Ro	Es	Moderada	America do Sul
Lopholejeunea nigricans (Lindenb.) Schiff.	H			2	2			Ca, So, Ro	Es	Ampla	Pantropical
Lopholejeunea subfusca (Nees) Schiffn.	H		11	10	1	2	3	Ca, So, Ro	Es	Ampla	Pantropical
Mastigolejeunea innovans (Spruce) Steph.	H			3	1	1		Ca, Ro	Es	Moderada	Neotropical
Metalejeunea cucullata (Reinw. et al.) Grolle	H			3				Ca, So	N	Rara	Pantropical
Microlejeunea bullata (Taylor) Steph.	H	3	9	2	5	2	5	Ca, So, Ro	N	Ampla	Neotropical
Schiffneriolejeunea polycarpa (Nees) Gradst.	H	5					3	Ca, So	Es	Ampla	Neotropical

Tabela 2 Continuação...

Espécies	**Filo**	**RM1**	**RM2**	**RM 3**	**RM4**	**RM5**	**RM6**	**Substrato**	**Estrutura de dispersão**	**Distribuição no Brasil**	**Distribuição mundial**
Leucobryaceae											
Campylopus carolinae Grout	M		2					So, Ro	Es	Moderada	Américas
Campylopus julaceus A. Jaeger	M	16	46	22	9	10	11	Ca, So, Ro	Pro	Moderada	Pantropical
Campylopus julicaulis Broth.	M			4				So	Pro	Moderada	América do Sul
Campylopus lamellinervis (Müll.Hal.) Mitt.	M	7	6	1	4	11	1	Ca, So, Ro	Pro	Ampla	Neotropical
Campylopus occultus Mitt.	M	2	1	2				Ca, Ma, So	Pro	Ampla	Neotropical
Campylopus pilifer Brid.	M	69	168	44	20	38	57	Ca, Ma, So, Ro	Pro	Ampla	Neotropical
Campylopus savannarum (Müll. Hal.) Mitt.	M	24	75	34	18	28	14	Ca, Ma, So, Ro	Pro	Ampla	Pantropical
Leucobryum clavatum Hampe	M		1			2		Ro	Pro	Moderada	América do Sul
Pilopogon peruvianus (R.S. Williams) J.-P. Frahm	M			2				So, Ro	Pro	Rara	Neotropical
Lophocoleaceae											
Lophocolea bidentata (L.) Dumort.	H	1			6		1	Ca, Ro	N	Ampla	Cosmopolita
Metzgeriaceae											
Metzgeria albinea Spruce		1					1	Ca, So	Ge	Ampla	Pantropical
Metzgeria lechleri Steph.	H	1	1	1	5		8	Ca, Ma, So, Ro	Ge	Ampla	Neotropical
Myriniaceae											
Helicodontium capillare (Hedw.) A. Jaeger	M			1				Ro	Es	Ampla	Neotropical
Octoblepharaceae											
Octoblepharum albidum Hedw.	M	1	1		8		3	Ca, Ma, So, Ro	Es, Ge	Ampla	Pantropical
Orthotrichaceae											
Groutiella tomentosa (Hornsch.) Wijk. & Margad.	M		1		8	1	1	Ca, So, Ro	Es	Moderada	Cosmopolita
Macrocoma orthotrichoides (Raddi) Wijk. & Margad.	M	1	1	3	7		3	Ca, Ma, So, Ro	Es	Moderada	Pantropical
Macromitrium punctatum (Hook. & Grev.) Brid.	M	1	2		1		4	Ca, Ro	Es	Ampla	Neotropical
Schlotheimia rugifolia (Hook.) Schwägr.	M	1	5	4	5	3	2	Ca, Ma, So, Ro	Es	Ampla	Pantropical

Tabela 2 Continuação...

Espécies	Filo	RM1	RM2	RM 3	RM4	RM5	RM6	Substrato	Estrutura de dispersão	Distribuição no Brasil	Distribuição mundial
Schlotheimia fuscoviridis Hornsch.	M		2		10	8	6	Ca,Ma,So, Ro	Es	Moderada	Neotropical
Zygodon reinwardtii (Hornsch.) A.Braun var. reinwardtii	M	1	1				1	Ca, Ma, So, Ro	Es	Moderada	Pantropical
Plagiochilaceae											
Plagiochila corrugata (Nees) Nees & Mont.	H				7	1	7	Ca, Ma, So, Ro	Es, Pro	Ampla	Neotropical
Polytrichaceae											
Polytrichum juniperinum Willd. ex Hedw.	M	11	31	3	5	4	4	Ca, So, Ro	Es, Pro	Ampla	Cosmopolita
Pottiaceae											
Didymodon rigidulus Hedw.	M		1					So	Ge	Rara	Cosmopolita
Hyophila involuta (Hook.) A. Jaeger	M		2					Ca, So, Ro	N	Ampla	Cosmopolita
Syntrichia amphidiacea (Müll.Hal.) R.H.Zander	M				2			Ca, Ro	Ge	Moderada	Pantropical
Tortella humilis (Hedw.) Jenn.	M	2	10	14	8	4	3	Ma, So	Es	Ampla	Cosmopolita
Trichostomum weisioides Müll. Hal.	M	3	3	3	1	6	4	Ca, Ma, So, Ro	N	Moderada	América do Sul
Weissia controversa Hedw.	M		1					Ro	Es	Ampla	Cosmopolita
Pylaisiadelphaceae											
Isopterygium tenerum (Sw.) Mitt.	M	2	2		1		7	Ca, So, Ro	Es	Ampla	Cosmopolita
Wijkia flagellifera (Broth.) H.A. Crum	M				5			Ro	Pro	Moderada	Neotropical
Racopilaceae											
Racopilum tomentosum (Hedw.) Brid.	M			5				Ro	Es	Ampla	Cosmopolita
Sematophyllaceae											
Donnellia commutata (Müll. Hal.) W.R. Buck	M	5		5	1	3	4	Ca, Ma, So, Ro	Es	Ampla	Neotropical
Sematophyllum galipense (Müll. Hal.) Mitt.	M	3	10	6	1	3	7	Ca, Ma, So, Ro	Es	Ampla	Neotropical
Sematophyllum subpinnatum (Brid.) E. Britt.	M	6	19	33	12	10	17	Ca, Ma, So, Ro	Es	Ampla	Pantropical
Stereophyllaceae											
Entodontopsis nitens (Mitt.) W. R. Buck & Ireland	M			2				Ro	Es	Ampla	Pantropical

As briófitas presentes no RM apresentam padrões de distribuição mundial predominantemente neotropical, seguido de cosmopolita e pantropical (Tab. 3). *Campylopus julicaulis* e *Leucobryum clavatum* foram as únicas espécies classificadas como endêmicas do Brasil. Quanto à distribuição no Brasil, 66% das espécies de briófitas são amplamente distribuídas no país; e localmente, destacam-se as espécies com distribuição restrita no parque. De forma geral, as espécies de briófitas em Cangas do RM parecem se dispersar especialmente por esporos. Espécies com padrões de distribuição mais restritos, em escalas mundial e regional, apresentam também propágulos vegetativos como importantes formas de dispersão. Por outro lado, na escala do parque, propágulos vegetativos foram aparentemente mais importantes paras as espécies mais abundantes (Tab. 3).

Tabela 3. Distribuição geográfica de espécies de briófitas, com diferentes estruturas de dispersão, presentes no Parque Estadual da Serra do Rola-Moça, Minas Gerais.

Distribuição mundial	**Riqueza**	**Esporos (%)**	**Gemas (%)**	**Propágulos (%)**
Cosmopolita	15	69	8	23
Pantropical	16	56	38	6
Américas	6	71	14	14
Neotropical	29	63	10	27
America do Sul	4	33	0	67
Distribuição no Brasil				
Ampla	45	68	13	19
Moderada	19	53	21	26
Rara	6	40	20	40
Distribuição no Parque				
Ampla	9	50	8	42
Moderada	10	75	13	13
Restrita	51	63	18	20

O elevado número de espécies de briófitas no RM, especialmente com padrão de distribuição neotropical, chega a superar a riqueza de briófitas registrada por trabalhos em outros tipos de afloramentos rochosos. Espécies com padrões fitogeográficos amplos e poucas espécies endêmicas são frequentes nestes ambientes, principalmente devido a maior colonização de espécies sobre solo em áreas abertas (*e.g.*, *Campylopus pilifer*;

Silva e Pôrto 2013; Silva *et al*. 2014a; Silva *et al*. 2014b; Fantecelle *et al*. 2017). O papel dos esporos como importante forma de dispersão entre as espécies mais amplamente distribuídas, no mundo e no Brasil, pode sugerir que as espécies de briófitas nas Cangas do RM dispersam-se efetivamente a longas distâncias (Longton 1992; Miller e McDaniel 2004; Pohjamo *et al*. 2006; Frahm 2008). Por outro lado, a contribuição dos propágulos vegetativos nas espécies com distribuição mais ampla no parque, juntamente aos esporos (*e.g., Bryum argenteum*), favorece uma dispersão efetiva a curta e longa distância, e garante a manutenção e crescimento das colônias (Ozinga *et al*. 2004; Stöcklin e Winkler 2004; Pohjamo *et al*. 2006).

As Cangas do Parque Estadual da Serra do Rola-Moça apresentam uma alta diversidade de espécies de briófitas, de similar importância à registrada em outros tipos de afloramentos rochosos no país. Observamos também uma preferência das espécies de musgos e hepáticas em colonizar solo, rocha e cascas de árvore/arbustos. Michohabitats mais expostos abrigam espécies generalistas e/ou especialistas de sol, que caracterizam os afloramentos rochosos. As distribuições geográficas ampla da maioria das espécies do RM, junto à elevada incidência de esporos, sugerem que essas espécies são boas dispersoras a longas distâncias. Já em escala loca, os propágulos vegetativos parecem desempenhar esse papel para a manutenção das colênias de espécies mais abundantes. É importante ampliar o conhecimento sobre as briófitas em formações de Canga, pois estas são áreas únicas e ricas que abrigam alta diversidade taxonômica e ecológica do grupo.

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CONCLUSÕES

I. Afloramentos rochosos ferruginosos do Quadrilátero Ferrífero de Minas Gerais abrigam uma alta diversidade de briófitas. Estes resultados destacam a importância da conservação de diferentes sítios de Cangas, pois essas áreas podem sustentar comunidades únicas de briófitas **(Capítulos I, II e III)**;

II. Diferentes espécies de musgos e de hepáticas conseguem se estabelecer e sobreviver nas Cangas, tolerando às condições ambientais adversas presentes nestas áreas **(Capítulos I, II e III)**;

III. A expressão sexual e o sucesso reprodutivo foram influenciados principalmente pelos sistemas sexuais das espécies de briófitas, refletindo o papel relevante de espécies de musgos dioicos em Cangas (**Capítulo I)**;

IV. Espécies dioicas chave, cuja propagação se dá especialmente por propágulos caducos, foram muito informativas sobre as estratégias de reprodução de briófitas nas Cangas (**Capítulo I)**;

V. Pela primeria vez, foram caracterizados os microhambientes: *Insect Nests, Shrub Associations, Tree Associations, Soil Islands* e *Exposed Rocks* que são colonizados por briófitas nos afloramentos rochosos ferruginosos. Evidenciando a importância de investigar as diferentes comunidades vegetais e seus habitats (**Capítulo II)**;

VI. Comunidades de briófitas de diferentes áreas de Canga podem ser estruturadas diferencialmente em resposta a filtros ambientais locais ou regionais, resultando em composições distintas. Tal fato deve ser cuidadosamente levado em conta para medidas de conservação (**Capítulo II**).

VII. A distribuição geográfica ampla das espéceis do RM, junto com a elevada incidência de esporos, sugere que muitas espécies de musgos e hepáticas em Cangas se dispersam efetivamente a longas distâncias (**Capítulo III)**;

VIII. É importante ampliar o conhecimento sobre as briófitas em formações de Canga, pois estas são áreas únicas e ricas que abrigam alta diversidade taxonômica e ecológica do grupo (**Capítulo III)**.

APÊNDICE

Apêndice A: Musgos do gênero *Campylopus* Brid. (Leucobryaceae) em Cangas do Parque Estadual da Serra do Rola-Moça, Minas Gerais, Brasil. In Rapid Color Guide of the Field Museum.

MUSGOS do gênero *Campylopus* Brid. (Leucobryaceae) em Cangas do Parque Estadual da Serra do Rola-Moça, Minas Gerais, BRASIL

1

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O Parque Estadual da Serra do Rola-Moça é uma importante área de conservação localizada no noroeste do Quadrilátero Ferrífero em Minas Gerais, em uma região de transição entre o Cerrado e a Mata Atlântica. Um elemento peculiar do Parque são os afloramentos rochosos ferruginosos, conhecidos como Cangas e presentes acima de 800 m de altitude. As Cangas abrigam os campos rupestres ferruginosos, uma fitofisionomia pouco compreendida e fortemente ameaçada pela exploração do minério de ferro. A combinação de um mosaico de micro-habitats com fatores como alta incidência solar, ventos fortes e elevada restrição hídrica promoveu altos níveis de diversidade e endemismo nas Cangas, especialmente da comunidade de plantas xerotolerantes. Nestes ambientes, espécies de musgos geralmente formam extensos tapetes sobre rochas e ilhas de solo, e adaptações como a poiquiloidria e a propagação vegetativa devem ser estratégias chave para dispersão, estabelecimento e manutenção do grupo em Cangas. Apesar do generalizado reconhecimento da presença de musgos em campos ferruginosos, a escassez de informação elementar sobre a diversidade destas plantas impossibilita investigações mais aprofundadas. O objetivo deste trabalho foi gerar um guia a cores das espécies do gênero *Campylopus* presentes em Cangas do Parque Estadual da Serra do Rola-Moça, sendo esta a primeira contribuição para o estudo da brioflora em Cangas no estado de Minas Gerais.

1-a ***Campylopus carolinae* Grout.** Plantas secas

1-b ***Campylopus carolinae* Grout.** Plantas hidratadas

1-c Gametófitos com esporófitos

1-d Filídio

1-e Região apical

1-f Região mediana

1-g Região basal

1-h Secção transversal

MUSGOS do gênero Campylopus Brid. (Leucobryaceae) em Cangas do Parque Estadual da Serra do Rola-Moça, Minas Gerais, BRASIL

2

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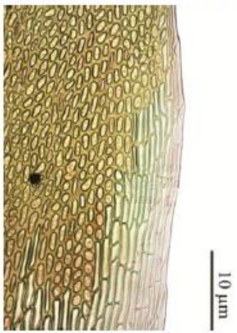
2-a *Campylopus julaceus* **A. Jaeger**
Plantas secas

2-b *Campylopus julaceus* **A. Jaeger**
Plantas hidratadas

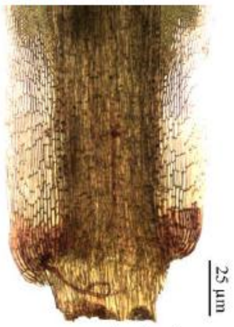
2-c Gametófitos: seco e hidratado

2-d Filídio

2-e Região apical



2-f Região mediana



2-g Região basal

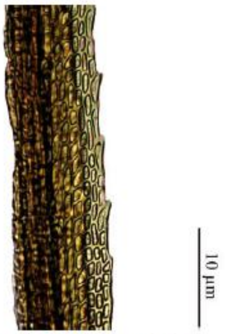
2-h Secção transversal

3-a *Campylopus lamellinervis* **(Müll. Hal.) Mitt.**
Plantas secas

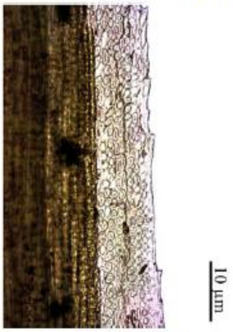
3-b *Campylopus lamellinervis* **(Müll. Hal.) Mitt.**
Plantas hidratadas

3-c Gametófitos: seco e hidratado

3-d Filídio



3-e Região apical



3-f Região mediana

3-g Região basal

3-h Secção transversal

MUSGOS do gênero *Campylopus* Brid. (Leucobryaceae) em Cangas do Parque Estadual da Serra do Rola-Moça, Minas Gerais, BRASIL

3

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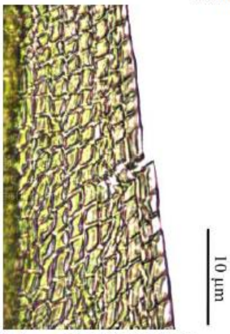
4-a *Campylopus occultus* **Mitt.**
Plantas secas

4-b *Campylopus occultus* **Mitt.**
Plantas hidratadas

4-c Gametófitos: seco e hidratado

4-d Filídio

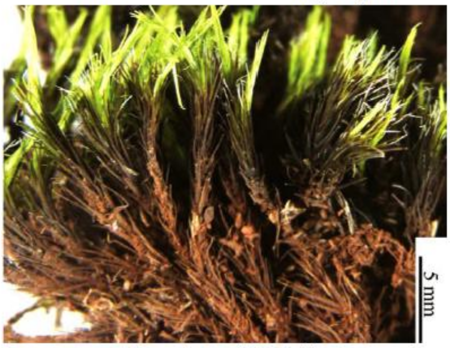
4-e Região apical



4-f Região mediana

4-g Região basal

4-h Secção transversal



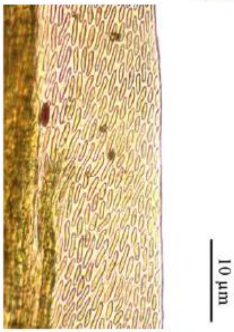
5-a *Campylopus pilifer* **Brid.**
Plantas secas

5-b *Campylopus pilifer* **Brid.**
Plantas hidratadas

5-c Gametófitos: seco e hidratado

5-d Filídio

5-e Região apical



5-f Região mediana

5-g Região basal

5-h Secção transversal

MUSGOS do gênero *Campylopus* Brid. (Leucobryaceae) em Cangas do Parque Estadual da Serra do Rola-Moça, Minas Gerais, BRASIL

4

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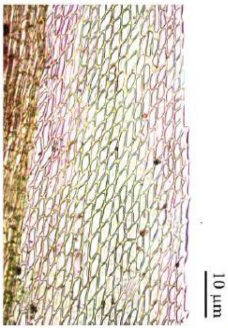
6-a ***Campylopus savannarum* (Müll. Hal.) Mitt.**
Plantas secas

6-b ***Campylopus savannarum* (Müll. Hal.) Mitt.**
Plantas hidratadas

6-c Gametófitos: seco e hidratado

6-d Filídio

6-e Região apical

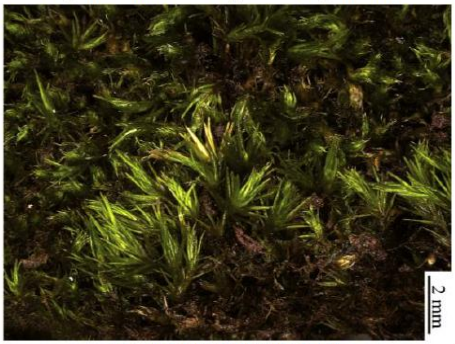


6-f Região mediana

6-g Região basal

6-h Secção transversal

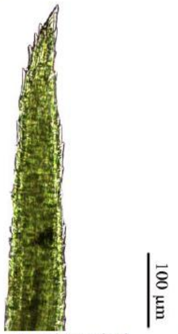
7-a ***Campylopus julicaulis* Broth.**
Plantas secas



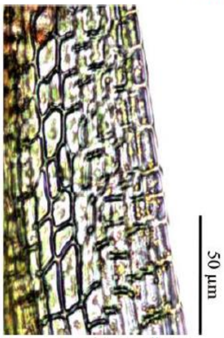
7-b ***Campylopus julicaulis* Broth.**
Plantas hidratadas

7-c Gametófitos: seco e hidratado

7-d Filídio



7-e Região apical



7-f Região mediana

7-g Região basal

7-h Secção transversal