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Litter thickness and soil pH influence the diversity of saprotrophic fungi in primary forest fragments in the Amazon

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ABSTRACT

Plant communities influence the composition of local fungi, and this has been verified in different biomes around the world. The analysis of the litter structure in a forest reserve in the Amazon has shown that floristic diversity and substrate morphology affect fungal diversity at different scales. Our results revealed that the α diversity of the fungi was positively correlated with the substrate quality in the litter, while β diversity showed differences within and among the floristic groups identified in the reserve. In addition to litter morphology, some soil physicochemical variables were considered as predictors, of which only the soil pH affected the fungal richness. Therefore, our results support the hypotheses that: 1) plant identity and substrate deposition time in soil have an effect on microbial communities, and 2) a greater leaf diversity correlates to increased fungal variety.

1. Introduction

Fungi play an important role in nutrient cycling and forest dynamics (Baldrian, 2017; Lavelle et al., 2020; Rousk et al., 2009). Despite several advancements in the study of ecological patterns of the fungal community structure, the distribution of fungal species is still unclear, especially when considering different spatial scales (Tedersoo et al., 2014). For example, at the global scale, climatic and edaphic variables are the best predictors for determining the richness and composition of the fungal community (Tedersoo et al., 2014). In contrast, locally, there is evidence that the diversity and composition of plant communities directly influence the fungal variety, which has been verified in different biomes, such as the Amazon (Peay et al., 2013), Taiga (Tedersoo et al., 2016), and temperate forests (Yang et al., 2017a, 2017b). This demonstrates the ability of vegetation in a given region to hierarchically control the organisms that depend on it for survival (Lavelle et al., 1993; Mori et al., 2016).

In small forest remnants, natural disturbances such as heavy rains can accelerate the dynamics of succession (Machado and Oliveira-Filho, 2010). The emergence of new patterns of tree distribution with changes in plant structure and composition favors the formation of distinct floristic clusters (Laurance et al., 2002), although it is unclear how changes in vegetation affect fungal communities (Kivlin and Hawkes, 2020, 2016). Saprotrophic fungi are dependent on dead materials that accumulate at the bottom of the forest, such as branches, leaves, flowers, and fruits, which in turn are controlled by the phenological behavior of botanical species in response to environmental factors, such as temperature, humidity, and soil physicochemical variables (Becklin et al., 2016; Chapin et al., 1987; Sakai and Kitajima, 2019). The time and decomposition dynamics of this material can be evaluated by analyzing the litter profile, which can have up to three organic horizons: organic and litter (OL), organic and fragmented (OF), and organic and humus (OH), distinguishable by the recognition rate of the remaining material and the humic components present (Zanella et al., 2018b).

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The interaction between these horizons and the organisms that decompose their substrate components form a complex known as the litter system (Lavelle and Spain, 2001; Zanella et al., 2018a). Leaves typically comprise most of this system, and studies have shown that leaf mixtures of distinct quality decompose more effectively than single types (Chapman et al., 2013; Chapman and Newman, 2010; McGuire et al., 2010). Saprotrophic fungi are sensitive to changes in plant substrate composition (Huang et al., 2019; Laurance et al., 2002; Rambelli et al., 2004), and studies based on diversity metrics help elucidate the patterns of vegetation distribution that affect the community of these organisms. A valuable metric for detecting community distribution patterns is additive partitioning of diversity, a multiscale assessment method that proportionally divides the total γ diversity (regional diversity) into its α (local diversity, e.g., average species richness in minor scales) and β (differentiation among scales) components (Veech et al., 2002)

Megadiverse forest environments, such as the Amazon, are expected to present a large microbial diversity (Ritter et al., 2018), and changes in the vegetation structure can cause changes in the organization of fungal communities (Mori et al., 2018). To clarify these effects on the diversity of these organisms, the following predictions were tested in the fungal community: 1) the α diversity varies in response to the litter substrate type and plant species composition, represented by the leaves of the OL horizon; 2) β diversity varies in response to the plant community composition between sampling points and distinct floristic clusters; and 3) γ diversity is an expression of the spatial variation of forest plants as a function of litter mosaics and the physicochemical properties of the soil.

2. Material & methods

2.1. Study site

The study was conducted in the Mocambo Reserve, a 5.7 ha dense ombrophilous forest fragment, which is a part of the Ecological Research Area of Guamá (APEG, 1°26′20″ S, 48°25′18″ W), with 506 ha of dense rainforest that includes the Aurá (Várzea Forests, 400 ha) and Catu (Igapó Forest, 100 ha) reserves (Pires and Salomão, 2005). The area is located in the city of Belém, Pará, Brazil. The fragment is bordered by the Guamá River to the south and by the city's metropolitan region to the north and west. The climate of the region is type *Af* (tropical humid, according to the Köppen-Geiger classification) with an annual average rainfall of 3000 mm, and an annual average air temperature ranging between 23 °C and 31 °C (INMET, 2019). The soil in this area is of an oxisol group, yellow latosol with a sandy-clay texture, with relatively flat relief, and an upper quaternary terrain (Rodrigues et al., 2004).

2.2. Study design and sample point selection

The Mocambo Reserve has a permanent plot for floristic studies, and its vegetation dynamics have been monitored since 1956 (Pires and Salomão, 2000). An analysis of the species components with the highest relative frequency, collected from a forest inventory of tree species with diameter at breast height (DBH) > 10 cm conducted in 2016 resulted in four distinct floristic groups in this plot. Each grouping was defined according to the relative density of the species *Cecropia sciadophylla* and *Pourouma mollis*, as: (i) D20 – with more than 20 % relative density for both tree species mentioned; (ii) D15 – with up to 15 % relative density for both species; (iii) D10 – with up to 10 % relative density for both species and; (iv) D5 – with less than 5 % relative density for both species. This classification takes into account a slow decomposition of the leaves of these plants, with accumulation in litter (Mesquita et al., 1998; Bakker et al., 2011).

The organic horizons (OL and OF) of the litter system were analyzed with a transect for each floristic group (D5, D10, D15, and D20), approximately 40 m apart, that was arranged in the permanent plot. Each transect measured 15 m in length and contained 10 sample points distributed every 1.5 m. The sample points measured 0.5 × 0.5 m and the thickness (cm) of the horizons was estimated in the field, according to the method described by Zanella et al. (2018a).

2.3. Measurement of leaf litter characteristics

The litter components (leaves, branches, reproductive parts, roots, plant material adhered to the roots, and miscellaneous) were collected from the field and separated in the Laboratory of Sustainable Systems Analysis of EMBRAPA, Eastern Amazon, dried in a forced circulation oven at a temperature of 60 °C for 48 h, and weighed on a precision scale (BL 320H, Shimadzu, 0.001 g) to obtain the dry mass. The identification of leaves present in the OL horizon was compared to the herbarium material from EMBRAPA, using the Angiosperm Phylogeny Group (APG III) classification system.

2.4. Measurement of soil physicochemical properties

After collecting the litter from each sampling point, three soil subsamples were taken at a depth of 10 cm and reunited to form a soil sample of approximately 500 g. In the laboratory, the samples were in open-air dried and sifted to a size of 2 mm. The following attributes were determined: texture (pipette method; fine sand, clay, and silt concentration), pH (in water), organic matter (calculated from organic carbon, analyzed by wet oxidation), total nitrogen (Kjeldahl by vapor distillation), sodium (Flame Spectrophotometry), aluminum, calcium, and magnesium (Atomic Absorption Spectrometry), according to the manual of soil analysis methods (EMBRAPA; Centro Nacional de Pesquisa de Solos, 1997). All analyses were conducted at the Soil Laboratory of the Emílio Goeldi Museum of Pará (MPEG).

2.5. Leaf litter fungi assemblage collection and identification

From each sampling point, 10 leaves and 10 fresh branches were removed from each OL and OF organic horizon to identify the fungal community present in the substrate. In the laboratory, the material was washed under running water, packed in an adapted wet chamber (Santos et al., 2018), and incubated at room temperature (25–30 °C) inside polystyrene boxes (80 L) that were opened for light entry and air exchange for 30 min each day, over a maximum period of 60 days (adapted from (Castañeda-Ruíz et al., 2016). After 10 days of incubation, semi-permanent and/or permanent slides of reproductive structures were prepared with lactoglycerol (Carmo et al., 2016) and PVL resin (polyvinyl + alcohol + lactophenol) (Trappe and Schenck, 1982). The species were identified by morphological analysis and measurements of microstructures with taxonomic value under an optical microscope (magnification × 400 and ×1000), with the aid of specialized literature (Ellis, 1971, 1976; Seifert et al., 2011). Vouchers and slides of the identified fungi were deposited in the João Murça Pires Herbarium at the Emílio Goeldi Museum of Pará.

2.6. Additive partitioning diversity and fungal community

An additive partitioning structure was used, in which diversity-γ was determined as the sum of α- and β-diversity. Total diversity was partitioned into its components (α- and β-diversity), and the contribution of each nested spatial scale to the fungal species diversity was calculated. The average richness of fungal species found in a type of substrate (leaves or branch) associated with a horizon of the litter system (OL or OF horizon) (α1) was defined as α-diversity. Diversity-γ was defined as the total number of species found in the study area. Thus, to

calculate the spatial hierarchy of the diversity of fungal species, the data were gathered in four spatial scales: 1) substrate within the horizon (β1); 2) horizons within the sampling point (β2); 3) sampling points within a floristic group (β3); and 4) and floristic groups within the terra firme forest fragment in the Mocambo Reserve (β4). Given that α and β diversity were mean values expressed in the same units, it was possible to evaluate the contribution of each nested spatial level to the total γ-diversity and, therefore, the significance of each spatial component (Veech et al., 2002). The null hypothesis was that the diversity of fungi is uniform at all spatial scales. Therefore, to assign certain ecological processes to the β diversities, it is first necessary to verify whether the observed values are higher or lower than those expected by the random variation due to the sample design (Crist et al., 2003; Gotelli and Graves, 1996).

To quantify which processes contribute the most to the β-diversity of fungi, the β-diversity was decomposed, and proportional turnover (βsim) and nesting (βnes) values were calculated based on total dissimilarity (βsor) as follows: contribution of βsim = βsim/βsor, and that of βnes = βnes/βsor (Baselga, 2010, 2012). The βsor index ranged from 0 (clusters of identical species) to 1 (clusters of different species). Using this approach for the data set not only enabled testing differences in the total dissimilarity values (βsor) between the different scales studied, but also the relative contribution of species turnover (βsim) and the dissimilarity resulting from nesting (βnes) in each scale.

To reduce the effect of rare species on community turnover, species that occurred in less than four samples were removed from partition calculations and diversity-β, leaving 55 species of fungi in the matrix. As the size of the samples differed for the floristic clusters due to the lack of fungi in some samples at the substrate level, it was necessary to resample the data to obtain comparable values of β-diversity among the floristic groups (Baselga, 2010). This step is important because the analysis of diversity-β is sensitive to sample size, leading to biased results (Baselga, 2010).

Finally, a permutational multivariate analysis of variance (PERMANOVA; (Anderson, 2001) was performed to verify differences in the fungal composition between the floristic groups (9999 permutations, Bray-Curtis dissimilarity index). The PERMANOVA results were represented using a principal coordinate analysis (PCoA). All stages of analysis were conducted using the vegan and betapart packages in the R platform for additive partitioning of diversity and decomposition of β-diversity, respectively (R Core Team, 2020).

2.7. Data analysis

Multivariate methods are useful for exploring how floristic groups generate spatial heterogeneity using different ecological factors. Thus, empirical information was collected from the litter system characteristics and physicochemical properties of the soil for extracting, summarizing, and visualizing the pattern to test the predictions (Chi, 2012). PCoA was used to explore the general patterns of leaf composition that form the organic horizons, based on the Bray-Curtis dissimilarity distances. As the matrix is filled with mass data, this index (modified from the Sørensen index) is suitable for verifying the dissimilarity pattern (Zak and Willig, 2004).

Principal component analysis (PCA) was used to summarize the data of the litter system physical structure (OL and OF horizon thickness, leaf mass, and branch mass), soil chemical properties (concentrations of organic matter, sodium, aluminum, nitrogen, calcium, magnesium, and pH), and soil physical properties (percentage of clay, silt, and fine sand). As the data of the physical structure of litter and chemical properties of the soil are expressed in different measurement scales, a PCA with a correlation matrix (standardization of variables) was calculated, while a PCA with a variance and covariance matrix (without standardization of variables) was used for the soil physical properties.

Rarefaction and extrapolation curves based on samples were used to estimate the richness of saprotrophic fungi species for each floristic group (Chao et al., 2014; Colwell et al., 2012). Extrapolation was performed considering the presence and absence of data, thus reducing potential bias caused by rarely sampled species (Chao et al., 2014), with 1000 randomizations to compare diversity between groups.

A Mantel test with Pearson's correlation was performed with 10,000 permutations using paired matrices to inspect the relationships between the dissimilarity matrices of the fungal and litter communities (Nekola and White, 1999). The fungal dissimilarity matrix was created using presence/absence data and eliminating species that appeared in less than four samples to reduce the effect of turnover caused by rare species. This generated a matrix of 55 species (26 % of the total). Therefore, the β-diversity was calculated using the Sørensen index, which represents the total compositional variation among all pairs of sample points. The peer-to-peer dissimilarity matrix for the litter leaf community was calculated using the Bray-Curtis dissimilarity distances for the biomass data.

Finally, the effects of environmental variables on the richness of species of saprotrophic fungi on the sample point scale (β3) were calculated. As explanatory variables, we used i) total thickness of the OL and OF horizons, ii) leaf mass, iii) branch mass, iv) pH, v) first axis of the ordering of a PCA of the soil chemical properties (representing 34.94 % of variation), vi) first axis of the ordering of a PCA of the soil physical properties (representing 52.61 % of the variation); and vii) first axis of the ordering of a PCoA for the leaf composition that forms the substrate for the litter system (responsible for 32.66 % of the variation). A linear mixed effects model was built, where the fixed effect was natural logarithmic (richness of fungi species), and the effects of all explanatory variables and floristic groups were random. As the range of absolute values of variables i, ii, iii, and iv varied relative to the others, they were centered at zero, and staggered by subtracting their average value and dividing by its standard deviation (mean equal to 0, deviation equal to 1).

The complete model was used to select models using multi-model inference (Burnham et al., 2011). This statistical approach differs from the traditional zero hypothesis test, as it can be used to identify a better model, supporting a specific hypothesis or inferences based on the weighted support of a complete set of competing models (Monteiro et al., 2017). The relative performance of the models was evaluated based on the second-order Akaike information criterion (AICc), which corrects small sample sizes. The best set of models was selected among all the possibilities derived from the complete model, where ΔAICc < 2, thus capturing greater uncertainty in the final set of candidate variables (Vierling et al., 2013).

To plot curves and derive the biological meaning of the variables, we used coefficients that excluded zero in their confidence intervals and the relative importance value of the predictor variable (RVI). The coefficients were calculated based on the averaging model of the complete model, representing the average coefficients of all the candidate models. The RVI is the sum of the Akaike weights (probability of a model being the most plausible model) for the models with a predictor. Therefore, a predictor included in models with high Akaike weights will receive a higher value.

These values can be used to support each predictor variable for all models. The 50 % cutoff point is arbitrary and differentiates important and non-important predictors (Burnham and Anderson, 2002; Deschutter et al., 2017; Everaert et al., 2018; Terrer et al., 2016). The complete model was subjected to hierarchical partitioning to calculate the independent contribution of each variable to evaluate its percentage of explanation (Mac Nally, 2000; Murray and Conner, 2009).

All stages of the analysis were conducted using the R platform (R Core Team, 2020). The following packages were used: i) multivariate methods – cmdscale function of the stats package (PCoA) with rda function of the vegan package (PCA); ii) rarefaction and extrapolation curve

– iNEXT function; iii) Mantel test – Mantel function of the vegan package; iv) selection of models and medium model – dredge and model.avg functions, respectively, from the MuMIn package; and v) hierarchical partitioning – hier. part function.

3. Results

3.1. Description of leaf litter characteristics and soil physicochemical properties by sample points

The multivariate methods used to explore the spatial heterogeneity of the samples highlighted a distinct separation between the four floristic groups (D20, D15, D10 and D5), compatible with the general observation of the Mocambo Reserve, for all analyzed parameters (Fig. 1A–D). The PCoA revealed an evident separation of groups for 266 leaf species in the OL horizon (Fig. 1A). The first axis of the PCA for soil chemical variables (34.95 % of the explained variance) showed sites D5 and D10, where soils are richer in organic matter, aluminum, and sodium, as opposed to D20, which is relatively rich in calcium. The second axis (22.08 %) showed soils rich in magnesium and nitrogen at sites D15 and D5, in contrast to D10, which is rich in aluminum (Fig. 1B).

Regarding the physical properties of forest soil, the finer fractions (clay and silt) contributed significantly to differentiating the floristic groups compared to the sand fraction (Fig. 1C), which was greater than 70 % in D20, D15, D5, and approximately 60 % in D10, the only group with a higher proportion of clay and silt (Table 1). For the physical structure of the litter system, the first axis of the PCA demonstrated that the thickness and dry mass of leaves of the OL/OF horizons were the most determining attributes in differentiating the floristic groups (54.14 %, Fig. 1D). In general, the sampled soils presented an acidic pH (Table 1), with lower D20 and higher D5 values. These two floristic groups also showed higher organic matter content than the other floristic groups.

3.2. Leaf litter fungal assemblage and β-diversity pattern

From the 40 sampling points, a total of 208 species belonging to 86 genera, 33 families, 22 orders, and five classes in the phylum Ascomycota, were identified. One hundred and nine strains were recognized as Sordariomycetes (52.40 %); 22 as Dothideomycetes (10.58 %); 22 as Leotiomycetes (10.58 %); one as Orbiliomycetes (0.48 %); and four strains were identified as Eurotiomycetes (1.92 %) (Table S1). The remaining 50 species (24.04 %) did not have a defined class; thus, they were included as unclassified Ascomycota (Fig. 2A). The genera *Codinaea*, *Dictyochaetopsis*, and *Dactylaria* were the most representative in terms of the number of species, with 10, 8 and 8, respectively, followed by *Thozetella* (7 species).

Most species (153) were rare, with less than four occurrences among the sample points, with 43 % Sordariomycetes species, 27 % incertae sedis, and the remaining distributed in other classes. For the fungal species richness, a similar result was found for floristic groups D20 and D15, which had the least species (64 ± 17.97 and 69 ± 17.68, respectively), while D10 presented intermediate species richness (91 ± 25.41), and D5 had the richest assemblage in species (126 ± 22.21) (Fig. 2B).

There was a gradual increase in the contribution of each spatial scale to the γ-diversity (Fig. 3A). The type of substrate, whether branch

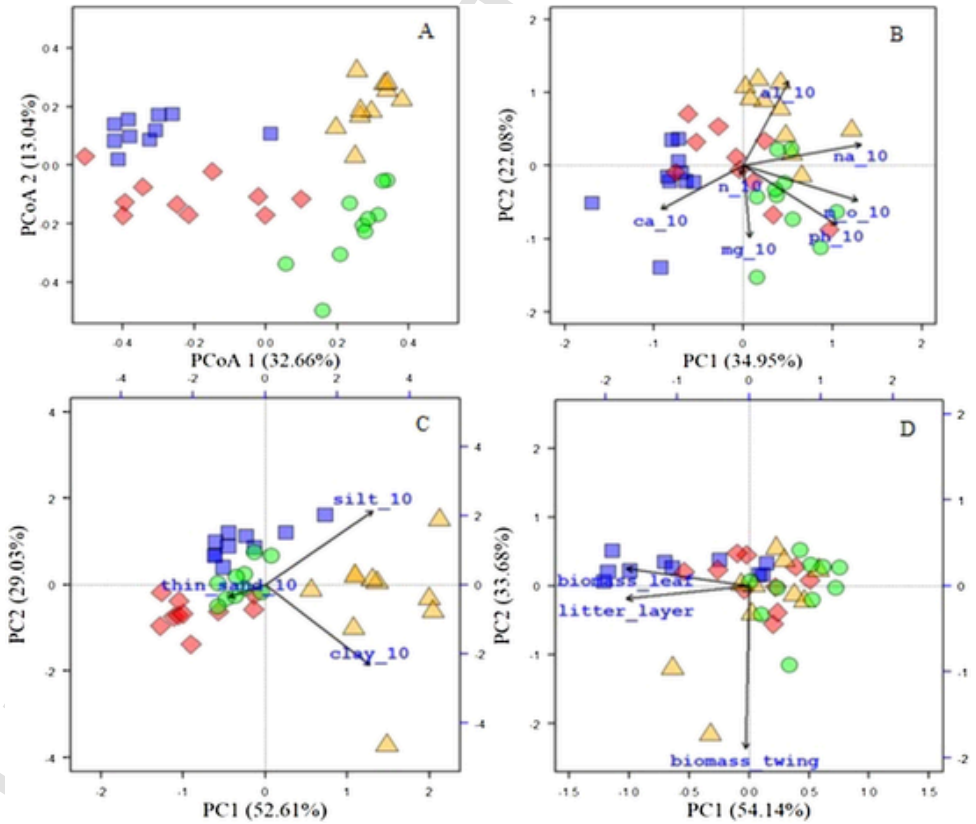

Fig. 1. Spatial heterogeneity of the 40 sampling points (AD—), located in the four floristic groups of the Mocambo Reserve. A – PCoA of the floristic groups for the leaf species composition that constitute the litter of the OL horizon; B – Axes 1 and 2 of a PCA based on soil chemical characteristics (calcium, nitrogen, aluminum, sodium, organic matter, and magnesium); C – Axes 1 and 2 of a PCA based on the soil physical properties (sand, clay, and silt); D – Axes 1 and 2 of a PCA based on the thickness of the organic horizons and the dry mass of leaves and branches. Each geometric figure represents a group: D20 – blue square; D15 – red diamond; D10 – orange triangle and D5 – green circle. $p < 0.001$ (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

Table 1
Soil physicochemical variables (mean ± standard deviation) for the four floristic groups: D20, D15, D10 and D5. pH: Hydrogen potential; N: Nitrogen; Na: Sodium; Al: Aluminum; Ca: Calcium; Mg: Magnesium.

Soil physicochemical variables	Floristic groups											
	D20			D15			D10			D5		
Coarse sand (%)	58.90	±	3.908	61.40	±	2.085	49.70	±	4.416	56.20	±	2.747
Thin sand (%)	17.20	±	1.856	18.00	±	2.755	16.20	±	1.911	19.30	±	2.356
Clay (%)	10.30	±	0.911	12.30	±	1.203	18.30	±	3.204	12.50	±	0.816
Silt (%)	13.60	±	2.085	8.30	±	1.018	15.80	±	3.532	12.00	±	1.109
pH	3.81	±	0.066	4.06	±	0.326	4.08	±	0.337	4.26	±	0.217
Organic matter (g/kg)	32.91	±	7.575	44.14	±	9.859	45.21	±	9.889	63.78	±	9.043
N (g/kg)	1.24	±	0.182	1.43	±	0.290	1.10	±	0.244	1.02	±	0.285
Na (mg/kg)	2.8	±	1.1	6.2	±	2.5	8.8	±	1.6	6.9	±	1.7
Al (mg/kg)	159.7	±	23.4	163.1	±	30.9	234.1	±	27.8	167.1	±	25.4
Ca (mg/kg)	17.1	±	10.7	9.6	±	4.5	5.9	±	3.7	7.8	±	4.2
Mg (mg/kg)	16.5	±	5.6	11.9	±	1.4	13	±	1.6	18.4	±	7.9

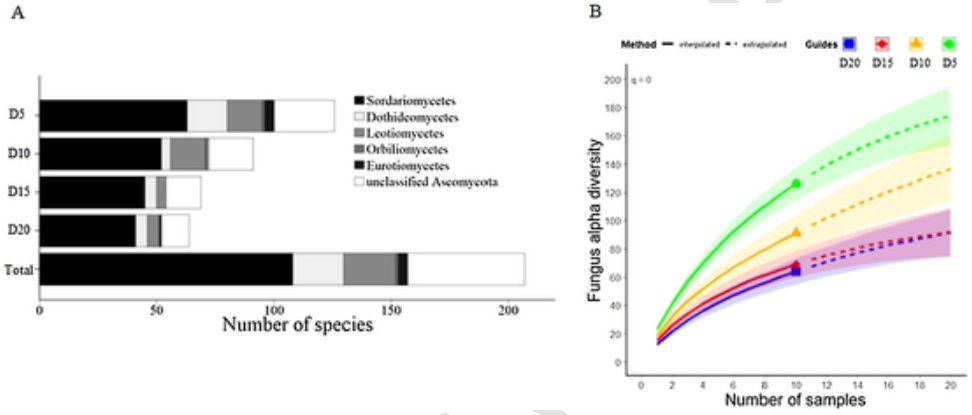

Fig. 2. Taxon distribution along the 40 sampling points, located in the forest groupings of Mocambo Reserve, Belém, PA. **A** - Total of 208 species of Ascomycota litter fungi, represented by class Sordariomycetes = 109 (52.4 %), Dothideomycetes = 22 (10.58 %), Leotiomycetes = 22 (10.58 %), Orbiliomycetes = 1 (0.48 %), Eurotiomycetes = 4 (1.92 %), and 50 more species of unclassified Ascomycota. **B** - Fungal species richness for groups: D20 – blue square = 64 ± 17.97, D15 – red diamond = 69 ± 17.68, D10 – orange triangle = 91 ± 25.41 and D5 – green circle = 126 ± 22.21 (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

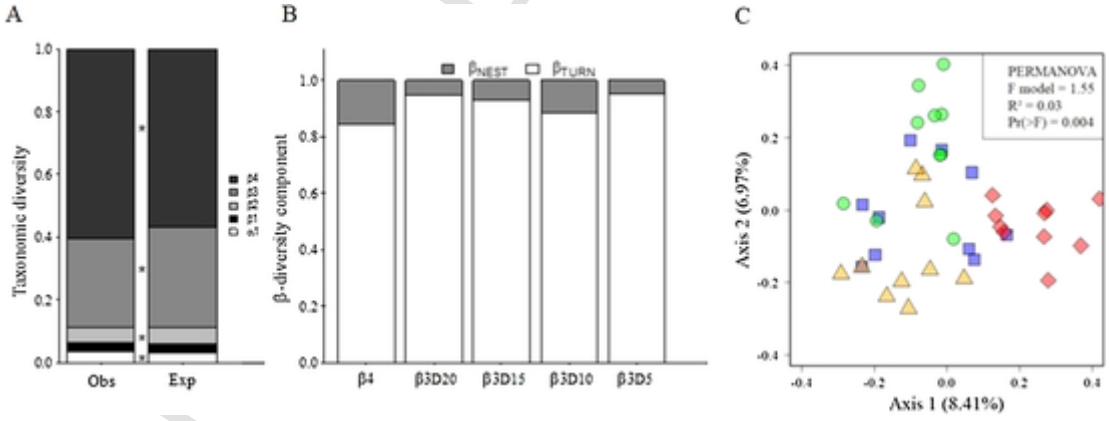

Fig. 3. Spatial hierarchy of the diversity of fungal species in four scales (β1 – β4) located in the floristic groups. **A** – Contribution of each spatial scale (α1: average fungal richness within each substrate; β1: diversity between substrate within litter horizon; β2: diversity between litter horizons within of the sampling point; β3: diversity between the sampling points within a floristic group; and β4: diversity between floristic groups within the terra firme forest fragment) to γ diversity; **B** – Dissimilarity in the fungal community composition among the floristic groups, indicating the turnover process (βTURN: replacement of species) that contributed the most to the β4 scale, as well as for all β3 scales (> 0.8), with low contribution by nesting (βNEST: lost/gain of species); **C -** PCoA showing the dissimilarity in the composition of fungal species between the floristic groups: D20 – blue square; D15 – red diamond; D10 – orange triangle and D5 – green circle (PERMANOVA $F_{1,39}$ = 1.55; $p < 0.01$) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

or leaf, has an influence on α1 diversity, which was significantly higher than that expected by chance. However, no difference was observed in the composition of fungi when the two types of substrate were present on the same horizon (β1, less than 0.003 contribution), unless they were in distinct organic horizons (β2, 0.05 contribution between OL/OF horizons within a sampling point). The contributions of β3-diversity (0.28 between sampling points within a floristic grouping) and β4 (0.59 among floristic clusters within the reserve fragment) were distinct. Even with the differentiation observed in species richness, the contribution of the turnover process was highest for the β4 scale, as well as for

all β3 scales (Fig. 3B, greater than 0.8). There was a clear distinction between the fungal communities of groups D20 to D5 through PCoA (Fig. 3C).

3.3. Correlation of fungal β diversity with plant community

The β-diversity of fungi (different compositions between pairs of sampling points) was positively correlated with the β-diversity of plants that comprised the OL horizon of the litter system (Fig. 4). The Mantel test showed that the most distinct sample points in leaf composition on the OL horizon harbored a distinct assembly of saprotrophic fungi (Mantel r = 0.13; p < 0.05).

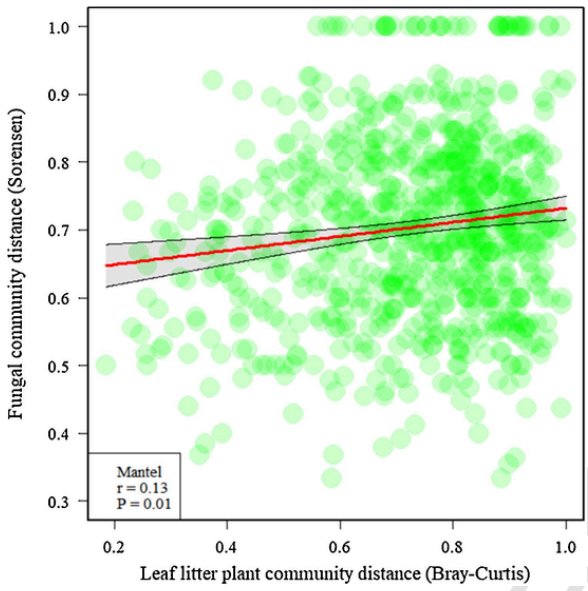

Fig. 4. Correlation between the dissimilarity of saprotrophic fungi communities and the dissimilarity of leaves identified in the OL horizon of the litter system, in the floristic groups: D20, D15, D10 and D5.

3.4. Response of leaf litter fungal richness to leaf litter characteristics, soil physicochemical properties, and plant communities

Among the floristic clusters, the thickness of the OL/OF horizons and pH were the only predictors that influenced fungal richness (Fig. 5), with an approximately 0.7 contribution to the total (p < 0.05). The variables had opposite effects: pH had a positive effect, while the thickness of the OL/OF horizons had a negative effect (Fig. 6) on richness. A large substrate accumulation was verified in the OF horizon at all sampling points, and D20 recorded the greatest thickness for the OL and OF horizons, in contrast to D5, with the lowest measurements for both (Table S2).

4. Discussion

The partitioning of diversity into its spatial components improves the understanding of species distribution and highlights the importance of the plant community and spatial heterogeneity of the fungal assemblage. Plant diversity contributes to litter variation, providing an assortment of materials (e.g., branches and leaves), and selected fungi that assist in soil processing (e.g., decomposition). Our results are consistent with those of other studies that showed that local and regional effects such as plant diversity, substrate type, and physical and chemical soil attributes (Chen et al., 2018; Yang et al., 2017a, 2017b) can overcome global effects such as climate and latitude changes (Prober et al., 2015; Tedersoo et al., 2014) in predicting the succession of fungal diversity.

Most leaf dry mass in the OL horizon originates from the most common species found in the reserve (Table S2). Pires and Salomão (2000) monitored the Mocambo Reserve over 36 years (1956–1992) and recorded continuous changes in plant dynamics. At the end of the evaluation, the authors reported that species loss was higher than recruitment. Invasion by pioneer species (*Pourouma mollis* and *Cecropia sciadophylla*) (Amaral et al., 2012), indicated that variations in dynamics generated an increased amount of light inside the forest, favoring the recruitment and development of those species (Laurance and Vasconcelos, 2009). In the last 20 years, the main reason for increased light inside the reserve was treefall gaps caused by tree mortality (Salomão, personal comment).

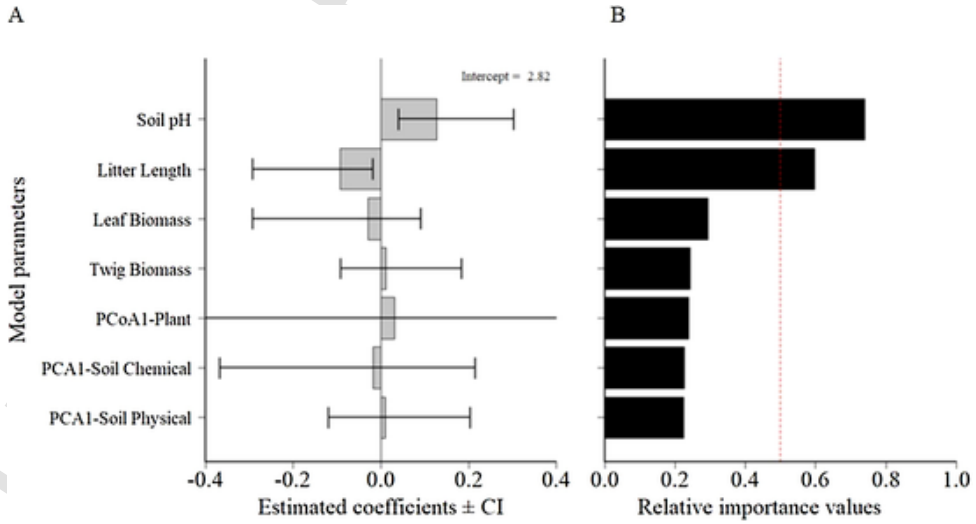

Fig. 5. Linear model of the effects of the environmental variables on the fungal species richness within of the sampling point (n = 40), located in the floristic groups of the Mocambo Reserve, Belém, PA. **A** – Influence of predictors on the fungi richness: pH; Litter length: total thickness of the organic horizons (OL/OF) of the litter system; Leaf Biomass: leaf and branch mass; PCoA1-Plant: first axis of the ordering of a PCoA for the litter leaf composition (responsible for 32.66 % of the variation between clusters); PCA1-Soil Chemical: first axis of the ordering of an PCA with soil chemical properties (representing 34.94 % of the variation); PCA1-Soil Physical: first axis of the ordering of an PCA with soil physical properties (representing 52.61 % of the variation); **B** – Proportion contribution of predictors (pH and total thickness of the litter layer) that significantly influenced the fungal richness (0.7, p < 0.01).

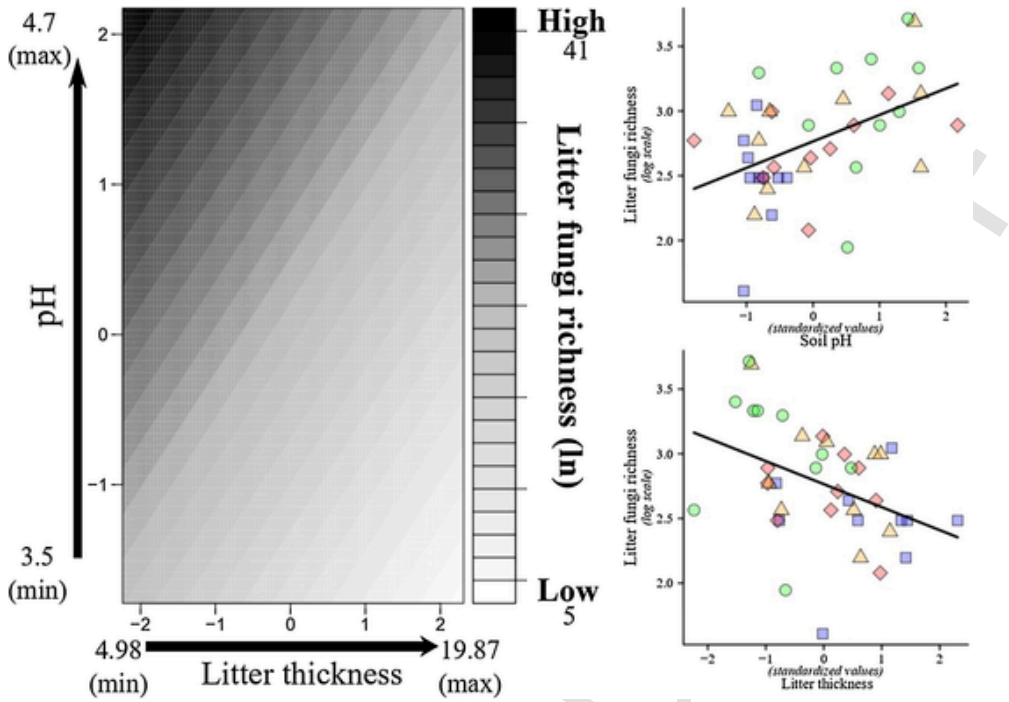

Fig. 6. Simultaneous effects of the soil pH and litter thickness (predictor variables) over the litter fungi richness (response variable) in the Mocambo Reserve, Belém, Brazil. The x-axis corresponds to the standardized values. Subplots on the right side highlight the effect direction and the colors indicate the floristic groups: D20 – blue square; D15 – red diamond; D10 – yellow triangle; D5 – green circle (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

Leaf composition in the organic horizons was an important factor for the gradual increase in the α diversity of fungi present in litter substrates (Fig. 2B), confirming the first hypothesis. The substrate type can influence the abundance of fungi and stages of fungal succession, in addition to representing specific niches such as foliar and lignin materials (Buresova et al., 2019; Izabel and Gusmão, 2018; Vivelo and Bhatnagar, 2019). Horizon formation is a process primarily related to plant composition, followed by the ability to attract decomposer organisms, and the related responses of both factors (Hättenschwiler et al., 2005; Zanella et al., 2018b). Thus, the thickness of a horizon represents the decomposition time of the substrates and depends on the quality of the forming material (Zanella et al., 2018b).

Physical and chemical leaf traits, such as morphology (shape, size, resistance, and hardness) and permanence of secondary plant metabolites (condensed tannins, phenolic compounds, and aldehydes), can accelerate or prolong decomposition (Krishna and Mohan, 2017). In the floristic groups with the highest OL and OF horizons (Table S2), the species *Cecropia sciadophylla*, *Pourouma mollis,* and *Eschweilera coriacea* recorded the largest accumulation of leaves, presenting the morphology and chemical composition typical of slow decomposition (Berg, 1978; Berg et al., 1990; Cárdenas et al., 2014; Hättenschwiler et al., 2008; Lopes et al., 2002). In group D5, with a lower horizon thickness, there was little variation in the mass accumulation of leaves and a greater richness of plant and fungal species.

In the fungal community, most species belong to the class Sordariomycetes, known cosmopolitans that are often isolated from the leaves of terrestrial plants and important cellulose decomposers (Krishna and Mohan, 2017; Tedersoo et al., 2014; Zhang and Wang, 2015). Among them, only *Thozetella cristata*, *Menisporopsis theobromae*, and *Chloridium virescens* were sampled from the substrate of both organic horizons (OL and OF) at all sampling points. Approximately 74 % of the species were identified in less than four sampling points, which may explain the significance of the turnover component that contributed mostly to both the β3 and β4 scales (Fig. 3B). This means that communities within and between floristic clusters are not a subset of species, but rather a different community of saprotrophic fungi, possibly because of the large number of specialist species identified in the samples, confirming the second hypothesis.

In tropical forests, where temperature and humidity are generally stable, specialist species are more resistant, propagate vegetatively, and have little competition, because their specialization is related to nutritional factors and secondary chemistry of the substrates (Rambelli et al., 2004). Conversely, generalist species have greater colonization capacity but shorter lifetimes (Rambelli et al., 2004). Both scales show how soil heterogeneity and vegetation composition are important for determining the litter fungal composition (Huang et al., 2019; Seaton et al., 2020; Weißbecker et al., 2018; Yang et al., 2017a). According to Barberán et al. (2015), plants can influence microbial communities via specific traits, root distribution, and exudate release, which reflects fungal growth and nutrient absorption.

The substances released into the soil due to the catabolism of macromolecules by fungi can modify the local pH (Deacon, 2006; Purahong et al., 2016), influencing the distribution of groups such as Ascomycota, which are sensitive to changes in vegetation composition (Kivlin and Hawkes, 2016; Vivelo and Bhatnagar, 2019). These results are consistent with those of Peay et al. (2013); Yang et al. (2017a, 2017b), and Kivlin and Hawkes (2020), which suggest that the plant community is a strong predictor of fungal communities.

In the four floristic groups, the plant composition explained some of the variations observed among the fungal communities (Fig. 4, Mantel $r = 0.13$; $p < 0.05$). This suggests that the mosaic of physical structures in the litter system can exert greater influence on the organization of microorganisms in this reserve and confirms the third hypothesis that γ-diversity is an expression of the spatial variation of plants in the forest as a function of litter mosaics. This positive relationship corroborates previous research on plant identity and spatialization reflecting the community of decomposer microorganisms (Barberán et al., 2015; Peay et al., 2013; Schimann et al., 2017; Yang et al., 2017b). This could be due to the specialization of some fungal groups in using organic resources, such as the differentiated leaves in litter (Barberán et al., 2015;

Schimann et al., 2017), and chemical differences in the substrate, which influence species growth (McGuire et al., 2010). Fungal specialization refers to the functionality of these organisms in forest soils and their roles in the nutrient cycle (McGuire et al., 2010). This result reinforces that changes or loss of vegetation cover can have a marked impact on the ecosystem, both for the biota below ground and those above it (Tedersoo et al., 2014). This relationship has previously been verified in other tropical forests (Peay et al., 2013; Qian et al., 2013) and subtropical forests (Weißbecker et al., 2018).

As for the mosaic of physical structures of litter, the thickness of the organic horizons was the only variable that significantly influenced fungal richness. This shows how these organisms are dependent on the composition and nutritional sources available within these systems (Pioli et al., 2020; Posada et al., 2012). The physical attributes of litter, such as mass, thickness of the organic horizons, leaf size, and texture can be indirect ways of demonstrating this relationship (Bernier, 2018; Posada et al., 2012). The description of the plant-fungus relationship in organic horizons, based on the composition and how these litter mosaics are formed on the forest floor (Bernier, 2018) may represent an important tool in understanding the patterns that maintain the functionality of tropical forests.

The pH was the only soil variable that influenced the richness of fungi in this fragment. In our study, higher pH was associated with a greater richness of fungi, consistent with the responses of other soil organisms with positive effects. This pattern can also be observed for other soil biota within a latitudinal gradient (Chapman et al., 2013; Huang et al., 2019; Kivlin and Hawkes, 2016). The pH is an environmental factor that influences the net load of membrane proteins and directly affects the absorption of specific nutrients (Deacon, 2006). However, soils with low pH may contain toxic levels of trace elements, such as aluminum, manganese, copper, and molybdenum, preventing the growth of more sensitive species (Webster and Weber, 2007). Thus, pH acts as an environmental filter and can explain the contribution of γ in both tropical and temperate climates (Huang et al., 2019; Purahong et al., 2016).

The dynamic cycle of tropical forests increases rapidly in small fragments, causing important differences in the spatial structures of these ecosystems (Laurance et al., 2002; Machado and Oliveira-Filho, 2010). By partitioning total diversity at different scales, we were able to confirm statements made in previous studies on how plant identity and substrate leaf type predict microbial communities. In these forests, maintaining plant diversity guarantees successful fragment regeneration after a disturbance, because the speed at which the nutrients immobilized in the substrate, return to mineral conditions, and reintegrate into plant living tissue depends on efficient interactions with decomposers (Barberán et al., 2015; Peay et al., 2013; Schimann et al., 2017; Yang et al., 2017a, 2017b). Diverse fungi capable of accessing and providing nutrients by catabolizing large molecules may be more efficient for the resilience of forests under constant disturbance (Webster and Weber, 2007). This information is applicable to conservation and restoration biology, owing to the possible identification of strategies for reforestation and recovery of microbial functions in degraded areas.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.pedobi.2021.150771.

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