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Distribution, ecology, and reproduction of bryophytes in a humid enclave in the semiarid region of northeastern Brazil

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ABSTRACT

The ready availability of water resources distinguishes the humid forest of Chapada do Araripe, Ceará State, Brazil, from the semiarid vegetation around it. The regional climate demonstrates a marked seasonality of rainfall that affects the ecological strategies of the species found there. We studied the bryophytes of the humid forest of Chapada do Araripe, analyzing their diversity, geographic distributions, and ecological and reproductive aspects. Bryophytes were collected from different substrates using the random-walk method. We gathered information concerning the geographic distribution, functional groups (life forms, light tolerance guilds, and habits) and reproductive aspects of each taxon. We found 76 bryophyte species, predominantly mosses (45 species). Ten new occurrences were recorded for Ceará State, including a new taxon for northeastern Brazil. Most species are widely distributed in that country. Desiccation tolerant (turf) and intermediate (mat and weft) life forms predominated, as well as generalist species in terms of their light requirements. Sixty eight percent of the species demonstrated substrate preferences. Monoicous (67 %) sexual systems predominated over dioicous. The species displayed functional groups and reproductive aspects tolerant to adverse conditions that maximized the use of available resources and allowed their persistence under the seasonal conditions of the forest.

Keywords: mosses, liverworts, floristics, enclave forest, seasonality

Introduction

The Chapada do Araripe (CA), Ceará State, Brazil, harbors humid a forest enclave within the dry forest mosaic of the Caatinga dryland domain. The humid forest grows in an area with relatively abundant water resources provided by many streams and springs, in spite of the long, regional dry season (DNPM 1996) constituting a type of oasis in the midst of a semiarid region that supports a wide floral and faunal diversity (FLONA 2004; Silva *et al*. 2011). The humid forest acts as a refuge for many species specific to that region, including endemic taxa such as *Antilophia bokermanni* (the Araripe manakin,"soldadinho do Araripe") which is critically threatened with extinction (Auler *et al*. 2004; Linhares & Silva 2015), and other taxa with disjunct distributions between the Atlantic and Amazon forests (e.g., spermatophytes and ferns; Loiola et al. 2015; Reinaldo et al. 2015) – illustrating the biological importance of that area and the necessity of its protection (MMA 2000).

Other humid enclaves (i.e., Montane forests, locally known as "Brejos de Altitude") found in Ceará State, (e.g., Chapada do Ibiapaba, Serra Maciço de Baturité, and Serra de Pirapora) likewise harbor high vascular and non-vascular plant diversities, including bryophytes (Yano & Pôrto 2006; Oliveira & Alves 2007; Oliveira & Bastos 2009a; b; 2010a; b;

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Lima & Mansano 2011; Lima *et al*. 2011; Ribeiro-Silva *et al*. 2012). Those enclaves, like the humid forests of Chapada do Araripe, demonstrate amenable climatic conditions with higher precipitation and lower temperatures than the surrounding matrix of dry forest (Tabarelli & Santos 2004; Silva & Casteleti 2005; Moro *et al*. 2015). Many species of bryophytes are found in those environments, including taxa with limited distributions and vulnerable to extinction (Pôrto *et al*. 2004). In general, little is known about the ecology and reproduction of the species found in humid forest enclaves in northeastern Brazil (Pôrto *et al*. 2004). Studies of the bryophytes of Ceará State have largely focused on species compositions, the microhabitats they colonize, and their taxonomies and geographic distributions (Yano & Pôrto 2006; Oliveira & Alves 2007; Oliveira & Bastos 2009a; b; 2010a; b). Information currently available concerning bryophytes in Chapada do Araripe is restricted to data from sporadic collections made between 1844 and 1994 – with 25 species being recognized for the region (see the Supplementary Material section, based on Brito & Pôrto 2000; Yano & Pôrto 2006).

Bryophytes are intimately influenced by environmental conditions and demonstrate extreme requirements of water/humidity to maintain their correct hydration and biological processes (e.g., sexual reproduction) (Proctor 1999; Proctor & Tuba 2002; Glime 2007). The responses of those plants to environmental conditions reflect ecological and reproductive strategies that guarantee their establishment, persistence, and dispersal. Those strategies are reflected in their life forms as well as in physiological aspects related to light tolerance, habitat specialization, and reproductive modes (Bates 1998; Alvarenga & Pôrto 2007; Germano & Pôrto 2006; Bisang & Hedenäs 2005). While researchers have identified numerous strategies utilized by bryophytes in different tropical ecosystems (Fatoba 1998; Maciel-Silva *et al*. 2012b; 2013), little information is currently available concerning the ecology of that group in ecological transition zones (IBGE 2012) such as those encountered within humid forests in the heterogeneous landscapes of the Brazilian semiarid region. We studied the bryophytes of the humid forest of Chapada do Araripe, analyzing their diversity, geographic distributions, and ecological and reproductive aspects.

Materials and methods

Study area

Our research was undertaken in a humid forest enclave on the northeastern slope of the Chapada do Araripe Range (Ceará State, northeastern Brazil) at elevations between 600 and 950 m a.s.l. (DNPM 1996) – a transition zone between seasonally dry tropical forests (Caatinga) and Neotropical Savanna (Cerrado) vegetations. Those humid forest formations occupy parts of the municipalities of Crato (7°13’66”S 39°24’32”W), Barbalha (7°18’20”S 39°18’9”W), and Missão Velha (7°15’26”S 39°8’45”W). The vegetation there is classified as Seasonal Semi-Deciduous Montane Forest (Veloso *et al.* 1991), which, in spite of the strong regional seasonality, retains 80 % of its leaf cover during the year (Loiola *et al.* 2015). The region experiences two well-defined seasons: a dry season (0-60 mm of rainfall per month) that generally extends from May through November, and a rainy season that lasts from December to April, with the heaviest rainfall from January to March (with a mean of 600 mm during those months, during the years between 1971 and 2000; FUNCEME 2000); total mean annual rainfall can reach 1,033 mm (DNPM 1996). According to the Koeppen-Geiger classification, the regional climate can be defined as Aw (*A- Equatorial w- equatorial savanna with dry winters*), hot and humid with (Austral) summer rains. The humid forests in Chapada do Araripe are partially protected by two conservation areas: the Chapada do Araripe Environmental Protection Area (APA), and (principally) the Araripe National Forest (FLONA). The area is nonetheless subject to numerous anthropogenic impacts, such as the presence of domestic animals, grazing, the extraction of natural resources, and the presence of garbage in localities frequented by tourists – as has been noted in other studies (FLONA 2004; Silva *et al.* 2011).

Sampling methods

A random-walk technique was adopted for sampling bryophytes in 12 localities (with a minimum distance of 1 km between them) throughout the extension of the humid forest enclave. The bryophyte inventory was undertaken by searching different available substrates (soil, rocks, tree bark, decaying tree trunks, leaves, and artificial substrates) in the understory (to a maximum height of 2 m). Collections were made during both the dry and rainy seasons (with priority given to the latter).

Treatment of the material

The identifications of the materials collected were based mainly on Sharp *et al.* (1994), Buck (1998), Gradstein & Costa (2003), and Gradstein & Ilkiu-Borges (2009), among other more specialized texts, as well as consultations with specialists. The species were classified in terms of the life form of the colony with which they were associated (e.g. turf (dense), mat, thalloid mat, weft, and fan), following Bates (1998), with the additional consideration of “sparse turf” (when portions of the larger colony demonstrated sparsely spaced individuals). According to Gimingham & Birse (1957), and considering Bates (1998), life forms respond to decreasing levels of moisture (or desiccation), so we also included life forms classification of: tolerant (turf and sparse turf), intermediate (mat, thalloid mat and weft), or vulnerable (fan) in relation to desiccation.

The guilds of tolerance to light intensity were classified based on Richards (1954); Gradstein (1992); Costa (1999); Gradstein & Costa (2003); Alvarenga & Pôrto (2007); Silva & Pôrto (2009) with the assistance of specialists and field observations: "generalist species" are considered those without special restrictions of tolerance to micro-environmental conditions (in terms of humidity or light conditions); specialist species demonstrate preferences for certain types of microenvironments (such as those requiring constantly shaded environments "shade species", as opposed to "sun species" tolerant of high light levels) (Richards 1954; Gradstein 1992; Costa 1999). In terms of the geographic distributions of the taxa, we evaluated their occurrence in different phytogeographic domains, and by state, in Brazil, classifying them as: widely-distributed (when encountered in more than five Brazilian states), or rare, when found in four states or less. We also classified their distributions as either disjunct between humid forests (Atlantic and Amazon forests) and enclaves of humid forest in the Cerrado domain (Gallery forests) and/or Caatinga (northeastern montane forests). Distribution data was obtained from Costa & Peralta (2015), as well as from floristic databanks (WVSM Batista unpubl. res), compiled during various floristic surveys of bryophytes in Brazil published between 1990 and the first half of 2017. Each specimen was examined to determine its sexual expression and type of reproduction: sexual (with sporophytes), or asexual (with asexual diaspores). The species were classified based on their sexual systems (monoicous and dioicous) in conformity with the specialized literature (Hell 1969; Sharp *et al*. 1994; Buck 1998; 2003; Gradstein & Costa 2003; Pursell 2007; Silva *et al.* 2014b) as well as the databank of Bryophytes from the Laboratório Biologia de Briófitas available at the Universidade Federal de Pernambuco.

Results

Floristics and geographic distributions

We recorded a total of 76 species, considering both mosses (45 species) and liverworts (31), including four varieties (Tab. 1). Those taxa were distributed among 25 families (14 moss families and 11 liverworts). The most well-represented moss family was Fissidentaceae (16 spp.), while the most well-represented liverwort family was Lejeuneaceae (14 spp.). The most abundant liverwort species was *Frullania ericoides* (152 occurrences) and the most important moss species was *Entodontopsis leucostega* (98 occurrences). We reported here 10 new species occurrences for Ceará State, including one for northeastern Brazil, *Fissidens steerei* Grout (Tab. 1).

In terms of the occurrence of taxa according to their phytogeographical domains, 79 % of the species occur in more than three different domains, principally the Atlantic and Amazon forests and Cerrado (20 % of the species); only two species are restricted to a single domain (the Atlantic Forest. In addition to the geographic distributions of the species in Brazil, 96 % were known to be widely distributed, with only a few being considered rare; 22 % of the species demonstrated disjunct distributions between humid forests and humid enclaves (Tab. 1).

Ecological aspects

Four different life forms were identified: mat, weft, turf, and fan, with two variations (sparse turf and thalloid mat) (Fig. 1). Some colonies were associated with more than one type of life form (17 % of the species). Intermediate life forms predominated in relation to desiccation tolerance (67 %), followed by tolerant (30 %) and low tolerance species (3 %). In terms of tolerance to light intensity, most species were generalists (55 %), principally mosses (60 %), as opposed to liverworts (40 %). Among the specialists, there was a prevalence of species tolerant of shaded environments (25 %) as opposed to those typical of more direct sunlight (20 %). In terms of the available substrates, 68 % of the species demonstrated preferences for a single type of substrate, predominately tree bark, rocks, or soil (Fig. 2).

Reproductive aspects

The predominant sexual system was monoicous (67 %), followed by dioicous (31 %); only 2 % of the species demonstrated both sexual systems (Fig. 3). In terms of their sexual expression, 58 % of the species were observed expressing sex; 72 % of those species were observed with sporophytes, those being principally monoicous (80 %); 21 % of those species utilized asexual reproduction (e.g., the production of gemma, regenerating plantlets, and caducous leaves), with approximately 75 % of them being dioicous; 7 % of the species demonstrated sexual and asexual reproduction simultaneously.

Discussion

Floristics and geographic distributions

Sixty-one taxa were added to the floristic composition of bryophytes previously known to the study area (Tab. S1 in supplementary material), totaling 91 species of bryophytes for the CA enclave, with greater moss than liverwort richness. Greater moss richness would be expected in dry forests, with liverworts being more predominant in humid forests (Gradstein *et al*. 2001). Mosses demonstrate wide morphological varieties (in relation to liverworts), which lends them greater tolerance to stress conditions in semiarid environments (Goffinet *et al*. 2009). The study area demonstrated high levels of available water and humidity due to the presence of springs and small streams, as well as

Table 1. List and characteristics of bryophytes species of Chapada do Araripe. Phytogeographic domains (Phyt. dom.): AM = Amazon Rainforest; AF = Atlantic Forest; CA= Caatinga; CA* = enclaves within the Caatinga; CE =Cerrado; CE* = enclaves within Cerrado; PM = Pampa; and PL = Pantanal. Geographic distribution in Brazil: Wide = Wide distribution; Disjunct = Disjunct distribution within rain forests; Rare = Rare distribution. Life forms: Fan, Mat, Thalloid Mat, Turf, Turf* = sparse colony of Turf and Weft. Light tolerance Guilds (Guilds): generalists = generalist species; sun = sun species; shade = shade species. Substrate: Art = Artificial; DT = Decaying trunk; Le = Leaf; Ro = Rock; So = Soil; and T = Tree bark. Sexual System: D = Dioicous; M = Monoicous. Sexual Structures: FG = Female gametangia; MG = Male gametangia; Sp = Sporophytes; Asex = Asexual propagule. Symbol: * in species = New record for State of Ceará; ** in species = New record for northeastern Brazil.

Species	Geographic distribution	Ecologycal Strategies	Reproduction Strategies				
	Phyt. Dom.	Brazil	Life Form	Guilds	Substrate	Sexual System	Sexual structures
Marchantiophyta							
Calypogeia laxa Gottsche & Lindenb.	AM/AF	Wide/Disjunct	Weft	generalists	So/Ro	Dioicous	-
Cheilolejeunea rigidula (Nees ex Mont.) R. M. Schust.	AF/CA/CE/PL	Wide	Weft	generalists	T	Dioicous	FG
Chiloscyphus liebmannianus (Gottsche) J. J. Engel & R. M. Schust.	AM/AF/CE*	Wide/Disjunct	Weft	generalists	Ro	Monoicous	-
Chiloscyphus martianus (Nees) J. J. Engel & R. M. Schust.	AM/AF/CE/PL	Wide	Mat/Weft	generalists	Ro	Monoicous	-
Cololejeunea camillii (Lehm.) A. Evans	AM/AF	Wide/Disjunct	Mat	generalists	Ro/T	Monoicous	FG
Cololejeunea contractiloba A. Evans*	AM/AF/CE	Wide	Mat	generalists	T	Monoicous	FG
Cololejeunea minutissima (Sm.) Schiffn.	AM/AF/CE/PL	Wide	Mat	generalists	T	Monoicous	-
Cololejeunea obliqua (Nees & Mont.) Schiffn.	AM/AF	Wide/Disjunct	Mat	generalists	T	Monoicous	-
Cylindrocolea rhizantha (Mont.) R. M. Schust.	AM/AF/CE*	Wide/Disjunct	Weft	shade	Ro	Monoicous	FG
Diplasiolejeunea pellucida (Meissn.) Schiffn.	AM/AF	Wide/Disjunct	Mat	sun	Le	Dioicous	FG/MG
Fossombronia porphyrorhiza (Nees) Prosk.	AF/CA/CE/PL	Wide	Mat	generalists	Ro	Monoicous	-
Frullania dusenii Steph.	AM/AF/CA/CE	Wide	Weft	sun	Ro/T	Monoicous	FG/Sp
Frullania ericoides (Nees) Mont.	all	Wide	Mat/Weft	sun	Ro/T	Dioicous	FG/MG/Sp
Frullania kunzei (Lehm. & Lindenb.) Lehm. & Lindenb.	AM/AF/CE/PL	Wide	Weft	sun	T	Monoicous	FG
Frullania platycalyx Herzog	CE/AF	Wide	Mat/Weft	sun	DT/T	Monoicous	FG/MG/Sp
Lejeunea controversa Gottsche	AM/AF/PL	Wide	Mat	generalists	T	Monoicous	FG/MG/Sp
Lejeunea flava (Sw.) Nees	all	Wide	Mat	generalists	T	Monoicous	-
Lejeunea glaucescens Gottsche	AM/AF/CE/PL	Wide	Mat	generalists	DT/Ro/So	Monoicous	FG/MG
Lejeunea phyllobola Nees & Mont.	AM/AF/CA/ CE/PL	Wide	Mat/Weft	generalists	Ro/T	Dioicous	FM/Asex
Lophocolea bidentata (L.) Dumort.	AM/AF/CE*	Wide/Disjunct	Weft	shade	Ro/T	D/M	-
Microlejeunea bullata (Taylor) Steph.	all	Wide	Mat	generalists	T	Dioicous	FG
Microlejeunea epiphylla Bischl.	AM/AF/CA/ CE/PL	Wide	Mat	sun	T	Dioicous	FG
Micropterygium trachyphyllum Reimers*	AM/AF/CE*	Wide/Disjunct	Mat	shade	T	Dioicous	-
Plagiochila raddiana Lindenb.	AM/AF/CE*	Wide/Disjunct	Fan	shade	Ro/T	Dioicous	FG/Asex
Pycnolejeunea contigua (Nees) Grolle	AM/AF	Wide/Disjunct	Mat	sun	Ro/T	Dioicous	FG
Riccardia chamedryfolia (With.) Grolle*	AF/CE*	Wide/Disjunct	Thalloid Mat	shade	Ro	Monoicous	-
Riccardia tenuicula (Spruce) Meenks*	AM/AF/CE*	Wide/Disjunct	Thalloid Mat	shade	Ro	Dioicous	MG/Sp
Schiffneriolejeunea polycarpa (Nees) Gradst.	AM/AF/CA/ CE/PL	Wide	Mat	sun	T	D/M	MF/MG/Sp
Symphyogyna aspera Steph.	AM/AF/CE/PL	Wide	Thalloid Mat	shade	Art/Ro	Dioicous	-
Telaranea nematodes (Gottsche ex Austin) M. A. Howe	AM/AF/CE*	Wide/Disjunct	Weft	shade	Art/So	Monoicous	FG
Zoopsidella macella (Steph.) R. M. Schust.	AM/AF/CA/CE	Wide	Weft	generalists	Ro/So	Monoicous	FG
Bryophyta							
Bryum huillense Welm. & Duby*	AF/CE	Wide	Turf	shade	Ro	Dioicous	-
Bryum limbatum Müll. Hal.	AF/AM	Wide	Weft	shade	Ro	Dioicous	-
Callicostella pallida (Hornsch.) Ångström	all	Wide	Weft	generalists	Art/Ro	Monoicous	Sp

Table 1. Cont.

Species	Geographic distribution	Ecologycal Strategies	Reproduction Strategies				
	Phyt. Dom.	Brazil	Life Form	Guilds	Substrate	Sexual System	Sexual structures
Calymperes afzelii Sw.	AM/AF/CE	Wide	Turf	generalists	T	Dioicous	FG/Asex
Calymperes palisotii Schwägr.	AM/AF/CA/CE	Wide	Turf/Weft	generalists	T	Dioicous	MG/Asex
Campylopus cuspidatus (Hornsch.) Mitt.*	AM/AF/CE	Wide	Turf	sun	So	Dioicous	-
Campylopus julicaulis Broth.*	AF/PA	Wide	Turf	sun	Ro/So	Dioicous	-
Donnellia commutata (Müll. Hal.) W. R. Buck	AM/AF/CE/PL	Wide	Mat	generalists	T	Monoicous	-
Entodontopsis leucostega (Brid.) W. R. Buck & Ireland	AM/AF/CA/CE/PL	Wide	Mat/Weft	generalists	DT/T	Monoicous	Sp
Erpodium coronatum (Hook. & Wilson.) Mitt.	AF/CE/PL	Wide	Mat/Weft	generalists	T	Dioicous	Sp
Fabronia ciliaris (Brid.) Brid. subsp. *ciliaris*	AM/AF/CA/CE/PL	Wide	Mat	generalists	T	Monoicous	Sp
Fabronia ciliaris (Hook.) W. R. Buck var. *polycarpa*	AM/AF/CA/CE/PL	Wide	Mat	generalists	T	Monoicous	-
Fabronia macroblepharis Schwägr.	AF/CA/CE/PL	Wide	Weft	sun	T	Monoicous	Sp
Fissidens angustifolius Sull.	all	Wide	Turf	generalists	So	Monoicous	-
Fissidens brevipes Besch.	all	Wide	Turf/Weft	generalists	T	Monoicous	-
Fissidens bryoides Hedw.	AF	Rare/Disjunct	Turf*	shade	So	Monoicous	-
Fissidens cryptoneuron P. de la Varde	CA*/CE	Rare	Weft	generalists	T	Monoicous	-
Fissidens elegans Brid.	all	Wide	Weft	generalists	T	Monoicous	MG/Sp/Asex
Fissidens gardneri Mitt.*	AF/CA/CE	Wide	Mat	shade	T	Monoicous	-
Fissidens hornschuchii Mont.	all	Wide	Turf	generalists	So	Monoicous	-
Fissidens inaequalis Mitt.	AM/AF/CE*	Wide/Disjunct	Weft	shade	Ro	Monoicous	-
Fissidens lagenarius Mitt. var. *lagenarius*	AF/CA/CE/PL	Wide	Fan/Weft	shade	Ro	Monoicous	Sp
Fissidens neglectus H. A. Crum*	AF	Rare/Disjunct	Turf*	generalists	So	Monoicous	-
Fissidens pallidinervis Mitt.	AM/AF/CA/CE/PL	Wide	Fan/Weft	shade	DT/T	Monoicous	FG/MG
Fissidens pellucidus Hornsch. var. *pellucidus*	all	Wide	Fan/Weft	generalists	Ro	Monoicous	-
Fissidens radicans Mont.	AM/AF/CA/CE	Wide	Turf/Weft	generalists	Ro/T	Monoicous	MG/Sp
Fissidens steerei Grout**	AF/CE*	Rare/Disjunct	Fan	shade	Ro	Monoicous	-
Fissidens submarginatus Bruch	all	Wide	Turf*	shade	So	Monoicous	Sp
Fissidens zollingeri Mont.	AM/AF/CA/CE/PL	Wide	Turf	generalists	T	Monoicous	-
Hyophyla involuta (Hook.) A. Jaeger	all	Wide	Turf	sun	Ro	Dioicous	-
Isopterygium tenerifolium Mitt.	AM/AF/CE	Wide	Weft	generalists	T/Wa	Monoicous	Sp
Isopterygium tenerum (Sw.) Mitt.	all	Wide	Mat	generalists	T	Monoicous	Sp
Jaegerina scariosa (Lorentz) Arzeni	AM/AFCE/PL	Wide	Fan	generalists	T	Dioicous	-
Macrocoma sp.	AF/CE	-	Mat	-	T	-	-
Ochrobryum gardneri (Müll. Hal.) Mitt.	AM/AF/CE/PL	Wide	Turf	sun	T	Dioicous	Sp
Octoblepharum albidum Hedw.	all	Wide	Turf/Turf*	generalists	T	Monoicous	Asex/Sp
Ptychostomum capillare (Hedw.) Holyoak & Pedersen	AF/CA/CE/PA/PL	Wide	Turf	generalists	DT/So/T	Dioicous	Sp
Schlotheimia rugifolia (Hook.) Schwägr.	AM/AF/CE	Wide	Mat	sun	DT	Dioicous	Sp
Sematophyllum galipense (Müll. Hal.) Mitt.	AM/AF/CE*	Wide/Disjunct	Mat	generalists	Ro/T	Monoicous	Sp
Sematophyllum subpinnatum (Hedw.) Mitt. J. Linn. Soc.	all	Wide	Mat	generalists	Ro/T	Monoicous	Sp
Sematophyllum subsimplex (Brid.) E. Britton	AM/AF/CA/CE/PL	Wide	Mat	generalists	Ro/T	Monoicous	Sp
Stereophyllum radiculosum (Hook.) Mitt.	AM/AF/CE/PL	Wide	Turf	generalists	T	Monoicous	Sp
Syrrhopodon ligulatus Mont.	AM/AF/CE*	Wide/Disjunct	Turf	shade	T	Dioicous	FG/Asex
Syrrhopodon parasiticus (Brid.) Paris	AM/AF/CE/PL	Wide	Turf	sun	T	Dioicous	FG/Asex
Tortella lilliputana (Müll. Hal. ex Roth) R. H. Zander.*	AF/CE*	Rare/Disjunct	Turf	shade	Ro	-	-

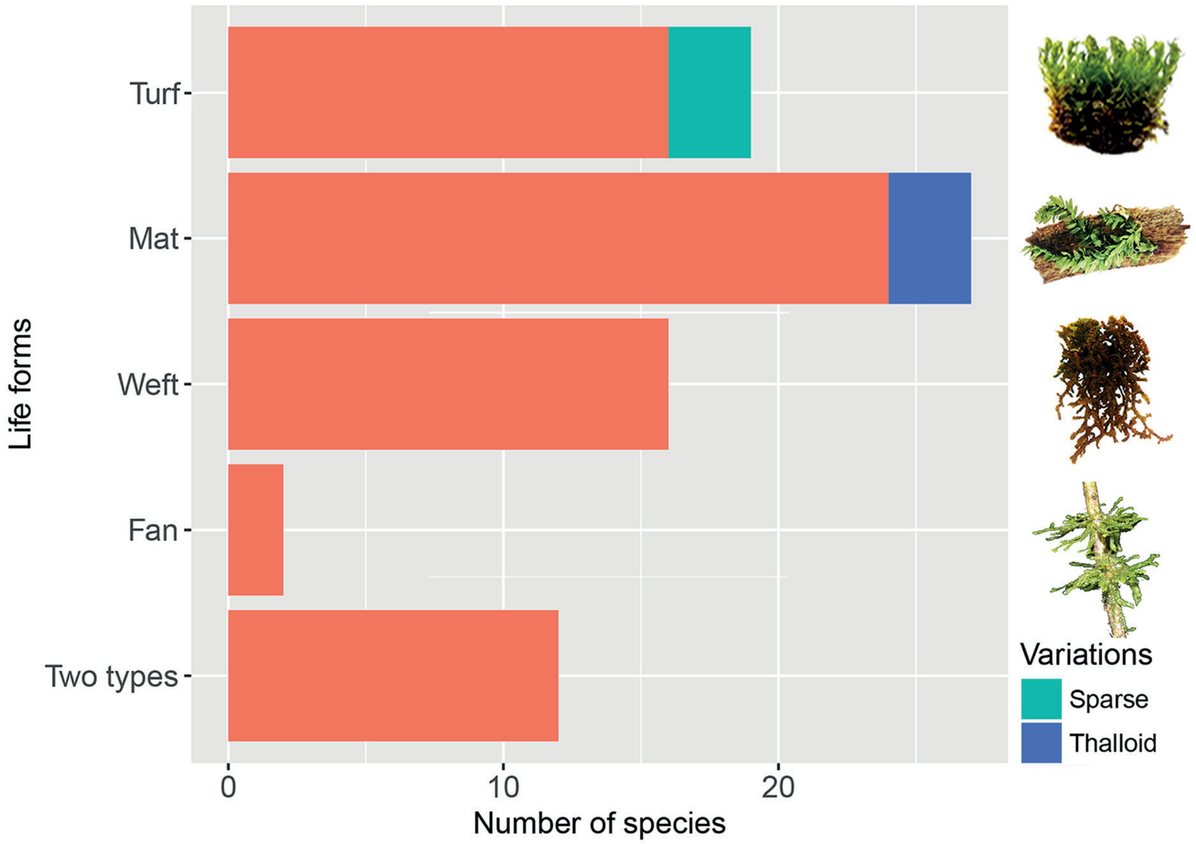

Figure 1. Numbers of species per life form: Fan; Mat; Turf and variation: colony sparse turf (sparse); Thalloid mat (thalloid) and Weft. Species with more than one type of life form (two types).

the effects of orographic rainfall (mean annual rainfall of 1,030 mm in the humid forest and 720 mm in the adjacent dry forests) – in spite of the strong seasonality of the regional climate, with 80 % of the mean annual precipitation being concentrated in just four months of the year (the rainy season) (DNPM 1996; Zanella 2005). Inventories of the bryofloras of six other humid enclaves in the states of Ceará, Paraíba, and Pernambuco in northeastern Brazil also demonstrated greater moss richness in relation to liverworts (Pôrto *et al.* 2004; Oliveira 2008; Silva 2013); the family Fissidentaceae was the most representative in five of those areas (Pôrto *et al.* 2004; Oliveira 2008; Oliveira & Bastos 2010b; Silva 2013). In spite of the fact that the family comprises only a single genus (*Fissidens*), its species are quite diverse in terms of a variety of morphological attributes, including limbidium and papillae (which are considered adaptive to desiccation tolerance); its species are found in many different environments, from natural to disturbed/urban (Pursell 2007; Bordin & Yano 2013). *Fissidens* is also the most diversified moss genus in the Caatinga domain (Bordin 2015), where the present study was undertaken, reinforcing the contributions that dry forests make to the pool of regional species. The CA forest harbors other representatives of the genus *Fissidens*, such as *F. neglectus* and *F. cryptoneuron,* which are considered vulnerable (VU) to extinction in Brazil (Bordin & Yano 2013).

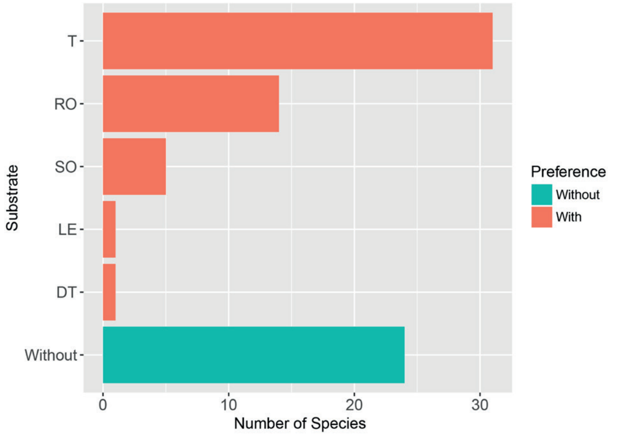

Figure 2. Numbers of species with substrate preferences (With), on tree bark (T), rocks (RO), soil (SO), leaves (LE), and on decaying tree trunks (DT). Species that colonize more than one type of substrate (two types), those that do not demonstrate any preference (Without).

Lejeuneaceae was the most representative family among the liverworts, as expected, as it is the most diverse family in Brazil (Costa & Peralta 2015), comprising taxa principally inhabiting humid tropical forests, such as *Cololejeunea*

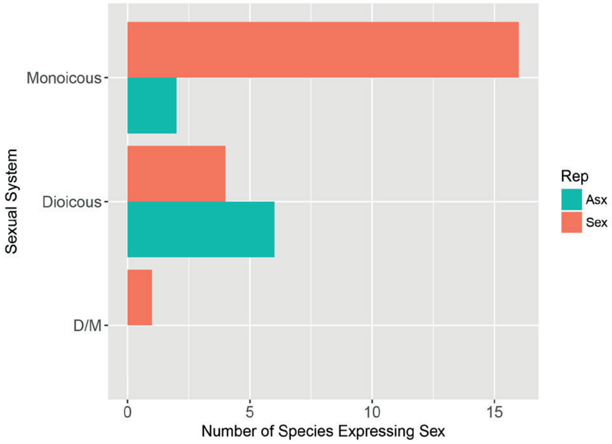

Figure 3. Numbers of species according to their reproductive strategies: monoicous and dioicous (both: D/M). Type of reproduction (Rep), sexual (Sex) and asexual (Asx).

contractiloba, *Cololejeunea obliqua*, and *Diplasiolejeunea pellucida*; other of its members occur in dry forests, such as *Lejeunea flava*, *Lejeunea glaucescens*, and *Lejeunea phyllobola*.

Most of the bryophyte species reported here are widely distributed throughout Brazil, being frequent in both humid and dry forests and in different phytogeographic domains – as seen in surveys undertaken in dry forests and disturbed areas (Silva *et al.* 2014a; b; Carmo *et al.* 2015). Generalist species usually have functional traits that provide them with tolerance to adverse conditions (Glime 2007), such as the presence of papillae on the leaves (an adaptation to dry environments) (Kürschner 2004). Papillae were principally observed on mosses (16 spp.) of the genera *Fissidens*, *Syrrhopodon, Stereophyllum, Callicostella*, and *Tortella*, as opposed to liverworts (the species *Micropterygium trachyphyllum* and *Cololejeunea contractiloba*). The presence of costae on the leaves (exclusive to mosses) also represents a functional trait that facilitates water transport (Glime 2007; Goffinet *et al.* 2009). Fully 89 % of the moss species of the CA had costae and some of those structures were quite broad (ca. 50 % of the surface area of the leaves) (Sharp *et al.* 1994; Yano & Peralta 2011; Santos 2011), including representatives of the genera *Octoblepharum, Ochrobryum,* and *Campylopus*. Additionally, accessory pigments that aid in protecting the plants against solar radiation were observed (Seel *et al.* 1992), principally among species of *Frullania*.

Ecological aspects

The predominant life forms of the bryophytes observed in the CA were intermediate: mat and weft – forms generally associated with perennial life strategies and therefore commonly encountered (During 1979; 1992). Life forms represent functional groups molded by ambient light intensity and humidity conditions that allow individuals and/or populations to minimize water losses and maximize primary production (Mägdefrau 1982; Bates 1998). Mat-forming populations demonstrate strong fixation to the substrate, which facilitates their establishment on many types of surfaces and leaves them less exposed to impacts by external factors (such as strong winds) (Bates 1998). Turf life forms are more tolerant and are typically encountered in sites exposed to high incident light intensities and low humidity levels. It is important to note that dense turf forms predominated over sparse turf assemblages, which reflects the responses of those bryophytes to the microclimatic conditions of the area. According to Skre *et al.* (1983), high colony densities favor self-shading of the gametophytes, minimizing the negative effects of high light levels that could otherwise damage their photosynthetic systems. Specialist life forms, such as fan, are more typical of shaded environments, with minimum direct exposure to sunlight while retaining viable water resources (Mägdefrau 1982; Bates 1998). It is noteworthy that the two species encountered showing fan life forms occurred in forest sites where access is generally forbidden to the general public (near the headquarters of the FLONA-Araripe); that site was also the sampling area at the highest altitude (ca. 950 m), and showed high humidity levels.

Bryophyte species demonstrate individual preferences for colonizing exposed or shaded microhabitats (Gradstein 1992). A predominance of generalist species (e.g., *Cheilolejeunea rigidula*, *Octoblepharum albidum* and *Calymperes afzelii*) was expected based on other studies of bryophytes in tropical environments, as that group is less demanding in terms of the micro-environmental conditions necessary for growth and establishment (Silva & Pôrto 2009; Brito & Ilkiu-Borges 2014). Specialist species encountered in humid forest environments are predominantly shade-demanding types (e.g. *Syrrhopodon ligulatus*) (Alvarenga & Pôrto 2007; Silva & Pôrto 2009; Santos *et al.* 2011; Brito & Ilkiu-Borges 2014; Visnadi 2015; Fagundes *et al.* 2016), while those encountered in dry forests (such as the Caatinga) are typically tolerant (e.g. *Schiffneriolejeunea polycarpa*) of high light intensity levels (Silva *et al.* 2014b). It is important to remember that light intensities in the forest interior are quite dynamic due to the structural complexity of those sites and the various disturbances that can affect them (such as the occurrence of temporary clearings) (Richards 1988; Acebey *et al.* 2003; Frahm 2003). We observed that specialist species (typical of either high sunlight or deep shade sites) were well-represented, which reflects the micro-environmental variety encountered in those dry forests due to natural and/or anthropogenic disturbances, as well as to the phytogeographic character of the region – an area of ecological contact that mixes elements of humid and dry forests.

Most of the bryophytes demonstrated substrate type preferences, with a predominance of species that colonize tree bark. Different substrate types are known to create different micro-environments that can directly influence species richness, composition, and abundance (Crites &

Dale 1998; Hodge 2005). Frahm (2003) in a study of tropical rain forest bryophytes, however, observed that substrate influences can be neutralized when regional climatic conditions (high humidity levels) are very favorable; in those cases, most species do not demonstrate particular preferences for substrate types, being capable of colonizing a wide range of available surfaces. Germano & Pôrto (2006) observed that most of the bryophytes (87 %) encountered in a remnant area of Atlantic Forest with a very high mean annual precipitation rate (2,450 mm – much higher than the humid forest of CA, with 1,033 mm) did not demonstrate strong preferences for specific substrates. As such, the predominance of species demonstrating distinct preferences for certain substrates in CA appears to reflect the low humidity in the region (with high seasonal rainfall variations) and the necessity of occupying specialized microhabitats to take advantage of their particular conditions (such as greater or lesser water retention capacities).

A number of studies have demonstrated the existence of bryophyte specificities for distinct phorophytes in tropical and temperate forests (Cornelissen & Steege 1989; Schmitt & Slack 1990; Wolf 1994; Mancebo *et al.* 2003; Batista & Santos 2016), and related the heterogeneity of tree trunk conditions (*e.g.,* their diameters and bark attributes such as roughness, pH, porosity, and water retention capacity, etc.) with greater microhabitat availability (i.e., more available colonization niches) (Smith 1982; Frahm 1990; Bates 1992). That type of heterogeneity is not seen with other substrates such as soil, however.

Only one species was exclusively found on a temporary substrate (the epiphyllous species *Diplasiolejeunea pellucida*). All of the individuals of that species were observed with sporophytes (eight occurrences). The short life spans of those substrates require specific strategies of the occupying species to effectively maintain their populations (Frahm 2003) – such as a prostrate growth habit and/or a short life cycle – with high fertility and high diaspore production levels (Zartman 2003; Alvarenga *et al.* 2013).

Reproductive aspects

Most bryophyte species (mosses and liverworts) are dioicous, with the exception of hornworts (Wyatt 1982; Villarreal & Renner 2013). The few studies that have examined the reproductive aspects of bryophytes at the community level reported monoicous species predominating on rock outcrops in the Caatinga domain (Silva *et al.* 2014b), with dioicous species predominating in areas of Atlantic Forest and on rock outcrops in Cerrado sites (Silva 2013; Santos *et al.* 2017; Peñaloza-Bojacá *et al.* 2017). Environmental conditions (such as humidity) will directly influence the reproductive processes of bryophytes (Milne 2001; Oliveira & Pôrto 2001; Maciel-Silva & Válio 2011), as they have adopted wider varieties of reproductive strategies than seed-producing plants (Glime & Bisang 2007). The sexual systems of bryophytes can facilitate sexual reproduction, as monoicous plants do not spatially segregate their reproductive organs – with the opposite occurring in dioicous individuals (Bisang & Hedenäs 2005; Stark *et al.* 2005). This pattern was confirmed in the present study, as the highest fertilization rates (the presence of sporophytes) were associated with monoicous species, demonstrating the efficiency of monoicous systems in carrying out sexual reproduction (Longton 1992; 1997; Laaka-Lindberg *et al.* 2000; Söderström & During 2005).

Sexual reproduction strategies (predominate among monoicous plants) result in the production of spores – creating the possibility of dispersal over much larger distances than are possible with asexual propagules (Longton 1997; Pohjamo *et al.* 2006). Spores are also more resistant to desiccation and can remain dormant in spore banks (Leck & Simpson 1987; Maciel-Silva *et al.* 2012a). Species invest in the production of spores that can persist during dry periods and then germinate under more favorable conditions, although it is important to note that some species produce very short-lived spores (Jonsson 1993; Maciel-Silva *et al.* 2012a). Asexual structures are largely produced by dioicous species, as observed in our study (e.g. *Lejeunea phyllobola*, *Plagiochila raddiana*, and including representatives of the genera *Syrrhopodon* and *Calymperes*). It is known that asexual structures can help guarantee the maintenance of populations at local scales, principally when environmental factors are unfavorable to sexual reproduction, which requires conditions of greater humidity (Newton & Mishler 1994; Longton 1997; Glime & Bisang 2007). Clonal reproduction by dioicous species contributes to the segregation of male and female gametophytes, and the frequent creation of unisexual colonies – which tends to make fertilization more difficult (McLetchie & Puterbaugh 2000; Bisang & Hedenäs 2005).

Conclusion

The ecological aspects identified here provide important information for understanding the distributions and ecology of bryophyte species in an area of ecological transition (humid enclaves in the Caatinga domain). The general patterns encountered indicate the influence of long dry periods (associated with low and irregular regional precipitation) on bryophyte strategies, with a greater representivity of mosses with intermediate tolerance to desiccation, wide geographic distributions, specific substrate requirements, and a low richness of epiphyllous species; likewise, there is a prevalence of species with monoicous sexual systems that facilitate fecundity, together with investments in resistant propagules – reflecting the highly seasonal regional climate. The existence of species typical of shaded environments and the presence of taxa showing disjunct distributions between humid forests and humid enclaves suggest that local humidity in CA, maintained by the presence of streams and springs, allows colonization by groups of species highly demanding of humid conditions. Our data provides the basis for future ecological investigations addressing some of the questions raised here, such as identifying the structuring processes determining those assemblages and identifying the environmental filters (both natural and anthropogenic) that affect the distributions of those taxa.

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