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Original Paper

Bryophyte flora in an Amazon island: structure of communities in areas of different levels of anthropization

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Abstract

The present study is aimed to evaluate the richness, composition and spatial distribution of bryophytes occurring in Mosqueiro Island, in the Amazon forest. Forty-one 100-m² plots in 37 flooded and 4 non-flooded environments were selected for data collection, all substrate found were considered. The results were compared with surveys in other islands from the state of Pará and were analyzed according to frequency of populations, colonized substrates, light tolerance guilds, and distribution in Brazilian biomes. Ninety-seven species were recorded, distributed in 36 genera and 17 families, being 57 (58.7%) liverwort and 40 (41.2%) moss species. The rare species stood out with 53 species (54.08%). High similarity was observed between corticolous and epixylic communities, and between the terricolous community and the bryophytes found growing on charcoal, which is an artificial substrate. In relation to light tolerance guilds, generalist species prevailed (52 species, 53.6%). As for phytogeographic distribution, there was a predominance of taxa with occurrence in the Amazon and Atlantic rainforest (35 species, 37.11%). *Ceratolejeunea ceratantha* is reported for the first time for the state of Pará. The level of anthropization in the island was showed mainly by high richness and occurrence of generalist species underscores and well-adapted species to stressed conditions, evidencing changes in the bryophyte community structure.

Key words: amazonian estuaries, anthropization, bryophyte flora, ecology, environmental modification.

Resumo

O presente estudo teve como objetivo avaliar a distribuição espacial de briófitas ocorrentes na Ilha de Mosqueiro, na Amazônia. Foram selecionadas 41 parcelas de 100 m² em ambientes alagados e não alagados para coleta de dados. Os resultados foram comparados com os levantamentos de outras ilhas do estado do Pará e analisados segundo frequência de populações, substratos colonizados, guildas de tolerância à luz e distribuição nos biomas brasileiros. Foram registradas 97 espécies, distribuídas em 36 gêneros e 18 famílias, sendo 57 (58,7%) hepáticas e 40 (41,2%) espécies de musgo. As espécies raras se destacaram com 53 espécies (54,08%). Observou-se alta similaridade entre as comunidades corticícolas e epíxilas, e entre a comunidade terrícola e com as briófitas encontradas crescendo no carvão, que é um substrato artificial. Em relação às guildas de tolerância à luz, prevaleceu a espécie generalista (52 espécies, 53,6%). Quanto à distribuição fitogeográfica, houve predomínio de espécies com ocorrência na Amazônia e Mata Atlântica (35 espécies, 37,11%) e espécies endêmicas da Amazônia (10 espécies, 10,3%). *Ceratolejeunea ceratantha* é relatada pela primeira vez para o estado do Pará. O nível de antropização na ilha foi evidenciado principalmente pela alta riqueza e ocorrência de espécies generalistas e bem adaptadas às condições de estresse, evidenciando alterações na estrutura da comunidade de briófitas.

Palavras-chave: estuário amazônico, antropização, brioflora, ecologia, modificação ambiental.

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Introduction

Tropical forests hold the greatest richness and diversity on planet Earth (Myers 1991), and around 40% of the remaining tropical rainforests in the world belong to the Amazon forest, playing a key role in maintaining biodiversity and climate (Laurance *et al*. 2001; Phillips & Brienen 2017). However, the fragmentation of these ecosystems has considerably grown with the increase of human occupation, which has also created a necessity for more areas for exploitation of forest products and food cultivation (Ramankutty & Foley 1998; Arroyo-Rodríguez *et al.* 2017). This has resulted in the loss or decrease of biodiversity, isolation of populations, and changes in the migration and dispersal patterns of species (Laurance *et al.* 2002; Shackleton *et al.* 2018).

Anthropic pressures on natural ecosystems are the main cause of losses in biodiversity and ecological processes in the Amazon, creating highly fragmented landscapes in which the remaining forest patches become smaller and more susceptible to edge effects, changing the dynamics of populations and communities (Viana & Pinheiro 1998; Renó *et al*. 2016). The effects of fragmentation are even more severe in island environments because of geographical restrictions and a high rate of species with endemic and restricted distribution (Kier *et al.* 2009). In this sense, extinction thresholds may increase with habitat loss, because adequate environments are necessary for the persistence of communities (Fahrig 2002).

Increased stress and biotic decay caused by anthropic pressures in forests, such as creation of unproductive pastures, selective logging and burning, can be considered sources of greenhouse gas emission, as carbon stored in forest biomass is lost to the atmosphere (Fearnside 2003). Thus, the substitution of forests with other land cover types has generated a discussion on how to protect the intact remaining biodiversity (Laurance *et al.* 2012).

Studies have revealed strong human impact over the years in Mosqueiro Island, in the Amazon, including exploitation of natural resources and fragmentation of forest remnants caused mainly by logging and burning (Venturieri *et al.* 1998). These activities have probably caused loss of habitats and modification of local diversity. Thus, studies to produce information about effects of environmental changes caused by human impact on the biological dynamics of plant communities are sorely needed. In this context, bryophytes act as an excellent biological model for monitoring disturbed habitats (Hallingbäck & Hodgetts 2000), as they are sensitive to small environmental fluctuations (Robinson & Waterman 2014).

Brazil has relevant works on the dynamics of bryophytes on islands, Pará being the state with the largest number of works, mainly addressing anthropic pressure. For example, the study of the bryophyte flora of the artificial island of Germoplasma in Tucuruí Lake showed a low richness of species and predominance of generalist taxa, which the authors believed to be associated with anthropic disturbances (Ilkiu-Borges *et al*. 2004). Also, a strong influence of tourism was observed in the marine island of Algodoal (Ilkiu-Borges *et al.* 2009). In Marajó Island, Brito & Ilkiu-Borges (2013) reported that there was a significant difference between the bryophyte flora of the municipalities of Soure and Cachoeira do Arari, with the species in the former presenting niches of greater tolerance as a possible result of forest degradation in the area. Still in Marajó Island, in the municipality of Salvaterra, environmental changes and extreme conditions in mangroves and sandbanks of the Bacurizal Ecological Reserve may have altered the quality of the bryophyte flora (Garcia *et al.* 2014). All these works showed changes in the bryophyte flora of islands, highlighting the high richness of species well adapted environmental changes caused by human impact.

Based on the above-mentioned results, bryophytes have been shown to be an efficient organism that can be used as a biological model to understand forest dynamics, this study aimed to compare the structure of bryophyte communities in areas of different levels of anthropization of forest remnants in Amazon.

Materials and Methods

Study area

The study area has remnants of Amazon secondary forests, including flooded (várzea) and non-flooded (Terra Firme) forests, fragmented by anthropic action associated mainly with urbanization, road opening and family crops, located at the Marí-Marí road that assess road to the communities of Caruaru and Castanhal do Marí-Marí (01°10’09”S, 48°24’28.8”W) (Fig. 1), in Mosqueiro Island, Pará, Brazil. The region has a hot equatorial climate (AM type) according to Köppen classification, with annual temperature and precipitation of 25.9 ºC and 2,900 mm, respectively, and 84% relative humidity on average. This information was obtained from the database of the National Institute of Meteorology (<http://www.inmet.gov.br/portal/index.php?r=home2/index>).

Sampling, collection and taxonomic identification

Six collection trips were undertaken from January 2015 to April 2016. Understory samples (0–2 meters high) were randomly collected within a total of forty-one 100-m² plots. Those plots were arranged 100 meters or more from the nearest plot, avoiding repetition of bryophyte assemblages by proximity (Fig. 1d), using usual sampling techniques for bryophytes (Vanderpoorten *et al.* 2010) and the methodology of Glime (2017) for field collection and preservation of botanical material. Of the total plots, 37 were located in non-flooded forest and four in flooded forest. Nineteen plots occurred in clearings (logging and burning areas), 17 in secondary forest areas (Capoeiras) and five in cultivations areas.

Each substrate colonized by bryophytes was defined as a sample, and each colonizing species was considered as one occurrence. Specialized literature and identification keys were used for the taxonomic study of the samples (Florschütz 1964; Lisboa 1993; Reese 1993; Gradstein 1994; Ilkiu-Borges 2000; Dauphin 2003; Gradstein & Costa 2003; Yano & Peralta 2007; Zartman & Ilkiu-Borges 2007; Gradstein & Ilkiu-Borges 2009). The families and species sampled were organized following the taxonomic classification system based on Goffinet *et al.* (2009) for Bryophyta and Crandall-Stotler *et al.* (2009) for Marchantiophyta, with modifications. Scientific names were confirmed by consultation to the online database the Brazil Flora Group (BFG 2018). Vouchers were incorporated into the Prof. Dr. Marlene Freitas da Silva (MFS) herbarium of the State University of Pará.

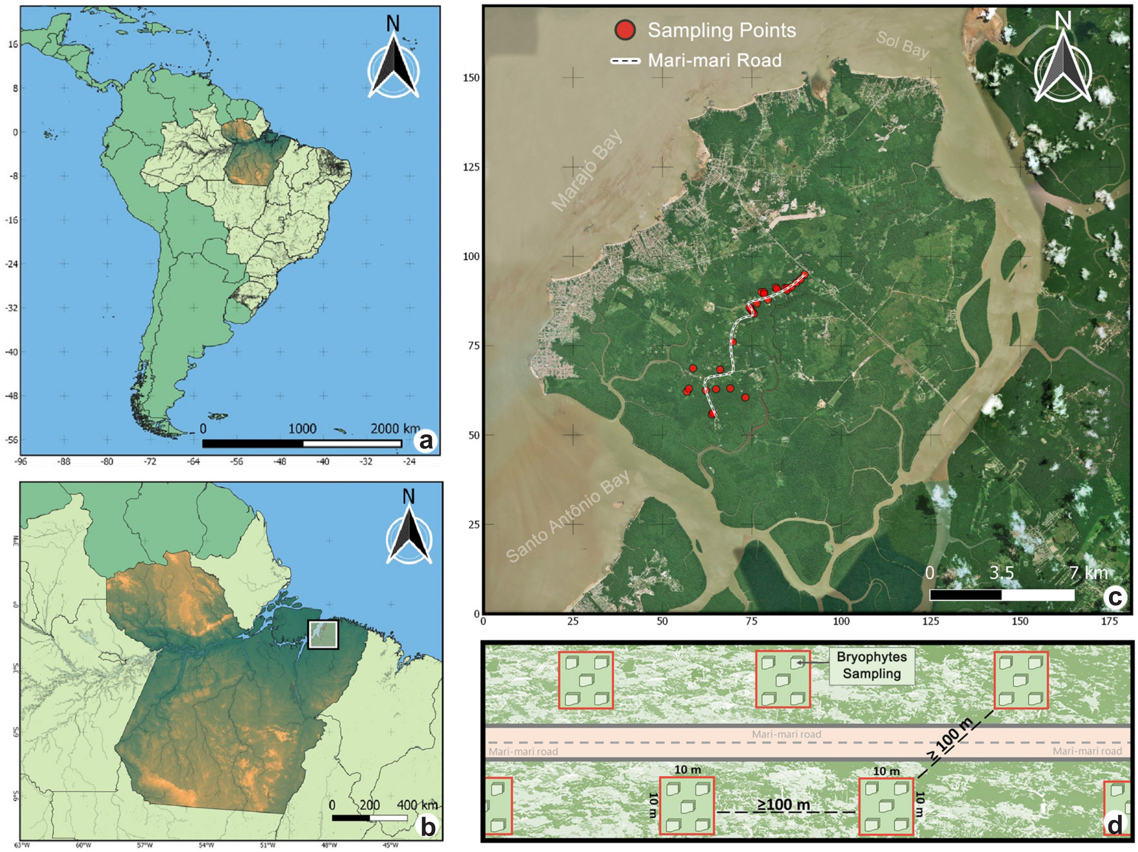

Figure 1 – a-d. Location map of collection points Mosqueiro Island, Belém, Pará, Brazilian Amazon – a. localization of Brazil in South America; b. localization of Pará in Brasil; c. localization of sampling points in Mosqueiro Island, Pará; d. methodology scheme adopted for the collection of bryophytes end plot distance along Mari-mari road.

Data analysis

Species presence/absence matrices prepared for each plot were used to compute the Mao Tau function to test the sampling effort based on accumulation curves (Colwell *et al*. 2004). The expected richness for the area was predicted through the estimator Jackknife (Meyer et al. 1986). This test was run in the EstimateS 9.1.0 software (Colwell 2009). The absolute frequency of the species was classified according to Silva & Pôrto (2007) and adapted according to Fagundes *et al*. (2016), where species with > 1 and < 5 occurrences are considering rare, > 5 and < 20 occurrences common, and > 20 occurrences constant.

The bryophyte flora of Mosqueiro was compared to surveys of liverworts and mosses from other islands in the state of Pará available in the literature, namely, Marajó Island (Lisboa & Maciel 1994; Lisboa *et al*. 1998, 1999; Brito & Ilkiu-Borges 2013; Garcia *et al*. 2014), the artificial fluvial island of Germoplasma in the Tucuruí reservoir (Ilkiu-Borges *et al*. 2004), Algodoal-Maiandeua Island in Maracanã municipality (Ilkiu-Borges *et al*. 2009), and Combú Island in Belém (Moura *et al*. 2013). The matrix consisted of 158 taxa; species with only one occurrence per island were removed in order to increase the efficiency of the analysis. Similarity was calculated using the Sørensen coefficient. The unweighted pair group method using arithmetic averages algorithm (UPGMA) was adopted for calculations and construction of a dendrogram. The MVSP 3.0 software was used in this analysis (Kovach 2011).

For the study of species distribution, the species were classified according to the ecological groups of light tolerance, namely, sun specialists, shade specialists, and generalists. The literature used to support this classification was Richards (1984), Cornelissen & ter Steege (1989), Gradstein *et al*. (2001), Pantoja *et al*. (2015), and Fagundes *et al*. (2016). The species were classified as to substrate colonized, based on Robbins (1952); they were live trunk (Corticolous), dead trunk (Epixylic), leaf (Epiphyllous), soil (Terricolous) and rocks (Rupicolous), with an adaptation to include termite mounds and charred trunks (Charcoal). The floristic similarity between substrates was analyzed with basis on a presence/absence binary matrix with information on 77 taxa. In this case, species with only one occurrence were excluded to increase the efficiency of the analysis. The same methods above mentioned for calculations and generation of dendrograms were used in this analysis.

The distribution of the species in the phytogeographic domains of Brazil on which they have been recorded was investigated. To this end, the online databases the Brazil Flora Group (BFG 2018), SpeciesLink and the works of Peralta & Yano (2008) and Yano (2004, 2012, 2014) were consulted.

Results

Floristic composition

Four hundred and forty-five (445) samples were analyzed, resulting in the record of 955 individuals from 97 species and 17 families(Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.16863670.v1). Liverworts were more prevalent both in terms of richness (57 spp.) and number of individuals (596), with a predominance of *Lejeuneaceae* (49 spp. and 536 individuals) and highlight to *Ceratolejeunea cornuta* (Lindenb.) Schiffn. with 114 individuals. Mosses (40 spp., 359 individuals) were represented mainly by *Calymperaceae* (16 spp. 126) and *Sematophyllaceae* (five spp., 81 individuals), with *Octoblepharum pulvinatum* (Dozy & Molk.) Mitt. (48) and *Microcalpe subsimplex* (Hedw.) W.R. Buck (52) being the species with the highest number of individuals in each family, respectively. *Ceratolejeunea ceratantha* (Nees & Mont.) Steph. is being cited for the first time for the state of Pará (Fig. 2). The fundamental niche of the most common species found in this study contributes to draw a picture of the current state of conservation of the forest fragment of Mosqueiro Island, where there is intense anthropization resulting from logging and burning. Species with narrower niches and that do not tolerate such pressure can be extinct at local scale, giving rise to the colonization of more generalist species, modifying the real biological diversity of the site.

The estimated richness observed for the total set of samples was 122 species. Rare species represented about 54.08% (53 spp.) of the total pool of species, followed by common species with 33.61% (30 spp.) and constant species with 14.28% (14 spp.).

Similarity between the bryophyte flora of islands

In the analysis of floristic similarity between bryophytes from the forest fragment of Mosqueiro Island and other non-flooded ecosystems studied in the state of Pará, two distinct groups were distinguished (Fig. 3). The group with greatest similarity was formed by Combu Island, Marajó Island and Mosqueiro Island, and the second comprised Tucuruí Island and Algodoal Island, the two islands with lower richness in relation to the others.

Ecological groups

The generalist guild corresponded to more than half of the species. This guild prevailed not only in terms of richness, with 53.6% (52 spp.) of the species, but also occurrences, with 75.65% (721) of the individuals. Among the most representative generalist taxa, *Calymperes erosum* Müll. Hal. (27), *Ceratolejeunea cornuta* (Lindenb.) Steph. (114), *Cheilolejeunea oncophylla* (Aongström) Grolle & E. Reiner. (39), *Cheilolejeunea rigidula* (Mont.) R.M.Schust. (53), *Octoblepharum pulvinatum* Dozy and Molk. Mitt. (48), *Microcalpe subsimplex* (Hedw.) Mitt. (52) and *Taxithelium planum* (Brid.) Mitt. (27) stood out. The group of shade specialists had the second highest richness, with 24.75% (26 spp.) of the sampled species and 11.75% of the individuals (112). Sun specialists were represented by 21.65% (21 spp.) of the species and 12.6% (120) of the individuals.

Species distribution by substrate

Corticolous species were predominant, with 46.9% (447) of the individuals, observed in different heights in the host trees. Dead trunk was the second most colonized substrate, with 35.5% (339) of the individuals, followed by leaf 9.7% (92), soil 3.2% (31), charred trunk 2.7% (26), termite mound 1.7% (17), and rock 0.3% (3).

The bryophyte communities colonizing the studied substrates were grouped into three

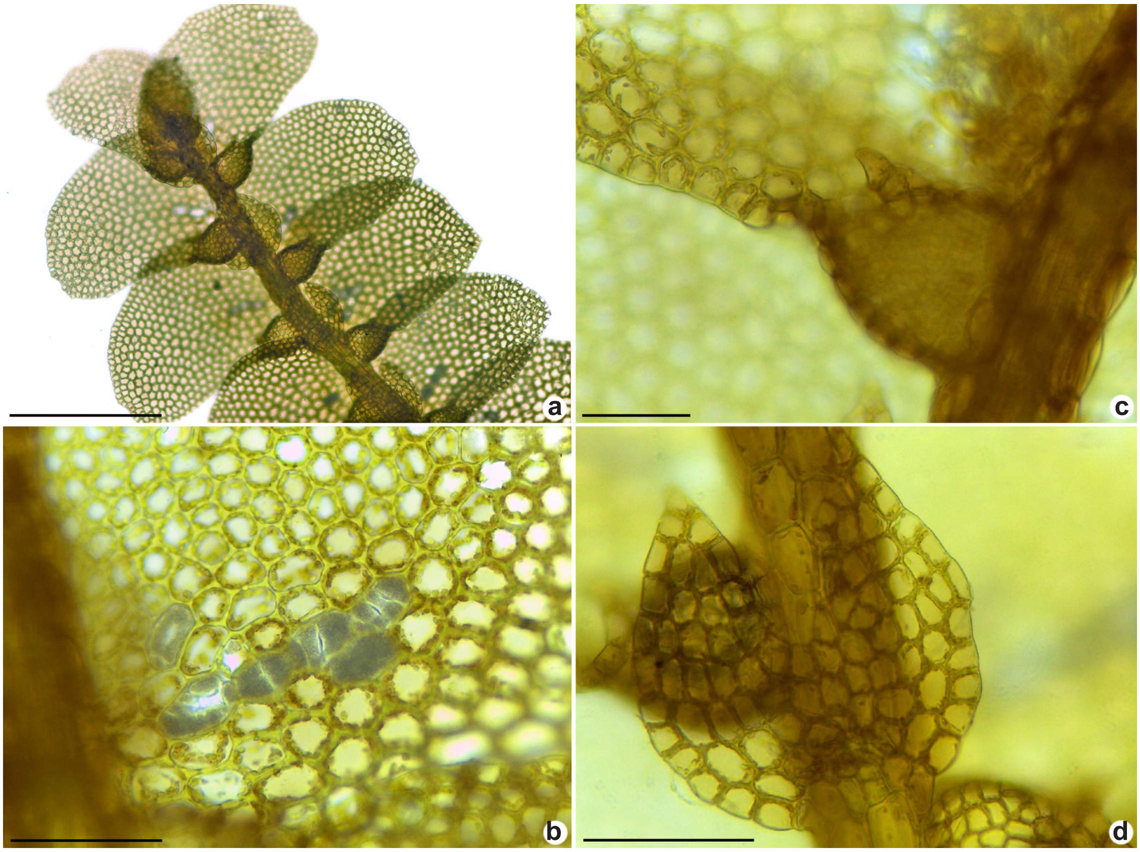

Figure 2 – a-d. *Ceratolejeunea ceratantha* – a. stem portion; b. lobule; c. ocelli; d. underleaves.

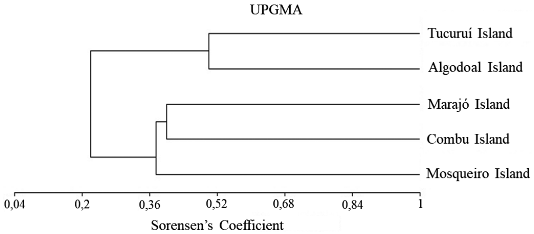

Figure 3 – Floristic similarity dendrogram between islands of the state of Pará, Brazilian Amazon.

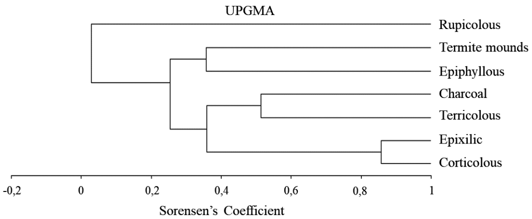

Figure 4 – Floristic similarity dendrogram of bryophyte species colonizing substrates inventoried in Mosqueiro Island, Belém, Pará, Brazilian Amazon.

groups with different levels of similarity (Fig. 4). The greatest similarity was found between the corticolous and epixylic communities, which shared 27 exclusive species, with high occurrence of *Calymperes erosum* Müll. Hal. and *Octoblepharum pulvinatum* (Dozy & Molk.) Mitt. The second greatest similarity was seen between the charcoal and terricolous communities, sharing nine species, with prominence of *Callicostella pallida* (Hornsch.) Ångström, *Campylopus surinamensis* Müll. Hal., *Ceratolejeunea cornuta* (Lindenb.) Schiffn., *Fissidens zollingeri* Mont., *Trichosteleum papillosum* (Hornsch.) A. Jaeger and *Taxithelium planum* (Brid.) Mitt. Epiphyllous and termite mound communities showed the third greatest similarity with five shared species, namely, *Ceratolejeunea cornuta* (Lindenb.) Schiffn., *Cheilolejeunea rigidula* (Mont.) R.M.Schust., *Lejeunea laetevirens*, *Harpalejeunea stricta* (Lindenb. & Gottsche) Steph., and *Rectolejeunea berteroana* (Gottsche ex Steph.) A. Evans, Nees & Mont. The low similarity between the rupicolous community and all the others occurred because rocks were colonized only by *Taxithelium concavum* (Hook.) Spruce *ex* J. Florsch.

Species distribution in Brazilian phytogeographic domains

The species registered in Mosqueiro Island showed a wide distribution in Brazilian phytogeographic domains. Approximately 37.11% were restricted to the Amazon and Atlantic Forest phytogeographic domains, with emphasis on *Ceratolejeunea cornuta* (Lindenb.) Schiffn., *Ceratolejeunea coarina* (Gottsche) Steph., *Cheilolejeunea oncophylla* (Aongström) Grolle & E.Reiner, *Cyclolejeunea convexistipa* (Lehm. & Lindenb.) A.Evans, *Harpalejeunea stricta* (Lindenb. & Gottsche) Steph., and *Symbiezidium transversale* (Sw.) Trevis.

Discussion

Species accumulation curves

In floristic studies conducted in tropical forests, species accumulation curves tend to non-stabilization due to the high frequency of rare species, which contribute to the steep growth of the curves (Schilling & Batista 2008). In the case of bryophytes in other non-flooded areas in the Amazon, the predominance of rare species has been cited for Caxiuanã National Forest, Pará (Alvarenga & Lisboa 2009). In this sense, rare species are important for the conservation of the biodiversity of these ecosystems and yet are still largely neglected in conservation decision-making. Non-stabilization of curves was also observed in non-flooded forests fragments of the Environmental Protection Area of Tucuruí Lake (Garcia *et al.* 2014), Volta Grande do Xingu (Pantoja *et al.* 2015), and Gunma Ecological Park (Fagundes *et al.* 2016), all in the state of Pará.

Areas that lose a large proportion of their original habitat or are severely fragmented eventually lose some of their species (MacArthur & Wilson 1967). In this context, high frequency of rare species and advanced stages of anthropization, as in the case of the forest fragment studied here, are considered by Myers *et al.* (2000) as indicators of priority for biodiversity conservation, because of their susceptibility to local extinction.

Floristic composition

The greater representativeness of liverworts in terms of richness and occurrences is recurrent in humid tropical forests (Gradstein & Costa 2003). Liverworts were represented here mainly by Lejeuneaceae, which holds about 70% of the richness of bryophyte species in the Amazon and the largest number of individuals in the neotropics (Gradstein *et al.* 2001). In the Amazon, some Lejeuneaceae taxa have morphological characteristics that contribute to their adaptation to different microhabitats and height gradients on host trees (Mota-de-Oliveira 2018). Such characteristics guarantee the wide distribution of these taxa in the studied fragment.

Calymperaceae and Sematophyllaceae are the most represented moss families reported for the Amazon (Gradstein *et al*. 2001). In Brazil, these families have a history of predominance in disturbed environments and are mainly represented by *Calymperes palisotii* Schwägr. and *Microcalpe subsimplex* (Hedw.) W.R. Buck, two species that are considered to indicate environmental changes (Visnadi & Monteiro 1990; Bastos & Yano 1993; Lisboa & Ilkiu-Borges 1995; Santos & Lisboa 2008).

The species registered in this study have morphological traits that provide them with greater resistance to colonize different habitats, which are in turn subject to a high level of anthropization in the forest fragment of Mosqueiro Island. The most frequent species in areas exposed to intense light incidence in this study, *Ceratolejeunea cornuta* (Lindenb.) Schiffn., had inflated lobes, utricles and dark leaves. According to Cornelissen & ter Steege (1989), morphometric variation of lobes is a response of the plant to environmental conditions of low humidity and intense sun exposure. Utricles, on the other hand, are characterized by Dauphin (2003) as structures adapted to extracellular water retention. Dark pigmentation blocks excess light in photosynthetic cells, reduces reactive oxygen generated by solar radiation, and assists in antimicrobial protection (Chen *et al*. 2018). The great representativeness of *Cheilolejeunea rigidula* (Mont.) RM Schust. is probably related to its wide phenotypic plasticity, which allows it to develop aptitudes in different environments (Ilkiu-Borges 2000; Zartman & Ilkiu-Borges 2007) and tolerate the wide variety of microhabitats (Rydin 2009). Another species with wide occurrence was *Cyclolejeunea convexistipa* (Lehmann & Lindenberg) A. Evans, characterized by phenotypic plasticity and dark pigmentation (Evans 1904).

Among mosses, the greater representation of *Octoblepharum pulvinatum* (Dozy & Molk.) Mitt. may be related to the functional traits of this species, such as the presence of a costa that assists in the rapid absorption and transport of water, in addition to structural support to leaves during desiccation (Frahm 1985), and the stratified layer of leucocysts (Yano 1992) that protects photosynthetic chlorocysts from intense sunlight incidence (Glime 2014). The large occurrence of *Calymperes erosum* Müll. Hal. can also be related to its functional traits, including the presence of papillose cells that facilitate the absorption of water from the atmosphere (Gradstein *et al.* 2001; Buck 2003), and hyaline cells (cancellinae and teniolae) (Lisboa 1993) which are responsible for the retention and rapid absorption of water, retarding dehydration (Goffinet *et al*. 2009). Futhermore, *C. erosum* is a fundamental indicator of habitat quality, since this species has frequently been associated with the recovery of degraded areas (Lopes *et al.* 2016).

Microcalpe subsimplex (Hedw.) Mitt. and *Taxithelium planum* (Brid.) Mitt. individuals are also reported in the literature as presenting a wide occurrence and features that aid in water absorption, such as hyaline (alar) and papillose cells (Buck 2003; Yano & Peralta 2007). *Ceratolejeunea ceratantha* (Nees & Mont.) Steph., which is cited for the first time for the state of Pará, is found mainly in submontane non-flooded forests, colonizing live trunks, crowns and wet rocks (Dauphin 2003; Bastos & Yano 2008; Dauphin *et al.* 2015). Fagundes *et al.* (2016) stressed that the new occurrences of bryophytes for the state of Pará reinforce the importance of forest fragments and their conservation, mainly in the Amazon, a region with high biodiversity.

Similarity between the bryophyte flora of islands

The greater similarity between the Marajó, Mosqueiro and Combu islands can be attributed to the similar microclimate conditions of the studied areas, which are formed by non-flooded forests with similar phytophysiognomy. In addition, these islands are estuarine and bathed by the Pará River (Gregorio & Mendes 2009a), which may also influence and lead to similar microclimate conditions. Marajó Island is influenced by tributaries of the Marajó Bay, and Combu Island by tributaries of the Guajará Bay, while Mosqueiro Island is bathed by tributaries of both bays (Gregorio & Mendes 2009b). Five species, *Archilejeunea parviflora* (Nees) Schiffn., *Callicostella pallida* (Hornsch.) Ångstr., *Cheilolejeunea adnata* (Kunze) Grolle., *Taxithelium planum* (Brid.) Mitt. and *Trichosteleum papillosum* (Hornsch.) A. Jaeg. occurred in a restricted way in the islands, (Lisboa & Maciel 1994; Lisboa *et al*. 1998, 1999; Ilkiu-Borges *et al*. 2009; Moura *et al*. 2013; Garcia *et al*. 2014).

The similarity between the marine island of Algodoal (Oliveira-Brito & Aquino 2013) and the fluvial island of Germoplasma in Tucuruí Lake (Ilkiu-Borges *et al.* 2004) may be related by the island size, the conservation status of these areas, under high anthropization and loss of forest integrity. These aspects possibly influence the bryophyte flora more intensively than the origin of the water and the distance between the islands. Three restricted generalist species, *Calymperes palisotii* Schwägr., *Lejeunea laetevirens* Nees & Mont., and *Microcalpe subsimplex* (Hedw.) Mitt., occurred in these two areas, reinforcing their high degree of disturbance.

Brito & Ilkiu-Borges (2013) analyzed the bryophyte flora of the municipalities of Soure and Cachoeira do Arari Marajó Island and noted a significant difference between them, where Soure presented species of wide ecological range, as a possible result of forest degradation in the area. Then, in Bacurizal Ecological Reserve in the municipality of Salvaterra, Garcia *et al.* (2014) analyzed the proportion of tolerance guilds and confirmed that environmental changes and extreme conditions in mangroves and sandbanks can alter the quality of the bryophyte flora. These two studies demonstrated changes in the bryophytes growing on islands, highlighting the high richness of species well adapted to abiotic variations in response to environmental changes.

Ecological groups

The predominance of the group of generalist species may be associated with environmental changes (Fagundes *et al.* 2016), which are frequent in the studied area. These species are indifferent to forest degradation. On the other hand, specialist species have narrow fundamental niches that make them more fragile to environmental disturbances (Acebey *et al*. 2003). In a non-flooded forest fragment in Gunma Ecological Park, Fagundes *et al.* (2016) registered 103 species, of which 48 were generalists. Twenty three of these generalist species also occurred in the present study. In an open ombrophilous forest fragment in the municipality of Porto Velho, in the state of Rondônia, 33 species bryophytes were recorded, and 15 were generalists (Cerqueira *et al.* 2015).

Both in Gunma Ecological Park (Fagundes *et al*. 2016) and Porto Velho (Cerqueira *et al.* 2015) forest fragments, some of the shared species were also recorded in the forest fragment of Mosqueiro Island. They were *Calymperes erosum* Müll. Hal., *Calymperes palisotii* Schwägr., *Ceratolejeunea cornuta* (Lindenb.) Schiffn., *Cheilolejeunea oncophylla* (Aongström) Grolle & E.Reiner, *Cheilolejeunea rigidula* (Mont.) R.M.Schust., *Fissidens prionodes* Mont., Micr. Buck, *Octoblepharum albidum* Hedw., and *Octoblepharum pulvinatum* (Dozy & Molk.) Mitt. These results show that there is a specific group of bryophytes that occurs more frequently in forest fragments, emphasizing its importance as an indicator of environmental quality.

Specialist species in the Amazon occur along specific height and microhabitat gradients (Mota-de-Oliveira *et al.* 2009). In an analysis of the vertical gradient in forests with different succession stages in the state of Pará, sun specialists [*Harpalejeunea oxyphylla* (Nees & Mont.) Steph., *Radula javanica* Gottsche, *Symbiezidium transversale* (Sw.) Trevis., *Stictolejeunea squamata* (Willd, *ex*. Weber) Schiffn., and *Thysananthus amazonicus* (Spruce) Schiffn] were present above 12 to 20 meters in host trees (Tavares-Martins *et al.* 2014). All these species were registered in the present study, but in the understory, at heights below two meters. Such modification may be a response to the loss of typical canopy microhabitats due to fragmentation and opening of the forest structure. The predominance of shade specialists is directly related to the area studied, as they are the more common group in humid and shaded forest areas (Gradstein *et al*. 2001).

Species distribution by substrate

The similarity and specificity regarding the substrates may be related to the physical-chemical properties of the substrates, which can act as environmental filters that determine the colonization of communities (Hespanhol *et al.* 2011; Gosselin *et al.* 2017). The greater occurrence of corticolous species found in this work is based on the fact that there is a greater availability of live and decomposing trunks in tropical forests (Hallingbäck & Hodgetts 2000). In the Amazon, corticolous species predominated in the non-flooded forest in the municipality of Benjamin Constant (MA) (Saldanha *et al*. 2018) and in the open forest fragment in Porto Velho (Cerqueira *et al.* 2015), followed by epixylic species (Richards 1984). Colonization of dead trunks occurs in succession as a result of the levels of decomposition of organic matter. These substrates are first colonized by facultative epixylic taxa, then by late epixylics, and finally by specialist epixylics (Rydin 2009). Facultative epixylics occur in the early stages of decomposition, where the properties of the dead barks are similar to that of live trunks (Söderstrom 1988). This is a possible explanation for the marked similarity between these two substrates, considering that clearings in the collection sites were recent and the decomposition of trunks was probably at initial stages.

The low representativeness of terrestrial species may be related to the accumulation and deposition of litter in tropical forests that prevents bryophytes from colonizing the soil (Wagner *et al.* 2014). The opening of clearings and consequently the burning of wood provides greater availability of these two substrates, thus being the first sites to be colonized by bryophytes (Maytby *et al*. 1990). Charcoal is considered an artificial substrate generated in response to the degradation of natural habitats by human activity, with creation of new microhabitats for the colonization of bryophytes. Bryophytes colonizing carbonized trunks are recurrent in areas degraded by burning (Duncan & Dalton 1982; LaGreca *et al*. 2005; Ryömä & Laaka-Lindberg 2005) and are reported together with soil species as pioneers in the ecological succession following burning (Maltby *et al.* 1990).

Humidity in the habitats acts as a limiting factor for epiphyllous communities. These communities are vulnerable to environmental stress and require high humidity for their establishment (Richards 1984; Zartman 2003). In this study, only seven species were exclusively epiphyllous and 14 were facultative, as they can colonize other substrates (Cornelissen & ter Steege 1989). This richness may be related to the proliferation of generalist species that resulted from the deterioration of microhabitats. Termite mounds showed a great capacity of water retention in the surveyed environments, which favored their colonization by bryophytes. The similarity between the epiphyllous and termite communities is possibly associated with the transience of the substrates that filter species with a life cycle associated with rapid replacement of the substrate.

Low richness of rupicolous species has been mentioned for the Amazon (Brito & Ilkiu-Borges 2013; Garcia *et al.* 2014; Cerqueira *et al*. 2015) and associated with the shortage of rocks in humid tropical forests (Hallingbäck & Hodgetts 2000). However, plants that colonize rocks are important for retaining particles carried off in water runoff, as well as preventing substrate erosion (Ando & Matsuo 1984).

Species distribution in Brazilian phytogeographic domains

The occurrence of species well distributed in Brazilian biomes may be the result of their production of small, light and desiccation-tolerant spores, easily transported over long distances by the air and water streams (Mogensen 1981; Vanderpoorten & Hallingbäck 2009). The Amazon and the Atlantic Forest are phytogeographic domains composed of dense and humid rainforests (Méio *et al.* 2003) with biogeographic connection in past times, forming an extensive forest cover (Sobral-Souza *et al.* 2015). This history probably explains the greater representativeness of species restricted to these two biomes, highlighting the floristic similarity of bryophytes shared by them until present days (Silva *et al.* 2004).

The fragmented areas in Mosqueiro Island have potential for biodiversity conservation, indicated by the high frequency of rare species, with restricted and endemic distribution, and the occurrence of a bryophyte species reported for the first time for the state of Pará. It was observed that the islands with similar ecosystems and microclimate conditions tend to present a bryophyte floristic composition with niches in the same ecological tolerance range, with greater occurrence of species with functional characteristics that confer them desiccation tolerance. In addition, the high richness and occurrence of generalist species underscores the high degree of anthropization of the studied site, reinforcing the need to expand collections and studies in estuarine and island environments in the Amazon in order to collaborate with the development of measures for the conservation of biological diversity.

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