



## DISTRIBUTION, ECOLOGY AND REPRODUCTION OF BRYOPHYTES IN A PRESERVED REMNANT OF ATLANTIC FOREST IN SOUTH OF BAHIA, BRAZIL

*Luciana Carvalho dos Reis<sup>1</sup>\*, Hermeson Cassiano de Oliveira<sup>2</sup> & Kátia Cavalcanti Pôrto<sup>1</sup>*

<sup>1</sup> Universidade Federal de Pernambuco, Departamento de Botânica, Programa de Pós-Graduação em Biologia Vegetal, Rua Professor Moraes Rego, s/n. Cidade Universitária, CEP: 50.670-901, Recife, PE, Brasil.

<sup>2</sup> Universidade Estadual do Piauí, Campus Heróis do Jenipapo, Avenida Santo Antônio, s/n, CEP: 64280-000, Campo Maior, PI, Brasil.

E-mails: luciana\_cr@hotmail.com (corresponding author); hermeson123@gmail.com; kcncporto@gmail.com

**Abstract:** The continuous and intense process of habitat loss and fragmentation has reduced the Atlantic Forest to less than 12% of its original area, with 80% of the remaining fragments smaller than 50 ha and only 9% protected within conservation units. One of the largest Brazilian Atlantic Forest remnants is protected inside the Una Biological Reserve – REBIO Una and Una Wildlife Refuge – REVIS UNA (designated here as “Una Region”). Una Region has fundamental importance to many biological groups due to their endemic species, most of them threatened, but with regard to bryophytes in Una Region there are still knowledge gaps. We carried out a bryofloristic survey in Una Region and analyzed floristic, ecological and reproductive aspects of the bryoflora. Bark, leaf and decaying wood samples were collected within 15 10 x 10 m plots resulting in the identification of 140 species (95 liverworts and 45 mosses), including five new records for Bahia State and 11 for the Northeastern region of Brazil, one endangered (EN) species, and one species recently described. Richness estimators revealed high proportions of undetected species, varying according to substrate type. The bryoflora was dominated by life forms of intermediate desiccation tolerance and shade specialists. Asexual or sexual reproductive structures were observed in nearly 60% of the species. Our results indicate that Una Region plays a fundamental role in the maintenance of the taxonomic, functional and genetic diversity of bryophytes and in the conservation of this group not only in Bahia, but also in the Atlantic Forest.

**Keywords:** Diversity; Functional groups; Life forms; Light tolerance; Sexual forms.

### INTRODUCTION

The Atlantic Forest is the largest biosphere reserve designated by UNESCO and one of the priority regions for biodiversity conservation worldwide (Rodrigues *et al.* 2009). It originally covered an area of more than 130 million hectares along the Brazilian east coast, ca. 88% of which has been lost due to intense degradation, leaving forest remnants that mostly consist of small,

isolated, unprotected and, often, strongly altered fragments (Ribeiro *et al.* 2009). Nevertheless, this biome still harbors very high levels of biodiversity and endemism (Myers *et al.* 2000). Specifically for bryophytes, the Atlantic Forest represents the Brazilian biome with the greatest diversity of species and the third largest center of diversity in the Neotropical region (Gradstein & Costa 2003). It also has three potential distribution centers of bryophytes and the highest environmental

suitability for establishment and development of key species, that is, species considered bioindicators of environmental quality, endemic to the Atlantic Forest or endemic to Brazil (Silva *et al.* 2014).

Bryophytes are extremely sensitive to changes in environmental factors, such as light incidence and air humidity (Glime 2017a, 2017b) resulting from anthropic activities (Sporn *et al.* 2009). Some negative effects on bryophyte communities include loss of taxonomic diversity and replacement of less desiccation tolerant species with others more tolerant (Alvarenga *et al.* 2010), loss of functional diversity (Henriques *et al.* 2017, Souza *et al.* 2020), decreased sexual reproduction and increased asexual reproduction (Oliveira & Pôrto 2001, Maciel-Silva & Válio 2011). The fine ecological responses of these plants to environmental conditions make them useful ecological indicators of forest quality (Spitale *et al.* 2020).

Assuming that undisturbed habitats are necessary to maintain the diversity of bryophytes in the Atlantic Forest (Silva & Pôrto 2015), legally protected areas are expected to play a fundamental role in the conservation of this group (Brasil 2000). However, recent analyses have shown that only 27% of the total area potentially suitable for the occurrence of key species falls within protected areas established in this biome (Silva *et al.* 2014), which is considered less than adequate for efficient conservation of the group. The Una Biological Reserve (REBIO Una) and Una Wildlife Refuge (REVIS Una) are two of these few conservation units, which are superimposed and together they protect one of the largest remaining fragments of Atlantic forest (Ribeiro *et al.* 2009). The aforementioned conservation units are located in the central corridor of potential distribution of bryophytes (Silva *et al.* 2014), within the Bahia Center of Endemism (Galindo-Leal & Câmara 2003), and has a high biodiversity, including many species with some degree of threat or rarity (Fontoura & Santos 2010, Nemésio 2013). From this point on, we will designate the union of REBIO Una and REVIS Una as “Una Region”.

Despite the considerable body of knowledge on the biodiversity of Una Region, no bryological studies have been conducted in this fragment remnant. The information currently available

about bryophytes is restricted to data from few sporadic collections available in the Herbário Virtual da Flora e dos Fungos – HVFF (<https://incthvff.wixsite.com/inct-hvff>) and one paper reporting the rediscovery of a rare species from Brazil (Reis *et al.* 2020). Floristic surveys represent a supporting tool not only for taxonomic studies, but also for meta-analyses in ecology, biogeography, and evolutionary biology (Söderström *et al.* 2008). Considering the ecological relevance of Una Region for the biodiversity of the Atlantic Forest, we aimed to analyze floristic, ecological and reproductive aspects of the bryoflora of this conservation unit and surroundings. Data obtained may serve as a basis for assessing the environmental quality of the remaining forest.

## MATERIALS AND METHODS

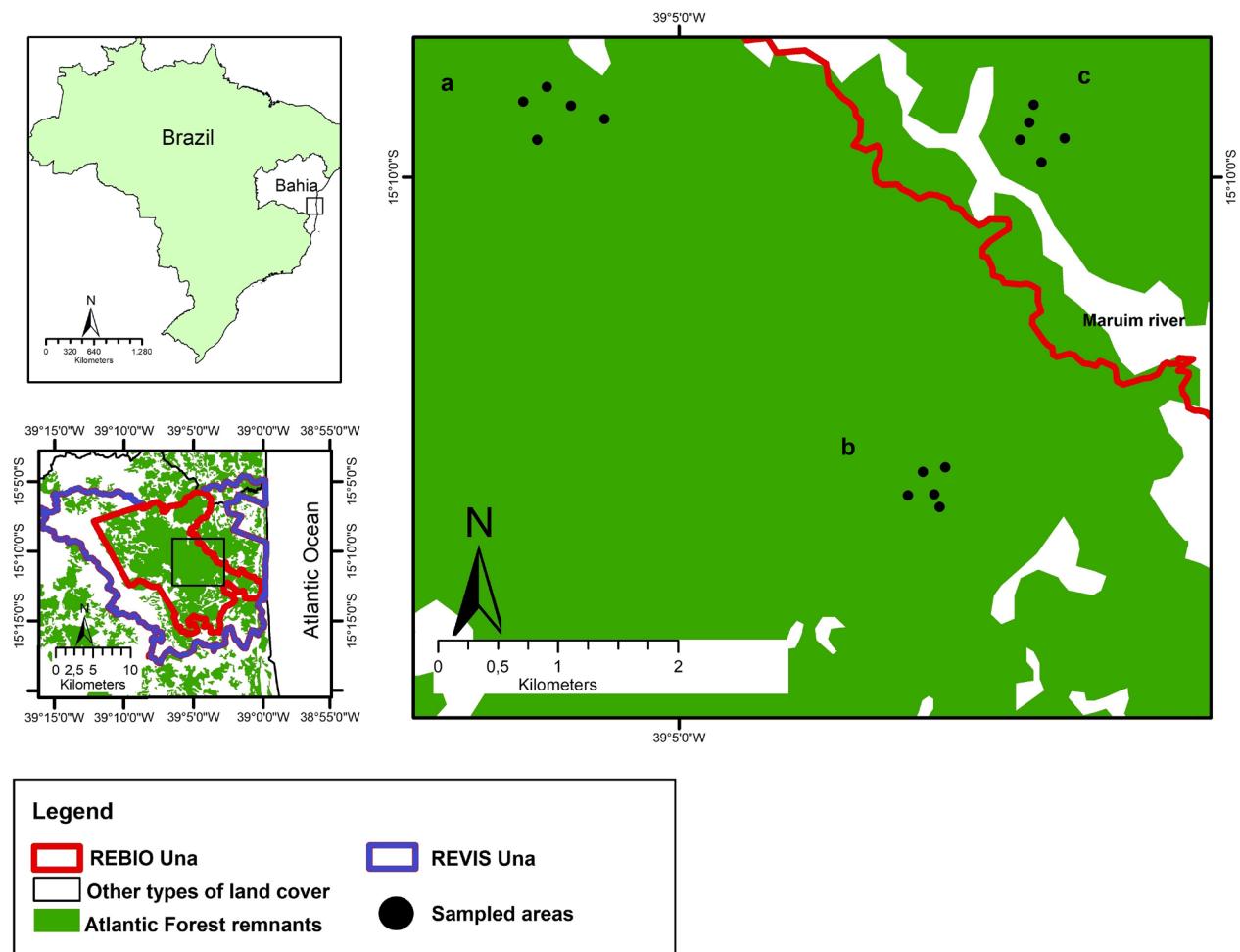
### *Study area*

The study was carried out in one large forest remnant inserted in the conservation units Biological Reserve – REBIO Una and Una Wildlife Refuge – REVIS UNA (designated in this study as “Una Region”), in the municipality of Una, Bahia, Brazil (14° 41’– 15° 22’ S and 39° 02’–39° 11’ W) (Figure 1). The REBIO Una is a conservation unit of integral protection inserted in the Atlantic Forest domain. The surroundings of the REBIO Una are part of the REVIS Una, and together constitute the Una Region with an area of 23,404 ha. The original vegetation in the region is classified as Tropical Lowland Rainforest and the average annual precipitation and temperature in the municipality of Una are approximately 1,300 mm and 24 °C, respectively (Thomas & Carvalho 2003). The altitude in the study area ranged from 12 to 107 m.a.s.l.

### *Sampling methods and checklist*

The floristic list of bryophytes from Una Region was produced based on data obtained during three field expeditions, lasting seven days each one, between September/2014 and January/2015, complemented with data from botanical collections available in the HVFF.

The samplings of bryophytes were performed on three types of substrates in the forest understory of Una Region: tree bark, leaves and decaying wood (corticicolous, epiphyllous



**Figure 1.** Location of sampling sites (a = “*Trilha 10 do macaco*”, b = “*Mata do Príncipe*”, and c = “*Ecoparque*”) in Una Region, southern Bahia, Brazil.

and epixyloous species, respectively). Bark was sampled from trees with diameter at breast height (DBH)  $\geq 5$  cm and leaves from shrubs and young trees within 15  $10 \times 10$  m plots. In this substrate, were collected bryophytes up to 2 m tall in the trunk of each shrub and tree sampled. The plots were located at least 100 m apart from each other. Decaying wood samples were collected along trails inside the forest, not limited to the plots.

Records referring to bryophyte collections carried out in the Una Region were searched in virtual collections available at the HVFF on July 10, 2020. In the SpLink tool, search form of the HVFF, we use the keywords “Reserva Biológica de Una; Rebio Una; Refúgio da Vida Silvestre de Una; Revis Una” in the field ‘busca livre’, and the keywords “Bahia” and “Una” in the fields ‘Estado’ and ‘Município’, respectively. We did not use the field ‘Filo’ due to the high frequency of records without information for this field in

virtual collections of bryophytes (Reis & Valente 2022). Carrying out searches for bryophyte data in the virtual collections with field “Filo” filled in can have the opposite effects of what was expected because records with empty in this field will not be returned in the search, causing an underestimation of obtained data (Reis *et al.* 2022).

As a result of our search we obtained one list containing 589 records corresponding to 332 species representatives of all plant groups already collected in the region of interest. We downloaded the data into an excel spreadsheet in which we proceed to the selection of the bryophyte species.

#### Treatment of material

Botanical identifications were based on specialized literature. The classification systems adopted follow Crandall-Stotler *et al.* (2009) for liverworts and Goffinet *et al.* (2009) for mosses.

The samples were deposited in the Geraldo Mariz Herbarium (UFP) of the Federal University of Pernambuco.

The geographic distribution of the species in the country was classified according to Valente & Pôrto (2006), as “restricted” in the case of species occurring in 1-4 states as, “moderate” in the case of those occurring in 5-9 states, and “wide” in the case of those occurring in 10 or more states. To determine the number of states in which each species occurred, we used information provided in the literature and in the Flora e Funga do Brasil (2022) database.

Bryophyte species were classified into two functional groups related to desiccation (life forms) and light tolerance (shade specialists, sun specialists and generalists). Information on light tolerance of each species was based on literature data (e.g. Acebey *et al.* 2003, Alvarenga *et al.* 2010, Oliveira *et al.* 2011) and the opinion of specialists. Life form classification was based on Bates (1998).

Information on sexual system was obtained from observations of the collected material and information available in the literature (e.g. Sharp *et al.* 1994, Gradstein & Ilkiu-Borges 2009). Each specimen was examined to check the presence of sexual (sporophytes and/or male and female gametangia) and asexual (e.g. gemmae, caducous leaves, fragmentation of leaves, specialized propagules) reproductive structures.

### Data analyses

Sample-based accumulation curves (100 permutations) were plotted for the species inventoried during the field expeditions in the area using the Coleman method (Coleman *et al.* 1982). In order to estimate substrate-specific differences in species detectability, accumulation curves were generated for the entire dataset and then for each of the three sampled substrate types. Species richness was estimated for the entire dataset and for substrate types using the nonparametric Chao estimator with standard error (Chao 1987) and the first-order Jackknife estimator (Gotelli & Colwell 2001). All analyses were carried out using R software (version 3.6.3) (2020).

## RESULTS

### **Floristics and geographic distribution**

A total number of 140 bryophyte species (95 liverworts and 45 mosses) belonging to 68 genera and 24 families were registered in Una Region, of which 132 species were collected in the area during the field expeditions and 8 were found only in virtual herbaria database (Table 1). The most diverse liverwort families were Lejeuneaceae (64 spp.) and Plagiochilaceae (8 spp.) and moss families were Calymperaceae (12 spp.) and Sematophyllaceae (6 spp.), together accounting for 64% of the bryoflora of the reserve.

Among the 140 species, 33 (23.6%) had a restricted geographic distribution, 34 (24.3%) had a moderate distribution, and 73 (52.1%) had a wide distribution in Brazil. Thirteen species were endemic to Brazil (ten liverworts and three mosses) (Table 1). Among the species with a restricted distribution, six are recorded only in the state of Bahia (*Drepanolejeunea pinnatiloba*, *Hypnella symphyodontoides*, *Lejeunea herminieri*, *Prionolejeunea trachyodes*, *Pseudotrichopus martinicensis* and *Pycnolejeunea porrectilobula*), and seven occur only in two states (*Lopholejeunea euplopha*, *Microlejeunea acutifolia*, *Micropterygium campanense*, *Plagiochila lamyana*, *Prionolejeunea muricato-serrulata*, *Rectolejeunea emarginuliflora* and *R. flageliformis*) (Table 1). Eleven species – nine liverworts (*Cololejeunea gracilis*, *Saccogynidium caldense*, *Leptolejeunea moniliata*, *Lopholejeunea euplopha*, *Microlejeunea acutifolia*, *Prionolejeunea muricato-serrulata*, *Bazzania cuneistipula*, *Plagiochila lamyana* and *Radula elliotii*) and two mosses (*Aerobryopsis capensis* and *Syrrhopodon incompletus* var. *luridus*) – are new records for the Northeast region of Brazil. Four liverworts (*Cololejeunea camillii*, *Cololejeunea gracilis*, *Harpalejeunea uncinata* and *Leptoscyphus porphyrius*) and one moss (*Schlottheimia tecta*) are new records for Bahia.

A total of 965 specimens of 132 species in 274 samples were found in the three types of substrates: 93 species were found as corticolous in 116 samples, 47 as epiphyllous in 132 samples, and 44 as epixyloous in 26 samples. Forty-nine species were found exclusively colonizing live trunks, 18 exclusively colonizing leaves, and 17 exclusively colonizing decaying wood.

**Table 1.** List of bryophyte species occurring in the understorey of Una Region with respective reproductive and ecological data, number of specimens (Records), geographic distribution, and reference. Type of reproduction: sexual (sex), asexual (asex), sexual and asexual (sex; asex), no reproduction observed (-). Light tolerance: generalist (gen), sun tolerant (sun), and shade tolerant (sh) species. Substrate: Decaying wood (DW), Leaf (Le) and Tree bark (T). Symbol: \* = Endemic to Brazil; 1 = New record for Bahia State; 2 = New record for Northeastern Brazil.

Phylo/Family/Species	Reproductive aspects			Ecological aspects			Geographic distribution	Records	Reference
	Sexual system	Strategy	Life form	Light tolerance	Substrate				
<b>Liverworts</b>									
Aneuraceae									
<i>Riccardia digitiloba (Spruce ex Steph.) Pagán</i>	M	Asex	Thalloid mat	Sun	DW	AC, AM, BA, CE, ES, MG, MT, MS, PE, RJ, SP	4	This study	
Frullaniaceae									
<i>Frullania apiculata (Reinw. et al.) Nees</i>	M	-	Weft	Sun	T/Le/DW	AM, BA, DE, GO, MS, PA, PE, RJ, SC, SP	3	This study	
<i>Frullania kunzei</i> (Lehm. & Lindenb.) Lehm. & Lindenb	M	-	Weft	Sun	Le	AC, AM, BA, CE, DE, ES, GO, MG, MT, PA, PB, PE, PR, RI, RR, RS, SC, SE, SP	1	This study	
Geocalycaceae									
<i>Leptoscyphus gibbosus</i> (Taylor) Mitt.	D	-	Weft	Sh	DW	BA, RJ, SP	1	This study	
<sup>1</sup> <i>Leptoscyphus porphyrius</i> (Nees) Grolle	D	-	Weft	Sh	DW	ES, MG, PA, PE, PR, RJ, SP	1	This study	
<sup>2</sup> <i>Saccogynidium caldense</i> (Angström) Grolle	D	-	Weft	Sun	T	MG, RJ, SP	1	This study	
Herbertaceae									
<i>Herbertus juniperoides</i> (Sw.) Grolle	D	-	Weft	Sh	DW	AM, BA, CE, ES, MG, PE, PR, RJ, RR, RS, SC, SP	1	This study	
Lejeuneaceae									
<i>Archilejeunea fuscescens</i> (Hampe ex Lehm.) Fulford	M	Sex	Mat	Gen	T/DW	AC, AL, AM, BA, ES, MG, PA, PE, RJ, RR	7	This study	
<i>Ceratolejeunea coarina</i> (Gottsche) Steph.	M	-	Weft	Gen	Le/DW	AC, AL, AM, AP, BA, MA, PA, PR, SE, SP	3	This study	

**Table 1.** Continues on next page...

Table 1. ...continued

Phylo/Family/Species	Reproductive aspects			Ecological aspects			Geographic distribution	Records	Reference
	Sexual system	Strategy	Life form	Light tolerance	Substrate				
<i>Ceratolejeunea cornuta</i> (Lindenb.) Schiffn.	D	-	Weft	Gen	T/le		AC, AM, AP, BA, CE, MG, PA, PE, PR, RJ, RO, RR, SC, SP	3	This study
<i>Ceratolejeunea cubensis</i> (Mont.) Schiffn.	M	Sex	Weft	Gen	T/DW		AC, AL, AM, AP, BA, CE, ES, PA, PB, PE, RJ, RO, SC, SP	17	This study
<i>Ceratolejeunea minuta</i> Dauphin	D	Sex	Weft	Gen	T/le		AM, BA, PA, PE BA, PA, RJ	21	This study
<i>D</i>	-	Mat	Gen	Le			AC, AL, AM, AP, BA, ES, MG, MT, PA, PE, PR, RN, RR, SC, SP	1	This study
<i>Ceratolejeunea minuta</i> Dauphin	D	Sex; Asex	Mat	Gen	T		AM, AL, BA, ES, MG, PE, RR, SP	4	This study
<i>*Cheilolejeunea adnata</i> var. <i>autoica</i> Gradst. & Ilk.-Borg.	M	Sex	Mat	Gen	T		AM, AL, BA, ES, MG, PE, PR, RJ, SP	5	This study
<i>Cheirolejeunea holostipa</i> (Spruce) Grolle & R.-L.Zhu	D	-	Weft	Gen	Le		AM, BA, ES, MG, PA, PE, PR, RJ, SP	4	This study
<i>*Cheilolejeunea rigidula</i> (Nees ex Mont.) R.M. Schust.	D	Sex; Asex	Weft	Gen	T/Le/DW		AC, AL, AM, AP, BA, CE, DE, ES, GO, MA, MG, MT, MS, PA, PB, PE, PR, RI, RR, RO, SC, SE, SP, TO	41	This study
<sup>1</sup> <i>Cololejeunea camillii</i> (Lehm.) A. Evans	M	-	Mat	Sh	Le		AL, AM, CE, DF, MG, PA, PE, RJ, SP	2	This study
<i>Cololejeunea contractiloba</i> A. Evans	M	-	Mat	Sh	Le		BA, AM, PA	6	This study
<sup>2</sup> <i>Cololejeunea gracilis</i> (Ast.) Pócs	M	-	Mat	Sh	Le		AM, ES, MG, MT, PA, RJ, SP	3	This study
<i>Cololejeunea obliqua</i> (Nees & Mont.) Schiffn.	M	Sex	Mat	Gen	Le		AC, AL, AM, BA, ES, PA, PE, PR, RI, SC, SP,	8	This study
<i>Cololejeunea diaphana</i> A. Evans	M	-	Mat	Sh	Le		AM, BA, ES, GO, MT, PA, PE, RI, RS, SC, SP	2	This study

Table 1. Continues on next page...

Table 1. ...continued

Phylo/Family/Species	Reproductive aspects			Ecological aspects			Geographic distribution	Records	Reference
	Sexual system	Strategy	Life form	Light tolerance	Substrate				
<i>Cololejeunea sicaefolia</i> (Gottsche) Pócs & Bermecker	M	-	Mat	Sh	DW	BA, PA, PE, PR, SC, SP	1	This study	
<i>Colura greig-smithii</i> Jovet-Ast	D	-	Weft	Sun	Le	AM, BA, MT, PE, SP	2	This study	
<i>Colura tortifolia</i> (Nees & Mont.) Steph.	D	Sex; Asex	Weft	Sun	Le	AC, BA, PA, PE, SP	4	This study	
<i>Cyclolejeunea convexisipa</i> (Lehm. & Lindenb.) A.Evans	D	Sex; Asex	Weft	Sh	T/Le	AL, AM, AP, BA, CE	73	This study	
<i>Cyclolejeunea luteola</i> (Spruce) Grolle	D	Asex	Weft	Sh	T	AM, BA, MG, MT, PA, PE, RI, RR, SP	3	This study	
<i>Diplasiolejeunea brunnea</i> Steph.	D	Sex	Mat	Sun	Le	AC, AL, AM, BA, CE, ES, MT, PA, RI, RO, SC, SP	17	This study	
<i>Diplasiolejeunea peltucida</i> (Meisn.) Schiffn.	M	Sex	Mat	Sh	T/Le	AM, BA, ES, MG, PA, PE, PR, RI, SC, SP	44	This study	
<i>Drepanolejeunea bidens</i> (Steph.) A.Evans	D	-	Mat	Sun	Le/DW	AL, AM, BA, MG, PE, RR, SP	2	This study	
<i>Drepanolejeunea crucianella</i> (Taylor) A.Evans	D	Sex	Mat	Gen	T/Le/DW	AM, BA, PA	23	This study	
<i>Drepanolejeunea fragilis</i> Bischl.	-	-	Mat	Gen	Le	AL, AM, AP, BA, CE, ES, MG, PA, PE, RI, RR, SP	1	This study	
<i>Drepanolejeunea mosenii</i> (Steph.) Bischl.	-	-	Mat	Gen	DW	AM, BA, ES, MG, PE, PR, RI, RR, SC, SP	1	This study	
<i>Drepanolejeunea pinnatiloba</i> Schiffn.	M	-	Mat	Sh	DW	BA	1	This study	
* <i>Harpalejeunea schiffneri</i> S.W. Arnell	D	-	Mat	Sun	Le	BA, ES, MG, MT, MS, PR, RI, SP	1	This study	
<sup>1</sup> <i>Harpalejeunea uncinata</i> Steph.	D	-	Mat	Sun	Le	PE, RI, SP	1	This study	
<i>Lejeunea acanthogona</i> var. <i>grossiretis</i> (Steph.) Grdast, & C.J. Bastos	M	-	Mat	Gen	T	BA, ES, SP	1	This study	
<i>Lejeunea aphanes</i> Spruce	M	Sex	Mat	Gen	T/Le	AL, BA, CE, ES, MS, SP	3	This study	
<i>Lejeunea boryana</i> Mont.	M	Sex	Mat	Gen	T	AC, AM, BA, CE, PA, RR	6	This study	

Table 1. Continues on next page...

Table 1. ...continued

Phylo/Family/Species	Reproductive aspects				Ecological aspects			Geographic distribution	Records	Reference
	Sexual system	Strategy	Life form	Light tolerance	Substrate					
<i>Lejeunea controversa</i> Gottsche	M	Sex	Mat	Gen	T/le	AC, AL, AM, BA, MS, PA, PE, RI, SP		7	This study	
<i>Lejeunea glaucescens</i> Gottsche	M	Sex	Mat	Gen	T	AC, AM, BA, CE, DE, ES, GO, MA, MG, MT, MS, PA, PE, PR, RR, RS, SC, SP		2	This study	
<i>Lejeunea herminieri</i> (Steph.) R.L. Zhu	M	-	Mat	-	T	BA	AM, BA, MG, PA, PR, SP	1	This study	
<i>Lejeunea parvula</i> (L.) Angstr.	D	Sex; Asex	Weft	Gen	T	AC, AL, AM, BA, CE, DE, ES, GO, MA, MG, MT, MS, PA, PE, RI, RN, SC, SP		5	This study	
<i>Lejeunea phyllobola</i> Nees & Mont.	M	Sex; Asex	Mat	Gen	T/le	MT, MS, PA, PE, RI, RN, SC, SP		27	This study	
<sup>1</sup> <i>Lejeunea subsessilis</i> Spruce	M	-	Mat	Gen	T	BA, MG, SC	AM, BA, ES, PA, PE, PR, RJ, RR, RO, SP	1	This study	
<i>Lepidolejeunea involuta</i> (Gottsch.) Grolle	M	Sex	Mat	Sh	T/le/DW	AC, AL, AM, AP, BA, CE, DE, ES, GO, MG, MT, PA, PE, PR, RI, RR, SC, SE, SP		11	This study	
<i>Leptolejeunea elliptica</i> (Lehm. & Lindenb.) Schiffn.	M	Sex	Mat	Sun	Le	PA, PE, PR, RI, RR, SC, SE, SP		23	This study	
<sup>2</sup> <i>Leptolejeunea moniliata</i> Steph.	M	-	Mat	Sun	T/le	AM, RJ	AM	2	This study	
<sup>2</sup> <i>Lopholejeunea euplopha</i> (Taylor) Schiffn.	M	Sex	Weft	Sun	T/DW	AC, AL, AM, BA, CE, DE, ES, GO, MA, MG, MT, MS, PA, PE, PR, RI, RR, SC, SP		7	This study	
<i>Lopholejeunea nigricans</i> (Lindenb.) Schiffn.	M	-	Weft	Sun	T	AC, AL, AM, AP, BA, CE, DE, ES, GO, MA, MG, MT, MS, PA, PE, PR, RI, RR, SC, SP		1	This study	
<i>Lopholejeunea subfusca</i> (Nees) Schiffn.	M	Sex	Weft	Sun	T/le/DW	PR, RI, RR, RO, SC, SE, SP, TO		11	This study	

Table 1. Continues on next page...

Table 1. ...continued

Phylo/Family/Species	Reproductive aspects			Ecological aspects			Geographic distribution	Records	Reference
	Sexual system	Strategy	Life form	Light tolerance	Substrate				
<i>Metalejeunea cucullata</i> (Reinw. et al.) Grolle	M D	Sex -	Mat Mat	Gen Sun	T/Le/DW T	BA, RJ, SP PA	18	This study	
<sup>2</sup> <i>Microlejeunea acutifolia</i> Steph.	M	-	Mat	Sun	T	AC, AM, BA, CE, DF, ES, GO, MA, MG, MT, MS, PE, PR, RJ, RN, RR, RS, SC, SE, SP	2	This study	
<i>Microlejeunea bullata</i> (Taylor) Steph.	M	-	Mat	Sun	T	AL, BA, CE, ES, GO, MA, MG, MS, PB, PE, RJ, SE, SP	3	This study	
<i>Microlejeunea epiphylla</i> Bischl.	D	Sex	Mat	Sun	T/Le	AM, BA, DF, ES, PA	18	This study	
<i>Neurolejeunea seminervis</i> (Spruce) Schiffn.	D	-	Weft	Sun	T/Le/DW	AM, BA, PA, BA	4	This study	
<i>Otigonirolejeunea huctumalensis</i> (Lindemb. & Gottsche) Y.M. Wei, R.I. Zhu & Gradst.	M	Sex	Mat	Gen	T	AM, PA, BA	2	This study	
<i>Prionolejeunea denticulata</i> (Weber) Schiffn.	M	Sex	Mat	Gen	T/DW	AM, BA, PA, PE, RJ, RR, SP	10	This study	
<sup>2</sup> <i>Prionolejeunea muricato-serrulata</i> (Spruce) Steph.	M	Sex	Mat	Sh	T/Le	PA	4	This study	
* <i>Prionolejeunea scaberula</i> (Spruce) Steph.	M	Sex	Mat	Sh	T	AM, BA, MA, SP	2	This study	
<i>Prionolejeunea trachynodes</i> (Spruce) Steph.	D	-	Mat	Sh	T	BA	6	This study	
<i>Pycnolejeunea contigua</i> (Nees) Grolle	M	-	Mat	Sun	T	AM, BA, CE, ES, MG, PA, PE, RR, RS, SC, SP	2	This study	
<i>Pycnolejeunea macroloba</i> (Nees e Mont.) Schiffn.	M	Sex	Mat	Sun	T/Le	AL, AM, BA, CE, ES, PA, PE, SP	10	This study	
* <i>Pycnolejeunea porrectilobula</i> Bastos & Vano Evans	M	Asex	Mat	Gen	Le	BA	12	This study	
<i>Rectolejeunea flagiformis</i> A. Evans	D	Asex	Mat	Gen	Le	BA, SP	1	This study	
					BA, PE	BA, PE	1	This study	

Table 1. Continues on next page...

Table 1. ...continued

Phylo/Family/Species	Reproductive aspects		Ecological aspects			Geographic distribution	Records	Reference
	Sexual system	Strategy	Life form	Light tolerance	Substrate			
<i>Schiffnerolejeunea polycarpa (Nees) Gradst</i>	M	-	Mat	Sun	T/DW	AC, AL, AM, BA, CE, DF, ES, GO, MG, MT, MS, PA, PB, PE, RJ, RO, RS, SC, SE, SP	3	This study
<i>Strictolejeunea squamata</i> (Willd. ex Weber) Schiffn.	D	Sex	Mat	Gen	T/DW	AC, AL, AM, AP, BA, ES, GO, MA, PA, PE, RJ, RS, SC, SP	8	This study
<i>Symbiezidium barbiflorum</i> (Lindenb. & Gottsche) A. Evans	M	Sex	Weft	Gen	T/Le	AC, AM, BA, ES, PA, PE, RJ, SC, SP	12	This study
<i>Thysananthus amazonicus</i> (Spruce) Schiffn.	M	Sex	Weft	Gen	T/Le	AC, AM, AP, BA, GO, MT	3	This study
<i>Xylolejeunea crenata</i> (Nees e Mont.) X.-L. He & Grolle	M	Sex	Mat	Sh	T/DW	AL, AM, AP, BA, ES, MA, MG, PA, PE, RJ, RO, RR, SC, SP	22	This study
Lepidoziaceae								
<sup>2</sup> <i>Bazzania cuneistipula</i> (Gottsche & Lindenb.) Trevis.	D	-	Mat	Sh	DW	MG, RJ, SP	1	This study
<i>Bazzania hookeri</i> (Lindenb.) Trevis	D	-	Mat	Sh	DW	AM, BA, ES, GO, MG, PR, RO, RS, SC, SP	1	This study
<i>Micropterygium campanense</i> Spruce ex Reimers	D	Sex	Mat	Sh	T/DW	BA, MG	18	This study
<i>Micropterygium trachyphyllum</i> Reimers	D	Mat	Sh	-	AM, BA, DF, MT, PA, RR	-		
<i>Telaranea diacantha</i> (Mont.) Engel & Merr.	M	Weft	Sh	DW	AC, AM, BA, DF, ES, GO, PA, PE, RJ, RS, SC, SP	1	This study	
<i>Telaranea nematodes</i> (Gottsche ex Austin) M.A. Howe	M	-	Weft	Sh	T	AC, AM, BA, CE, DF, ES, GO, MG, MT, MS, RJ, RR, RS, SC, SE, SP	3	This study
<i>Zoopsidella integrifolia</i> (Spruce) R.M.Schust.	D	-	Weft	Sun	DW	AM, BA, DF, GO, MG, MT, PA, SE, SP	2	This study

Table 1. Continues on next page...

Table 1. ...continued

Phylo/Family/Species	Reproductive aspects			Ecological aspects			Geographic distribution	Records	Reference
	Sexual system	Strategy	Life form	Light tolerance	Substrate				
<i>Lophocoleaceae</i>									
* <i>Cryptolophocolea martiana</i> (Nees) L.Soderstr. et al.	M	Sex	Weft	Gen	T	BA, SC, SE, SP	5	This study	
<sup>1</sup> <i>Lophocolea bidentata</i> (L.) Dumort	D	-	Weft	Sh	T	AC, AM, BA, CE, DF, ES, GO, MG, MS, MT, PE, PR, RJ, RR, RS, SC, SP	1	This study	
<i>Metzgeriaceae</i>									
* <i>Metzgeria bahiensis</i> Schiffn.	M	-	Thalloid mat	Sh	T	BA, RS, SP	2	This study	
<i>Plagiochilaceae</i>									
<i>Plagiochila aerea</i> Taylor	D	-	Fan	Sh	T	BA, PE, RJ	7	This study	
<i>Plagiochila disticha</i> (Lehm. & Lindenb.) Lindenb.	D	Asex	Fan	Sh	T	AC, AL, AM, AP, BA, CE, DF, ES, GO, MG, MT, MS, PA, PB, PE, PR, RJ, RR, SC, SE, SP	12	This study	
<sup>2</sup> <i>Plagiochila lamyana</i> Gradst. & D.P. Costa	D	-	Fan	Sh	-	RR	-	Virtual collection	
<i>Plagiochila montagnei</i> Nees	D	Assex	Fan	Sh	T	AC, AL, AM, AP, BA, CE, ES, MG, PA, PB, PE, PR, RJ, RS, SC, SP	3	This study	
<i>Plagiochila raddiana</i> Lindenb.	D	-	Fan	Sh	T	AC, AL, AM, AP, BA, CE, ES, GO, MG, MT, PA, PB, PE, PR, RJ, RS, SC, SP	1	This study	
<i>Plagiochila rutilans</i> Lindenb.	D	-	Fan	Sh	-	AC, AM, AP, BA, CE, ES, MT, PA, PE, PR, RJ, RO, RR, RS, SC, SP	-	Virtual collection	
<i>Plagiochila simplex</i> (Sw.) Lindenb.	D	-	Fan	Sh	T	AM, BA, ES, MG, MT, PA, PE, PR, RJ, RS, SC, SP	1	This study	

**Table 1.** Continues on next page...

Table 1. ...continued

Phyllo/Family/Species	Reproductive aspects		Ecological aspects			Geographic distribution	Records	Reference
	Sexual system	Strategy	Life form	Light tolerance	Substrate			
<i>Plagiochila subplana</i> Lindenb.	D		Fan	Sh	T/Ie	AM, AP, BA, ES, MG, MT, PA, PE, RI, RR, SC, SP	4	This study
<i>Radulaceae</i>								
<sup>2</sup> <i>Radula elliotii</i> Castle	D	-	Mat	Sh	T	PR, SP	1	This study
<i>Radula flaccida</i> Lindenb. & Gottsche	D	Sex; Asex	Mat	Sh	Le	AC, AL, AM, BA, ES, MG, PA, PE, RO, RR, SP	55	This study
<i>Radula javanica</i> Gottsche	D	Sex; Asex	Mat	Gen	T	AC, AM, AP, BA, CE, ES, GO, MG, MT, MS, PA, PE, PR, RI, RO, RS, SC, SP	20	This study
<i>Radula kegelii</i> Gottsche ex Steph.	D	Sex	Mat	Sh	T	AL, BA, PE, PR, RI, RS, SC, SP	7	This study
<i>Radula ligula</i> Steph.	D	-	Mat	Sh	T	AL, BA, PE, PR, RI, RS, SC, SP	1	This study
<sup>2</sup> <i>Radula mexicana</i> Lindenb. & Gottsche	D	-	Mat	Sh	T	BA, ES, MG, PA, PE, PR, RI, RS, SC, SP	1	This study
Mosses								
Brachytheciaceae								
<i>Meteoriidium remotifolium</i> (Muell.Hal.) Manuel	D	Sex	Pendant	Gen	T/Ie	BA, ES, GO, MG, MT, PB, PE, PR, RI, RR, RS, SC, SP	7	This study
<i>Pseudotrichypus martinicensis</i> (Broth.) W.R. Buck	D	-	Pendant	Sh	T	BA	1	This study
<i>Squamidium brasiliense</i> Broth.	-	-	Pendant	Sh	T	BA, ES, MG, PR, RI, RS, SC, SP	1	This study

Table 1. Continues on next page...

Table 1. ...continued

Phylo/Family/Species	Reproductive aspects		Ecological aspects			Geographic distribution	Records	Reference
	Sexual system	Strategy	Life form	Light tolerance	Substrate			
<b>Calymperaceae</b>								
<i>Calymperes afzelii</i> Sw.	D	Asex	Turf	Gen	T	AC, AM, BA, ES, MG, MT, MS, PA, PB, PE, RJ, RR, RO, SC, SP, TO	1	This study
<i>Calymperes lonchophyllum</i> Schwägr.	D	Asex	Turf	Gen	T	AC, AL, AM, AP, BA, ES, GO, MA, MG, MT, MS, PA, PE, PI, PR, RN, RJ, RR, RO, SE, SP, TO	27	This study; Virtual collection
<i>Calymperes platyloma</i> Mitt.	D	-	Turf	-	-	AM, AP, BA, PA	-	Virtual collection
<i>Octoblepharum albidum</i> Hedw.	M	-	Turf	Gen	T/DW	AC, AL, AM, AP, BA, CE, DF, ES, GO, MA, MG, MT, MS, PA, PB, PE, PI, PR, RN, RJ, RR, RO, RS, SC, SE, SP, TO	3	This study; Virtual collection
<i>Octoblepharum coeruleum</i> Mitt.	M	-	Turf	Gen	T	AC, AM, BA, CE, ES, GO, MG, MT, MS, PA, RJ, RR, RO, SP	9	This study
<i>Octoblepharum pulvinatum</i> (Dozy e Molk.) Mitt	M	-	Turf	Sh	T	AC, AL, AM, AP, BA, CE, ES, GO, MA, MG, MT, MS, PA, PE, RJ, RR, RO, SC, SE, SP, TO	4	This study; Virtual collection
<i>Syrrhopodon incompletus</i> Schwägr.	D	Asex	Turf	Sh	T/Le	AC, AM, AP, BA, DF, GO, MG, MT, MS, PA, PE, PR, RJ, RR, RO, SC, SP, TO	6	This study
<i>Syrrhopodon incompletus</i> var. <i>luridus</i> (Paris e Broth.) Florsch.	D	-	Turf	Sh	T	AM, PA, RR	2	This study
<i>Syrrhopodon leprieurii</i> Mont.	D	-	Turf	Sh	T	AC, AM, AP, BA, MT, PA, RO, RR	5	This study

Table 1. Continues on next page...

Table 1. ...continued

Phyllo/Family/Species	Reproductive aspects			Ecological aspects			Geographic distribution	Records	Reference
	Sexual system	Strategy	Life form	Light tolerance	Substrate				
<i>Syrrhopodon ligulatus</i> Mont.	D	-	Turf	Sh	T/DW	AC, AL, AM, AP, BA, DE, MG, MT, MS, PA, PE, RJ, RO, RR, SP	3	This study	
<i>Syrrhopodon parasiticus</i> (Brid.) Besch.	D	-	Turf	Sun	T/DW	AC, AM, BA, DF, ES, GO, MG, MT, MS, PA, PE, PR, RJ, RO, RR, SC, SP	2	This study	
* <i>Syrrhopodon prolifer</i> Schwägr.	D	Asex	Turf	Gen	T/Le/DW	AC, AL, AM, AP, BA, CE, DF, ES, GO, MG, MT, PA, PE, PI, PR, RJ, RO, RS, SC, SE, SP, TO	30	This study	
Dicranaceae									
<i>Campylopus filicifolius</i> (Hornschr.) Mitt.	PA	-	Turf	Sun	-	BA, CE, ES, MG, PE, PR, RJ, RR, RS, SC, SP	-	Virtual collection	
<i>Campylopus occultus</i> Mitt.	PA	-	Turf	Sun	-	AP, BA, DF, ES, GO, MA, MG, MT, MS, PA, PE, PR, RJ, RR, RS, SC, SP	-	Virtual collection	
<i>Campylopus trachylepharon</i> (Müll. Hal.) Mitt.	PA	-	Turf	Gen	-	AC, AM, BA, ES, GO, MG, MT, PE, PR, RI, RS, SC, SE, SP, TO	-	Virtual collection	
<i>Leucoloma cruegerianum</i> (Müll.Hal.) A.Jaeger	D	-	Turf	Gen	DW	AL, BA, ES, GO, MG, PE, PR, RI, SP	1	This study	
<i>Leucoloma serrulatum</i> Brid.	D	Asex	Turf	Sh	T/DW	AL, BA, DF, ES, MG, PE, PR, RI, SP	16	This study; Virtual collection	
Fissidentaceae									
<i>Fissidens asplenoides</i> Hedw.	M	Sex	Fan	Gen	T	BA, PB, MG, MT, PR, RJ, RS, SC, SP	7	This study	
<i>Fissidens radicans</i> Mont.	M	-	Weft	Gen	T	BA, DF, ES, MA, MG, PA, PB, SE, SP	1	This study	

Table 1. Continues on next page...

Table 1. ...continued

Phylo/Family/Species	Reproductive aspects		Ecological aspects			Geographic distribution	Records	Reference
	Sexual system	Strategy	Life form	Light tolerance	Substrate			
<b>Hypnaceae</b>								
<i>Isopytergium tenerum</i> (Sw.) Mitt.	M	Sex	Mat	Gen	T	AC, AM, AP, BA, CE, DF, ES, GO, MA, MG, MT, MS, PA, PB, PE, PI, PR, RJ, RR, RS, SC, SP, TO	1	This study
<b>Leucobryaceae</b>								
<i>Leucobryum albicans</i> (Schwägr.) Lindb.	PA	-	Turf	Sh	-	BA, CE, DF, ES, MG, MT, PA, PE, PR, RI, RS, SC, SP	-	Virtual collection
<i>Leucobryum crispum</i> Müll. Hal.	PA	-	Turf	Sh	-	AM, AP, BA, CE, DF, ES, GO, MG, MT, PA, PR, RI, RO, RR, RS, SC, SP, TO	-	Virtual collection
<i>Leucobryum marinum</i> (Hornsch.) Hampe ex Müll. Hal.	D	-	Turf	Sh	T	AC, AL, AM, AP, BA, CE, DE, ES, GO, MA, MG, MT, MS, PA, PE, PR, RI, RR, RO, RS, SC, SE, SP, TO	6	This study; Virtual collection
<i>Ochrobdryum gardneri</i> (Müll.Hal.) Lindb.	D	Asex	Turf	Sun	T/DW	AL, AM, AP, BA, CE, DF, ES, GO, MG, MT, MS, PA, PE, RI, RO, SC, SE, SP, TO	16	This study
<b>Meteoriaceae</b>								
<sup>2</sup> <i>Aerobryopsis capensis</i> (Müll.Hal.) M.Fleisch.	M	-	Mat	Sh	T	MG, RI, RS, SP	2	This study
<b>Neckeraceae</b>								
<i>Homaliodendron piniforme</i> (Brid.) Emroth	D	-	Dendroid	Sh	T	BA, PE, RI, RS, SC, SP	3	This study
<i>Porotrichum substriatum</i> (Hampe) Mitt.	M	-	Weft	Sh	T/Le	AC, AL, AM, BA, MG, MT, PA, PE, RO, RI, RR, RS, SC, SP	2	This study

Table 1. Continues on next page...

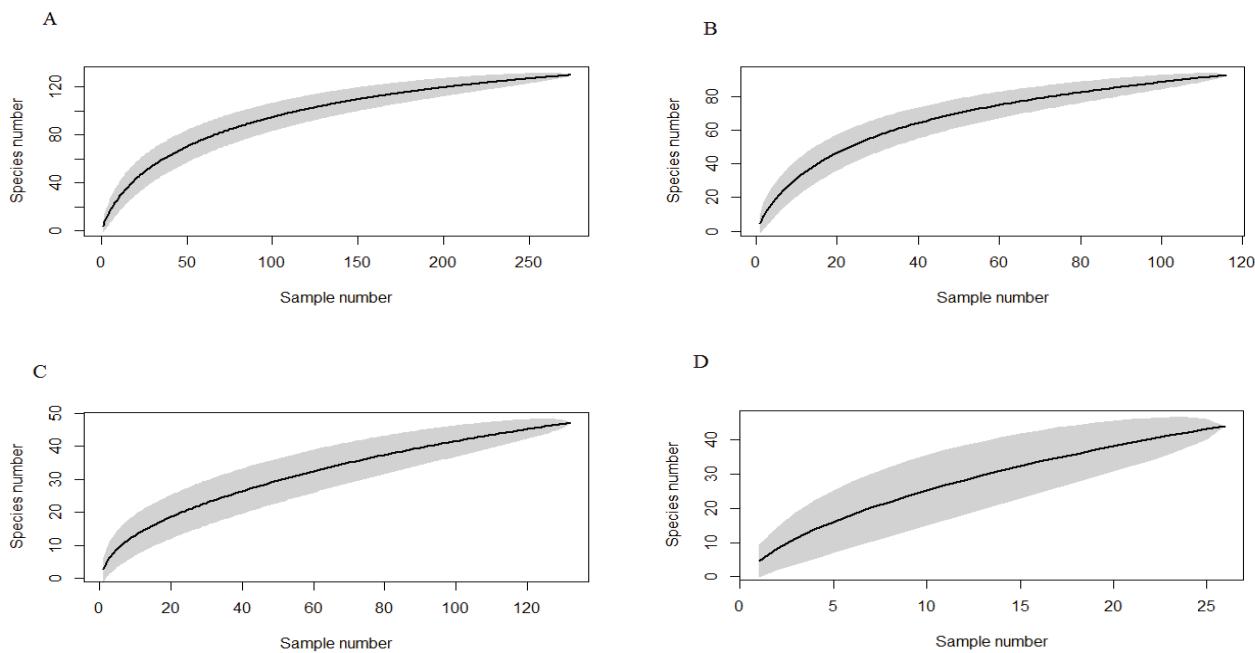
Table 1. ...continued

Phylo/Family/Species	Reproductive aspects			Ecological aspects			Geographic distribution	Records	Reference
	Sexual system	Strategy	Life form	Light tolerance	Substrate				
<b>Orthotrichaceae</b>									
<i>Schlottheimia rugifolia</i> (Hook.) Schwägr.	PA	-	Turf	Sun	DW		AC, AM, BA, CE, DE, ES, GO, MG, MT, MS, PA, PE, PR, RJ, RO, RS, SC, SP	1	This study
<i>Schlottheimia recta</i> Hook. f. & Wilson	PA	-	Turf	Sun	DW		CE, ES, MG, PR, RJ, RS, SC, SP	1	This study
<b>Phyllogoniaceae</b>									
<i>Phyllogonium viride</i> Brid.	D	-	Pendant	Sh	T		AL, BA, CE, ES, MG, MT, PE, PR, RJ, RS, SC, SP	1	This study
<b>Pilotrichaceae</b>									
<i>Callicostella pallida</i> (Hornsch.) Angstr.	M	Sex	Weft	Gen	T/DW		AC, AL, AM, AP, BA, CE, DE, ES, GO, MG, MT, MS, PA, PE, PR, RN, RJ, RR, RO, RS, SC, SE, SP, TO	4	This study
<i>Crossomitrium patrisiae</i> (Brid.) Müll. Hal.	D	-	Weft	Gen	T/Le		AC, AL, AM, BA, CE, PA, PE, PR, RO, RJ, RR, SC, SP	3	This study
<i>Pilotrichum bipinnatum</i> (Schwägr.) Brid.	M	Sex	Dendroid	Sh	T		AC, AL, AM, BA, MA, MG, PA, RJ, RO, RR, SP	3	This study
<b>Pterobryaceae</b>									
* <i>Hypnella symphyodontoides</i> S. Vilas Bôas-Bastos	M	Sex	Mat	-	DW		BA	4	This study
<i>Jaegerina scariosa</i> (Lorentz) Arzeni	D	-	Fan	Gen	T		AC, AL, AM, BA, CE, DF, ES, GO, MG, MT, MS, PA, PE, PR, RJ, RR, RO, RS, SC, TO	1	This study

Table 1. Continues on next page...

Table 1. ...continued

Phylo/Family/Species	Reproductive aspects		Ecological aspects			Geographic distribution	Records	Reference
	Sexual system	Strategy	Life form	Light tolerance	Substrate			
Sematophyllaceae								
<i>Brittonodoxa subspinata</i> (Brid.) W.R. Buck P.E.A.S. Câmara & Cary.-Silva	M	-	Mat	Gen	T/Le	AC, AM, AP, BA, CE, DF, ES, GO, MG, MT, PA, PB, PE, PI, PR, RJ, RR, RO, RS, SC, SP	2	This study
* <i>Microcalpe subsimplex</i> (Hedw.) W.R. Buck	M	Sex	Mat	Gen	T/DW	AC, AL, AM, AP, BA, CE, DF, ES, GO, MA, MG, MT, MS, PA, PE, PI, PR, RI, RO, RR, RS, SC, SE, SP, TO	40	This study; Virtual collection
<i>Sematophyllum swartzii</i> (Schwägr.) W.H.Welch & H.A.Crum	M	-	Mat	Gen	-	BA, DF, ES, MG, RJ, RS, SC, SP	-	Virtual collection
<i>Taxithelium planum</i> (Brid.) Mitt.	M	Sex	Mat	Gen	T/DW	AC, AL, AM, AP, BA, ES, GO, MA, MG, MT, PA, PB, PE, PR, RJ, RO, RR, SC, SP, TO	18	This study
<i>Taxithelium pluripunctatum</i> (Renauld & Cardot) Broth.	M	-	Mat	Sun	DW	AM, BA, PA, PE, RR	1	This study
<i>Trichosteleum papillosum</i> (Hornschr.) A.Jaeger	M	Sex	Mat	Gen	T/DW	AC, AM, AP, BA, ES, GO, MG, MT, PA, PE, RO, RJ, RR, SE, SC, SP	19	This study
Stereophyllaceae								
<i>Pilosium chlorophyllum</i> (Hornschr.) Müll.Hal.	M	-	Weft	Gen	-	AC, AL, AM, AP, BA, DF, ES, GO, MG, MT, MS, PA, PE, RO, RJ, RR, SP, TO	-	Virtual collection



**Figure 2.** Species accumulation curves (Coleman method) for the entire dataset (A) and the corticicolous (B), epiphyllous (C), and epixyloous (D) assemblages in Una Region. Gray shades represent confidence intervals.

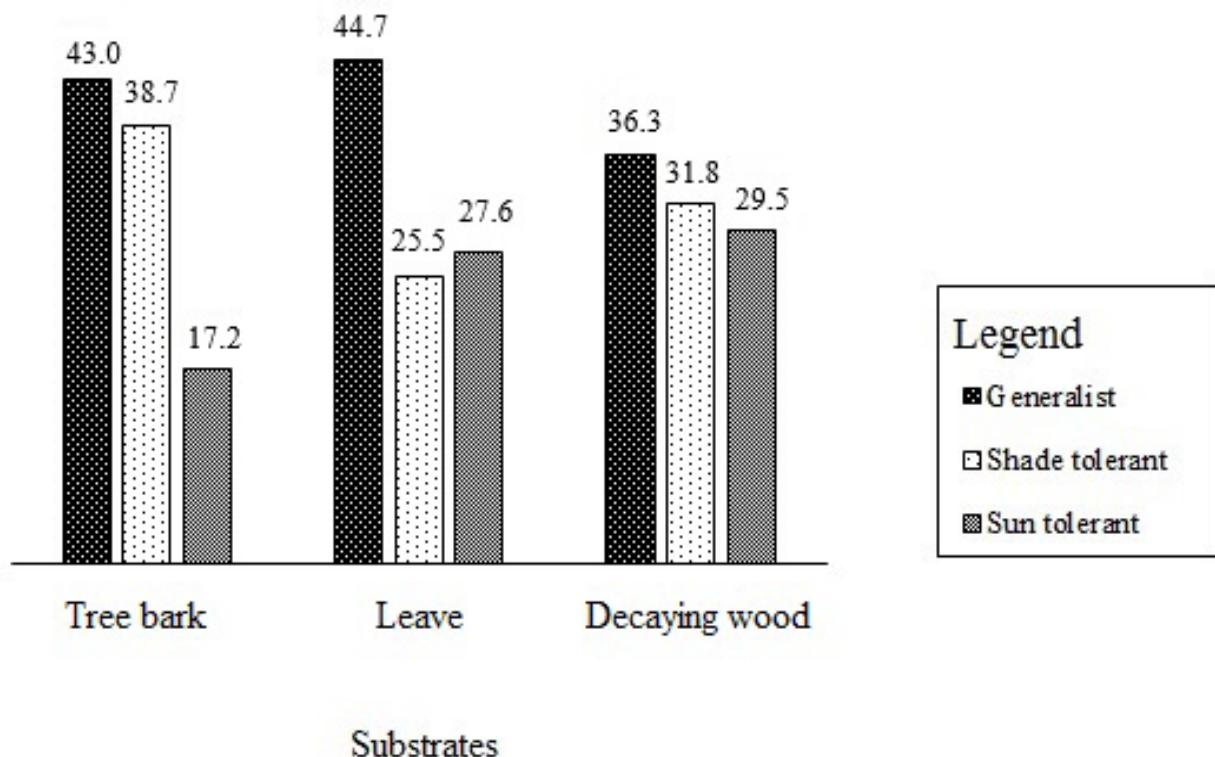
Considering the entire dataset resulting from the material collected at Una Region, 57 species (43.8%) were singletons (*sensu* Chao 1987), recorded once (38 spp.) or twice (19 spp.). Rarefaction curves showed that species richness was closer to saturation in the analysis of the entire dataset (Figure 2A) and of the corticicolous species (Figure 2B). In turn, rarefaction curves of the epiphyllous (Figure 2C) and epixyloous (Figure 2D) assemblages showed a strong upward trend and did not approach saturation. The richness estimators showed considerably greater estimated than observed richness for all sampled substrates (Table 2). The proportion of undetected species varied according to substrate type: decaying wood (52.4% – 78.6%), tree bark (30.9% – 44.8%), and leaves (42.2%).

### Ecological aspects

Seven different life forms were identified in Una Region: dendroid, fan, mat (including the thalloid mat variation), pendant, turf and weft. About 72.3% of the 140 bryophyte species had life forms displaying intermediate desiccation tolerance (mat and weft), 16.3% desiccation tolerant life forms (turf), and 11.3% drought-sensitive life forms (dendroid, fan and pendant). In terms of light tolerance, there was a balance between the number of shade specialist and generalist species (54 spp. And 52 spp., 38% and 37%, respectively), but the latter stood out in terms of abundance (445 vs. 358 specimens). Thirty-two species (23%), represented by 157 specimens, were classified as sun specialists (Table 1). The shade tolerant species colonized mainly tree barks, while sun

**Table 2.** Species richness estimation for the entire dataset and each substrate type according to the nonparametric Chao and first-order Jackknife estimators.

	Total	Corticicolous	Epiphyllous	Epixyloous
Species pool	130	93	47	44
Chao Index	156.50	134.68	66.84	78.61
First order Jackknife	162.88	121.75	66.84	67.07
Sample number (n)	274	116	132	26



**Figure 3.** Percentage of species belonging to functional groups of light tolerance in Una Region according to type of substrate.

tolerant species were more frequent in decaying wood and leaves (Figure 3).

#### ***Sexual systems and reproductive strategies***

Seventy-three (51.8%) species had a dioicous sexual system, among which seven are classified as pseudautoicous (i.e. dioicous species with dwarf males growing on the leaves of female plants), and 65 (46%) had a monoicous system. The sexual system was not identified in two species.

Approximately 60% of the species presented asexual or sexual reproductive structures. Sexual reproduction was observed in 49.2% of the monoicous and 24.2% of the dioicous species. Asexual reproduction was observed in only 1.5% of the monoicous species and in almost 50% of the dioicous species that also presented sexual reproduction; 15.2% of the dioicous species presented only asexual reproduction (Figure 4). Considering the total number of specimens, 518 (53.7%) were dioicous and 444 (46%) monoicous. The presence of reproductive structures (sexual, asexual or both) was observed in 81.5% of the

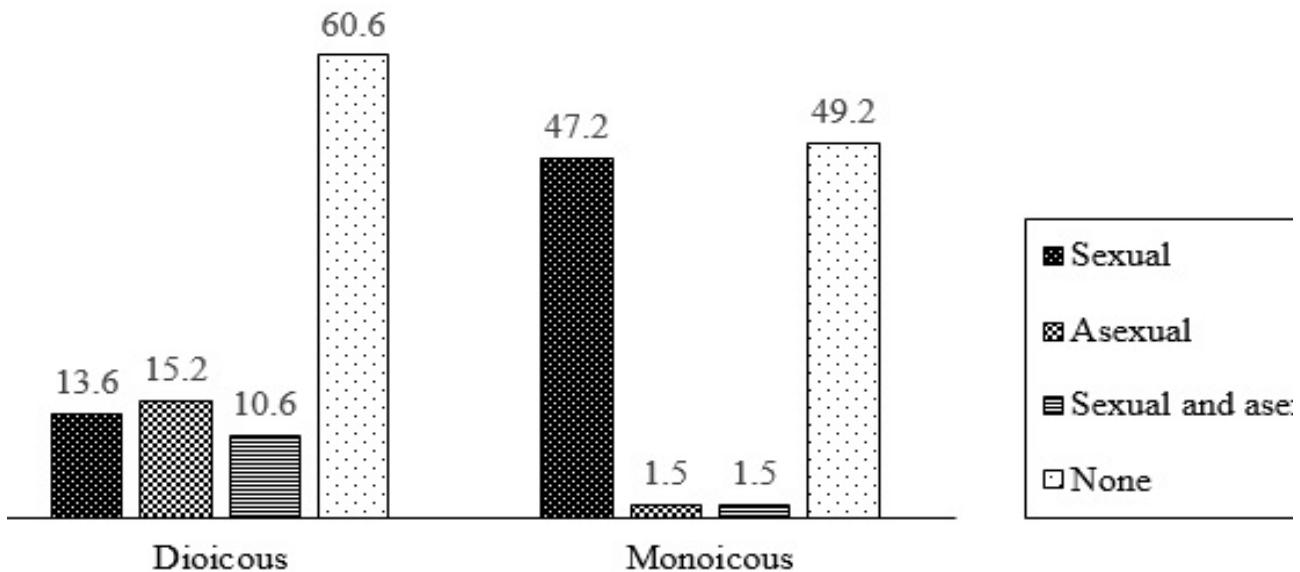
dioicous and 75% of the monoicous specimens (Table 1).

## **DISCUSSION**

#### ***Floristics and geographic distribution***

The present study revealed the greatest diversity of bryophytes in the Una Region, which corresponds to ca. 19.8% of the total richness described for the northeastern Atlantic Forest (Flora e Funga do Brasil 2022) and evidences the importance of forest remnant in this region for the bryophyte diversity in this phytogeographic domain. The dominance of liverworts was due to the high number of Lejeuneaceae species, the most representative family in lowland Tropical Forests (Cornelissen & Gradstein 1990). This family, together with Plagiochilaceae, comprise the most diverse pantropical families of liverworts in terms of number of species (Gradstein *et al.* 2001).

Most of bryophyte species reported for Una Region are widely distributed throughout Brazil, but there were also species with restricted distribution cited only for the Northern region



**Figure 4.** Occurrence (%) of sexual and asexual reproduction in bryophytes according to sexual system.

(Amapá, Amazônia, Pará and Roraima) and to the state of Bahia, indicating a disjunct distribution between the Atlantic and the Amazon Forests (Batista *et al.* 2018). Also noteworthy is the occurrence of thirteen species considered endemic to Brazil. Other three species have been rarely found in other floristic surveys carried out in the northeastern Atlantic Forest: *Plagiochila lamyana*, *Drepanolejeunea pinnatiloba* and *Syrrhopodon leprieurii*.

*Plagiochila lamyana* is a species recently described by Gradstein & Costa (2018) from the Mount Roraima National Park, Roraima State, Northern Brazil, occurring as corticolous on trunk bases and restricted to areas with high air humidity as summit areas. *Drepanolejeunea pinnatiloba* is described in the literature as exclusive species of preserved native old-growth Tropical Forests. This species presents highly restricted distribution in Brazil, with very small population sizes and Endangered (EN) conservation status (Reis *et al.* 2020). *Syrrhopodon leprieurii*, in turn, although it has moderate distribution in Brazil it occurs more frequently in the Amazon Forest and southeastern Atlantic Forest, according to data available on the HVFF. For the Atlantic Forest, data available on the SpeciesLink platform show only two old records of *S. leprieurii* from the northeastern portion of the biome (1978 and 2005 yr). Valente *et al.* (2013) mention the occurrence of *S. leprieurii* in the

vegetation of rupestrian fields and lower montane fields in the Chapada Diamantina region, but these authors used information from specimens previously collected in the region and deposited in herbaria (secondary data).

The occurrence of the above mentioned species shows that the forest in Una Region may have an important role for the maintenance of the diversity of bryophytes in the Atlantic Forest, because despite the significant increase in bryofloristic studies carried out in this biome over the last decades, including protected areas (e.g. Alvarenga *et al.* 2008, 2010, Bastos & Valente 2008, Evangelista *et al.* 2019, Reis *et al.* 2015, Valente & Pôrto 2006), this species had not been recollected for at least fifteen years until now.

Although corticolous species predominated in Una Region, it is important to highlight the considerable representativeness of the epiphyllous assemblage. Species that colonize living leaves have peculiar characteristics, occurring only in conditions of high air humidity, and are extremely vulnerable to any structural alteration of the forest (Richards 1984). Although the richness observed in this study can be considered high for lowland forests, richness estimators showed high percentages of undetected species in the entire dataset and in the three sampled substrates. The literature shows that the highly ephemeral nature of leaves as substrates can decrease the detectability of

epiphyllous assemblages in the habitat (Sierra *et al.* 2018). Epixyloous assemblages are considered very diverse, but there is a strong turnover of species following the process of decomposition of trunks (Sastre-De Jésus 1992) and few species occur exclusively on this substrate (Richards 1984).

### **Ecological aspects**

Our results suggest that the forest in Una Region has favorable environmental conditions for the maintenance of a highly rich and diverse bryoflora. In tropical forests, drought-sensitive life forms (dendroid, fan and pendant) are significantly associated with shaded and humid conditions typical of forest interior sites, while drought-tolerant forms (turf) are more related to sun-exposed and arid conditions like those in forest edges (Oishi 2009). Life forms exhibiting intermediate desiccation tolerance (mat and weft) present mechanisms of attachment to the substrate that protect their leaves against impacts caused by external factors such as strong winds (Bates 1998), and are often predominant in bryophyte communities from lowland tropical forests (Oliveira & Oliveira 2017).

The similar proportions of generalists and shade specialists suggest that the environmental conditions in the area of Una Region allow the more ecologically demanding species to compete for niche with generalist species. Shade specialists are strongly demanding of specific micro-environmental conditions for the growth and establishment of populations (Gradstein *et al.* 2001, Brito & Ilkiu-Borges 2014). Contrary to our finding, other studies have often reported an imbalance in the proportions of these two functional groups, with a predominance of generalist species over shade specialists (Silva & Pôrto 2010, Oliveira *et al.* 2011). The lower representation of sun specialists in our study area was expected because the increase of these species in the understory is normally associated with forest degradation (Alvarenga *et al.* 2010), which is not the case of the sampled forest in Una Region.

### **Sexual systems and reproductive strategies**

Reproduction among bryophytes in Una Region was frequent, with ca. 60% of the species showing reproductive strategies. High sexual reproductive

success rates (sporophyte production) were observed in the monoicous assemblage, which was expected in view of the possibility of self-fertilization in these taxa (Bisang & Hedenäs 2005). The dioicous assemblage also showed expressive rates of sporophyte production in addition to a high incidence of asexual reproduction. Dioicous species showing simultaneous asexual and sexual reproduction (*e.g.* *Cyclolejeunea convexistipa*, *Radula flaccida* and *Cheilolejeunea rigidula*) were among the most abundant in Una Region. It is possible that the occurrence of large populations and extensive colonized surface areas promoted by asexual reproduction (Frey & Kürchner 2011) are decreasing the distance between female and male plants and thus increasing the mating chances and, consequently, sexual reproduction in our study area. This hypothesis, however, was not tested.

The knowledge about the reproductive strategies used by bryophyte species can be useful to support conservation strategies for the group, because different reproductive modes can promote distinct ecological patterns and bring different evolutionary consequences for the species: while high out-crossing rates and levels of genetic variation are expected among dioicous species, self-fertilization and low genetic variation is common among monoicous taxa (Longton & Schuster 1983).

## **CONCLUSION**

The floristic, ecological and reproductive aspects identified in this study provide information for understanding the distribution and maintenance of bryophytes in an important area of Atlantic Forest. The general patterns found in the study, such as the significant proportion of shade specialists and species with intermediate tolerance to desiccation, and the high frequency of sexual reproduction, especially among dioicous species, reflect the influence of the humid conditions in Una Region. More preserved remnants present better physiognomic structure, with taller trees and a homogeneous canopy, allowing the maintenance of more stable microclimatic conditions (temperature and humidity) and, thus, a rich bryoflora.

The presence of endemic species, one

endangered species, one recently described species, and taxa with disjunct distribution between the Atlantic and the Amazon forests indicate the biological relevance of Una Region for the conservation of bryophytes in the Atlantic Forest and the need to protect both conservation units. Furthermore, the eleven species newly recorded from the Northeastern region of Brazil and the five newly reported for the state of Bahia, as well as the high proportion of undetected species indicated by richness estimators reinforce the need for more research on the bryoflora of this region and of other insufficiently sampled forest remnants of Atlantic Forest.

In summary, our results indicate that the forest in Una Region plays a fundamental role for the taxonomic, functional and genetic diversity and conservation of bryophytes not only from Bahia, but also from the Atlantic Forest. Since the studied forest are preserved areas, permanently protected from local anthropogenic disturbance, we suggest that the patterns observed there can be used as a “reference” in studies on the effects of habitat disturbance on taxonomic, ecological and reproductive aspects of bryophyte species in the Atlantic Forest.

## ACKNOWLEDGMENTS

The authors thank the Fundação de Amparo à Ciência e à Tecnologia do Estado de Pernambuco (FACEPE) for PhD fellowship to the first author; the Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB) for financing the Project PAM 0003/2013; INCT – Herbário Virtual da Flora e dos Fungos - for financial support; the management team of REBIO Una for the logistic support; Maxwell Silveira, Robson Oliveira and Rafael Santos for the help in the field work; and Dr. Anna Luiza Ilkiu Borges and Dr. Juçara Bordin for confirming the identification of some species.

## REFERENCES

- Acebey, A., Gradstein, S. R., & Krömer, T. 2003. Species richness and habitat diversification of bryophytes in submontane rainforest and fallows of Bolivia. *Journal of Tropical Ecology*, 19, 9–18. DOI: 10.1017/S026646740300302X
- Alvarenga, L. D. P., Oliveira, J. R. P. M., Silva, M. P., Costa, S. O., & Pôrto, K. C. 2008. Liverworts of Alagoas State, Brazil. *Acta Botanica Brasilica*, 22, 878–890. DOI: 10.1590/S0102-33062008000300023
- Alvarenga, L. D. P., Pôrto, K. C., & Oliveira, J. R. P. M. 2010. Habitat loss effects on spatial distribution of epiphytic bryophytes in a Brazilian Atlantic forest. *Biodiversity and Conservation*, 19, 619–635. DOI: 10.1007/s10531-009-9723-2
- Bastos, C. J. P., & Valente, E. B. 2008. Hepáticas (Marchantiophyta) da Reserva Ecológica da Michelin, Igrapiúna, Bahia, Brasil. *Sitientibus, Série Ciências Biológicas*, 8, 280–293.
- Bates, J. W. 1998. Is ‘life-form’ a useful concept in bryophyte ecology? *Oikos*, 82, 22–237. DOI: 10.2307/3546962
- Batista, W. V. S. M., Santos, N. D., & Pôrto, K. C. 2018. Distribution, ecology, and reproduction of bryophytes in a humid enclave in the semiarid region of northeastern Brazil. *Acta Botanica Brasilica*, 32(2), 303–313. DOI: 10.1590/0102-33062017abb0339
- Bisang, I., & Hedenäs, L. 2005. Sex ratio patterns in dioicous bryophytes revisited. *Journal of Bryology*, 27, 207–219. DOI: 10.1179/174328205X69959
- Brasil. Presidência da República. Lei nº 9.985, de 18 de julho de 2000. SNUC – Sistema Nacional de Unidades de Conservação da Natureza. Brasília, DF. (Retrieved on August 11th, 2021, from [http://www.planalto.gov.br/ccivil\\_03/leis/l9985.htm](http://www.planalto.gov.br/ccivil_03/leis/l9985.htm)).
- Brito, E. S., & Ilkiu-Borges, A. L. 2014. Briófitas de uma área de Terra Firme no município de Mirinzal e novas ocorrências para o estado do Maranhão, Brasil. *Iheringia, Série Botânica*, 69, 133–142.
- Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics*, 43, 783–91. DOI: 10.2307/2531532
- Coleman, B. D., Mares, M. A., Willis, M. R., & Hsieh, Y. 1982. Randomness, area and species richness. *Ecology*, 63, 1121–1133. DOI: 10.2307/1937249
- Cornelissen, J. H. C., & Gradstein, S. R. 1990. On the occurrence of Bryophytes and macrolichens in different lowland rain forest types at Mabura Hill, Guyana. *Tropical Bryology*, 3, 29–35. DOI: 10.11646/bde.3.1.4
- Crandall-Stotler, B., Stotler, R. E., & Long, D. G.

2009. Morphology and classification of the Marchantiophyta. In: B. Goffinet & A. J. Shaw (Eds.), *Bryophyte Biology*. pp. 1–54. New York: Cambridge University Press.
- Evangelista, M., Valente, E. B., Bastos, C. J. P., & Vilas Bôas-Bastos, S. B. 2019. Musgos (Bryophyta) da Estação Ecológica Wenceslau Guimarães, Estado da Bahia, Brasil. *Hoehnea*, 46(4), e092019. DOI: 10.1590/2236-8906-09/2019
- Flora e Funga do Brasil 2022. Jardim Botânico do Rio de Janeiro. Disponível em: <<http://floradobrasil.jbrj.gov.br/>>. Acesso em: 26 fev. 2022
- Fontoura, T., & Santos, F. A. M. 2010. Geographic distribution of epiphytic bromeliads of the Una region, Northeastern Brazil. *Biota Neotropica*, 10(4), 127–132. DOI: 10.1590/S1676-06032010000400017
- Frey, W., & Kürschner, H. 2011. Asexual reproduction, habitat colonization and habitat maintenance in bryophytes. *Flora*, 206(3), 173–184. DOI: 10.1016/j.flora.2010.04.020
- Galindo-Leal, C., & Câmara, I. G. 2003. The Atlantic Forest of South America: biodiversity status, threats, and outlook. Washington. Center for Applied Biodiversity Science at Conservation International: Island Press: p. 488.
- Glime, J. M. 2017a. Adaptive Strategies: Growth and Life Forms. In: J. M. Glime (Ed.), *Bryophyte Ecology*. E-book sponsored by Michigan Technological University and the International Association of Bryologists. [accessed 2019 Dez 13]. <http://digitalcommons.mtu.edu/bryophyte-ecology1/>.
- Glime, J. M. 2017b. Light: The Shade Plants. In: J. M. Glime (Ed.), *Bryophyte Ecology*. E-book sponsored by Michigan Technological University and the International Association of Bryologists. [accessed 2019 Dez 13]. <http://digitalcommons.mtu.edu/bryophyte-ecology1/>.
- Goffinet, B., Buck, W. R., & Shaw, A. J. 2009. Morphology and classification of the Bryophyta. In: B. Goffinet & A. J. Shaw (Eds.), *Bryophyte Biology*. pp. 55–138. New York: Cambridge University Press.
- Gotelli, N. J., & Colwell, R. K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379–391. DOI: 10.1046/j.1461-0248.2001.00230.x
- Gradstein, S. R., & Churchill, S. P., Salazar-Allen, N. & Reiner-Drehwald, M. E. 2001. Guide to the bryophytes of Tropical America. *Memoirs of the New York Botanical Garden*, 86, 1–577.
- Gradstein S. R., & Costa D. P. 2003. The Hepaticae and Anthocerotae of Brazil. *Memoirs of the New York Botanical Garden*, 87, 1–336.
- Gradstein, S. R., & Costa, D. P. 2018. *Plagiochila lamyana*, a New Liverwort Species from the Guayana Highland of Brazil. *Cryptogamie Bryologie*, 39(2), 147–153. DOI: 10.7872/cryb/v39.iss2.2018.147
- Gradstein, S. R., & Ilkiu-Borges, A. L. 2009. Guide to the plants of Central French Guiana. *Memoirs of the New York Botanical Garden*, 76, 1–140.
- Henriques, D. S. G., Rigal, F., Borges, P. A. V., Ah-Peng, C., & Gabriel, R. 2017. Functional diversity and composition of bryophyte water-related traits in Azorean native vegetation. *Plant Ecology & Diversity*, 10(2-3), 127–137. DOI: 10.1080/17550874.2017.1315839
- Longton, R. E., & Schuster, R. M. 1983. Reproductive biology. In: R. M. Schuster (Ed.), *New manual of Bryology*. The Journal of the Hattori Botanical Laboratory, 386–462.
- Maciel-Silva, A. S., & Válio, I. F. M. 2011. Reproductive phenology of bryophytes in tropical rain forests: the sexes never sleep. *The Bryologist*, 114, 708–719. DOI: 10.1639/0007-2745-114.4.708
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B., & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858. DOI: 10.1038/35002501
- Nemésio, A. 2013. The orchid-bee fauna (Hymenoptera: Apidae) of ‘Reserva Biológica de Una’, a hotspot in the Atlantic Forest of southern Bahia, eastern Brazil. *Brazilian Journal of Biology*, 73(2), 347–352. DOI: 10.1590/S1519-69842013000200014
- Oishi, Y. 2009. A survey method for evaluating drought-sensitive bryophytes in fragmented forests: a bryophyte life-form based approach. *Biological Conservation*, 142, 2854–2861. DOI: 10.1016/j.biocon.2009.04.011
- Oliveira, H. C., & Oliveira, S. M. 2017. Vertical distribution of epiphytic bryophytes in

- Atlantic Forest fragments in northeastern Brazil. *Acta Botanica Brasilica*, 30(4), 609–7. DOI: 10.1590/0102-33062016abb0303
- Oliveira, J. R. P. M., Pôrto, K. C., & Silva, M. P. P. 2011. Richness preservation in a fragmented landscape: a study of epiphytic bryophytes in an Atlantic forest remnant in Northeast Brazil. *Journal of Bryology*, 33(4), 279–290. DOI: 10.1179/1743282011Y.00000000017
- Oliveira, S. M., & Pôrto, K. C. 2001. Reproductive phenology of the moss *Sematophyllum subpinnatum* in a tropical lowland forest of north-eastern Brazil. *Journal of Bryology*, 23(1), 17–21. DOI: 10.1179/jbr.2001.23.1.17
- Pôrto, K. C., Silva, I. C., Reis, L. C., & Maciel-Silva, A. S. 2016. Sex ratios and sporophyte production in the moss *Bryum argenteum* Hedw. on a rock outcrop, north-eastern Brazil. *Journal of Bryology*, 38(4), 1–5. DOI: 10.1080/03736687.2016.1232012
- Reis, L. C., Oliveira, H. C., & Bastos, C. J. P. 2015. Hepáticas (Marchantiophyta) epífitas de duas áreas de Floresta Atlântica no Estado da Bahia, Brasil. *Pesquisas, Botânica*, 67, 225–241.
- Reis, L. C., Oliveira, H. C., & Pôrto, K. C. 2020. *Drepanolejeunea pinnatiloba* Schiffn. (Lejeuneaceae): a rare species in Brazil rediscovered after 17 years. *Check List*, 16(3), 593–596. DOI: 10.15560/16.3.593
- Reis, L. C., & Valente, E. B. 2022. Qualidade da informação em herbários virtuais no Brasil: Coleções de briófitas como estudo de caso. *Pesquisas, Botânica*, 76, 306–315.
- Ribeiro, M. C., Metzger, J. P., Martensen, A. A., Ponzoni, F. L., & Hirota, M. M. 2009. The Brazilian Atlantic Forest: How much is left, and how is there remaining forest distributed? Implications for conservation. *Biological Conservation*, 142, 114–1153. DOI: 10.1016/j.biocon.2009.02.021
- Richards, P. W. 1984. The ecology of tropical forest bryophytes. In: R. M. Schuster (Ed.), *New Manual of Bryology*. pp. 1233–1270. Nichinan: The Hattori Botanical Laboratory.
- Rodrigues, R. R., Lima, R. A. F., Gndolfi, S., & Nave, A. G. 2009. On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. *Biological Conservation*, 142, 1242–1251. DOI: 10.1016/j.biocon.2008.12.008
- Sastre-De Jesús I. 1992. *Estudios Preliminares sobre Comunidades de Briófitas en Troncos en Descomposición en el Bosque Subtropical Lluvioso de Puerto Rico*. *Tropical Bryology*, 6, 181–191. DOI: 10.11646/BDE.6.1.21
- Sharp, A. J., Crum, H., & Eckel, P. M. 1994. The moss flora Mexico. *Memoirs of the New York Botanical Garden*, 69, 1–113.
- Sierra, A. M., Vanderpoorten, A., Gradstein, S. R., Pereira, M. R., Bastos, C. J. P., & Zartman, C. E. 2018. Bryophytes of Jaú National Park (Amazonas, Brazil): Estimating species detectability and richness in a lowland Amazonian megareserve. *The Bryologist*, 121(4), 571–588. DOI: 10.1639/0007-2745-121.4.571
- Silva, M. P. P., Kamino, L. H. Y., & Pôrto, K. C. 2014. Is the current network system of protected areas in the Atlantic Forest effective in conserving key species of bryophytes? *Tropical Conservation Science*, 7(1), 61–74. DOI: 10.1177/194008291400700110
- Silva, M. P. P., & Pôrto, K. C. 2010. Spatial structure of bryophyte communities along an edge-interior gradient in an Atlantic Forest remnant in Northeast Brazil. *Journal of Bryology*, 32(2), 101–112. DOI: 10.1179/037366810X12578498136110.
- Silva, M. P. P., & Pôrto, K. C. 2015. Diversity of bryophytes in priority areas for conservation in the Atlantic forest of northeast Brazil. *Acta Botanica Brasilica*, 29(1), 16–23. DOI: 10.1590/0102-33062014abb3534
- Söderström, L., Hagborg, A., von Konrat, M., & Renner, M. 2008. Chapter ten: Early Land Plants Today: Liverwort checklist of checklists. *Fieldiana Botany*, 47, 105–130. DOI: 10.3158/0015-0746-47.1.105
- Souza, J. P. S., Silva, M. P. P., & Pôrto, K. C. 2020. Spatial distribution of functional traits of bryophytes along environmental gradients in an Atlantic Forest remnant in north-eastern Brazil. *Plant Ecology & Diversity*, 13, 1–12. DOI: 10.1080/17550874.2019.1709227
- Spitale, D., Maira, P., & Nascimbene, J. 2020. Patterns of bryophyte life-forms are predictable across land cover types. *Ecological Indicators*, 109, 105799. DOI: 10.1016/j.ecolind.2019.105799
- Sporn, S. G., Bos, M. M., Hoffstätter-Müncheberg, M., Kessler, M., & Gradstein, S.R., 2009. Microclimate determines community

- composition but not richness of epiphytic understory bryophytes of rainforest and cacao agroforests in Indonesia. *Functional Plant Biology*, 36(2), 171–179. DOI: 10.1071/FP08197
- Thomas, W. M. W., & Carvalho, A. M. V. 2003. Zoneamento Ecológico do Sudeste da Bahia, Brasil (mapa em formato digital). In: P. I Prado, E. C. Landau, R. T. Moura, L. P. S. Pinto, G. A. B. Fonseca & K. Alger (Eds), Corredor de biodiversidade da Mata Atlântica do sul da Bahia. IESB/Conservation International, Ilhéus, CD-ROM.
- Valente, E. B., & Pôrto, K. C. 2006. Hepáticas (Marchantiophyta) de um fragmento de Mata Atlântica na Serra da Jibóia, Município de Santa Teresinha, BA, Brasil. *Acta Botanica Brasilica*, 20(2), 433–441. DOI: 10.1590/S0102-33062006000200018
- Valente, E. B., Pôrto, K. C., Bastos, C. J. P., & Ballejos-Loyola, J. 2013. Diversity and distribution of the bryophyte flora in montane forest in the Chapada Diamantina region of Brazil. *Acta Botanica Brasilica*, 27, 506–518. DOI: 10.1590/S0102-33062013000300008

*Submitted: 26 February 2022*

*Accepted: 14 July 2022*

*Published online: 27 October 2022*

*Associate Editor: Bianca Andrade*