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Bryophyte flora in upland forests at different successional stages and in the various strata of host trees in northeastern Pará, Brazil[1]

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ABSTRACT

In the northeastern region of the Brazilian state of Pará, approximately 90% of the forested areas are secondary forests. Secondary forests are interesting areas for floristic studies aimed at determining the effects that clear-cutting has on bryophyte communities. The aim of this study was to compare upland forests at different successional stages and the various strata of host trees, in terms of the bryophyte species composition. Bryophyte specimens were collected between August 2005 and September 2006 from host trees in primary and secondary forests of different ages and of different heights, within the municipality of Capitão Poço, in the state of Pará. The vertical distribution of bryophytes was evaluated in 15 host trees within the primary forest. We identified a total of 99 bryophyte species: 33 mosses and 66 liverworts. The dominant family was Lejeuneaceae, with 56 species. Most of the species (n = 60) had a neotropical distribution, and 3 species were endemic to Brazil. *Cololejeunea minutissima* var. *myriocarpa* (Nees & Mont.) R.M.Schust., *Pycnolejeunea papillosa* X.-L. He, *Radula mammosa* Spruce and *Verdoornianthus marsupiifolius* (Spruce) Gradst. represent new records for the state of Pará. In the successional forests evaluated, we identified 78 species, most of which (n = 38) occurred in primary forest. On the host tree trunks evaluated in the primary forest, we observed 31 species occurring at heights ranging from 2 m to 20 m. Despite the fact that secondary forests account for such a large proportion of the forested areas in Capitão Poço, we found that the bryoflora was relatively rich, comprising 31% of the species recorded for the state. The fact that 40% of the species recorded occurred exclusively in the secondary forests and the fact that 45.5% of the species recorded in primary forest occurred within the 2-20 m height range show the importance of studies focusing on bryophytes in secondary forests and in the upper strata of host trees in primary forests.

Key words: bryophytes, northeastern Pará, primary forests, secondary forests, vertical distribution

Introduction

Brazil has a rich bryoflora, with approximately 1,650 species, comprising 35% of all neotropical species, which have been estimated to number 4,700 (Gradstein *et al.* 2001, Gradstein & Costa 2003, Costa & Luizi-Ponzo 2010). In the Brazilian state of Pará, there are an estimated 317 species of bryophytes (Costa 2013), which correspond to approximately 20% of the bryophyte flora known in the country, demonstrating the level of knowledge and the importance of bryophytes in the state. The state of Pará is divided geographically into six mesoregions and 22 microregions (SEPOF 2008), and the mesoregion of the northeastern part of the state is one of the oldest agricultural frontiers in the Amazon, caused by the migration of northeasterners fleeing drought (IBGE 1991). The northeastern mesoregion comprises the microregions of Salgado, Bragantina, Cametá, Tomé-Açu and Guamá (IDESP 1992). Currently, the landscape of those microregions is highly disturbed due to subsistence farming of crops such as cassava, corn and rice (Wiesenmüller 2004). This dynamic gave rise to the appearance of ecosystems, at different successional stages, which are highly depleted in terms of genetic resources (Vieira 1996).

Regarding the bryoflora of northeastern Pará, Santos & Lisboa (2003) conducted a survey of mosses in eight municipalities within the Salgado, Bragantina and Guamá microregions. The same authors subsequently investigated whether bryophyte species could be employed as indicators of disturbed environments (Santos & Lisboa 2008). In another study, Lisboa & Santos (2005) published the first record of the genus *Papillaria* (Müll. Hal.) Müll. Hal. for the Amazon.

In the Chocoaré-Mato Grosso Extractive Reserve, located in the municipality of Santarém Novo, within

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the Bragantina microregion, the same authors observed a predominance of bryophyte species typical of disturbed habitats, cultivated areas and the forest canopy, indicating the high degree to which the area had been disturbed (Lisboa & Tavares 2008). The microregions of Cametá, Tomé-Açu and Guamá, all of which have been disturbed in large part, are the regions for which the least is known of the bryophyte flora and are therefore considered priority areas for the execution of future floristic inventories. The municipality of Capitão Poço, which is within the microregion of Guamá, is among the municipalities in northeastern Pará where there has been considerable deforestation, 64% of Capitão Poço having been deforested by 2007 (INPE 2009). The municipality encompasses upland areas, floodplains and swamps that have been progressively altered, only 2.5% of primary forests remaining, and are now dominated by secondary forests, which cover 43.1% of the total area (Wiesenmüller 2004). Currently, as in the other regions of northeastern Pará, the landscape of Capitão Poço presents a mosaic of secondary forests of different ages, as well as temporary and permanent pastures and plantations. These secondary forests are considered priority areas for the study of the local flora, given that epiphytes in disturbed areas have received little attention (Wolf 2005) and that there is a need for studies of ecological succession in neotropical bryophytes (Gradstein & Raeymaekers 2000).

In the Brazilian Amazon, there is a lack of studies involving bryophytes, not only of bryophyte species in secondary forests but also on the vertical distribution of bryophyte species on host trees (on the upper trunk and in the crown). Because bryophytes species in the forest canopy are difficult to access and have therefore been less widely studied, it is possible that some bryophytes are exclusive to the canopy (Rhoades 1995). Therefore, the study of such bryophytes could result in a more comprehensive inventory of the bryophyte flora of a given area.

In Brazil, studies of epiphytic bryophytes in host trees have been restricted to the Atlantic Forest biome and have been conducted in forests at different successional stages (Costa 1999) or in forest fragments in different states of conservation (Alvarenga *et al.* 2009). In the Brazilian Amazon, the first and only such study in preserved upland forests was conducted by Oliveira (2010), who reported that species richness was highest in the canopy and that species composition, at the base of the host tree trunk as well as in the canopy, is determined by environmental filters.

In the present study, we sought to identify the bryophytes species that occur in forests at different successional stages, as well as to determine their vertical distribution on their host trees. The objective of this study was to compare upland forests at different successional stages, as well as the various strata of host trees, in terms of the bryophyte species composition, in northern Brazil.

Material and methods

Study area

The municipality of Capitão Poço (01°44'54"S; 47°03'42"W) encompasses an area of approximately 2900 km^2, at an elevation of 40 m, and is the seventh largest municipality in Pará, in terms of area (SEPOF 2008). According to the Köppen system of classification, the climate of the region is type Am (Bastos *et al.* 1984), categorized as tropical monsoon climate. The mean monthly maximum temperature ranges from 28.7°C to 30.2°C, whereas the mean monthly minimum ranges from 24.9°C to 29.8°C (data obtained from the rainfall measurement station operated by CITROPAR - Cítricos do Pará S/A. The vegetation cover in the area is dense tropical rain forest, comprising areas of upland forest, floodplain forest and swamp forest (Wiesenmüller 2004, Almeida *et al.* 2005).

Sampling and evaluation of botanical material

Botanical material was collected in areas of upland forest between August 2005 and September 2006. We selected four areas of secondary forest of different successional ages (6, 10, 20 and 40 years, respectively) and one fragment of primary forest (with no evidence of timber extraction). For the comparison between primary and secondary forest, bryophyte specimens were randomly collected from the understory of both forest types, within a 2000 m^2 plot. The methods employed in the collection, storage and herbarium preservation of specimens followed Yano (1984a).

In order to evaluate the vertical distribution of bryophytes on host trees (which was studied only in the area of primary forest), we selected 15 host trees (located outside of the 2000 m^2 plot) whose crowns were visible from the understory, as recommended by Gradstein *et al.* (1996). From the base to the crown of each tree, we delineated 20 × 20 cm plots at 2 m vertical intervals, as described by Frahm (2003), within which we collected addition bryophyte specimens. Each host tree was therefore divided into three zones, by height: base; 2-10 m; and 12-20 m.

The botanical material was identified by reference to the studies conducted by Dauphin (2003), Engel & Smith Merrill (2004), Florschütz (1964), Florschütz-De Waard (1986; 1996), Florschütz-De Waard & Veling (1996), Fulford (1968), Gradstein (1994), Gradstein & Costa (2003), He (1999), Heinrichs *et al.* (1999), Ilkiu-Borges & Lisboa (2002a; 2002b; 2002c; 2002d; 2004), Inoue & Gradstein (1980), Lisboa (1993), Lisboa & Ilkiu-Borges (1997), Reese (1961; 1993), Reiner-Drehwald (1994; 1998; 2000; 2007), Reiner-Drehwald & Goda (2000), Reiner-Drehwald & Ilkiu-Borges (2007), Schuster (1980), Tixier (1980), Yamada (1993), Yano (1985). Mosses were classified according to Goffinet *et al.* (2009), and liverworts were classified according to Crandall-Stotler *et al.* (2009). The study specimens were deposited in the Herbar-

ium of the Research Institute of the Rio de Janeiro Botanical Garden (code, RB) and the João Murça Pires Herbarium of the Museu Paraense Emílio Goeldi (code, MG).

Data analysis

We evaluated species richness, floristic composition, geographic distribution and vertical distribution of bryophyte species, as well as the relationship between primary and secondary forest. The distribution of taxa was determined in accordance with the information available in the online databases *Lista de Espécies da Flora do Brasil* (List of Species of the Brazilian Flora, Costa 2013) and *Banco de Briófitas do Estado do Rio de Janeiro* (Rio de Janeiro State Bryophyte Database, Costa *et al.* 2012a), as well as with the studies conducted by Gradstein & Costa (2003), Lisboa *et al.* (2006), Gradstein & Ilkiu-Borges (2009), Peralta & Yano (2011), Tavares *et al.* (2006), Yano (1984b; 1989; 1995; 2006; 2008; 2011a; 2011b) and Yano & Peralta (2011). The two-letter abbreviations of state names employed are those established the Brazilian Institute of Geography and Statistics.

The relationship between primary and secondary forest was evaluated on the basis of quantitative and qualitative data related to the bryophyte species observed in each forest type. The comparison among the different vertical zones of the host trees was based on the bryophyte species richness observed in each zone.

When multiple specimens were collected for a species, we opted to cite only two voucher specimens. Species representing new records for the state of Pará are indicated with an asterisk and are illustrated.

Results and discussion

Overall species richness

Within the study area as a whole, we identified 99 bryophyte species (33 mosses and 66 liverworts), within 15 families and 47 genera (Tab. 1), representing approximately 31% of the known bryophyte flora in the state of Pará (Costa 2013). The species richness found in Capitão Poço was similar to that reported for other upland forests in the state, such as that within Caxiuanã National Forest, where 126 bryophyte species have been recorded (Lisboa & Nazaré 1997, 2002; Ilkiu-Borges & Lisboa 2002d; Alvarenga *et al.* 2007). In Capitão Poço, we identified 62 (49.2%) of those 126 species. Lisboa & Ilkiu-Borges (1995) also identified 126 bryophyte species in a variety of vegetation formations, including upland forest, on the outskirts of the city of Belém, also in the state of Pará. Of those, we identified 37 species (29.4%) in Capitão Poço. In the Guamá Ecological Research Area, known as the Mocambo Reserve, also near Belém, those same authors identified 113 bryophyte species (Lisboa & Ikiu-Borges 2007), 45 of which (39.8%) were also found to occur in our study area.

Despite the fact that the Capitão Poço region is dominated by secondary forest, we found that it has a rich bryophyte flora, comprising 31% of the species recorded for the state. In addition, the bryophyte species richness in the study area was similar to that reported for other areas in the state presenting varying degrees of conservation (37-50%).

Floristic composition

In our study area, the family Lejeuneaceae showed the highest species richness, with 56 of the 99 taxa identified. The importance of Lejeuneaceae has also been reported for the Amazon, Atlantic Forest, *caatinga* (shrublands) and *pantanal* (swampland) in Brazil, as well as for French Guiana (Lisboa *et al.* 2006; Lisboa & Ilkiu-Borges 2001, 2007; Lisboa & Tavares 2008; Yano & Câmara 2004; Pôrto *et al.* 2004; Campelo & Pôrto 2007; Siqueira *et al.* 2011; Costa *et al.* 2005; Valente *et al.* 2013; Câmara & Vital 2004; Gradstein 2006). In addition, Gradstein *et al.* (2001) reported that more than 70% of the liverwort species found in neotropical forests belong to Lejeuneaceae. In the present study, the most well-represented moss family was Calymperaceae, with 12 species, followed by Sematophyllaceae, with five (Fig. 1). Lisboa *et al.* (1998; 1999), Santos & Lisboa (2003) and Souza & Lisboa (2005; 2006) obtained similar results, and Gradstein *et al.* (2001) reported that Calymperaceae and Sematophyllaceae were among the four most well-represented moss families in areas of lowland moist forest.

Geographic distribution

We observed seven different patterns of geographic distribution (Fig. 2), the predominant pattern being neotropical, with 60 species, followed by pantropical, with 15, South American (restricted to the countries of South America), with 8, and the tropics of Africa and the Americas, with 10. Of the 99 species identified, three are exclusive to Brazil, two are widely distributed worldwide, and one is restricted to Brazil and French Guiana. Similar results have been obtained in studies conducted in various forest types in the Amazon, Atlantic Forest and other regions of South America (Ilkiu-Borges & Lisboa 2002d; Ilkiu-Borges *et al.* 2004; Valente & Pôrto 2006; Costa & Lima 2005; Rico & Pócs 2004; Parolly *et al.* 2004).

The species *Micropterygium leiophyllum* Spruce, *Pycnolejeunea papillosa* X.-L. He and *Verdoornianthus marsupiifolius* (Spruce) Gradst. are endemic to Brazil, the last two previously being reported only for the state of Amazonas (Gradstein & Costa 2003; Bastos 2012; Costa *et al.* 2012b) and here recorded for the first time for the state of Pará, as were *Cololejeunea minutissima* subsp. *myriocarpa*, (Nees & Mont.) R.M.Schust. and *Radula mammosa* Spruce (Fig. 3, 4 and 5). In Brazil, the species *Microlejeunea acutifolia* Steph. and *Prionolejeunea muricatoserrulata* (Spruce) Steph. occur exclusively in Pará.

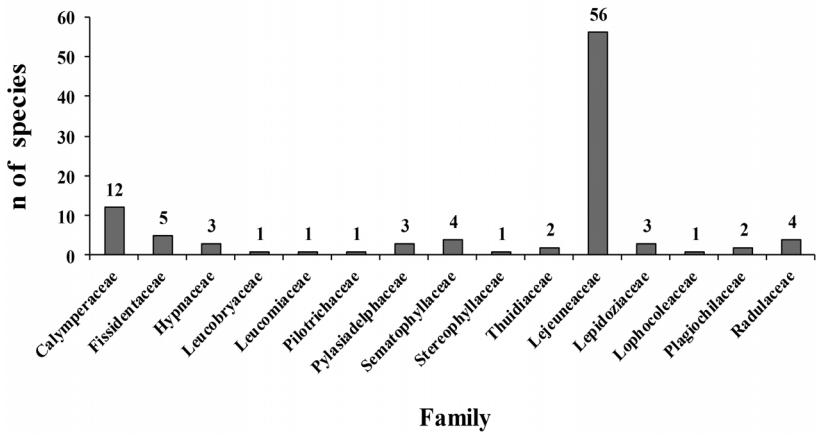

Figure 1. Species richness, by family, for bryophytes identified in the municipality of Capitão Poço, in the state of Pará, Brazil.

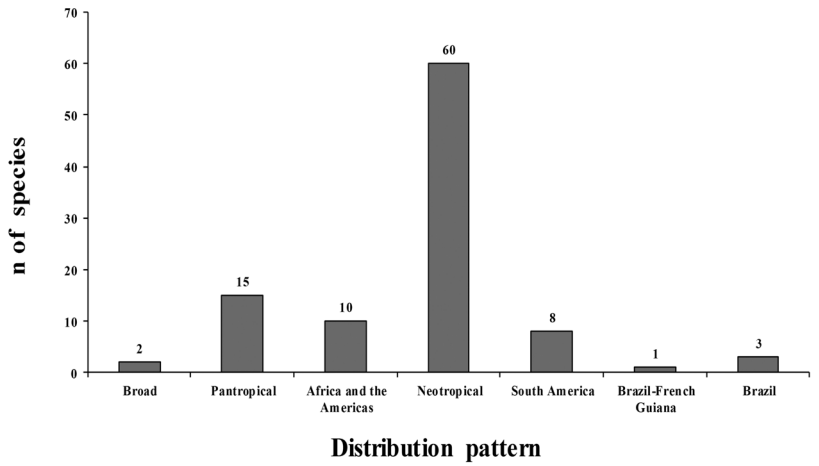

Figure 2. Distribution patterns of bryophyte species identified in the municipality of Capitão Poço, in the state of Pará, Brazil.

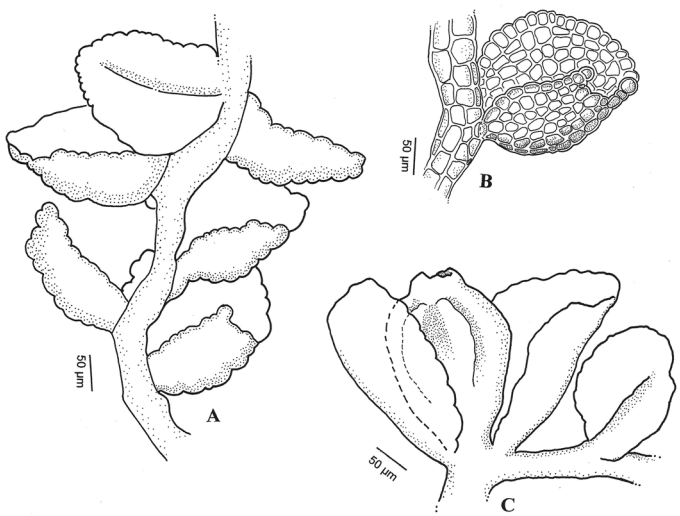

Figure 3. A-C. *Cololejeunea minutissima* subsp. *myriocarpa* (Nees & Mont.) R.M. Schust. A. habit. B. leaf. C. perianth. (A-C from specimen *ACCTavares 782*).

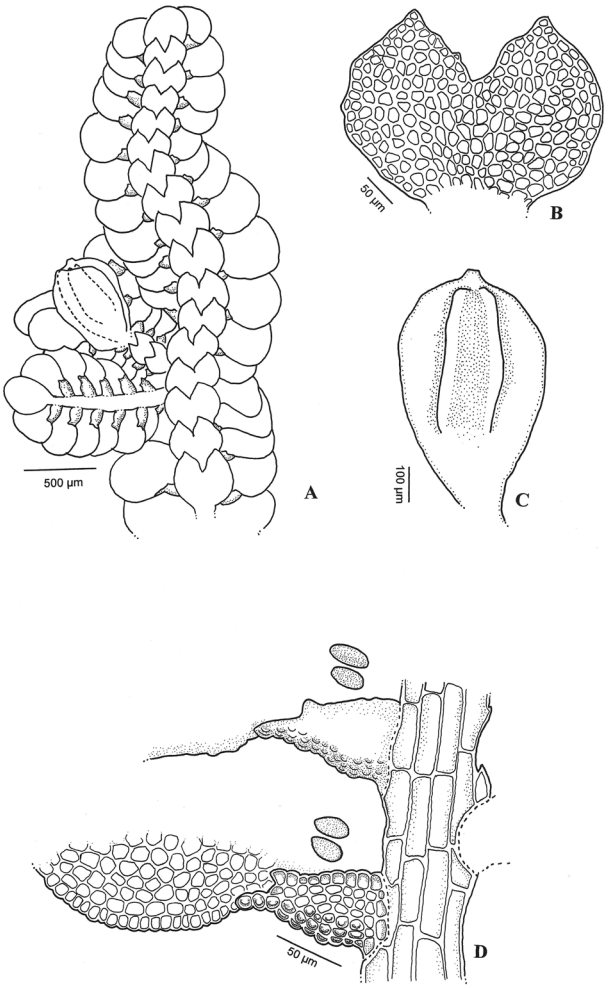

Figure 4. A-C. *Pycnolejeunea papillosa* X.-L. He. A. habit. B. underleaf. C. perianth. D. leaf margin and keel. (A-D from specimen *ACCTavares 791*).

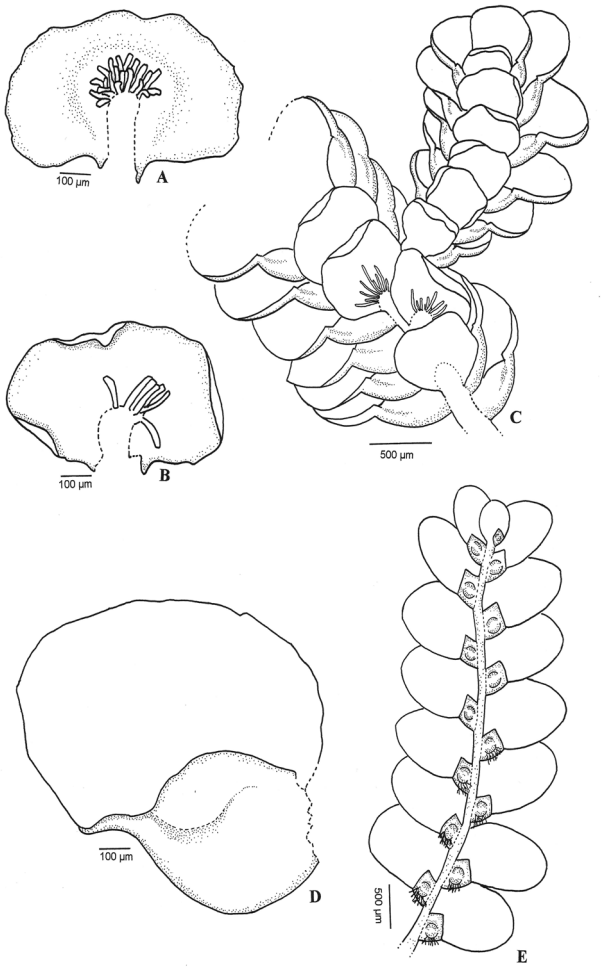

Figure 5. A-D. *Verdoornianthus marsupiifolius* (Spruce) Gradst. A and B. underleaf. C. habit. D. leaf. E. *Radula mammosa* Spruce, habit. (A-D from *ACCTavares 787*; E from specimen *ACCTavares 829*).

Primary versus secondary forest

In the areas of successional forest evaluated, we identified 78 bryophyte species. Bryophyte species richness was higher in the primary forest, where 38 species were identified, than in any of the areas of secondary forest (Fig. 6). Analyzing the species identified in the areas of successional forest, we found that 23 (29.5%) occurred exclusively in the primary forest only, whereas 40 (51.3%) were exclusive to the areas of secondary forest (Tab. 1). The difference between primary and secondary forest, in terms of bryophyte species richness, has previously been reported in field studies. For example, in studies conducted in different types of tropical forests, Lisboa *et al.* (1987), Costa (1999) and Acebey *et al.* (2003) also reported that bryophyte species richness was lower in areas of secondary forest. The fact that approximately half of the species identified in the present study were exclusive to the areas of secondary forest underscores the importance of conducting additional studies in such areas, in order to determine which taxa are exclusive to those environments, given that such species appear to be

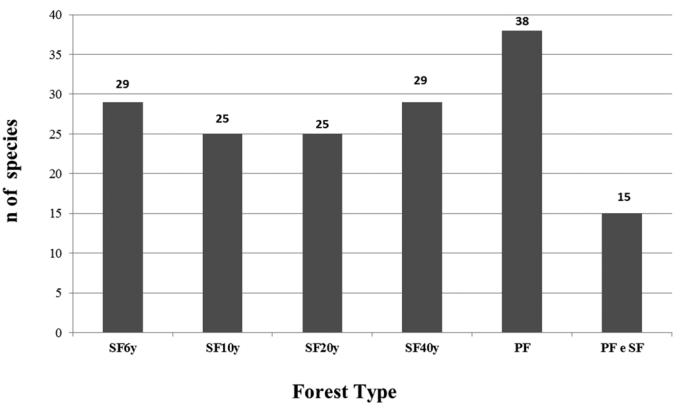

Figure 6. Bryophyte species richness in the areas sampled in the municipality of Capitão Poço, in the state of Pará, Brazil.
SF6y – secondary forest in its sixth year of regeneration; SF10y – secondary forest in its tenth year of regeneration; SF20y – secondary forest in its twentieth year of regeneration; SF40y – secondary forest in its fortieth year of regeneration; PF – primary forest; SF – secondary forest.

more well-adapted to the environmental changes caused by agricultural activity in the region.

Vertical gradient

On the 15 host trees evaluated, we identified 68 bryophyte species. Of those, 37 were found to occur in the base zone of the tree, 11 being exclusive to that zone. In the 2-10 m zone, we identified 45 species, eight of which were exclusive to that zone. In the 12-20 m zone, we identified 44 species, 11 of which were exclusive to that zone. Only 20 species occurred in all three zones (Fig. 7). Among the 11 species that occurred exclusively in the 12-20 m zone, *Harpalejeunea oxyphylla* (Nees & Mont.) Steph., *Radula javanica* Gottsche, *Symbiezidium transversale* (Sw.) Trevis., *Stictolejeunea squamata* (Willd. ex. Weber) Schiffn. and

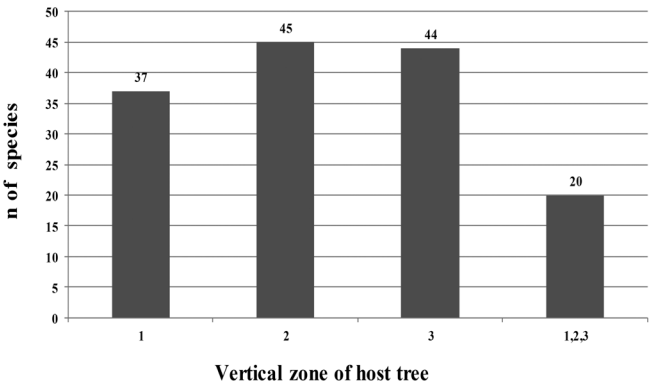

Figure 7. Bryophyte species richness in the different vertical zones of the host trees evaluated in primary forest in the municipality of Capitão Poço, in the state of Pará, Brazil.
zone 1 – base; zone 2 – 2-10 m; zone 3 – 12-20 m.

Table 1. Bryophyte species identified in the municipality of Capitão Poço, in the state of Pará, Brazil.

FAMILY Species	Type of sucessional forest	Vertical zone of host trees in primary forest	Worldwide distribution; distribution in Brazil (by state)	Voucher specimen
CALYMPERACEAE				
Calymperes afzelii Sw.	SF	2, 3	Pantropical; AC, AL, AM, AP, BA, CE, ES, MS, MT, PA, PB, PE, RJ, RO, RR, SC, SP and TO	AC768
C. erosum Müll. Hal.	SF	1, 2, 3	Pantropical; AC, AM, AP, BA, CE, DF, ES, GO, MG, MT, MS, PA, PB, PE, RJ, RO, RR, SC, SP and TO	AC766, AC1019
C. lonchophyllum Schwägr.	PF	1, 2, 3	Pantropical; AC, AL, AM, AP, BA, ES, GO, MA, MG, MT, MS, PA, PE, PR, RJ, RO, RR, SP and TO	AC832
C. pallidum Mitt.	SF	--	Neotropical; AC, AM, BA, GO, MT, PA and RO	AC849
C. alymperes platyloma Mitt.	PF, SF	2, 3	South America; AM, AP, BA, MT, PA and RR	AC758, AC1086
Octoblepharum albidum Hedw. var. *albidum*	SF	1, 2, 3	Pantropical; AC, AL, AM, AP, BA, CE, DF, ES, GO, MA, MG, MS, MT, PA, PB, PE, PI, PR, RJ, RN, RR, RO, RS, SC, SE, SP and TO	AC759, AC1080
O. albidum var *violascens* Müll. Hal.	SF	--	Neotropical; AC, AM, BA, MT, MS, PA, RJ, RO, RR, SE and SP	AC879
O. cylindricum Schimp. ex Mont.	SF	--	Neotropical; AC, AM, AP, BA, CE, DF, GO, MG, MS, MT, PA, PB, PI, RJ, RO, RR, SP, DF, SE and TO	AC871
O. pulvinatum (Dozy & Molk.) Mitt.	PF, SF	1, 2, 3	Neotropical; AC, AL, AM, AP, BA, CE, ES, GO, MA, MG, MS, MT, PA, PE, RJ, RO, RR, SC, SP and TO	AC764, AC1092
Syrrhopodon incompletus Schwägr.	--	1, 2, 3	Africa and the Americas; AC, AL, AM, AP, BA, DF, GO, MG, MS, MT, PA, PB, PE, PR, RJ, RO, RR, SC, SP and TO	AC920, AC1087
S. ligulatus Mont.	--	2, 3	Neotropical; AC, AM, AP, BA, DF, GO, MT, MS, MG, PA, PE, RJ, RO, RR and SP	AC1014
S. prolifer Schwägr.	--	1, 2, 3	Neotropical; AL, AM, AP, BA, CE, DF, ES, GO, MG, MT, PA, PE, PI, PR, RJ, RO, RS, SC, SE, SP and TO	AC1000
FISSIDENTACEAE				
Fissidens elegans Brid.	--	1, 2, 3	Neotropical; AC, AM, BA, CE, DF, ES, GO, MA, MG, MS, MT, PA, PB, PE, PI, PR, RJ, RN, RS, RO, RR, SC, SP and TO	AC1061
F. guianensis Mont.	PF	2	Neotropical; AC, AL, AM, AP, BA, CE, DF, ES, GO, MA, MG, MT, MS, PA, PB, PE, PI, RJ, RO, RR, RS, SP and TO	AC816
F. flaccidus Mitt.	SF	--	Africa and the Americas; AC, AM, BA, CE, DF, ES, GO, MA, MG, MS, MT, PA, PB, PE, PR, RJ, RO, RS, SE, SP and TO	AC845
F. pellucidus Hornsch.	--	1	Neotropical; AC, AM, BA, CE, DF, ES, GO, MG, MT, PA, PB, PE, PR, RJ, RO, RR, RS, SC, SP and TO	AC1046
F. zollingeri Mont.	SF	--	Pantropical; AC, AL, AM, AP, BA, CE, DF, ES, GO, MA, MG, MS, MT, PA, PB, PE, PI, PR, RJ, RO, RR, RS, SC, SP and TO	AC790

Continues

Table 1. Continuation.

FAMILY Species	Type of sucessional forest	Vertical zone of host trees in primary forest	Worldwide distribution; distribution in Brazil (by state)	Voucher specimen
HYPNACEAE				
Chryso-hypnum diminutivum (Hampe) W.R.Buck	SF	2, 3	Widespread; AC, AL, AM, AP, BA, DF, ES, GO, MA, MG, MS, MT, PA, PE, PR, RJ, RO, RS, RR, SC, SP and TO	AC771, AC1056
Ectropotecium leptochaetum (Schwägr.) W.R.Buck	SF	--	Pantropical; AM, BA, ES, MG, MS, MT, PA, PE, PR, RJ, SC and SP	AC837
Vesicularia vesicularis (Schwägr.) Broth.	SF	--	Neotropical; AC, AL, AM, AP, BA ES, GO, MG, MS, MT, PA, PE, PI, PR, RJ, RS, SC, SP, RO, RR and TO	AC780
LEUCOBRYACEAE				
Leucobryum martianum (Hornsch.) Hampe	PF	--	South America; AC, AL, AM, AP, BA, CE, DF, ES, GO, MA, MG, MS, MT, PA, PE, PR, RJ, RO, RR, RS, SC, SE, SP and TO	AC812
LEUCOMIACEAE				
Leucomium strumosum (Hornsch.) Mitt.	PF	--	Pantropical; AC, AL, AM, AP, BA, ES, MG, PA, PE, RJ, RO, RR, SC and SP	AC828
PILOTRICHACEAE				
Callicostella pallida (Hornsch.) Ångstr.	--	1	Neotropical; AC, AL, AM, AP, BA, CE, DF, ES, GO, MT, MS, MG, PA, PR, PE, RJ, RS, RO, RR, RS, SC, SE, SP and TO	AC883
PYLAISIADELPHACEAE				
Isopterygium subbrevisetum (Hampe) Broth.	SF	--	Neotropical; AC, AM, AP, BA, CE, MG, PA, RJ, RO, SC and SP	AC803
I. tenerum (Sw.) Mitt.	--	2, 3	Neotropical; AC, AM, BA, CE, ES, DF, GO, MA, MG, MS, MT, PA, PB, PE, PI, PR, RJ, RR, RO, RS, SC, SP and TO	AC1087
Taxithelium planum (Brid.) Mitt.	PF, SF	1	Widespread; AC, AL, AM, AP, BA, DF, ES, GO, MA, MG, MS, MT, PA, PB, PE, PR, RJ, RO, RR, SC, SP and TO	AC803, AC880
SEMATOPHYLLACEAE				
Potamium lonchophyllum (Mont.) Mitt.	PF	--	South America; AM, BA, MT, PA and RJ	AC816
Sematophyllum subsimplex (Hedw.) Mitt.	PF, SF	1, 2, 3	Africa and the Americas; AC, AM, AP, BA, CE, DF, ES, GO, MA, MG, MT, MS, PA, PB, PE, PI, PR, RJ, RO, RR, RS, SC, SE, SP and TO	AC762, AC1080
Trichosteleum subdemissum (Besch.) A.Jaeger	--	1	Africa and the Americas; AM, BA, DF, GO, MA, MG, MT, PA, PI, PR, RJ, RO, RR, RS, SC, SP	AC956
T. papillosum (Hornsch.) A.Jaeger	PF, SF	2, 3	South America; AC, AP, AM, BA, ES, GO, MG, MT, PA, PE, RJ, RO, RR, SC, SE, SP and TO	AC777, AC1042
STEREOPHYLLACEAE				
Pilosium chlorophyllum (Hornsch.) Müll. Hal.	PF, SF	1	Neotropical; AC, AL, AM, AP, BA, CE, DF, ES, GO, MG, MT, MS, PA, PE, RJ, RO, RR, SP and TO	AC766, AC1018
THUIDIACEAE				
Pelekium scabrosulum (Mitt.) Touw	SF	--	Neotropical; AC, AM, AP, BA, DF, GO, MT, PA, PE, RO and RR	AC876
P. schistocalyx (Müll. Hal.) Touw	SF	--	Neotropical; AC, AM, AP, GO, MA, MT, PA, RO and RJ	AC771
LEJEUNEACEAE				
Acrolejeunea torulosa (Lehm. & Lindenb.) Schiffn.	SF	3	Neotropical; AC, AL, AM, BA, CE, DF, ES, GO, MA, MG, MS, MT, PA, PE, PR, RJ, RO, RR, RS and SP	AC786
Archilejeunea auberiana (Mont.) A.Evans	SF	2	Neotropical; AC, AP, AM, BA, ES, MS, MT, PA, PE, PR, RJ, RO, RR, RS and SP	AC878
A. fuscescens (Hamp. ex. Lehm.) Fulford	PF, SF	1, 2, 3	Neotropical; AC, AL, AM, BA, PA, PE, RJ and RR	AC838, AC1077

Continues

Table 1. Continuation.

FAMILY Species	Type of sucessional forest	Vertical zone of host trees in primary forest	Worldwide distribution; distribution in Brazil (by state)	Voucher specimen
A. parviflora (Nees) Schiffn.	PF	1, 2	Neotropical; AC, AP, AM, BA, ES, GO, MG, MS, MT, PA, PE, RJ, RO, RR, RS, SC, SP and TO	AC832
Caudalejeunea lehmanniana (Gottsche) A.Evans	SF	--	Pantropical; AL, AP, AM, BA, CE, ES, MT, PA, PE, PR, RJ, RO, RS, RR, SC, SE and SP	AC791
Ceratolejeunea coarina (Gottsche) Steph.	PF	--	Neotropical; AC, AL, AM, AP, BA, MA, PA, PE, PR, SE and SP	AC827
C. cornuta (Lindenb.) Steph	PF, SF	1, 2, 3	Neotropical; AC, AL, AM, AP, BA, CE, GO, MG, PA, PE, PR, RJ, RO,RR, SC, SE and SP	AC1060
C. cubensis (Mont.) Schiffn.	--	2, 3	Neotropical; AC, AL, AM, AP, BA, CE, ES, GO, MG, PA, PB, PE, PR, RJ, RO, RR, RS, SC, SP and TO	AC1041
C. guianensis (Ness & Mont.) Steph.	--	1, 2, 3	Neotropical; AM, BA, PA and PE.	AC954
C. laetefusca (Austin) R.M. Schust.	--	3	Neotropical; AC, AM, BA, ES, GO, MG, PA, PE, RJ, RR and SP	AC907
C. minuta G. Dauphin	PF	1, 2, 3	Brazil and the French Guiana; AL, AM, BA, PA and PE	AC811, AC1097
C. rubiginosa Steph.	--	2	Neotropical; AP, CE, PA, RJ, SP	AC905
Cheilolejeunea adnata (Kunze) Grolle	--	2, 3	Neotropical; AC, AL, AM, AP, BA, ES, MG, MT, PA, PE, PR, RN,RR, SC and SP	AC925, AC1098
C. aneogyna (Spruce) A. Evans	PF, SF	1, 2, 3	South America; AM, BA, ES, MA, PA, PE MG, RO and SP	AC764, AC1085
C. clausa (Nees & Mont.) R.M.Schust.	SF	3	Neotropical; AC, AL, AM, AP, BA, CE, ES, GO, MG, MS, MT, PA, PE, PR, RJ, RS, SC and SP	AC845
C. discoidea (Lehm. & Lindenb.) Kachr. & R.M.Schust.	--	2,3	Neotropical; AL, BA, CE, DF, ES, GO, MG, MS, MT, PA, RJ, RS, SE and SP	AC903
C. holostipa (Spruce) Grolle & R.-L.Zhu	--	2, 3	Neotropical; AL, AP, BA, ES, GO, MG, PA, PE, PR, RJ, SC, and SP	AC978, AC 1029
C. oncophylla (Ångstr.) Grolle & Reiner	SF	1, 2, 3	Neotropical; AC, AP, AL, BA, ES, GO, MG, MT, PA, PR, RJ, RR, SE, SC and SP	AC757, AC847
C. rigidula (Nees & Mont.) R.M.Schust.	PF, SF	1, 2, 3	Africa and the Americas; AC, AL, AM, AP, BA, CE, DF, ES, GO, MA, MG, MS, MT, PA, PB, PE, PR, RJ, RR, SC, SE, SP and TO	AC757, AC1045
C. trifaria (Reinw., Blume & Nees) Mizut.	SF	3	Pantropical; AC, AM, AP, BA, CE, DF, ES, GO, MG, MS, MT, PA, PB, PE, PR, RJ, RR and SP	AC790
Cololejeunea diaphana A. Evans	PF, SF	1	Pantropical; AL, AM, BA, DF, ES, GO, MG, MS, MT, PA, PE, RJ, RS, SC and SP	AC773
C. minutissima subsp. *myriocarpa* (Nees & Mont.) R.M.Schust.*	SF	--	Pantropical; AM, BA, MG, MS, PA, RJ and SP	AC782
C. subcardiocarpa Tixier	SF	--	Neotropical; AC, AL, AM, BA, CE, ES, GO, MG, MT, PA, PE, PR, RJ, SC and, SP	AC868
C. surinamensis Tixier	PF	--	South America; AM, MG, MS, MT, PA, RJ, SC and SP	AC830
Drepanolejeunea fragillis Bischl.	SF	3	Neotropical; AM, AL, AP, BA, CE, ES, MG, PA, PE RJ, RR, SE and SP	AC777
Haplolejeunea cucullata (Steph.) Grolle	PF	1	Africa and the Americas; BA, CE, PA and SP	AC813, AC1093
Harpalejeunea oxyphylla (Nees & Mont.) Steph	--	3	Neotropical; AL, AM, BA, PA, PB, PE, RJ, RR and SP	AC982
H. stricta (Lindenb & Gott.) Steph.	SF	1, 2, 3	Neotropical; AL, AC, BA, CE, MG, PA, PE, RJ, SC and SP	AC1026
Lejeunea adpressa Nees	SF	--	Africa and the Americas; AC, AL, AM, BA, CE, BA, ES, MG, MS, MT, PA, PE, PR, RJ, RR, SE, SC, SP and TO	AC773, AC875
L. boryana Mont.	--	2	Neotropical; AC, AM, BA, PA and RR	AC886

Continues

Table 1. Continuation.

FAMILY Species	Type of sucessional forest	Vertical zone of host trees in primary forest	Worldwide distribution; distribution in Brazil (by state)	Voucher specimen
L. caulicalyx (Steph.) E.Reiner & Goda	PF, SF	2	Neotropical; AC, BA, CE, DF, ES, MG, MS, MT, PA, PE, PR, RJ, RR, SC, SP and TO	AC762, AC861
L. cerina (Lehm. & Lindenb.) Gottsche	--	1, 2, 3	Neotropical; AC, BA, ES, MG, PA, PE, RJ, SP and TO	AC890
L. controversa Gottsche	PF	--	Neotropical; AC, AM, BA, MS, PA, PE, RJ and SP	AC836
L. flava (Sw.) Nees	SF	1, 2, 3	Pantropical; AC, AL, AM, BA, CE, DF, ES, GO, MA, MG, MS, MT, PA, PB, PE, PR, RJ, RS, RR, SE, SC, SP and TO	AC 1038
L. huctumalcensis Lindenb. & Gottsche	PF	1, 2	Neotropical; AL, AM, BA, PA, PE and SP	AC827, AC1077
L. laetevirens Nees & Mont.	SF	1	Neotropical; AC, AL, AM, AP, BA, CE, DF, ES, GO, MA, MG, MS, MT, PA, PB, PE, RJ,RN, RR, RS, SC, SE and SP	AC870
L. tapajosensis Spruce	SF	3	South America; AC, AM, BA, ES, PA, PE, RJ and TO	AC777
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.	SF	--	Neotropical; AC, AL, AM, AP, BA, CE, DF, ES, GO, MG, MT, PA, PE, PR, RJ, RR, RS, SC, SE, SP and TO	AC878
Lopholejeunea subfusca (Nees) Schiffn.	SF	1, 2	Pantropical; AC, AL, AM, AP, BA, CE, DF, ES, GO, MG, MS, MT, PA, PB, PE, RJ, RO, RR, SC, SP and TO	AC859
Microlejeunea acutifolia Steph.	PF, SF	2	Neotropical; PA	AC761, AC970
M. epiphylla Bischl.	SF	2, 3	Neotropical; AL, AP, BA, CE, ES, GO, MA, MG, MS, PA, PB, PE, RJ, SE, SP and TO	AC844, AC986
Odontolejeunea lunulata (Weber) Schiffn.	SF	--	Africa and the Americas; AC, AL, AM, AP, BA, CE, ES, MG, MT, PA, PE, PR, RJ, RS, RR and SP	AC850
Pictolejeunea picta (Gottsche ex. Steph.) Grolle	PF	1, 2	Neotropical; AM, PA, RJ and SC	AC816, AC1070
Prionolejeunea denticulata (Weber) Schiffn.	PF, SF	1	Neotropical; AC, AM, BA, CE, ES, GO, PA, PE, RJ, RR and SP	AC772, AC1017
P. muricatoserrulata (Spruce) Steph.	PF	1, 2	Neotropical; PA	AC816
Pycnolejeunea contigua (Nees) Grolle	SF	1, 2, 3	Pantropical; AM, BA, CE, ES, MG, PA, PE, PR, RR, RS, SC and SP	AC783, AC1029
P. macroloba (Nees & Mont.) Schiffn.	--	2, 3	Neotropical; AL, AM, BA, CE, ES, PA, PE and SP	AC983, AC1015
P. papillosa X.-L. He*	SF	2	Brazil; AM and PA	AC791
Rectolejeunea berteroana (Gottsche) A.Evans	SF	1, 2, 3	Neotropical; AC, AL, AM, AP, BA, ES, GO, MG, MT, PA, PE, PR, RJ, SC, SP and TO	AC781, AC1083
Stictolejeunea squamata (Willd. ex Weber) Schiffn.	--	3	Neotropical; AC, AL, AM, AP, BA, ES, GO, MA, MT PA, PE, MG, RJ, RS, SC, SP and TO	AC1071
Symbiezidium transversale (Sw.) Trevis.	SF	3	Neotropical; AC, AM, AP, CE, BA, ES, GO, MG, MT, PA, PE, RJ, SP and SC	AC1090
S. transversale var. *hookerianum* (Gottsche) Gradst. & Van Beek	SF	--	Neotropical; AM, AP, BA and PA	AC866
Taxilejeunea lusoria (Lindenb. & Gottsche) Steph.	PF	--	Neotropical; AM, AP, BA, ES, MG, PA,PR, RJ and SP	AC813
Thysananthus amazonicus (Spruce) Schiffn.	--	3	Neotropical; AC, AP, AM,BA, GO, MT and PA	AC 982, AC1012
Verdoornianthus marsupiifolius (Spruce) Gradst.*	SF	--	Brazil; AM, PA	AC782
Xylolejeunea crenata (Nees & Mont.) X.-L. He & Grolle	PF, SF	1	Neotropical; AL, AM, AP, BA, ES, GO, MA, MG, MT, PA, PE, RJ, RO, RR, SC and SP	AC779, AC871
LEPIDOZIACEAE				
Micropterygium leiophyllum Spruce	PF	--	Brazil; AM, GO, MG, MT, PA, RO, RJ and RR	AC812

Continues

Table 1. Continuation.

FAMILY Species	Type of sucessional forest	Vertical zone of host trees in primary forest	Worldwide distribution; distribution in Brazil (by state)	Voucher specimen
Monodactylopsis monodactyla (Spruce) R.M. Schust.	SF	--	Neotropical; AM, ES, PA, RJ, RO, RR,	AC779
Zoopsidela integrifolia (Spruce) R.M. Schust.	PF	--	Neotropical; AM, BA, DF, GO, MG, MT, PA, SE and SP	AC820
LOPHOCOLEACEAE				
Lophocolea martiana Nees	PF	--	Afro-Americana; AL, AM, AP, BA, CE, ES, GO, MG, MT, PA, PE, PR, RJ, RS, SC, SE and SP	AC835
PLAGIOCHILACEAE				
Plagiochila rutilans Lindenb.	PF	1	Neotropical; AC, AM, AP, BA, CE, ES, GO, MG, MT, PA, PE, RJ, RR, RS, SC and SP	AC828
P. subplana Lindenb.	PF	1, 3	Neotropical; AC, AM, AP, BA, DF, ES, GO, MG, MT, PA, PE, RJ, RR, RS, SC and SP	AC814, AC1049
RADULACEAE				
Radula flaccida Lindenb. & Gottsche	PF	--	Africa and the Americas; AC, AL, AM, BA, ES, MG, PA, PR, RR and SP	AC804
R. javanica Gottsche	SF	3	Pantropical; AC, AP, AM, BA, ES, GO, MG, MS, MT, PA, PE, PR, RJ, RS, SC and SP	AC870
R. surinamensis Steph.	PF	--	South America; SP and PA	AC836
R. mammosa Spruce*	PF	2	Neotropical; AM, BA, PA, RJ, SC and SP	AC829

PF – primary forest; SF – secondary forest; zone 1 – base; zone 2 – 2-10 m; zone 3 – 12-20 m; AC – Acre; AL – Alagoas; AM – Amazonas; AP – Amapá; BA – Bahia; CE – Ceará; DF – Distrito Federal (Federal District of Brasília); ES – Espírito Santo; GO – Goiás; MA – Maranhão; MG – Minas Gerais; MS – Mato Grosso do Sul; MT – Mato Grosso; PA – Pará; PB – Paraíba; PE – Pernambuco; PI – Piauí; PR – Paraná; RJ – Rio e 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 the state of Pará.

Thysananthus amazonicus (Spruce) Schiffn were of note because they are species typical of open environments. The bryophytes that occurred only in the 2-10 m and 12-20 m zones, together with those that occurred exclusively in either of those two zones, totaled 31 species, accounting for 45.5% of the species identified on the host trees evaluated (Tab. 1). Therefore, at least within the area studied, collecting samples only from the base zone of host trees could result in an underestimation of the extent of the bryophyte flora. The presence of species that occur above a height of 2 m lends credence to the supposition made by Gradstein (1995), who suggested that bryophyte species richness can be underestimated in studies that do not involve sampling of the upper trunk and canopy of host trees.

Despite the fact that our study was conducted in region that had been deforested by extensive human activity, the species identified corresponded to 31% of the bryophyte flora of the state, as well as including species that represented new records for the state and species endemic to Brazil. Nevertheless, we also found that bryophyte species richness was lower in secondary forest than in primary forest. The fact that 45.5% of the species recorded in primary forest occurred within the 2-20 m height range shows the importance of sampling the upper trunk and canopy zones in floristic studies of bryophytes.

Our findings indicate the need for further floristic inventories of bryophytes in other areas of Amazon forest within the state of Pará, such as the southeastern and southwestern mesoregions. The data presented here increase the existing knowledge of the biological diversity within the state of Pará, by identifying species that are indicative of certain environments and including new records of species considered endemic, thus contributing to the implementation of conservation policies.

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