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ABSTRACT:

The influence exerted by tree communities, topography and soil chemistry on the assembly of macrofungal communities remains poorly understood, especially in highly diverse tropical forests. Here, we used a large dataset that combines inventories of macrofungal Basidiomycetes fruiting bodies, tree species composition and measurements for 16 soil physico-chemical parameters, collected in 34 plots located in four sites of lowland rainforests in French Guiana. Plots were established on three different topographical conditions: hilltop, slope and seasonally flooded soils. We found hyperdiverse Basidiomycetes communities, mainly comprising members of Agaricales and Polyporales. Phosphorus, clay contents and base saturation in soils strongly varied across plots and shaped the richness and composition of tree communities. The latter composition explained 23% of the variation in the composition of macrofungal communities, probably through high heterogeneity of the litter chemistry and selective effects of biotic interactions. The high local heterogeneity of habitats influenced the distribution of both macrofungi and trees, as a result of diversed local soil hydromorphic conditions associated to contrasting soil chemistry. This first regional study across habitats of French Guiana forests revealed new niches for macrofungi, such as ectomycorrhizal ones, and illustrate how macrofungi inventories are still paramount to can be to understand the processes at work in the tropics.

KEY-WORDS: composition, communities, diversity, macrofungi, habitat, lowland neotropical rainforest, trees, soil properties

COMMUNITY ASSEMBLY RULES ARE THE RESULT OF FOUR PRIMARY MECHANISMS, SPECIATION, DISPERSAL, drift and selection, taking both neutral and niche-based processes into account (Nemergut *et al*. 2013). This conceptual framework paves the way toward more mechanistic understandings of observed community patterns. Regarding fungi specifically, dispersal limitation impacts diversity at all scales by maintaining regional endemism but also by structuring local assemblages of communities (Hanson *et al*. 2012, Peay *et al*. 2016). At small spatial scales, habitat filtering is an important determinant of fungal community assembly (Feinstein & Blackwood 2013, Crowther *et al.* 2014) but it differentially affects symbiotic, saprophytic or pathogenic fungi (Kerekes *et al*. 2013, Tedersoo *et al*. 2015). As an example, soil phosphorus in particular is known to differentially affect ectomycorrhizal fungi (symbiont of tree roots, van der Linde *et al.* 2018) or saprophytic (Kerekes *et al*. 2013) fungi. Soil pH is universally related to both environmental filtering and niche partitioning (Tedersoo *et al*. 2015) but in tropical areas, the trophic status of fungi affects the relationship between fungal communities and soil pH, which could result from both local and regional mechanisms (Pärtel et *al*. 2016).

As many fungi interact with plants, either by building symbioses (mycorrhizal and endophytic fungi), degrading tree leaves and woody tissues, or being plant-pathogens, several studies have investigated how tree diversity could shape fungal diversity. This relationship was often hypothesised (Waldrop *et al*. 2006) and confirmed at a broad scale (Schmit *et al.* 2005). Recently, Schappe *et al.* (2017) investigated fungal communities in Panama and showed that local tree community equivalently shaped saprophytes, pathogens and symbiotic fungal communities, in agreement with the study of Peay *et al.* (2013) in the western Amazon basin in Peru. Soil properties also had a local effect in both studies, suggesting that abiotic gradients would influence soil fungal community assembly.

Plant ecologists have detected in the Guianas both local and regional variations of tree communities, partly correlated with soils and changes of topography (Guitet *et al*. 2015). The Guianas are placed upon a Proterozoic exposed craton, situated in Eastern Amazonia that has been highly weathered (Hoorn *et al.* 2010) and exhibit very low soil fertility and weak geological and altitudinal gradients (ter Steege *et al.* 2006). However, the relief displays a substantial geomorphodiversity that generates a variety of landforms and soil covers, which have shaped the regional floristic pool (Guitet *et al*. 2018). The variation of soil hydrological and physico-chemical properties between hilltops and seasonally flooded forests strongly contribute in driving the structure of tree communities (Ferry, Morneau, Bontemps, Blanc & Freycon 2010), and it has been suggested that tolerance to prolonged water saturation is the main factor explaining species distribution at a fine scale (Allié *et al.* 2015, Ferry, Morneau, Bontemps, Blanc & Freycon 2010). Moreover, Fortunel et al. (2013) have shown that tree communities are functionally different between habitats characterized by contrasting soil water retention and other physico-chemical properties (clay-rich *terra-firme*, seasonally flooded bottomlands and white-sand forests). Therefore, we can expect that a change in tree functional traits determining decomposition properties of the wood or leaves (e.g. leaf thickness, leaf carbon content, wood density, Yamashita et al., 2015) , and a change in the identity of tree species (determining e.g. the nature of fungi-tree symbioses) across habitats may in turn induce a turn-over in fungal community composition. In this context, we aimed at testing if and how tree diversity and soil properties shape fungal communities across environmental gradients, both at a local and regional scales.

Fungal communities are more and more studied through environmental sequencing, but in the Neotropics, the low number of reference sequences could also limit the assignation to species and to trophic guilds. More generally in the Neotropics, only a minority of fungi have been described up until now (Mueller & Schmit 2007) and data on their ecology and distribution

remain largely fragmentary (Osmundson *et al*. 2013). Indeed, in South America, the interest in mycology has only begun in the 19th century (Montagne 1855). In between, mycologists have gathered specimens throughout Amazonia (for example Singer & Aguiar 1986, Henkel *et al.* 2014, Matheny *et al.* 2003, Vasco-Palacios, Hernandez, Peñuela-Mora, Franco-Molano & Boekhout 2018, Trierveiler-Pereira & Baseia 2009, Sánchez-García *et al.* 2016). Nevertheless, the known distribution of neotropical fungi remains patchy and biased towards accessible sites (Roy *et al*. 2016, Sulzbacher *et al*. 2017) and little is known on their ecology or their habitat. In particular, few studies have examined the phenology of fungal fruiting-bodies and showed the key role of rainfall seasonal patterns and litter humidity particularly on leaf-decomposing fungi (Osono, 2017; Piepenbring et al., 2015) . From this perspective, French Guiana largely remains an uncharted territory, and existing collections of fungi have been confined to few coastal localities. Both taxonomists and ecologists have claimed that there is an urgent need to systematically collect and document fungal specimens from undersampled areas to fill the gaps of knowledge in a region where fungal diversity may be much higher than actually known (Truong *et al.* 2017, Barnes, Maldonado, Frøslev, Antonelli & Rønsted 2016, Roy *et al.* 2017). This sampling effort could last for years, but could be guided by community-level analysis, for example to detect favorable habitats (Roy *et al.* 2017) or sampling periods (Braga-Neto *et al.* 2008) that may not appear at a first glance.

Here, we aimed at disentangling the relative effects of tree community composition and abiotic factors on the structure of macrofungi communities collected in French Guiana. To achieve this objective, we comprehensively sampled 34 plots distributed in four remote sites in French Guiana. The dataset comprises inventories of macrofungal fruiting-bodies and tree species, as well as soil physico-chemical characteristics. The sampling encompassed the main forests habitats encountered in the region, mainly distinguished by their local topography and water drainage. We addressed the following questions: i) how diverse are macrofungal

communities; ii) to what extent does macrofungal community composition vary across contrasting forest habitats; iii) what are the relative effects of tree communities and soil properties on the richness and composition of macrofungal communities across habitats ?

METHODS

SAMPLING SITES

French Guiana is situated at the eastern limit of the Guiana Shield in South America. Soils are ancient, heavily eroded and chemically poor. The country's relief is fairly flat, rarely exceeding 200m (Guitet *et al*. 2013). The climate is characterized by a clear seasonal pattern: a wet season from December to July, interrupted in February or March by a short dry period, and a long dry season from August to November. Average annual precipitation reaches 2200 mm, with a mean annual temperature of 25°C (Gourlet-Fleury *et al.* 2004). Since 2013, the authors have collected sporocarps in 34 2-ha plots distributed in four sites across French Guiana (Figure S1, Supporting Information SI). Limonade (3°33'36"N,53°12'W), Itoupé (3°1'12"N, 53°6'W), and Mitaraka (2°13'12"N, 54°27'36"W) are part of the National Amazonian Park of French Guiana (PAG, www.pag.fr). Trinité (4°24'36"N, 53°24'47"W) is a natural reserve part of the Network of Natural Reserve of French Guiana (www.guyane-parcregional.fr). The 34 plots were assigned to one of three topographical habitats according to the classification of (Ferry *et al.* 2010): hilltop if the plot is situated on upper part of a hill with vertical water drainage; slope if the plot is situated along a slope and exhibited a superficial lateral drainage; seasonally flooded forest if the plot is situated downhill where the soil is regularly inundated during the rainy season and characterized by a water table that is always above 60 cm depth and reaches the surface soil for at least two consecutive months. The three habitats were found together in Limonade, Mitaraka and Trinité but not in Itoupé (Table 1), and plots were set up to be at least 500 m distant. At each site, trees and fungi were

sampled together at the beginning of the rainy season during the same field trips of fifteen days long.

TREE INVENTORIES AND TREE COMMUNITY DIVERSITY

We used a modification of the Gentry protocol used by Phillips *et al.* (2003). The protocol consists of ten parallel transects of 10 × 50 m disposed within a 2 ha area (Baraloto et al. 2011 and see Figure S2 and following details). Each tree was identified and recorded as morphospecies. At least one voucher specimen for each species was collected and stored whenever there was any uncertainty in the identification. A full duplicate set of collections is deposited in KOU collection associated to CAY herbarium (herbier-guyane.ird.fr). A team of 6 persons was dedicated to the sampling of trees. Because they were not very accessible, each site was visited once (Table 1) during a 15-days field trips, and the sampling of trees and fruiting-bodies was carried in parallel.

SPOROCARPS FIELD SAMPLING

We developed an easily and reproducible field experimental procedure to collect fruiting bodies. Inventories were carried out on the same 2-ha plots as for tree communities, and conducted as follows: two collectors collected all visible sporocarps on three sub-samples of 20 x 20 m randomly positioned in the 2-ha plot and for a period of 1.5 h maximum per plot. Hypogeous fungi were not targeted during these inventories. They were rarely observed and collectors focused on Basidiomycota. All visible sporocarps were photographied, numbered and dried within 24h for at least 48h. For each specimen, taxonomic identification was done by Mélanie Roy, Cony Decock and Gérald Grühn in the field based on existing literature (Pegler 1983) or later from vouchered specimens by Annemieke Verbeken, Felipe Wartchow, and Bart Buyck. Homogeneity and consistency of all taxonomic names were controlled. All dry voucher specimens were deposited at the following herbaria: LIP, University of Lille; PC,

Paris Natural History Museum; MUCL, Catholic University of Louvain. For most specimens, identification at the genus level was obtained. As species descriptions are still in process and to allow a more regional study, and comparisons across sites and habitats, we handled further statistical analyses based on genus-level identifications. We used these identifications to attribute trophic status to specimens, following FUNGUILD database (Nguyen *et al.* 2016).

ENVIRONMENTAL PARAMETERS

Bulked soil cores were collected at 0-30 cm depth in each plot, at each of the ten intersection points between parallel transects and the main central line (Figure S2). They were combined into a composite 500g sample. The latter was dried at 25°C, sieved to 2mm and shipped within 3 months for physical and chemical laboratory analyses at CIRAD (France). 16 soil physico-chemistry variables were then measured using standard soil analysis protocol (Pansu and Gautheyrou 2006). Physical properties were soils texture (clay, silt and sand content), and chemical properties were pH in water (pH), soil organic matter (OM), carbon (C), nitrogen (N), available phosphorus (P), the effective cation exchange capacity (CEC) and six bioavailable cations (Ca, Mg, K, Na, Al and Mn). Base Saturation was computed as the ratio between CEC and the base cations (Ca, Mg, K and Na).

STATISTICAL ANALYSIS

Analyses were conducted in R statistical environment (R.3.5.3, R Core Team, 2019), using packages vegan (Oksanen et al. 2017), entropart (Marcon & Hérault 2015), adespatial (Dray et al. 2018) and lme4 (Bates et al. 2015). As ecological guilds are often conserved at the genus level for fungi (Tedersoo & Smith, 2013), we based analyses of beta-diversity at the genus level.

Soil properties

The data for 16 soil variables for the three topographical habitats were normalized with a Box-Cox transformation and standardized (z-score transformation). Pairwise comparisons of each variable across the three topographies were tested with an analysis of variance. We determined the patterns of relationships between the 16 soil variables by performing a principal component analysis (PCA) on the correlation matrix between normalized (Box-Cox transformation) centred-reduced soil variables values. The clustering of plots by topographical habitats was checked by running an analysis of variance of the coordinates of the plot on the three first axis.

Diversity of tree and fungal communities

Proportions of classes, orders and families were computed on all sites for trees and fungi. The diversities of tree and fungi were described as proposed by Chao et al. (2014) and Jost (2006, 2007) at the plot level. This approach represents diversity in terms of effective numbers of taxa which are calculated with different weights (q) placed on abundant taxa (Marcon et al 2014, Jots 2007). The effective numbers of taxa is the number of equally abundant taxa that would be needed to give the same value of a diversity measure. When q= 0, all taxa are weighted equally and Richness is estimated; when q=1 all taxa are weighted by their relative abundance and Shannon diversity is estimated; and when q=2 more weight is placed on abundant taxa and Simpson diversity is estimated. We also estimated the alpha parameter of Fisher's logarithmic series per plot. Average values of each index (Richness, Shannon, Simpson and Fisher'Alpha) were compared across topographical habitats and sites with a Kruskal-Wallis rank test.

Effects of tree communities and soils on the richness of macrofungal communities

The response of macrofungal genus richness to soil environment and tree community diversity and composition was tested with a linear mixed model. First, the scores of the three

first axis of the PCA conducted on the 16 soil variables and which explained 81% of the variance, were used to describe soil properties in all subsequent analyses. Second, the richness of tree communities as estimated above was included. Tree species composition was quantified according to the plot scores along the first four axes extracted from a Principal Coordinate Analysis (PCoA) based on Bray-Curtis dissimilarity. We used Hellinger-transformed data to downweight the rare species (Legendre & Gallagher, 2001). We then built a linear mixed model with tree community richness and composition and soil parameters as fixed effects and site as random effect with the function lmer (lme4). The significant effect of each factor on macrofungal richness was evaluated with a Wald Chi-square test. The relative importance of variables in the final model was calculated as the R^2 contribution averaged over orderings among regressors (lmg, Grömping 2006). Lmg values were tested by comparing their observed values with 4999 null values obtained using Moran Spectral Randomizations (MSR, Wagner & Dray 2015), in order to take into account spatial autocorrelation in our data. MSR allow reproducing variables displaying spatial structures that are very similar to the original ones. The method first consists of generating Moran Eigenvector's Maps (MEM, Dray et al. 2006) to extract information on the connection properties from the set of MEM that best fit the data (see Dray et al. 2006 and Bauman et al. 2018). Using this information, the MSR method performs a conditional simulation procedure that preserves the original structure of the data (see Wagner & Dray 2015 for details). To calculate the MEM, the spatial connections among plots were modelled using a graph-based configuration (Gabriel's graph) which has been shown suitable for nested samplings (Bauman et al. 2018). Lmg values were considered significant when they were higher than 95% of the null values.

Effects of tree communities and soils on macrofungal community composition

First we determined the effects of soil chemistry on tree community composition by conducting a redundancy analysis (RDA, Legendre & Gallagher 2001) as follows. Tree

occurrence table was first Hellinger-transformed and included as response variable. The explanatory variables were the scores of the three first axis of PCA conducted on soil variables. An ANOVA-like permutation test for RDA was then performed to assess the significance of individual terms. Relationships between soil variables and tree community composition was visualized with a RDA biplot.

We then tested the effect of soil variables and tree community composition on the macrofungal community composition with a RDA as follows: macrofungal occurrence table was first Hellinger-transformed and included as response variable. Tree community composition (the sites scores of the four first axis of a PCoA) and soil variables (the scores of the three first axis of the PCA) corresponded to the explanatory variables. Then we applied a variance partitioning method (Peres-Neto *et al.* 2006, Peres-Neto & Legendre 2010) to quantify the pure and shared proportion of variation explained by trees, soils and spatial components . Explanatory variables included : i) tree species composition summarized by the scores of four first axis of a PCoA (PCoA1 to PCoA4) and ii) soil variables taken either all together or corresponding to the scores of the three first axes of the PCA conducted on the sixteen variables (PC1 to PC3). The adjusted R^2 values obtained for each fraction were systematically tested using the MSR method described above in order to take into account spatial autocorrelation in our data.

RESULTS

DIVERSITY OF BASIDIOMYCETES COMMUNITIES

We collected 2150 fruiting bodies of Basidiomycota, of which 3.58% were classified as unknown at the Genus level. Our sampling covered 17 orders, 63 families and 161 genera, mainly belonging to the class of Agaricomycetes, of which 26.5% only were identified at the species level. Specimens unidentified at the genus level (4%) were not taken into account for

diversity estimates. Within this class, 62% of the specimens were Agaricales, 24% Polyporales, 5% Hymenochaetales (Figure 1a). At the family level, there were some differences in proportions between sites, with more Marasmiaceae at Trinité (37%), more Polyporaceae at Itoupé, more Tricholomataceae at Limonade or more Ganodermataceae at Mitaraka (Figure S3). Genus accumulation curves showed that sampling effort was equivalent between sites except for Limonade which was more intensively sampled (Figure S4). However, the curves didn't reach an asymptote which indicated that the sampling effort didn't allow to fully capture the fungal diversity in each site. Alpha diversity estimates (Richness, Shannon Index, Simpson Index and Fisher'Alpha) showed no significant difference among topographical habitats (Figure S5 a-d). Among sites, there was only a significant difference of the average Simpson index between Trinité and the three other sites (Figure S6 a-d). *Marasmius*, the most abundant genus (14% of specimens) was found in all plots, with 304 fruiting-bodies collected. 37% of genera were observed only once like *Armillaria*, *Thelephora* or *Xerocomus*. Saprotrophs were predominant in the three habitats (Figure 2) while ectomycorrhizal fungi appeared to be more abundant in the slopes as compared to the two other habitats (28% in the slopes vs 8% and 5% in the seasonally flooded forest and hilltops respectively, Figure 2).

DIVERSITY OF TREE COMMUNITIES

9847 trees were inventoried in the four sites, and belonged to 1194 identified species and morphospecies. The most abundant families were the Arecaceae, Fabaceae, Burseraceae, Meliaceae and Myrtaceae (14, 11, 7, 6 and 5% respectively, Figures 1b and S3b) which represented 37% of the individuals. There were differences of floristic composition between topographical habitats, seasonally flooded forest plots hosting a large proportion of Arecaceae (45%), a family known to be particularly abundant in these habitats (Figure 1b). The Fabaceae were the second most abundant family and present equally in the three habitats (Figure 1b).

The Burseraceae were more abundant on slope and hilltop (11% and 6% respectively) than seasonally flooded forest (2%), as were the Meliaceae and the Myrtaceae (Figure 1b). Some particular plant families like Vochysiaceae and the Nyctaginaceae were only recorded on hilltop and slope, respectively (Figure 1b). Plant families known as potential host for ECM fungal species, which represented 21% of the trees sampled, were more abundant on slopes and hilltops (Table S3).

SOIL VARIATION AND SPATIAL STRUCTURES

Top soils showed significant differences between topographical habitats in terms of percentage of clay, pH-H_2O, available phosphorus, available calcium, magnesium and manganese content, and base saturation (Kruskall-Wallis test significant at $p \leq 0.05$, Figure 3 and S7). Apart for magnesium content, values in hilltops and slopes showed no significant differences. On the contrary, values in seasonally flooded forest appeared in most case significantly different from either hilltops or slopes (Figure 3 b and c, Figure S7). The PCA performed on soil variables produced three main axes which explained more than 81% of the edaphic variation (Figure 3a Figure S7 and Table S2). The first PCA axis (45.6%) was mostly explained by soil fertility, with CEC, available phosphorus, K, Ca, Mg, Na, total contents in N and C. The second PCA axis (21.5%) was explained by Al and clay contents. The third PCA axis (14.18%) was mainly defined by soil texture, with the percentage of sand and to some extent the percentage of clay (Figure S8). The projection of scores in two dimensions for the 34 plots (Figure 3a) displayed a significant clustering by topography with soils in seasonally flooded forest plots being much more variable than in the two other habitats (ANOVA, $p<0.05$).

PLANT COMMUNITIES AND SOILS EFFECTS ON MACROFUNGAL COMMUNITIES

We first tested the effects of tree community (diversity and composition) and soil variables on the richness of Basidiomycetes communities. We found a significant effect of tree composition (PCoA axis2, 34.3% of variation, Table2) and no significant effects of soil properties or tree richness.

Soil variables had a significant effect on tree community composition and RDA axes 1 and 2 explained 75.4 % of the variation in plant community (ANOVA-like permutations test, p=0.001,Figure 4a). An ANOVA-like permutation test on individual terms of the RDA showed that the structuring effect of soil on plant communities was mainly due to the axis 2 (Al, pH and clay) and 3 (sand, clay, Mn) of the PCA on soil variables.

Soil and tree community composition significantly structured macrofungal community composition and explained up to 64.2% of the variation as shown by the RDA analysis conducted (ANOVA-like permutations test, p=0.001, Figure 4b). In parallel, the variance partitioning (Table 3) analyze showed that tree community composition and soil significantly structured macrofungal community composition. Tree community composition was the first structuring factor (23 % of the variation explained, Table 3), while soil effect and spatial factors explained together 13.3% of the fungal composition variation (Table 3). The effect of soil was mainly due to the third axis of the PCA (Table 3), which was mainly explained by soil texture, especially the percentage of sand (Figure S8).

DISCUSSION

Our study aimed at testing how much tree diversity and composition, soil properties and topography affect fungal community assembly (in terms of taxonomic richness and composition) at a local and regional scale in the neotropical forests of French Guiana. By sampling fruiting-bodies, we were able to gather more than 2400 specimens of fruiting-bodies mainly represented by Basidiomycetes, in remote sites of French Guiana, which constitutes an

original collection of fungi for the region. 96% of our specimens were identified to the genus level, and several new species are already described (Henkel *et al.* 2014, Crous *et al.* 2018, Gruhn *et al.* 2017). The large proportion of specimens unidentified at the species level confirms the need to carry out further field sampling and joint-projects, as pointed by Truong *et al*. (2017). We compared Basidiomycetes communities across sites and detected more than 161 genera belonging to 63 families largely distributed across forest habitats (Figure 1). Based on fruiting-bodies, the most abundant families found in French Guiana are also among the most abundant ones found in Amazonian Brazilian forests (*http://splink.cria.org.br/*, keywords search = Basidiomycota AND Acre, Amapa, Amazonas, Para, Roraima, 12754 records). Around one quarter of these genera were also recorded in the Amazonian part of Columbia by Vasco-Palacios & Franco-Molano (2013). Interestingly, thirteen genera known to be ectomycorrhizal were found, representing only 3.13 % of the fungal specimens collected (Figure 2), and 21% of tree species were potential host (Figure 1), based on Steidinger *et al.* (2019) . All genera are distributed in other neotropical forests, such as the monodominant leguminous forests in Guyana (Henkel *et al*. 2012), but species might differ, as suggested by comparisons of Roy *et al*. (2016).

Instead of setting a long-term survey, recommended to detect rare species (Aime & Brearley 2012), we inventoried Basidiomycetes once on distant and remote sites across French Guiana. Even if accumulation curves demonstrated that we missed a part of diversity, such inventories represent a solid framework to investigate ecological processes shaping macrofungal communities. Sampling at different periods has probably contributed in differences of abundance, but not in presence of Basidiomycetes. Seasonal variations of fruiting bodies production in the tropics have been recorded in tropical regions with strongly contrasting dry and rainy seasons (Yorou *et al*. 2001, Munguia *et al*. 2005), suggesting that the phenology of fructification might follow the same path in French Guiana. Nevertheless, we always sampled

after or during a rainy period, which is determinant for fruiting-bodies production in the Amazon (Braga-Neto *et al.* 2008).

To better understand how tree diversity and soil properties may interact, we first investigated tree communities' variations. Indeed, tree communities were strongly impacted by soil chemistry (aluminium and pH on axis 2 of the PCA), and texture (sand and clay on axis 3 of the PCA, Figure 3). The strong effects of topography and geomorphology on the distribution of tree species in the Guiana Shield have been previously noted (Guitet et al. 2015). Across the Amazon, soil fertility and particularly phosphorus content affect tree community composition (ter Steege et al. 2006, Quesada et al. 2010). In the Guiana Shield region, trees appear less limited by direct nutrient uptake and rely more on nutrient resorption and storage of nutrient in the biomass to complete their nutritional requirements (Grau et al., 2017) .Tree communities were highly distinct between local habitats with seasonally flooded forests dominated by plants of the Arecaceae family, and some families more abundant on hilltops and slopes (Figure 1). At a local scale, tree species have already shown pervasive habitat preference for soil hydrological and physico-chemical properties (Allié et al. 2015). In the present study, the significant effect of aluminium, pH and soil texture is probably explained by the local topography. The leaching of well-drained hilltops towards seasonally flooded forests explained the decrease in clay content and increase of nutrients between them (Allié *et al.* 2015, Ferry, Morneau, Bontemps, Blanc & Freycon 2010), but also the release of phosphorus in seasonally flooded forests through the reduction of the iron and other metals like aluminium (Baldwin et al. 2000). The axis 2 of the PCA, which was explained mainly by aluminium and pH, was the only PCA axis significantly correlated with fungal community composition (Figure 4, Table 3). Soils were rather poor in aluminium as compared to the rest of Amazonia (Quesada et al. 2010) but had also low pH (soils in most plots were at pH < 4.5) favouring aluminium solubility and decreasing phosphorus solubility (Fujii 2014, Liptzin &

Silver 2015). These significant effects on both plant and fungal communities probably reflected the effect of contrasted hydromorphic conditions between the three habitats.

As expected, and in line with Waldrop *et al*. (2006) who showed a relationship between plant and fungi through resources availability, we found that plant communities were one of the main drivers of Basidiomycetes communities. More precisely, we detected that changes in tree community composition but not tree richness had an effect on Basidiomycetes communities. This was in disagreement with Dassen et al. (2017); Peay et al.(2013) and Schmit et al. (2005) in previous studies but consistent with the findings of other authors (Weißbecker et al. 2018, Vleminckx et al. 2019). For instance, Vleminckx *et al*. 2019 detected coordinated turnover of community composition between plant and fungi in French Guiana, at the same spatial scale encompassed by our sampling, beyond any effects of soil properties (Vleminckx *et al*., 2019) . This apparent discrepancy between effects of richness and composition may be partially explained because the relative effect of soil properties and tree diversity may differ among fungal guilds (Dassen et al., 2017; Schappe et al., 2017) . Therefore, ectomycorrhizal fungal community appear more strongly coupled to tree communities than saprotroph or endomycorrhizal community, with a strong effect of dispersal limitation (Weißbecker *et al.*, 2018) or resource availability (Gilbert *et al.* 2007, Waldrop *et al.* 2006). These effects may also partly reflect habitat preferences of fungi. In Colombian Amazon forests, López-Quintero *et al.* (2012) demonstrated an effect of forest habitats on fungal diversity, with disparities between flooded and hilltop forests. Our study confirms that Basidiomycetes do also follow this Amazonian gradient, partly correlated with changes in tree communities. Moreover, slopes hosted distinct Basidiomycetes communities, particularly rich in ectomycorrhizal taxa, expanding the distribution of these taxa in the Amazon (Roy *et al.* 2016, Vasco-Palacios *et al.* 2018) and revealing new favorable habitats. Interestingly, some plant families, such as Malvaceae, Myrtaceae and Nyctaginaceae, were more abundant on

hilltops and slopes and represent possible host families for these fungi (Tedersoo *et al.* 2009, Steidinger *et al.* 2019). Slopes are barely investigated in long term surveys for practical reasons but may be important niches for fungi poorly adapted to hydromorphic sites such as seasonally-flooded forests. More generally, this prominent effect of plant species was described as a bottom-up effect shaping multitrophic interactions networks (Scherber *et al.* 2010). But Schuldt *et al.* (2017) on the contrary suggested cascading effects of soil biota on above-ground organisms across trophic levels. Irrespective of the direction of links, plants and Basidiomycetes communities appear strongly coupled.

By comparing tree and Basidiomycetes community variations, we also detected distinct drivers for the composition of these two communities. As already shown by Allié *et al.* (2015) and Ferry *et al.* (2010), plant communities were more strongly influenced by topographical and chemical conditions of soils than macrofungal communities, which displayed a less distinct distribution among seasonally flooded, slope and hilltops forests (Figure 4). Saprobes and wood-decay macrofungi were particularly frequent and were found in all habitats, and known for their wide distribution and low host preference (Gilbert *et al.* 2002, Lodge & Cantrell 1995). Basidiomycetes communities may display very local variations due to the high heterogeneity of the quality and quantity of nutritional resources at a small scale that we didn't take into account considering the size of the plots (1ha). Macrofungi can be sensitive to decay stage of the litter (Gibertoni *et al.* 2016), which can be highly heterogeneous at a small scale and depend on leaf chemistry (Hättenschwiler *et al.* 2008). As soil microfungi communities in neotropical forests are hyperdiverse and exhibit a high percentage of uncharacterized fungi (Barnes, Maldonado, Frøslev, Antonelli & Rønsted 2016), we surely missed a great part of this diversity by focusing only on fruiting-bodies. Therefore, as a first approach, barcoding herbarium collections and high-throughput inventories of fresh fruiting-bodies are necessary to document fungal diversity (Halme *et al.* 2012, Barnes, Maldonado,

Frøslev, Antonelli & Rønsted 2016), particularly in neotropical forests where large territories remain unexplored (Truong *et al.* 2017, Blackwell & Vega 2018). By sampling macrofungi in remote areas of French Guiana, we also unraveled factors shaping Basidiomycetes distribution in this region. Notably, we showed that the distribution of both trees and macrofungi were shaped by the high local heterogeneity of habitats originating from contrasted topographical and soil hydromorphic conditions. Basidiomycetes communities were also affected by tree communities, probably through the high heterogeneity of the litter chemistry and selective effects of biotic interactions. However, the mechanisms behind the relationships between tree and fungal diversity and composition remain poorly understood. Further investigations are necessary to understand to what extent top-down and bottom-up feedbacks between plant and fungi account for the distribution of species across contrasted habitats in hyperdiverse forests.

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AUTHORS' CONTRIBUTIONS

CB coordinated the project. HS, CB and MR developed the tree and fungi sampling design. CB, HS, MR, JE, EL, SM, AS collected the specimens in the field. GJ gathered and checked data and metadata and built the database. HS and JV analysed the results. HS and JV wrote the first draft of the manuscript and all authors contributed to revisions.

DATA AVAILABILITY

Data are available as supporting information .

SUPPORTING INFORMATION

Figure S1: Map of French Guiana showing the localization of the sites. Isohyet lines of annual precipitation are indicated as information

Figure S2 : Configuration of the modified Gentry plot used to inventory trees and fungi. Blue solid lines represent the main 200m-long and perpendicular lines along which trees were sampled. Green squares represent the three 20X20m subplots settled to inventory fruiting-bodies. Trees and fungi were sampled in parallel by two teams of 6 and 2 people respectively.

Figure S3: Proportions of the main families of fungi (A) and trees (B) in the four sites. Itou=Itoupe, Lim=Limonade, Mit=Mitaraka, Tri Trinite

Figure S4: Genus accumulation curves by sites (left) and by topographical habitats (right)

Figure S5: fungi and tree alpha diversity per topography with a) Richness; b) Simpson index; c) Shannon index; d) Fisher's alpha for fungi; and e) Richness; f) Simpson index; g) Shannon index; h) Fisher's alpha for trees . P-values of ANOVA are given. P= Hilltop, SFF = Seasonally flooded forest, S = Slope.

Figure S6: fungi and tree alpha diversity per site with a) Richness; b) Simpson index; c) Shannon index; d) Fisher's alpha for fungi; and e) Richness; f) Simpson index; g) Shannon index; h) Fisher's alpha for trees . P-values of ANOVA are given. Itou = Itoupe, Lim=Limonade, Mit = Mitaraka, Tri = Trinite

Figure S7: Variation of soil properties among habitats. P = Hilltop, SFF=Seasonally flooded forest, S= slope. Values have been transformed with a Box-Cox transformation and standardized. Significant differences between habitats after an ANOVA are shown (ns : p > 0.05, *: p <= 0.05, **: p <= 0.01).

Figure S8: Contribution of soil variables to axes 1 to 3 of the PCA. Dashed line corresponds to the expected value if the contribution were uniform.

Tables S1: Databases for fungi, trees and soils

Table S2: Pearson Pairwise Correlation Matrix of the 16 soil variables

Table S3: Numbers of tree samples and belonging to families known as Ectomycorrhizal according to Steindinger et al (2019), spread by topographical habitats. They represent 21% of the trees sampling.

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TABLES

TABLE 1 : Characteristics of the main sites, with number of 2-ha plots per site, number of fruiting bodies and trees sampled, topography, latitude, longitude and annual rainfall. Topography types were defined according to Ferry et al. (2010) and soil types according to Baraloto et al. (2011) and Guitet et al. (2013).

Site	Topography	Numbers of 2ha-plots	Number of fruiting-bodies	Number of trees	Latitude	Longitude	Altitude (m)	Annual precipitation (mm)	Date of sampling
Itoupe	hilltop (4) slope (5)	9	521	2567	3°1'12"N	53°6'O	300-800	2000	Nov-14
Limonade	hilltop (3), slope (3), seasonally flooded forest (4)	10	796	3226	3°33'36"N	53°12'O	100-280	2250	Oct-13
Mitaraka	hilltop (3), slope (3), seasonally flooded forest (3)	9	654	2569	2°13'12"N	54°27'36"O	300-600	1750	Mar-05
Trinité	hilltop(4), seasonally flooded forest (2)	6	588	1485	4°24'36"N	53°24'47"O	100-460	2584	Apr-16

TABLE 2: Linear mixed model results with fixed effects corresponding to tree species richness and composition (PCoA 1 to 4), soil properties (PC 1 to 3) and spatial effects (significant inter-site MEM vectors), and the response variable corresponding to the genus richness of fungal communities. The three variables that correlated most strongly with each PC are listed in decreasing order of correlation. Estimates, standard errors (SE), *t* and *p*-values following an analysis of deviance (Type II Wald chi^2 test), lmg (relative contribution of variables) and *p*-values calculated with the MSR method are given. Significant lmg values ($p \leq 0.05$) are indicated in bold.

	Estimate	SE	t value	p value	lmg	MSR
Fixed effects						
Intercept	49.23	46.29	1.06			
Tree Richness	0.08	0.18	0.41	0.684	0.127	0.44
PCoA axis 1	86.41	116.07	0.74	0.456	0.069	0.526
PCoA axis 2	-247.43	111.85	-2.21	**0.026**	**0.343**	**0.058** *
PCoA axis 3	-5.97	79.17	-0.08	0.939	0.033	0.666
PCoA axis 4	22.36	84.40	0.27	0.791	0.181	0.287
PC 1 : CEC, P, K	0.69	3.71	0.19	0.851	0.111	0.553
PC 2 : Al, pH-H_2O, Clay	7.54	5.17	1.46	0.144	0.066	0.408
PC 3 : Sand , Clay, Mn	7.54	7.78	0.97	0.332	0.066	0.521

TABLE 3: Relative importance (quantified by the adjusted R^2) of tree community composition (PCoA 1 to 4) and soil properties (PC1 to 3) on the macrofungal community composition, as revealed by the partition of variance. Soil effect was tested using all soil variables together or the scores of the three first PCA axes taken separately. Significant R^2 values ($P \leq 0.05$ according to the MSR method) are indicated in bold. Unexplained variation (residuals) is also given.

Fractions		Soil total	PC1 CEC, P, K	PC2 Al, pH, Clay	PC3 Sand, Clay, Mn
Tree community composition	a+b		**0.230**		
Shared soil and spatial effects	b+c	**0.080**	0.000	0.012	**0.064**
Soil	b	**0.052**	0.003	0.024	**0.054**
Residuals	d	0.742	0.773	0.747	0.761

FIGURE CAPTIONS

FIGURE 1: Proportions of the main families of fungi (A) and Trees (B) in the three topographical habitats. P =Hilltop, SFF= Seasonally flooded forest, S= Slope

FIGURE 2: Proportions of the main functional guilds of fungi observed in Seasonally flooded forest (a), Hilltop (b) and Slope (c). Based on assignation at the genus level with Funguild (Nguyen *et al.* 2016).

FIGURE 3: Differences in physico-chemical characteristics of soils according to the topographical habitat with P = Hilltop, SFF = Seasonally flooded forest and S = Slope. A) Biplot on the two first axis from the PCA performed on the 16 soil variables. The clustering of plots by habitats was significant (ANOVA, $p<0.05$). Red, green and blue points correspond to plots situated on hilltop, seasonally flooded forest and slope, respectively. Axes 1 and 2 represent, respectively, 45.6 and 21.5% of the overall soil inertia. Variations across topographical habitats in Phosphorus (B), pH (C) and Clay (D). Significance of the pairwise comparisons between the three habitats resulting from a Kruskal-Wallis test is shown (ns : $p > 0.05$, *: $p <= 0.05$, **: $p <= 0.01$). Values have been transformed with a Box-Cox transformation and standardized.

FIGURE 4: Constrained redundancy analysis of plot-based tree community composition (A) and macrofungal community composition (B). Dispersions (ellipses, 0.95 SD around sites centroids) are shown. Arrows represent correlations of variables with community structure along the first two RDA axes: tree community composition (PCoA1 to 4) and soil properties (PC1 : CEC, P, K ; PC2 : Al, Clay and pH ; PC3 : Sand, Clay, Mn). Red dots and ellipse represent Hilltops, blue ones represent Slopes, green ones represent Seasonally flooded forest . PC2 and PC3 significantly clustered tree community composition (ANOVA-like

permutation at $p<0.05$,A) and PCoA1 to 4 significantly clustered fungal community composition (ANOVA-like permutations test at $p<0.05$, B).