Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

Root-associated fungal diversity in Central Africa's most logged timber species (Aucoumea klaineana Pierre) suggests monodominance is independent of mycorrhizal associations

Quentin Guidosse

qguidosse@uliege.be

TERRA Teaching and Research Centre, University of Liège

Mélanie Roy

University Paul-Sabatier Toulouse III

Sébastien Massart

TERRA Teaching and Research Centre, University of Liège

Jean-Louis Doucet

TERRA Teaching and Research Centre, University of Liège

Ludivine Lassois

TERRA Teaching and Research Centre, University of Liège

Caroline De Clerck

TERRA Teaching and Research Centre, University of Liège

Research Article

Keywords: Monodominance, Root-associated fungi, Okoumé, Soil microbiota, Tropical forest ecology, Mycorrhiza, Timber

Posted Date: April 11th, 2025

DOI: https://doi.org/10.21203/rs.3.rs-6261557/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Mycorrhiza on November 13th, 2025. See the published version at https://doi.org/10.1007/s00572-025-01239-y.

Abstract

Aucoumea klaineana is the most important timber species in Central Africa, forming monodominant stands. While soil fungi are crucial for plant growth, their role in promoting monodominance and supporting suppressed, light-demanding trees remains underexplored. This study, the first to analyze the root mycobiota of *A. klaineana*, investigates fungal communities in monodominant stands and old-growth mixed forests in Gabon, and plantations in the DRC using ITS2 rDNA and SSU rRNA high-throughput sequencing. We identified high fungal diversity in both regions but found no "core mycobiota" across stand types or tree social status. Fungal communities varied significantly between stand types, emphasizing a context-dependent nature. Monodominance was not linked to ectomycorrhizal fungi (EcM), as no EcM OTUs were found in monodominant stands. While arbuscular mycorrhizal (AM) fungi exhibited high richness, their abundance was low, possibly due to the scarcity of arbuscules. No distinct fungal communities were found in suppressed trees. These findings challenge the assumed link between EcM associations and monodominance in *A. klaineana*, suggesting alternative mechanisms, such as root grafting, may influence stand dynamics. This study provides a foundation for future research on the belowground strategies that contribute to the persistence and sustainable management of *A. klaineana*.

Introduction

African tropical forests are highly diverse ecosystems, harboring between 4,600 and 6,000 tree species (Slik et al., 2018). In Central Africa, one hectare of forest can host between 50 and 150 tree species (diameter at breast height > 10 cm) (Day et al., 2014; Gourlet-Fleury et al., 2013). However, locally, a single tree species, such as *Gilbertiodendron dewevrei* (De Wild.) J.Léonard or *Julbernardia seretii* (De Wild.) Troupin (Peh et al., 2011) can cover more than 60% of the canopy, forming so-called monodominant stands (Connell and Lowman, 1989; Hart et al., 1989; Peh et al., 2014; Torti et al., 2001). While the processes by which a single tree species becomes monodominant have been extensively studied, a complete understanding remains elusive. Connell and Lowman (1989) suggested that species monodominance could arise through rapid recruitment in frequently disturbed environments, or competitive exclusion in stable ones. Building on this, Peh et al. (2011) compared eight hypotheses to explain this phenomenon.

Although no single factor can solely explain persistent monodominance, they emphasized the importance of ectomycorrhizal (EcM) associations and slow decomposition rates, both linked to soil microbiota, as key processes that may generate positive feedbacks contributing to species dominance. For instance, in the well-studied *G. dewevrei* forests, monodominance is associated with positive feedback between EcM associations and slow leaf litter decomposition, as well as other life-history traits such as shade tolerance and large seed production (Peh et al., 2011a; 2011b; Torti et al., 2001).

As monodominant stands age, stratification among conspecifics occurs. Surprisingly, some tree individuals survive despite limited light availability, even in stands dominated by light-demanding pioneer

species (Connell and Lowman, 1989), then referred as suppressed trees. While this phenomenon has received limited attention, increasing evidence suggests that plant responses to abiotic factors are mediated by soil microorganisms (Friesen et al., 2011; Xi et al., 2019). Although few studies have examined soil feedback under varying light conditions (Mccarthy-Neumann and Kober, 2010), Xi et al. (2019) demonstrated that, at least at the seedling stage, soil microorganisms can influence plant light responses through traits related to carbon gain and nutrient availability. Soil microorganisms might also help understory trees survive in low light via common mycorrhizal networks (Balandier et al., 2022; McGuire, 2007; Sen, 2000; Simard et al., 1997), allowing them to benefit from resources acquired by neighboring canopy-reaching trees. However, how these belowground processes mediate interactions between understory and overstory trees remains unclear (Deng et al., 2023).

Okoumé (*Aucoumea klaineana* Pierre, Burseraceae, Sapindale), is the most harvested timber species in Central Africa (FRMi, 2018). This tree species is light-demanding, thriving in areas receiving 10–60% of relative irradiance (Guidosse et al., 2024a). Established individuals form dense, monospecific stands, eventually becoming monodominant (e.g., Delègue et al., 2001; Fuhr, 1999; Pangou et al., 2003; White et al., 2000), similar to the process described for *G. dewevrei* by Leroy Deval (1974). However, the mechanisms driving this monodominance have never been elucidated for this major commercial species. While Burseraceae species typically do not form ectomycorrhizal associations (Bâ et al., 2011), some researchers have hypothesized that *A. klaineana* might be an exception (Leroy Deval, 1974; Peh et al., 2011). However, studies on its root-associated fungi are lacking, likely due to methodological barriers (Guidosse et al., 2024b). The only existing records include a single *Endogone* sp. observation (Leroy Deval, 1976) and a brief mention of arbuscular mycorrhizal (AM) fungi based on root staining (Onguene et al., 2002). Considering the coarse and shallow morphology of the tree rootlets (Guidosse et al., 2022), similar to structures formed by EcM fungi (Smith and Read, 2008), this assumption requires further investigation.

In logging concessions, the natural regeneration of *A. klaineana* is constrained by the sedentarization of human populations, leading to a decrease in open fallow lands (Biraud and Catinot, 1960; Morin-Rivat et al., 2017). Additionally, sustainable logging practices create gaps that are too small and sparse (Blaser et al., 2021; Ezzine De Blas and Ruiz Pérez, 2008; Nasi et al., 2012; Van Gemerden et al., 2003) for new populations to establish. This lack of disturbance causes the natural ageing of the forest and the closure of its canopy with the consequence that long-lived, light-demanding commercial species are progressively replaced by poorly harvested, shade-tolerant species (Morin-Rivat et al., 2017; Van Gemerden et al., 2003). In Gabon, forest managers addressed this challenge early on with extensive plantation campaigns (Brunck et al., 1990; Guidosse et al., 2022). However, in some cases, the results have been inconclusive probably due to a lack of understanding of the species' ecology, a challenge common to many tropical timber species (Dos Santos and Ferreira, 2020).

Unraveling the root-associated fungi of *A. klaineana* could contribute to improving the species' management and performance, especially in plantations. Root-associated fungi, which are key components of the soil microbiota, may explain the poor performance of *A. klaineana* in some artificial

stands (Van Der Heijden and Horton, 2009). Based on findings from other timber trees (Sawada et al., 2021), natural mixed forests may host a higher taxonomic and functional diversity of soil and root associated microbes as compared to monospecific stands of *A. klaineana* in plantations. Additionally, suppressed trees may also host distinct microbial communities, associated with their lower photosynthetic activity in low-light conditions (Alsanius et al., 2019; Balandier et al., 2022; Konvalinková and Jansa, 2016), compared to local canopy-reaching individuals. Understanding the variations in these fungal communities is thus essential for sustainable forest management in *A. klaineana*-dominated forests, including the understanding of the role and functions of root mycobiota.

Among fungal trophic guilds, AM fungi are ideal candidates for such investigations. They are essential for tropical forest resilience and play a pivotal role in these ecosystems (Martinez-Garcia et al., 2017; Sousa et al., 2022). They form symbiotic associations that support plant-soil feedbacks and nutrient exchange (Van Der Heijden et al., 2015) with approximatively 70% of terrestrial plant species (Brundrett and Tedersoo, 2018) including a wide range of tree species, particularly in Central Africa (Bâ et al., 2012). AM fungal communities are shaped primarily by niche-based processes, such as environmental filtering driven by soil pH, precipitation, and temperature, though they can also be influenced by neutral (stochastic) processes like spore dispersal limitation (Dumbrell et al., 2010; Horn et al., 2014; Roy et al., 2017). Their specialization makes them valuable bioindicators of soil properties and forest health (De Assis et al., 2016; Weber et al., 2021), with their adaptability underscoring their ecological significance and relevance in forest management.

The advent of high-throughput sequencing (HTS) technologies in ecology over the past few years (Hu et al., 2021) offers an excellent opportunity to explore the fungal assemblages (Miyauchi et al., 2020) associated with *A. klaineana* roots using molecular methods.

The objectives of this study are to: (1) identify any specific fungal taxa or functional groups that are more closely associated with dominant tree individuals, potentially contributing to the maintenance of high-density populations of *A. klaineana*, or supporting the survival of suppressed trees in natural and artificial forest stands ; (2) evaluate whether these communities are shaped by neutral or niche-based processes, and assess the effects of stand type and tree social status ; (3) explore the variability of fungal communities associated with *A. klaineana* roots through its distribution across different contexts: in plantations, monodominant natural forests, and old-growth mixed forests, while considering tree social status (canopy-reaching versus suppressed trees).

Materials and Methods

Two sampling campaigns were carried out in two different regions (Fig. 1), both on ferralsols (Jones et al., 2013) and within the so-called “SW Gabon” climatic region (Philippon et al., 2019, 2018). The first one took place in February 2021 (rainy season), in two plantations (Minkuku, Ntozi) within the Luki Biosphere Reserve, Mayombe, west of the Democratic Republic of Congo (DRC) (5°36’53”S–13°05’55”E). The Minkuku plantation was established on savanna along a roadside, with trees planted at regular 3 × 2.5 m

spacing. It is reportedly still managed despite substantial undergrowth clearing during sampling. In contrast, the unmanaged Ntozi plantation, located at the bottom of a valley near the Ntozi River, features irregularly spaced trees, including some codominant *Terminalia superba* Engl. & Diels. The second collection period extended from July to August 2021 (dry season). Sampling sites were located in the FSC-certified logging company *Precious Woods - Concession Equatoriale des Bois* (PW-CEB) in Bambidie, Ogooué-Lolo, Gabon (0°41’65”S–12°59’01”E). Samples were collected in young monodominant *A. klaineana* forests, with plots ranging from 0.25 to 1 ha, where *A. klaineana* dominates the canopy but the understory hosts more shade-tolerant species. Old-growth mixed forests were sampled over larger areas (6.25 ha per plot) to obtain sufficient samples, as *A. klaineana* has largely been replaced by other species and is now mostly found as isolated individuals.

3.1 Sampling protocols

For each randomly chosen tree, from the trunk and by following three different directions, roots were tracked and excavated to the finest rootlets (< 2 mm diameter). Rootlets were collected, washed and pooled into a ca. 20 g sample. During the first collection campaign (the DRC), rootlets were put in a porous paper bag then in a sealable bag filled with silica beads for desiccation. Due to significant issues with DNA extraction, including poor DNA recovery, low quality, and PCR inhibition supposedly caused by dry root materials in this initial batch (Guidosse et al., 2024b) the storage protocol differed during the second sampling campaign. During the second campaign in Gabon, rootlets were directly poured in 2 mL tubes containing 1 mL of 2% Cetyltrimethylammonium bromide (CTAB) for future DNA extraction. In total, 113 samples were collected: 68 in natural stands from Gabon and 45 from the DRC plantations.

3.2 PCR protocols

Rootlets (including rhizoplane) from the DRC, kept dry by silica beads, were shredded using liquid nitrogen, mortar and pestle. Those from Gabon were grounded in a FastPrep-24^{TM} bead beater (MP Biomedicals, France) by 4 cycles of 30 seconds at 4.5 M.S^{-1} after adding 3 ceramic beads (Ø 2 mm) and 10 mg of Carborundum coarse powder (Prolabo, France).

DNA extraction and amplification followed our adapted protocol (Guidosse et al., 2024b). The ITS2 rDNA region was targeted and amplified by the fungal-specific ITS86F and ITS4 primer pair (Vancov and Keen, 2009; Waud et al., 2014). From each sample the nuclear SSU rRNA gene was also amplified by the glomeromycotinan specific primer pair NS31 and AML2 (Morgan et al., 2017), providing a better precision for this functionally important group. Adaptations were made to these primer pairs for compatibility with Illumina MiSeq sequencing by adding nucleotides at the 5' end, enabling dual-indexed paired-end sequencing (Kozich et al., 2013). For each PCR reaction, 1 µl of DNA template, 0.5 µl of 10 µM forward primer, 0.5 µl of 10 µM reverse primer, 2 µl of 2% (w/v) bovine serum albumin (Sigma-Aldrich, Darmstadt, Germany), 12.5 µl of Q5 High-Fidelity 2× Master Mix (NEB, Ipswich, MA, USA), and PCR-grade

water were added to reach a final volume of 25 µl. The PCR thermal cycle used with ITS86F-ITS4 primer pair corresponded to: denaturation step 5’ at 95°C, 35 cycles of 30” at 95°C, 30” at 55°C, 20” at 72°C and a final extension phase of 10’ at 72°C. The PCR thermal cycle used with the NS31-AML2 primer pair corresponded to: denaturation step 15’ at 94°C, 35 cycles of 55” at 94°C, 40” at 58°C, 30” at 72°C and a final extension of phase of 5’ at 72°C.

Amplicons were handed over to the GIGA-Genomics platform at the University of Liège (Belgium) for outsourced sequencing according to the Illumina 16S metagenomic workflow protocol. The workflow included the following steps: purification of PCR products from the first amplification using AMPure XP beads (Beckman Coulter, USA), addition of Illumina adapter overhangs and dual-index barcodes through a second limited-cycle PCR, and a second purification step using AMPure XP beads. During the second PCR step, Illumina adapter overhang sequences were appended to the locus-specific primers. The forward overhang sequence was 5' TCGTCGGCAGCGTCAGATGTGTATAAGAGACAG-[locus-specific sequence], while the reverse overhang sequence was 5' GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG-[locus-specific sequence]. The dual-index barcodes enabled multiplexing libraries by appending unique 8-base sequences to each sample for demultiplexing during downstream bioinformatics analyses.

The concentration of the final library was normalized to 7 ng·µL⁻¹ using the Quant-iT™ PicoGreen™ dsDNA Assay Kit (ThermoFisher, USA), and quality control was performed on the QIAxcel Advanced System (Qiagen, Germany). Before proceeding to high-throughput sequencing, the concentration of the final pool was quantified by qPCR using KAPA SYBR® FAST qPCR Kits (Sopachem, Netherlands) and Illumina Library Quantification DNA Standards (Roche, Switzerland). Sequencing was carried out on an Illumina MiSeq system (version 3) with a v3 reagent kit (2 × 300 cycles), using a final denatured library pool concentration of 8.5 pM.

3.3 Quality control, clustering and taxonomic assignation

Initial control of raw sequencing data was performed using FastQC to assess reads quality. Using DADA2 (Callahan et al., 2016) from the QIIME2 pipeline (Bolyen et al., 2019), demultiplexed reads of sequencing were merged for the ITS2 rDNA region and chimeric sequences were identified and removed. Regarding the SSU rRNA gene, sequences quality did not allow for a paired-end approach after sequencing. Downstream analyses were then performed using only the forward reads (ca. 240 bp). Samples presenting < 40 % of non-chimeric sequences, or sequences < 300 reads were removed. The resulting high-quality reads were clustered into Operational Taxonomic Units (OTUs) at a 97 % similarity threshold. Taxonomic assignment of the OTUs was performed against the UNITE database (Abarenkov et al., 2024) for fungal ITS2 sequences and against the MaarjAM database (Öpik et al., 2010) for SSU glomeromycotinan sequences. OTUs obtained from the ITS2 rDNA region were assigned to functional guilds using the FUNGuild database (Nguyen et al., 2016) when classifications were deemed "Probable" to "Highly Probable”. FUNGuild was preferred over FungalTraits (Põlme et al., 2020) due to its cautious

assignment of pathogens, reflecting the context-dependent nature of fungi. Samples were classified by trophic guild, separating saprotrophs and pathotrophs, while symbiotrophs were divided into ectomycorrhizal (EcM) fungi, arbuscular mycorrhizal (AM) fungi, and others through the ITS2 rDNA region. Every relevant sequences were deposited in GenBank Bioproject accession No. PRJNA1214243.

3.4 Diversity analyses

Downstream analyses were performed in R (R Core Team, 2021). The initial data in QIIME2 format (.qza, .tsv) were converted to R-compatible objects using the 'qiime2R' package (Bisanz, 2018) and subsequently formatted into phylogenetic sequence data using the 'phyloseq' package (McMurdie and Holmes, 2013) for data manipulation and visualization.

Rarefaction curves were generated using the 'vegan' R package (Oksanen and et al., 2024), which determined optimal sampling depths of 10,000 sequences for ITS2 rDNA and 3,000 sequences for SSU rRNA. Due to the clear differences in sample processing between the two sampling campaigns (e.g., storage and grounding methods, country, stand types, seasonality, and soil), data analyses were conducted separately : for the natural stands in Gabon, and the plantations in the DRC. Extremely rare fungal OTUs, representing < 0.001 % of the total sequences, were removed. Subsequently, the impact of stand type on the mycobiota was examined by comparing two plantations in the DRC and young monodominant stands with old-growth mixed forests in Gabon. Additionally, the interaction between fungal communities and the social status of the trees was explored by comparing canopy-reaching trees (dominant, codominant) with those surviving in the shade (suppressed) for all sites.

Diversity analyses were performed using the 'MicrobiotaProcess' R package (Xu et al., 2023). Alpha diversity was assessed using the OTU richness, the Shannon index, and the Pielou evenness index. Kruskal-Wallis non-parametric tests were applied to check for significant differences for these indexes. Fungal community comparisons (beta diversity) were conducted by constructing Bray-Curtis dissimilarity and Jaccard distance matrices from abundance tables. Principal Coordinates Analysis (PCoA) was used to visualize the Bray-Curtis dissimilarity matrices. To test for significant differences among fungal communities, permutational multivariate analysis of variance (PERMANOVA) was performed with 9,999 permutations using the 'vegan' R package (Oksanen and et al., 2024), applying Bray-Curtis and Jaccard matrices. To assess the nestedness of fungal communities, the weighted nestedness metric based on overlap and decreasing fill (WNODF) (Almeida-Neto and Ulrich, 2011) was calculated, ranging from 1 (no nestedness) to 100 (maximum nestedness).

To provide insights into any stable and functionally important fungal taxa associated with the studied trees and stands, the core mycobiota was investigated by identifying OTUs that were consistently present in 10–100 % of the samples, both in general and for each factor separately, specifically stand types and tree social status. Finally, an indicator species analyses (Dufrêne and Legendre, 1997) was performed on size-equalized groups using the 'indicspecies' R package (De Cáceres et al., 2010; De Cáceres and Legendre, 2009). Indicator taxa were identified as described by Bakker (2008).

$$A_{ij} = {\bar{x}_{ij}}/{\sum_j x_{i\cdot}}$$

$$B_{ij} = {n_{ij}}/{n_{\cdot j}}$$

$$Indval_{ij} = \sqrt{A_{ij} \times B_{ij}}$$

with A defined as specificity or relative abundance, and B defined as fidelity or relative frequency. The indicator value (Indval) ranges from 0 to 1. Indicator taxa were identified using Monte Carlo randomization tests based on 9,999 permutations. Following this, indicative taxa across studied factors and guilds were visualized on heatmaps using the 'pheatmap' R package (Kolde, 2018).

Results

4.1 Fungal composition (ITS2 rDNA region)

A total of 3,549,465 high quality reads assigned to 4,119 fungal OTUs were obtained from sequencing the ITS2 rDNA region across samples from Gabon. After removing the rarest (< 0.001% of reads), 1,694 fungal OTUs were retained (41%, 3,522,826 sequences). Among the seven identified phyla, the five most represented were Ascomycota (60.8% sequences, 961 OTUs), Basidiomycota (37.6% sequences, 547 OTUs), Glomeromycota (1.3% sequences, 166 OTUs), Mucoromycota (0.1% sequences, 28 OTUs) and Mortierellomycota (0.03% sequences, 9 OTUs). The rest of the phyla (Chytridiomycota, Entomophtoramycota) were represented by less than 120 sequences and one OTU each, or were unidentified (0.2% sequences, 15 OTUs). Functional guilds were assigned to 861.801 sequences (24.5%) represented by 719 (42.4%) fungal OTUs (Fig. 2), unsure trophic mode (Mixed, 55.6% sequences, 258 OTUs) and saprotrophic fungi were dominant (28.9% sequences, 222 OTUs). Symbiotrophic OTUs accounted for only a tenth of representative reads (10.1% sequences, 203 OTUs) and a low pathogenic charge was observed (5.7% sequences, 36 OTUs).

Among the symbiotrophic fungal OTUs, half of the sequences (49.4%, 165 OTUs) was represented by AM fungi and a small part by lichenized OTUs (11 OTUs, 0.007% symbiotic sequences) and epiphytic OTUs (4 OTUs, 0.003% symbiotic sequences).

Another large proportion of symbiotrophic sequences (46.1%) was assigned to EcM fungi. They comprised 23 OTUs distributed across four taxa: *Russula* spp. (Russulaceae, 61.1% of EcM sequences), *Lactifluus* spp. (Russulaceae, 31.8% of EcM sequences), *Lactarius* spp. (Russulaceae, 0.06% of EcM sequences), and *Laccaria* spp. (Hydnangiaceae, 0.009% of EcM sequences).

In the DRC, 2,016,514 reads from 45 samples, passed the quality filtering and were assigned to 4,502 fungal OTUs. After removing the rarest (< 0.001% of reads), 2,003 fungal OTUs were retained (44%,

1,997,950 sequences). Among the seven identified phyla, the five most represented were Ascomycota (63.4% sequences, 1,129 OTUs), Basidiomycota (32.9% sequences, 604 OTUs), Mucoromycota (2.6%, 44 OTUs), Glomeromycota (1.0% sequences, 189 OTUs), and Mortierellomycota (0.04% sequences, 9 OTUs). The rest of the phyla (Rozellomycota, Chytridiomycota) were represented by less than 488 and 65 sequences respectively and two OTU each, or were unidentified (0.12% sequences, 24 OTUs). Functional guilds were assigned to 945,709 sequences (47.3%) represented by 1,015 (50.7%) fungal OTUs (Fig. 2). Saprotrophic fungi (48.4% sequences, 440 OTUs) and mixed trophic modes (43.67% sequences, 348 OTUs) were dominant. Symbiotrophic OTUs had only a few representative reads (3.4% sequences, 196 OTUs) and a low pathogenic charge was observed (4.5% sequences, 31 OTUs).

Among the symbiotrophic fungal OTUs, 59.6% of the sequences and 96.4% the OTUs were represented by AM fungi. Another large proportion (40.1% of the sequences) was represented by epiphytic fungi, but clustered into 6 OTUs only. The 115 other sequences were assigned to lichenized OTUs. No EcM OTUs have been found in the DRC.

Regarding the SSU rRNA gene for samples from Gabon (Fig. 3), 1,187,360 reads from 49 samples passed the quality filtering and were assigned to 625 glomeromycotinan OTUs. After removing the rarest (< 0.001% of reads), 526 fungal OTUs remain (84%, 1,186,767 sequences). Three classes have been identified: Glomeromycetes (95.7% sequences, 440 OTUs), Paraglomeromycetes (3.9% sequences, 74 OTUs) and Archaeosporomycetes (0.4% sequences, 9 OTUs), the rest was unidentified (0.03% sequences, 3 OTUs). At the genus level, a large majority were represented by *Glomus* spp. (93.4% sequences, 362 OTUs). The rest was shared by *Paraglomus* spp. (3.9% sequences, 74 OTUs), *Acaulospora* spp. (1.3% sequences, 61 OTUs), *Scutellospora* spp. (0.9% sequences, 16 OTUs) and *Archaeospora* spp. (0.4% sequences, 5 OTUs). 0.04% of the sequences (8 OTUs) were unassigned.

In the DRC, 1,331,094 reads from 39 samples passed the quality filtering and were assigned to 1,037 glomeromycotinan OTUs (Fig. 3). After removing the rarest (< 0.001% of reads), 951 fungal OTUs remained (91.7%, 1,330,094 sequences). Three classes have been identified : Glomeromycetes (98.7% sequences, 850 OTUs), Paraglomeromycetes (1.0% sequences, 85 OTUs) and Archaeosporomycetes (0.2% sequences, 8 OTUs), the rest was unidentified (0.1% sequences, 8 OTUs). At the genus level, the majority were represented by *Glomus* spp. (73.6% sequences, 523 OTUs). Almost a quarter of the sequence was also represented by *Acaulospora* spp. (23.7% sequences, 286 OTUs). The rest was shared by *Scutellospora* spp. (1.4% sequences, 39 OTUs), *Paraglomus* spp. (1.0% sequences, 85 OTUs), *Archaeospora* spp. (0.07% sequences, 5 OTUs) and *Diversispora* spp. (0.01% sequences, 2 OTUs). 0.24% of the sequences (11 OTUs) were unassigned.

4.2 Diversity analyses

To assess within-sample fungal diversity, we calculated OTU richness, Shannon diversity index, and Pielou's evenness for all fungi as per trophic guild. For EcM-associated OTUs, only their richness was calculated, but could not be compared across all samples, as their presence was largely restricted (with the exception of one OTU) to canopy-reaching trees in old-growth mixed forests in Gabon (Fig. 4). Alpha

diversity metrics for other trophic guilds and for all fungi showed no consistent variation across stand types and tree social status, regardless of the country (**Supplementary Materials 1**).

In natural stands (Gabon), canopy-reaching trees exhibited higher specific diversity of saprotrophic OTUs (Shannon index: mean = 1.33, SD = 0.09; Kruskal-Wallis test, p = 0.043) compared to suppressed trees. However, this slight variation was not observed in plantation samples from the DRC. In these artificial stands, Pielou evenness (mean = 0.94, SD = 0.007; Kruskal-Wallis test, p = 0.043) was higher at the Minkuku site compared to Ntozi, indicating a more balanced saprotrophic community at Minkuku.

4.3 Community composition

The PERMANOVA analysis on Bray-Curtis dissimilarity and Jaccard distance matrices revealed a strong and significant differentiation in fungal community composition between monodominant stands and old-growth mixed forests in Gabon, regardless of trophic guild (all p-values < 0.001).

A similar differentiation was observed between plantations in the DRC, with significant differences for saprotrophs (Bray-Curtis p-value = 0.043), pathotrophs (Bray-Curtis p-value = 0.005), symbiotrophs (ITS2, Bray-Curtis p-value = 0.021), and AM fungi (SSU, Bray-Curtis p-value = 0.002). However, no significant difference was found when considering all fungal OTUs (Bray-Curtis p-value = 0.426) (**Supplementary Material 2**).

In natural stands, tree social status significantly influenced saprotrophic (Bray-Curtis p-value = 0.003) and AM fungal communities (SSU, Bray-Curtis p-value = 0.004), as well as symbiotrophs (ITS2, Bray-Curtis p-value = 0.008). In contrast, no significant differences were found for pathogenic fungi in natural stands (Bray-Curtis p-value = 0.192) or across social status in DRC plantations for any fungal trophic guild.

These differences were visualized in a PCoA plot for trophic guilds of interest (Fig. 5) and for every obtained fungal OTUs (**Supplementary Material 2–3**) where samples from different stand type and tree social status formed separate clusters. Symbiotrophic OTUs obtained from the ITS2 rDNA region are presented only in **Supplementary Materials 3**, as EcM fungi were found solely in canopy-reaching trees from old-growth mixed forests, and the resolution for AM fungi was better with the SSU rRNA region. Interestingly, the stand type showed a higher impact than tree social status on every fungal assemblage.

4.4 Community Structure

To assess the nestedness of fungal communities, the weighted nestedness metric based on overlap and decreasing fill (WNODF) was calculated (Table 1). Overall, fungal communities exhibited a low nestedness, showing a high turnover, with a WNODF score ranging between 1.3 and 10.8 (mean = 4.0, SD = 3.0), no matter the trophic guild. This pattern suggested for instance that the fungal communities in monodominant stands are not subsets of more diverse community associated with, old-growth mixed forests and even at the individual level this turnover occurred locally between trees.

Table 1
Weighted Nestedness (WNODF, scaled 1-100) calculated for fungal communities in Gabon and the DRC, for all fungi and per trophic guild, with values presented overall, per sample, per OTU, and matrix fill (density of non-zero values in abundance matrix).

WNODF [1-100]		Overall	Per sample	Per OTU	Fill
Gabon	All (ITS2)	1.35	1.32	2.87	0.03
	Saprotrophs (ITS2)	2.11	2.01	0.28	0.04
	Pathotrophs (ITS2)	4.53	4.34	4.70	0.09
	Symbiotrophs (ITS2)	2.82	2.77	3.35	0.05
	EcM fungi (ITS2)	4.69	4.91	3.91	0.14
	AM fungi (SSU)	2.27	2.31	1.98	0.06
the DRC	All (ITS2)	1.31	1.30	1.58	0.04
	Saprotrophs (ITS2)	2.14	2.03	3.00	0.05
	Pathotrophs (ITS2)	10.82	11.26	10.69	0.15
	Symbiotrophs (ITS2)	2.61	2.59	2.80	0.05
	AM fungi (SSU)	1.69	0.17	1.43	0.06

4.5 Core versus specific indicator mycobiota

4.5.1 Core mycobiota

A very low proportion of shared OTUs was observed between samples, irrespective of the country, stand type, or tree social status, which hindered any identification of core mycobiota (Fig. 6). The only exception is for the suppressed trees in Gabon, where, when studying the SSU rRNA gene (Fig. 6C), three *Glomus* OTUs were common across all samples (n = 11).

For the ITS2 rDNA region, in natural stands (Gabon), 0.69% of OTUs (25.0% of sequences) were present in at least 50% of the samples, while only 0.11% of OTUs (13.0% of sequences) were found in 70% or more. In plantations (DRC), the proportions were higher, with 2.96% of OTUs (40.11% of sequences) present in at least 50% of the samples and 1.10% of OTUs (26.93% of sequences) found in 70% or more. When considering each factor separately, the proportion did not exceed 4.74% of OTUs (5.78% of sequences) for 50% of the samples and 1.84% of OTUs (1.56% of sequences) for 70% or more. The higher proportions observed in the DRC are primarily due to the smaller number of samples. For the SSU rRNA gene concerning AM fungi, in natural stands (Gabon), 3.66% of OTUs (58.92% of sequences) were

present in at least 50% of the samples, while only 0.77% of OTUs (21.82% of sequences) were found in 70% or more. In plantations (DRC), 2.94% of OTUs (48.78% of sequences) were present in at least 50% of the samples, and 0.76% of OTUs (20.55% of sequences) were found in 70% or more.

4.5.2 Indicator taxa

Among the considered trophic guilds, 161 fungal OTUs were identified as potential indicator taxa associated with stand types and tree social status (Fig. 7). Canopy-reaching trees harbored the fewest indicator taxa in both the DRC and Gabon (Fig. 7), with the exception that all EcM-associated OTUs were obtained from samples collected from dominant trees in the old-growth mixed forests of Gabon (Fig. 4). In the DRC plantations, only four OTUs were identified as indicators of canopy-reaching trees. They belonged to four genera: *Umbelopsis* sp. (saprotroph), one *Castanediella* sp. (pathotroph), as well as *Glomus* sp. and *Scutellospora* sp. as AM fungi. In natural stands, only one *Glomus* sp. was identified.

The indicator OTUs of canopy-reaching trees displayed markedly different trends between Gabon and the DRC. In Gabon, they were characterized by a high diversity of AM fungi and four genera of saprotrophs, with *Exobasidium* sp. serving as the only indicator pathogen. In contrast, the suppressed trees in the DRC were characterized by four pathogenic OTUs (*Coniella* sp., two *Tetragoniomyces* spp., and another *Castanediella* sp.) and four OTUs associated with *Trechispora* spp.(saprotrophic).

The plantations in the DRC exhibited distinctly different indicator taxa. Among them, four *Acaulospora* sp. (AM fungi) were identified at Minkuku. Finally, the old-growth mixed forests housed the most specific taxa, comprising 12 saprotrophs, six pathotrophs, and 30 AM fungi.

Discussion

Our study based on the HTS sequencing of ITS2 rDNA and SSU rRNA regions provided for the first time a detailed overview of root-associated fungi of *Aucoumea klaineana*, Central Africa's most harvested timber species. Fungal communities were investigated both in monodominant stands and old-growth mixed forests from Gabon and in plantations from the DRC, as well as through a comparison of two different tree social status, illustrating the wide ecological range of *A. klaineana*. Our results showed a highly diverse community, extremely variable between stand types and tree social status, at a regional and local scale. Our results did not reveal any “core mycobiota” (Fig. 6) but instead complex and diverse fungal assemblages, of symbiotic as well as saprotrophic and pathogenic fungi.

As previously hypothesized by Leroy Deval (1974) and Peh et al. (2011), and confirmed for various tree species, EcM fungi often support monodominance in tropical ecosystems (e.g., Diedhiou et al., 2014; Ebenye et al., 2017; Fukami et al., 2017; Henkel, 2003; Liang et al., 2020). However, according to our results, it was not observed for *A. klaineana*. Instead, EcM fungal OTUs were only found in old-growth mixed forests, primarily associated with larger, canopy-reaching trees (Fig. 4). In contrast, EcM fungi were notably absent in monodominant stands (except for one OTU) and plantations. Their presence and mostly their high read counts (5% of sequences, equal to AM fungi, Fig. 2) in old-growth mixed forests

might represent a specific biological reality but might also come from potential bias such as (i) contamination from fungi associated with neighboring tree without functional relevance to *A. klaineana* (Amend et al., 2010; Smith and Read, 2008), or (ii) potential amplification bias during analysis (Amend et al., 2010; Buée et al., 2016). More than 90% of the reads associated with EcM fungi (43% of every symbiotrophic sequences from Gabon, Fig. 2) belonged to the *Russula-Lactarius* lineage, which is the most represented in the Afrotropical region (Corrales et al., 2022). Given these potential biases, complementary studies are needed to validate these findings.

Root-associated fungi appeared to have minimal impact on the survival of suppressed *A. klaineana*, as these trees did not host any distinct fungal communities (Fig. 6). In natural forests, only slight differences in saprotrophic and AM fungal guild composition were observed (Fig. 5). Despite minor richness differences, suppressed trees hosted more AM fungal indicator taxa (43 OTUs) compared to just one in canopy trees. This trend was absent in plantations, maybe due to an insufficient stand age for clear stratification. This also contrasts with Neuekemp et al. (2021), who suggested that favorable light conditions reduce selectivity for specific AM fungi and promote compatibility with a broader range of taxa.

Overall, our findings indicated that the root-associated fungal communities in *A. klaineana* forests were shaped more by processes linked to stand type context rather than tree social status (Fig. 6). This pattern may align with stochastic neutral processes of fungal assemblage (Dumbrell et al., 2010) (Table 1) or reflect the influence of soil physicochemical differences between monodominant versus old-growth mixed forests in Gabon (Bonito et al., 2014; Covacevich and Berbara, 2011).

However, no consistent trends emerged across the factors studied, highlighting the complexity of these interactions.

Considering the variability of root-associated fungal communities of *A. klaineana* characterized for the first time, the ITS2 fungal diversity observed across both countries was substantial, with 1,694 OTUs identified across 68 samples in Gabon (3,522,826 sequences) and 2,003 OTUs across 45 samples in the DRC (1,997,950 sequences), following quality filtering and removal of rare taxa. This richness is similar to what is known for temperate forest soils, studies reporting between 600 and over 5,000 fungal OTUs (e.g., Bahnmann et al., 2018; Buée et al., 2016; Kujawska et al., 2021; Lynikienė et al., 2020), whereas roots generally exhibit lower fungal richness than soils (e.g., Boeraeve et al., 2019; Olanipon et al., 2024; Větrovský et al., 2023). By comparison, studies focusing on root-associated fungi report approximately 2,200 OTUs in Serbian riparian forests (Marjanović et al., 2020) and around 1,000 OTUs in neotropical forests in Mexico (Schroeder et al., 2018) after data curation, but from multispecific rootlets samples.

However, this richness was shaped by environmental factors and methodologies, potentially underestimated due to fungal hyperdiversity (Buée et al., 2009; Taylor et al., 2014) and the removal of singletons in molecular analyses (Tedersoo et al., 2010b) which may represent rare taxa (Kauserud et al., 2012).

Tropical forests are underrepresented in fungal diversity studies (Powell and Rillig, 2018), leading to a sampling bias toward temperate regions (Větrovský et al., 2023). A notable data gap in Central Africa (Bahram et al., 2018; Cameron et al., 2019; Díaz-Vallejo et al., 2021) could have limited the taxonomic classification of OTUs, with 42.3% assigned to at least a "mixed" trophic guild in Gabon and 50.7% in the DRC. Nevertheless, the overall functional guild composition was consistent across both sampling campaigns, suggesting that these patterns are recurrent.

In both Gabon and the DRC, the dominant fungal phyla were Ascomycota and Basidiomycota, reaching together more than 95% of sequences for both countries. These phyla are part of the Dikarya clade, encompassing about 98% of known fungal species (James et al., 2006). Ascomycota were almost twice as abundant as Basidiomycota in both countries. This contrasts with other fungal assemblages from temperate forests soils, which show a majority of Basidiomycota (Goldmann et al., 2015; Kujawska et al., 2021). The Basidiomycota phylum primarily comprises ectomycorrhizal (EcM) and saprotrophic fungi (He et al., 2022; Smith and Read, 2008; Tedersoo et al., 2010a). Saprotrophic fungi were the most represented in our study no matter the phylum, while EcM fungal OTUs were rare in Gabon and absent in the DRC (Fig. 4). This difference between biomes is likely due to the prevalence of EcM-associated trees in temperate forest ecosystems (Smith and Read, 2008; Tedersoo et al., 2014).

Among minor phyla, Glomeromycota harbored the largest part of symbiotrophic OTUs, consistently present among samples but comprising only 1.0% of reads in Gabon and 1.2% in the DRC. This low proportion was also reported in temperate (Schröter et al., 2019), boreal (Nagati et al., 2018), and subtropical (Li et al., 2021) regions. This may be due to lower primer affinity and the high proportion of non-glomeromycotan sequences, which could result in the loss of rare AM fungi because of low yield or amplification bias (Řezáčová et al., 2016; Stockinger et al., 2010; Tedersoo et al., 2010b).

Mortierellomycota and Mucoromycota were also found in Gabon and the DRC, with proportions varying relative to Glomeromycota. In natural forests (Gabon), Glomeromycota were more abundant than Mortierellomycota, as in Serbian temperate forests (Marjanović et al., 2020) but unlike in subtropical regions (Li et al. 2021). They were also more prevalent than Mucoromycota in natural stands, in contrast to the previous results of Nagati et al. (2018) (boreal forests), but not in the DRC plantations. These two groups encompass numerous plant decomposers and also mycorrhizal fungi, root endophytes, and plant pathogens (Bonfante and Venice, 2020).

A consistent pathogenic prevalence was also observed across sampling campaigns and sites: 5% of OTUs in Gabon (6% of sequences), 3% in the DRC (5% of sequences) (Fig. 2). This is higher than those found in soils from Scots pine forests (Kujawska et al., 2021) or beech forests (Raimbault et al., 2024). Pathogenic fungal OTUs presented a higher read abundance than symbiotrophic in both countries. Among them, *Xylogone* and *Phaeocremonium* were indicators in old-growth mixed forests, benefiting from the variety of wood substrates and root structures that enhance decay. However, no symptoms of tree decline were observed and only generalist taxa have been identified as indicators (Fig. 7).

Symbiotrophic fungi were diverse in both regions, accounting for 28% of OTUs and 10% of reads in Gabon, and 20% of OTUs and 3% of reads in the DRC. Most of these fungi were AM fungi, reflecting the dominance of AM fungi-associated tree species across Central Africa (Bâ et al., 2012). For this guild, the ITS2 rDNA dataset showed many AM fungi OTUs but at low abundance. Supporting this, Onguene et al. (2002) found AM fungi in every stained *A. klaineana* rootlets samples from plantations, however, only a few arbuscules were observed, indicating low nutrient exchange activity (Smith and Read, 2008). A similar pattern was noted by Onguene and Kuyper (2001) in Anacardiaceae and Sapindaceae (other Sapindales) tree species from Cameroon, as well as in *Protium sagotinium* March. (Burseraceae) in French Guiana (Béreau et al., 1997). These species, like *A. klaineana*, have large rootlets with few hairs, which contrasts with the typical 'outsourcing' strategy of directing carbon to mycorrhizal partners (Bergmann et al., 2020; Hogan et al., 2023; McCormack and Iversen, 2019). Instead, this trait suggests a 'do-it-yourself' approach where roots primarily obtain nutrients independently, without relying on fungal symbioses, characteristic of saprotrophic fungi dominance.

According to the Gadgil effect, saprotophic and EcM fungi compete for organic matter decomposition, which can slow down the carbon decomposition rate in forest litter (Fernandez and Kennedy, 2016; Gadgil and Gadgil, 1971, 1975). In our study, saprotrophic fungi represented the largest share of assigned OTUs richness (31% in Gabon and 43% in the DRC, Fig. 2) and counts (29% in Gabon and 48% in the DRC, Fig. 2). These fungi play essential roles in carbon and nutrient cycling, and soil decomposition (Talbot et al., 2015), aligning with the fast litter decomposition rate observed in *A. klaineana* stands (Leroy Deval, 1974), even after logging activities (Midoko Iponga et al., 2019). Indicator saprotrophs in old-growth mixed forests, showed greater diversity due to the variety of decomposable materials. *Trechispora* and *Botrybasidium* decompose lignin-rich wood, while *Thozetella*, *Gynotrichum*, *Lauriomyces*, and *Hyaloscyphaceae* break down finer debris like leaves, releasing nutrients into the soil (Cannon and Kirk, 2007; Põlme et al., 2020; Tedersoo et al., 2014). In contrast, fungal communities in plantations in the DRC showed less differentiation overall, especially among saprotrophs, likely due to the small surface of study sites (0.5 ha in Minkuku, 0.2 ha in Ntozi), and to lower tree diversity. Interestingly, the dominance of saprotrophic fungi over other guilds was not found in soils from Scots pine (*Pinus sylvestris* L.) Polish forests (Kujawska et al., 2021) or beech (*Fagus sylvatica* L.) French forests (Raimbault et al., 2024), where EcM fungi were reported as the predominant group.

Sequencing the SSU rRNA region with glomeromycotinan-specific primers enhanced resolution for AM fungi identification (Öpik et al., 2010, 2014), despite shorter reads resulting from the single-end approach. *Glomus* was systematically the dominant taxon, consistent with prior research on AM fungal composition in forest communities (e.g., Boeraeve et al., 2019; da Silva et al., 2005; Olanipon et al., 2024; Tchiechoua et al., 2023). While other taxa were less abundant, they were more diverse, indicating high turnover rates and niche partitioning among taxa. In the DRC plantations, *Acaulospora* was the second most abundant genus, representing 24% of reads and 30% of OTUs. This is often the second most abundant AM genus in perturbed (Suárez et al., 2023) and natural forests (Kebede et al., 2023; Wang and Jiang, 2015), and it can exceed *Glomus* in some cases (Belay et al., 2020). However, it can also be poorly represented (Tchiechoua et al., 2023), as in Gabonese natural forests in our study (1% of reads and 12%

of OTUs). The rapid nuclear multiplication of *Glomus* and *Acaulospora*, particularly during spore formation, contribute to their dominance in plant roots, enhancing their resilience to soil disturbances and ecosystem changes (Hart and Reader, 2002; Lindhal et al., 2013; Muleta et al., 2008; Sanders and Croll, 2010; Wang and Jiang, 2015).

Overall, our study did not detect clear fungal compositional distinctions across tree social status or stand type. Interestingly, the concept of "core mycobiota" was not observed in our data, and the level of nestedness was very low, whether considering stand type or tree social status. This suggests that fungal communities are highly variable and context-dependent rather than forming stable, core associations with *A. klaineana*. One possible explanation for this variability is root grafting, a resource-sharing adaptation that could facilitate nutrient transfer among trees and commonly observed for *A. klaineana* (Leroy Deval, 1974, 1973). This process may occur alongside common mycorrhizal networks (Deslippe and Simard, 2011), enhancing the resilience of shaded trees (Bormann, 1966; Lev-Yadun, 2011) and supporting the stability of monodominant stands by extending their root systems and occupying available space. Root grafting could help suppressed trees survive and explain how *A. klaineana* maintains its monodominance, despite the lack of consistent fungal community patterns and limited reliance on symbiotic partnerships. Future research should also explore other factors, such as root exudates and allelopathic compounds, which can influence microbial community structure and dynamics (Balandier et al., 2022; Gris et al., 2019). These hypotheses highlight the need for a deeper understanding of *A. klaineana*'s belowground strategies, its interactions with microbial species, and the potential genetic traits that enable it to thrive in shaded, nutrient-limited conditions while sustaining monodominance.

Conclusion

This study provides the first comprehensive analysis of root-associated fungal communities in *Aucoumea klaineana*, Central Africa's most harvested timber species, using ITS2 rDNA and SSU rRNA high-throughput sequencing. We found no consistent “core mycobiota” associated with *A. klaineana*; instead, fungal assemblages were highly variable and diverse across stand type, tree social status, and regions. This suggested a context-dependent, neutral assemblage driven more by other ecological factors than by stable host associations.

Our results indicated that *A. klaineana*'s monodominance was not driven by EcM fungi associations, given the absence of EcM OTUs in monodominant stands. Instead, AM fungi were consistently present, but their low abundance suggested a limited functional activity. Notably, suppressed trees showed no distinct fungal communities related to their status, hinting at minimal impact of root-associated fungi on tree survival under light deprivation. This opens the possibility that *A. klaineana*'s persistence and monodominance may rely on alternative mechanisms, such as root grafting, which could enhance nutrient-sharing and resilience among individuals, rather than on specific fungal partnerships. Further research should examine *A. klaineana*'s reliance on belowground strategies including root grafting, root exudate processing, and their interactions with root-associated fungi, to better understand the

mechanisms of persistent monodominance and the resilience of suppressed trees, laying the foundation for the sustainable management of this key timber species.

Declarations

Data availability

Data will be made available on request.

Acknowledgements

We extend our gratitude to the University of Liège and the MODUS grants 2020/MOB/01047 and 2021/MOB/00222 for funding the field missions. To the "Ecole Régionale Postuniversitaire d'Aménagement et de Gestion intégrés des Forêts et Territoires tropicaux" (ERAIFT) in Kinshasa, Democratic Republic of Congo, its director Baudouin Michel, and field manager Ernestine Tipi for their warm welcome. We also thank the Concession Equatoriale des Bois – Precious Wood (CEB-PW) in Bambidie, Gabon, for their hospitality. We acknowledge the Nature + grant that enabled us to sequence all our amplicons. Thanks to Prof. Patrick du Jardin from the Plant Biology department (Gembloux Agro-Bio Tech, University of Liège, Belgium) for initiating the thesis in which this article is embedded. We are also grateful to Mario Amalfi and Jérôme Degreef from the Meise Botanic Garden (Belgium) for their insights. The authors also express their gratitude to the colleagues of the Plant Science Department for their valuable advice.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethics Statement

The content and authorship of the submitted manuscript have been approved by all authors, and all prevailing local, national and international regulations and conventions, and normal scientific ethical practices, have been respected.

Credit authorship contribution statement

Quentin Guidosse: Conceptualization, Methodology, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, Visualization, Funding acquisition. **Mélanie Roy**: Formal analysis, Writing - Review & Editing. **Jean-Louis Doucet**: Conceptualization, Methodology, Resources, Writing - Review & Editing, Supervision, Project administration. **Ludivine Lassois**: Conceptualization, Methodology, Writing - Review & Editing, Project administration. **Sébastien Massart**: Formal analysis, Writing - Review & Editing. **Caroline de Clerck**: Writing - Review & Editing, Supervision.

References

1. Abarenkov, K., Nilsson, R.H., Larsson, K.-H., Taylor, A.F.S., May, T.W., Frøslev, T.G., Pawlowska, J., Lindahl, B., Põldmaa, K., Truong, C., Vu, D., Hosoya, T., Niskanen, T., Piirmann, T., Ivanov, F., Zirk, A., Peterson, M., Cheeke, T.E., Ishigami, Y., Jansson, A.T., Jeppesen, T.S., Kristiansson, E., Mikryukov, V., Miller, J.T., Oono, R., Ossandon, F.J., Paupério, J., Saar, I., Schigel, D., Suija, A., Tedersoo, L., Kõljalg, U., 2024. The UNITE database for molecular identification and taxonomic communication of fungi and other eukaryotes: sequences, taxa and classifications reconsidered. Nucleic Acids Research 52, D791–D797. https://doi.org/10.1093/nar/gkad1039
2. Almeida-Neto, M., Ulrich, W., 2011. A straightforward computational approach for measuring nestedness using quantitative matrices. Environmental Modelling & Software 26, 173–178. https://doi.org/10.1016/j.envsoft.2010.08.003
3. Alsanius, B., Karlsson, M., Rosberg, A., Dorais, M., Naznin, M., Khalil, S., Bergstrand, K.-J., 2019. Light and Microbial Lifestyle: The Impact of Light Quality on Plant–Microbe Interactions in Horticultural Production Systems—A Review. Horticulturae 5, 41. https://doi.org/10.3390/horticulturae5020041
4. Amend, A.S., Seifert, K.A., Bruns, T.D., 2010. Quantifying microbial communities with 454 pyrosequencing: does read abundance count?: Quantitative pyrosequencing of microbes. Molecular Ecology 19, 5555–5565. https://doi.org/10.1111/j.1365-294X.2010.04898.x
5. Bâ, A., Duponnois, R., Diabaté, M., Dreyfus, B., 2011. Les champignons ectomycorhiziens des arbres forestiers en Afrique de l'Ouest : méthodes d'étude, diversité, écologie, utilisation en foresterie et comestibilité, Didactiques. IRD Éditions.
6. Bâ, A.M., Duponnois, R., Moyersoen, B., Diédhiou, A.G., 2012. Ectomycorrhizal symbiosis of tropical African trees. Mycorrhiza 22, 1–29. https://doi.org/10.1007/s00572-011-0415-x
7. Bahnmann, B., Mašínová, T., Halvorsen, R., Davey, M.L., Sedlák, P., Tomšovský, M., Baldrian, P., 2018. Effects of oak, beech and spruce on the distribution and community structure of fungi in litter and soils across a temperate forest. Soil Biology and Biochemistry 119, 162–173. https://doi.org/10.1016/j.soilbio.2018.01.021
8. Bahram, M., Hildebrand, F., Forslund, S.K., Anderson, J.L., Soudzilovskaia, N.A., Bodegom, P.M., Bengston-Palme, J., Anslan, S., Coelho, L.P., Harend, H., Huerta-Cepas, J., Medema, M.H., Maltz, M.R., Mundra, S., Olsson, P.A., Pent, M., Põlme, S., Sunagawa, S., Ryberg, M., Tedersoo, L., Bork, P., 2018. Structure and function of the global topsoil microbiome. Nautre 560, 233–256. https://doi.org/10.1038/s41586-018-0386-6
9. Bakker, J.D., 2008. Increasing the utility of Indicator Species Analysis. Journal of Applied Ecology 45, 1829–1835. https://doi.org/10.1111/j.1365-2664.2008.01571.x
10. Balandier, P., Mårell, A., Prévosto, B., Vincenot, L., 2022. Tamm review: Forest understorey and overstorey interactions: So much more than just light interception by trees. Forest Ecology and Management 526, 120584. https://doi.org/10.1016/j.foreco.2022.120584
11. Belay, Z., Negash, M., Kaseva, J., Vestberg, M., Kahiluoto, H., 2020. Native forests but not agroforestry systems preserve arbuscular mycorrhizal fungal species richness in southern Ethiopia.

Mycorrhiza. https://doi.org/10.1007/s00572-020-00984-6

12. Béreau, M., Gazel, M., Garbaye, J., 1997. Les symbioses mycorhiziennes des arbres de la forêt tropicale humide de Guyane française. Can. J. Bot. 75, 711–716. https://doi.org/10.1139/b97-080
13. Bergmann, J., Weigelt, A., van der Plas, F., Laughlin, D.C., Kuyper, T.W., Guerrero-Ramírez, N.R., Valverde-Barrantes, O.J., Bruelheide, H., Freschet, G.T., Iversen, C.M., Kattge, J., McCormack, M.L., Meier, I.C., Rillig, M.C., Roumet, C., Semchenko, M., Sweeney, C.J., van Ruijven, J., York, L.M., Mommer, L., 2020. The fungal collaboration gradient dominates the root economics space in plants. Science Advances 6, 9.
14. Biraud, J., Catinot, R., 1960. Les plantations artificielles d'Okoumé au Gabon. Bois et Forêts des Tropiques 3–24.
15. Bisanz, J.E., 2018. qiime2R: Importing QIIME2 artifacts and associated data into R sessions.
16. Blaser, J., Frizzo, J.C., Norgrove, L., 2021. Not only timber: the potential for managing non-timber forest products in tropical production forests—a comprehensive literature review, in: 50. Presented at the w. ITTO Technical Series No. 50. International Tropical Timber Organization (ITTO), Yokohama, Japan.
17. Boeraeve, M., Honnay, O., Jacquemyn, H., 2019. Forest edge effects on the mycorrhizal communities of the dual-mycorrhizal tree species Alnus glutinosa (L.) Gaertn. Science of The Total Environment 666, 703–712. https://doi.org/10.1016/j.scitotenv.2019.02.290
18. Bolyen, E., Rideout, J.R., Dillon, M.R., Bokulich, N.A., Abnet, C.C., Al-Ghalith, G.A., Alexander, H., Alm, E.J., Arumugam, M., Asnicar, F., Bai, Y., Bisanz, J.E., Bittinger, K., Brejnrod, A., Brislawn, C.J., Brown, C.T., Callahan, B.J., Caraballo-Rodríguez, A.M., Chase, J., Cope, E.K., Da Silva, R., Diener, C., Dorrestein, P.C., Douglas, G.M., Durall, D.M., Duvallet, C., Edwardson, C.F., Ernst, M., Estaki, M., Fouquier, J., Gauglitz, J.M., Gibbons, S.M., Gibson, D.L., Gonzalez, A., Gorlick, K., Guo, J., Hillmann, B., Holmes, S., Holste, H., Huttenhower, C., Huttley, G.A., Janssen, S., Jarmusch, A.K., Jiang, L., Kaehler, B.D., Kang, K.B., Keefe, C.R., Keim, P., Kelley, S.T., Knights, D., Koester, I., Kosciolek, T., Kreps, J., Langille, M.G.I., Lee, J., Ley, R., Liu, Y.-X., Loftfield, E., Lozupone, C., Maher, M., Marotz, C., Martin, B.D., McDonald, D., McIver, L.J., Melnik, A.V., Metcalf, J.L., Morgan, S.C., Morton, J.T., Naimey, A.T., Navas-Molina, J.A., Nothias, L.F., Orchanian, S.B., Pearson, T., Peoples, S.L., Petras, D., Preuss, M.L., Pruesse, E., Rasmussen, L.B., Rivers, A., Robeson, M.S., Rosenthal, P., Segata, N., Shaffer, M., Shiffer, A., Sinha, R., Song, S.J., Spear, J.R., Swafford, A.D., Thompson, L.R., Torres, P.J., Trinh, P., Tripathi, A., Turnbaugh, P.J., Ul-Hasan, S., Van Der Hooft, J.J.J., Vargas, F., Vázquez-Baeza, Y., Vogtmann, E., Von Hippel, M., Walters, W., Wan, Y., Wang, M., Warren, J., Weber, K.C., Williamson, C.H.D., Willis, A.D., Xu, Z.Z., Zaneveld, J.R., Zhang, Y., Zhu, Q., Knight, R., Caporaso, J.G., 2019. Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. Nat Biotechnol 37, 852–857. https://doi.org/10.1038/s41587-019-0209-9
19. Bonfante, P., Venice, F., 2020. Mucoromycota: going to the roots of plant-interacting fungi. Fungal Biology Reviews 34, 100–113. https://doi.org/10.1016/j.fbr.2019.12.003

20. Bonito, G., Reynolds, H., Robeson, M.S., Nelson, J., Hodkinson, B.P., Tuskan, G., Schadt, C.W., Vilgalys, R., 2014. Plant host and soil origin influence fungal and bacterial assemblages in the roots of woody plants. Molecular Ecology 23, 3356–3370. https://doi.org/10.1111/mec.12821
21. Bormann, F.H., 1966. The Structure, Function, and Ecological Significance of Root Grafts in Pinus strobus L. Ecological Monographs 36, 1–26. https://doi.org/10.2307/1948486
22. Brunck, F., Grison, F., Maître, H.-F., 1990. L'okoumé, CIRAD-CTFT. ed. Nogent-sur-Marne.
23. Brundrett, M.C., Tedersoo, L., 2018. Evolutionary history of mycorrhizal symbioses and global host plant diversity. New Phytologist 220, 1108–1115. https://doi.org/10.1111/nph.14976
24. Buée, M., Reich, M., Murat, C., Morin, E., Nilsson, R.H., Uroz, S., Martin, F., 2009. 454 Pyrosequencing analyses of forest soils reveal an unexpectedly high fungal diversity. New Phytologist 184, 449–456. https://doi.org/10.1111/j.1469-8137.2009.03003.x
25. Buée, M., Sentausa, E., Murat, C., 2016. Molecular technologies applied to the ecology of ectomycorrhizal communities, in: Martin, F. (Ed.), Molecular Mycorrhizal Symbiosis. Wiley, pp. 323–339. https://doi.org/10.1002/9781118951446.ch18
26. Callahan, B.J., McMurdie, P.J., Rosen, M.J., Han, A.W., Johnson, A.J.A., Holmes, S.P., 2016. DADA2: High-resolution sample inference from Illumina amplicon data. Nat Methods 13, 581–583. https://doi.org/10.1038/nmeth.3869
27. Cameron, E.K., Martins, I.S., Lavelle, P., Mathieu, J., Tedersoo, L., Gottschall, F., Guerra, C.A., Hines, J., Patoine, G., Siebert, J., Winter, M., Cesarz, S., Delgado-Baquerizo, M., Ferlian, O., Fierer, N., Kreft, H., Lovejoy, T.E., Montanarella, L., Orgiazzi, A., Pereira, H.M., Phillips, H.R.P., Settele, J., Wall, D.H., Eisenhauer, N., 2019. Global gaps in soil biodiversity data. Nat Ecol Evol. 2, 1042–1043. https://doi.org/10.1038/s41559-018-0573-8
28. Cannon, P.F., Kirk, P.M., 2007. Fungal Families of the World. CAB International, Cambridge.
29. Connell, J.H., Lowman, M.D., 1989. Low-Diversity Tropical Rain Forests: Some Possible Mechanisms for Their Existence. The American Naturalist 134, 88–119. https://doi.org/10.1086/284967
30. Corrales, A., Koch, R.A., Vasco-Palacios, A.M., Smith, M.E., Ge, Z.-W., Henkel, T.W., 2022. Diversity and distribution of tropical ectomycorrhizal fungi. Mycologia 114, 919–933. https://doi.org/10.1080/00275514.2022.2115284
31. Covacevich, F., Berbara, R.L.L., 2011. Indigenous arbuscular mycorrhizae in areas with different successional stages at a tropical dry forest biome in Brazil. Afr. J. Microbiol. Res. 5, 2697–2705. https://doi.org/10.5897/AJMR11.435
32. da Silva, G.A., Trufem, S.F.B., Saggin Júnior, O.J., Maia, L.C., 2005. Arbuscular mycorrhizal fungi in a semiarid copper mining area in Brazil. Mycorrhiza 15, 47–53. https://doi.org/10.1007/s00572-004-0293-6
33. Day, M., Baldauf, C., Rutishauser, E., Sunderland, T.C.H., 2014. Relationships between tree species diversity and above-ground biomass in Central African rainforests: implications for REDD. Envir. Conserv. 41, 64–72. https://doi.org/10.1017/S0376892913000295

34. De Assis, D.M.A., Oehl, F., Gonçalves, C.M., Da Silva, D.K.A., Da Silva, G.A., 2016. Community structure of arbuscular mycorrhizal fungi in fluvial and maritime dunes of Brazilian Northeast. Applied Soil Ecology 108, 136–146. https://doi.org/10.1016/j.apsoil.2016.07.018
35. De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574. https://doi.org/10.1890/08-1823.1
36. De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. Oikos 119, 1674–1684. https://doi.org/10.1111/j.1600-0706.2010.18334.x
37. Delègue, M.-A., Fuhr, M., Schwartz, D., Mariotti, A., Nasi, R., 2001. Recent origin of a large part of the forest cover in the Gabon coastal area based on stable carbon isotope data. Oecologia 129, 106–113. https://doi.org/10.1007/s004420100696
38. Deng, J., Fang, S., Fang, X., Jin, Y., Kuang, Y., Lin, F., Liu, J., Ma, J., Nie, Y., Ouyang, S., Ren, J., Tie, L., Tang, S., Tan, X., Wang, X., Fan, Z., Wang, Q.-W., Wang, H., Liu, C., 2023. Forest understory vegetation study: current status and future trends. f 3, 0–0. https://doi.org/10.48130/FR-2023-0006
39. Deslippe, J.R., Simard, S.W., 2011. Below-ground carbon transfer among Betula nana may increase with warming in Arctic tundra. New Phytologist 192, 689–698. https://doi.org/10.1111/j.1469-8137.2011.03835.x
40. Díaz-Vallejo, E.J., Seeley, M., Peyton Smith, A., Marín-Spiotta, E., 2021. A meta-analysis of tropical land-use change effects on the soil microbiome: Emerging patterns and knowledge gaps. Biotropica 53, 738–752.
41. Diedhiou, A., Ebenye, C., Selosse, M.-A., Awana, N., Bâ, A., 2014. Diversity and Community Structure of Ectomycorrhizal Fungi in Mixed and Monodominant African Tropical Rainforests, in: Diédhiou, A. (Ed.), Ectomycorrhizal Symbioses in Tropical and Neotropical Forests. CRC Press, pp. 1–18. https://doi.org/10.1201/b16536-2
42. Dos Santos, V.A.H.F., Ferreira, M.J., 2020. Initial establishment of commercial tree species under enrichment planting in a Central Amazon secondary forest: Effects of silvicultural treatments. Forest Ecology and Management 460, 1–10. https://doi.org/10.1016/j.foreco.2019.117822
43. Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species:the need for a flexible asymmetrical approach. Ecological Monographs 67, 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2
44. Dumbrell, A.J., Nelson, M., Helgason, T., Dytham, C., Fitter, A.H., 2010. Relative roles of niche and neutral processes in structuring a soil microbial community. ISME J 4, 337–345. https://doi.org/10.1038/ismej.2009.122
45. Ebenye, H.C., Taudière, A., Niang, N., Ndiaye, C., Sauve, M., Awana, N.O., Verbeken, M., De Kesel, A., Séne, S., Diédhiou, A.G., Sarda, V., Sadio, O., Cissoko, M., Ndoye, I., Selosse, M.-A., Bâ, A.M., 2017. Ectomycorrhizal fungi are shared between seedlings and adults in a monodominant *Gilbertiodendron dewevrei* rain forest in Cameroon. Biotropica 49, 256–267. https://doi.org/10.1111/btp.12415

46. Ezzine De Blas, D., Ruiz Pérez, M., 2008. Prospects for Reduced Impact Logging in Central African logging concessions. Forest Ecology and Management 256, 1509–1516. https://doi.org/10.1016/j.foreco.2008.05.016
47. Fernandez, C.W., Kennedy, P.G., 2016. Revisiting the 'Gadgil effect': do interguild fungal interactions control carbon cycling in forest soils? New Phytologist 209, 1382–1394. https://doi.org/10.1111/nph.13648
48. Friesen, M.L., Porter, S.S., Stark, S.C., Von Wettberg, E.J., Sachs, J.L., Martinez-Romero, E., 2011. Microbially Mediated Plant Functional Traits. Annu. Rev. Ecol. Evol. Syst. 42, 23–46. https://doi.org/10.1146/annurev-ecolsys-102710-145039
49. FRMi, 2018. Vision stratégique et industrialisation de la filière Bois dans les 6 pays du Bassin du Congo. Horizon 2030. Accroitre/ Sécuriser/ Valoriser les ressources en bois (Rapport stratégique régional), Développement intégré et durable de la filière bois dans le Bassin du Congo: opportunités, défis et recommandations opérationnelles. Plan de travail issu de la mission de cadrage. Montpellier, France.
50. Fuhr, M., 1999. Structure et dynamique de la forêt côtière du Gabon. Implications pour une succession secondaire dérivant de la forêt monodominante à Okoumé (*Aucoumea klaineana* Pierre) (PhD Thesis). Université Montpellier II.
51. Fukami, T., Nakajima, M., Fortunel, C., Fine, P.V.A., Baraloto, C., Russo, S.E., Peay, K.G., 2017. Geographical Variation in Community Divergence: Insights from Tropical Forest Monodominance by Ectomycorrhizal Trees. The American Naturalist 190, S105–S122. https://doi.org/10.1086/692439
52. Gadgil, R.L., Gadgil, 1971. Mycorrhiza and litter decomposition. Nature 233, 133.
53. Gadgil, R.L., Gadgil, P.D., 1975. Suppression of litter decomposition by mycorrhizal roots of *Pinus radiata* . New Zealand Journal of Forestry Science 5, 35–41.
54. Goldmann, K., Schöning, I., Buscot, F., Wubet, T., 2015. Forest Management Type Influences Diversity and Community Composition of Soil Fungi across Temperate Forest Ecosystems. Front. Microbiol. 6. https://doi.org/10.3389/fmicb.2015.01300
55. Gourlet-Fleury, S., Beina, D., Fayolle, A., Ouédraogo, D.-Y., Mortier, F., Bénédet, F., Closset-Kopp, D., Decocq, G., 2013. Silvicultural disturbance has little impact on tree species diversity in a Central African moist forest. Forest Ecology and Management 304, 322–332. https://doi.org/10.1016/j.foreco.2013.05.021
56. Guidosse, Q., Biwolé, A., De Clerck, C., Ekome, S.N., Lassois, L., Doucet, J.-L., 2024a. Seedling ecology of *Aucoumea klaineana* Pierre, the most important timber species in Central Africa. Forest Ecology and Management 569, 10. https://doi.org/10.1016/j.foreco.2024.122221
57. Guidosse, Q., Jardin, P.D., White, L.J.T., Lassois, L., Doucet, J.-L., 2022. Gabon's green gold: a bibliographical review of thirty years of research on okoumé (*Aucoumea klaineana* Pierre). Biotechnol. Agron. Soc. Environ. 26, 30–42. https://doi.org/10.25518/1780-4507.19458
58. Guidosse, Q., Roy, M., Lassois, L., Doucet, J.-L., 2024b. Adapted molecular methods to unravel the recalcitrant mycorrhizal associations of *Aucoumea klaineana* Pierre. Journal of Microbiological

Methods 224, 4. https://doi.org/10.1016/j.mimet.2024.107000

59. Hart, M.M., Reader, R.J., 2002. Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. New Phytologist 153, 335–344.
60. Hart, T.B., Hart, J.A., Murphy, P.G., 1989. Monodominant and Species-Rich Forests of the Humid Tropics: Causes for Their Co-Occurrence. The American Naturalist 133, 613–633.
61. He, M.-Q., Zhao, R.-L., Liu, D.-M., Denchev, T.T., Begerow, D., Yurkov, A., Kemler, M., Millanes, A.M., Wedin, M., McTaggart, A.R., Shivas, R.G., Buyck, B., Chen, J., Vizzini, A., Papp, V., Zmitrovich, I.V., Davoodian, N., Hyde, K.D., 2022. Species diversity of Basidiomycota. Fungal Diversity 114, 281–325. https://doi.org/10.1007/s13225-021-00497-3
62. Henkel, T.W., 2003. Monodominance in the ectomycorrhizal *Dicymbe corymbosa* (Caesalpiniaceae) from Guyana. J. Trop. Ecol. 19, 417–437. https://doi.org/10.1017/S0266467403003468
63. Hogan, J.A., Jusino, M.A., Smith, M.E., Corrales, A., Song, X., Hu, Y., Yang, J., Cao, M., Valverde-Barrantes, O.J., Baraloto, C., 2023. Root-associated fungal communities are influenced more by soils than by plant-host root. New Phytologist 238, 1849–1864.
64. Horn, S., Caruso, T., Verbruggen, E., Rillig, M.C., Hempel, S., 2014. Arbuscular mycorrhizal fungal communities are phylogenetically clustered at small scales. The ISME Journal 8, 2231–2242. https://doi.org/10.1038/ismej.2014.72
65. Hu, T., Chitnis, N., Monos, D., Dinh, A., 2021. Next-generation sequencing technologies: An overview. Human Immunology 82, 801–811. https://doi.org/10.1016/j.humimm.2021.02.012
66. James, T.Y., Kauff, F., Schoch, C.L., Matheny, P.B., Hofstetter, V., Cox, C.J., Celio, G., Gueidan, C., Fraker, E., Miadlikowska, J., Lumbsch, H.T., Rauhut, A., Reeb, V., Arnold, A.E., Amtoft, A., Stajich, J.E., Hosaka, K., Sung, G.-H., Johnson, D., O'Rourke, B., Crockett, M., Binder, M., Curtis, J.M., Slot, J.C., Wang, Z., Wilson, A.W., Schüßler, A., Longcore, J.E., O'Donnell, K., Mozley-Standridge, S., Porter, D., Letcher, P.M., Powell, M.J., Taylor, J.W., White, M.M., Griffith, G.W., Davies, D.R., Humber, R.A., Morton, J.B., Sugiyama, J., Rossman, A.Y., Rogers, J.D., Pfister, D.H., Hewitt, D., Hansen, K., Hambleton, S., Shoemaker, R.A., Kohlmeyer, J., Volkmann-Kohlmeyer, B., Spotts, R.A., Serdani, M., Crous, P.W., Hughes, K.W., Matsuura, K., Langer, E., Langer, G., Untereiner, W.A., Lücking, R., Büdel, B., Geiser, D.M., Aptroot, A., Diederich, P., Schmitt, I., Schultz, M., Yahr, R., Hibbett, D.S., Lutzoni, F., McLaughlin, D.J., Spatafora, J.W., Vilgalys, R., 2006. Reconstructing the early evolution of Fungi using a six-gene phylogeny. Nature 443, 818–822. https://doi.org/10.1038/nature05110
67. Jones, A, Breuning-Madsen, H., Brossard, M., Dampha, A., Deckers, J., Dewitte, O., Gallali, T., Hallett, S., Jones, R, Kilasara, M., Le Roux, P., Micheli, E., Montanarella, L, Spaargaren, O., Thiombiano, L., Van Ranst, E., Yemefack, M., Zougmoré R, Jones, Arwyn, Montanarella, Luca, Jones, Robert, European Commission, Joint Research Centre, 2013. Soil Atlas of Africa. Commission européenne, Bureau des publications de l'Union européenne, Luxembourg.
68. Kauserud, H., Kumar, S., Brysting, A.K., Nordén, J., Carlsen, T., 2012. High consistency between replicate 454 pyrosequencing analyses of ectomycorrhizal plant root samples. Mycorrhiza 22, 309–315. https://doi.org/10.1007/s00572-011-0403-1

69. Kebede, J.Y., Pagano, M.C., Beyene, B.B., Tuji, F.A., 2023. Diverse arbuscular mycorrhizal fungi species associate with indigenous trees in a natural forest. Mycol Progress 22, 77. https://doi.org/10.1007/s11557-023-01922-4
70. Kolde, R., 2018. pheatmap: Pretty Heatmaps.
71. Konvalinková, T., Jansa, J., 2016. Lights Off for Arbuscular Mycorrhiza: On Its Symbiotic Functioning under Light Deprivation. Front. Plant Sci. 7. https://doi.org/10.3389/fpls.2016.00782
72. Kozich, J.J., Westcott, S.L., Baxter, N.T., Highlander, S.K., Schloss, P.D., 2013. Development of a Dual-Index Sequencing Strategy and Curation Pipeline for Analyzing Amplicon Sequence Data on the MiSeq Illumina Sequencing Platform. Appl Environ Microbiol 79, 5112–5120. https://doi.org/10.1128/AEM.01043-13
73. Kujawska, M.B., Rudawska, M., Wilgan, R., Leski, T., 2021. Similarities and Differences among Soil Fungal Assemblages in Managed Forests and Formerly Managed Forest Reserves. Forests 12, 353. https://doi.org/10.3390/f12030353
74. Leroy Deval, J., 1976. Biologie et sylviculture de l'Okoumé (*Aucoumea klaineana* Pierre). Tome 1: La sylviculture de l'Okoumé, CTFT. ed. Nogent-sur-Marne.
75. Leroy Deval, J., 1974. Structure dynamique de la rhizosphère de l'okoumé dans ses rapports avec la sylviculture. CTFT, Nogent-sur-Marne.
76. Leroy Deval, J., 1973. Les liaisons et anastomoses racinaires. Bois et Forêts des Tropiques 152, 37–49. https://doi.org/10.19182/bft1973.152.a19173
77. Lev-Yadun, S., 2011. Why should trees have natural root grafts? Tree Physiology 31, 575–578. https://doi.org/10.1093/treephys/tpr061
78. Li, W.-Q., Huang, Y.-X., Chen, F.S., Liu, Y.Q., Lin, X.F., Zong, Y.-Y., Wu, G.-Y., Yu, Z.-R., Fang, X.-M., 2021. Mixing with broad-leaved trees shapes the rhizosphere soil fungal communities of coniferous tree species in subtropical forests. Forest Ecology and Management 480, 10.
79. Liang, M., Johnson, D., Burslem, D.F.R.P., Yu, S., Fang, M., Taylor, J.D., Taylor, A.F.S., Helgason, T., Liu, X., 2020. Soil fungal networks maintain local dominance of ectomycorrhizal trees. Nat Commun 11, 2636. https://doi.org/10.1038/s41467-020-16507-y
80. Lindhal, A., Nilsson, R.H., Tedersoo, L., Abarenkov, K., Carlsen, T., Kjøller, R., Kõljalg, U., Pennanen, T.L., Rosendahl, S., Stenlid, J., Kauserud, H., 2013. Fungal community analysis by high-throughput sequencing of amplified markers – a user's guide. New Phytologist 199, 288–299. https://doi.org/10.1111/nph.12243
81. Lynikienė, J., Marčiulynienė, D., Marčiulynas, A., Gedminas, A., Vaičiukynė, M., Menkis, A., 2020. Managed and Unmanaged Pinus sylvestris Forest Stands Harbour Similar Diversity and Composition of the Phyllosphere and Soil Fungi. Microorganisms 8, 259. https://doi.org/10.3390/microorganisms8020259
82. Marjanović, Ž., Nawaz, A., Stevanović, K., Saljnikov, E., Maček, I., Oehl, F., Wubet, T., 2020. Root-Associated Mycobiome Differentiate between Habitats Supporting Production of Different Truffle

Species in Serbian Riparian Forests. Microorganisms 8, 1331. https://doi.org/10.3390/microorganisms8091331

83. Martinez-Garcia, L.B., De Deyn, G.B., Pugnaire, F.I., Kothamasi, D., Van Der Heijden, M.G.A., 2017. Symbiotic soil fungi enhance ecosystem resilience to climate change. Global Change Biology 23, 5228–5236. https://doi.org/10.1111/gcb.13785
84. Mccarthy-Neumann, S., Kober, R.K., 2010. Conspecific plant-soil feedbacks reduce survivorship and growth of tropical tree seedlings. Journal of Ecology 98, 396–407. https://doi.org/10.1111/j.1365-2745.2009.01619.x.
85. McCormack, M.L., Iversen, C.M., 2019. Physical and Functional Constraints on Viable Belowground Acquisition Strategies. Front. Plant Sci. 10, 1215. https://doi.org/10.3389/fpls.2019.01215
86. McGuire, K.L., 2007. Common ectomycorrhizal networks may maintain monodominance in a tropical rain forest. Ecology 88, 567–574. https://doi.org/10.1890/05-1173
87. McMurdie, P.J., Holmes, S., 2013. phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data. PLoS ONE 8, e61217. https://doi.org/10.1371/journal.pone.0061217
88. Midoko Iponga, D.M., Mpikou, R.G.J., Loumeto, J., Picard, N., 2019. The effect of different anthropogenic disturbances on litterfall of a dominant pioneer rain forest tree in Gabon. African Journal of Ecology 58, 281–290. https://doi.org/10.1111/aje.12696
89. Miyauchi, S., Kiss, E., Kuo, A., Drula, E., Kohler, A., Sánchez-García, M., Morin, E., Andreopoulos, B., Barry, K.W., Bonito, G., Buée, M., Carver, A., Chen, C., Cichocki, N., Clum, A., Culley, D., Crous, P.W., Fauchery, L., Girlanda, M., Hayes, R.D., Kéri, Z., LaButti, K., Lipzen, A., Lombard, V., Magnuson, J., Maillard, F., Murat, C., Nolan, M., Ohm, R.A., Pangilinan, J., Pereira, M.D.F., Perotto, S., Peter, M., Pfister, S., Riley, R., Sitrit, Y., Stielow, J.B., Szöllősi, G., Žifčáková, L., Štursová, M., Spatafora, J.W., Tedersoo, L., Vaario, L.-M., Yamada, A., Yan, M., Wang, P., Xu, J., Bruns, T., Baldrian, P., Vilgalys, R., Dunand, C., Henrissat, B., Grigoriev, I.V., Hibbett, D., Nagy, L.G., Martin, F.M., 2020. Large-scale genome sequencing of mycorrhizal fungi provides insights into the early evolution of symbiotic traits. Nat Commun 11, 5125. https://doi.org/10.1038/s41467-020-18795-w
90. Morgan, B.S.T., Egerton-Warburton, L.M., 2017. Barcoded NS31/AML2 Primers for Sequencing of Arbuscular Mycorrhizal Communities in Environmental Samples. Applications in Plant Sciences 5, 1700017. https://doi.org/10.3732/apps.1700017
91. Morin-Rivat, J., Fayolle, A., Favier, C., Bremond, L., Gourlet-Fleury, S., Bayol, N., Lejeune, P., Beeckman, H., Doucet, J.-L., 2017. Present-day central African forest is a legacy of the 19th century human history. eLife e20343, 1–18. https://doi.org/10.7554/eLife.20343
92. Muleta, D., Assefa, F., Nemomissa, S., Granhall, U., 2008. Distribution of arbuscular mycorrhizal fungi spores in soils of smallholder agroforestry and monocultural coffee systems in southwestern Ethiopia. Biol Fertil Soils 44, 653–659. https://doi.org/10.1007/s00374-007-0261-3
93. Nagati, M., Roy, M., Manzi, S., Richard, F., DesRochers, A., Gardes, M., Bergeron, Y., 2018. Impact of local forest composition on soil fungal communities in a mixed boreal forest. Plant Soil 432, 345–

357.

94. Nasi, R., Billand, A., van Vliet, N., 2012. Managing for timber and biodiversity in the Congo Basin. Forest Ecology and Management 268, 103–111. https://doi.org/10.1016/j.foreco.2011.04.005
95. Neuenkamp, L., Zobel, M., Koorem, K., Jairus, T., Davison, J., Öpik, M., Vasar, M., Moora, M., 2021. Light availability and light demand of plants shape the arbuscular mycorrhizal fungal communities in their roots. Ecology Letters 24, 426–437. https://doi.org/10.1111/ele.13656
96. Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., Kennedy, P.G., 2016. FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecology 20, 241–248. https://doi.org/10.1016/j.funeco.2015.06.006
97. Oksanen, J., et al., 2024. Vegan: Community Ecology Package.
98. Olanipon, D., Boeraeve, M., Jacquemyn, H., 2024. Arbuscular mycorrhizal fungal diversity and potential association networks among African tropical forest trees. Mycorrhiza 34, 271–282. https://doi.org/10.1007/s00572-024-01156-6
99. Onguene, N.A., Kuyper, T.W., 2001. Mycorrhizal associations in the rain forest of South Cameroon. Forest Ecology and Management 140, 277–287. https://doi.org/10.1016/S0378-1127(00)00322-4
100. Onguene, N.A., Tsimi, J.P.M., Balla, M.J.E., 2002. Statut mycorhizien de l'okoumé (*Aucoumea klaineana* Pierre) en régénération artificielle au sud Cameroun. Tropicultura 20, 104–108.
101. Öpik, M., Davison, J., Moora, M., Zobel, M., 2014. DNA-based detection and identification of Glomeromycota: the virtual taxonomy of environmental sequences. Botany 92, 135–147. https://doi.org/10.1139/cjb-2013-0110
102. Öpik, M., Vanatoa, A., Vanatoa, E., Moora, M., Davison, J., Kalwij, J.M., Reier, Ü., Zobel, M., 2010. The online database Maarj *AM* reveals global and ecosystemic distribution patterns in arbuscular mycorrhizal fungi (Glomeromycota). New Phytologist 188, 223–241. https://doi.org/10.1111/j.1469-8137.2010.03334.x
103. Pangou, S.V., Maury-Lechon, G., Moutanda, A., 2003. Monodominant forests of *Aucoumea klaineana* and *Terminalia superba* in the Chaillu forest (SW Congo, Africa). Polish Botanical Journal 48, 145–162.
104. Peh, Kelvin S.-H., Lewis, S.L., Lloyd, J., 2011. Mechanisms of monodominance in diverse tropical tree-dominated systems. Journal of Ecology 99, 891–898. https://doi.org/10.1111/j.1365-2745.2011.01827.x
105. Peh, Kelvin S. -H., Sonké, B., Lloyd, J., Quesada, C.A., Lewis, S.L., 2011. Soil Does Not Explain Monodominance in a Central African Tropical Forest. PLoS ONE 6, e16996. https://doi.org/10.1371/journal.pone.0016996
106. Peh, K.S.-H., Sonké, B., Séné, O., Djuikouo, M.N.K., Nguembou, C.K., Taedoumg, H., Begne, S.K., Lewis, S.L., 2014. Mixed-Forest Species Establishment in a Monodominant Forest in Central Africa: Implications for Tropical Forest Invasibility. PLOS ONE 9, 1–15.
107. Philippon, N., Cornu, G., Gond, V., Monteil, L., Moron, V., Pergaud, J., Bigot, S., Camberlin, P., Doumenge, C., Fayolle, A., 2018. Cycles diurnes de rayonnement solaire et forêts en Afrique centrale,

in: Martin, N. (Ed.), XXXIe Colloque de l'Association Internationale de Climatologie : Les Échelles Spatiales et Temporelles Fines. Presented at the Colloque annuel de l'Association internationale de climatologie (AIC 2018), AIC, Nice, France, pp. 38–42.

108. Philippon, N., Cornu, G., Monteil, L., Gond, V., Moron, V., Pergaud, J., Sèze, G., Bigot, S., Camberlin, P., Doumenge, C., Fayolle, A., Ngomanda, A., 2019. The light-deficient climates of western Central African evergreen forests. Environ. Res. Lett. 14, 1–12. https://doi.org/10.1088/1748-9326/aaf5d8
109. Põlme, S., Abarenkov, K., Henrik Nilsson, R., Lindahl, B.D., Clemmensen, K.E., Kauserud, H., Nguyen, N., Kjøller, R., Bates, S.T., Baldrian, P., Frøslev, T.G., Adojaan, K., Vizzini, A., Suija, A., Pfister, D., Baral, H.-O., Järv, H., Madrid, H., Nordén, J., Liu, J.-K., Pawlowska, J., Põldmaa, K., Pärtel, K., Runnel, K., Hansen, K., Larsson, K.-H., Hyde, K.D., Sandoval-Denis, M., Smith, M.E., Toome-Heller, M., Wijayawardene, N.N., Menolli, N., Reynolds, N.K., Drenkhan, R., Maharachchikumbura, S.S.N., Gibertoni, T.B., Læssøe, T., Davis, W., Tokarev, Y., Corrales, A., Soares, A.M., Agan, A., Machado, A.R., Argüelles-Moyao, A., Detheridge, A., De Meiras-Ottoni, A., Verbeken, A., Dutta, A.K., Cui, B.-K., Pradeep, C.K., Marín, C., Stanton, D., Gohar, D., Wanasinghe, D.N., Otsing, E., Aslani, F., Griffith, G.W., Lumbsch, T.H., Grossart, H.-P., Masigol, H., Timling, I., Hiiesalu, I., Oja, J., Kupagme, J.Y., Geml, J., Alvarez-Manjarrez, J., Ilves, K., Loit, K., Adamson, K., Nara, K., Küngas, K., Rojas-Jimenez, K., Bitenieks, K., Irinyi, L., Nagy, L.G., Soonvald, L., Zhou, L.-W., Wagner, L., Aime, M.C., Öpik, M., Mujica, M.I., Metsoja, M., Ryberg, M., Vasar, M., Murata, M., Nelsen, M.P., Cleary, M., Samarakoon, M.C., Doilom, M., Bahram, M., Hagh-Doust, N., Dulya, O., Johnston, P., Kohout, P., Chen, Q., Tian, Q., Nandi, R., Amiri, R., Perera, R.H., Dos Santos Chikowski, R., Mendes-Alvarenga, R.L., Garibay-Orijel, R., Gielen, R., Phookamsak, R., Jayawardena, R.S., Rahimlou, S., Karunarathna, S.C., Tibpromma, S., Brown, S.P., Sepp, S.-K., Mundra, S., Luo, Z.-H., Bose, T., Vahter, T., Netherway, T., Yang, T., May, T., Varga, T., Li, W., Coimbra, V.R.M., De Oliveira, V.R.T., De Lima, V.X., Mikryukov, V.S., Lu, Y., Matsuda, Y., Miyamoto, Y., Kõljalg, U., Tedersoo, L., 2020. FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. Fungal Diversity 105, 1–16. https://doi.org/10.1007/s13225-020-00466-2
110. Powell, J.R., Rillig, M.C., 2018. Biodiversity of arbuscular mycorrhizal fungi and ecosystem function. New Phytologist 220, 1059–1075.
111. R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.
112. Raimbault, A., Brin, A., Manzi, S., Gandois, L., Oliva, P., Fogliani, O., Roy-Camille, C., Gratacap, L., Roy, M., 2024. Influence of habitat fragmentation and habitat amount on soil fungi communities in ancient forests. Landsc Ecol 39, 19. https://doi.org/10.1007/s10980-024-01821-3
113. Řezáčová, V., Gryndler, M., Bukovská, P., Šmilauer, P., Jansa, J., 2016. Molecular community analysis of arbuscular mycorrhizal fungi—Contributions of PCR primer and host plant selectivity to the detected community profiles. Pedobiologia 59, 179–187. https://doi.org/10.1016/j.pedobi.2016.04.002
114. Roy, J., Reichel, R., Brüggemann, N., Hempel, S., Rillig, M.C., 2017. Succession of arbuscular mycorrhizal fungi along a 52-years agricultural recultivation chronosequence. FEMS Microbiology Ecology. https://doi.org/10.1093/femsec/fix102

115. Sanders, I.R., Croll, D., 2010. Arbuscular Mycorrhiza: The Challenge to Understand the Genetics of the Fungal Partner. Annu. Rev. Genet. 44, 271–292. https://doi.org/10.1146/annurev-genet-102108-134239

116. Sawada, K., Inagaki, Y., Sugihara, S., Funakawa, S., Ritz, K., Toyota, K., 2021. Impacts of conversion from natural forest to cedar plantation on the structure and diversity of root-associated and soil microbial communities. Applied Soil Ecology 167, 104027. https://doi.org/10.1016/j.apsoil.2021.104027

117. Schroeder, J.W., Martin, J.T., Angulo, D.F., Barbosa, J.M., Perea, R., Arias-Del Razo, I., Sebastián-González, E., Dirzo, R., 2018. Community composition and diversity of Neotropical root-associated fungi in common and rare trees. Biotropica 50, 694–703. https://doi.org/10.1111/btp.12553

118. Schröter, K., Wemheuer, B., Pena, R., Schöning, I., Ehbrecht, M., Schall, P., Ammer, C., Daniel, R., Polle, A., 2019. Assembly processes of trophic guilds in the root mycobiome of temperate forests. Molecular Ecology 28, 348–364. https://doi.org/10.1111/mec.14887

119. Sen, R., 2000. Budgeting for the wood-wide web. New Phytologist 145, 161–163. https://doi.org/10.1046/j.1469-8137.2000.00585.x

120. Simard, S.W., Perry, D.A., Jones, M.D., Myrold, D.D., Durall, D.M., Molina, R., 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. Nature 388, 579–582. https://doi.org/10.1038/41557

121. Slik, J.W.F., Arroyo-Rodríguez, V., Aiba, S.-I., Alvarez-Loayza, P., Alves, L.F., Ashton, P., Balvanera, P., Bastian, M.L., Bellingham, P.J., ..., 2018. An estimate of the number of tropical tree species. PNAS 112, 7472–7477.

122. Smith, S.E., Read, D.J., 2008. Mycorrhizal Symbiosis, 3th ed. Academic Press, Oxford, UK.

123. Sousa, N.M.F., Roy, J., Hempel, S., Rillig, M.C., Maia, L.C., 2022. Precipitation and temperature shape the biogeography of arbuscular mycorrhizal fungi across the Brazilian Caatinga. Journal of Biogeography 49, 1137–1150. https://doi.org/10.1111/jbi.14376

124. Stockinger, H., Krüger, M., Schüßler, A., 2010. DNA barcoding of arbuscular mycorrhizal fungi. New Phytologist 187, 461–474. https://doi.org/10.1111/j.1469-8137.2010.03262.x

125. Suárez, J.P., Herrera, P., Kalinhoff, C., Vivanco-Galván, O., Thangaswamy, S., 2023. Generalist arbuscular mycorrhizal fungi dominated heavy metal polluted soils at two artisanal and small – scale gold mining sites in southeastern Ecuador. BMC Microbiol 23, 42. https://doi.org/10.1186/s12866-022-02748-y

126. Talbot, J.M., Martin, F., Kohler, A., Henrissat, B., Peay, K.G., 2015. Functional guild classification predicts the enzymatic role of fungi in litter and soil biogeochemistry. Soil Biology and Biochemistry 88, 441–456. https://doi.org/10.1016/j.soilbio.2015.05.006

127. Taylor, D.L., Hollingsworth, T.N., McFarland, J.W., Lennon, N.J., Nusbaum, C., Ruess, R.W., 2014. A first comprehensive census of fungi in soil reveals both hyperdiversity and fine-scale niche partitioning. Ecological Monographs 84, 3–20. https://doi.org/10.1890/12-1693.1

128. Tchiechoua, Y.H., Odee, D.W., Ngonkeu, E.L.M., Kinyua, J., Ngumi, V.W., Machuka, E.M., Waweru, B., Le Roux, M., Pelle, R., 2023. DNA sequencing reveals high arbuscular mycorrhizal fungi diversity in the rhizosphere soil of Prunus africana trees in fragmented Afromontane forests. Ann Microbiol 73, 17. https://doi.org/10.1186/s13213-023-01720-z

129. Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V., Vasco-Palacios, A.M., Thu, P.Q., Suija, A., Smith, M.E., Sharp, C., Saluveer, E., Saitta, A., Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Põldmaa, K., Piepenbring, M., Phosri, C., Peterson, M., Parts, K., Pärtel, K., Otsing, E., Nouhra, E., Njouonkou, A.L., Nilsson, R.H., Morgado, L.N., Mayor, J., May, T.W., Majuakim, L., Lodge, D.J., Lee, S.S., Larsson, K.-H., Kohout, P., Hosaka, K., Hiiesalu, I., Henkel, T.W., Harend, H., Guo, L., Greslebin, A., Grelet, G., Geml, J., Gates, G., Dunstan, W., Dunk, C., Drenkhan, R., Dearnaley, J., De Kesel, A., Dang, T., Chen, X., Buegger, F., Brearley, F.Q., Bonito, G., Anslan, S., Abell, S., Abarenkov, K., 2014. Global diversity and geography of soil fungi. Science 346, 1256688. https://doi.org/10.1126/science.1256688

130. Tedersoo, L., May, T.W., Smith, M.E., 2010a. Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. Mycorrhiza 20, 217–263. https://doi.org/10.1007/s00572-009-0274-x

131. Tedersoo, L., Nilsson, R.H., Abarenkov, K., Jairus, T., Sadam, A., Saar, I., Bahram, M., Bechem, E., Chuyong, G., Kõljalg, U., 2010b. 454 Pyrosequencing and Sanger sequencing of tropical mycorrhizal fungi provide similar results but reveal substantial methodological biases. New Phytologist 188, 291–301. https://doi.org/10.1111/j.1469-8137.2010.03373.x

132. Torti, S.D., Coley, P.D., Kursar, T.A., 2001. Causes and Consequences of Monodominance in Tropical Lowland Forests. The American Naturalist 157, 141–153. https://doi.org/10.1086/318629

133. Van Der Heijden, M.G.A., Horton, T.R., 2009. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. Journal of Ecology 97, 1139–1150. https://doi.org/10.1111/j.1365-2745.2009.01570.x

134. Van Der Heijden, M.G.A., Martin, F.M., Selosse, M., Sanders, I.R., 2015. Mycorrhizal ecology and evolution: the past, the present, and the future. New Phytol 205, 1406–1423. https://doi.org/10.1111/nph.13288

135. Van Gemerden, B.S., Shu, G.N., Olff, H., 2003. Recovery of conservation values in Central African rain forest after logging and shifting cultivation. Biodviersity and Conservation 12, 1553–1570.

136. Vancov, T., Keen, B., 2009. Amplification of soil fungal community DNA using the ITS86F and ITS4 primers. FEMS Microbiology Letters 296, 91–96. https://doi.org/10.1111/j.1574-6968.2009.01621.x

137. Větrovský, T., Kolařík ová, Z., Lepinay, C., ..., Baldrian, P., Kohout, P., 2023. GlobalAMFungi: a global database of arbuscular mycorrhizal fungal occurrences from high-throughput sequencing metabarcoding studies. New Phytologist 240, 2151–2163. https://doi.org/10.1111/nph.19283

138. Wang, M., Jiang, P., 2015. Colonization and Diversity of AM Fungi by Morphological Analysis on Medicinal Plants in Southeast China. The Scientific World Journal 2015, 753842. https://doi.org/10.1155/2015/753842

139. Waud, M., Busschaert, P., Ruyters, S., Jacquemyn, H., Lievens, B., 2014. Impact of primer choice on characterization of orchid mycorrhizal communities using 454 pyrosequencing. Mol Ecol Resour 14, 679–699. https://doi.org/10.1111/1755-0998.12229

140. Weber, O.B., Da Silva, M.C.B., Da Silva, C.F., Correia, D., Dos Santos Garruti, D., Pagano, M.C., 2021. Diversity of mycorrhizal fungi and soil indicative species in coastal plantations of northeast Brazil. J. For. Res. 32, 1203–1211. https://doi.org/10.1007/s11676-020-01190-y

141. White, L., Oslisly, R., Abernethy, K., Maley, J., 2000. L'Okoumé (*Aucoumea klaineana*) : expansion et déclin d'un arbre pionnier en Afrique centrale atlantique au cours de l'Holocène, in: Servant, M., Servant-Vildary, S. (Eds.), Dynamique à long terme des écosystèmes forestiers intertropicaux. UNESCO, Paris, France, pp. 399–411.

142. Xi, N., Bloor, J.M.G., Wang, Y., Chu, C., 2019. Contribution of conspecific soil microorganisms to tree seedling light responses: Insights from two tropical species with contrasting shade tolerance. Environmental and Experimental Botany 166, 103826. https://doi.org/10.1016/j.envexpbot.2019.103826

143. Xu, S., Zhan, L., Tang, W., Wang, Q., Dai, Z., Zhou, L., Feng, T., Chen, M., Wu, T., Hu, E., Yu, G., 2023. MicrobiotaProcess: A comprehensive R package for deep mining microbiome. The Innovation 4, 100388. https://doi.org/10.1016/j.xinn.2023.100388

Figures

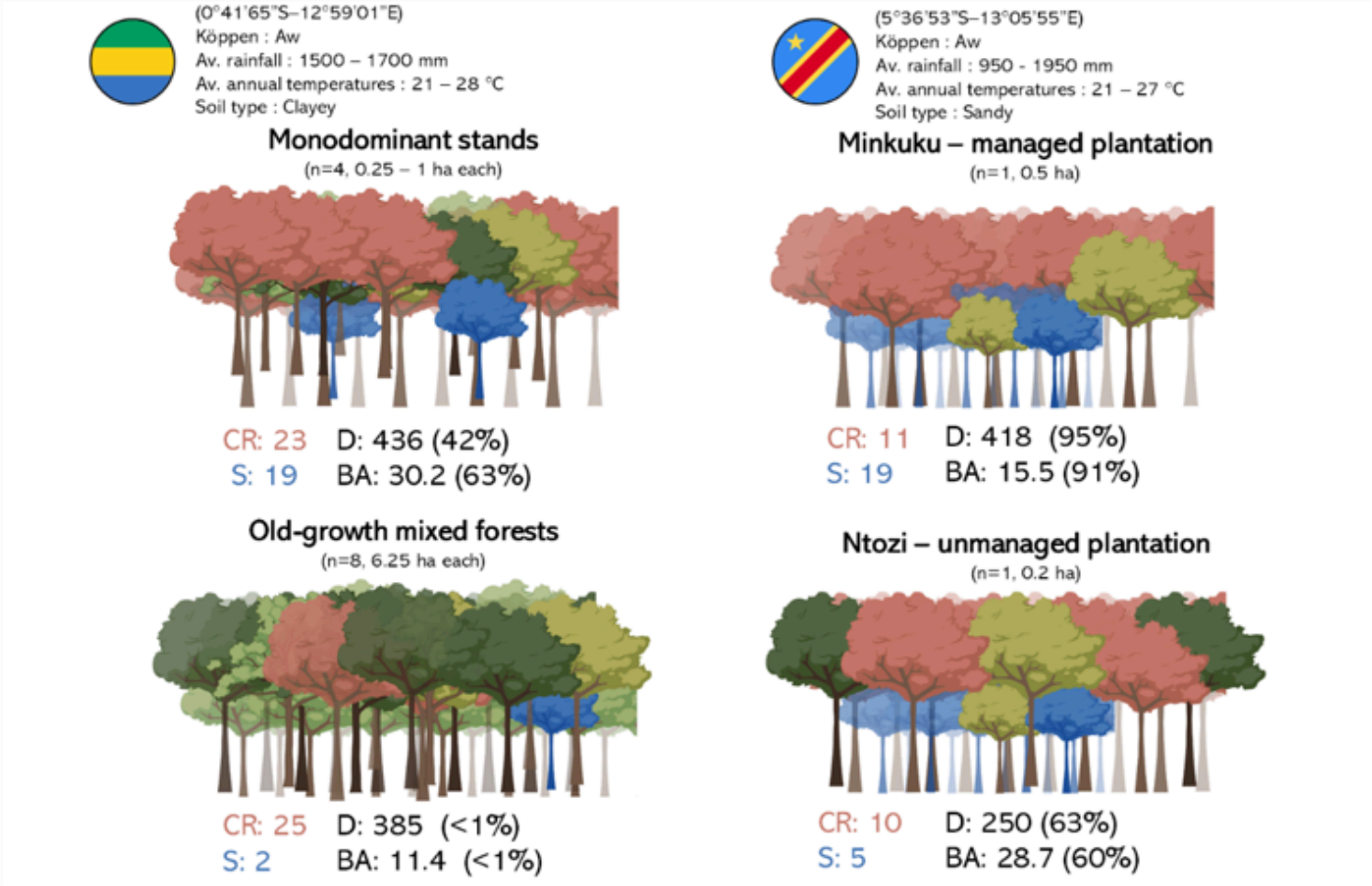


Figure 1

Characteristics of the study sites and stands. Distribution of tree types: canopy-reaching *A. klaineana* (red, CR), suppressed *A. klaineana* (blue, S), and other species (green). The amounts of collected samples are represented by corresponding colours for each stand type. Tree density (D, N/ha) and basal area (BA, m²/ha) are reported with the proportion of *A. klaineana* in parentheses. Note: the 42% proportion of *A. klaineana* in monodominant stands includes all trees, not only the canopy-reaching ones.

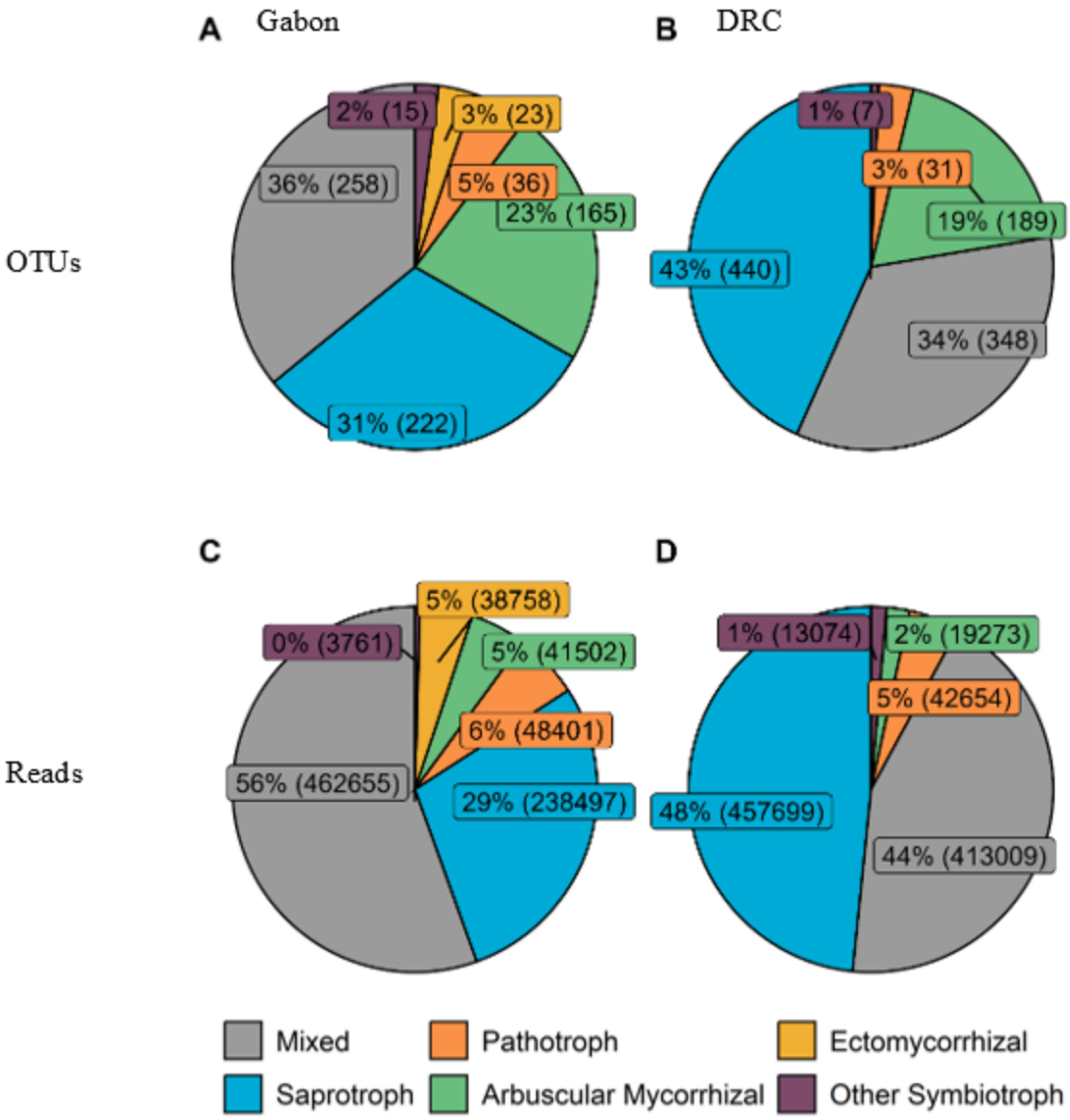


Figure 2

Trophic guild distribution based on the number of OTUs (A,B) and sequence reads (C,D) obtained for samples from Gabon (A,C) and the DRC (B,D) samples after sequencing the ITS2 rDNA region. Fungal OTUs with uncertain trophic associations are categorized as "Mixed". The “Other symbiotroph” group includes lichenized and epiphytic OTUs.

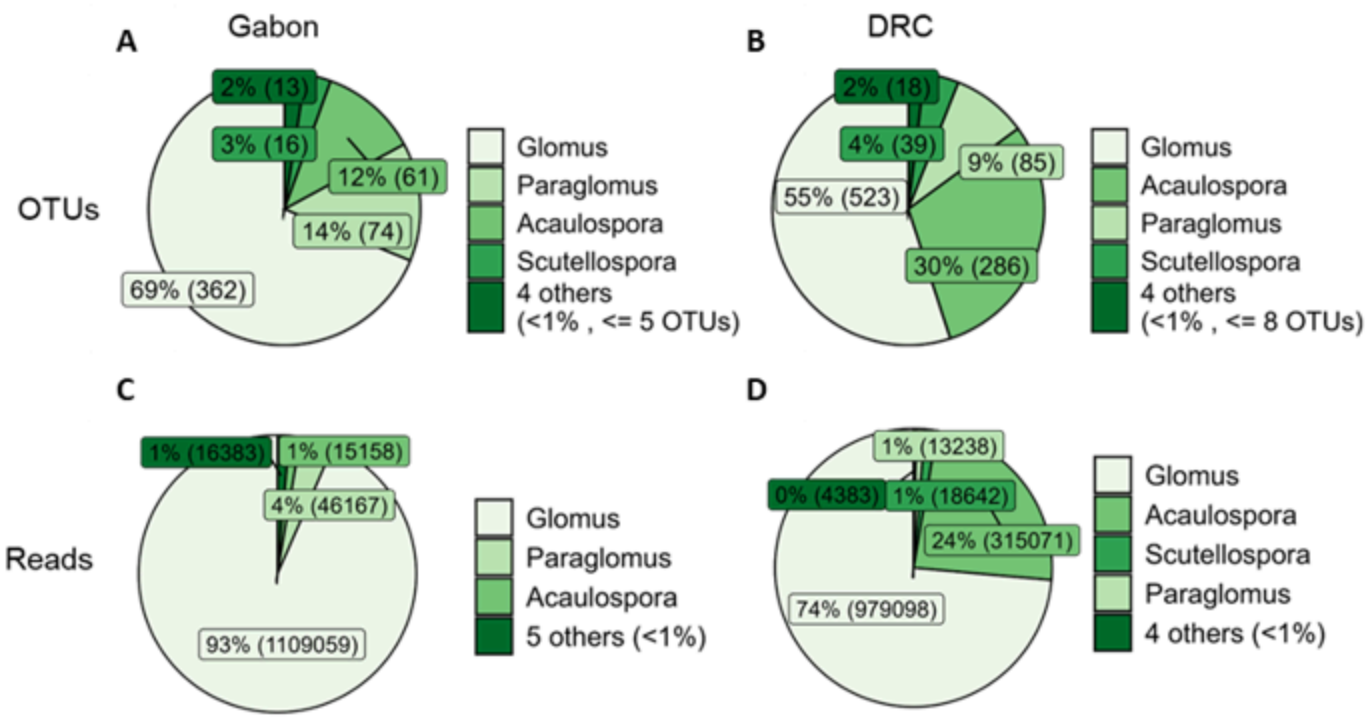


Figure 3

Distribution of arbuscular mycorrhizal (AM) fungal taxa at the genus level in terms of OTUs counts (A,B) and sequence reads (C,D) obtained from Gabon (A,C) and the DRC (B,D) based on the glomeromycotinan-specific SSU rRNA gene

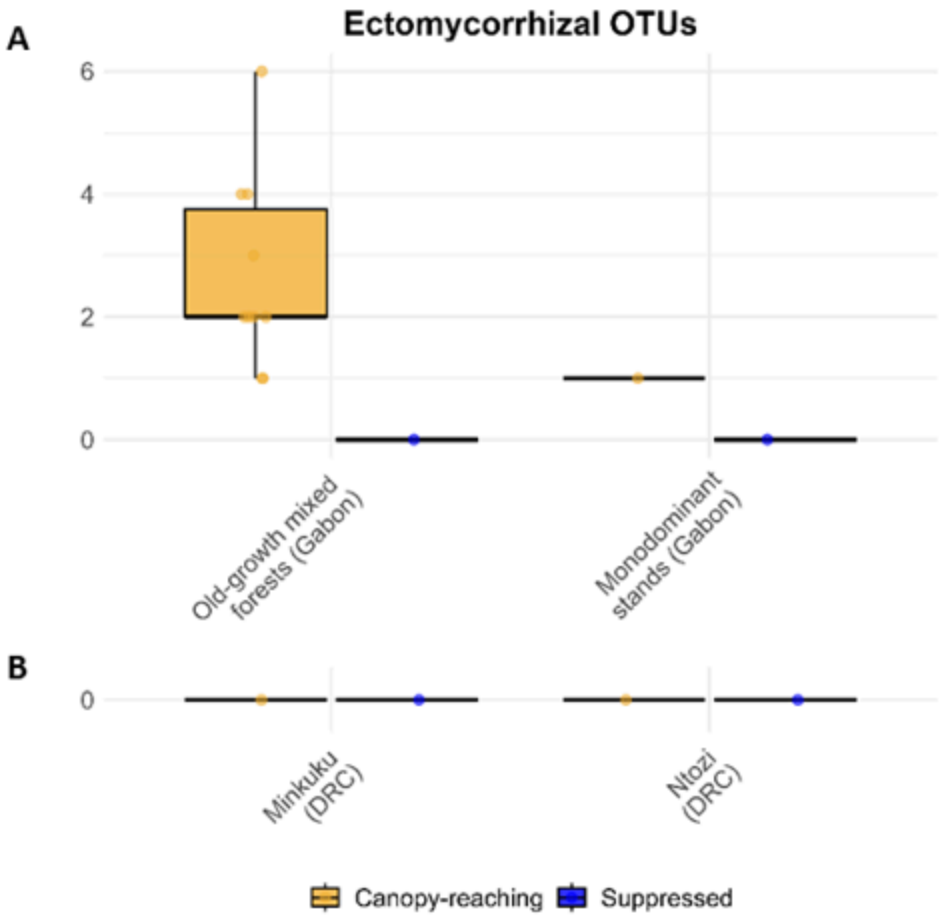


Figure 4

OTU richness obtained from samples in Gabon (A) and DRC (B) assigned as ectomycorrhizal (EcM) (n=23) across stand types and tree social status.

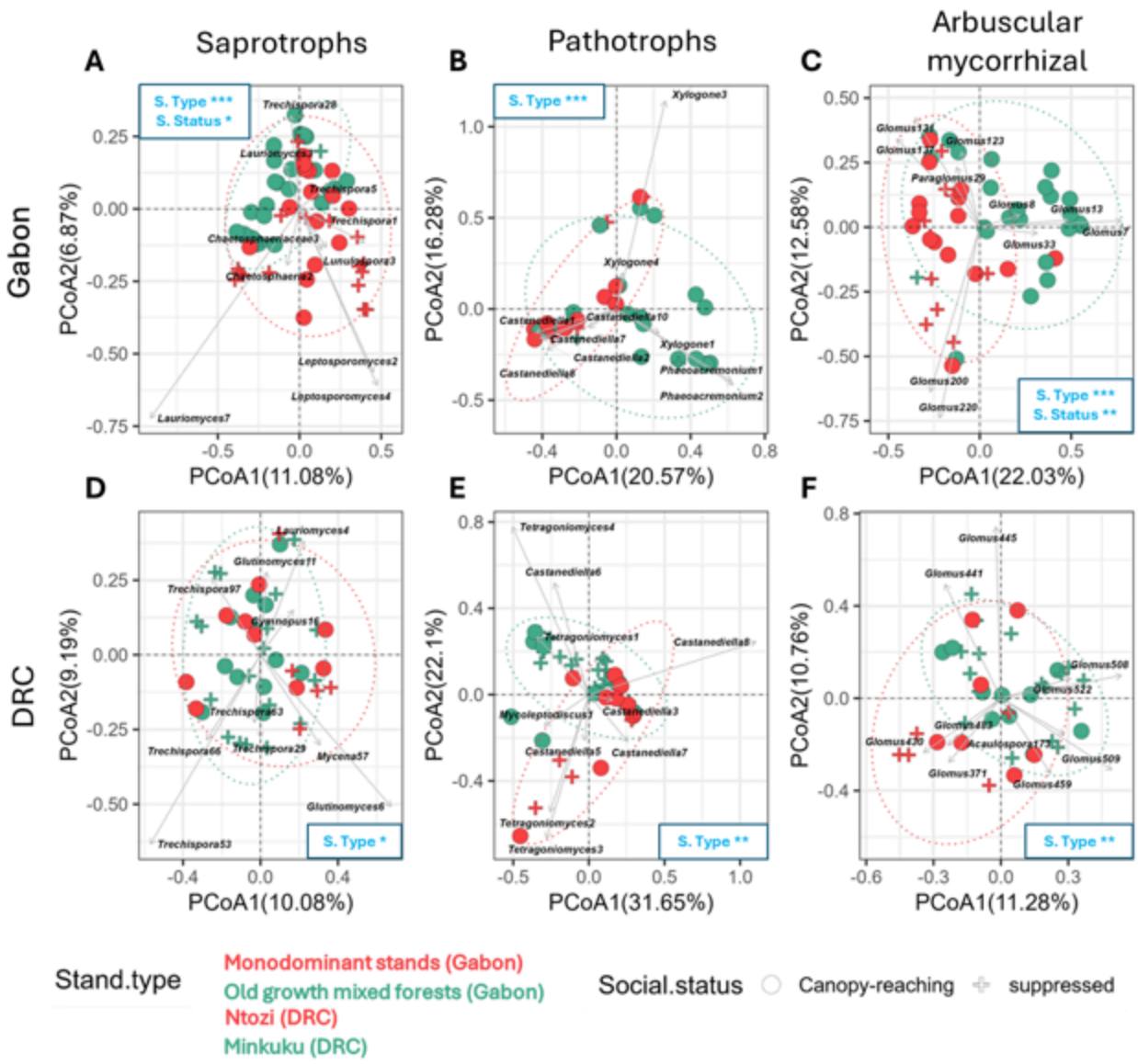


Figure 5

PCoA plots based on Bray-Curtis dissimilarity matrices on OTUs obtained from Gabon (A,B,C) and the DRC (D,E,F) assigned to saprotrophic (A,B), pathotrophic (B,E), and arbuscular mycorrhizal (C,F) trophic guilds. Significant differences between modalities were assessed using permutational multivariate analyses of variance (PERMANOVA) with 9,999 permutations. Blue labels indicate significant differences, with p-values categorized as follows: $p \leq 0.05$ (significant), $p \leq 0.01$ (highly significant), and $p \leq 0.001$ (very highly significant). The variables "S.type" stands for stand type and "S.status" for social status. The 10 taxa that have the highest contributions to the ordinations are labelled in each plot.

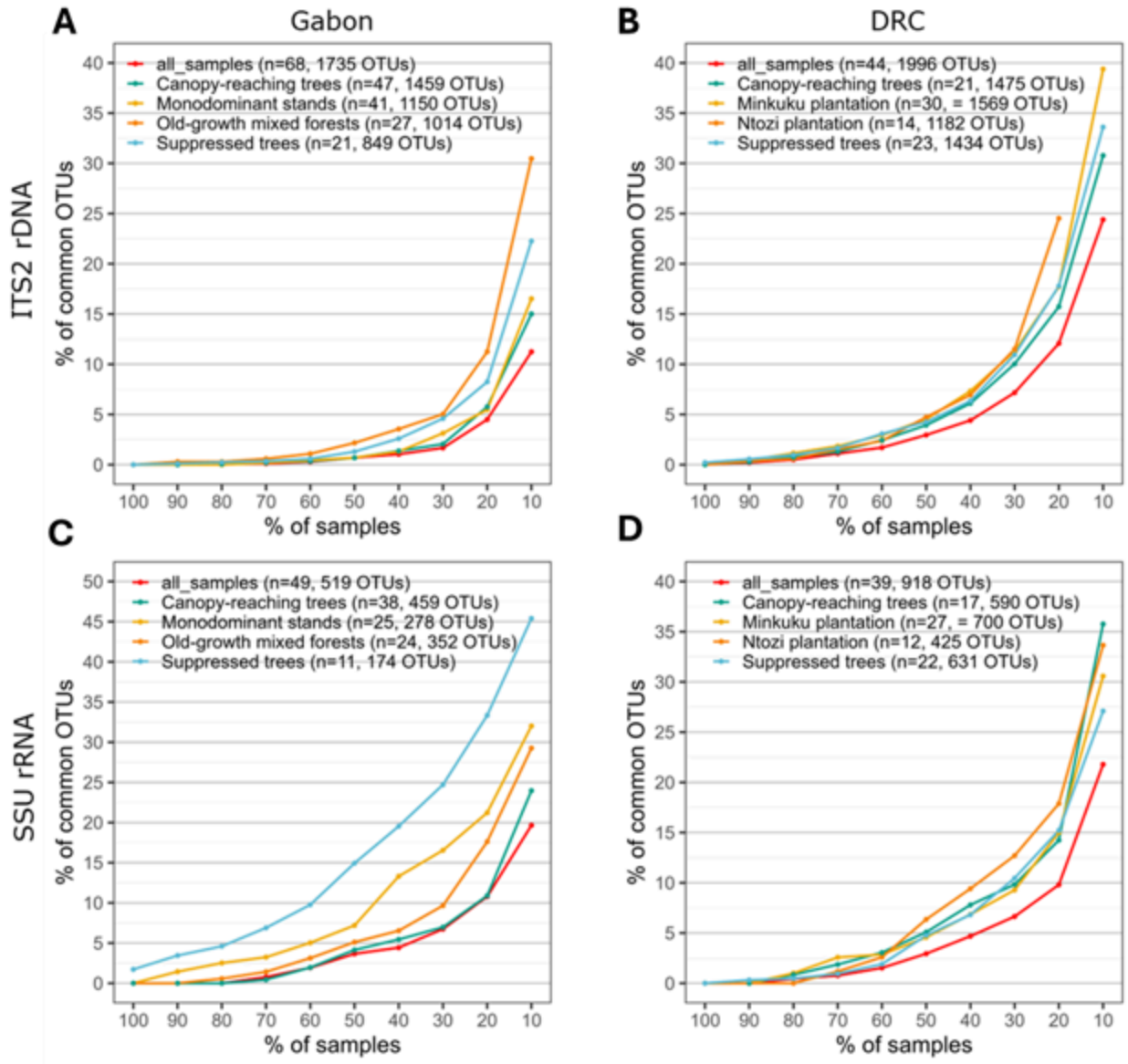


Figure 6

Proportions of shared OTUs between samples from natural stands in Gabon (A,C) and plantations in the Democratic Republic of Congo (DRC, B,D), based on the ITS2 rDNA (fungi-specific, A,B) and SSU rRNA gene (AM fungi-specific, C,D) regions.

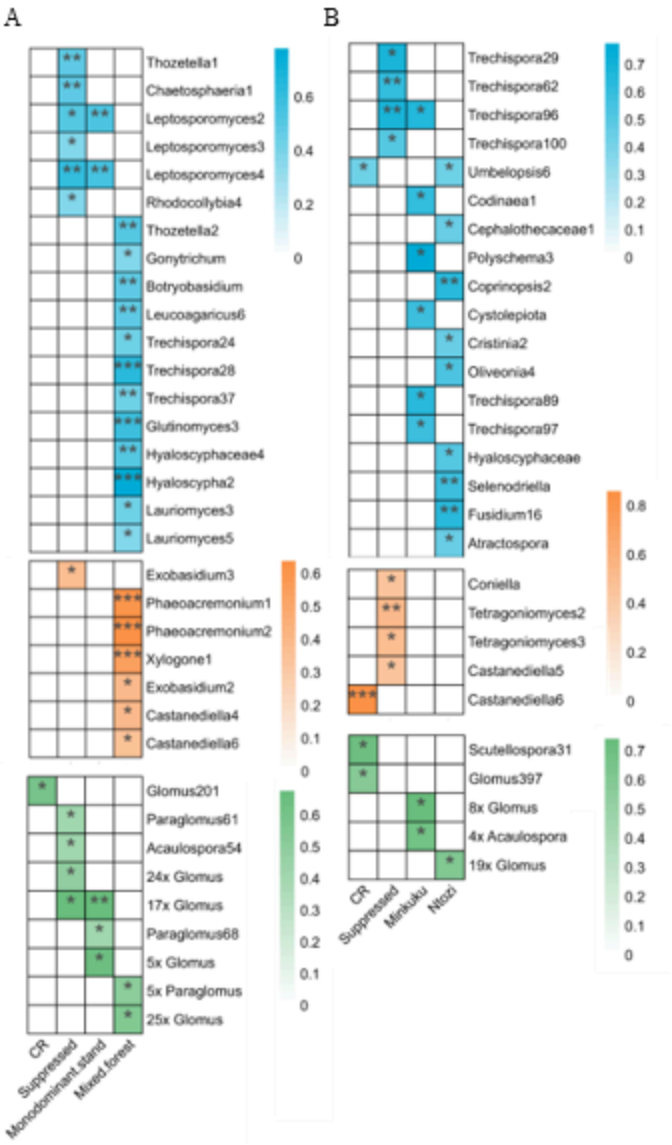


Figure 7

Heatmaps of significant taxa from Gabon (A) and the DRC (B) identified through indicator species analyses and Monte Carlo randomization tests. The color scale indicates indicator values (Indval). Asterisks represent p-values (** ≤ 0.05*significant, *** ≤ 0.01* highly significant, and **** ≤ 0.001* very highly significant). Heatmap colors correspond to trophic guilds: blue for saprotrophs, orange for pathotrophs, and green for arbuscular mycorrhizal (AM) fungi. Ectomycorrhizal (EcM) fungi are excluded, as they were only found in canopy-reaching trees (CR) of old-growth mixed forests (Mixed.forests) in Gabon. For AM fungi, the abundance of distinct OTUs within the same genus is grouped on a single line, with indicator values and p-values representing the mean of all OTUs.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- ArticleA.2.2SupplementaryMaterial.docx