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HIGH DIVERSITY AND VARIABILITY OF ROOT-ASSOCIATED FUNGI IN *AUCOUMEA KLAINEANA*, A MONODOMINANT CENTRAL AFRICAN TIMBER SPECIES

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Abstract

Aucoumea klaineana is the most important timber species in Central Africa, naturally forming monodominant stands. While soil fungi are crucial for plant growth, their role in promoting monodominance or supporting suppressed, lightdemanding 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, sampling both canopy-reaching vs. suppressed individuals, using ITS2 rDNA and 18S rDNA high-throughput sequencing. We identified high fungal diversity in both regions but found no "core mycobiota" across stand types or tree social status (canopy-reaching vs. suppressed). Fungal communities varied significantly between stand types, emphasizing a contextdependent nature. Moreover, no distinct fungal communities characterize the mycobiota of suppressed trees. Our findings indicate that fungal associations, including mycorrhizal ones, are unlikely to be a driver of monodominance in *A. klaineana*. These results highlight the need to consider alternative processes, not related to fungal interactions, such as root grafting, in explaining the persistence of suppressed trees and the dynamics of monodominant stands of *A. klaineana*. Finally, this study illustrates the highly variable and diverse belowground communities associated with *A. klaineana*, whose functions and interactions could contribute to the sustainable management of this major timber tree species.

Keywords

Monodominance ; Root-associated fungi ; Okoumé ; Soil microbiota ; Tropical forest ecology ; Mycorrhiza ; Timber

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Introduction

African tropical forests are highly diverse ecosystems, harboring between 4,600 and 6,000 tree species (Slik et al. 2015). 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. 2011a) 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. (2011a) 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, b; 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, Sapindales), is the most harvested timber species in Central Africa (FRMi 2018). This tree species is light-demanding, thriving in areas receiving 10% to 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. 2011a). However, studies on its root-associated fungi are lacking, likely due to methodological barriers (Guidosse et al. 2024b). The only existing records include

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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, lightdemanding 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 with 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 with 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 (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.

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The objectives of this study are to: (1) explore the diversity and identity 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); (2) evaluate whether these communities are shaped by neutral or nichebased processes, and assess the effects of stand type and tree social status on community diversity, composition and structure; and (3) identify any specific fungal taxa or functional groups that are more closely associated with dominant tree individuals, shaping a core microbiota 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.

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. 2018, 2019). 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).

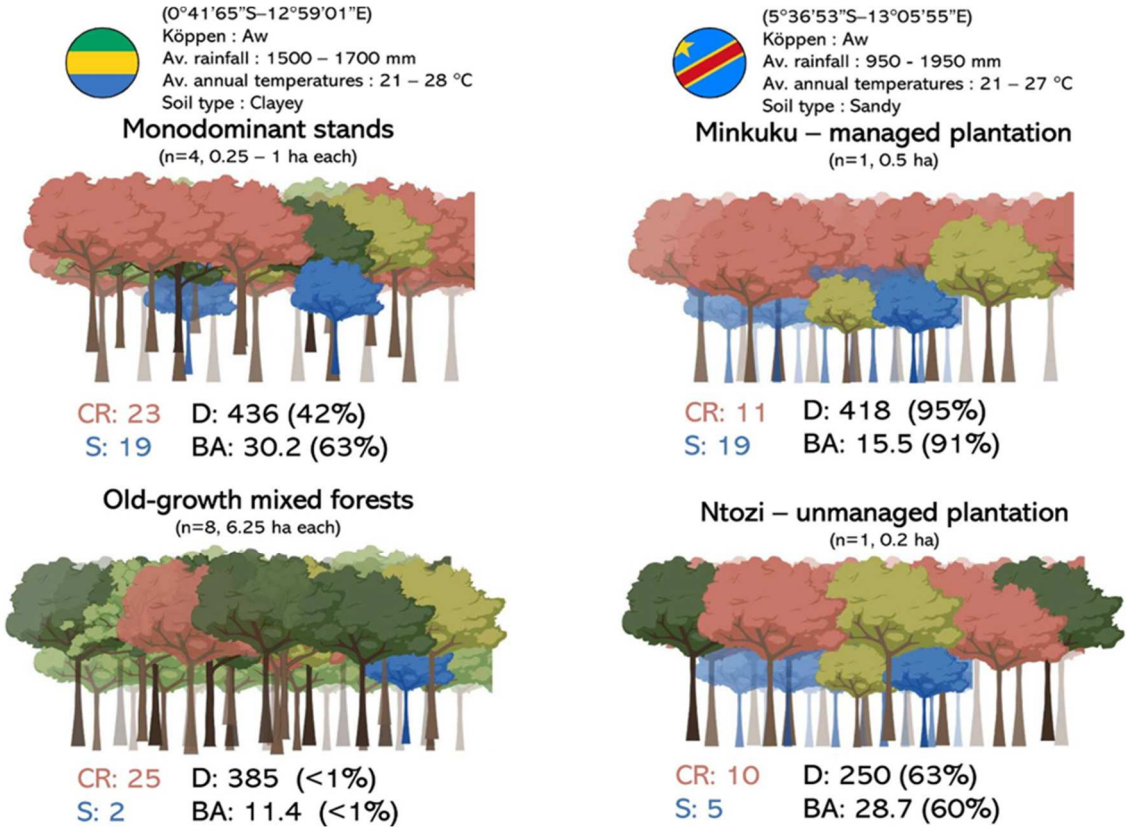

Fig. 1 Characteristics of the study sites and stands. Distribution of tree types: canopy-reaching A. klaineana (red, CR), suppressed A. klaineana (blue, S), and other species (green). The amounts of collected samples are represented by corresponding colours for each stand type. Tree density (D, N/ha) 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

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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.

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, gently washed with sterile water and passed through a 2 mm mesh sieve to remove soil and debris without damaging the tissue, 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.

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™ bead beater (MP Biomedicals, France) by 4 cycles of 30 s 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 18S rDNA gene was also amplified by the glomeromycotinan specific primer pair NS31 and AML2 (Morgan and Egerton-Warburton 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

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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′ T C G T C G G C A G C G T C A G A T G T G T A T A A G A G A C A G-[locus-specific sequence], while the reverse overhang sequence was 5′ G T C T C G T G G G C T C G G A G AT G T G T A T A A G A G A C A G-[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.

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 18S rDNA region, 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). Four samples presenting ≥ 60% of chimeric sequences or < 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 v10.0 (Abarenkov et al. 2024) for fungal ITS2 sequences and against the MaarjAM database v2021 (Öpik et al. 2010) for 18S rDNA 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 raw sequence reads were deposited in GenBank Bioproject accession No. PRJNA1214243.

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DIVERSITY ANALYSES

Downstream analyses were performed in 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 data using the 'phyloseq' package (McMurdie and Holmes 2013) for data manipulation and visualization.

Rarefaction curves were generated using the 'vegan' R package (Oksanen et al. 2025), which determined optimal sampling depths of 10,000 sequences for ITS2 rDNA and 3,000 sequences for 18S rDNA. 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 BrayCurtis 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 et al. 2025), 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.

Independently of the core mycobiota analysis, 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). This analysis was performed to test whether particular fungal taxa were consistently associated with the monodominance of *A. klaineana* or with the persistence of suppressed trees under low-light conditions. Indicator taxa were identified as described by Bakker (2008):

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$$A_{ij} = \overline{x}_{ij} \Big/ \sum\nolimits_j x_{i\bullet}$$

$$B_{ij} = n_{ij} \Big/ n_{\bullet j}$$

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

with A defined as specificity or relative abundance, i.e. the mean cover of taxa i in each stand types or tree social status modality (j) as a proportion of its mean cover in all groups; and B defined as fidelity or relative frequency, i.e. the proportion of trees in modality j on which taxa i occurs. 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

FUNGAL COMPOSITION

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 abundance of pathogenic fungi 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).

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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.

Regardless of the region, the most abundant families (Supplementary Materials 1–2) included Glomeraceae, as well as Chaetosphaeriaceae and Herpotrichiellaceae, which contain numerous endophytic fungi. Genera within these families, such as *Cladophialophora*, *Cyphellophora*, and *Knufia*, were frequently detected in root samples. Other detected genera, including *Hyaloscypha*, *Oidiodendron*, *Glutinomyces*, *Scytalidium*, and *Xylogone*, belonging to these families are largely composed of saprotrophs and potential pathogens that were also abundant across samples (Cannon and Kirk 2007; Newsham 2011; Vandepol et al. 2020).

Regarding the 18S rDNA 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.

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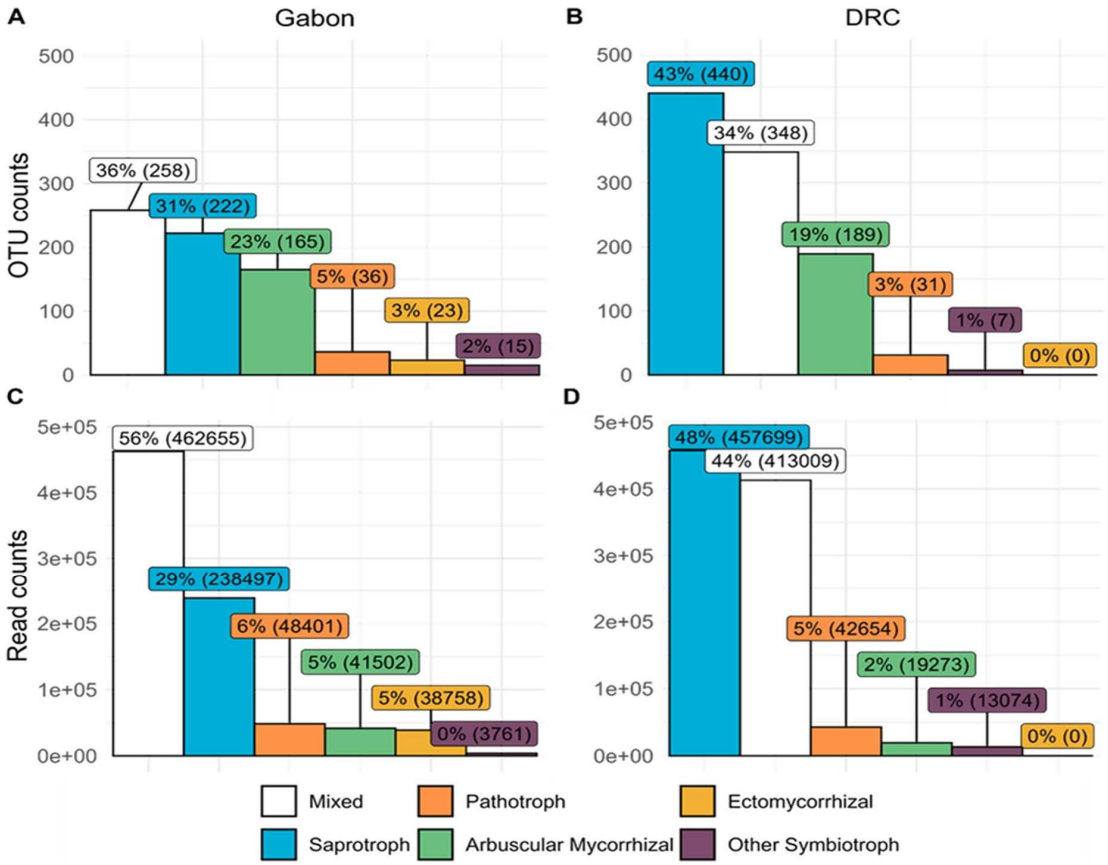

Fig. 2 Trophic guild distribution based on the number of OTUs (**A**, **B**) and sequence reads (**C**, **D**) obtained for samples from Gabon (**A**, **C**) and the DRC (**B**, **D**) samples after sequencing the ITS2 rDNA region. Fungal OTUs with uncertain trophic associations are categorized as "Mixed". The "Other Symbiotroph" group includes lichenized and epiphytic OTUs

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.

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ALPHA DIVERSITY ANALYSES

To assess within-sample fungal diversity, OTU richness, Shannon diversity index, and Pielou's evenness for all fungi as per trophic guild were calculated. 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. 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 or the primer pair (Supplementary Materials 3–6).

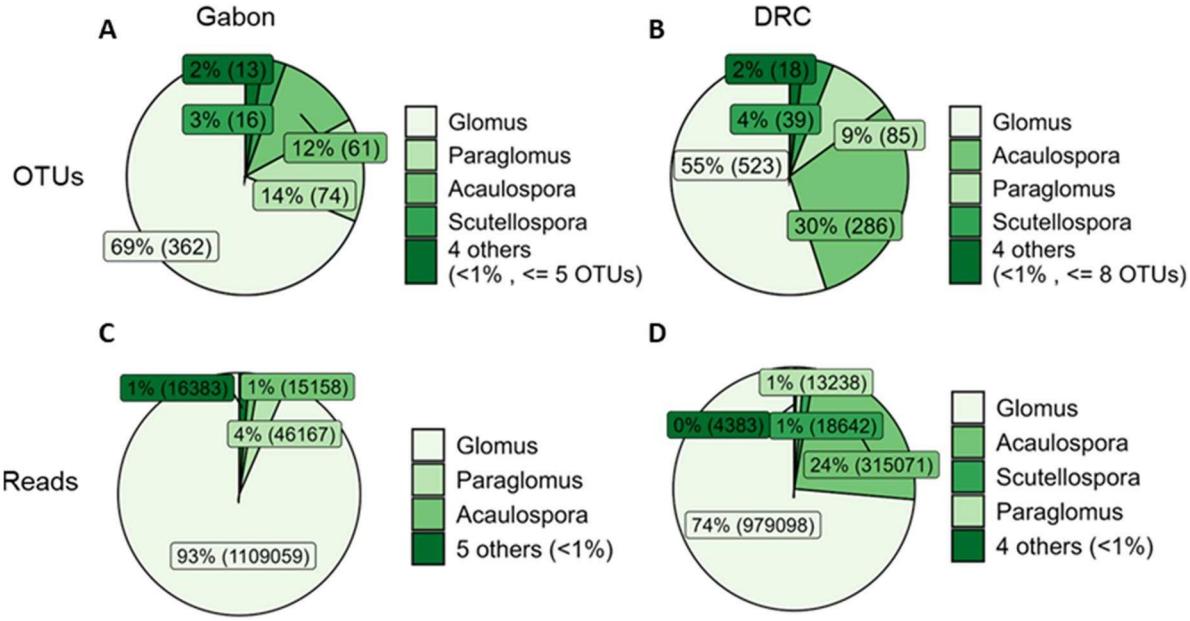

Fig. 3 Distribution of arbuscular mycorrhizal (AM) fungal taxa at the genus level in terms of OTUs counts (A, B) and sequence reads (C, D) obtained from Gabon (A, C) and the DRC (B, D) based on the glomeromycotinan-specific 18S rDNA

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 with 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 with Ntozi, indicating a more balanced saprotrophic community at Minkuku.

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, BrayCurtis p-value = 0.021), and AM fungi (18S, Bray-Curtis p-value = 0.002). However, no

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significant difference was found when considering all fungal OTUs (Bray-Curtis p-value = 0.426) (Supplementary Material 7).

In natural stands, tree social status significantly influenced saprotrophic (Bray-Curtis p-value = 0.003) and AM fungal communities (18S, 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. 4) and for every obtained fungal OTUs (Supplementary Materials 7–8) 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 Material 8, 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 18S rDNA region. Interestingly, the stand type showed a higher impact than tree social status on every fungal assemblage.

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 at genus level exhibited a low nestedness, showing a high turnover, with a WNODF score ranging between 0.70 and 19.75 (mean = 7.48, SD = 5.46), 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. However, symbiotrophic fungi in DRC plantations displayed a more structured pattern (overall WNODF = 19.75; genus-level = 40.07), suggesting that trees with fewer symbiotrophic taxa hosted subsets of richer communities. The low matrix fill (41%) indicates caution, as sparse data can constrain the detection of nestedness. Similarly, for AM fungi, although per-genus values reached relatively high levels (62.40 in the DRC), these results are difficult to interpret given the very limited genus pool (only *Glomus*, *Acaulospora*, *Scutellospora*, *Paraglomus*, and *Archaeospora).*

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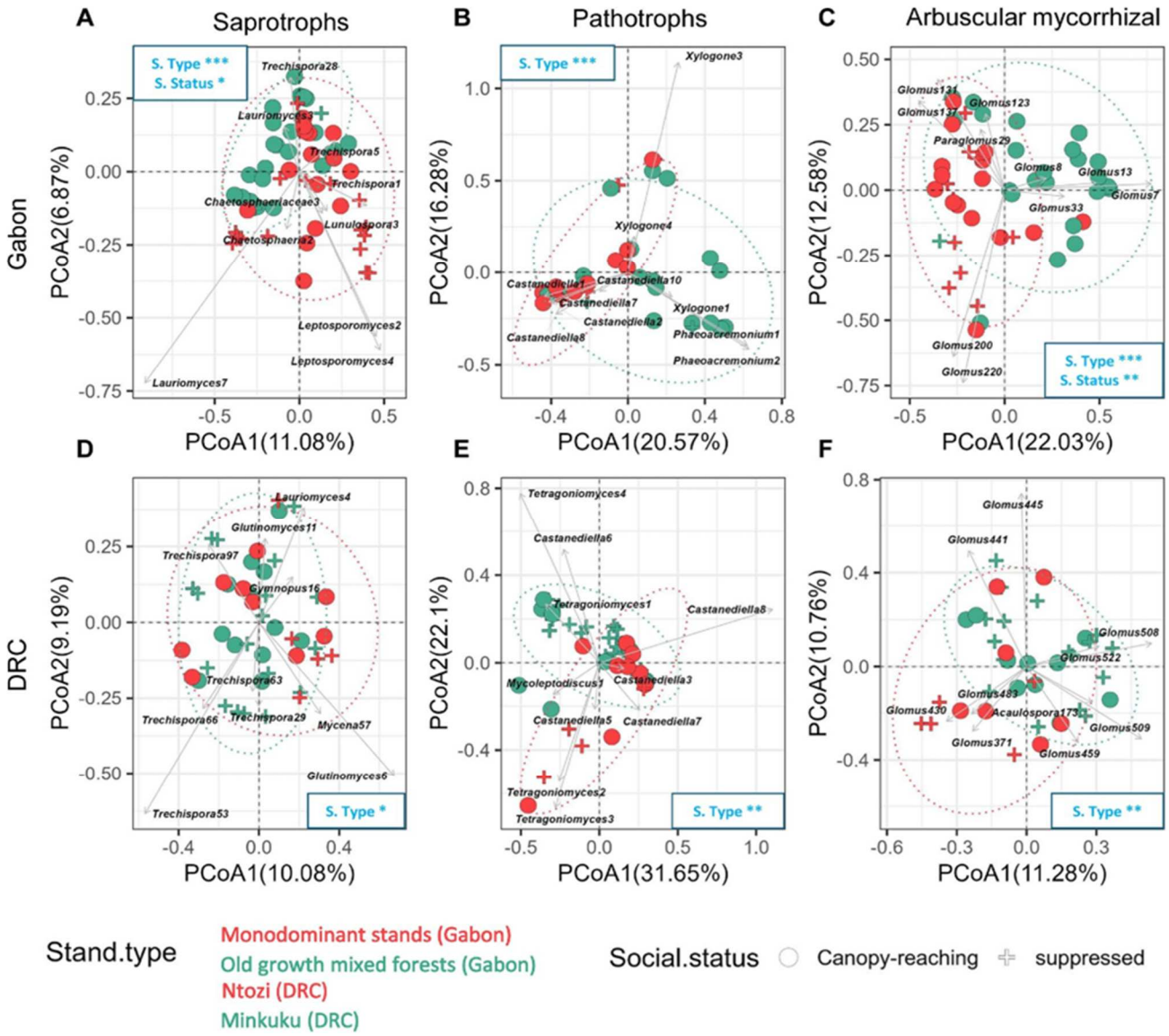

Fig. 4 PCoA plots based on bray-curtis dissimilarity matrices on OTUs obtained from Gabon (**A**, **B**, **C**) and the DRC (**D**, **E**, **F**) assigned to saprotrophic (**A**, **D**), pathotrophic (**B**, **E**) through the ITS2 rDNA region, and arbuscular mycorrhizal (**C**, **F**) through the 18S rDNA. 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

CORE AND SPECIFIC INDICATOR MYCOBIOTA

CORE MYCOBIOTA

A very low proportion of shared OTUs, or even genera, was observed between samples, irrespective of the country, stand type, or tree social status, which hindered any identification of core mycobiota (Fig. 5). The only exception is for the suppressed trees in Gabon, where, when studying the 18S rDNA (Fig. 5C), three *Glomus* OTUs were common across all samples (n = 11).

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WNODF [1–100]		Overall	Per sample	Per genus	Fill (%)
Gabon	All (ITS2)	4.75	5.80	3.74	53
	Saprotrophs (ITS2)	7.80	7.56	8.63	9
	Pathotrophs (ITS2)	3.11	2.83	10.44	21
	Symbiotrophs (ITS2)	8.44	8.37	13.35	18
	AM fungi (18S)	0.70	0.46	28.33	29
DRC	All (ITS2)	4.01	4.80	3.66	8
	Saprotrophs (ITS2)	12.56	12.89	12.10	14
	Pathotrophs (ITS2)	8.45	7.57	30.64	21
	Symbiotrophs (ITS2)	19.75	19.42	40.07	41
	AM fungi (18S)	5.25	4.79	62.40	50

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

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 18S rDNA 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.

Repeating the analysis at the genus level confirmed the absence of genera consistently shared across all ITS2 rDNA samples (Fig. 5E, F). This excludes the existence of a universal core mycobiota for *A. klaineana* in general, and even within monodominant stands, where only two genera were shared across 70% of samples (n = 28). The only genus detected in ≥ 80% of all samples was *Cladophialophora* spp. (Herpotrichiellaceae, Chaetothyriales; Supplementary Material 9), a dark septate endophyte known to influence plant growth (Diez-Hermano et al. 2024). In contrast, in the DRC 21 genera were shared among ≥ 80% of samples, occurring broadly across stand types and tree social statuses, without specificity to a given plantation or tree social status (Supplementary Material 9).

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. 6). Canopy-reaching trees harbored the fewest indicator taxa in both the DRC and Gabon (Fig. 6), with the exception that all EcM-associated OTUs were obtained from samples collected from dominant trees in the old-growth mixed forests of Gabon. 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

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Glomus sp. and *Scutellospora* sp. as AM fungi. In natural stands, only one *Glomus* sp. was identified as indicator.

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 high-throughput sequencing of ITS2 rDNA and 18S rDNA 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. 5) but instead complex and diverse fungal assemblages, of symbiotic as well as saprotrophic and pathogenic fungi.

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. 5). In natural forests, only slight differences in saprotrophic and AM fungal guild composition were observed (Fig. 4). Despite minor richness differences, suppressed trees hosted more AM fungal indicator taxa (43 OTUs) compared with 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 Neuenkemp 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. 4). 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 differences in terms of fungal communities emerged across the factors studied, highlighting the complexity of these interactions.

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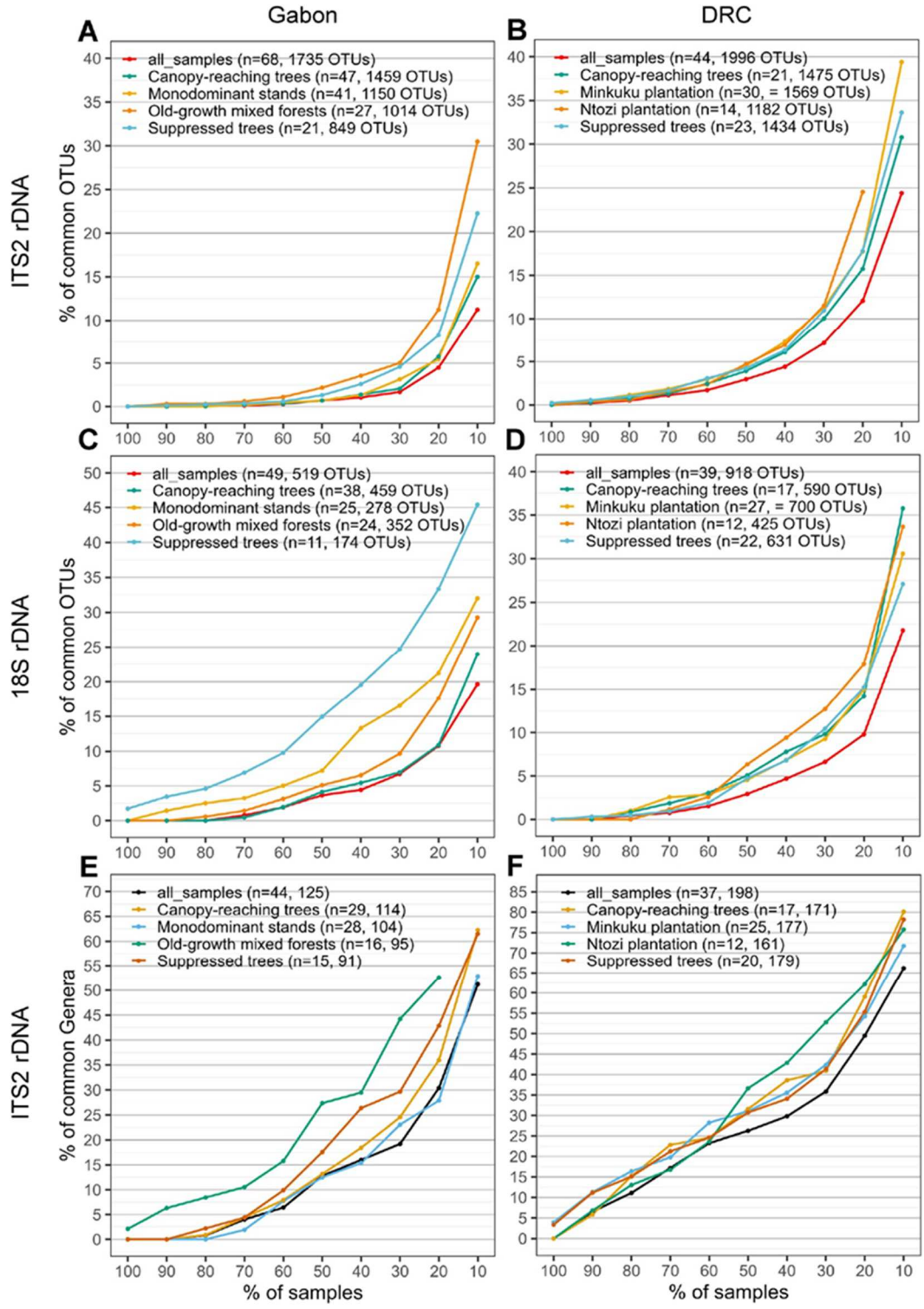

Fig. 5 Proportions of shared OTUs between samples from natural stands in Gabon (A, C, E) and plantations in the DRC (B, D, F), based on the ITS2 rDNA (fungi-specific, A,B) and 18S rDNA (glomeromycotinanspecific, C, D) regions. Shared proportions at the genus level are also shown for Gabon (E) and the DRC (F) using ITS2 rDNAProportions of shared OTUs between samples from natural stands in Gabon (A, C) and plantations in the DRC (B, D), based on the ITS2 rDNA (fungi-specific, A, B) and 18S rDNA (glomeromycotinan-specific, C, D) regions. Shared proportions at the genus level are also shown for Gabon (E) and the DRC (F) using ITS2 rDNA

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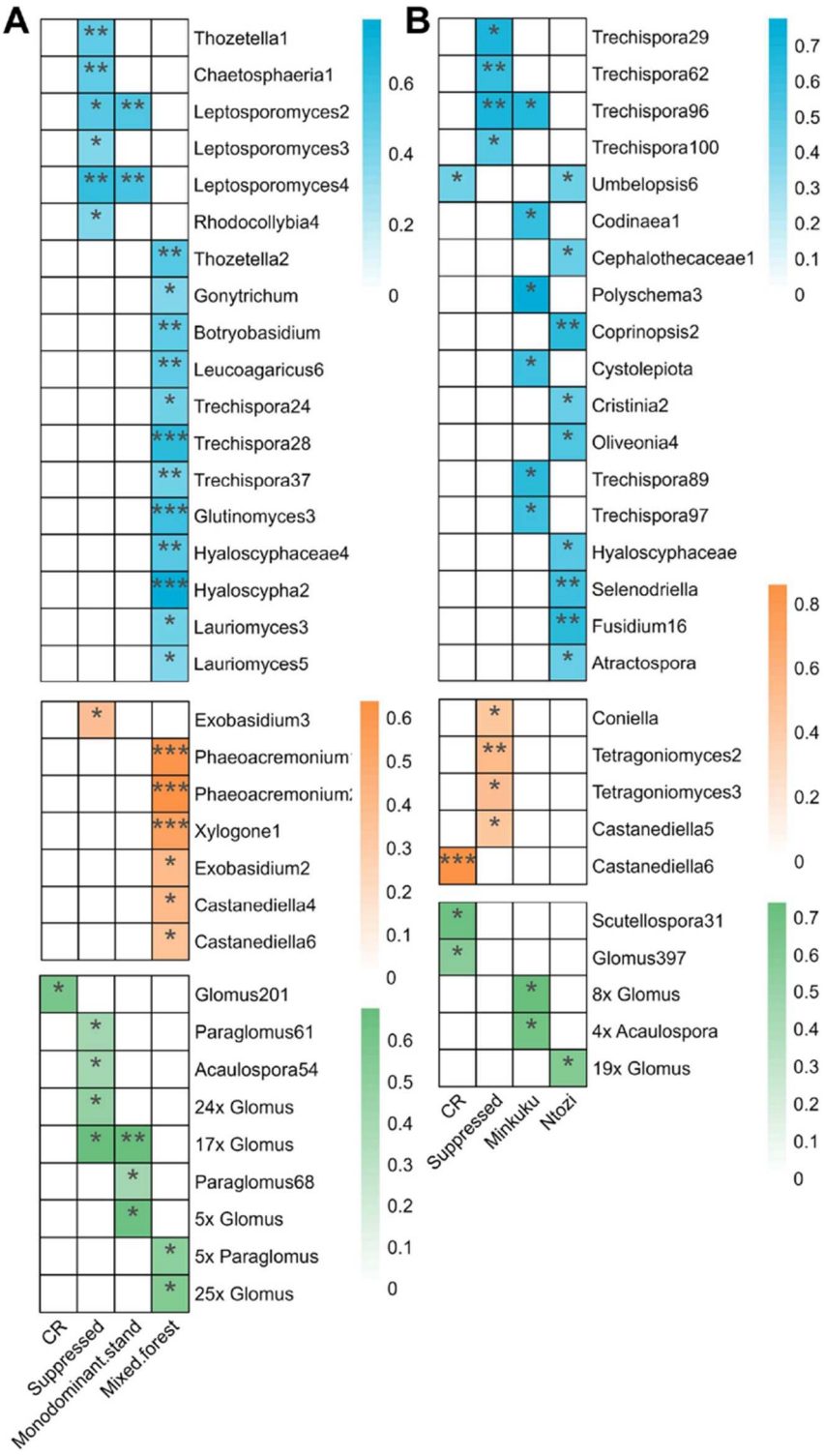

Fig. 6 Heatmaps of significant taxa from Gabon (A) and the DRC (B) identified through indicator species analyses and Monte Carlo randomization tests. The color scale indicates indicator values (indval). Asterisks represent p-values (* ≤ 0.05 significant, ** ≤ 0.01 highly significant, and *** ≤ 0.001 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

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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 multi-specific rootlets samples. 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. 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.

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. 6).

Regarding the ITS2 rDNA region, 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. 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, as in comparison, AM fungi were detected in all samples using the 18S rDNA barcode.

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). Like *A. klaineana*, these species possess large rootlets with few root hairs, with large cortical area and root diameter to facilitate colonization by mycorrhizal partners (Brundrett and Tedersoo 2018; Kong et al. 2014), consistent with

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the typical 'outsourcing' strategy of allocating carbon to symbionts. (Bergmann et al. 2020; Hogan et al. 2023; McCormack and Iversen 2019). Instead, it seems that *A. klaineana*'s rootlets primarily obtain nutrients independently, with limited use on fungal symbioses, which is characteristic of saprotrophic fungi dominance.

Sequencing the 18S rDNA 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).

Comparatively, EcM fungi were notably absent in *A. klaineana* monodominant stands (except for one OTU) and plantations, declining previous hypothesis by Leroy Deval (1974); Peh et al. (2011a) that suggested that EcM fungi may support *A. klaineana* monodominance as shown for many species in tropical ecosystems (e.g., Diedhiou et al. 2014; Ebenye et al. 2017; Fukami et al. 2017; Henkel 2003; Liang et al. 2020). In contrast their presence and mostly their high read counts (5% of sequences, equal to AM fungi, Fig. 2) in old-growth mixed forests might come from potential contact with fungi associated with neighboring tree without functional relevance to *A. klaineana* (Amend et al. 2010; Smith and Read 2008). Indeed, 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), and could associate with *Anthonotha fragrans* (Baker f.) Exell & Hillc and *Julbernardia pellegriniana* Troupin two EcM-associated trees species (Bâ et al. 2012; Bakarr and Janos 1996) observed at less than 10 m from our sampled *A. klaineana* trees from old-growth mixed forests (Supplementary Material 10).

Despite the low proportion of mycorrhizal sequences in *A. klaineana* compared with other trophic guilds, rootassociated fungal communities were nevertheless diverse. Instead, across both regions, the Chaetosphaeriaceae, and Herpotrichiellaceae families dominated the root mycobiota (Supplementary Materials 1, 2). Notably, *Cladophialophora* and *Knufia*, both dark septate endophytes (DSE) or closely related taxa, were particularly abundant and may play important roles in the persistence of *A. klaineana* monodominant stands by enhancing nutrient acquisition and stress tolerance of roots even though the role of these fungi are still unclear (Newsham 2011).

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 organic matter turnover (Talbot et al. 2015),

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aligning with the slow litter decomposition rate observed in *A. klaineana* stands (Leroy Deval 1974), even after logging activities (Midoko Iponga et al. 2020). 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.

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 1973, 1974). As for *Dacryodes excelsa* Vahl, another Burseraceae but shade-tolerant and late-successional (Basnet et al. 1993), root grafting in *A. klaineana* could help suppressed trees survive and explain how it maintains its dominance by enabling direct transfer of water and nutrients among conspecifics, as a potential alternative to the role attributed to consistent fungal community patterns and limited reliance on abundant mycorrhizal 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 rootassociated fungal communities in *Aucoumea klaineana*, Central Africa's most harvested timber species, using ITS2 rDNA and 18S rDNA 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 fungal associations were not a primary driver of monodominance in *A. klaineana* nor individual tree social status. This was also supported by the lack of distinct core fungal communities related monodominant stands and to the status of suppressed trees. Arbuscular mycorrhizal (AM) fungi were consistently present, confirming the AM status of *A. klaineana*, and rejecting the hypothesis of an EcM-related monodominance. Other mechanisms, such as the root grafting processes frequent in these stands, could enhance nutrient-sharing and shape stand monodominance. Further research should examine *A. klaineana*'s reliance on belowground strategies including root grafting, root exudate processing, and litter dynamics in interactions with root-

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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.

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AUTHOR CONTRIBUTIONS

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.

DATA AVAILABILITY

Data will be made available on request.

DECLARATIONS

Competing interests The authors declare no competing interests.

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