



Does the stage of decomposition of fallen logs influence the bryophyte community? Understanding the epixylic bryophytes in a Nebular Forest in Southeastern Brazil

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ABSTRACT

Epixylic bryophytes – colonizers of decaying logs – are the third most endangered group of these plants, but few studies have been focused on them. Thirty logs in the proximity of three trails in a nebular forest in the Serra da Bocaina National Park in the state of São Paulo, Brazil, were sampled. Our objective was to study and compare the composition of the communities in three levels of decomposition (10 plots per level): X = initial (solid wood and intact cortex); Y = intermediate (partially soft wood with cracks) and Z = advanced (completely soft wood with undefined shape). To compare the floristic relationships among plots, we used Sørensen's similarity coefficient and phytosociological parameters. We found 74 species of bryophytes (40 genera and 24 families), 80% of which were pleurocarpous mosses. The results showed no preference of the species for any level of decomposition and no spatial structure (similarity x distance). We conclude that epixylic bryophyte species in Atlantic Forest are generalists and colonize different types of environments and substrates.

Keywords: Bryophytes, ecology, epixylic.

Introduction

The Atlantic Forest is the richest Brazilian phytogeographic domain in species of mosses, liverworts and hornworts due its high humidity and availability of substrates, particularly promoted by the different environmental conditions present in mountainous tropical areas (Costa & Peralta 2015). The richness and diversity of

bryophytes is directly related to the availability of substrates (Frahm 2003), where the large amount of trees continues to serve as substrates for bryophytes even after their fall.

The decomposition of fallen logs, slowly releasing water and minerals to the environment, produces important substrates for bryophytes (Pócs 1982; Richards 1984; Mattila & Koponen 1999). Bryophyte species that colonize fallen logs are called epixylic and are the third most endangered

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group of bryophytes according to Vána (1996). However, few exclusive species of fallen logs in Brazil are cited in the list of the Brazilian bryophyte flora; they are *Lejeunea ramulosa* Spruce, *Syzygiella concreta* (Gottsche) Spruce, *Thamniopsis undata* (Hedw.) W.R. Buck (Reflora 2023).

Few studies have been developed in the world to describe and understand log communities. Söderström (1988) investigated the bryophyte and lichen species occurring on decaying logs in a forest in Northern Sweden, analyzing wood texture (degree of surface erosion) and diameter of the logs. Sastre-de-Jesús (1992), who used a similar methodology to that adopted in the current study, carried out a quantitative study of the bryophyte communities of fallen logs in different levels of decomposition in a humid forest of Puerto Rico.

In Brazil, only two studies have been carried out on epixylic bryophytes until now, namely, Germano and Pôrto (1997), who surveyed this group in a remnant of Atlantic Forest in the state of Pernambuco, and Silva and Pôrto (2007), who analyzed the epixylic bryophytes of the Murici Ecological Station, in the state of Alagoas.

Increasing the knowledge about the niche of epixylic bryophytes is fundamental for conservation purposes and to understand their occurrence, especially in threatened phytogeographic domains such as the Atlantic Forest. Massive deforestation and spontaneous forest death caused

by the change of environmental conditions are crucial to the balance and management of species diversity.

The objective of the present work was to verify whether there are qualitative and quantitative differences among the epixylic bryophyte communities growing on logs at different levels of decomposition. The study aimed to answer the following questions: What is the richness and abundance of bryophytes species on fallen logs? How do the floristic composition and structure of bryophyte communities differ according to the levels of decomposition of the substrate? As spatial distance between plots can influence the occurrence of the species, do closer plots have greater similarity?

Material and methods

Study area - The Serra da Bocaina National Park (SBNP) is located between the states of São Paulo and Rio de Janeiro (ICMbio 2015) and according to Lima and Peralta (2021), has 485 species of bryophytes. The park has an area of 104 thousand hectares, the climate is characterized by constantly high temperatures and high precipitation throughout the year, and altitudes range from sea level to over 2.000 m a.s.l.

Data were collected along three trails in Upper-Montane Dense Ombrophilous Forest (Nebular Forest) (Fig. 1A): trail after the Cachoeira do Santo Isidro - 1,521 m a.s.l.;

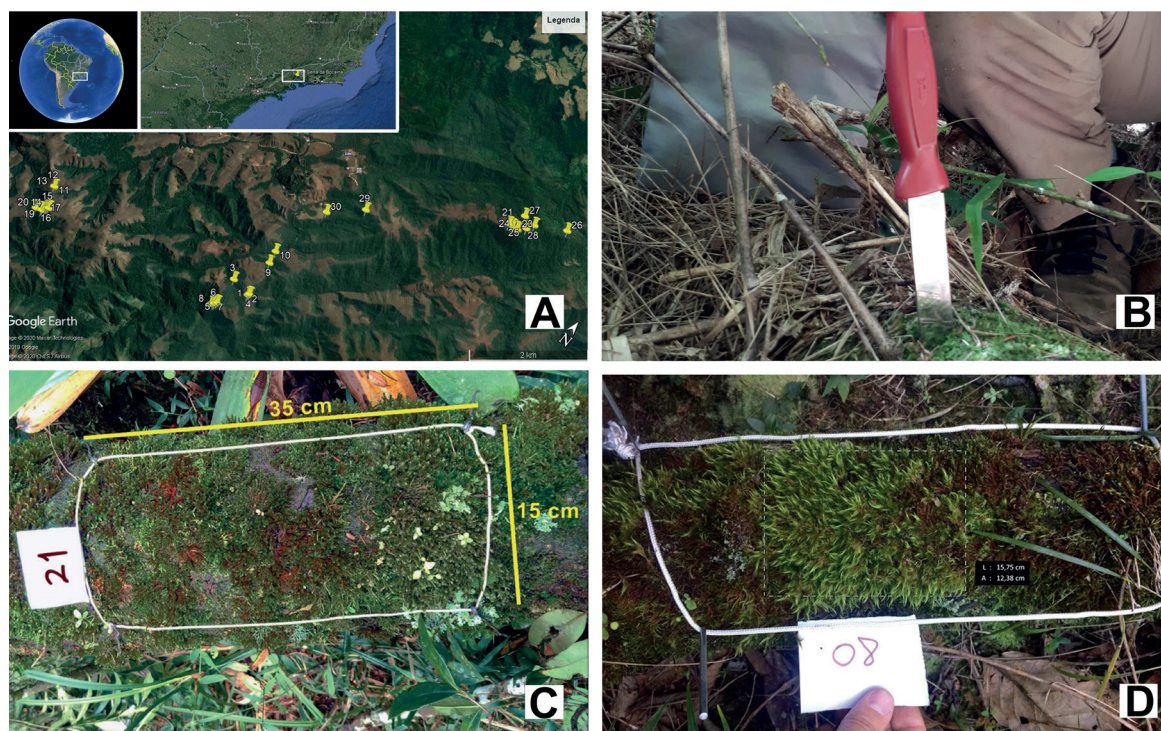


Figure 1. (A) Localities of the trails of the 30 plots sampling epixylic species by decomposition level in the Serra da Bocaina National Park, in the São José do Barreiro County (modified by Google Earth). (B). Method to evaluate the decomposition level (adopted by Frahm 2003), into three levels: X = initial (solid wood and intact cortex); Y = intermediate (partially soft wood with cracks) and Z = advanced (completely soft wood with undefined shape). (Photo: J.S.Lima 2018). (C) Images of the plots (525 cm²) (Photo: J.S.Lima 2019) (D) Method for the visual estimation of the epixylic species covered in the plots using the software Photoshop CC versão 21.0.3 2019 (Adobe© System 1990-2018) by decomposition level in the Serra da Bocaina National Park.

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trail to Pico do Tira Chapéu - 1,948 m a.s.l.; and trail to Pedra da Bacia - 1,923 m a.s.l. Bryophyte communities on fallen logs were surveyed within the area of the SBNP, at least 100 meters from the edge of the forest and the trail, from August 2018 to March 2019.

Sampling - In order to compare the epixylic bryophyte communities of logs at different levels of decomposition, 30 35 x 15 cm plots (525 cm² each, totaling 15,750 cm² plots) were established at a minimum distance of 100 meters from each other. Three decomposition levels were adopted from Frahm (2003): X = initial (solid wood and intact cortex); Y = intermediate (partially soft wood with cracks) and Z = advanced (completely soft wood with undefined shape) (see Fig. 2). The level of decomposition was determined by pushing a knife into the trunk and measuring the depth of penetration, as follows (adopted from Frahm (2003): 1. the knife does not penetrate the trunk (level X), 2. the knife penetrates the trunk up to one centimeter (level Y); and 3. the knife penetrates the trunk several centimeters (level Z) (Fig. 1B).

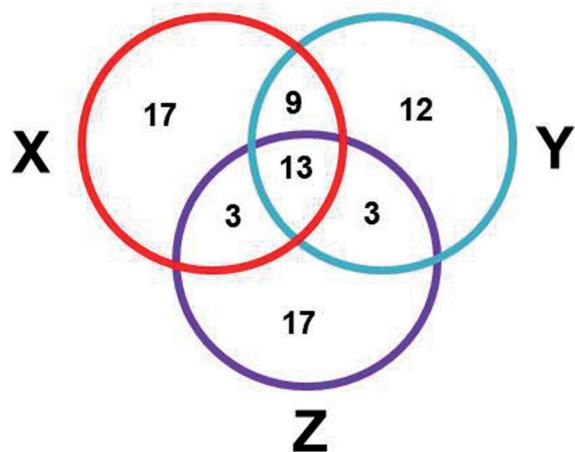


Figure 2. Venn distribution of the recorded epixylic species by decomposition level in the Serra da Bocaina National Park.

Ten 35 x 15 cm (525 cm²) plots were established per trail, totaling 30 plots (10 trunks of each level of decomposition). The plots were placed at least 100 meters from the edge of the forest and of the trail (Fig. 1A, Fig. 1C). The bryophytes in each plot were collected. After identifications, we built a dataset with the floristic list, the total number of species (richness) and their abundance per plot in each level of decomposition.

Abundance was measured in terms of area of the substrate covered by each species in cm². Standardized digital images of the plots were taken and analyzed using the “grid” function in Photoshop CC software version 21.0.3 2019 (Adobe © System 1990-2018). Each plot was covered with a checkered transparent screen and the number of “grids” (1 x 1-cm or 2 x 2-cm squares, depending on the case) in which each species occurred was counted. This analysis

was conducted after identification of all species and only when it was possible to visually distinguish the species in the images (Benavides & Sastre-de-Jesús 2009) (Fig. 1D).

Coverage values were used for the quantitative analysis of the structure of the communities and to calculate the community absolute coverage (AC) and relative coverage (RC).

Absolute coverage was calculated by summing the coverage values of a given species *i* in all sampled plots, expressed in gross numbers. Relative coverage, in turn, refers to the proportional area covered by each species in relation to the total area covered by all bryophyte species occurring in the plots, according to the formula $rc_i = (ac_i / \sum ac(\text{total})) * 100$, where *i* is the species in question and total refers to all sampled species (Colwell 2013).

The structure of the bryophyte community was characterized using the “number of occurrences” (number of plots (from 1 to 30) in which each species occurred), “absolute frequency” (AF = total number of occurrences of a given species *i* divided by the total - 30 plots), and “relative frequency” (RF = number of occurrences of a given species *i* divided by the sum of the absolute frequencies of all species (*n* species) expressed in percentage, $RF_i = (AF_i / \sum fa(i..n)) * 100$). Species with an absolute frequency greater than 20% were considered frequent and those with an absolute frequency lower than 10% were considered rare (Colwell 2013).

Collection and treatment of samples - All individuals of epixylic bryophytes present in each plot were collected following the techniques of Frahm (2003). The samples were placed in envelopes made of bond paper and information on the collector, date, number of the plot, and level of decomposition (X, Y or Z) of the log was noted.

Data analysis - In order to test whether there were significant differences in species richness and abundance of the epixylic bryophyte community among the levels of decomposition of fallen logs, a one-way analysis of variance (One-way ANOVA) was performed. Prior analyses of homogeneity of variances (homoscedasticity) were conducted using the Levene’s test. All tests were performed in the STATISTICA v.12 program (StatSoft © 2016).

Cluster analyses were performed with binary (presence/absence) and quantitative (coverage) data of the species per plot in order to analyze the floristic relationships among plots and whether there were well-defined floristic units according to the level of decomposition of the logs (X, Y, Z). Cluster analyses were performed according to the average linkage method (UPGMA - Unweighted Pair Group Mean Average), using the Sørensen similarity index for the presence/absence data and the Bray-Curtis similarity index for coverage data (Krebs 1999). Non-metric Multidimensional Scaling (NMS) (Clarke 1993) analyses were also performed with the coverage data using the Bray-Curtis index followed by Analysis of Similarities (ANOSIM) (Clarke 1993) to test whether any groups established in



the NMS were really distinct under the floristic-structural aspect. ANOSIM is analogous to a One-way ANOVA in which the preconceived categories (in this case, the levels of decomposition X, Y, Z) correspond to the 'factor' and the distances among all sampling units (similarity matrix) are the dependent variable.

The analyses were performed using the PRIMER software, version 5.2.2 (Clarke & Gorley 2001).

Identification of samples and data analysis - Samples were identified using methods and literature specific to each family, including the preparation of slides for observation under stereomicroscope and optical microscope, and all samples were deposited in the SP herbarium. The classification systems follow Renzaglia *et al.* (2009) for Anthocerotophyta, Crandall-Stotler *et al.* (2009) for Marchantiophyta, and Goffinet *et al.* (2009) for Bryophyta including adaptation cited in Reffora (2023). The geographic distribution of the species in Brazil was based on data added to Reffora (2023) and the works of Forzza *et al.* (2010) and Costa *et al.* (2011), Carmo and Peralta (2016), Carmo *et al.* (2016), and Amélio *et al.* (2019).

Results

General floristic composition - Seventy-four species (40 genera and 24 families) were found; 39 of these species occurred in only one plot. A maximum number of 10 species was found per plot and trunks in advanced decomposition (level Z) had greater numbers of species; only one plot presented only one species (Table 1).

Twenty-three species distributed in 18 genera and 12 families of the Bryophyta division were found. The best represented families were Orthotrichaceae, with five species, followed by Sematophyllaceae (four species) (Table 2). Orthotrichaceae, is constituted by species whose sporophytes develop along secondary branches and main branches are generally prostrate (La Farge-England 1996). Sematophyllaceae is exclusively composed of pleurocarpous mosses (whose gametophytes are prostrate, densely branched and form extensive tangles) (La Farge-England 1996). Acrocarpous mosses were the minority (three species) in the present study. Pleurocarpous mosses corresponded to about 70% of the total species of Bryophyta (14 species; 7 families).

In Marchantiophyta, 51 species, 21 genera and 12 families were found. Lejeuneaceae was the richest family with 19 species, representing 37% of the liverworts and 26% of the 74 bryophyte species found in the plots. Thallose liverworts were the minority, four species distributed in two families (Aneuraceae and Metzgeriaceae).

Regarding the distribution of the species in trunks at different levels of decomposition, 13 of them occurred in the three levels. Seventeen species occurred only in the level of decomposition X (solid wood) and three of

Table 1. Details of the 30 plots of 525cm² (15 x 35cm), carried out in the Serra da Bocaina National Park, 10 for each decomposition level (DL): X = initial (solid wood and intact cortex); Y = intermediate (partially soft wood with cracks) and Z = advanced (completely soft wood with undefined shape); SR - Species Richness.

Plot	DL	Plot ID	SR
1	Z	Z1	4
2	X	X1	9
3	Y	Y1	8
4	Z	Z2	2
5	X	X2	4
6	Y	Y2	7
7	X	X3	8
8	Y	Y3	4
9	Y	Y4	5
10	Y	Y5	5
11	Y	Y6	9
12	Z	Z3	7
13	X	X4	5
14	X	X5	8
15	Z	Z4	7
16	X	X6	1
17	Z	Z5	4
18	Y	Y7	5
19	X	X7	2
20	Y	Y8	2
21	X	X8	9
22	X	X9	4
23	Y	Y9	7
24	Z	Z6	3
25	Y	Y10	3
26	Z	Z7	6
27	Z	Z8	10
28	X	X10	5
29	Z	Z9	10
30	Z	Z10	6

them (*Cheilolejeunea acutangula* (Nees) Grolle, *Frullania brasiliensis* Raddi, and *F. caulisequa* (Nees) Nees) showed more than one occurrence in this level. Twelve species occurred exclusively on trunks at level of decomposition Y (partially soft wood), and *Schlotheimia rugifolia* (Hook.) Schwägr. was the only of them which occurred in more than one plot. Seventeen species were exclusively found on trunks at the level of decomposition Z (completely soft wood), and 13 of them occurred in only one plot (Table 2). The species *Cheilolejeunea filiformis* (Sw.) W. Ye, R.L. Zhu & Gradst. and *Cyclodictyon albicans* (Hedw.) Kuntze occurred



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only in the levels X and Z; *Lejeunea oligoclada* Spruce, *Lophocolea martiana* Nees and *Plagiochila punctata* (Taylor) Taylor in the levels Y and Z; and 9 species occurred in the levels X and Y (see Table 1 and Fig. 2). Some species were formerly cited as exclusively occurring on other types of substrates (Reflora 2023). Only five species collected in this work (*Chiloscyphus porphyrius* Nees, *Lophocolea bidentata* (L.) Dumort., *Lophocolea heterophylla* (Schrad.) Dumort.,

Lophocolea muricata (Lehm.) Nees, *Radula brasiliica* K. Yamada and *Syzygiella concreta* (Gottsche) Spruce) are described in the literature as exclusively epixylic.

Diversity - A total area of 9,762.64 cm² was covered by bryophytes (around 62% of the total area of the 30 plots analyzed). A total of 42 species distributed over 3,122.00 cm² were found on trunks at the level of decomposition X, while only 36 species were found on trunks at the levels Y

Table 2. Species list of the epixylic bryophytes in decomposing trunks in the Serra da Bocaina National Park, SP. Species distribution: occurrence, absolute frequency - AF and relative frequency - RF (%); Terms of abundance: by the values of absolute coverage - AC (cm²), relative coverage - RC (%). Survey carried out in 30 plots of 525cm² (15 x 35cm), 10 for each type of trunk: X = initial (solid wood and intact cortex); Y = intermediate (partially soft wood with cracks) and Z = advanced (completely soft wood with undefined shape).

Family	Species	Community data							
		Records				AF	RF	AC	RC
		X	Y	Z	Total				
THUIDIACEAE	<i>Thuidium delicatulum</i> (Hedw.) Schimp.	3	3	1	7	0,2	4,1	1048	10,7
LEUCOBRYACEAE	<i>Campylopus arctocarpus</i> (Hornsch.) Mitt.	2	6	4	12	0,4	7,1	1019	10,4
DICRANACEAE	<i>Holomitrium crispulum</i> Mart.	1	2	2	5	0,2	3	580	5,9
SEMATOPHYLLACEAE	<i>Trichosteleum glaziovii</i> (Hampe) W.R. Buck	2	3	6	11	0,4	6,5	523	5,4
LOPHOCOLEACEAE	<i>Lophocolea bidentata</i> (L.) Dumort.	0	0	1	1	0	0,6	357	3,7
ANEURACEAE	<i>Riccardia fucoidea</i> (Sw.) Schiffn.	0	0	1	1	0	0,6	303	3,1
SEMATOPHYLLACEAE	<i>Aptychopsis pyrrophylla</i> (Müll.Hal.) Wijk & Margad.	1	1	2	4	0,1	2,4	300	3,1
LEJEUNEACEAE	<i>Cheilolejeunea acutangula</i> (Nees) Grolle	2	0	0	2	0,1	1,2	273	2,8
LEJEUNEACEAE	<i>Lejeunea caulicalyx</i> (Steph.) M.E. Reiner & Goda	1	1	0	2	0,1	1,2	252	2,6
ANEURACEAE	<i>Riccardia glaziovii</i> (Spruce) Meenks	0	1	0	1	0	0,6	233	2,4
ANEURACEAE	<i>Riccardia digitiloba</i> (Spruce ex Steph.) Pagán	0	0	1	1	0	0,6	227	2,3
JAMESONIELLACEAE	<i>Syzygiella concreta</i> (Gottsche) Spruce	2	2	1	5	0,2	3	221	2,3
LEPIDOZIACEAE	<i>Bazzania hookeri</i> (Lindenb.) Trevis.	2	1	1	4	0,1	2,4	214	2,2
SEMATOPHYLLACEAE	<i>Sematophyllum swartzii</i> (Schwägr.) Welch & H.A. Crum	0	0	3	3	0,1	1,8	209	2,1
HYPNACEAE	<i>Mittenothamnium reptans</i> (Hampe) Cardot	3	1	1	5	0,2	3	191	2
PLAGIOCHILACEAE	<i>Plagiochila subbidentata</i> Taylor	1	1	0	2	0,1	1,2	179	1,8
THUIDIACEAE	<i>Thuidium brasiliense</i> Mitt.	0	0	1	1	0	0,6	177	1,8
LOPHOCOLEACEAE	<i>Cryptolophocolea martiana</i> (Nees) L.Soderstr. et al.	0	1	1	2	0,1	1,2	175	1,8
ORTHOTRICHACEAE	<i>Schlotheimia rugifolia</i> (Hook.) Schwägr.	0	2	0	2	0,1	1,2	163	1,7
HERBETACEAE	<i>Herbertus sendtneri</i> (Nees) A. Evans	0	0	1	1	0	0,6	154	1,6
PLAGIOCHILACEAE	<i>Plagiochila crispabilis</i> Lindb.	1	0	0	1	0	0,6	142	1,5
LEUCOBRYACEAE	<i>Campylopus filifolius</i> (Hornsch.) Mitt.	0	0	3	3	0,1	1,8	130	1,3
LEJEUNEACEAE	<i>Lejeunea diversicuspis</i> Spruce	1	0	1	2	0,1	1,2	129	1,3
LOPHOCOLEACEAE	<i>Lophocolea muricata</i> (Lehm.) Nees	1	4	3	8	0,3	4,7	125	1,3
RADULACEAE	<i>Radula brasiliica</i> K. Yamada	2	4	2	8	0,3	4,7	113	1,2
LEJEUNEACEAE	<i>Lejeunea cristulaeflora</i> (Steph.) M.E. Reiner & Goda	1	2	0	3	0,1	1,8	112	1,2
PLAGIOCHILACEAE	<i>Plagiochila punctata</i> (Taylor) Taylor	0	1	4	5	0,2	3	110	1,1
PYLAISIADELPHACEAE	<i>Microcalpe subsimplex</i> (Hedw.) W.R. Buck	0	1	0	1	0	0,6	108	1,1
ORTHOTRICHACEAE	<i>Macromitrium punctatum</i> (Hook. & Grev.) Brid.	1	0	0	1	0	0,6	108	1,1
JAMESONIELLACEAE	<i>Syzygiella anomala</i> (Lindenb. & Gottsche) Steph.	0	1	0	1	0	0,6	104	1,1
LEJEUNEACEAE	<i>Anoplolejeunea conferta</i> (C.F.W. Meissn.) A. Evans	1	1	1	3	0,1	1,8	103	1,1
LEPIDOZIACEAE	<i>Lepidozia brasiliensis</i> Steph.	2	1	0	3	0,1	1,8	100	1



Table 2. Cont.

Family	Species	Community data							
		Records				AF	RF	AC	RC
		X	Y	Z	Total				
LEPIDOZIACEAE	<i>Bazzania heterostipa</i> (Steph.) Fulford	0	0	1	1	0	0,6	89	0,9
LEJEUNEACEAE	<i>Lejeunea flava</i> (Sw.) Nees	1	1	1	3	0,1	1,8	87	0,9
LEJEUNEACEAE	<i>Harpalejeunea stricta</i> (Lindenb. & Gottsche) Steph.	1	1	1	3	0,1	1,8	81	0,8
LEJEUNEACEAE	<i>Cheilolejeunea filiformis</i> (Sw.) W. Ye, R.L. Zhu & Gradst.	1	0	1	2	0,1	1,2	80	0,8
LEJEUNEACEAE	<i>Lejeunea oligoclada</i> Spruce	0	1	2	3	0,1	1,8	80	0,8
HERBETACEAE	<i>Herbertus bivittatus</i> Spruce	1	1	0	2	0,1	1,2	79	0,8
ORTHOTRICHACEAE	<i>Groutiella wagneriana</i> (Müll.Hal.) H.A. Crum & Steere	1	0	0	1	0	0,6	71	0,7
SEMATOPHYLLACEAE	<i>Sematophyllum galipense</i> (Müll.Hal.) Mitt.	1	0	0	1	0	0,6	71	0,7
DALTONIACEAE	<i>Daltonia splachnoides</i> (Sm.) Hook. & Taylor	1	0	0	1	0	0,6	69	0,7
FRULLANIACEAE	<i>Frullania caulisequa</i> (Nees) Nees	2	0	0	2	0,1	1,2	64	0,7
PILOTTRICHACEAE	<i>Cyclodictyon albicans</i> (Hedw.) Kuntze	1	0	1	2	0,1	1,2	62	0,6
LEPIDOZIACEAE	<i>Telaranea nematodes</i> (Gottsche ex Austin) M. Howe	0	0	2	2	0,1	1,2	60	0,6
METEORACEAE	<i>Meteorium nigrescens</i> (Hedw.) Dozy & Molk.	1	0	0	1	0	0,6	55	0,6
LEJEUNEACEAE	<i>Lejeunea bermudiana</i> (A. Evans) R.M. Schust.	1	0	0	1	0	0,6	54	0,6
LEPIDOZIACEAE	<i>Lepidozia cupressina</i> (Sw.) Lindenb.	0	0	2	2	0,1	1,2	53	0,5
LOPHOCOLEACEAE	<i>Lophocolea heterophylla</i> (Schrad.) Dumort.	0	0	1	1	0	0,6	52	0,5
PLAGIOCHILACEAE	<i>Plagiochila rutilans</i> Lindenb.	1	1	0	2	0,1	1,2	47	0,5
PLAGIOCHILACEAE	<i>Plagiochila bifaria</i> (Sw.) Lindenb.	0	0	1	1	0	0,6	47	0,5
LEJEUNEACEAE	<i>Lejeunea aphanes</i> Spruce	0	1	0	1	0	0,6	44	0,5
LOPHOCOLEACEAE	<i>Chiloscyphus porphyrius</i> Nees	0	0	1	1	0	0,6	39	0,4
ANEURACEAE	<i>Riccardia chamedryfolia</i> (With.) Grolle	0	1	0	1	0	0,6	30	0,3
PLAGIOCHILACEAE	<i>Plagiochila patula</i> (Sw.) Lindenb.	1	0	0	1	0	0,6	27	0,3
FRULLANIACEAE	<i>Frullania brasiliensis</i> Raddi	2	0	0	2	0,1	1,2	23	0,2
ORTHOTRICHACEAE	<i>Schlotheimia jamesonii</i> (Arn.) Brid	0	0	1	1	0	0,6	23	0,2
METZGERIACEAE	<i>Metzgeria albinea</i> Spruce	1	1	0	2	0,1	1,2	21	0,2
LEJEUNEACEAE	<i>Drepanolejeunea fragilis</i> Bischl.	1	1	0	2	0,1	1,2	17	0,2
BRACHYTHECIACEAE	<i>Squamidium brasiliense</i> Broth.	0	1	0	1	0	0,6	16	0,2
LEJEUNEACEAE	<i>Cheilolejeunea insecta</i> Grolle & Gradst.	1	0	0	1	0	0,6	16	0,2
PILOTTRICHACEAE	<i>Thamniopsis langsdorfii</i> (Hook.) W.R. Buck	0	0	1	1	0	0,6	15	0,2
PILOTTRICHACEAE	<i>Lepidopilum sububulatum</i> Geh. & Hampe	0	1	0	1	0	0,6	14	0,1
FRULLANIACEAE	<i>Frullania apiculata</i> (Reinw. et al.) Dumort.	0	1	0	1	0	0,6	13	0,1
JAMESONIACEAE	<i>Syzygiella contigua</i> Steph.	1	0	0	1	0	0,6	13	0,1
LEJEUNEACEAE	<i>Drepanolejeunea araucariae</i> Steph.	1	0	0	1	0	0,6	12	0,1
LEJEUNEACEAE	<i>Drepanolejeunea mosenii</i> Bischl.	0	1	0	1	0	0,6	10	0,1
LEJEUNEACEAE	<i>Neurolejeunea breutelii</i> (Gottsche) A. Evans	1	0	0	1	0	0,6	9	0,1
LEJEUNEACEAE	<i>Lejeunea cerina</i> (Lehm. & Lindenb.) Gottsche et al.	1	0	0	1	0	0,6	9	0,1
ORTHOTRICHACEAE	<i>Macromitrium longifolium</i> (Hook.) Brid.	1	0	0	1	0	0,6	8	0,1
LEJEUNEACEAE	<i>Microlejeunea epiphylla</i> Bischl.	0	1	0	1	0	0,6	8	0,1
NECKERACEAE	<i>Porotrichum longirostre</i> (Hook.) Mitt.	1	0	0	1	0	0,6	5	0,1
TRICHOCOLEACEAE	<i>Trichocolea brevifissa</i> Steph.	0	1	0	1	0	0,6	5	0,1
LEJEUNEACEAE	<i>Microlejeunea cystifera</i> Herzog	0	0	1	1	0	0,6	2	0
JUNGERMANNIACEAE	<i>Jungermannia hyalina</i> Lyell.	0	0	1	1	0	0,6	1	0
	TOTAL	55	55	59	169	5,6	100	9763	100



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and Z, with total coverage values of 3,417.03 and 3,223.61 cm², respectively. However, the mean species richness ($F(2,27) = 0.078$; $p = 0.926$) (Fig. 3) and coverage values ($F(2,27) = 0.321$; $p = 0.728$) (Fig. 4) in the different levels of decomposition were not significantly different according to the ANOVA. The variation explained by chance of each tested factor was the same, ($F(2,27) = 0.478$; $p = 0.625$ for species richness and $F(2,27) = 0.178$; $p = 0.838$ for coverage).

The ANOVA showed similar values of species richness and coverage among the 10 plots in the levels of decomposition X, Y and Z. The mean species richness was 5.50 in the levels X and Y (± 2.87 in X and ± 2.22 in Y) and 5.90 ± 2.72 in Z. The mean coverage was 312.30 ± 89.12 cm² in the level of decomposition X, 341.70 ± 88.13 cm² in the level Y, and 322.36 ± 72.71 cm² in the level Z (see Fig. 3, Fig. 4). The richness in individual plots varied from one to 10 species, with the lowest value found in a plot on a trunk in the level of decomposition X and the highest in two plots on trunks in the level of decomposition Z. The lowest coverage (93.22 cm²) was found in a plot on a trunk in the level of decomposition X, while the highest coverage was found in a plot on a trunk in the level of decomposition Y (441 cm²).

These results indicate, therefore, that the richness and abundance of epixylic bryophyte species do not seem to be influenced by the degree of decomposition of the fallen logs.

Floristic similarity - Some relatively well-defined groups were observed in the three types of logs. The cluster analysis with binary data showed that the community with the highest similarity (65%) belonged to two plots of different levels of decomposition, X9 and Y8 (Fig. 5). This may have been due to two species shared between these plots, *Campylopus arctocarpus* and *Lepidozia brasiliensis* Steph., which were the only species occurring in Y8 and two of the four species occurring in X9.

Logs in the levels of decomposition X and Z showed less than 37% similarity (Fig. 5). The dendrogram also showed that the logs in the level Y were always associated with logs either in low or high levels of decomposition (X and Z), probably because the level Y is transitional between them. Four large groups including logs in all levels of decomposition (B, C, D, E; Fig. 5) showed 10% floristic similarity as well as one group (A) consisting only of the plot Z1. The latter presented four species that occurred exclusively on logs at the advanced level decomposition Z (*Campylopus filifolius* (Hornsch.) Mitt., *Lophocolea bidentata*

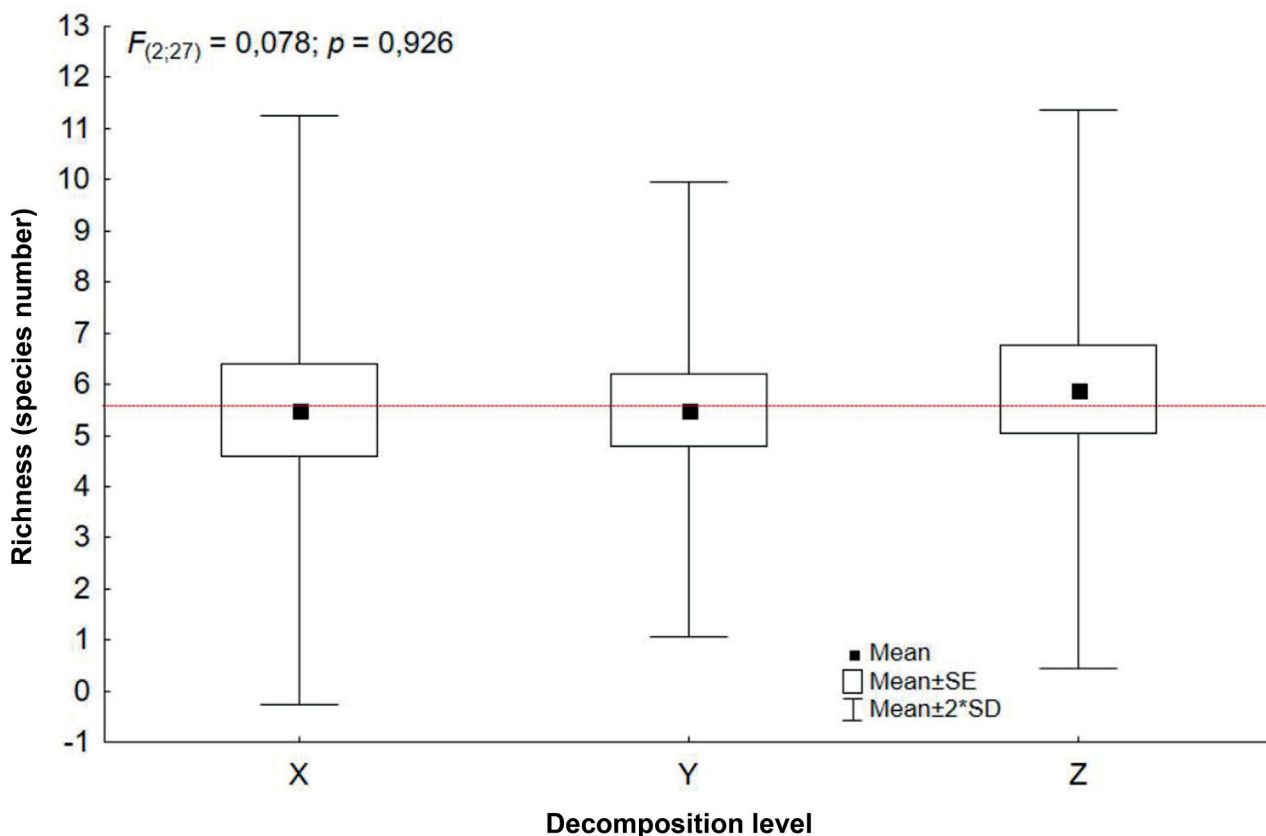


Figure 3. Species richness among the decomposition levels (X = initial (solid wood and intact cortex); Y = intermediate (partially soft wood with cracks) and Z = advanced (completely soft wood with undefined shape)), of the epixylic species by decomposition level in the Serra da Bocaina National Park. Total plots = 30 (10 plots by decomposition level). Red line indicates (5,63). X(méd)=5,50±2,87; Y(méd)=5,50±2,22; Z(méd)=5,90±2,72.

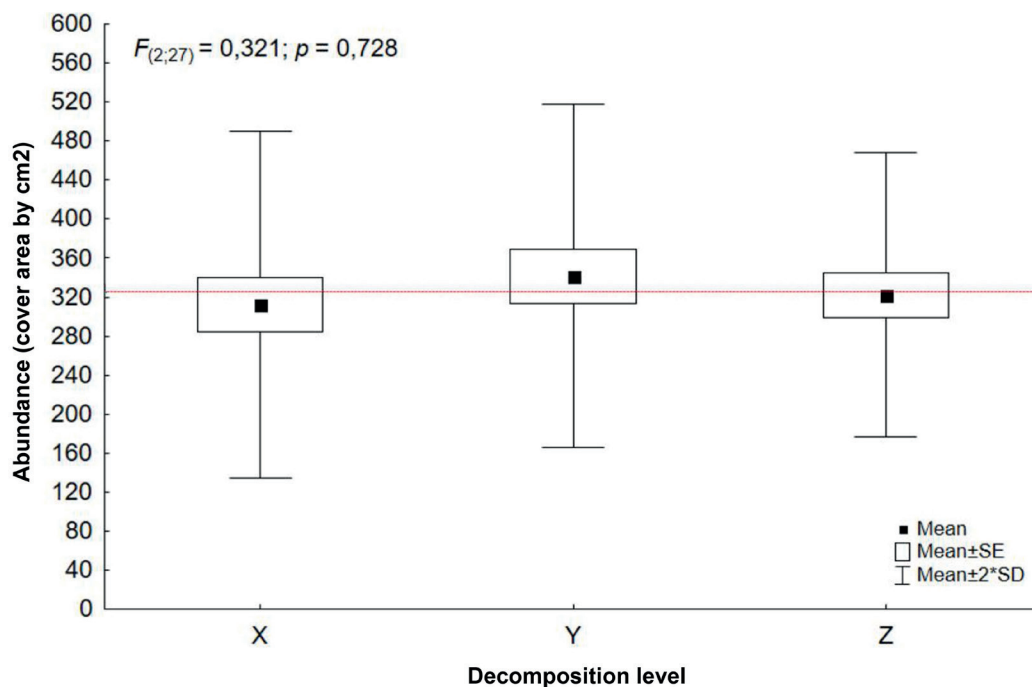


Figure 4. Species cover among the decomposition levels (X = initial (solid wood and intact cortex); Y = intermediate (partially soft wood with cracks) and Z = advanced (completely soft wood with undefined shape)), of the epixylic species by decomposition level in the Serra da Bocaina National Park. Total plots = 30 (10 plots by decomposition level). Red line indicates (325,42). X(méd) = 312,20±89,12; Y(méd) = 341,70±88,13; Z(méd) = 322,36±72,71.

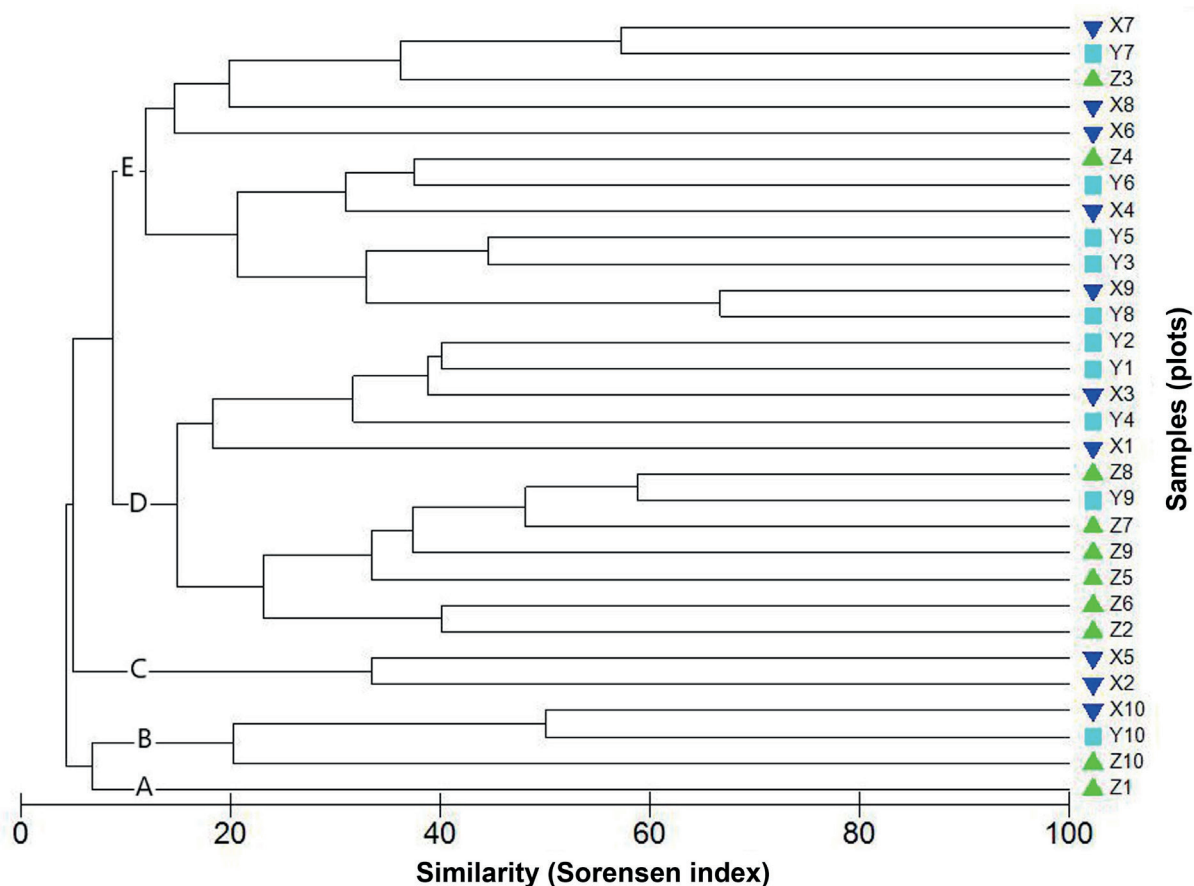


Figure 5. Clustering of the epixylic communities in the 30 plots using Average Association Method (or UPGMA - Unweighted Pair Group Mean Average), using the Sørensen Similarity.



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(L.) Dumort., *Sematophyllum swartzii* (Schwägr.) Welch & H.A. Crumi and *Thamniopsis langsdorffii* (Hook.) W.R. Buck).

Similarly to the cluster analysis with binary data, the analysis with abundance data showed an association of logs in intermediate level of decomposition with logs in initial and advanced level of decomposition, with 75% similarity between the plots X9 and Y10 (Fig. 6). The consistency of this group was mainly influenced by the abundance of *Thuidium delicatulum* (Hedw.) Schimp. This species presented the highest values of total coverage in the study, especially in these two plots. A community of logs in intermediate level of decomposition (Y3 and Y8) was found with almost 60% similarity. They had only the species *Campylopus arctocarpus* in common. Another group of logs in initial level of decomposition (X4 and X5) showed 50% similarity; they shared the species *Bazzania hookeri* (Lindenb.) Trevis., found at all levels of decomposition in the study, and *Cheilolejeunea acutangula* (Nees) Grolle, found only at the initial level, specifically in these two plots.

We are considering the similarity near 10%, when we observed different results from those of the analysis with binary data. In this case, groups were formed only between

logs in the levels Y and Z and between logs in the levels Y and X. The similarity between logs in initial and advanced level of decomposition was low than 5% (Fig. 6).

The NMS analysis (Fig. 7) corroborated the results obtained with the cluster analysis. Some groups remained close by sharing species and the plot Z1 remained distant from the others.

There was a tendency of plots in the level of decomposition Z to show greater similarity in terms of community structure (i.e., composition and abundance) with each other than with plots in the other levels of decomposition. Plots in the intermediate level of decomposition also tended to be in an intermediate position in the ordering in relation to plots in the other levels, while plots in the levels Z and X were almost always distant from each other. However, the relationships of similarity were non-significant (ANOSIM, $R = 0.069$; $p = 0.091$), showing that the plots of a certain level of decomposition do not necessarily form homogeneous and genuinely similar groups.

A regression analysis between the similarity values (Sorensen index) as a function of the distance between the plots revealed that there was no geographic structure (Fig 8).

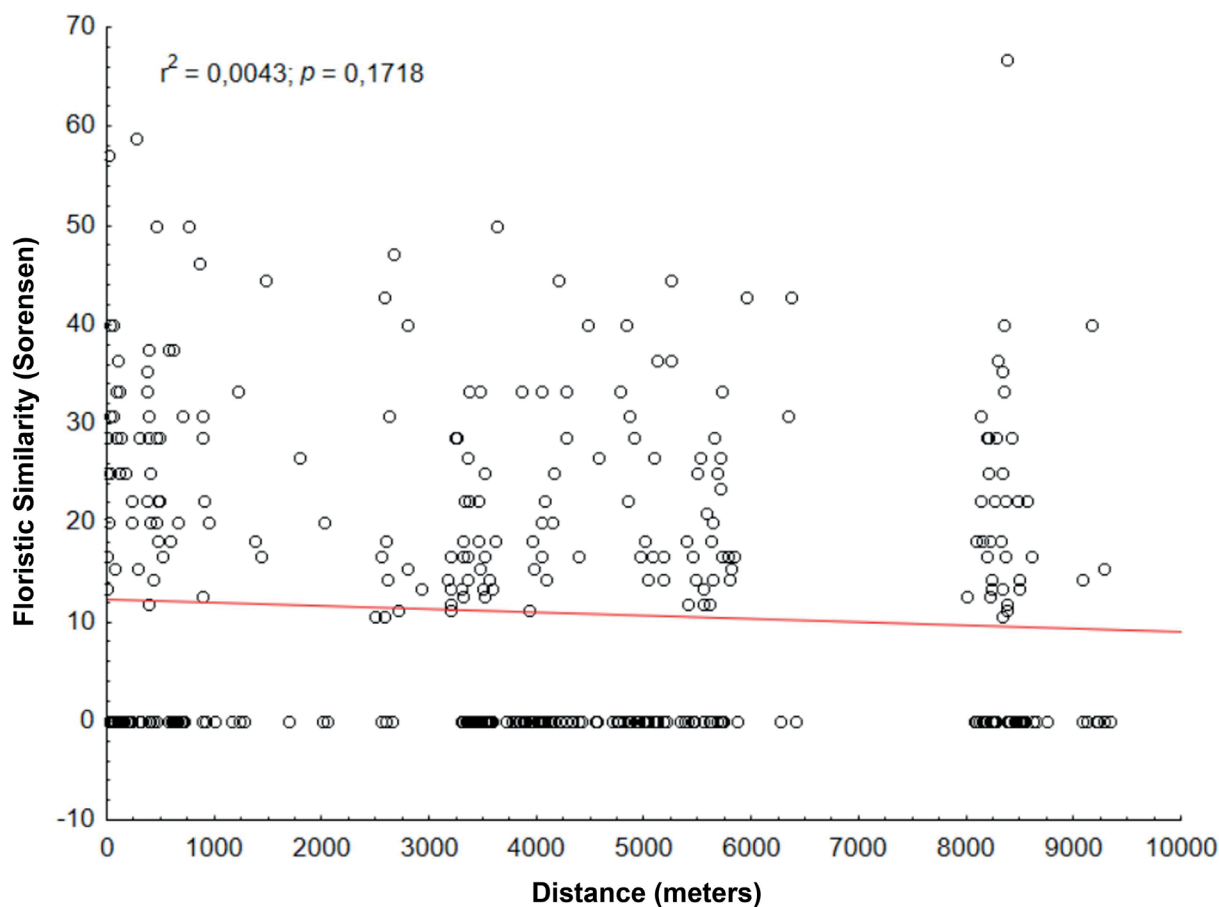


Figure 6. Clustering of the epixylic communities in the 30 plots (X = initial (solid wood and intact cortex); Y = intermediate (partially soft wood with cracks) and Z = advanced (completely soft wood with undefined shape)) using Average Association Method (or UPGMA - Unweighted Pair Group Mean Average), using the Bray-Curtis Similarity Index coverage data.



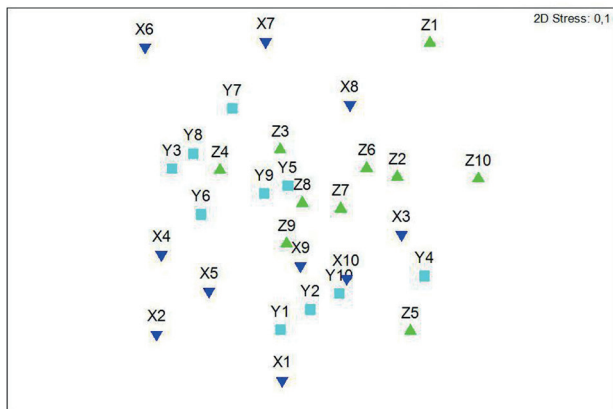


Figure 7. Non-metric Multidimensional Scaling (NMS) of the plots (X = initial (solid wood and intact cortex); Y = intermediate (partially soft wood with cracks) and Z = advanced (completely soft wood with undefined shape)) using the floristic similarity of epixylic species by decomposition level in the Serra da Bocaina National Park.

Frequency and abundance - Five species were considered frequent, namely: *Campylopus arctocarpus* (40% AF and 12 occurrences), *Trichosteleum glaziovii* (Hampe) W.R. Buck (37% AF and 11 occurrences), *Lophocolea muricata* (Lehm.) Nees (27% and 8 occurrences), *Radula brasiliica* K. Yamada

(27% AF and eight occurrences), and *Thuidium delicatulum* (23% AF and seven occurrences) (Table 2). *Campylopus arctocarpus* (24%) and *Trichosteleum glaziovii* (Hampe) W.R. Buck (22%) were the only species that showed more than 20% of relative frequency.

In terms of absolute coverage, only two species obtained values greater than 10%: *Thuidium delicatulum* (11%) and *Campylopus arctocarpus* (10%) (Table 2). In terms of relative coverage, *T. delicatulum* (11%) and *C. arctocarpus* (10%) had the greater values.

Campylopus arctocarpus was the most frequent and the second most abundant species, followed by *Trichosteleum glaziovii*, the second most frequent and fourth most abundant (5%) (Table 2). *Lophocolea muricata* was the third most frequent, but its coverage did not exceed 1.3% (Table 2).

Discussion

What is the richness and abundance of bryophytes species on fallen logs? In this study, many many species are being recorded for the first time on decomposed logs. This finding confirms the lack of studies on epixylic bryophytes. As observed in previous studies (Germano & Pôrto 1997;

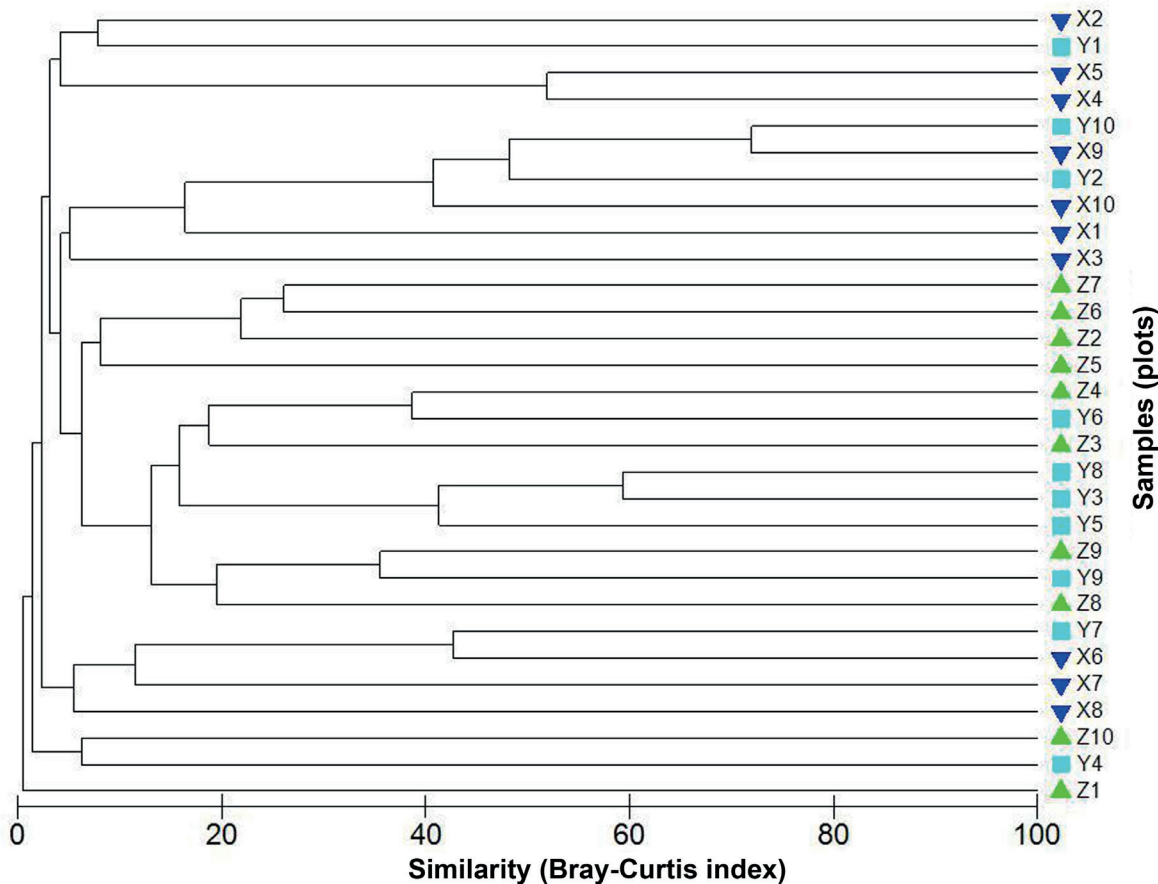


Figure 8. Linear Ordination of the Floristic similarity and distance of the plots of epixylic species found in the Serra da Bocaina National Park.

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Silva & Pôrto 2007), the vast majority of epixylic bryophytes can be classified as generalist species of decaying logs.

According to Sastre-de-Jesús (1992), when bryophytes are collected from trunks of a single phanerogam host species, there may be a pattern of epixylic species for each level of decomposition. The colonization of decomposing logs by bryophytes in our study have two possible explanations: either the species were colonizing the trees before they fell, remaining there later on, until our sampling, or the species found in the soil colonized the trunk after the trees fell. In the current study, bryophyte species were collected from native trees of different phanerogam species, similarly to Germano and Pôrto (1997), who also found similar results as ours.

Lejeuneaceae species require high levels of humidity and temperature to reach full development (Richards 1984; Schuster 1963; Germano & Pôrto 1997). Previous works developed in Brazil (Germano & Pôrto 1997; Silva & Pôrto 2007) also showed the predominance of Lejeuneaceae among liverworts and emphasized that this family is important in the bryophyte flora of the tropics, exhibiting wide ecological amplitude.

Sematophyllaceae also stood out in the community of decomposed logs in the studies by Germano and Pôrto (1997) and Silva and Pôrto (2007), similarly to our present finding.

Many species found here had hitherto been mentioned exclusively growing on live trees. Thus, in these cases, we can probably assume that the species were growing on the substrate before the trees fell and started to decompose or that these species were in the soil and colonized the trunks after their fall. Similar observations were made by Richards (1984) and Pôrto (1992).

How do the floristic composition and structure of bryophyte communities differ according to the levels of decomposition of the substrate? We observed that the most frequent species were not necessarily the most abundant. This proves that the frequent species have greater dispersal ability than the abundant ones in the plots. The abundant species, on the other hand, have a more successful establishment on the substrate. Pleurocarpous mosses were the most abundant, likely favored by the prostrate growth of their gametophytes, which spread like matted and branched carpets. However, the most frequent species was an acrocarpous moss.

Campylopus arctocarpus (Hornsch.) Mitt. was the most frequent species and the second most abundant, with a difference of only 1% of coverage in relation to the most abundant. *Campylopus arctocarpus* is a moss with upright, simple gametophytes growing like tufts and producing the sporophytes at the stem apices (La Farge-England 1996). However, different from all other species of this genus, it has frequently branched gametophytes, resembling a pleurocarpous moss. It was mentioned by Frahm (1991) as widely distributed in montane forests in the Neotropics, easily found on decomposing trunks. This description is

aligned with the successful colonization of plots by this species observed in the present study.

As spatial distance between plots can influence the occurrence of the species, do closer plots have greater similarity? No spatial structure was observed in our study. The similarity between plots was not influenced by the distance between them. The distributions of epixylic bryophyte species in Serra da Bocaina may be associated with some environmental (biotic or abiotic) factors not quantified in this work. The level of decomposition of the trunks could be one of the factors, but our results do not provide unequivocal evidence of that, as we did not find differences in richness and abundance between the levels of decomposition and inconclusive data regarding the floristic and structural composition of the communities on the logs.

Raschendorfer (1949) and McCullough (1948) mentioned that the succession process on decomposing logs can differ between a region with a constantly humid climate and another with dry periods during the year. However, even though the collections of this current work were carried out in different seasons of the year (winter and summer), the sampled area is extremely humid, thus corroborating the results of Raschendorfer (1949) and McCullough (1948).

We conclude, with our results, that there may be inconspicuous differences among the bryophyte communities developing on logs at different levels of decomposition. The richness and abundance of species showed to be similar among the different levels of decomposition. The floristic composition of these communities also showed non-significant differences in the NMS and ANOSIM analysis. Finally, the analysis of the relationship between similarity and the spatial distance between plots showed that the epixylic bryophytes in the studied area are highly adapted to different types of environment and substrates, since some species proved to be generalists, occurring on substrates other than fallen logs.

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References

- Amélio LA, Peralta DF, Carmo DM. 2019. Briófitas do Parque Estadual de Campos do Jordão, Estado de São Paulo, Brasil. *Hoehnea* 46: e962018.
- Benavides JC, Sastre-de-Jesús I. 2009. Digitized images provide more accuracy and efficiency to estimate bryophyte cover. *Bryologist* 112: 12–18.
- Carmo DM, Lima JS, Amélio LA, Peralta DF. 2016. Briófitas do Parque Estadual da Serra do Mar, Núcleo de Santa Virgínia, Estado de São Paulo, Brasil. *Hoehnea* 43: 265–287.



- Carmo DM, Peralta DF. 2016. Survey of bryophytes in Serra da Canastra National Park, Minas Gerais, Brazil. *Acta Botanica Brasilica* 30: 254–265.
- Clarke KR. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117–143.
- Clarke KR, Gorley RN. 2001. Primer v5: User Manual/Tutorial. Plymouth, Primer-E Ltd.
- Colwell K. 2013. EstimateS: Statistical Estimations of Species Richness and Shared Species from Samples. versão. 9.1.0. University of Connecticut, USA.
- Costa DP, Pôrto KC, Luiz-Ponzo AP *et al.* 2011. Synopsis of the Brazilian moss flora: checklist, distribution and conservation. *Nova Hedwigia* 93: 277–334
- Costa DP, Peralta DF. 2015. Bryophytes diversity in Brazil. *Rodriguésia* 66: 1063–1071.
- Crandall-Stotler B, Stotler RE, Long DG. 2009. Morphology and classification of the Marchantiophyta. In: Goffinet B, Shaw AJ (eds.). *Bryophyte Biology*. 2nd. edn. Cambridge, Cambridge University Press. p. 1–54.
- Forzza RC, Leitman PM, Costa AF *et al.* 2010. Introdução. In: Lista de espécies da Flora do Brasil. Rio de Janeiro, Jardim Botânico do Rio de Janeiro. vol. 1. p. 875.
- Frahm JP. 1991. Dicranaceae: Campylopoioideae, Paraleucobryoidae. *Flora Neotropica Monograph* 54: 1–238.
- Frahm JP. 2003. Manual of tropical Bryology. *Tropical Bryology* 23: 1–196.
- Germano SR, Pôrto KC. 1997. Ecological analyses of epixylic bryophytes in relation to the decomposition of the substrate (municipality of Timbaúba, Pernambuco, Brazil). *Cryptogamie, Bryologie Lichénologie* 18: 143–150.
- Goffinet B, Buck WR, Shaw AJ. 2009. Morphology, anatomy, and classification of the Bryophyta. In: Goffinet B, Shaw AJ (eds.). *Bryophyte Biology*. 2nd. edn. Cambridge, Cambridge University Press. p. 55–138.
- ICMbio - Instituto Chico Mendes de Conservação da Biodiversidade, Parque Nacional da Serra da Bocaina. 2015. Quem Somos. <https://www.icmbio.gov.br/parnaserradabocaina/quem-somos.html>. 18 Set. 2019.
- La Farge-England C. 1996. Growth form, branching pattern, and perichaetial position in mosses: Cladocarpus and pleurocarpus redefined. *The Bryologist* 99: 170–186
- Lima JS, Peralta DF. 2021. Brioflora do Parque Nacional da Serra da Bocaina, de São Paulo, Brasil. *Hoehnea* 48: e802020.
- Krebs C. 1999. *Ecological Methodology*. 2nd. edn. Califórnia, The Benjamin Curmmings Publishers.
- Mattila P, Koponen T. 1999. Diversity of the bryophyte flora and vegetation on rotten wood in rain and montane forests in northeastern Tanzania. *Tropical Bryology* 16: 39–164.
- McCullough HA. 1948. Plant succession on fallen logs in a virgin spruce-fir forest. *Ecology* 29: 508–513.
- Pócs T. 1982. Tropical Forest Bryophytes. In: Smith AJE. *Bryophyte Ecology*. New York, Chapman and Hall. p. 59–104.
- Pôrto KC. 1992. Bryoflores d'une forêt de plaine et d'une forêt d'altitude moyenne dans l'État de Pernambuco (Brésil). 2. Analyse écologique comparative des forêts. *Cryptogamie, Bryologie Lichénologie* 13: 187–219.
- Raschendorfer I. 1949. Beobachtungen über die Besiedlung von modernem Holz mit besonderer Berücksichtigung der adnaten Vereine. *Österreichische botanische Zeitschrift* 96: 232–280.
- Reflora. 2023. Flora e Funga do Brasil. <http://floradobrasil.jbrj.gov.br/>. 01 Jun. 2023.
- Renzaglia KS, Villarreal JC, Duff RJ. 2009. New insights into morphology, anatomy and systematics of hornworts. In: Goffinet B, Shaw AJ. *Bryophyte Biology*. 2nd. edn. Cambridge, Cambridge University Press. p. 139–171.
- Richards PW. 1984. The Ecology of Tropical Forest Bryophytes. In: Schuster RM (ed.). *New Manual of Bryology*. Nichinan: The Hattori Botanical Laboratory. vol. 2, p. 1233–1270.
- Sastre-de-Jesús I. 1992. Estudios preliminares sobre comunidades de briofitas en troncos en descomposición en el bosque subtropical lluvioso de Puerto Rico. *Tropical Bryology* 6: 181–191.
- Schuster RM. 1963. An annotated synopsis of genera and subgenera de Lejeuneaceae. I. Introduction; annotated keys subfamilies and genera. *Beihefte zur Nova Hedwigia* 9: 1–203.
- Silva MPP, Pôrto KC. 2007. Composição e riquezas de briófitas epixilas em fragmentos florestais da Estação Ecológica de Murici, Alagoas. *Revista Brasileira de Biociências* 5: 243–245.
- Söderström L. 1988. Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in Northern Sweden. *Nordic Journal of Botanic* 8: 89–97.
- Vána J. 1996. Notes on the Jungermaniineae of the World. *Anales del Instituto de Biología* 67: 99–107.

