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MICROBIOLOGY

Wood-inhabiting macrofungi Hymenochaetales and Polyporales (Basidiomycota) in the Amazon Forest: relationship the abiotic factors and substrate colonization

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Abstract: Hymenochaetales and Polyporales are important macrofungi for the maintenance of tropical forests, since they act directly in the nutrient cycling of the wood decomposition. In the Amazon, the largest tropical forest in the world, knowledge about Agaricomycetes is still insipient, since many areas have not yet been inventoried and new records appear each new study. To increase ecological knowledge about the Hymenochaetales and Polyporales, in the Brazilian Amazon region, collections were conducted in western Pará, Brazil, relating these fungi to the substrate they colonize and to environmental variables. 91 species were identified, with greater macrofungi richness associated with the rainy season; these fungi showed preferences for dead woods, of small diameter (class 1 = 5,9 ⊢ 39 cm) and, in stages of decomposition still rigid or intermediate. The abundance and richness of Hymenochaetales and Polyporales were influenced by air humidity and the assemblage composition was influenced by temperature, air humidity and rainfall. The results indicate a rich diversity for western Pará region, these species are associated with environmental conditions, and may be threatened by the increasing pressure of human activity in the Brazilian Amazon.

Key words: Amazon, ecology, funga, fungi assemblage, polypore.

INTRODUCTION

The Hymenochaetales Oberw. and Polyporales Gäum are macrofungi belonging the Phylum Basidiomycota, both popularly known as “shelf fungi” or “polypores”, which stand out for their interest in systematic and ecological studies among mycologists (Larsson et al. 2006, Justos et al. 2017). Currently, the constitute one of the main groups of wood-inhabiting macrofungi, comprising more than 3,182 species with very different anatomical and physiological characteristics (Larsson et al. 2006, Binder et al. 2013, Wijayawardene et al. 2020).

These macrofungi Hymenochaetales and Polyporales, focus of this study, are organisms of great ecological importance in tropical forests, mainly because they act in the decomposition of dead woods, facilitating nutrient cycling (Blackwell et al. 2006, Webster & Weber 2007), in addition to promoting population control of plant species due to phytopathogenic and mutualistic relationships established with some plant species (Petersen 2012).

These fungi are also important for biotechnology due to the production of cellulose and lignin degrading enzymes, with great value to the textile industry for cleaning oil-contaminated tributaries, as well as being useful in the production of pesticides (Maciel et al. 2010, Lomascolo et al. 2011, Bekai et al. 2012). Some species of Hymenochaetales and

Polyporales are used to generate products with medicinal properties such as antiviral, anti-inflammatory substances and cancer treatment (Grienke et al. 2014, Dos Reis et al. 2015, Bishop 2020).

Ecological information about Hymenochaetales and Polyporales is still scarce in tropical forests (e.g. Lindblad 2000, 2001, Gilbert & Sousa 2002, Gilbert et al. 2002, 2008, Yamashita et al. 2008). It is known that the occurrence and diversity of these fungi are directly related to environmental factors (Hawksworth & Müller 2005, Hawkes et al. 2011), to the physical-chemical characteristics of the substrate (Boddy et al. 2008), as well as to the structure habitat and environmental disturbances (Yamashita et al. 2008, Gates et al. 2011, Blaser et al. 2013).

Amazon forest is one of the richest biomes in the world in terms of biodiversity and has been threatened by overexploitation of wood, deforestation and burning, mainly to meet the interests of agribusiness and mining (Capobianco et al. 2001, Ritter et al. 2017). Thus, it is denoting that the advance of deforestation and the fragmentation of habitats are the main environmental disturbances that affect fungi (Pentillä et al. 2006, Yamashita et al. 2008) and considering the territorial extent of this biome, many areas have not been inventoried yet, resulting in risks to the Funga not known yet.

The most expressive studies on Hymenochaetales and Polyporales in the Amazon region were carried out by Gibertoni et al. (2016) who analyzed the distribution of Hymenochaetales and Polyporales assemblages in Amapá, Pará and Rondônia states, Gibertoni (2008) and Medeiros et al. (2015), observed the influence of the characteristics of the substrates on the fungal composition of the northern region of Pará, demonstrating that the richness and diversity of Hymenochaetales and Polyporales are positively related to their wood size or decomposition stage.

Our hypothesis is that the diameter and physical state of dead woods can influence the abundance and richness of Hymenochaetales and Polyporales, as well as local environmental variables. The objectives of this study were: i - investigate the influence of environmental variables on the abundance, richness and assemblage of Hymenochaetales and Polyporales, ii - determine the occurrence/preference of the abundance and richness of Hymenochaetales and Polyporales among living or dead woods, iii - evaluate the occurrence of abundance and richness of Hymenochaetales and Polyporales between the stages of decomposition and the diameter of dead woods.

MATERIALS AND METHODS

Study area

The study was carried out in an 8 km^2 Amazon Forest fragment near the Silvio Braga Hydroelectric Power Plant (HPP) (centroid coordinates: 2°49'11.49"S; 54°17'56.64"W), located in Santarém city, Pará state, Brazil. The study area has vegetation cover of dense ombrophylous forest (Veloso et al. 1991) and with yellow latosol (Jati & Silva 2017). The climate is classified as humid tropical, with an average annual temperature of 27 °C (± 5 °C). The average relative humidity of the air is 88% and the average annual rainfall is 2,200 mm, with greater rainfall occurring between the months of January to May (rainy season; monthly average of 231 mm) and lower rainfall from August to November (dry period; monthly average of 61 mm) (Alvares et al. 2013).

Collection and identification of Hymenochaetales and Polyporales

Excursions for the collection of Hymenochaetales and Polyporales were carried out quarterly in 2018 (January, April, July and October), with collections over 30 transects of 250 m each, equidistant of 250 m with the beginning of the transects at 50 m from the edge of the forest, demarcated by PA-370 (Figure 1).

The basidiomata (fruiting bodies) found along each transect were collected following the protocol of Fidalgo & Bononi (1984) and Lodge et al. (2004), which consists of photographing the basidiomata before they are removed and afterwards, perform manual removal using a chisel or pocket knife, followed by accommodation of the basidiomata in paper bags with the appropriate collection information (number of the collector, type of substrate, geographic coordinates). At the Laboratory, the specimens were dehydrated at 35 °C (± 2 °C) in a forced air circulation oven for a period of two to three days (Fidalgo & Bononi 1984) and then mounted on exsiccates.

The identification of Hymenochaetales and Polyporales was based on macro and microscopic analysis. The macroscopic analysis consisted of detailed observations of the basidiomata with the naked eye and/or with the aid of a stereoscopic microscope, analyzing their insertion in the substrate, size (length, width and thickness), color, consistency, characteristics of the surfaces of the cap and pores, the tubes, the context and the margin of the basidiome. The color of the basidiome was determined by comparing the color chart by Kueppers (1982).

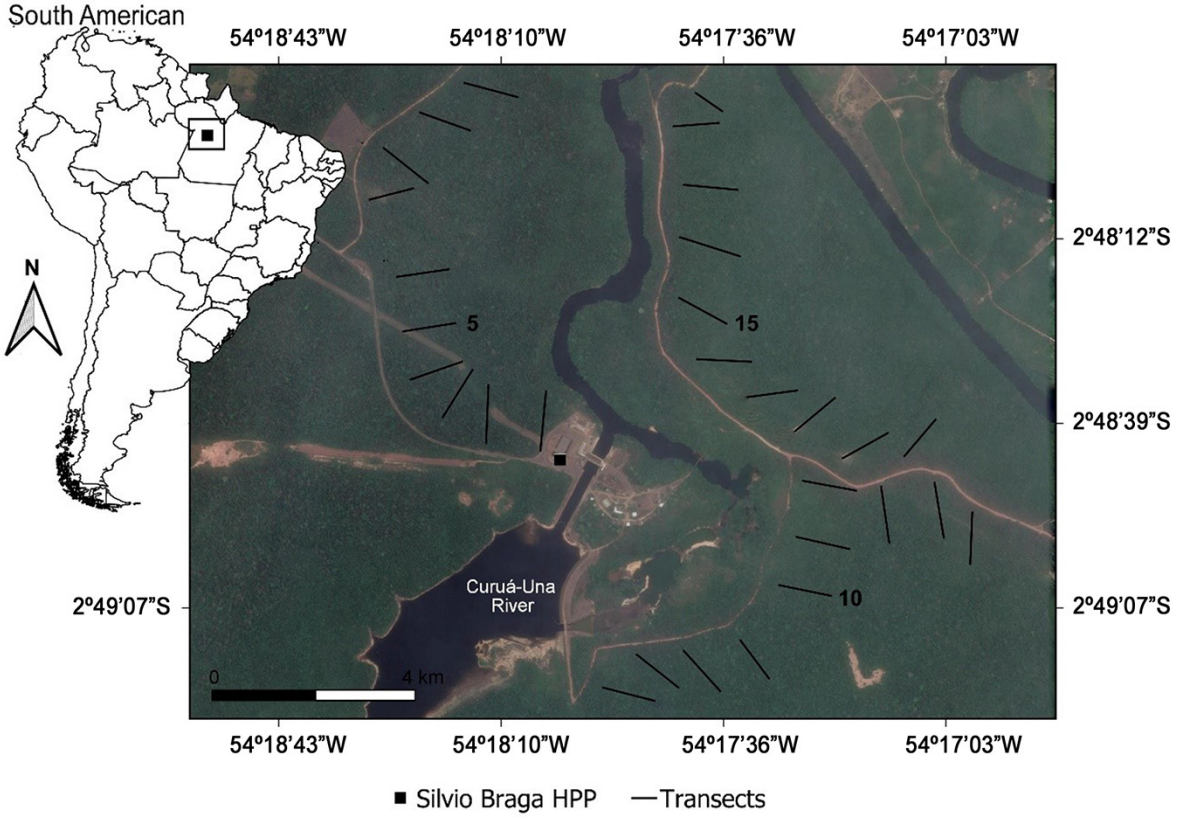

Figure 1. Study area with indication of transects (black lines) for Hymenochaetales and Polyporales collection. The numbers indicate the position of artisanal rain gauges in the study area.

For microscopic analysis, sections of different parts of the basidiomata (pileus, context and tubes) were made with the aid of a steel blade, under a binocular optical microscope. The cuts were arranged between slides and coverslips immersed in different aqueous solutions: 3% potassium hydroxide (moisturizer), phloxin, methylene blue (dyes) and, Melzer reagent to evidence the reactions of the microstructure walls, which can be positive or negative and, which vary according to each species: hyaline (colorless tone, with visible cell wall), amyloid (blue to purple/violet tone) or dextrinoid (gold to reddish tone) (Teixeira 1995, Ryvarden 2004). The hyphalic system (monomitic, di-trimitic), reproductive structures (basidia and basidiospores) and sterile structures (cistidia, cystidioles, setae, among others), were also analyzed.

After analyzed, the characteristics were compared with the specialized literature of the studied taxa Reid (1965), Ryvarden & Johansen (1980), Furtado (1981), Núñez & Ryvarden (1995), Ryvarden (2004, 2015, 2016), Dai (2010), Gomes-Silva et al. (2014, 2015), Costa-Rezende et al. (2016), Palacio et al. (2017) and used to identify and/or confirm the species. The species classification was continuously updated according to the Index Fungorum (http://www.indexfungorum.org) and the testimony material was deposited in the collection of fungi of the Herbarium HSTM of the Universidade Federal do Oeste do Pará (UFOPA).

Environmental variables

In each excursion the light input through the canopy, the temperature, the relative humidity and the rainfall were measured. Additionally, we categorized the substrates of occurrence of fungi in live or dead woods, diameter classes and decomposition stage for dead woods.

The entry of light through the canopy into the forest (canopy opening), temperature and relative humidity were measured every 50 m of each transect. Light input was estimated by canopy photographs taken at 1.30 m from the ground, transformed into black and white, of which white pixels were counted using Adobe Photoshop CC 2015© software, with the threshold function and the luminosity histogram (Marsden et al. 2002). Air temperature and relative humidity were measured with a digital thermo-hygrometer (Hikari, model HTH-240). And the rainfall was measured with the aid of handmade rain gauges composed of a 27.60 cm diameter funnel coupled to gallons of 20 L installed 125 m from the beginning of the 5th, 15th and 25th transects (Figure 1).

The diameter of the woods with the occurrence of Hymenochaetales and Polyporales were measured using a tape measure and grouped in a class interval table according to Sturges (1926), with eight classes being established: class 1 (5.9 ⊢ 39 cm), class 2 (39 ⊢ 72 cm), class 3 (72 ⊢ 105 cm), class 4 (105 ⊢ 139), class 5 (139 ⊢ 172 cm), class 6 (172 ⊢ 205 cm), class 7 (205 ⊢ 238 cm) and class 8 (271 ⊢ 305 cm).

The decomposition stages of the woods were also verified (D1 to D3) and determined according to Nordén & Paltto (2001). In the D1 stage, the wood fell recently, therefore, still rigid, so that a knife with the strength of the hand penetrates less than 2 mm. In the stage D2 the knife easily penetrates from 2 to 20 mm and in the stage D3 the knife easily penetrates more than 20 mm.

Data analysis

For data analysis, we built a spreadsheet with all the information in Microsoft Excel 2019© software relating abundance and richness, with the environmental variables collected in each sample period. As that the environmental

variables inhibit or not the growth of fungi (Núñez 1996, Meier et al. 2010), the differences among the variables registered in each sample period was considered as a sample and not a pseudo-reply, that is, each transect per excursion was considered a sample, totaling 120 samples, except for comparisons among substrates (live or dead wood, decomposition index and trunk diameter), in which each substrate was considered a sample.

Regarding fungi, we considered richness as the total number of species found and abundance as the sum of the occurrence of specimens found in different substrates. Data on light input, temperature and air humidity were measured by transect. Rainfall data were measured by month, using the sampling months for this study.

The relative frequency of species (*F*) was calculated using the function: $F = n / N \times 100$, where *n* is the number of specimens of a species and *N* is the total number of specimens found (Lindblad 2001), in order to present the dominance of the species found in the study area.

For all data, we tested the assumptions of normality (shapiro-wilk) and homogeneity (Breuch-Pagan). To remove the multicollinearity of the variables (linear relationship between the explanatory variables with a value above 10) we used a Variation Inflation Factor (*VIF*) and a correlation in order to remove the instability from the regression model and eliminate correlated variables (correlation above 70%). The Variation Inflation Factor analysis did not show multicollinearity or correlation between environmental variables.

The relationships between richness (total number of species) and abundance (total number of specimens) of Hymenochaetales and Polyporales with environmental variables (canopy opening, temperature and air humidity) were analyzed by multiple linear regressions, with the stepwise method using the Vegan package (Oksanen et al. 2015), all analyzes were performed on R 3.5.2 (R Core Team 2012).

To relate the assemblage (species composition) of Hymenochaetales and Polyporales with the environmental variables, a simple regression analysis was used. For this, the representative matrix of the assemblage of Hymenochaetales and Polyporales was reduced to the first axis of a Principal Coordinate Analysis (PCoA) based on Bray-Curtis dissimilarity, using the MASS (Ripley et al. 2013) and Vegan package (Oksanen et al. 2015). A similarity analysis (ANOSIM) based on Bray-Curtis dissimilarity, with 1,000 randomizations was used to assess the relationship between the collection periods, we used the Vegan package (Oksanen et al. 2015).

Environmental data, richness and abundance were compared between sample periods by one-way Analysis of Variance (ANOVA), followed by Tukey's test when necessary, using the Vegan package (Oksanen et al. 2015) and Car (Fox & Weisberg 2011), to indicate significant differences between standard deviation pairs we used the agricolae package (Mendiburu & Mendiburu 2019) and the Sciplot package (Morales & Morales 2017) for making graphs with standard deviation bars. These analyzes reinforced the results observed in the aforementioned regressions.

Chi-square adjustment tests (χ^2) were used to compare the abundance and richness of Hymenochaetales and Polyporales between live and dead woods, between the stages of decomposition and diameter classes of the wood using the Vegan package (Oksanen et al. 2015). An individual Indication Value (*IndVal*, Dufrêne & Legendre 1997) with 1,000 randomizations was used to assess the relationship between species abundance with dead and live woods.

In order to observe all species of Hymenochaetales and Polyporales found in

wood with different stages of decomposition, we generated an ordination chart using Comunidata 1.6. Finally, we performed analyze the association of Hymenochaetales and Polyporales with the stages of decomposition and with the diameter classes of the wood, utilization indices were applied (Kruys et al. 1999), using the labdsv package (Roberts 2016). When $U_i = 1$, there is no preference for a certain condition; $U_i > 1$, indicates preference for a certain condition. This analysis was performed for species with an abundance equal or greater than 10 specimens in woods with different stages of decomposition, due to the impossibility of inferring ecological patterns with low abundance of individuals (Yamashita et al. 2009).

RESULTS

A total of 545 specimens of Hymenochaetales and Polyporales were collected, identified and represented in 91 species. The species with the greatest abundance and frequency of occurrence were *Cerrena hydnoides* (Sw.) Zmitr. with 34 specimens, *Trametes elegans* (Spreng.) Fr. with 31 specimens and *Rigidoporus lineatus* (Pers.) Ryvarden with 30 specimens, corresponding to 22.5% of the specimens collected and occurring in 29 samples (24%) (Figure 2, Table I).

The abundance and the richness of Hymenochaetales and Polyporales were positively influenced by air humidity, although with low determination coefficient values of the multiple regression (Table II). These results were indirectly confirmed by comparing the abiotic variables, the abundance and richness of Hymenochaetales and Polyporales between the rainy (January and April) and dry (July and October) periods (Figures 3, 4, Tables III, IV).

The assemblage of Hymenochaetales and Polyporales was influenced by air humidity, temperature and rainfall in the study area (Table II), with emphasis on temperature that significantly contributed to the species distribution (Figure 5, Table V). These results were directly confirmed with the comparison between rainy and dry periods ($r = 0.24$, $p < 0.001$).

The abundance of Hymenochaetales and Polyporales differed significantly between live and dead woods ($r^2 = 154.63$, df = 1, $p < 0.0001$), being significantly higher in dead woods ($n = 210$) than in live woods ($n = 21$). Likewise, Hymenochaetales and Polyporales richness was significantly higher in dead than live woods ($r^2 = 28.45$, df = 1, $p < 0.001$), with 52 species of Hymenochaetales and Polyporales found in dead substrates and only 10 species in living substrates. However, a significant occurrence

Figure 2. Basidiome of the most abundant macrofungal species in the occurring near the Silvio Braga HPP, Santarém, PA. a) *Cerrena hydnoides*, b) *Rigidoporus lineatus* and c) *Trametes elegans*.

of the species in these substrates, only for *Rigidoporus lineatus* (*Indival* = 0.44, $p < 0.02$) and *Trametes elegans* (*Indival* = 0.44, $p < 0.02$) associated with dead woods and *Phylloporia chrysites* (*Indival* = 039, $p < 0.03$) associated with live woods.

Significant differences in abundance and richness of Hymenochaetales and Polyporales were also observed in relation to the decay stage of the dead woods ($\chi^2_{abundance} = 254.94$, gl = 2, $p = 0.001$; $\chi^2_{richness} = 38.87$, gl = 2, $p < 0.001$). Hymenochaetales and Polyporales were more abundant and representative in richness in the decomposition stage D1 (*n* = 179, richness = 51), compared to D2 (*n* = 19; richness = 12) or D3 (*n* = 12; richness = 7), being *Lenzites betulina*, *Perenniporia medulla-panis*, *Ranadivia modesta*, *Trametes elegans* and *T. variegata* were found in the three stages of decomposition (D1-D2-D3), while *Fomitopsis rosoealba*, *Ganoderma resinaceum*, *Lentinus crinitus*, *Rigidoporus lineatus* and *Truncospora ochroleuca* were found in two stages of decomposition (D1-D2), with emphasis on *Megasporporia setulosa*, *Nigrofomes melanoporus* and *Podoscypha nitidula* found in a single stage of decomposition, D2 and D3, respectively (Figure 6).

Regarding the abundant species (10 ≥ specimens) with the stages of wood decomposition *Perenniporia medulla-panis*, *Ranadivia modesta*, *Lenzites betulina* and *Trametes elegans* are related to the stage of decomposition (D2-D3), with the last two species being strongly related to stage of decomposition (D3), that is, soft substrate. *Cerrena hydnoides*, *Fuscoporia gilva* and *Rigidoporus lineatus* are related to the decomposition stage (D1), tough substrate. We did not record species that are related to the three stages of decomposition at the same time (Table VI).

Hymenochaetales and Polyporales were more abundant and representative in class 1 in diameter of woods (*n* = 97, richness = 95) and class 2 (*n* = 61; richness = 59), compared to the class 3 (*n* = 34; richness = 32), class 4 (*n* = 6; richness = 6), class 5 (*n* = 2; richness = 2), class 6 and 7 (*n* = 4; richness = 4) and class 8 (*n* = 1; richness 1). However, most species with more than ten specimens showed wood use pattern in class 3, the *Ranadivia modesta* species occurs in five diameter classes, with the preference strongly related to class 5, followed by *Rigidoporus lineatus* occurring in four classes in diameter and strongly related to class 6, and *Trametes elegans* occurring in three diameter classes with greater relation in class 8, four species were related in classes 1 (Table VII).

DISCUSSION

Data obtained show that the Hymenochaetales and Polyporales fungi from this region of the Amazon have a preference for dead woods with reduced diameters, in addition to the richness, abundance and assemblage of these fungi being influenced by the effects of environmental variables such as relative humidity, temperature and rainfall.

The relative humidity of the air is a factor that facilitates the growth of fungi (Núñez 1996, Hawkes et al. 2011), so that humid forests can serve as refuges for Hymenochaetales and Polyporales, facilitating their spread. The diversity of Hymenochaetales and Polyporales varies along a gradient or factors related to rainfall between dry and wet periods (Lindblad 2001), a fact observed in the present study, in which the greatest richness and abundance occurs in the rainy period (January and April).

However, it is not always possible to establish a direct correlation between environmental variables and the Hymenochaetales and Polyporales assemblage (e.g. Lindblad 2001, Laganà et al. 2002, Gibertoni 2008), this

Table I. Families, genera and species of Hymenochaetales and Polyporales with their respective frequencies of occurrence (FR), abundance (AB), type of substrate (SU) observed (BR = Branch, LT = living trunk, DT = dead trunk, SO = soil) and stage of decomposition (SD) with the categories (D1 = rigid, D2 = intermediary, D3 = fragile) found near the Silvio Braga HPP, in Santarém, PA.

Order/Family/Species	SU	SD	FR	AB
Hymenochaetales Oberw.				
Hymenochaetaceae Donk				
Coltricia barbata Ryvarden & de Meijer	SO	-	0.18	1
Coltricia cf. *focicola* (Berk. & M.A. Curtis) Murrill	SO	-	0.37	2
Coltricia cinnamomea (Jacq.) Murrill	SO	-	0.73	4
Coltricia globispora Gomes-Silva, Ryvarden & Gibertoni	SO	-	0.18	1
Fomitiporia cf. *maxonii* Murrill	DT	D1	0.18	1
Fomitiporia neotropica Camp.-Sant., Amalfi, R.M. Silveira, Robledo & Decock	DT	D1	1.47	8
Fomitiporia apiahyna (Speg.) Robledo, Decock & Rajchenb.	DT	D1	0.55	3
Fulvifomes imbricatus L.W. Zhou	DT	D1	0.18	1
Fuscoporia callimorpha (Lév.) Groposo, Log.-Leite & Góes-Neto	DT	D1	0.73	4
Fuscoporia chrysea (Lév.) Baltazar & Gibertoni	DT	D1	0.18	1
Fuscoporia gilva (Schwein.) T. Wagner & M. Fisch	DT-LT	D1	3.67	20
Fuscoporia rhabarbarina (Berk.) Groposo, Log.-Leite & Góes-Neto	BR	-	0.73	4
Fuscoporia undulata (Murrill) Bondartseva & S. Herrera	BR	-	0.18	1
Fuscoporia wahlbergii (Fr.) T. Wagner & M. Fisch.	DT	D1	0.18	1
Hymenochaete damicornis (Link) Lév.	SO	-	5.14	28
Hymenochaete luteobadia (Fr.) Höhn. & Litsch.	BR-DT	D1	2.02	11
Hymenochaete rubiginosa (Dicks.) Lév.	DT	D1	0.18	1
Inonotus tabacinus (Mont.) G. Cunn.	DT-LT	D1	0.55	3
Phellinus fastuosus (Lév.) S. Ahmad	DT	D1	0.37	2
Phellinus sp.	DT	D1	0.18	1
Phylloporia chrysites (Berk.) Ryvarden	LT	D1	2.02	11
Phylloporia spathulata (Hook.) Ryvarden	DT-SO	D1	0.55	3
Nigrofomitaceae Jülich				
Nigrofomes melanoporus (Mont.) Murrill	DT	D2	0.18	1
Incertae sedis				
Trichaptum byssogenum (Jungh.) Ryvarden	DT	D1	0.37	2
Trichaptum perrottetii (Lév.) Ryvarden	DT	D1	0.18	1
Polyporales Gäum.				
Cerrenaceae Miettinen, Justo & Hibbett				
Cerrena caperata (Berk.) Zmitr.	DT	D1	2.57	14
Cerrena hydnoides (Sw.) Zmitr.	DT	D1	6.24	34
Fomitopsidaceae Jülich				
Fomitella supina (Sw.) Murrill	DT	D1	0.18	1

Table I. Continuation.

Fomitopsis roseoalba A.M.S. Soares, Ryvarden & Gibertoni	DT-LT	D1-D2	1.10	6
Ganodermataceae Donk				
Amauroderma aurantiacum (Berk.) Torrend	SO	-	0.18	1
Amauroderma calcigenum (Berk.) Torrend	SO	-	1.10	6
Amauroderma elegantissimum Ryvarden & Iturriaga	SO	-	0.18	1
Amauroderma laccatostiptatum Gomes-Silva, Ryvarden & Gibertoni	SO	-	0.18	1
Amauroderma omphalodes (Berk.) Torrend	SO	-	1.47	8
Amauroderma partitum (Berk.) Wakef.	SO	-	1.28	7
Amauroderma praetervisum (Pat.) Torrend	DT-SO	D1	2.94	16
Amauroderma rude (Berk.) Torrend.	SO	-	0.55	3
Amauroderma schomburgkii (Mont. & Berk.) Torrend	SO	-	2.20	12
Amauroderma sprucei (Pat.) Torrend	SO	-	1.65	9
Amauroderma subsessile Gomes-Silva, Ryvarden & Gibertoni	DT	D1	0.18	1
Ganoderma amazonense Weir	SO	-	0.18	1
Ganoderma australe (Fr.) Pat.	DT	D1	0.37	2
Ganoderma resinaceum Boud.	DT	D1-D2	0.92	5
Haddowia longipes (Lév.) Steyaert	SO	-	0.37	2
Irpicaceae Spirin & Zmitr.				
Flavodon flavus (Klotzsch) Ryvarden	DT	D1	2.57	14
Meripilaceae Jülich				
Rigidoporus biokoensis (Bres. ex Lloyd) Ryvarden	DT	D1	2.94	16
Rigidoporus lineatus (Pers.) Ryvarden	DT	D1-D2	5.50	30
Meruliaceae Jülich				
Mycorrhaphium adustulum (Banker) Ryvarden	DT		0.18	1
Podoscypha nitidula (Berk.) Pat.	DT	D3	0.37	2
Podoscypha parvula (Lloyd) D.A. Reid	BR	-	0.37	2
Stereopsis hiscens (Berk. & Ravenel) D.A. Reid	SO	-	0.55	3
Stereopsis radicans (Berk.) Reid	SO	-	0.18	1
Phanerochaetaceae Jülich				
Inflatostereum glabrum (Lév.) D.A. Reid	BR	-	0.18	1
Panaceae Miettinen, Justo & Hibbett				
Cymatoderma caperatum (Berk. & Mont.) D.A. Reid	BR	-	0.55	3
Panus neostrigosus Drechsler-Santos & Wartchow	DT	D1	0.18	1
Polyporaceae Corda				
Atroporus diabolicus (Berk.) Ryvarden	BR	-	2.20	12
Atroporus rufoatratus (Berk.) Palacio, Reck & Robledo	BR	-	1.47	8
Bresadolia uda (Jungh.) Audet	DT-SO	D1	0.73	4
Cerioporus cavernulosus (Berk.) Zmitr.	DT	D1	0.55	3
Cerioporus flavus (Sw.) Zmitr.	BR	D1	0.73	4
Cerioporus mollis (Sommerf.) Zmitr. & Kovalenko	BR	-	0.18	1
Cerioporus varius (Pers.) Zmitr. & Kovalenko	DT	D1	0.55	3

Table I. Continuation.

Earliella scabrosa (Pers.) Gilb. & Ryvarden	BR	-	0.37	2
Favolus brasiliensis (Fr.) Fr.	BR	-	0.55	3
Favolus grammocephalus (Berk.) Imazeki	BR	-	0.37	2
Fomes fasciatus (Sw.) Cooke	DT	D1	0.37	2
Fomes fomentarius (L.) Fr.	DT	-	0.18	1
Lentinus crinitus (L.) Fr.	DT	D1-D2	1.83	10
Lentinus velutinus Fr.	DT	D1-D3	1.28	7
Lenzites betulina (L.) Fr.	DT	D1-D2-D3	3.49	19
Lopharia cinerascens (Schwein.) G.Cunn.	BR	D1	0.18	1
Megasporoporia setulosa (Henn.) Rajchenb	DT	D2	0.55	3
Microporellus dealbatus (Berk. & M.A. Curtis) Murrill	SO	-	1.47	8
Microporellus iguazuensis Rajchenb.	SO	-	0.37	2
Microporellus obovatus (Jungh.) Ryvarden	DT	D1	1.28	7
Neodictyopus atlanticae (Mont.) Palacio, Robledo & Drechsler-Santos	BR	-	0.37	2
Neodictyopus gugliottae Palacio, Grassi & Robledo	BR	-	0.18	1
Neofavolus alveolaris (DC.) Sotome & T. Hatt.	BR	-	0.37	2
Perenniporia medulla-panis (Jacq.) Donk	DT-LT	D1-D2-D3	2.57	14
Perenniporia stipitata Ryvarden	DT	D1	0.73	4
Polyporus guianensis Mont.	DT	D1	2.02	11
Polyporus leprieurii Mont.	DT	D1	0.55	3
Porogramme albocincta (Cooke & Massee) Gibertoni	BR	-	0.55	3
Pycnoporus sanguineus (L.) Murrill	DT	D1	1.28	7
Ranadivia modesta (Kunze ex Fr.) Zmitr.	DT	D1-D2-D3	3.30	18
Trametes elegans (Spreng.) Fr.	DT	D1-D2-D3	5.69	31
Trametes leonina (Klotzsch) Imazeki	DT	D1	0.18	1
Trametes pubescens (Schumach.) Pilát	DT	D1	0.18	1
Trametes variegata (Berk.) Zmitr., Wasser & Ezhov	DT	D1-D2-D3	3.12	17
Trametes versicolor (L.) Lloyd	DT	D1	0.73	4
Truncospora ochroleuca (Berk.) Pilát	DT	D1-D2	0.73	4
Total				545

relationship depends on the characteristics of each occurrence of these fungi. Gibertoni et al. (2007), for example, reported significant differences in the assemblage of Hymenochaetales and Polyporales found in different sample periods in thirteen areas of Atlantic Forest in the Northeast of Brazil, similar to that found in the present study, although it has diverged as to the period of the year in which these fungi were most often. Other studies were similar, comparing fungal assemblages, and did not observe significant differences between periods of greater or lesser drought (Núñez 1996, Gibertoni et al. 2015).

The richness and abundance of Hymenochaetales and Polyporales species were clearly higher in dead wood. This type of substrate allows greater use by fungi in relation to live woods, it indicates that are functional according to their ability to decompose by the conditions of the substrate found, and what varies according to the physical and chemical

Table II. Influence of environmental variables on the abundance and richness of Hymenochaetales and Polyporales collected near the Silvio Braga HPP, in Santarém, PA. *b* = slope of the line, Error = Standard Error, *t* = critical *t* value, *P* = *p* value, r = *r* value. Values in bold, significant at ≤ 0.05.

Variables	Abundance				Richness			
	b	**Error**	***t***	***P***	**B**	**Error**	***t***	***P***
Intercept	-18.48	12.58	-1.48	0.14	-14.77	8.67	-1.70	0.09
Canopy	0.02	0.08	0.23	0.82	-0.01	0.05	-0.26	0.79
Temperature	0.03	0.33	0.09	0.93	0.03	0.23	0.13	0.90
Humidity	0.27	0.06	4.87	**0.001**	0.23	0.04	5.84	**0.001**
r	0.19				0.25			

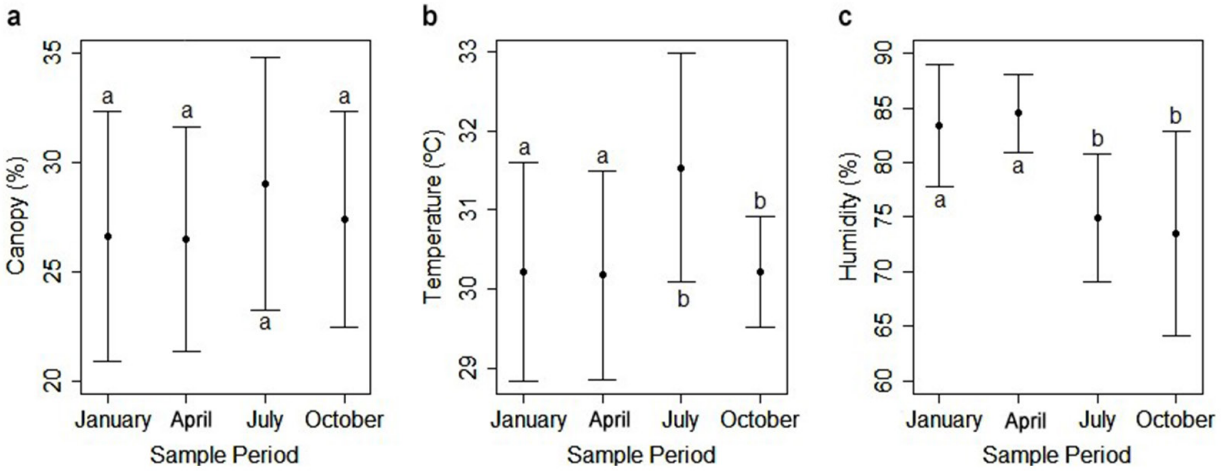

Figure 3. Comparisons of canopy opening (a), temperature (b) and air humidity (c) near the Silvio Braga HPP, in Western Pará between sample periods. Letters on the standard deviation bars indicate significant differences between pairs.

properties of the substrate (Adarsh et al. 2015). Thus, there is a generalization of the use of dead woods by species of fungi (Lindhe et al. 2004, Tikkanen et al. 2006, Wong 2009).

Species of the genus *Amauroderma*, *Coltricia* and *Phylloporia spathulata* were found in the soil, demonstrating specialization in accessing another niche, possibly ectomycorrhizal relationships with living tree roots or in buried debris (Tedersoo et al. 2007, Ryvarden 2004, Yamashita et al. 2009). In addition, the physical properties of soils can cause these species to occur in the study area (O'Hanlon & Harrington 2012).

Wood decomposition is a dynamic process linked to an ecological succession of the fungal community or assemblage (Rajala et al. 2012, Siitonen & Stockland 2012). The preferential occurrence of fungi at a given stage of decomposition is related to the degradation capacity of the fungus itself (Gibertoni 2008). In species of Hymenochaetales and Polyporales were observed occurring preferentially in woods in stages of decomposition D1 and D2, that is, in more intact woods.

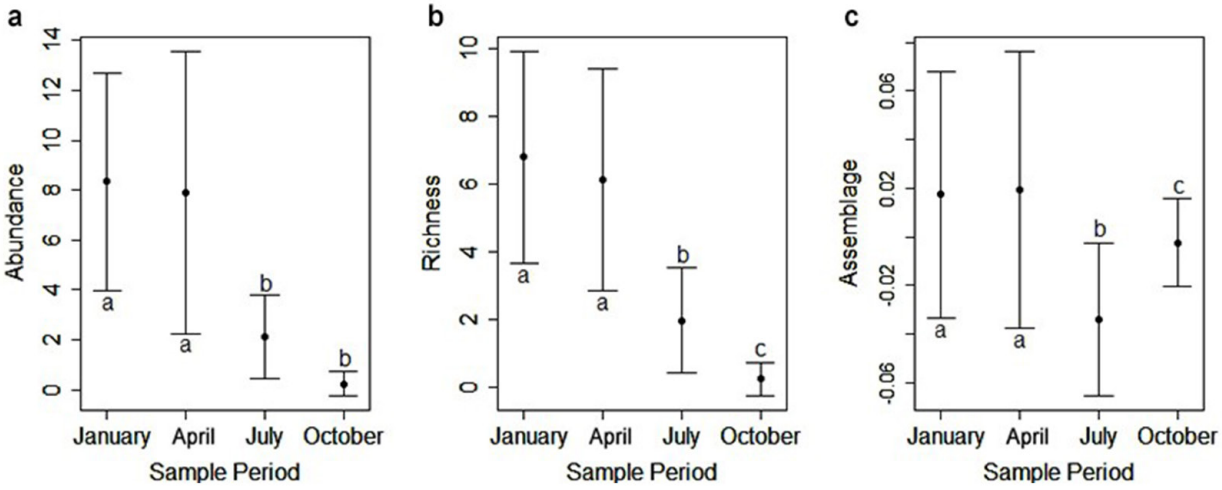

Figure 4. Comparisons of abundance (a), richness (b) and assemblage of Hymenochaetales and Polyporales (c) collected in the near the Silvio Braga HPP, in Western Pará between sample periods. Letters on the standard deviation bars indicate significant differences between pairs.

Table III. Analysis results of environmental variables variance between sample periods. SQ = Quadratic sum, df = Degree of freedom, *F = F statistic value*, *P = p* value. Values in bold, significant at ≤ 0.05.

Canopy opening					
Variation source	**df**	**SQ**	**Variance**	***F***	***P***
Factor	3	121	40.45	1.38	0.25
Residue	116	3389	29.22		
Temperature					
Variation source	**df**	**SQ**	**Variance**	***F***	***P***
Factor	3	39.58	13.19	8.58	**0.001**
Residue	116	178.35	1.53		
Relative humidity					
Variation source	**df**	**SQ**	**Variance**	***F***	***P***
Factor	3	2.90	965,4	23,2	**0.001**
Residue	116	4.83	41,6		

The decomposition process starts from the wood dense (D1), with low moisture content, low decomposition rate and have a higher amount of sapwood, facilitating the development of wood degrading fungi, the decay rate gradually increases to a peak during the intermediate stages (D2) which are characterized by a high diversity of basidiomata (Lindblad 2001, Mäkinen et al. 2006, Gibertoni et al. 2007). However, the decomposition rate gradually decreases (D3) to a minimum and wood decomposing fungi can no longer be detected, and the remaining wood contains only the most recalcitrant compounds (Mäkinen et al. 2006, Rajala et al. 2012), this entire process depends on abiotic factors such as relative humidity, temperature and even the floristic composition in a given place (Stokland et al. 2012). The same occurrence aspect was

Table IV. Analysis results of variance of environmental variables between sample periods. SQ = Quadratic sum, df = Degree of freedom, *F = F statistic value*, *P = p* value. Values in bold, significant at ≤ 0.05.

Abundance					
Variation source	**df**	**SQ**	**Variance**	***F***	***P***
Factor	3	1499	499.7	36.87	**0.001**
Residue	116	1572	13.6		
Total	119	3071	513.3		
Richness					
Variation source	**df**	**SQ**	**Variance**	***F***	***P***
Factor	3	915.8	305.26	52.49	0.001
Residue	116	674.6	5.82		
Total	119	1590.4	311.08		
Assemblage					
Variation source	**df**	**SQ**	**Variance**	***F***	***P***
Factor	1	10.7	10.70	9.14	**0.003**
Residue	117	137.0	1.17		
Total	118	147.7	11.87		

observed in the studies carried out in the Caxiuanã National Forest (Gibertoni 2008) and in the RAPELD sample system (Medeiros et al. 2015), both environments of the Amazon Forest, but it was different in areas of the Atlantic Forest (Gibertoni et al. 2007), the majority of Hymenochaetales and Polyporales species occurring on substrates in stages D2 and D3 of decomposition.

The knowledge about the decomposition stage still demands a greater study time, was also observed in Pasanen et al. (2014) and Kwaśna et al. (2017) where the study time was relatively short, and the perception of dead wood in different stages of decomposition in the study area was greater than the others, this factor being a tendency to find fungal species in the first stages of succession decomposition. Most Hymenochaetales and Polyporales have a strong tendency to produce basidiome at a certain stage of decomposition (Lindblad 1998, Gibertoni 2008), as species found mainly from pioneer decomposers, and lack of wood at advanced stages of decomposition other fungal species (Junninen & Komonen 2011), which corresponds to this study.

The abundance and richness of Hymenochaetales and Polyporales decreased with the increase in the diameter of the wood, with the largest records being in woods with a diameter class of 5 to 39 cm, data that corroborate studies conducted in tropical forests in other parts of the Amazon and also in Malaysia (Yamashita et al. 2009, Medeiros et al. 2015). In the rainforest of Costa Rica and in the alder forest in Argentina, Hymenochaetales and Polyporales occur preferably in woods over 40 cm in diameter (Lindblad 2001, Urcelay & Robledo 2009), as in boreal and temperate forests (Junninen & Komonen 2011, Abrego & Salcedo 2013). The abundance and richness of fungi in larger diameter class woods is probably due to the greater availability of resources, microhabitat, space and humidity (Bader et al. 1995, Lindblad 2001, Stokland et al. 2012, Halme et al. 2013).

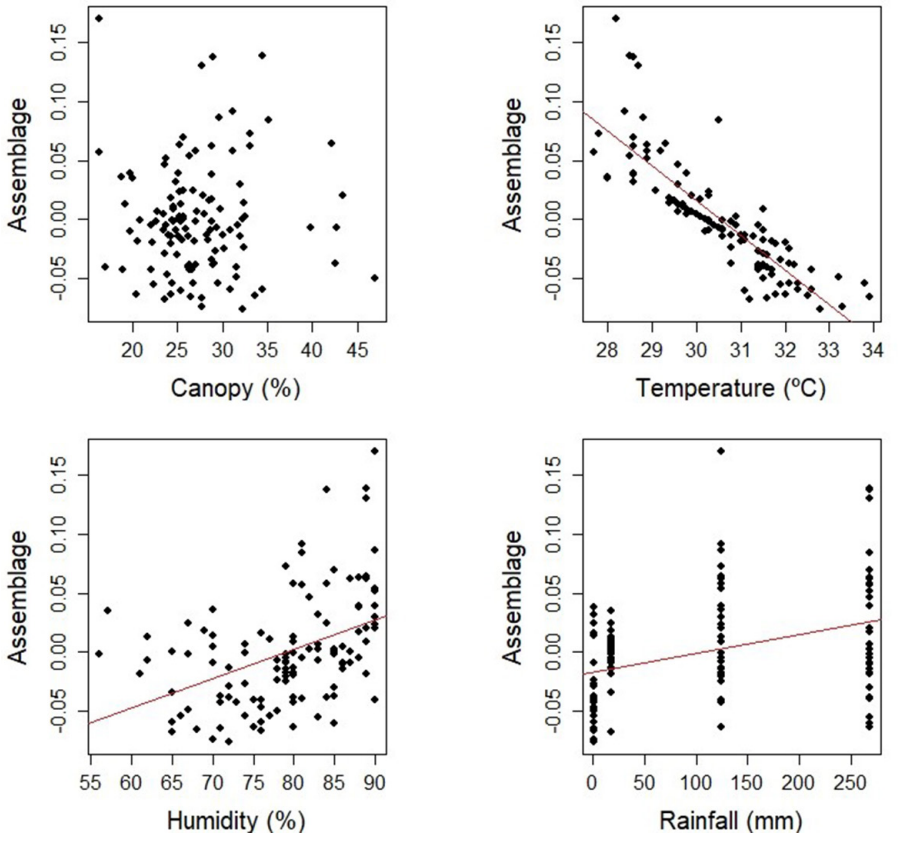

Figure 5. Relationship of environmental variables with the assemblage of Hymenochaetales and Polyporales (axis 1 of PCoA, with Bray-Curtis dissimilarity distance) occurring near the Silvio Braga HPP, Santarém, PA.

Table V. Influence of environmental variables on the assemblage of Hymenochaetales and Polyporales near the Silvio Braga HPP, in Santarém, PA. *b* = slope of the line, Error = Standard Error, *t* = critical *t* value, *P* = *p* value, r^2 = adjusted *r* value. Values in bold, significant at ≤ 0.05.

Variables	*b*	Error	*t*	*P*	r^2
Canopy	0.10	10.57	0.01	0.99	0.00
Temperature	-24.64	1.38	-17.81	**0.001**	0.73
Humidity	72.92	14.32	5.09	**0.001**	0.18
Rainfall	838.62	197.39	4.25	**0.001**	0.13

The abundance and richness of Hymenochaetales and Polyporales in dead wood depend on sample size (Fukasawa 2021). Our sample data by diameter classes is an attempt to make a compromise in relation to wood diameter at large and small scales, thus providing conditions for producing adequate and reliable results on fungal abundance and richness for future studies. For example, our data corroborate Medeiros et al. (2015) and Gibertoni (2008) in relation to species with more than ten records, all have a wide distribution of frequency and preference in the first class of dead wood diameter (5.9 ⊦ 39 cm), with the exception of *Lenzites betulina* which has preference only by one diameter class, data that differ from those obtained by Kwaśna et al. (2017) where fungal species are found in larger diameters. Diameter size is important in studies of dead wood and wood-dwelling fungi (Juutilainen et al. 2011).

Among the species found in the present study, the only one common to the work of

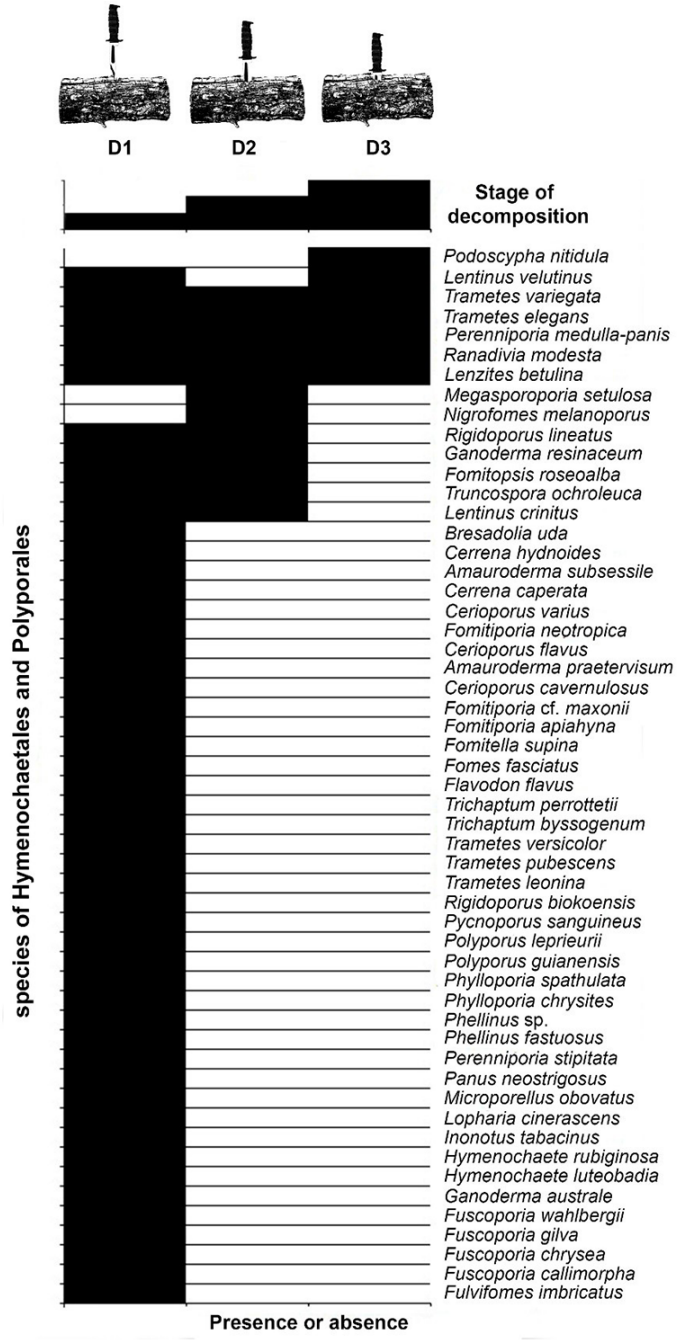

Figure 6. Ordering of Hymenochaetales and Polyporales species found at different stages of decomposition wood (D1 = rigid, D2 = intermediate and D3 = fragile) near the Silvio Braga HPP, Santarém, PA.

Medeiros et al. (2015) was *Fuscoporia gilva*, *Rigidoporus lineatus* and *Ranadivia modesta* that presented a wide frequency distribution in the different diameter classes in both. This could be explained by the fact that the species are perennial and, therefore, could be found in the same wood throughout its decomposition process (Halbwachs et al. 2016, Maurice et al. 2021).

Our standardized sampling indicates that environmental variables influence the richness, abundance and assemblage of Hymenochaetales and Polyporales in this region of the Amazon. The data on substrates demonstrate that the

Table VI. Usage index (U_i) of Hymenochaetales and Polyporales species in dead trunks near the Silvio Braga HPP, Santarém, PA, second stage of decomposition of the trunks (D1, D2 and D3). N = abundance. Values in bold significant to preference.

Species	N	U_i(D1)	U_i(D2)	U_i(D3)
Cerrena hydnoides	10	**1.20**	0.00	0.00
Fuscoporia gilva	11	**1.20**	0.00	0.00
Perenniporia medulla-panis	11	0.76	**2.79**	**1.30**
Lenzites betulina	12	0.70	**1.70**	**3.58**
Rigidoporus lineatus	17	**1.13**	0.60	0.00
Trametes elegans	18	0.80	**1.70**	**2.38**
Ranadivia modesta	18	0.93	**1.13**	**1.59**

Table VII. Substrate utilization index (U_i) by class of Hymenochaetales and Polyporales substrate diameter with more than ten records at Silvio Braga HPP, Santarém, PA. Values in bold significant to preference.

Species	Number	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6	Class 7	Class 8
Cerrena hydnoides	10	**1.21**	0.55	**1.10**	0.00	0.00	0.00	0.00	0.00
Fuscoporia gilva	11	**1.10**	0.77	**1.50**	0.00	0.00	0.00	0.00	0.00
Perenniporia medulla-panis	11	0.92	0.00	**1.50**	0.00	0.00	0.00	**4.33**	0.00
Lenzites betulina	12	0.50	0.70	**2.29**	0.00	0.00	0.00	0.00	0.00
Rigidoporus lineatus	17	**1.07**	**1.07**	0.32	**2.80**	0.00	**8.41**	0.00	0.00
Trametes elegans	18	**1.01**	**1.50**	0.92	0.00	0.00	0.00	0.00	**7.94**
Ranadivia modesta	18	0.22	**1.00**	**1.53**	**5.30**	**7.94**	0.00	**2.65**	0.00

studied richness and abundance is affected by the quality and diameter of the substrate, thus indicating a possible diversity of broad-lived strategies, since these species are capable of occupying all types of substrates available. In addition, the knowledge about Hymenochaetales and Polyporales for the Brazilian Amazon region has been expanded, as well as the certainty of the importance of encouraging mycological research in such a little-explored location.

These data may promote subsidies and framework for assessing the state of conservation at the community/assemblage level and in making decisions about the management of natural resources.

Our data emphasize the need for collections elsewhere, whether in fragmented forest areas or in Conservation Units (UC) such as Private Natural Heritage Reserve (RPPN), Biological Reserves (REBIO), National Forest (FLONA) and National Park (PARNA), explore these places in short and long-term monitoring projects to understand the funga as well as its successional role in wood decomposition, unify these data and promote subsidies and structure to assess the conservation status for each species found

in the decisions about the management of natural resources.

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