

# Bryophytes on rocky outcrops in the *caatinga* biome: A conservationist perspective<sup>1</sup>

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## ABSTRACT

In the state of Paraíba, Brazil, there is an abundance of rocky outcrops, which are typical elements of the semi-arid landscape. Those outcrops provide refuge to species with morphological adaptations to stressful climates and to rare communities of plants, including bryophytes. Nevertheless, there have been no studies of bryophytes in such habitats in the state. Therefore, this work aimed to inventory bryophytes on two outcrops in the municipality of Puxinanã, in Paraíba, addressing some of the ecological aspects of survival in xerophytic environments. Samples were collected once every two weeks from February 2010 to May 2011. The usual techniques of bryophyte sampling and herbarium preservation were employed. We recorded 21 bryophyte species (six liverworts and 15 mosses), some of which are rare for Brazil. We performed cluster analysis, using the unweighted pair group method with arithmetic mean, based on the Sørensen similarity index. We thus defined three clusters among the studied outcrops and similar areas recorded in the literature. The rocky outcrops proved to be singular in terms of bryophyte species composition, which, as in most xerophytic environments, included light-demanding and generalist species, featuring various morphological adaptations to resist water stress, primarily in terms of their leaf structure. Our results demonstrate the urgent need for additional studies in the state of Paraíba, including floristic, conservation, evolutionary and biogeographic studies.

**Key words:** bryophyte, inselberg, morphological adaptations, nonvascular flora, semi-arid, northeastern Brazil

## Introduction

Featuring a semi-arid climate, the northeastern region of Brazil has a large number of rocky outcrops, which are defined as monolithic rocks or rock clusters that appear abruptly in the midst of the surrounding shrublands, known as *caatinga* (Porembski *et al.* 1997). Such outcrops are typically composed of granite or gneiss (Porembski *et al.* 1998; Sarthou *et al.* 2003), with foci of rare, endemic plant communities (Oliveira & Godoy 2007). Because they provide habitats in which there is constant exposure to wind and sunlight (Araújo *et al.* 2008) and, consequently, rapid evaporation (Willis 1934), these rocky outcrops are classified as xeric environments. Nevertheless, they are excellent sites for comparative geophysical studies, as well as for studies of the factors influencing floristic diversity (Porembski 2007). Although plant communities are commonly found on these formations, there have been few studies of such communities (Araújo *et al.* 2008). In the northeastern Brazilian state of Paraíba, there have been some studies of vascular flora among rocky outcrops (Fevereiro & Fevereiro 1980; Almeida *et al.* 2007a, 2007b; Porto *et al.* 2008; Tölke *et al.*

2011). However, studies of bryophytes in the state have been restricted to forest environments (Yano & Andrade-Lima 1987; Pôrto & Germano 2002; Lüt & Schafer-Verwimp 2004; Yano 2004; Pôrto *et al.* 2004).

Consequently, the present study is the first of its kind, in that it was aimed at providing data related to bryophyte communities among rocky outcrops in the state of Paraíba.

## Material and methods

### Study area

The study was conducted in the municipality of Puxinanã, within the Agreste region of the state of Paraíba, Brazil. In the study area, the climate is dry and the topography comprises deep, narrow valleys (Beltrão *et al.* 2005), where there are extensive groups of rock formations (Oliveira & Godoy 2007).

On the basis of visits and prior surveys, we selected two study sites, designated rocky outcrops 1 and 2 (RO1 and RO2, respectively). At RO1, which is near the middle of the most urbanized sector of Puxinanã (at 07°08'62"S;

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35°58'31"W), the elevation is 661 m, the average annual temperature is 23.7°C, and the average annual rainfall is 520 mm. At RO2, located on the Beija-Flor Grange (also within Puxinanã, at 07°14'91"S; 35°97'64"W), the elevation is 575 m, the average annual temperature is 24.2°C, and the average annual rainfall is 428 mm. At both sites, the tree and shrub vegetation at the top of the outcrop is typical of the *caatinga*, whereas in the lower, surrounding areas, the native flora has been supplanted by cultivated vegetation.

### Sampling and study of the material

Specimens were collected once every two weeks between February 2010 and May 2011. We sampled all available substrates from the bottom to the top of each outcrop, following the techniques for collection and herbarium preservation of bryophytes described in Yano (1984), Gradstein *et al.* (2001) and Frahm (2003).

Samples were deposited in the Manoel de Arruda Câmara Herbarium (ACAM), located on Campus I of Paraíba State University, in the city of Campina Grande. The identification of the taxa was based on the works of Gradstein & Buskes (1985), Gradstein (1989; 1994), Sharp *et al.* (1994), Buck (1998), Reiner-Drehwald (2000), Gradstein *et al.* (2001), Gradstein & Costa (2003) and Goffinet & Buck (2004), as well as on other specialized articles and monographs. The classification systems adopted for compiling the floristic list of bryophytes were those devised by Crandall-Stotler *et al.* (2009) for liverworts and by Goffinet *et al.* (2009) for mosses. The taxonomic nomenclature was updated according to recent studies and through a review of the database of the Missouri Botanical Garden (W<sup>3</sup> TROPICOS 2010). The identities of species that were difficult to distinguish were confirmed by experts.

The geographical distribution was obtained from the databases of the Rio de Janeiro Botanical Garden (Costa 2012) and the Missouri Botanical Garden (W<sup>3</sup> TROPICOS 2010), as well as from the catalogs published by Yano (1989; 1993; 1995; 1996; 2004; 2006; 2010; 2011).

The growth forms were determined in accordance with Mägdefrau (1982) and Gradstein *et al.* (1996). The specific synusia was determined on the basis of the data contained in Gradstein (1992) and in other works dealing with ecology.

Information on the conservation status of the species identified were obtained from Ganeva (1998), from the Red List of Threatened Bryophytes in Brazil, published by the Biodiversitas Foundation (Biodiversitas 2005), and from the New Zealand Threat Classification System lists compiled by Hitchmough *et al.* (2005).

### Data analysis

The climatic conditions (resolution, 2.5 min) were obtained from the WorldClim database (Hijmans *et al.* 2005b) via the program DIVA-GIS, version 5.2 (Hijmans

*et al.* 2005a). We compared bryophyte species composition between the two outcrops sampled (RO1 and RO2), as well as between the sampled sites and other areas with similar abiotic characteristics, in terms of aspects such as rainfall and temperature—*caatinga* area 1 (CA1), *caatinga* area 2 (CA2), an area within the dry, rocky grasslands known as *campos rupestres* (CR) and another rocky outcrop, located in the state of Bahia (RO3). To that end, we performed cluster analysis using the unweighted pair group method with arithmetic mean (UPGMA), based on the Sørensen similarity index, which excludes double absence and assigns greater weight to co-occurrence (Valentin 2000). The calculation of the Sørensen similarity index and the UPGMA were both achieved with the program Fitopac 2.1 (Shepherd 2010). For a list of the species occurring at the comparison sites, see Pôrto *et al.* (1994) for CA1, Pôrto & Bezerra (1996) for CA2, Bastos *et al.* (2000) for CR and Pôrto & Valente (2006) for RO3.

## Results and discussion

At the two study sites, we identified 21 bryophyte species (Tab. 1): 15 mosses, belonging to 11 genera within eight families; and six liverworts, belonging to three genera within three families. The bryophyte species richness at our study sites was comparable to that reported for inselbergs in the African nation of Benin by Frahm & Porembski (1997), who recorded 18 species, although lower than that reported for inselbergs in the Ivory Coast and Zimbabwe, for which 31 and 25 bryophyte species, respectively, have been recorded (Frahm 1996). In addition, there is a clear dissimilarity in the composition of species, as only *Gemmabryum exile* (also known as *Brachymenium exile*) and *Octoblepharum albidum* are common to the regions of Africa studied.

The families with the highest species richness in the present study (Bryaceae and Frullaniaceae) are among the top 10 families found in inventories of various vegetation types in tropical regions (Gradstein & Pócs 1989). Representatives of those families seem to have great ability to colonize rock surfaces, making them important pioneer species. Such species include *Frullania gibbosa* and *Bryum argenteum*, which were also the most common species in the present study (respectively accounting for 18.7% and 15.6% of the total species richness), followed by *Fabronia ciliaris* var. *wrightii* (15.6%), *B. argenteum* (15.6%) and *Gemmabryum exile* (12.5%). In addition, Bryaceae and Frullaniaceae were the only families to be represented in all of the areas evaluated (*caatinga* and rocky outcrops), although there were no species that occurred in all six areas.

Due to the inherent morphology of their gametophytes, mosses typically outnumber liverworts in tropical rain forests (Gradstein *et al.* 2001). However, on rocky outcrops and in other xeric environments, that relationship is inverted, as shown by the results obtained here and in (the few) other studies of bryophytes in such environments.

**Table 1.** Characteristics of bryophytes found on rocky outcrops. Municipality of Puxinanã, state of Paraíba, Brazil.

DIVISION						
Family						
Species	Publication	Material examined	Worldwide Distribution	Distribution in Brazil	Growth form	Synusia
<b>BRYOPHYTA</b>						
Bryaceae (3/4)						
<i>Bryum argenteum</i> Hedw.	Sp. Musc. Frond. 181. 1801	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 26/III/2010, RO1, top, on soil, Silva s/n (ACAM); 30/V/2011, RO2, top, on a patch of soil, Silva & Germano s/n (ACAM); <i>ibid.</i> side of the outcrop on a patch of soil s/n (ACAM).	Widely distributed	AL, AM, BA, CE, DF, ES, GO, MG, MT, PE, PB, PR, RJ, RR, RS, SC, SP	Turf	Generalist
* <i>Gemmabryum exile</i> (Dozy & Molck.) J.R. Spence & H.P. Ramsay	Phytologia 87(2): 67. 2005	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 30/V/2011, RO2, top, on a patch of soil, Silva & Germano s/n (ACAM).	Pantropical	BA, DF, ES, GO, PE, MS, RJ, RR, RS, SP	Turf	Generalist
* <i>Rosulabryum billardieri</i> (Schwagr.) J.R. Spence	Bryologist 99 (2): 223. 1996.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 12/III/2010, RO1, top, on soil, Silva s/n (ACAM).	Pantropical	AC, AM, BA, CE, DF, ES, GO, MA, MG, MS, MT, PA, PE, RJ, RO, SC, SP	Turf	Generalist
* <i>Rosulabryum capillare</i> (Hedw.) J.R. Spence	The Bryologist 99: 223. 1996.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 30/V/2011, RO2, top, on patches of soil, open environment, Silva & Germano s/n (ACAM).	Widely distributed	BA, CE, DF, ES, GO, MG, MT, PA, PE, PI, RJ, RO, SC, SP	Turf	Generalist
Calymperaceae (2/3)						
* <i>Calymperes lonchophyllum</i> Schwägr.	Suppl. 1 2: 333. pl. 98, 1816.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 30/V/2011, RO2, top, on shaded patches of soil, Silva & Germano s/n (ACAM).	Pantropical	AC, AL, AP, AM, BA, ES, GO, MA, MG, MS, MT, PA, PE, PR, RJ, RO, RR, SP, TO	Turf	Generalist
<i>Calymperes palisotii</i> Schwägr.	Suppl. 1 2: 334. pl. 98. 1816	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 30/V/2011, RO2, top, on branches and rock, Silva & Germano s/n (ACAM).	Widely distributed	AC, AL, AM, AP, BA, ES, GO, MA, MG, MS, MT, PA, PB, PE, PI, PR, RN, RJ, RO, RR, SE, SP, TO	Turf	Generalist
<i>Octoblepharum albidum</i> Hedw.	Sp. Musc. Frond. 50. 1801	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 26/III/2010, RO1, top, on a root, Silva s/n (ACAM); 30/V/2011, RO2, base, on a tree trunk, Silva & Germano s/n (ACAM).	Pantropical	AC, AL, AM, AP, BA, CE, DF, ES, GO, MA, MG, MS, MT, PA, PB, PE, PI, PR, TO, RJ, RN, RO, RS, SE, SC, SP	Turf	Generalist
Fabroniaceae (1/2)						
<i>Fabronia ciliaris</i> var. <i>polycarpa</i> (Hook.) W.R. Buck	Brittonia 35: 251. 1983.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, RO2, 30/V/2011, top, in a crevice near vascular vegetation, Silva & Germano s/n (ACAM).	Neotropical	AL, AM, BA, CE, PB, PE, MT, GO, DF, MS, MG, ES, SP, RJ, PR, SC, RS, SE	Mat	Generalist
*** <i>Fabronia ciliaris</i> var. <i>wrightii</i> (Sull. ex Sull. & Lesq.) Buck	Brittonia 35: 249. 1983.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, RO1, top, on shaded rock, Silva s/n (ACAM); 30/V/2011, RO2, top, on rock, soil and tree trunk, Silva & Germano s/n (ACAM).	Brazil	RJ	Mat	Generalist
Fissidentaceae (1/1)						
<i>Fissidens intromarginatus</i> (Hampe) Mitt.	Enum. Fissident. 14. 1869.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 23/IV/2010, RO1, top, Silva s/n (ACAM); 30/V/2011, RO2, top, shaded area, Silva & Germano s/n (ACAM).	Africa and the Americas	AC, BA, CE, ES, GO, MG, MS, MT, PA, PB, PR, RJ, RO, RS, SC, SP	Branching	Shade-tolerant

Continues

Table 1. Continuation.

DIVISION							
Family				Worldwide Distribution	Distribution in Brazil	Growth form	Synusia
Species	Publication	Material examined					
Helicophyllaceae (1/1)							
<i>Helicophyllum torquatum</i> (Hook.) Brid.	Bryologia Universa 2: 771. 1827.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 21/V/2010, RO1, top, on the posterior face of a shaded rock formation, Silva s/n (ACAM).		Neotropical	AL, AM, BA, CE, ES, GO, MG, MS, MT, PA, PB, PE, PI, PR, RJ, RS, SC, SP, TO	Weft	Light-demanding
Pottiaceae (1/1)							
<b>**Aschisma carniolicum</b> (Web & Mohr.) Lindb.	Utkast Eur. Bladmoss. 28. 1878	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 30/V/2011, RO2, base, on soil near agricultural activity, Silva & Germano s/n (ACAM).		Europe and Africa	BA, PE	Turf	Light-demanding
Sematophyllaceae (1/2)							
<i>Sematophyllum subpinatum</i> (Hedw.) Mitt., J. Linn. Soc.	Bot. 12: 494. 1869.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 30/V/2011, RO2, top, on tree trunk, Silva & Germano s/n (ACAM).		Pantropical	AC, AL, AM, AP, BA, CE, DE, ES, GO, MA, MG, MS, MT, PA, PB, PE, PR, RJ, RO, RR, RS, SC, SP, TO	Mat	Generalist
<i>Sematophyllum subsimplex</i> (Brid.) E. Britton	Bryologist 21: 28. 1918.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 30/V/2011, RO2, top, on branch, Silva & Germano s/n (ACAM).		Neotropical	AC, AM, AP, BA, CE, DE, ES, GO, MA, MG, MS, MT, PA, PB, PE, PI, PR, RJ, RO, RR, RS, SC, SE, SP, TO	Mat	Generalist
Stereophyllaceae (1/1)							
<i>Entodontopsis leucostega</i> (Brid.) W.R.Buck & Ireland	Nova Hedwigia 41: 103. 1985.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 23/IV/2010, RO1, top, at the base of a well-shaded tree trunk, Silva s/n (ACAM); 30/V/2011, RO2, top, on tree trunk, Silva & Germano s/n (ACAM).		Pantropical	AC, AM, BA, CE, DE, GO, MA, MG, MS, MT, PA, PB, PE, PI, RJ, RN, RO, SP, TO	Mat	Generalist
Marchantiophyta							
Cephaloziellaceae (1/1)							
<b>**Odontoschisma longiflorum</b> (Taylor) Steph.	Sp. Hepat.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 12/III/2010, RO1, top, on a well-shaded tree trunk, Silva s/n (ACAM); 30/V/2011, RO2, top, on tree trunk, rock, root and invertebrate, Silva & Germano s/n (ACAM).		Brazil	GO, MG, MT, PR, RJ, SP	Mat	Shade-tolerant
Frullaniaceae (1/4)							
<i>*Frullania dusenii</i> Steph.	Arquivos do Museu Nacional do Rio de Janeiro 13: 115. 1905.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 26/III/2010, RO1, base, on rock, Silva s/n (ACAM); 30/V/2011, RO2, top, on rock, Silva & Germano s/n (ACAM).		Brazil	AL, BA, ES, GO, MG, PE, RJ, RR, RS, SC, SE, SP	Mat	Light-demanding
<i>Frullania ericoides</i> (Nees ex Mart.) Mont.	Phytologia 57: 371. 1985.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 26/III/2010, RO1, base, on rock, Silva s/n (ACAM); 30/V/2011, RO2, top, on rock, Silva & Germano s/n (ACAM).		Widely distributed	AC, AL, AM, BA, CE, DE, ES, GO, MA, MG, MS, MT, PA, PB, PE, PR, RJ, RS, SC, SE, SP	Mat	Light-demanding

Continues

Table 1. Continuation.

DIVISION						
Family						
Species	Publication	Material examined	Worldwide Distribution	Distribution in Brazil	Growth form	Synusia
<i>Frullania gibbosa</i> Nees	Syn. Hepat. 411. 1847.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 26/III/2010, RO1, top, in crevices, Silva s/n (ACAM); 30/V/2011, RO2, base, on tree trunk, Silva & Germano s/n (ACAM).	Neotropical	AC, AM, BA, DF, ES, GO, MG, MS, MT, PA, PB, PE, RJ, RR, SC, SP	Mat	Light-demanding
<i>Frullania kunzei</i> (Lehm. & Lindenb.) Lehm. & Lindenb	Syn. Hepat. 449. 1845.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 12/III/2010, RO1, top, in crevices, Silva s/n (ACAM).	Neotropical	AC, AM, BA, CE, DF, ES, GO, MG, MT, PA, PB, PE, PR, RJ, RR, RS, SE, SP	Mat	Light-demanding
Lejeuneaceae (1/1)						
* <i>Acanthocoleus aberrans</i> var. <i>laevis</i> (Lindemb. E Gottsche) Gradst.	Flora Neotropica 62: 193. 1994.	<b>BRAZIL. Paraíba:</b> munic. Puxinanã, 30/V/2011, RO2, top, on tree trunk, Silva & Germano s/n (ACAM).	Neotropical	BA, DF, GO, MG, PR, RJ, RS, SC, SP	Mat	Light-demanding

AC – Acre; AL – Alagoas; AM – Amazonas; AP – Amapá; BA – Bahia; CE – Ceará; DF – Federal District of Brasília; ES – Espírito Santo; GO – Goiás; MA – Maranhão; MS – Mato Grosso do Sul; MT – Mato Grosso; MG – Minas Gerais; PA – Pará; PB – Paraíba; PE – Pernambuco; PI – Piauí; PR – Paraná; RJ – Rio de Janeiro; RN – Rio Grande do Norte; RO – Rondônia; RR – Roraima; RS – Rio Grande do Sul; SC – Santa Catarina; SE – Sergipe; SP – São Paulo; TO – Tocantins.

\*New record for Paraíba; \*\*New record for the northeast of Brazil; \*\*\*Species of rare occurrence for the country.

The UPGMA cluster analysis identified three principal clusters (RO1/RO2; CA1/CA2; and CR/RO3), with a cophenetic correlation of 0.98 (Fig. 1). The Sørensen similarity index ranged from 0.60 (between RO1 and RO2) to 0.00 (between RO3 and CA2). We found no significant similarity among the various areas of *caatinga* evaluated. This confirms the uniqueness of the rock formations. Among rocky outcrops within the *caatinga* biome, the relationship between the top of each outcrop and its surroundings is dependent on how similar the two zones are in terms of their flora (Gomes *et al.* 2011). The members of each cluster identified here were also within close geographical proximity of each other. Nevertheless, the only significant correlation (Sørensen similarity index > 0.5; Valentin 2000) was between RO1 and RO2. Further studies might elucidate the factors that best explain the similarity among communities of bryophytes on rocky outcrops.

It is noteworthy that little is known of the bryophyte flora in Paraíba. The few bryophyte studies of conducted in the state have focused on forest areas (Yano & Andrade-Lima 1987; Pôrto & Germano 2002; Lüth & Schafer-Verwimp 2004; Yano 2004), resulting in a lack of bryophyte studies in the *caatinga*. This explains also the high number of first records, which are mostly of bryophytes recorded extensively for other states in Brazil, except for *Fabronia ciliaris* var. *wrightii* (recorded only for Rio de Janeiro) and *Aschisma carniolicum* (recorded only for Bahia and Pernambuco), which are rare species for Brazil.

Most of the species identified in the present study were classified as neotropical or pantropical (28% each), although 19% were classified as widely distributed. Species unique to Brazil, collectively with species occurring in Africa and the

Americas, accounted for 10% of the total, whereas those occurring in Europe and the Americas accounted for only 5% (Tab. 1). This pattern of geographical distribution mirrors that commonly found in forest regions dominated by neotropical and pantropical species that generally occur in the Atlantic Forest ecosystem.

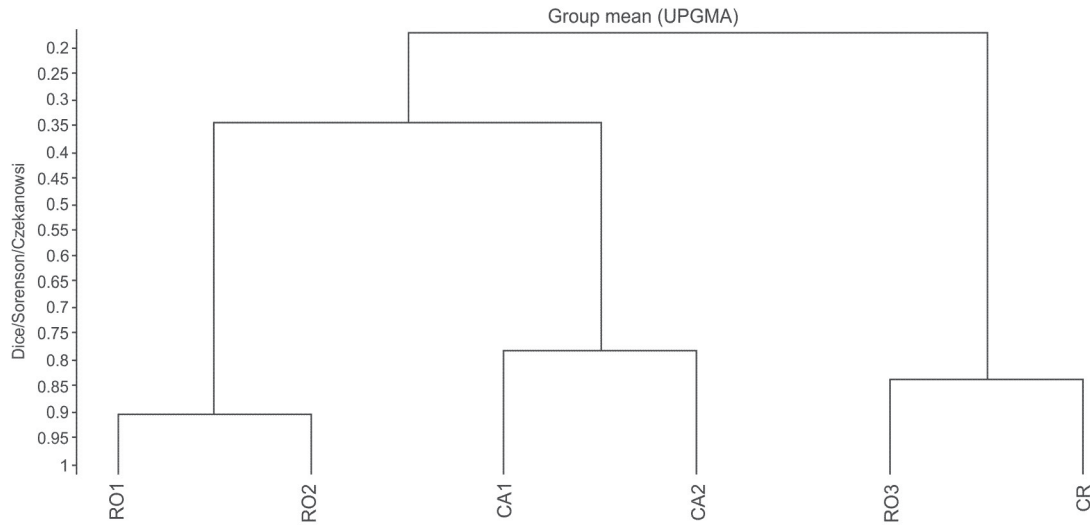
### Morphological attributes

We recorded three growth forms (Tab. 1): mat, turf and weft. The prevailing form was turf. In studies of lowland tropical forests, Costa (1999) and Montefort & Ek (1990) found that the aggregated forms, such as mat, weft and turf, were characteristic and were predominant in open areas, with high light intensity and air humidity, high. The liverworts showed the mat growth form.

The predominance of the turf growth form was expected, because that form is more desiccation tolerant (poikilohydric), facilitating the conduction of water to the surface (Watson 1914; Magdefraü 1982).

The rapid absorption and conduction of water through the aerial portions of their bodies make bryophytes excellent colonizers of environments such as rocky outcrops, given that, except in those with crevices or dense vegetation, the rainwater that falls on such environments drains to the rock below (Neves & Conceição 2007). Together with rapid evaporation (Willis 1934), this makes rocky outcrops environments that are deficient in water. The ability of bryophytes to absorb water and nutrients from rain, fog droplets and atmospheric dust make these plants specialists in nutritionally limited environments (Proctor 2008).





**Figure 1.** Cluster analysis, with the unweighted pair group method with arithmetic mean (UPGMA), of the rocky outcrops sampled and similar areas, in relation to the presence of bryophyte species. The cophenetic correlation was 0.8840. The exclusion of rare species (those occurring in only one area) resulted in the same cluster pattern (not shown), although with stronger clustering (cophenetic correlation of 0.9577). RO1 – rocky outcrop 1 (Puxinanã, Paraíba, Brazil); RO2 – rocky outcrop 2 (Puxinanã, Paraíba, Brazil); CA1 – *caatinga* area 1 (Agronomy Institute of Pernambuco Experimental Station at Caruaru, Pernambuco, Brazil); CA2 – *caatinga* area 2 (Agrestina, Pernambuco, Brazil); CR – *campos rupestres* (dry, rocky grasslands, Chapada Diamantina, Bahia, Brazil); RO3 – rocky outcrop 3 (Bahia, Brazil).

Bryophytes have developed several other attributes to resist the water stress inherent to rocky environments: leaf pattern, hairiness and characteristics specific to sporophytes (in the fertile species), as well as poikilohydry, which is a mechanism of defense against periods of drought (Porembski *et al.* 1997, 1998; Gignac 2001; Frahm 1996, 2004; Proctor 2008).

The leaf pattern seems to be especially crucial as an adaptive character. The species *Bryum argenteum*, *Rosulabryum billarderi* and *Acanthocoleus aberrans* var. *laevis* have an imbricate (overlapping) leaf pattern, whereas *Gemmabryum exile*, *Rosulabryum capillare*, *Helicophyllum torquatum* and *Aschisma carniolicum* have curled leaves. According to Watson (1914; 1933), curled and overlapping leaves are both excellent in dry environments, because they reduce the amount of water lost through transpiration.

*Entodontopsis leucostega* (Stereophyllaceae), as well as representatives of Sematophyllaceae and Fabroniaceae, present concave leaves, the adaxial surface of which is used for storing water, while the abaxial surface is used for gas exchange (Proctor 2008). This leaf pattern also facilitates the conduction of water to the surface (Frahm 2003). *Gemmabryum exile*, *Calymperes palisotii* Schwägr., *Fabronia ciliaris* var. *wrightii* and *F. ciliaris* var. *polycarpa* show the patent leaves, which decrease the absorption of light, resulting in less damage (Grebe 1913).

The liverworts display quadrate leaves, which protect themselves from desiccation by curling during times of drought and absorb water rapidly during rehydration (Watson 1914). In the present study, this pattern was seen in *Frullania ericoides* and *F. gibbosa*.

With the exception of the Sematophyllaceae species, a central strand was present in all of the mosses evaluated. According to Watson (1914), the enlargement of this structure, as seen in the Calymperaceae species cataloged, reduces the surface area available for water loss and compensates for photosynthesis by the presence of vertical lines of cells, thus adapting the plants to hostile climates.

Completing the set of traits that allow bryophytes to adapt to xeric environments are the mechanisms of storage, such as the separate lobes seen in Frullaniaceae and Lejeuneaceae (Thiers 1988; Frahm 2003), the hairy structures seen in *Helicophyllum torquatum*, the leaf borders seen in *Calymperes palisotii*, and the hyalocysts seen in Calymperaceae and Pottiaceae (Frahm 2000; 2003).

Evaluating reproduction, we observed low fertility rate in the samples collected. That might be a consequence of the habitat fragmentation caused by human activities on the outcrops studied in Puxinanã. In addition, in bryophytes adapted to xeric climates, reproduction peaks during milder (wetter) periods, because there is a considerable loss of metabolic power during periods of desiccation (Proctor 2008), which impedes reproduction, limiting dispersal and interspecific exchange.

In the present study, the only species found to present vegetative reproduction (gemmae) were *Calymperes palisotii* and *Odontoschisma longiflorum*. According to Magnusson (1983), species employing this type of reproduction are generally pioneers. Thiers (1988) argued that gemmae can arise from a lack of a spore dispersal mechanism. According to Gradstein & Pócs (1989), gemmae are excellent structures for dispersion over short distances, because they

are vegetative sprouts, providing an alternative mechanism for bryophytes that need to survive drought conditions (Proctor 2008).

In *Aschisma carniolicum*, the sessile sporophyte is protected by perichaetial leaves. The curvature and roughness of the capsule (both seen in *Bryum argenteum*) promote the full use of the capsular space without exposing the entire structure to desiccation (Watson, 1914; 1933). Grebe (1913) stated that the main sporophyte adaptation to xeric conditions (water storage and the prevention of transpiration) is seen in the sessile or capsule-down condition.

According to Patterson (1964), there are no structures effectively able to circumvent transpiration. Grebe (1913) and Frahm (2000) agree that some typical forest species have characters that can adapt them to xeric environments, suggesting that the characteristics are common and nonspecific.

### Conservation

According to the Red List of Threatened Bryophytes in Brazil published by the Biodiversitas Foundation (Biodiversitas 2005), which lists 17 species of mosses and liverworts, none of the species identified in the present study are classified as threatened.

The fact that the bryophytes recorded in this study have not appeared on the list of threatened species in Brazil or on the International Union for Conservation of Nature Red List of Threatened Species, both published in 2005, does not preclude the need for conservation studies. According Fife *et al.* (2010), many species of mosses and liverworts have, over the years, been excluded and included in the listings of endangered species within the same area.

It is known that rocky outcrops are refuges for species that suffer from grazing and human activities (Burke *et al.* 1998; Oliveira & Godoy 2007). At both of our study sites, we recorded species that are typical forest formations and not yet registered for the *caatinga* (Costa 2012): *Acanthocoleus aberrans* var. *laevis*; *Fabronia ciliaris* var. *wrightii*; and *Odontoschisma longiflorum*. That gives greater weight to such information and underscores the need for studies dealing with the conservation, evolution and biogeography of bryophytes in Brazil.

At both of our study sites, there is constant human activity, most recently at RO1. This explains the high proportion of generalist species at both sites (50.0% and 62.5% at RO1 and RO2, respectively). According to Alvarenga *et al.* (2010), such species are common in disturbed areas. In addition, exposed areas, such as rocky outcrops, favor the occurrence of light-demanding species at the expense of those that are shade-tolerant (Gradstein *et al.* 2001; Frahm 2003). In the present study, light-demanding species accounted for 41.6% and 31.25% of the species richness at RO1 and RO2, respectively. Among the species occurring at both study sites, only one (*Odontoschisma longiflorum*) was shade-tolerant. The recording of that species could indicate the refuge potential

of these ecological nooks, given the constant degradation of their surroundings. In addition, the recording of species typical of the *caatinga* can be explained by the uniqueness of the rocky outcrops.

Therefore, there is a need for additional floristic surveys of bryophytes in the state of Paraíba, which is rich in these formations. Including these environments in detailed studies could further the creation of conservation areas, as suggested by Burke (2003).

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