Beyond seasonal and host factors: ecosystem dynamics drive palm-associated root fungal communities at a local scale

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Universidad del Rosario
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Beyond seasonal and host factors: ecosystem dynamics drive palm-associated root fungal communities at a local scale

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Resumen

Antecedentes y objetivos

El aumento de fenómenos meteorológicos extremos debido al cambio climático puede alterar la dinámica de los ecosistemas. En los trópicos se sabe poco sobre cómo responderán los ecosistemas y las especies a las sequías e inundaciones. Identificar los factores bióticos y abióticos más importantes en los ecosistemas a nivel local es clave para desarrollar mejores prácticas de gestión forestal y comprender los efectos del cambio climático en las comunidades fúngicas.

Métodos

Realizamos un muestreo aleatorio de individuos adultos de varias especies de palmeras en tres ecosistemas cercanos con diferentes condiciones hidrológicas, durante las estaciones lluviosa y seca. Mediante secuenciación de nueva generación, identificamos las comunidades fúngicas y determinamos la influencia de las propiedades fisicoquímicas del suelo, las variables estacionales y la identidad del hospedador sobre la abundancia relativa de las comunidades fúngicas asociadas a la raíz y a la rizósfera.

Resultados

La composición de las comunidades fúngicas fue similar entre el bosque estacionalmente inundable y el bosque de tierra firme, mientras que en el pantano divergió debido a diferencias en las propiedades fisicoquímicas del suelo. Los análisis estacionales revelaron diferencias significativas en la abundancia relativa de varios taxones, principalmente asociados al bosque estacionalmente inundable. Sin embargo, no se detectó ninguna influencia de la especie de palmera en la abundancia de hongos a ningún nivel taxonómico.

Conclusión

Este estudio resalta la importancia de estudiar los ecosistemas a escala local y de considerar la dinámica de los ecosistemas en el estudio de las comunidades fúngicas y de otros microorganismos. Este enfoque es crucial para mejorar las predicciones en escenarios de cambio climático y comprender las consecuencias de alterar estas dinámicas en ecosistemas vulnerables y a menudo poco estudiados.

Palabras clave

Orinoquia, rizósfera, hongos asociados a raíces, inundación, estacionalidad, palmeras

Abstract

Background and Aims

The increase of extreme weather events due to climate change may alter ecosystem dynamics. In the tropics, little is known about how ecosystems and species will respond to droughts or floods. Identifying the most important biotic and abiotic factors in ecosystems at the local level is key to developing better forest management practices and understanding the effects of climate change on the fungal community.

Methods

We conducted a random sampling of adult individuals from several palm species across three adjacent ecosystems with different hydrological conditions, during rainy and dry seasons. Using next-generation sequencing, we identified fungal communities and determined the influence of soil physicochemical properties, as well as host and seasonal variables, on the relative abundance of the root- and rhizosphere-associated fungal communities.

Results

The composition of the fungal communities was similar between the seasonally flooded forest and the *terra-firme* forest, while the palm swamp diverged due to differences in soil physicochemical properties. Seasonal analyses revealed significant differences in the relative abundance of several taxa, mainly associated with the seasonally flooded forest. However, no influence of palm species on fungal abundance was detected at any taxonomic level.

Conclusion

This study highlights the importance of studying ecosystems at the local scale and considering ecosystem dynamics into the study of fungal communities and other microorganisms. Such an approach is crucial for improving predictions under climate change scenarios and understanding the consequences of altering these dynamics in vulnerable, often understudied ecosystems.

Keywords

Orinoquia, rhizosphere, root-associated fungi, flood, seasonality, palms

Introduction

Fungi play a key role in the regulation and maintenance of biogeochemical cycles as well as in the functioning of ecosystem processes such as decomposition, efficient water use by plants, and improved productivity (de Vries et al. 2018; Wei et al. 2022). The rhizosphere is a thin layer between the soil and plant roots that is characterized by a large diversity of microorganisms, and a high concentration of sugars, amino acids, and organic acids (Liu et al. 2012; Qiao et al. 2017; Zhang et al. 2021). The rhizosphere facilitates signaling and interactions between plants and soil microorganisms, affects the development, growth, and resistance to biotic and abiotic stressors, improves plant health, productivity, and adaptability through alterations in nutrient uptake, chemical signaling, and enzyme activity in metabolic processes (Qiao et al. 2017; Zhang et al. 2017).

Soil fungi are affected by edaphic variables such as pH, organic carbon, phosphorus (P), and total nitrogen (N), which are key elements for the different roles fungi play in the ecosystem as pathogens, decomposers, mutualists, nutrient cycling or as disease suppressors (Rodríguez-Echeverría et al. 2017; Egidi et al. 2019; Ballauff et al. 2021). Soil pH strongly influences the structure of fungal communities in general, while soil P may be an important driver for mycorrhizal fungi (Ballauff et al. 2021; Wei et al. 2022; Hogan et al. 2023). This is important because in tropical regions, P is a limiting factor, and a decrease in pH has been identified with an increase in the availability of nutrients such as N, P, Ca, K, Mg, and heavy metals in flooded forests and after flooding in tropical forest of the Amazon basin (Henrique et al. 2021; Trujillo et al. 2021).

Seasonality is also a driver for soil fungi; variables associated with temperature and precipitation can affect the composition and abundance of these communities. For example, in tropical forests, a positive correlation has been found between fungal composition and temperature, while precipitation is a dominant driver for fungal alpha diversity (Wei et al. 2022; Mikryukov et al. 2023). In addition, changes associated with precipitation may also affect soil moisture which affects fungal community composition. However, high tolerance to soil moisture has been reported, especially for fungi in both flooded ecosystems and drought scenarios (Bohrer et al. 2004; de Vries et al. 2018). Therefore, it is possible that variations in the fungal communities at local scales can be due to changes associated with seasonally affected soil resources, such as the availability of water, nutrients, or heavy metals. However, little is known about how tropical forest communities are affected (e.g., Nielsen et al. 2010; Wei et al. 2022).

Rhizosphere and root-associated fungi can facilitate growth and promote host protection through the production of induced systemic resistance and competition with pathogens (Berendsen et al. 2012; Li et al. 2022). Host-related factors such as plant species, genotype, stage of development as well as the microbial community previously established in the soil are key aspects that can alter the fungal-root relationship (Nielsen et al. 2010; Qiao et al. 2017; Wei et al. 2022; Mikryukov et al. 2023). In addition, root morphological and chemical traits can also influence fungus-root relationships by promoting associations with host plants that can shape the root traits, such as diameter and cortical area (Bergmann et al. 2020; Hogan et al. 2023). However, vegetation type can also affect these fungal communities through indirect changes by regulating the physicochemical properties of the soil and the accumulation of organic matter from its litter (Santonja et al. 2017; Canini et al. 2019; Han et al. 2021). The fungal-host relationship has been studied mainly in symbiotic relationships such as ectomycorrhizae and arbuscular mycorrhizae (Calaça and Bustamante 2022; Beidler et al. 2023). Recently, some degree of specificity between arbuscular mycorrhizae and their host in tropical ecosystems has been identified, mainly in Africa and dry ecosystems (Yamato et al. 2009; Mangan et al. 2010; Rodríguez-Echeverría et al. 2017). Other fungal lifestyles such as plant pathogens and saprophytes have been more associated to soil properties than to plant communities (Schappe et al. 2020).

In the plant family Arecaceae, a low level of fungal-host specificity has been suggested (Taylor et al. 2000). The palm family is widely distributed in the tropics and is ecologically, culturally, economically and medicinally important (Cámara-Leret et al. 2017; Muscarella et al. 2020; Lueder et al. 2022). However, research on root-associated fungi remains largely unexplored, leaving these communities virtually unknown (Taylor et al. 2000; Fan et al. 2023). This gap is particularly evident in ecosystems with seasonally shifting water regimes, where environmental filters may strongly influence both fungal and plant communities (Wang et al. 2011; Polanía et al. 2020; Henrique et al. 2021).

To develop more sustainable forest management practices as well as to improve predictions around climate change scenarios, we need to increase our understanding of the drivers that affect the fungal communities at a local scale. For instance, a rise in extreme weather events associated with changes in temperature and precipitation is expected (IPCC 2023). In the context of the rhizosphere, this is relevant because extreme droughts can reduce microbial activity as well as alter the composition and development of plant communities (Meisner et al. 2013; de Vries et al. 2018). However, not all ecosystems may respond in a similar way under extreme drought or flood. Seasonally flooded ecosystems, for example, may experience a reduction in fungal abundance due to heavy metal runoff, changes in soil properties and the development of anaerobic conditions that hinder plants establishment in these environments (Somenahally et al. 2011; Rodríguez-Echeverría et al. 2017; Li et al. 2021). The fungal community in the palm swamp ecosystem may thrive during dry periods due to its high carbon content and the absence of anaerobic conditions. In non-flooded forests (such as the *terra-firme* forest), soil variables may play an important role since they are generally nutrient poor (Vasco-Palacios et al. 2020; Trujillo et al. 2022). However, the high C content from leaf litter in these forests may favor some groups of fungi such as saprophytes (González and Rial 2011; Ritter et al. 2018; Schappe et al. 2020).

In this study, we focus on the community of palm root-associated fungi (root and rhizosphere) in characteristic ecosystems of the Colombian Orinoquia, such as palm swamps*,* terra firme*,* and seasonally flooded forests (Cámara-Leret et al. 2017; Muscarella et al. 2020; Lueder et al. 2022). These ecosystems are threatened due to the expansion of the agricultural frontier and extensive cattle ranching in the Orinoquia region (Castro et al. 2013; Aldana and Stevenson 2016). Here, we aim to identify the biotic and abiotic factors that influence the distribution of their root-associated fungi along a flood gradient. We hypothesize that there will be differences in the fungal community composition between palm swamps, *terra-firme* forests, and seasonally flooded forests due to changes in soil physicochemical properties. We also hypothesize that root-associated fungi are more strongly influenced by the ecosystem they inhabit than by their host species, as most fungi exhibit low host specificity. Additionally, root-associated fungi will be more affected by strong seasonality (related to flooding), such as in the swamps and seasonally flooded forests due to changes in aerobic conditions and soil moisture. Finally, we highlight the lack of knowledge about fungi in these tropical ecosystems, not only in identity but also in their trophic modes and habitat.

Material and methods

Study area

This study was conducted in the Rey Zamuro-Matarredonda Natural Reserve in the municipality of San Martin, Meta, Colombia (Fig. 1). The vegetation corresponds to the region of the *Serrania del Manacacias* in the Colombian Orinoquia, where different types of forest and other ecosystems occur over short distances, such as the seasonally flooded gallery forest (SFF), the *terra-firme* forest (TFF) and the palm swamp (PS). The mean annual temperature is 27.5 °C with a range from 19 to 35 °C. The rainfall regime is unimodal with a yearly precipitation between 2600 and 3000 mm. The dry season begins in the first days of December and finishes at the end of April, and the lowest precipitation occurs in the months of January and February (Aldana and Stevenson 2016; Minorta-Cely et al. 2019; Polanía et al. 2020). The rainy season is from June to the end of November, with the heaviest rainfall between May and July (Minorta-Cely et al. 2019).

In the *Serranía del Manacacías* there are upper tertiary strips that have been formed by fluvial action, forming a system of hills or elevated terrain, with a large number of interfluves that form valleys or lowlands with variable drainage, ranging from well to poorly drained. The soil, relief, and water characteristics play an important role in the floristic composition and structure of vegetation in these ecosystems (Minorta-Cely et al. 2019). The seasonally flooded forest is established in a valley along the Cumaral river, a white-water river that floods for 5 months, from June to November, and where flooding can reach between 1 to 1.2 m in the month of June (Polanía et al. 2020). The *terra-firme* forest is characterized by a higher number of species in well-drained hilly areas (Polanía et al. 2020). The palm swamp, also locally known as *morichal*, is dominated by the species *Mauritia flexuosa* that grows in areas with poor drainage where the soil is characterized by high contents of sand and gravel (González and Rial 2011). Due to their position in valleys, *morichales* are usually flooded throughout the year with a low level of nutrients and a high content of organic carbon. This is one of the most characteristic and threatened ecosystems in the region (González and Rial 2011; Minorta-Cely et al. 2019).

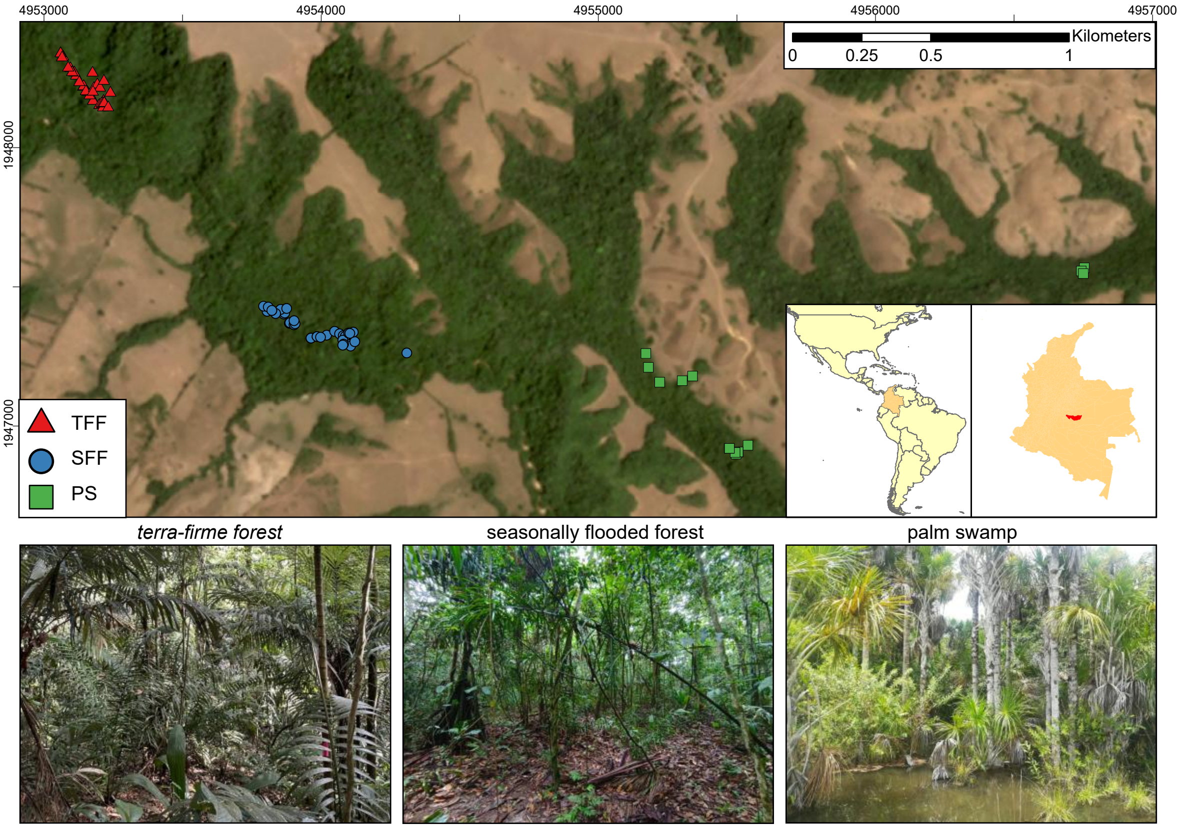

Fig 1. Location of the study site in the Colombian Orinoquia, municipality of San Martin, Department of Meta. Photographs of the three ecosystems: *terra-firme* forest (TFF), seasonally flooded forest (SFF), and palm swamp (PS) included in this study. Imagery © 2023 Planet Labs Inc. All use subject to the Participant License Agreement (https://planet.widen.net/s/zfdpf 8qxwk/participantlicenseagreement_nicfi_2024). Photos by M. Salamanca-Fonseca and A. Sanchez

Root and soil sampling

Healthy looking roots located in the first 30 cm from the soil surface were sampled using the root tracing method. They were collected with soil adhered at less than 1 cm after shaking, in five random adult individuals per palm species in each of the three ecosystems. We sampled all palm species present in each ecosystem (Table S1), with a total of eight species in the SFF, nine in the TFF, and three in the PS at the end of the rainy season, in early December 2022. Each individual palm was marked and georeferenced so that it could be sampled again at the end of the dry season in February 2023. Once collected, the roots were immediately placed in a portable fridge and then stored in a freezer at -20 °C at University of Rosario in Bogotá, and until the DNA extraction was performed. For soil physicochemical analyses, we obtained three composite soil samples, each consisting of three subsamples from each ecosystem and season. The three subsamples were collected from the top 30 cm of soil, excluding the organic horizon. The following variables were analyzed: pH, electrical conductivity (EC), effective cation exchange capacity (ECEC), mean moisture saturation, oxidizable organic carbon (OxOC), organic matter, total nitrogen (Total N), bulk density (B.d), clay percentage, sand percentage, silt percentage, interchangeable potassium (K), interchangeable calcium (Ca), interchangeable magnesium (Mg), interchangeable sodium (Na), exchangeable acidity, phosphorus (P), sulfur (S), aluminum saturation (Al Sat) in the commercial soil laboratory Agrilab (Bogotá, Colombia).

Molecular analyses

DNA was extracted from 20 cm of fine roots with soil attached using the CTAB-chloroform method following Gardes and Bruns (1993). The ITS2 rDNA was amplified as a fungal barcode by PCR using primers ITS7F-ITS4R tagged with unique molecular identifiers (MIDs). The PCR cycling conditions described by the manufacturer of the Q5 polymerase (Biolabs) were followed with minor changes: 5 min at 95 °C, 28 cycles of denaturation for 30 s at 95 °C, 45 s at 56 °C in the annealing phase and 60 s at 72 °C in the extension phase, then a final extension at 72 °C for 5 min. Negative DNA extraction controls and positive DNA controls from a distant and known fungal community were added in each run. We controlled each PCR product with an electrophoresis using a 1% agarose gel. Dilutions of x10 and x100 were performed to obtain as many PCR products as possible (80 per season) due to high DNA concentration. All samples were normalized using The SequalPrep Normalization Plate Kit (ThermoFisher Scientific, MA, USA) following the manufacturer's instructions. Samples were quantified on a Qubit flourometer and sequenced using Illumina Miseq 2 x 250 bp V3 at Fasteris SA.

Bioinformatics

Bioinformatic analyses were run on the Saga cluster of the Norwegian Research Infrastructure Services (NRIS). The raw sequences were independently demultipexed together with tag and primer removal using CUTADAPT (Martin 2011). The sequences with a low number of reads were then removed and a quality profile of the sequences was generated. Sequences were denoised, chimeras removed, and a table of amplicon sequence variants (ASVs) was created using the DADA2 algorithm (Callahan et al. 2016) in the R environment version 4.2. (R Core Team 2022). The ITS2 marker region was extracted using ITSx (Bengtsson-Palme et al. 2013) and additional clustering was performed with 97% similarity using VSEARCH (Rognes et al. 2016). Post-clustering curation was performed using the LULU algorithm (Frøslev et al. 2017). Taxonomic assignment was done based on the SINTAX predictive algorithm (Edgar 2016) against the UNITE database version 9.0 (Abarenkov et al. 2024). Finally, an "_X" was added to the last taxonomic level identified for analysis with unidentified taxa at higher resolutions, this was done each time higher levels were unknown.

Statistical Analysis

All statistical analyses were run in R (R Core Team 2022). All operational taxonomic units (OTUs) that had greater or equal proportions in the controls than in the root samples were removed. OTUs from positive controls were not found in the root samples. We normalized OTU abundance using the total-sum scaling (TSS) technique based on the total abundance per sample using the Dplyr package (Wickham et al. 2014). This approach helps preserve rare species information and improve comparability between samples. To understand the ecological roles of the fungi, we assigned habitat and trophic mode based on fungal genera using the FungalTraits version 1.2 database (Põlme et al. 2020). The trophic mode was assigned based on the fungi's primary lifestyle. Fungi whose primary lifestyle was classified as endophytic or associated with animals were grouped under the category 'other' due to their variable lifestyles (Põlme et al. 2020). Subsequently, we investigated fungal class composition variations across ecosystems, employing the phyloseq package (McMurdie and Holmes 2013) and ggplot (Wickham 2016) to generate a bar chart. Fungal classes with a relative abundance below 1% were grouped into a new category for better visualization. We further assessed the influence of ecosystems and palm species identity on fungal community abundance through differential abundance analysis. A heat tree was generated to visualize the abundance of fungal taxa up to the Order level, highlighting the taxa with significant differences according to their log2_median_ratio value and the abundance values using the metacoder package (Foster et al. 2017). To determine the impact of seasonality on fungal community abundance, we followed a heat tree approach comparing fungal communities in different seasons. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis distance calculated using the metaMDS function was employed to visualize changes in fungal community composition using the vegan package (Oksanen et al. 2020). The EnvFit function of the vegan package was used to adjust soil variables that showed low correlation using Spearman's correlation (Fig. S1). We tested whether the data fulfilled the assumptions of normality using the Shapiro-Wilk test and equality of variance between groups using the Levene’s test from the CAR package (Fox and Weisberg 2019). Finally, ANOVA and Kruskal-Wallis tests were conducted on the soil variables across the three ecosystems.

Results

Fungal community composition

After quality control analysis, chimera detection, and sequence management with a taxonomic identity threshold of 97% in the control samples, a total of 4036 fungal OTUs were detected. Agaricomycetes, Ascomycota_X, Dothideomycetes, Eurotiomycetes, and Sordariomycetes were the most dominant classes in all ecosystems and seasons (Fig. 2a; Figs. S2, S3). When exploring the classes with less than 1% relative abundance, there was a higher relative abundance of taxa in PS (Fig. 2b). The abundance of the classes Glomeromycetes and Endogonomycetes increased significantly in the PS ($p < 0.05$) compared to other ecosystems. The orders Glomerales, Diversisporales increased in PS compared to TFF, while no differences were found with the order Diversisporales in SFF (Fig. S3). Furthermore, a significant decrease of the order Trechisporales was observed in PS. When comparing SFF and TFF, only the orders Venturiales and Capnodiales showed significant differences ($p < 0.05$). Their abundance decreased in SFF, while the order Botryosphaeriales increased (Fig. S3).

In the dry season, the abundance of the classes Glomeromycetes and Monoblepharidomycetes in the PS was higher compared to SFF and TFF (Fig. S4a). In the rainy season there was an increase in the abundance of Agaricomycetes, Glomeromycetes, and unidentified fungi (Fungi_X_X), along with a decrease in Dothideomycetes (Fig. S4b). At the palm species level, we found no significant differences in the fungal community abundance at any taxonomic level ($p > 0.05$; Fig S5).

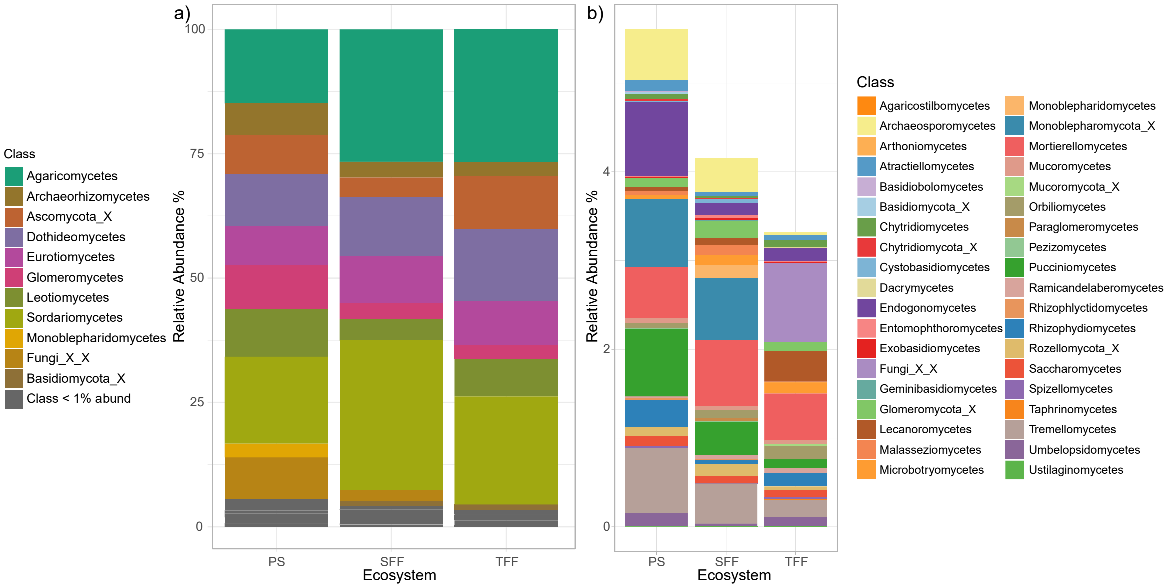

Fig 2. Relative abundance in the palm swamp (PS), seasonally flooded forest (SFF), and *terra-firme* forest (TFF) ecosystems. a) Abundance for dominant fungal classes; b) zoom in to fungal classes with less than 1% abundance.

Environmental drivers of the fungal community

Ordination based on Bray-Curtis dissimilarity revealed a strong clustering between SFF and TFF fungal communities, while PS communities were separated especially along the NMDS2 axis (Fig. 3a). When including the non-correlated edaphic variables to the ordination (Fig. S1), the variables that separated PS from the other ecosystems were high values in sulfur (S), electrical conductivity (EC), effective cation exchange capacity (ECEC), total nitrogen (Total_N), and exchangeable sodium (Na). Significant differences between ecosystems were found in pH, ECEC, Total_N, bulk density, P, Al_Sat, and Na ($p < 0.05$; Fig. 3a, Table S2). Marginal differences were found for EC ($p < 0.1$), while no differences were found for S despite its higher average value in PS (Table S2). These differences were mainly between PS and TFF, although P and Al_Sat were significantly different between PS and SFF (Table S3).

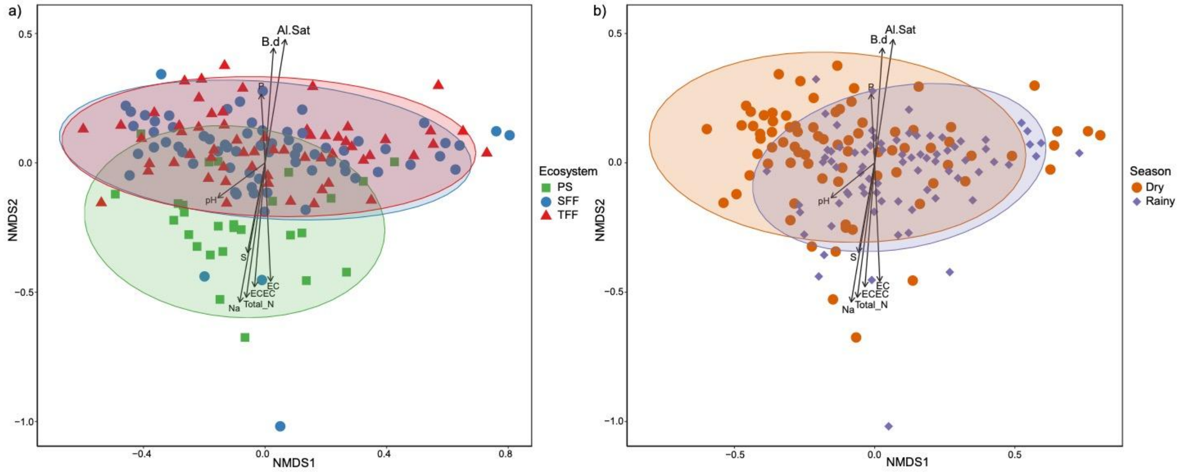

Fig 3. NMDS ordination of fungal community compositions based on Bray-Curtis distances. a) Ellipses represent the confidence regions (95%) for ecosystems: palm swamp (PS, green), seasonally flooded forest (SFF, blue), and *terra-firme* forest (TFF, red). b) Ellipses represent the confidence regions for the dry (orange) and rainy (purple) seasons. Arrow length and orientation indicate the strength and direction of the correlation between the significant soil variables and the ordination.

Effect of seasonality on the fungal community

NMDS ordination showed a separation between the fungal communities of all ecosystems in the dry and rainy seasons (Fig. 3b). Significant differences were found between seasons. In the dry season there was a significant decrease in Basidiomycota, Glomeromycota, and Mortierellomycota, while Ascomycota was the only one showing an increase compared to the rainy season (Fig. 4).

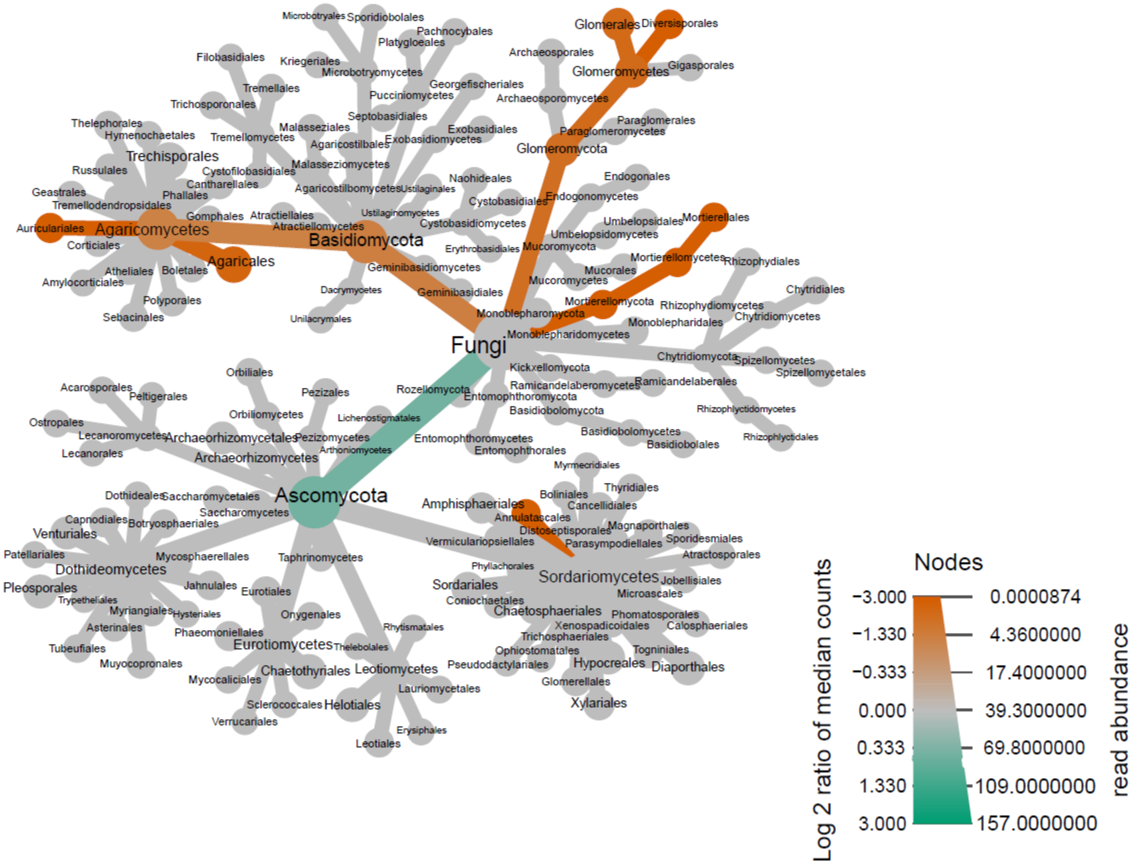

Fig 4. Heat tree showing the fungal communities and the changes found in the dry compared to the rainy season. Color changes are associated with significant changes in abundance ($p < 0.05$). Negative values (orange) indicate a decrease in taxa during the dry season, while positive values (green) indicate a significant increase in abundance during the dry season compared to the rainy season. Zero values (gray) indicate that no significant differences were found.

Seasonal changes by ecosystem indicated that the fungal community within TFF and PS did not change significantly. In the TFF dry season, there was only a significant reduction in the order Mortierellales (Fig. S6). In contrast, in the SFF, several seasonal changes were observed, mainly associated with a reduction of the orders Glomerales, Diversisporales, Mortierellales, Agaricales and Annulatascales in the dry season. The order Thyridiales was the only one increasing during the dry season (Fig. S6).

Comparing fungal communities in each season separately and between ecosystems revealed a distinct pattern. During the dry season, a higher number of taxa exhibited significant differences in abundance between PS and the other ecosystems (Fig. S7). Conversely, the rainy season only showed an increase in the order Leotiales in the PS, along with reductions in the orders Capnodiales and Venturiales in SFF compared to TFF (Fig. S8).

Fungal trophic modes

From the 4036 OTUs, we assigned trophic modes to 1674 based on reported lifestyles of fungal genera in the FungalTraits database. This means that only 41% of OTUs were classified into a specific trophic mode. Most of the fungi were identified as saprotrophs (26%), followed by pathotrophs (11%) (Fig. 5a). Classifications by habitat revealed that most of the OTUs could not be assigned (Fig. 5b). However, from the remaining OTUs, most were non-aquatic (23%) or partly aquatic (14%). Interestingly, 1% were aquatic, which could reflect the flooding conditions of SFF and PS.

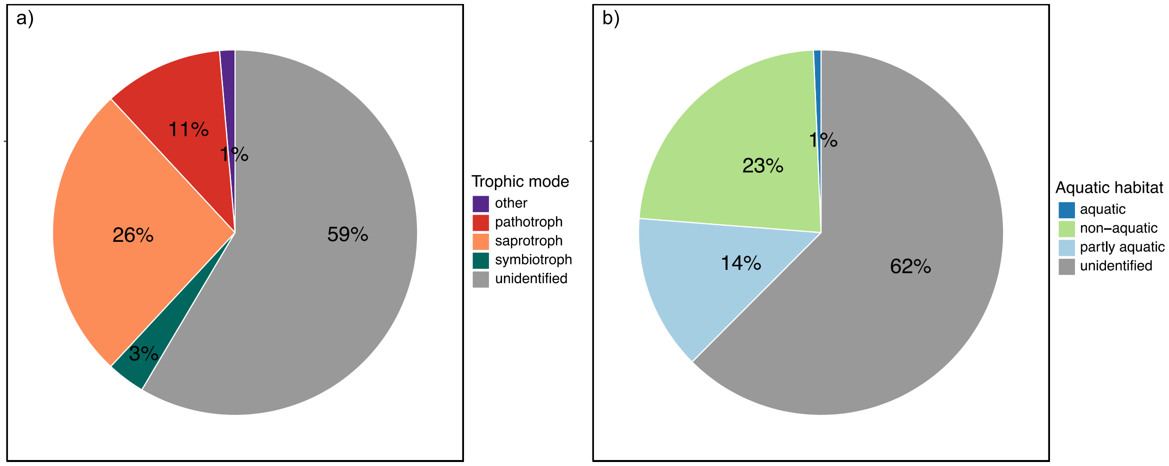

Fig 5. Pie chart showing the percentages of fungal operational taxonomic units (OTUs) identified in this study associated with a) trophic mode and b) habitat.

Discussion

As far as we know, this is the first study exploring the fungal communities associated with palms in three ecosystems of the Colombian Orinoquia. We found differences in the fungal community composition associated with the palm roots between the ecosystems of palm swamp (PS), *terra-firme* forest (TFF), and seasonally flooded forest (SFF). This is in agreement with our first hypothesis. Our results suggest the significant influence of edaphic factors, such as aluminum saturation (Al. Sat), bulk density (B.d), sulfur (S), sodium (Na), total nitrogen (Total_N), effective cation exchange capacity (ECEC), electrical conductivity (EC) and pH, on fungal community structure. In addition, we found that the fungal community composition of TFF and SFF were similar, while PS diverged from these ecosystems, reflecting differences in their beta diversity. We did not observe significant differences in fungal communities associated with different host plants, supporting our second hypothesis that the ecosystem exerts more influence than host identity in Arecaceae. In our third hypothesis, we proposed that seasonality would affect PS and SFF more than TFF. We detected seasonal differences in fungal community composition, along with a decrease in the abundance of Basidiomycota, Glomeromycota and Mortierellomycota, and an increase in Ascomycota during the dry season. These changes were observed mainly in the SFF, revealing the important role of ecosystem dynamics for the fungal community. Finally, more than half of the OTUs could not be assigned to a specific trophic mode or associated habitat, and many of these OTUs were not identified at high taxonomic levels. This reflects a significant gap in our knowledge of fungal diversity in these tropical ecosystems.

Ecosystem characteristics Shaping Fungal Community Composition

Plant communities, soil properties, and environmental conditions are known to influence fungal community composition (Nielsen et al. 2010; Qiao et al. 2017; Wei et al. 2022; Mikryukov et al. 2023). Our results showed similar community compositions between the SFF and the TFF, where the most abundant classes were the Agaricomycetes, Dothiomycetes, and Sordaryomycetes (Fig 2). This is in line with a previous study in tropical forests where the most abundant classes were Agaricomycetes and Sordariomycetes (Wei et al. 2022). Previous studies on plant communities of the SFF and TFF showed that they only share about one-third of the species, showing high diversity values and high equity in the species present in these ecosystems (Polanía et al. 2020). For Arecaceae, Polanía et al. (2020) reported this family as the most abundant and shared species between SFF and TFF. In contrast, PS were characterized by a dominant palm species, *Mauritia flexuosa*, and a low abundance of other plants species (Minorta-Cely et al. 2019), which could alter the fungal community. Although the role that the plant community exerts on the root-associated fungi is poorly understood in the ecosystems of the Orinoquia, it has been proposed that this relationship is dependent upon the scale used (Peay et al. 2013; Han et al. 2021). In this study, we worked at a local scale where ecosystems are found within a 3 km radius (Fig. 1) and share the same climatic conditions. Therefore, variables such as mean annual temperature and mean annual precipitation, which have been identified as drivers of the fungal community in other studies (Wei et al. 2022; Beidler et al. 2023; Mikryukov et al. 2023), may be less relevant in the ecosystems studied here. Another key factor that can affect the fungal community was associated with changes in the physicochemical properties of the soil (Schappe et al. 2020; Ballauffde vries et al. 2021; Wei et al. 2022), which can be influenced by the plant community (de Vries et al. 2018). Additionally, the flooding regime was another important characteristic of the ecosystems studied. The SFF is flooded by a white-water river for five months, resulting in nutrient deposition (Polanía et al. 2020), while the PS is subjected to organic matter accumulation due to the stagnant water. These regimes create different soil properties (González and Rial 2011), and coupled with the flooding regime, could partly explain the differences found between the fungal communities of these ecosystems (Fig 3a). We found a lower abundance of Agaricomycetes and Sordariomycetes in PS compared to TFF and SFF, which could be associated with pH differences (Fig. 2). A negative correlation between Agaricomycetes abundance and pH has been reported in subtropical forests (Wang et al. 2021). However, Sordariomycetes has been positively correlated with pH, which was not consistent with our results (Wang et al. 2021; Wei et al. 2022). This may be due to a negative correlation with NH_4 and NO_3. Although we did not measure these variables, we found a high value of total N in PS compared to TFF and SFF (Table S3). Another class that showed differences was the Glomeromycetes, which are mostly arbuscular mycorrhizae (Wang et al. 2021). This group showed a high relative abundance in PS. Interestingly, PS had the lowest values of P, but high values of nutrients such as K, Ca, Mg, Na, S (Table S2). The arbuscular mycorrhizae may thus be crucial for facilitating the absorption of nutrients, especially phosphorus (Bohrer et al. 2004; Calaça and Bustamante 2022; Qin et al. 2022). Additionally, a high number of Monoblepharidomycetes were detected in PS (Figs. 2, S4), a class that contains many saprotrophs and parasites. Their taxonomic position is still not very clear, and novel families and genera with new ecological roles are still being discovered (Karpov et al. 2017; Duo Saito et al. 2018). Monoblepharidomycetes have been isolated from freshwater, brackish water, marine, and soil samples as well as extreme environments (Dee et al. 2015; Duo Saito et al. 2018). Their association with freshwater environments coincides with our results, given that this group was found in PS and SFF. Many of them, however, were only identified at the phylum level (Table S4).

Seasonal Dynamics of Fungal Communities

We found differences in the composition of fungal communities between the dry and rainy season (Fig. 3b), as well as significant differences in several orders (Fig 4), especially related to a reduction of relative abundance in several taxa in the dry season. The changes in relative abundance between seasons were associated with SFF, while TFF and PS had barely any difference (Fig S6). Other studies have reported that soil fungal communities tend to remain stable over the seasons, with changes primarily associated with shifts in the plant community or the ecosystem, rather than seasonality itself (de Vries et al. 2018; Han et al. 2021; Wang et al. 2021). However, seasonal changes in SFF may be greater due to the seasonal flooding. A study comparing the same SFF and TFF sampled here, determined that flooding acts as a filter for the plant community (Polanía et al. 2020). Therefore, seasonal flooding could act as an abiotic filter for the fungal community, reflected in a decrease in abundance during the dry season (Fig S6). Given that many OTUs (e.g. Sordariomycetes and Dothideomycetes) are associated with aquatic or partially aquatic habitats, the end of the flooding cycle entails a reduction in the abundance. These findings support our hypothesis that the fungal community is more affected in ecosystems with a strong seasonality. Compared to SFF and TFF, the abundance of various orders (e.g., Glomerales, Diversisporales, Monoblepharidales, Jahnulales) in PS increased during the dry season, while Archaeosporales and Mortierellales were higher in PS compared to TFF (Fig S7). This is relevant because it has been reported that variations in humidity influence fungal communities (Han et al. 2021; Wang et al. 2021; Beidler et al. 2023), including arbuscular mycorrhizae of the phylum Glomeromycota (Schappe et al. 2020) and in tropical flooded savannas (Rodríguez-Echeverría et al. 2017). For example, Bohrer et al. (2004) suggested that arbuscular mycorrhizae were tolerant to a wide range of soil moisture and flooding conditions in wetland soils (Bohrer et al. 2004). This agrees with recent reports for some families that have higher diversity in PS in the dry season such as Acaulosporaceae, Archaeosporacea, Ambisporaceae and Glomeraceae which have been associated with wetlands and lentic bodies of water (de Queiroz et al. 2020). The relative importance of moisture for soil and ectomycorrhizae fungi has been reported to be greater in the dry season than in the wet season (Beidler et al. 2023). The same may be true for other trophic modes, where high soil moisture is important, and therefore, they may not be as affected by the rainy season (Fig S8). While the fungal community in SFF was negatively affected in the dry season (Fig S6), PS may act as a “water refuge” for the community, remaining unchanged between seasons (Fig S6). Even more, in the dry season the abundance increases compared to TFF and SFF (Fig S7). This “refuge” condition has also been observed in other organisms, such as animals and plants (González and Rial 2011; Trujillo et al. 2011).

Host Influence on Root-Associated Fungal Communities

In this study, we compared the fungal community using different palm species. Our results indicate that the host had no significant influence on fungal community composition and abundance, at least among different species (Fig S5). Although a high level of host specificity has been reported for some fungi, this has been mostly associated with ectomycorrhizae (Tedersoo et al. 2008; Vasco-Palacios et al. 2020; Beidler et al. 2023). Arbuscular mycorrhizae are known for their low specificity and wide distribution (Davison et al. 2015), with some exceptions (Husband et al. 2002; Yamato et al. 2009; Mangan et al. 2010). Recent studies in Ecuador suggest that the families Glomeraceae, Acaulosoraceae, and Archaeosporaceae are widely distributed and adapted to diverse soil conditions and a wide range of plant hosts (Garcés-Ruiz et al. 2017), which is in agreement with our results (Figs. 4, S3). Additionally, pathogenic and saprotrophic root and soil fungi have been related to soil properties in the tropics (i.e., pH, moisture, and nutrients) rather than to the tree community (Schappe et al. 2020). Additionally, some of the palm species are found in more than one ecosystem (Table S1) and may mask the effect of soil versus host. Some studies have reported that the root-associated fungal community of palms could show some specificity (Taylor et al. 2000; Zhang et al. 2019). There are also differences in the palm fungal communities between the temperate and tropical regions (Taylor et al. 2000; Fan et al. 2023). However, in a global scale study comparing fungi from three palm species, less than 10% of the fungal species collected showed host specificity indicating low specificity within palms (Taylor et al. 2000). This corroborates our findings, where there was a more pronounced effect of the ecosystem, followed by seasonality, than palm host.

Another reason why host identity may not show significant differences could be related to the sampling over relatively short spatial distances. Studies have shown that as the spatial distance increases, the similarity between the fungal communities decreases (Zhou and Ning 2017; Ballauff et al. 2021). In addition, a recent review of palm-associated fungi (Fan et al. 2023) indicates that they rarely associate with other plants. Since our study focused only on palms, we may not have captured the full extent of host-specific fungal communities. However, the complex interactions between palms and their associated fungi are still not fully understood, and many palm species along with their fungi remain understudied (Fan et al. 2023).

Tropical Ecosystems and Fungal Diversity

We highlight the role of ecosystem dynamics in shaping fungal communities. We found that higher water availability was associated with fungal relative abundance. During the dry season, with less water available, there was a significant reduction in the relative abundance of several fungal groups in ecosystems sensitive to drought, such as the SFF (Fig. S6). The PS generally maintained high moisture levels throughout the year, and higher fungal relative abundances in the dry season compared to SFF and TFF (Fig S7). This is relevant for the Orinoquia, since there have been land cover changes, such as the drainage of flooded ecosystems such as PS, due to the expansion of the agricultural frontier and extensive cattle ranching (Castro et al. 2013; Aldana and Stevenson 2016).

The transformation of this region, coupled with rising global temperatures and intensifying droughts, makes these ecosystems particularly vulnerable to climate change (IPCC 2023). We detected 3% of the identified OTUs as symbiotrophic fungi. However, more than half of the OTUs identified here could not be assigned to a trophic mode, because the required taxonomic resolution (genus) could not be assigned, or a trophic mode had not been previously reported. Interestingly, many of the compositional changes in seasons and ecosystems were linked to the Glomeromycota, a phylum historically associated with symbiotic relationships (Garcés-Ruiz et al. 2017; Schappe et al. 2020). In addition, in PS a higher amount of Monoblepharidomycetes were identified, a group that has recently been associated with pathotrophs and saprotroph fungi (Dee et al. 2015; Duo Saito et al. 2018). Unfortunately, we could not assign a trophic mode to the OTUs from this class. This clearly shows a lack of knowledge of taxa associated with aquatic environments, particularly in tropical ecosystems. Once swamps are drained, these fungi may become extinct, affecting the diversity that has not yet been explored (Fan et al. 2023). A recent study reported that although South America is considered a biodiversity hotspot and contains many native palm species, it is poorly studied in terms of fungal diversity (Fan et al. 2023). This is consistent with our results, where 59% of the OTUs identified could not be assigned a trophic mode, and 62% were unknown for their habitat type (Fig. 5).

Conclusion

We identified that beyond seasonality and associated palm species, the fungal community is influenced by local ecosystem dynamics. In our study we found that the root and rhizosphere fungal community of TFF and SFF are associated with similar soil physicochemical variables and share most of the fungal community across seasons. In contrast, the PS fungal community diverges from TFF and SFF. In addition, the ecosystem influence on the relative abundance of fungi was greater than the host palm. Although we found seasonality-related differences, these were mainly due to changes in the fungal relative abundance in the SFF, suggesting that the effect of seasonality is greater in ecosystems with pronounced seasonal dynamics. These results are key to our understanding of poorly studied tropical ecosystems such as those of the Orinoquia. They emphasize the importance of understanding the specific dynamics of each ecosystem and their impact on the fungal community, particularly in light of climate change scenarios that may alter ecosystem dynamics through more extreme events, changing flooding regimes and increasing droughts. We ought to continue studying these tropical ecosystems, especially those with changing flooding regimes, to increase our knowledge about the fungi of the Orinoquia and understand the effect of extreme events driven by climate change on these understudied communities and ecosystems.

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Contributions

A.S., A.C, M.S-F. conceived the idea and designed the methodology; A.S., M.S-F. collected the samples in the field; H.K., I.S., E.T., A.K.K., M.S-F. prepared the material and data analyses; M.S-F. wrote the first draft of the manuscript, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

Raw ITS sequences are available in the Sequence Read Archive (SRA) database at NCBI under accession number PRJNA1198099.

Ethics declarations

The authors declare no conflicts of interest.

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Supplementary material

Table S1. Palm species found in *Terra-Firme* Forest (TFF), Seasonally Flooded Forest (SFF) and Palm Swamp (PS) ecosystems.

TFF	**SFF**	**PS**
Astrocaryum gynacanthum	*Attalea insignis*	*Euterpe precatoria*
Attalea insignis	*Bactris brongniartii*	*Mauritia flexuosa*
Geonoma deversa	*Geonoma deversa*	*Socratea exorrhiza*
Oenocarpus bataua	*Euterpe precatoria*	
Oenocarpus minor	*Oenocarpus bataua*	
Socratea exorrhiza	*Oenocarpus minor*	
Syagrus orinocensis	*Socratea exorrhiza*	
	Syagrus orinocensis	

Table S2. Number of individuals (n), mean, standard deviations (sd) of ecosystems, p-value and statistics (F or H) from ANOVA (A) and Kruskal-Wallis (K) statistical tests for the soil variables between *Terra-Firme* Forest (TFF), Seasonally Flooded Forest (SFF) and Palm Swamp (PS). In **bold** are variables with low correlation that were adjusted for the NMDS.

Soil Variable	**n**	**Mean±sd**			**F / H**	***p-value***	**A / K**
		TFF	**SFF**	**PS**			
pH	18	3.68±0.13	3.78±0.15	4.02±0.22	5.713	0.0143*	A
Electrical Conductivity (EC)	18	0.472±0.10	0.635±0.18	1.05±0.65	4.797	0.0922°	K
Effective Cation Exchange Capacity (ECEC)	18	3.47±0.99	4.81±1.20	7.54±3.42	5.469	0.0165*	A
Mean Moisture Saturation	18	24.0±4.08	32.7±5.74	70.7±29.1	7.0292	0.0297*	K
Oxidizable Organic Carbon	18	1.99±0.61	3.50±1.96	14.8±7.32	6.4678	0.0394*	K
Organic Matter	18	3.43±1.07	6.02±3.37	25.4±12.60	6.4678	>0.001***	K
Total Nitrogen	18	0.16±0.05	0.29±0.16	1.23±0.60	6.4678	0.0394*	K

Bulk Density	18	1.30±0.11	1.12±0.20	0.71±0.39	6.0124	0.0494*	K
Clay	18	33.7±4.46	31.0±8.74	7.0±3.29	11.598	0.0030**	K
Sand	18	47.7±12.2	35.3±9.00	15.7±33.5	3.47	0.0577°	A
Silt	18	18.7±8.64	33.7±17.4	77.3±35.1	6.2351	0.0442*	K
K	18	41.0±7.48	71.5±20.4	449.0±282.0	8.4327	0.0147*	K
Ca	18	40.6±18.2	56.0±17.4	138.0±110.0	5.6667	0.0588°	K
Mg	18	18.9±7.48	33.3±7.55	118.0±79.5	7.6842	0.0214*	K
Na	18	13.4±1.88	15.6±2.55	39.2±17.2	11.111	0.0038**	K
Exchangeable Acidity	18	265.0±80.4	361.0±91.4	411.0±210	1.695	0.217	A
P	18	8.44±4.43	26.0±23.3	6.89±0.659	10.516	0.0052**	K
S	18	7.87±1.57	8.47±1.25	12.8±6.99	2.5494	0.2795	K
Aluminum Saturation	18	84.4±4.05	83.3±0.66	61.4±14.3	10.14	0.0062**	K

Note: Asterisks (*) represent significant p-values * <0.05, **<0.01, ***<0.001, while dots (°) marginal significant values ° <0.1

Table S3. p-value of the Tukey (T) or Dunn (D) post hoc analysis for the soil variables between *Terra-Firme* Forest (TFF), Seasonally Flooded Forest (SFF) and Palm Swamp (PS).

Soil Variable	**Mean±sd**			**T/D**
	TFF- SFF	**PS-SFF**	**PS-TFF**	
pH	0.607	0.083°	0.012*	T
Electrical Conductivity (EC)	0.369	0.401	0.091°	D
Effective Cation Exchange Capacity (ECEC)	0.544	0.108	0.014*	T
Total Nitrogen (Total_N)	0.234	0.352	0.033*	D
Bulk Density (B.d)	0.329	0.287	0.044*	D
Na	0.213	0.079°	0.002**	D
P	0.027*	0.006**	0.551	D
S	0.448	0.803	0.331	D
Aluminum Saturation (Al.Sat)	1.000	0.017*	0.011*	D

Note: Asterisks (*) represent significant P values * <0.05, **<0.01, ***<0.001, while dots (°) marginal significant values ° <0.1.

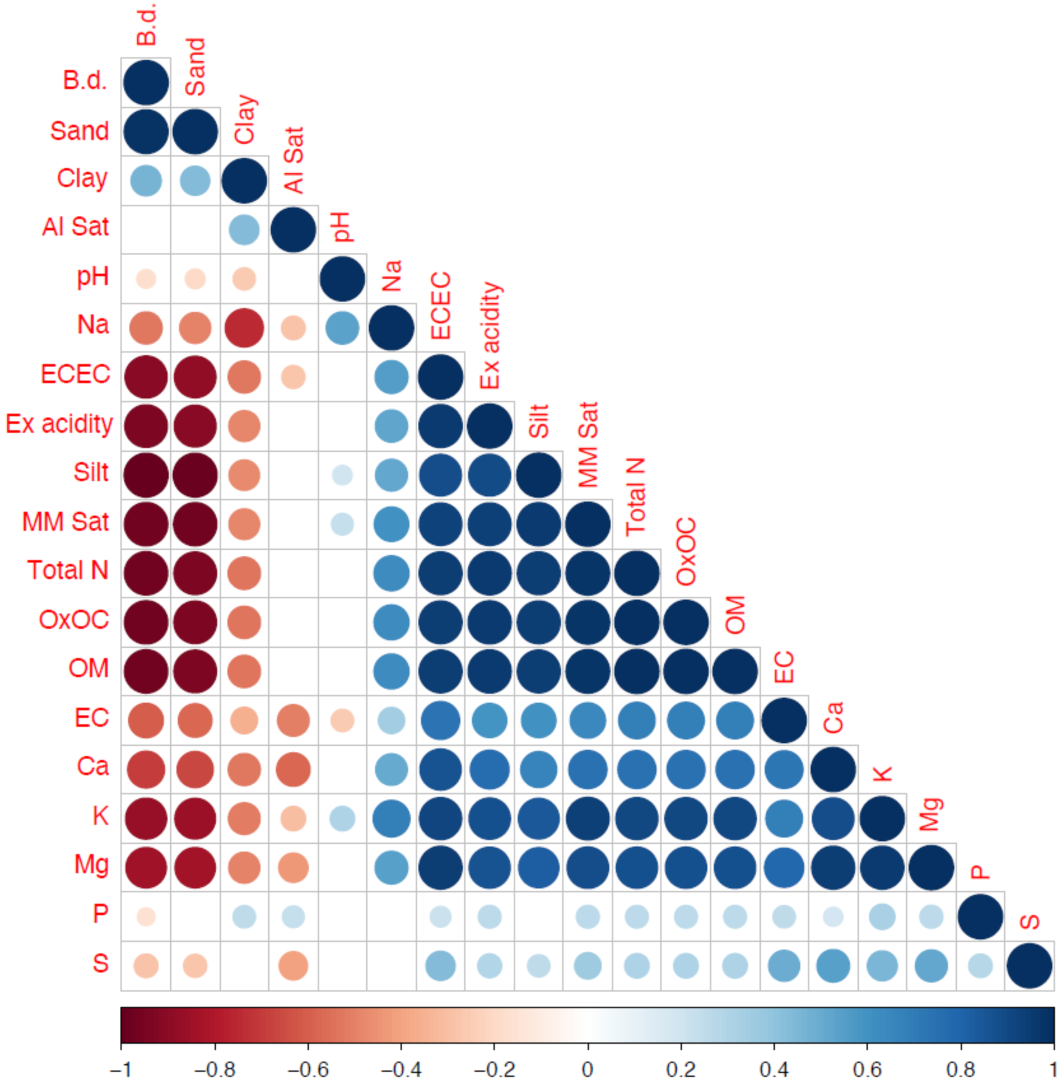


Fig S1. Heat map based on Spearman's correlation between the soil variables of the studied ecosystems. Red colors indicate a negative correlation and blue colors a positive correlation; empty cells indicate no correlation ($p > 0.05$).

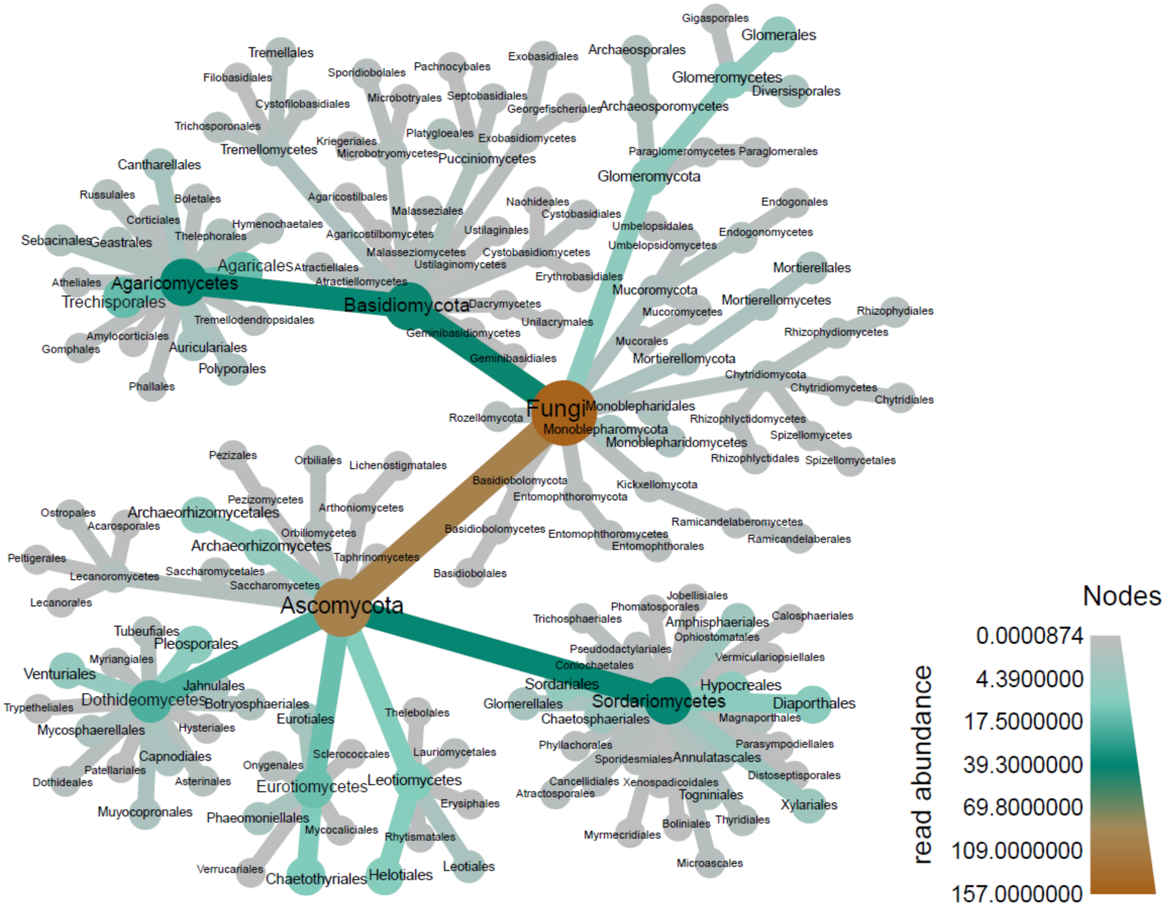


Fig S2. Heat tree showing the fungal communities and associated abundance in each of the taxa found in this study.

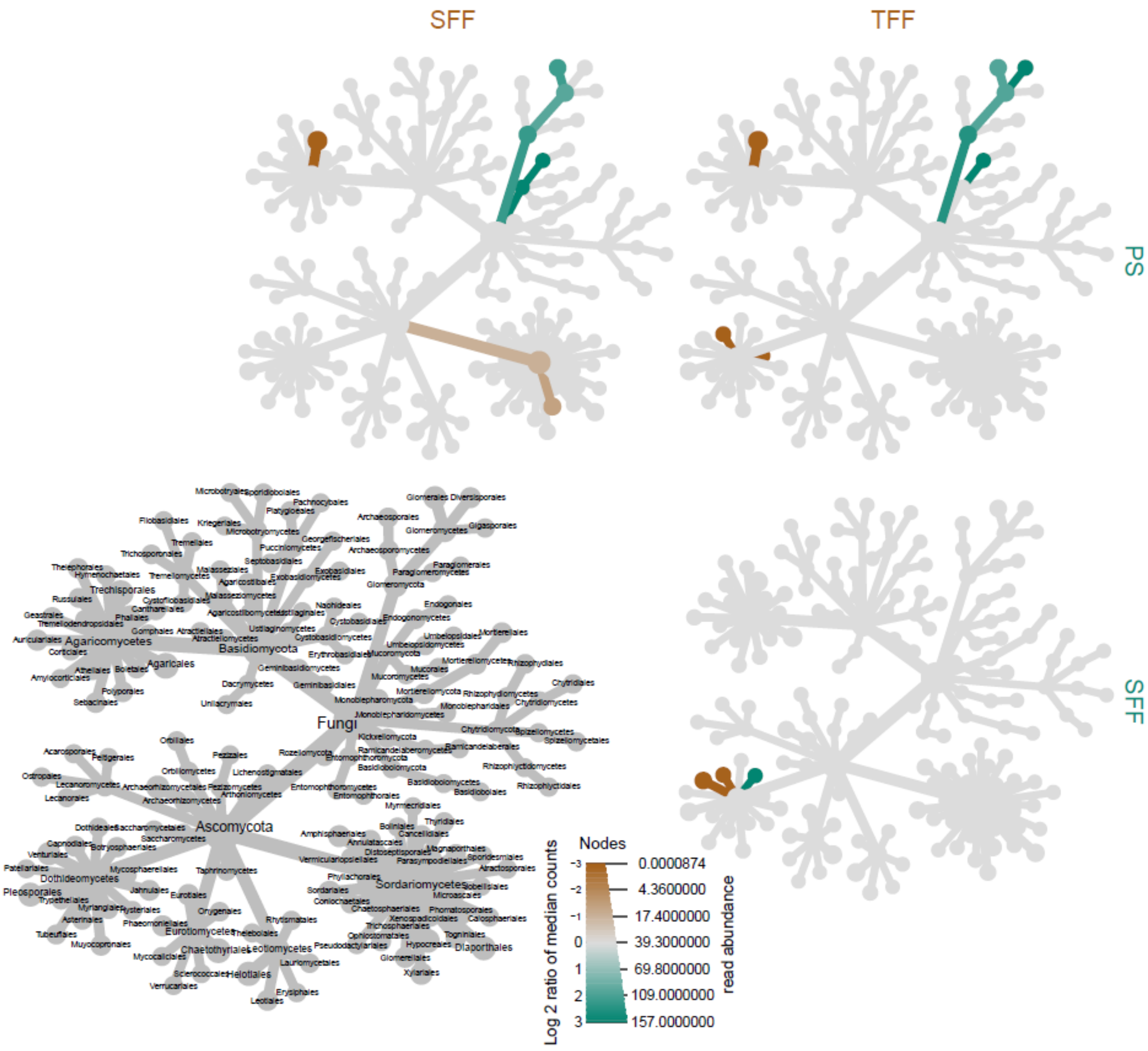


Fig S3. Heat tree showing the fungal communities and the changes found between the different ecosystems. Color changes are associated with significant changes in abundance ($p < 0.05$). Changes in colors indicate increases or decreases depending on the combination of ecosystems. Green colors indicate an increase in palm swamp (PS) or seasonally flooded forest (SFF) while brown colors indicate an increase in seasonally flooded forest (SFF) or *terra-firme* forest ecosystems (TFF). Zero values (gray) indicate that no significant differences were found.

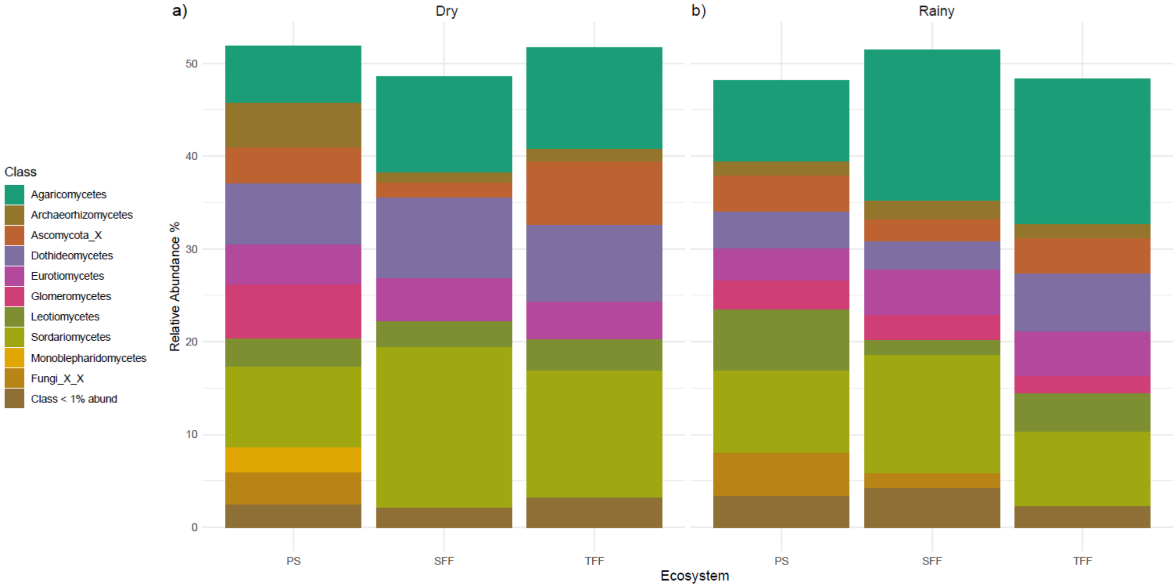


Fig S4. Relative abundance of dominant fungal classes in the dry and rainy seasons present in *terra-firme* forest (TFF), seasonally flooded forest (SFF), and palm swamp (PS) ecosystems.

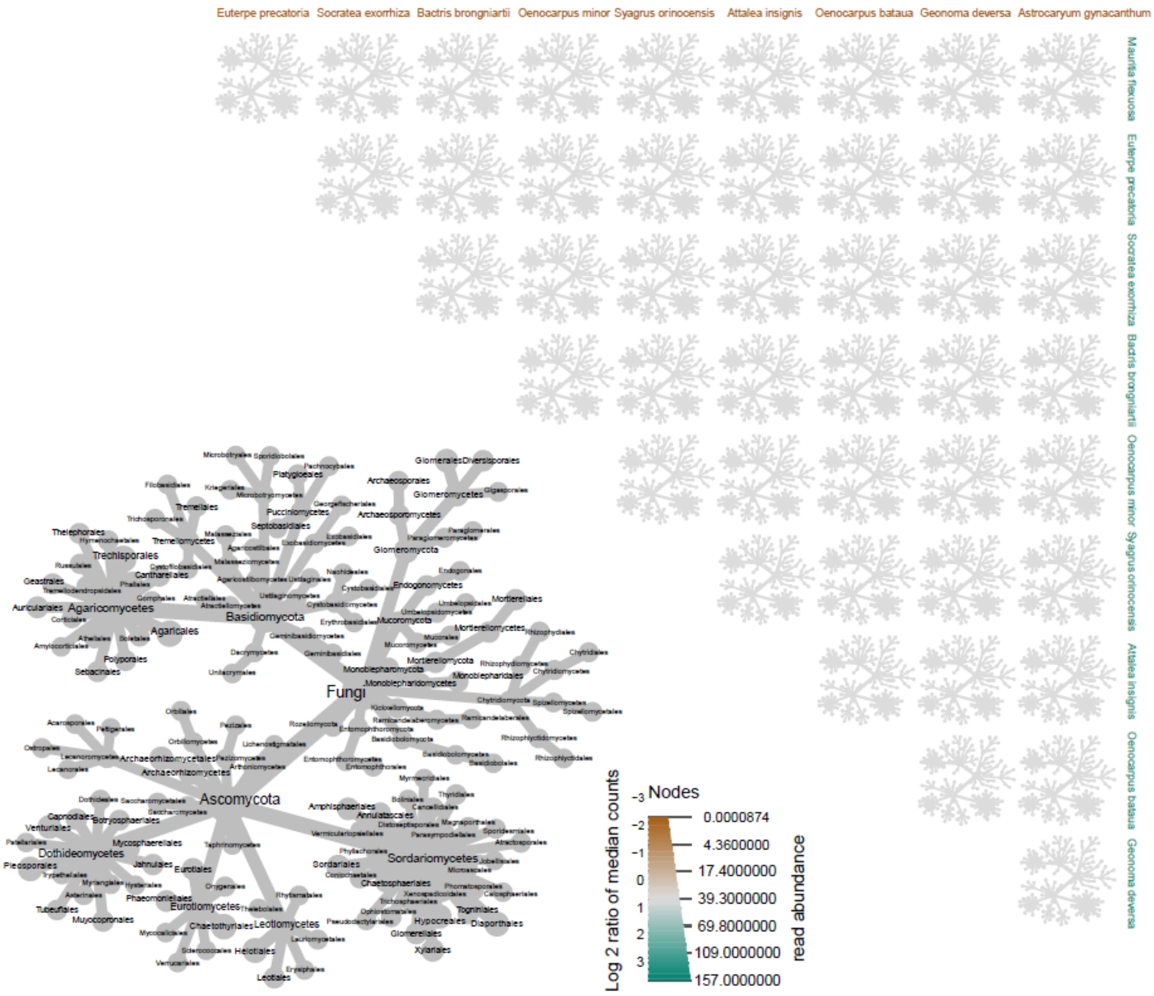
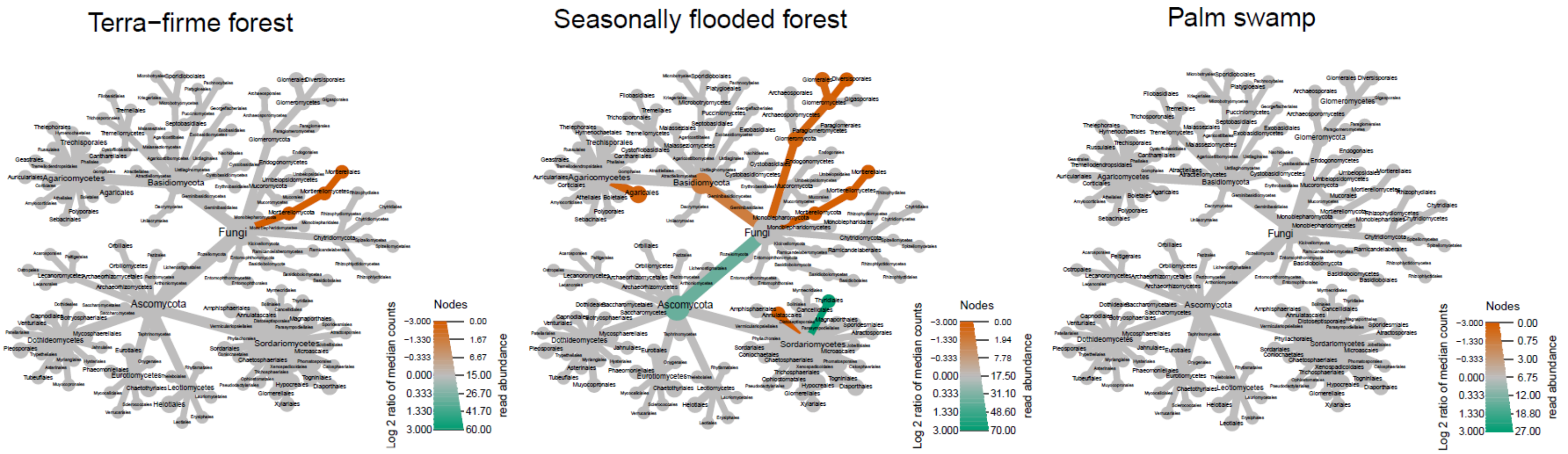


Fig S5. Heat tree showing the fungal communities and the changes found when comparing between palm species. Color changes are associated with significant changes in abundance ($p < 0.05$). Changes in colors indicate increases or decreases according to the comparison between species. Zero values (gray) indicate that no significant differences were found.


Terra−firme forest

Seasonally flooded forest

Palm swamp

Fig S6. Heat tree showing the fungal communities and the changes found in the dry season compared to the rainy season in each ecosystem. Color changes are associated with significant changes in abundance ($p < 0.05$). Negative values (orange) indicate a decrease of taxa in the dry season, while positive values (green) indicate a significant increase in abundance in the dry season compared to the rainy season. Zero values (gray) indicate that no significant differences were found.

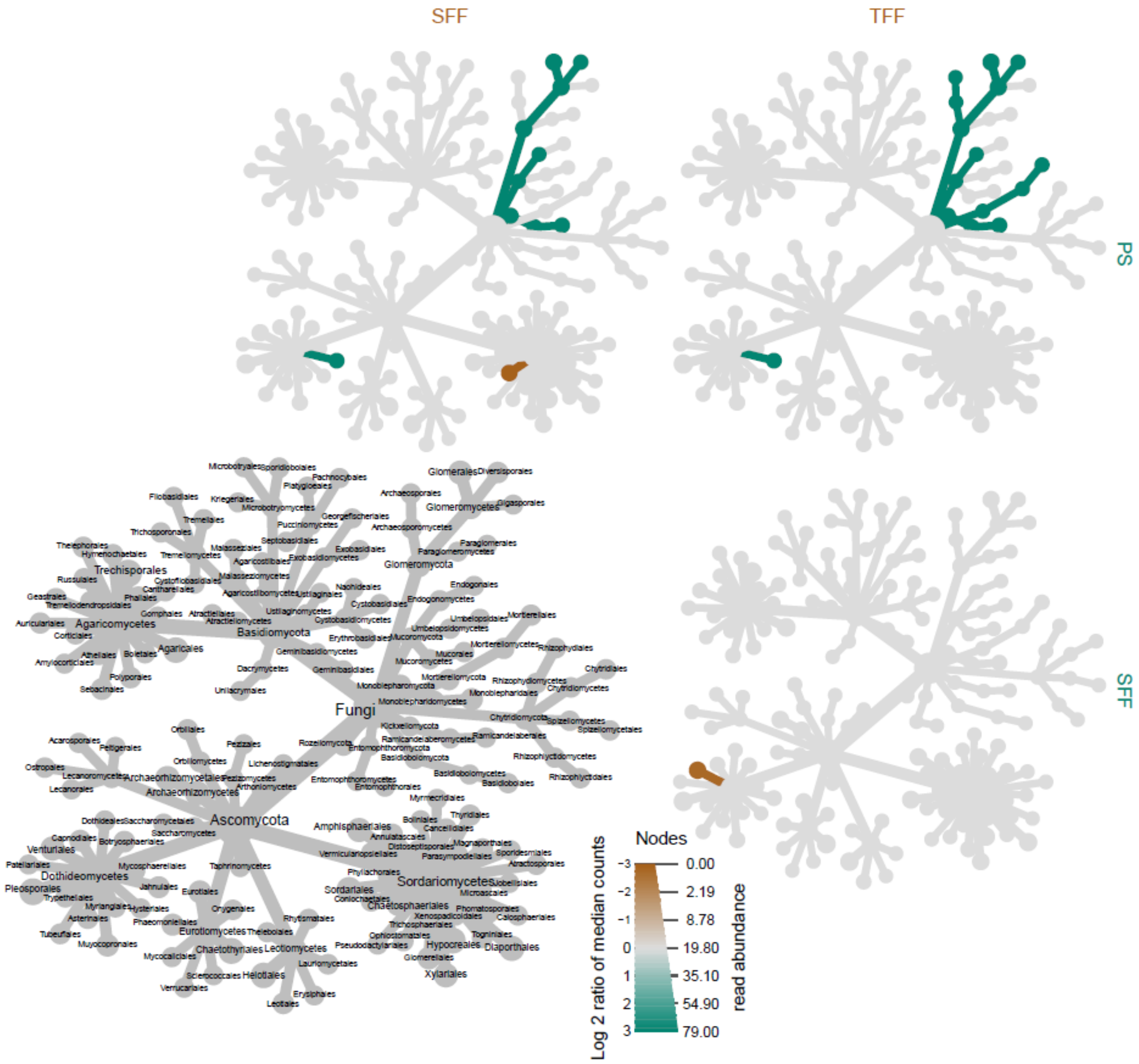


Fig S7. Heat tree showing the fungal communities and the changes found between the different ecosystems for the dry season. Color changes are associated with significant changes in abundance ($p < 0.05$). Changes in colors indicate increases or decreases depending on the combination of ecosystems. Green colors indicate an increase in palm swamp (PS) or seasonally flooded forest (SFF), while brown colors indicate an increase in seasonally flooded forest (SFF) or *terra-firme* forest ecosystems (TFF). Zero values (gray) indicate that no significant differences were found.

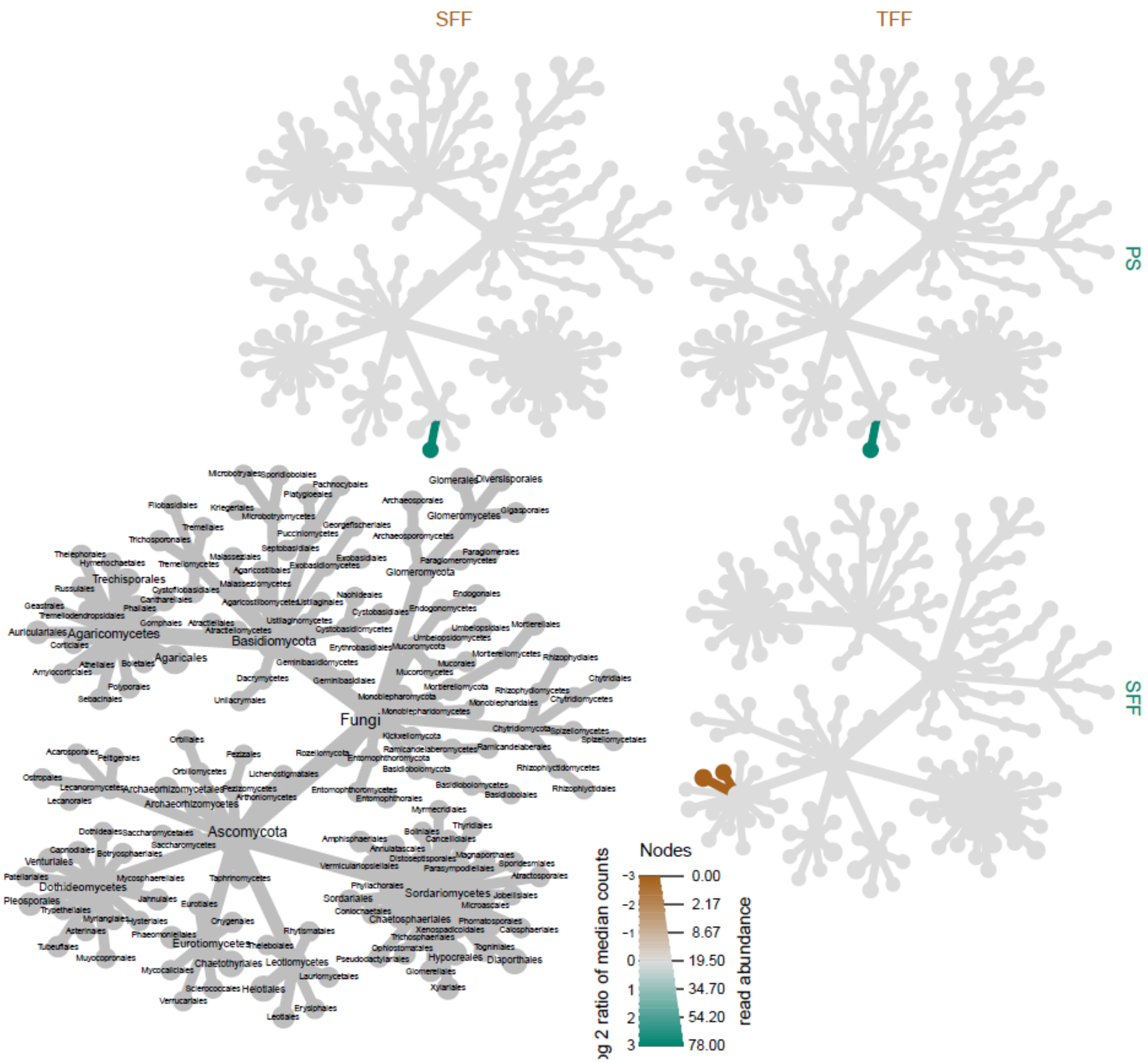


Fig S8. Heat tree showing the fungal communities and the changes found between the different ecosystems for the rainy season. Color changes are associated with significant changes in abundance ($p < 0.05$). Changes in colors indicate increases or decreases depending on the combination of ecosystems. Green colors indicate an increase in palm swamp (PS) or seasonally flooded forest (SFF), while brown colors indicate an increase in seasonally flooded forest (SFF) or *terra-firme* forest ecosystems (TFF). Zero values (gray) indicate that no significant differences were found.