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RESEARCH ARTICLE

Fungal succession, litter decomposition and root nitrogen supply in a tropical oil palm plantation

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Abstract

Background and Aims Industrial oil palm plantation management degrades tropical soils and disrupts ecosystem functions. Applying oil palm leaf litter can help restore soil fertility, but the underlying fungal-driven decomposition and nitrogen recycling remain understudied. This study examines fungal succession in degrading oil palm leaf litter, the fate of litter-derived nitrogen in soil and roots, and the potential for the restoration of fungal biodiversity.

Methods We produced ^{15}N-labelled oil palms and exposed dry leaf litter in 2-mm and 37-µm mesh bags within a plantation. The finer mesh allowed microbial access but restricted roots and most detritivores. We measured litter mass loss, carbon and nitrogen dynamics, and fungal communities via ITS barcoding over six months. Root ingrowth and soil chemistry were also analyzed.

Results Litter mass decreased by 70% in both mesh types, with soil accumulating litter-derived ^{15}N. Fine roots grew into the mesh after three months and took up ^{15}N**,** demonstrating nitrogen recycling. Fungal succession displayed clear temporal patterns: early colonizers thrived with higher C/N ratios (Hypocreales, Pleosporales, Chaetothyriales), while late colonizers (e.g., Sordariales, Pleosporales, Chaetosphaeriales)

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correlated with C degradation. Arbuscular mycorrhizal fungi increased with declining C/N ratios and coincided with root growth.
Conclusions Oil palm litter enhances nitrogen availability, fosters AMF diversity**,** and improves degraded soils. The numerous uncharacterized fungi in litter decomposition highlight the need for further research into their functional roles for sustainable soil restoration.

Keywords Arbuscular mycorrhiza · *Elaeis guineensis* · Diversity · Functional traits · Fungal metabarcoding · Litter degradation · Mycorrhiza · Nitrogen uptake · Soil restoration

Introduction

In south-east Asia, palm oil production is a major source of income but has detrimental effects on the abiotic and biotic environment (Dislich et al. 2017; Iddris et al. 2023). In Indonesia, the world-largest producer of palm oil (Monzon et al. 2021), the area of oil palm plantations increased massively in the past decades, now replacing approximately 32% of the country´s native forests (Gaveau et al. 2022). Most oil palms (*Elaeis guineensis*) are grown in industrial plantations covering large areas (> 50 ha per plantation) with even-aged mono-specific palm trees planted at regular distances. These plantations are managed for high productivity through the extensive use of fertilizers and herbicides for weed control (Dislich et al. 2017; Wenzel et al. 2024). These treatments have a significant negative impact on the biodiversity of most groups of above- and belowground taxa, except for soil microbes (Montoya-Sánchez et al. 2023; Zemp et al. 2023). Microbial diversity is not or very little affected in plantation soil, but its composition is drastically altered (Berkelmann et al. 2018; Ballauff et al. 2021; Carneiro De Melo Moura et al. 2025).

Soil fungi are critical drivers of biogeochemical processes. Saprotrophic fungi mine litter for carbon, thereby, making nitrogen (N) and other minerals available for plants (Setälä and McLean 2004; Talbot et al. 2013). This process is promoted by a succession of fungi, usually starting with the degradation of simple organic compounds, followed by the breakdown of more complex polymers (Voříšková and Baldrian 2013; Purahong et al. 2016). Mycorrhizal fungi form symbiotic associations with roots, utilizing carbon from photosynthesis to supply minerals to the trees (Van Der Heijden et al. 2008). Mycorrhizal hyphae play a crucial role in carbon allocation from above- to belowground compartments (Brundrett and Tedersoo 2018). The interplay of fungal soil communities is vital for ecosystem functions and services such as nutrient supply, carbon sequestration, and pathogen protection (Baldrian 2017).

Efforts are being made to implement sustainable management practices in oil palm plantations to increase biodiversity and ecological functions without or minimal economic tradeoff (Darras et al. 2019; Grass et al. 2020; Montoya-Sánchez et al. 2023; Paterno et al. 2024). For example, a moderate reduction in fertilizer use, which does not affect yield (Darras et al. 2019) can increase arbuscular mycorrhizal fungal (AMF) root colonization (Ryadin et al. 2022). Mulching with palm fronds can enhance beneficial microbial activities, stimulate soil N cycling, thereby increasing soil fertility and health (Comte et al. 2012; Rüegg et al. 2019; Formaglio et al. 2021). Given that oil palms require large amounts of N to sustain their high productivity and their roots are highly efficient at N uptake (Edy et al. 2020), these practices offer a promising route to maintaining yields while reducing reliance on synthetic fertilizers. In addition to microbes, soil fauna is also involved in nutrient turnover by feeding on roots, fungi, and bacteria (Filser et al. 2016; Tao et al. 2016).

Our knowledge on the composition of fungal decomposer communities in typically managed oil palm plantations and their contributions to root nutrient uptake is limited. To address this gap and distinguish between the impact of microbes and other soil processes, we exposed leaf litter in two different mesh bag types: one with pore widths of 37-µm, allowing fungal ingrowth, and another with pore widths of 2-mm, additionally permitting access for fine roots and soil fauna to the litter. We expected that mesh bags with larger pores would result in greater fungal diversity because mobile organisms can disperse fungal spores in their environment and increase substrate availability from root exudates and necromass ingress (Philippot et al. 2013; Yang et al. 2017; Rivera et al. 2025). We hypothesized (1) that the differences in litter accessibility result in different fungal communities and different decomposition rates. We further

hypothesized (2) that the ecological functions of the fungal communities are associated with distinct stages of litter decay and (3) promote litter-derived N supply to fine roots. The overarching aim of this study was to investigate fungal communities during the degradation of oil palm frond leaflets and track the path of litter-derived nitrogen (N) into roots using ^{15}N-labelled frond leaf litter.

Materials and methods

Sample preparation

Young oil palm (*Elaeis guineensis*) saplings were purchased from a local tree nursery (Jambi, Indonesia). They were potted in growth containers, grown for 11 months, and irrigated with tap water as needed. Every 24 days, the saplings were irrigated with 100 ml of 2 mM $^{15}NH_4Cl$ (99% ^{15}N, CK Isotopes, Leicestershire, United Kingdom). Control saplings were irrigated with $^{14}NH_4Cl$. After 11 months, both labelled and non-labelled saplings were harvested. The newly formed leaves were collected, dried at 40 °C, and used as leaf litter in the experiment.

Nylon fabric (CRP Import—Export GmbH, Hamburg, Germany) with pore sizes of 2 mm (for root and hyphal ingrowth) and of 37 µm (for hyphal ingrowth) were used to prepare mesh bags. The fabric was cut into 3 cm × 10 cm pieces, sewn into bags, and filled with 3.0 g of either ^{15}N-labelled or non-labelled fragmented oil palm leaflets (without fronds) and sealed by stitching.

Site, exposure and harvest of the mesh bags

We used the experimental area in a state-owned, large-scale (2025 ha) industrial oil palm plantation (PTPN VI, central coordinates: longitude 103.27056, latitude −1.786861), which was part of the EFForTS CRC 990 (Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems) project, located in Jambi province on Sumatra (Indonesia). Details on oil palm management and environmental conditions have been reported previously (Drescher et al. 2016; Darras et al. 2019). The climate is humid tropical with an average annual precipitation of 2075 ± 94 mm and two rainy seasons peaking around March and December. The average annual temperature is 26.7 ± 0.2 °C. The soil is an Acrisol with a sandy loam structure and a pH of 4.3. The soil contained the following nutrient elements (mg g^{-1} d.wt.): N 1.4, C: 23.7, K: 0.101, Ca: 0.201, Mg: 0.021, Mn: 7.156, Fe: 37.259, P: 0.130 (Iddris et al. 2023).

The oil palms were planted at a density of 142 plants ha^{-1} with a spacing of 8 m and were approximately 17- to 19-year-old during the experiment. The rows between the palms were alternatingly free alleys (inter-rows) or used for depositing palm fronds obtained during pruning and oil palm bunch harvesting (Comte et al. 2012). The plantation was managed conventionally, including fertilization (N-P-K: 260–50–220 kg ha^{-1} a^{-1}, split into two doses per year) and herbicide treatments (1.5 l glyphosate ha^{-1}, split into four doses per year). Fertilization and herbicide treatments were applied to the soil underneath the palms in a circle of 2 m around each tree. The inter-rows were not fertilized but were treated with 0.75 l glyphosate ha^{-1} (split into two applications per year) (Iddris et al. 2023).

We installed our experiment in the inter-rows because they were not affected by a previous influence of degrading palm fronds and were in areas least exposed to fertilizer. Small holes, approximately 7 cm deep, were dug into the mineral soil. A litter layer was not present and marginal organic debris was removed. Each mesh bag, containing either ^{15}N-labelled or non-labelled litter, was inserted upright (5 cm long) into the hole and covered with a 2-cm-thick soil layer. Pairs of mesh bags with 2 mm and 37 µm pore size were placed next each other. The distance to the next pair of mesh bags was 40 to 60 m.

Soil exposure of the mesh bags started on February 13, 2019. Collection of the mesh bags ($n = 5$ for ^{15}N-labelled samples per mesh bag type, $n = 3$ for non-labelled samples per mesh bag type) took place after 1, 3 and 6 months. At the harvest time points, we measured mean soil humidity of 28.6 ± 11.5%, 17.3 ± 3.1%, and 45.9 ± 9.0% and mean soil temperatures of 28.0 ± 1.3 °C, 27.9 ± 1.3 °C, and 29.4 ± 1.0 °C for February, May and August, respectively. At harvest, the mesh bags were removed from the soil, placed individually in plastic bags and transported on cool packs in cooling boxes to Jambi University, where they were stored at −15 °C. For transfer to Göttingen University (Göttingen, Germany), the frozen samples were transported by airfreight with cool

packs in cool boxes. On arrival, the samples were still frozen and stored at −20 °C.

Sample preparation

Each frozen mesh bag was weighed, opened and its content collected in a Petri dish, which was placed on ice. The empty bag weight was subtracted from the total mesh bag weight to determine the weight of the mesh bag content. The content of the bag was sorted according to litter, roots and soil under a dissecting microscope (Leica M205 FA; Leica Microsystems GmbH, Wetzlar, Germany). We controlled few root samples by cross-sectioning; they had a diameter of approximately 100 µm. The weight of each fraction was recorded. Aliquots of litter samples were removed and stored at −20 °C. All remaining samples were dried for one week at 40 °C (dry mass). Total dry litter biomass was calculated using the dry to fresh mass ratio.

Carbon, nitrogen, ^{13}C and ^{15}N analyses

Dry soil and litter samples were milled in a ball mill (Type MM400, Retsch, Haan, Germany) to a fine powder. We weighed 10 mg of soil or 2 mg of litter per sample into tin capsules (VA Analysentechnik, Meerbusch, Germany) on a super-micro balance (S4; Sartorius, Göttingen, Germany). Roots were present in low amounts (< 10 mg in 11 out of 17 root-containing samples) as small fragments. Milling results in electrostatic attachment of small amounts of powder to the container walls and thereby causing loss of low amounts of samples, which was critical for the roots. Therefore, we weighed 1 mg of root fragments without milling into the tin capsules (Khokon et al. 2023). The contents of N and C and the fractions of ^{15}N and ^{13}C in the samples were analyzed using separate isotope mass spectrometers for the measurements of labelled and non-labelled samples (labelled: Delta C, Finnigan MAT, Bremen, Germany; Interface: Conflo III; Thermo Electron Corp., Bremen, Germany; element analyser: NA1108; Fisons-Instruments, Rodano, Milano, Italy and non-labelled samples: Delta V Plus, Finnigan MAT; Interface: Conflo III; Finnigan MAT; element analyzer: NA1110; Fisons-Instruments). Acetanilide was used as the calibration standard.

All ^{15}N data presented in the figures and the tables pertain to ^{15}N originating from the labelled oil palm leaf litter after correction for the natural abundance of ^{15}N. The natural abundance of ^{15}N in litter (0.3686 ± 0.0005), roots (0.3670 ± 0.0005), and soil (0.3683 ± 0.0005) was determined and these values were used to calculate the enrichment of ^{15}N as follows:

^{15}N atom-% excess (APE) = ^{15}N atom-% in the labelled sample – ^{15}N atom-% in the non-labelled sample.

The ^{15}N concentration per unit of dry sample was calculated as:

^{15}N (µg g^{-1} d.wt.) = APE * 1000/100 * N.

Here, N represents the N concentration of the sample (mg N g^{-1} d.wt.). The total dry mass of the sample was used to determine the amount of C, N and ^{15}N per mesh bag:

C amount (mg mesh bag^{-1}) = C (mg g^{-1} d.wt.) * total sample dry mass (g).

N amount (mg mesh bag^{-1}) = N (mg g^{-1} d.wt.) * total sample dry mass (g).

^{15}N amount (µg mesh bag^{-1}) = ^{15}N (µg g^{-1} d.wt.) * total sample dry mass (g).

DNA extraction and fungal community analysis

Frozen leaf litter was milled in a ball mill (Type MM400, Retsch, Haan, Germany) to a fine powder. DNA extraction and processing were conducted as previously described (Brandt et al. 2024). DNA was extracted from milled litter samples using the DNeasy PowerSoil Kit (Qiagen, Venlo, Netherlands) and subsequently cleaned with the DNeasy PowerClean Cleanup Kit (Qiagen, Venlo, Netherlands) following the manufacturer´s instructions. The ITS2 region was amplified using the fungal specific markers ITS3 KYO2 (Toju et al. 2012) and ITS4 (White et al. 1990) and cleaned with MagSi-NGSPreb Plus Magnetic Beads (MagnaMedics GmbH, Aachen, Germany). Amplicon sequencing was performed on the MiSeq platform using the MiSeq Reagent Kit v3 (Illumina Inc., San Diego, USA) at the Göttingen Genomics Laboratory. Primer sequences were removed using cutadapt v.2.1 (Martin 2014) and quality filtering was carried out using fastp v.0.21.0 (Chen et al. 2018) with a size filter of minimum 120 base pairs and a mean quality ≥ 20 on a sliding window of 10 base pairs. An amplicon sequence variant (ASV) library was generated using vsearch v.2.7.0

(Rognes et al. 2016) for dereplication, denoising (using the unoise algorithm) and chimera detection both de-novo and against the fungal reference database UNITE v.8.97 (Kõljalg et al. 2013). Taxonomic annotation was performed using the blast algorithm (Camacho et al. 2009) as implemented in the classify-consensus-blast function of qiime2 v.2020.8.0 (Bolyen 2019). Functional annotation of fungal ASVs was carried out using FunGuild v1.1 (Nguyen et al. 2016). All quality filtered reads were mapped against the ASV library with a similarity threshold of 0.97 (corresponding to "operational taxonomic units", OTU) using vsearch to generate the count table. OTUs not classified as fungi were excluded from the count table and the table was rarefied to the minimum number of counts per sample (37,267).

Statistical analyses

Statistical analyses were performed using the program Statgraphics Centurion v 18.1.12 (Statgraphics Technologies, The Plains, Virgina, USA). Data are presented as means of $n=5\pm$SE, unless otherwise specified. Normal distribution (Skewness and Kurtois ranging from −2 to 2) and variance homogeneity (modified Levene test) were tested and data were log-transformed when necessary to meet the assumptions of the model. General Linear Models (GLM) with "mesh type" and "exposure time" as fixed factors were developed. In cases where the models indicated significant differences between means at $p<0.05$, a post hoc test (Tukey HSD) was conducted. If transformation did not result in normally distributed data structures, a rank test (Kruskal Wallis) was applied, followed by pairwise comparisons of rank groups using the Bonferroni procedure. Associations between fungal abundances and leaf traits were determined using Spearman rank correlations. Diversity indices of fungi (Richness, Shannon Index, Chao1), redundancy analysis (RDA) based on Bray Curtis distances, and PERMANOVA were calculated using the software PAST version 5 (Hammer and Harper 2001). Heatmaps were generated with Clustvis (Metsalu and Vilo 2015).

Results

Biomass, C, N and ^{15}N dynamics in litter bags

After one month of exposure in soil, 2-mm mesh bags lost about half of their initial mass, while 37-µm mesh bags lost about 30% (Fig. 1a). By six months, both mesh bag types had similar losses accounting for 82% and 79% of their initial mass, respectively (Fig. 1a). An interesting difference was the massive soil incorporation in the 2-mm mesh bags (Fig. 1a). The contrasting dynamic of litter loss and soil incorporation resulted in a final total mass similar to the initial weight in the 2-mm mesh bags (Fig. 1a).

The initial N concentration in the litter was 22.8 ± 0.3 mg N g^{-1} dry mass corresponding to approximately 68 mg N in the mesh bags. After one month, the 2-mm mesh bags lost 55% and the 37-µm mesh bags 27% of their N content (Fig. 1b). The decline rate in the 37-µm mesh bags was not significantly different from that in the 2-mm mesh bags (see slopes in Fig. 2). However, the intercept indicated greater initial loss from the 2-mm than from the 37-µm mesh bags (17% versus −2.7%, $p<0.001$). The overall N loss in the 2-mm mesh bags was partially compensated by N in newly captured soil (2.5 ± 0.7 mg N g^{-1}) within the mesh bags (Fig. 1b).

The initial ^{15}N enrichment in the litter was 1.58 ± 0.23 APE, corresponding to a total amount of 828 µg ^{15}N per mesh bag. The loss of ^{15}N from the litter bags was similar to that of N (Fig. 1c, slopes in Fig. 2). Additionally, ^{15}N was present in newly accumulated soil in the 2-mm mesh bags, showing that litter degradation contributed to soil N enrichment (Fig. 1c). The accumulation of soil in the 2-mm mesh bags increased the amount of ^{15}N from 1 to 37 µg per mesh bag within six months ($F_{2,14}=24.0$, $p_{time}<0.001$).

C and N concentrations in litter bags

The initial C concentration in the litter was 437 ± 7 mg g^{-1} dry mass and remained stable in the 37-µm mesh bags over the 6-month exposure (Fig. 1d). In the 2-mm mesh bags, litter C concentrations were lower after 3- and 6-month exposure than in the 37-µm mesh bags (Fig. 1d). In contrast to C, the N concentrations increased in litter in the 37-µm mesh bags and remained stable in the 2-mm mesh bags (Fig. 1e). As a result, the C/N ratios declined during the 6-month exposure from 19 at the start to about 12 in the 37-µm mesh bags (Fig. 1f).

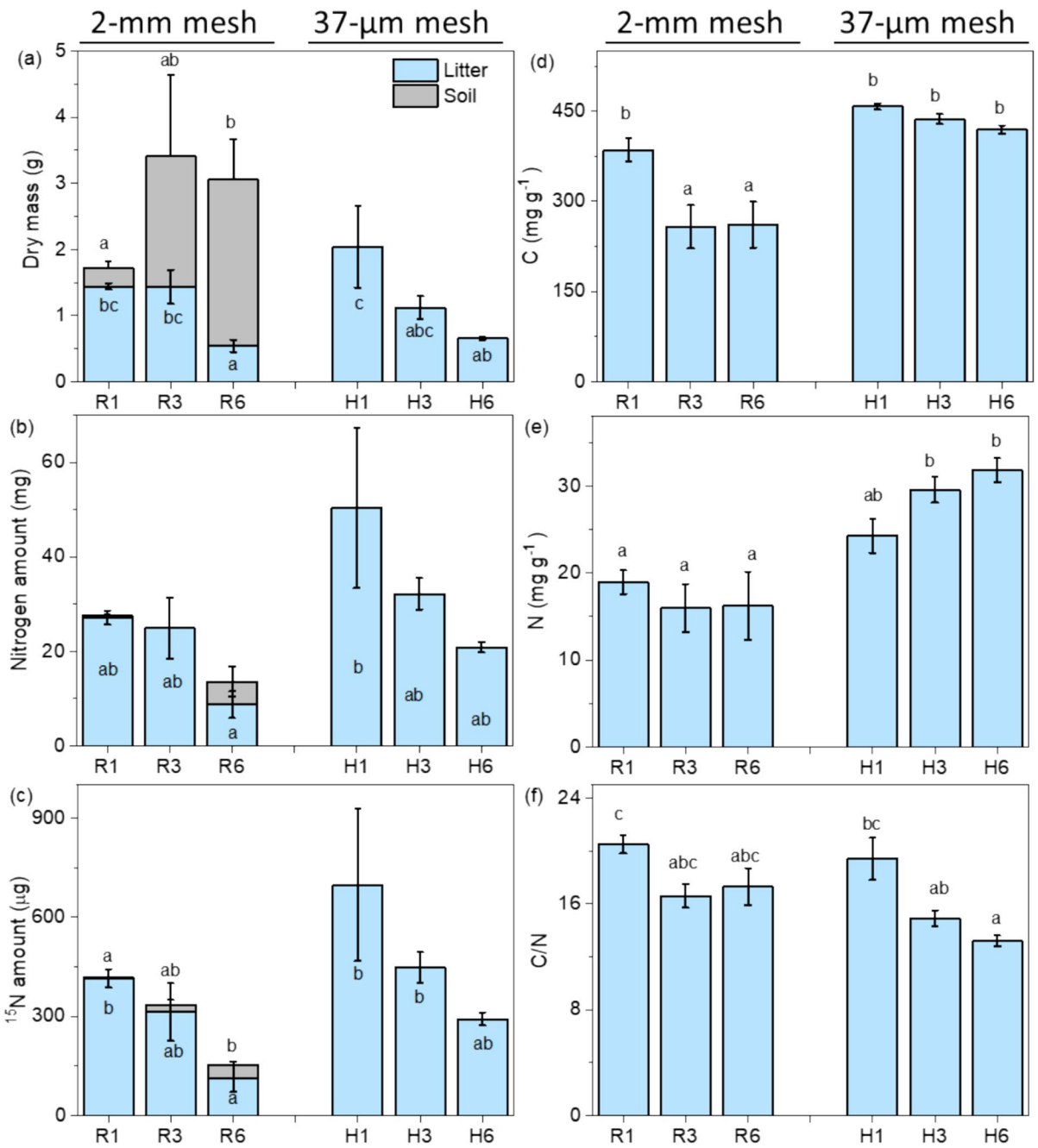

Fig. 1 Total amounts of dry mass (**a**), nitrogen (**b**), and ^{15}N (**c**) in mesh bags and concentrations of carbon (**d**) and nitrogen (**e**) and C/N-ratio (**f**) of leaf litter. R1, R3, and R6 refer to 2-mm ("root-accessible") and H1, H3 and H6 to 37-µm mesh bags ("hyphal-accessible") harvested after 1-, 3- and 6-month exposure in soil of an oil palm plantation. Blue bars show means for oil palm leaf litter and grey bars for soil, which accumulated in the mesh bags ($n = 5 \pm$ SE). Data were analyzed by GLM followed by Tukey HSD post-hoc test. Different letters indicate significant differences of means at $p < 0.05$

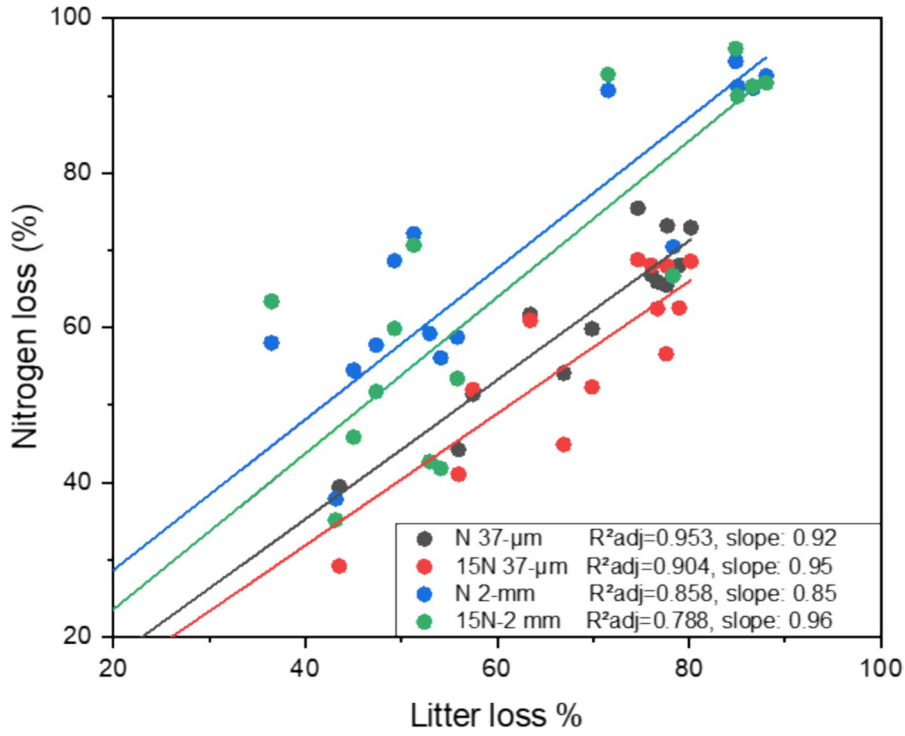

Fig. 2 Linear relationship of litter loss and nitrogen loss. Data points show individual measurements for 37-µm mesh bags: N (black), ^{15}N (red), and for 2-mm mesh bags: N (blue), ^{15}N (green). Inset: adjusted R^2 values and slopes of GLM

Root ingrowth and ^{15}N signatures inside the mesh bags in roots, litter and soil

We expected root ingrowth into the 2-mm but not into the 37-µm mesh bags. Unexpectedly, both mesh bag types contained very fine, thin roots (about 5 mg after 3 months and 14 mg after 6 months), although all mesh bags, except one (without roots), were visually intact at harvest. Because of high variation of root presence, the differences in root mass were not significant (GLM: $F_{3,19} = 1.35$, $p = 0.292$).

However, roots in the 37-µm mesh bags showed significantly higher ^{15}N enrichment than those in the 2-mm mesh bags ($F_{12,1} = 5.63$, $p = 0.042$, Fig. 3a). In the 37-µm mesh bags, APE in roots (1.23 ± 0.07 APE) was similar to that in litter (1.36 ± 0.12 APE, Fig. 3b). In the 2-mm mesh bags root APE (0.77 ± 0.17 APE) was similar to that in soil (0.66 ± 0.22 APE, Fig. 3c).

A temporal change in APE was neither observed in roots (GLM: $F_{2,12} = 1.88$, $p_{time} = 0.199$) nor in soil ($F_{2,18} = 0.84$, $p_{time} = 0.455$) (Fig. 3a,c). In litter, marginal changes ($p < 0.1$) were found ($F_{5,29} = 2.39$, $p_{time} = 0.068$) (Fig. 3b).

Taxonomic dynamics of fungi during litter degradation

The taxonomic composition of the fungal community in litter changed during exposure in soil (Fig. 4a). The compositional changes were mainly associated with shifts in litter C/N and APE (Fig. 4a). Significant differences between fungal communities were observed between the first and later time points, while no differences were noted between three- and six-month exposure (Table 1). The composition of fungal communities in 2-mm and 37-µm mesh bags did not differ significantly (Table 1, Fig. 4a).

OTU richness and Shannon diversity indices did not differ between the two types of mesh bags. OTU richness increased by 20% from month 1 to month 3 (Table 2). The Shannon index was higher in month 6 than in the previous months (Table 2).

Inspection of the taxonomic composition showed that fungi of the order Hypocreales were initially the most abundant (Fig. 4b). Their abundances declined with increasing incubation time, regardless of mesh bag type (Fig. 4b). Other orders with high relative abundances at the beginning were Botryosphaeriales,

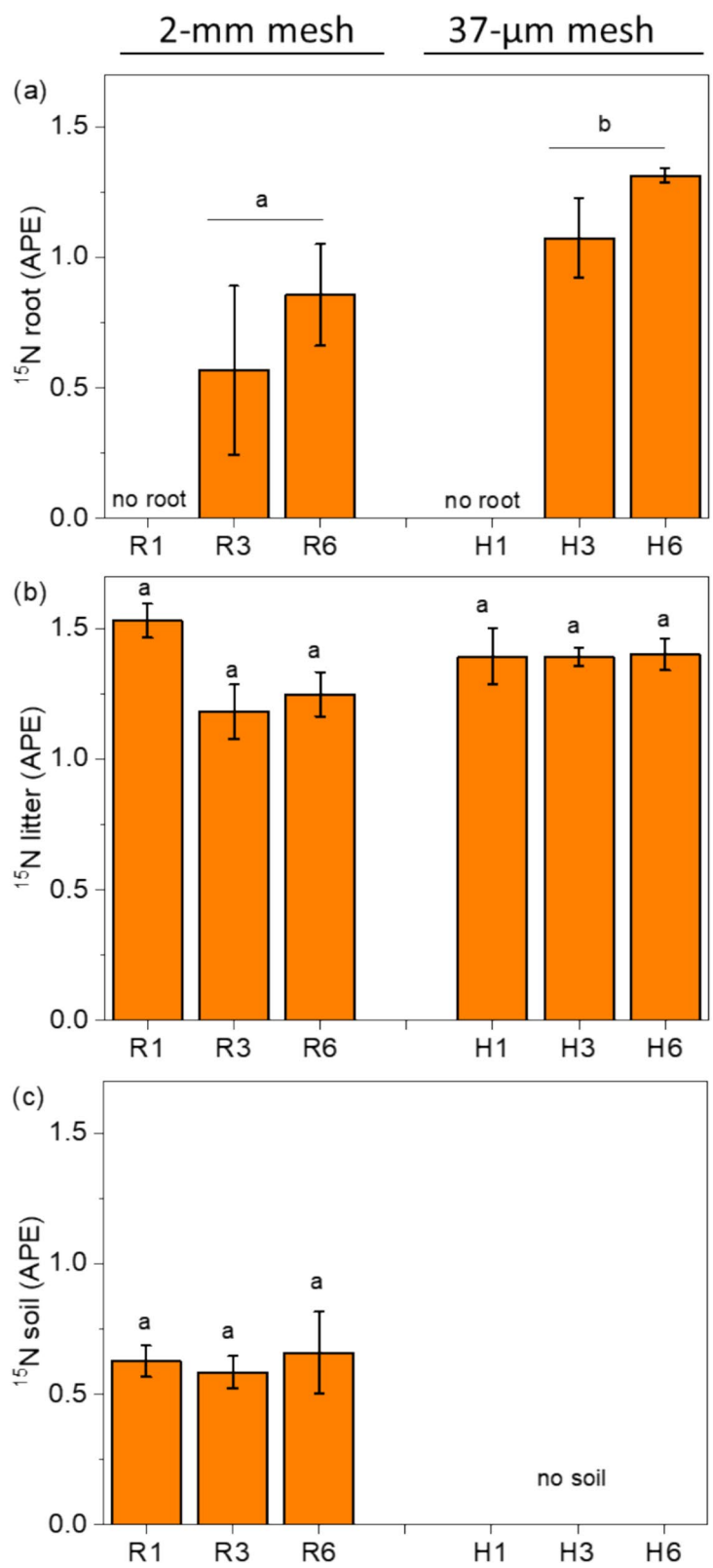

Fig. 3 ^{15}N (atom-% excess) in roots (**a**), leaf litter (**b**) and soil (**c**). Atom-% excess (APE) is the fraction of ^{15}N per N corrected for the natural abundance of ^{15}N. R1, R3, and R6 refer to 2-mm and H1, H3 and H6 to 37-µm mesh bags harvested after 1-, 3- and 6-month exposure in soil of an oil palm plantation. Bars show means ($n = 5 \pm$ SE). Data were analyzed by ANOVA followed by Tukey HSD post-hoc test. Different letters indicate significant differences of means at $p < 0.05$

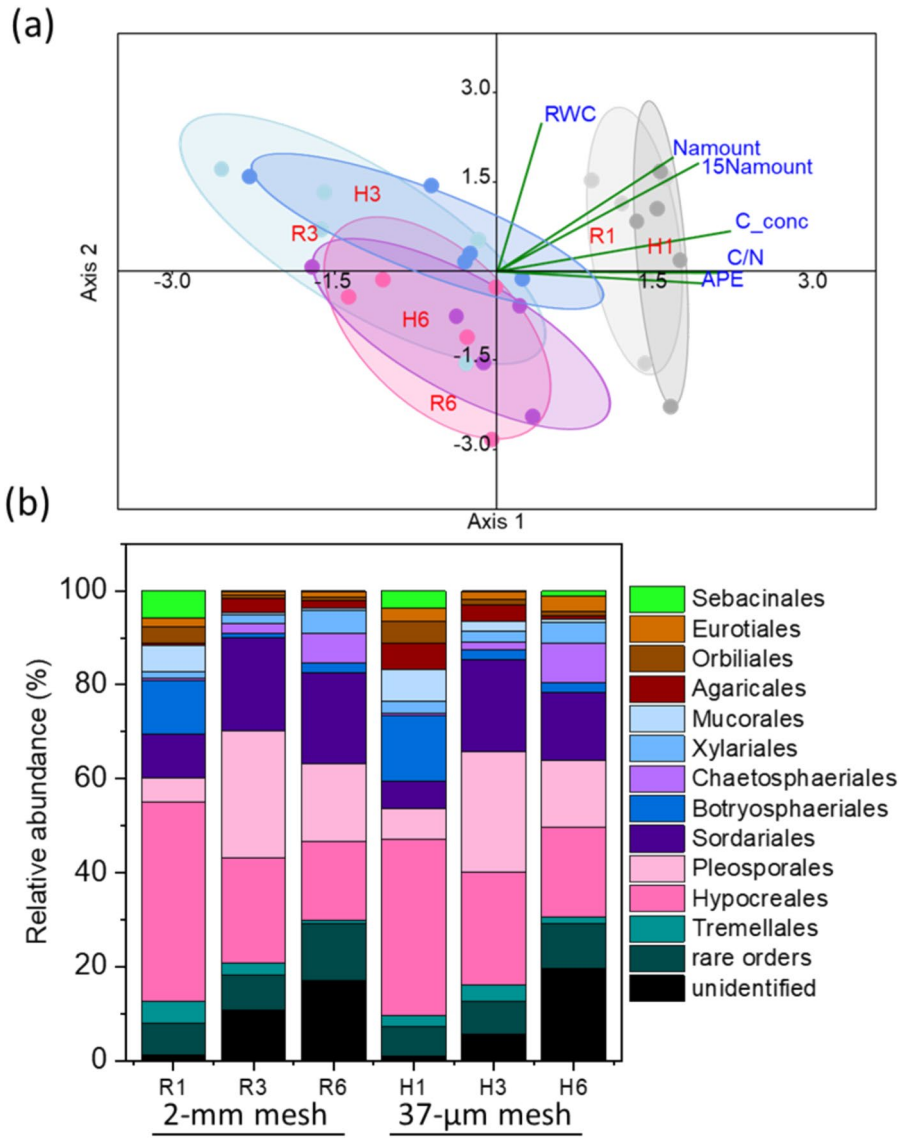

Fig. 4 Redundancy analysis of the taxonomic fungal community composition (**a**) and relative abundances of fungal orders in oil palm leaf litter (**b**). The redundancy analysis was performed with 9999 permutations (F = 2.09, p = 0.0004). Vectors show RCW (relative water content of soil) and litter traits: atom-% excess (APE), C/N ratio, C_conc = C concentration, N_amount and 15N_amount in litter. The relative abundances were determined for counts of the rarefied data set (37,267 counts per sample). R1, R3, and R6 refer to fungal orders in litter of 2-mm and H1, H3 and H6 to that in 37-µm mesh bags harvested after 1-, 3- and 6-month exposure in soil of an oil palm plantation

Table 1 PERMANOVA of similarity of the fungal community composition in leaf litterbags with pore sizes of 2-mm (R) or 37-µm (H) after 1-, 3-, and 6-month exposure in soil of an oil palm plantation

	R1	R3	R6	H1	H3
R3	**0.0091**				
R6	**0.0077**	0.1919			
H1	0.9036	**0.0086**	**0.0067**		
H3	**0.0156**	0.7515	0.1924	**0.008**	
H6	**0.0071**	0.1426	0.9082	**0.0073**	0.1984

PERMANOVA was conducted for pairwise comparisons using Bray Curtis distances and 9999 permutations. The table shows $p < 0.05$ in bold.

Sordariales and Mucorales (Fig. 4b). Mucorales almost disappeared at later stages of litter degradation, while Sordariales, Pleosporales, Chaetosphaeriales and Xylariales increased (Fig. 4b). Litter contained over 40 different fungal orders but most were rare, accounting for less than 1.5% of total counts (Supplement Data 1). They were summarized as rare orders (Fig. 4b). Overall, the phylum Ascomycota was dominant, while Mucoromycota and Basidomycota (mainly Agaricales, Sebacinales and Cantharellales) were less abundant. Glomeramycota (Archeosporales, Diversisporales, Gigasporales and Glomerales), representing AMF were relatively rare.

Table 2 Diversity indices of fungi colonizing oil palm leaf litter

Time (month)	$OTU_{(obs)}$ #	Chao-1#	Shannon H
1	325 ± 9a	395 ± 11a	3.34 ± 0.05ab
3	395 ± 19b	475 ± 26b	3.24 ± 0.13a
6	362 ± 11ab	442 ± 14b	3.55 ± 0.09b

# indicates results of the Kruskal Wallis test; other analyses were conducted with an ANOVA followed by Tukey HSD post hoc test. Different letters in columns indicate significant differences at $p < 0.05$.

Data from different mesh bag types showed no differences ($p > 0.05$) and were pooled. Data indicate means ($n = 10 \pm$ SE per time point). $OTU_{(obs)}$ = observed number of Amplicon Sequence Variants with 97% sequence similarity. Chao-1 = estimated maximum OTU richness.

Fungal OTUs without any taxonomic assignment at the order level increased in litter with increasing leaf degradation (Fig. 4b).

Functional dynamics of fungi during litter degradation

Functional assignments of fungal taxa to trophic guilds revealed a significant increase in the abundance of saprotrophic fungi with increasing degradation (Fig. 5a). Surprisingly, the steepest increases were found for AMF, although the overall OTU abundances for this group were low compared to other fungal guilds (Fig. 5b). Notably, not only did count abundances increase but also richness, from initially 9 OTU-based taxa to 69 and 89 OTU-based taxa (cf. Supplement Data sheet 1). Fungi for which no functional classification was available also increased massively (Fig. 5f).

Multi-trophic fungi, which can live as pathogens, symbionts or saprotrophs, declined approximately threefold during the six-month exposure time (Fig. 5c). Plant pathogens showed a similar pattern; they were strongly enriched in litter after one month of exposure and declined 4- to fivefold, thereafter (Fig. 5d). The litter also contained parasitic fungi (mainly mycoparasites) but their abundances were unaffected by exposure time (Fig. 5e). Furthermore, litter contained low abundances of fungi that can form orchid mycorrhizae, ectomycorrhizae or endophytic interactions (means: 241 ± 68 counts across all treatments, Fig. 5e, triangles).

Changes in the abundances of saprotrophic fungi were unrelated to litter traits (concentrations of N, C, ^{15}N, C/N ratio or the amounts of litter, C, ^{15}N or N per mesh bag) (Table 3). The abundances of multitrophic fungi, parasitic fungi, and pathogens were positively associated with the amounts of N, ^{15}N, and C in the litter bags, while AMF and unclassified fungi showed negative relationships with these traits (Table 3). Furthermore, AMF were negatively related to the C/N ratio of the litter, while pathotrophic fungi were positively associated with the C concentration and the C/N ratio (Table 3). Fungi without functional classification showed negative relationships with APE and C concentrations (Table 3).

We identified the 10 most abundant fungal species for each time point and mesh bag type (Fig. 6). This resulted in 23 different taxa because 14 taxa were shared among two or more conditions. Among the most abundant fungal species, four (ASV_00003, ASV_00004, ASV_00005 and ASV_00015) were found across all conditions (Fig. 6). They represented multitrophic Hypocreales (*Trichoderma* sp., Nectriaceae: *Fusarium* sp. and an unknown Nectriaceae) and a taxon from the Chaetomiaceae family (Sordariales), for which a functional annotation was lacking. In addition to these taxa, two species of the pathotrophic-saprotrophic genus *Rhizopus* and a potential ectomycorrhizal taxon (*Sebacina* sp.) were among the most abundant early stage fungi. At later stages, saprotrophic genera (*Tubeufia* sp., *Leptodiscella* sp., *Acrocalymma* sp.) and several taxa without a functional but a taxonomic assignment at the order level (Hypocreales, Sordariales, Pleosporales, Trechisporales) were present in the group of the most abundant taxa (Fig. 6).

Discussion

Litter degradation and colonization by roots foster fungal richness and N recycling

We investigated the dynamics of the taxonomic and functional profiles of litter-colonizing fungi in an industrial oil palm plantation in relation to litter decay. Within six months, approximately 70% of the oil palm leaf litter was degraded, which is line with previous studies conducted in humid tropical climate, including forests, oil palm plantations and

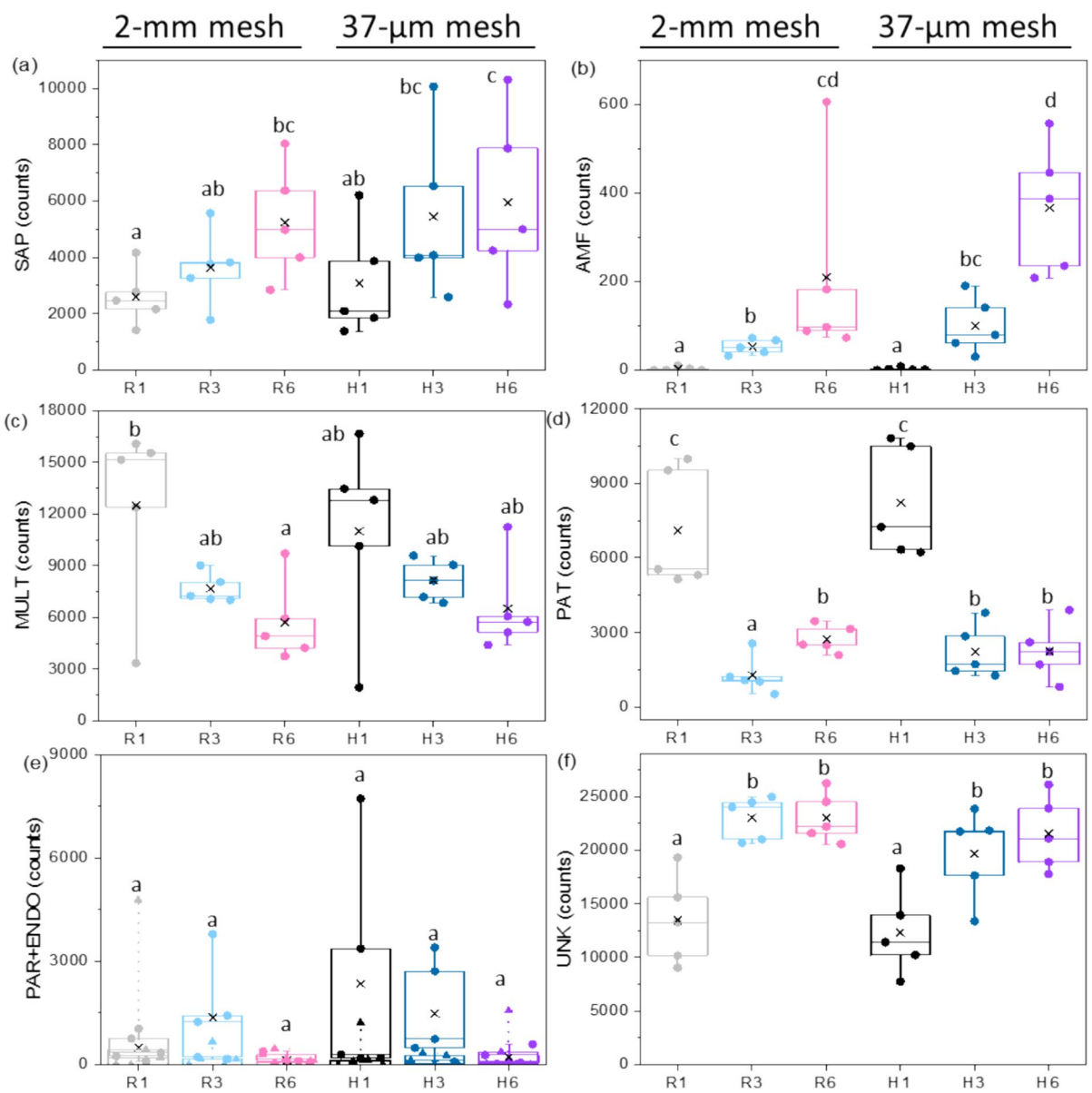

Fig. 5 Fungal abundances in oil palm leaf litter according to trophic groups. **a** Saprotrophs (SAP), **b** arbuscular mycorrhizal fungi (AMF), **c** multitrophic fungi (MULT), **d** pathogenic fungi (PAT, including PAT-SAP fungi), **e** parasitic fungi (PAR, circles) and endophytes and symbionts (ENDO, triangles), **f** fungi without trophic assignment (UNK). Data show box-plots with the mean as cross and the median as horizontal line. Dots show individual measurements. R1, R3, and R6 refer to fungi in litter of 2-mm and H1, H3 and H6 to that in 37-µm mesh bags harvested after 1-, 3- and 6-month exposure in soil of an oil palm plantation. Different letters indicate significant differences (Kruskal Wallis test)

other land use systems (Moradi et al. 2014; Pulunggono et al. 2019; Kerdraon et al. 2020). The initial loss depended on the accessibility of the litter, as the intercepts of the decay rates in mesh bags with wider or smaller pores differed significantly. Reasons for rapid losses in mesh bags with wider pores might be accessibility to meso- and macrofauna (Scheu and Setälä 2002) and greater wash out of small particulate materials by rainfall. The accumulation of soil in the 2-mm mesh bags indicates profound exchange

Table 3 Spearman Rank Correlations for the association of different fungal life styles and the amounts of litter mass, carbon and nitrogen and their concentrations

Coeff./p-value	SAP	AMF	MULT	PAT	PAR	UNK
litter amount (g)	−0.359	0.634	0.490	0.313	0.378	−0.443
p-value	0.053	**0.001**	**0.008**	0.092	**0.032**	**0.017**
^{15}N amount (µg)	−0.162	−0.437	0.550	0.453	0.389	−0.625
p-value	0.383	**0.019**	**0.003**	**0.015**	**0.036**	**0.001**
N amount (mg)	−0.200	−0.442	0.508	0.365	0.398	−0.504
p-value	0.282	**0.017**	**0.006**	**0.049**	**0.032**	**0.007**
C amount (mg)	−0.334	−0.657	0.552	0.566	0.425	−0.648
p-value	0.072	**0.000**	**0.003**	**0.002**	**0.022**	**0.001**
APE	−0.030	−0.185	0.154	0.256	0.200	−0.399
p-value	0.873	0.318	0.408	0.168	0.281	**0.032**
^{15}N (µg g^{-1} d.wt.)	0.123	0.294	0.146	0.060	0.056	−0.232
p-value	0.509	0.114	0.433	0.745	0.762	0.212
N (mg g^{-1} d.wt.)	0.111	0.312	0.129	0.043	−0.103	−0.173
p-value	0.552	0.093	0.488	0.819	0.579	0.351
C (mg g^{-1} d.wt.)	−0.072	−0.213	0.357	0.471	0.235	−0.573
p-value	0.697	0.251	0.055	**0.011**	0.205	**0.002**
C/N	−0.217	−0.645	0.073	0.429	0.271	−0.269
p-value	0.243	**0.001**	0.695	**0.021**	0.139	0.147

For each parameter, the upper row shows the coefficient (coeff.) and the lower row the p-value. Significant relationships ($p < 0.05$) are highlighted bold.

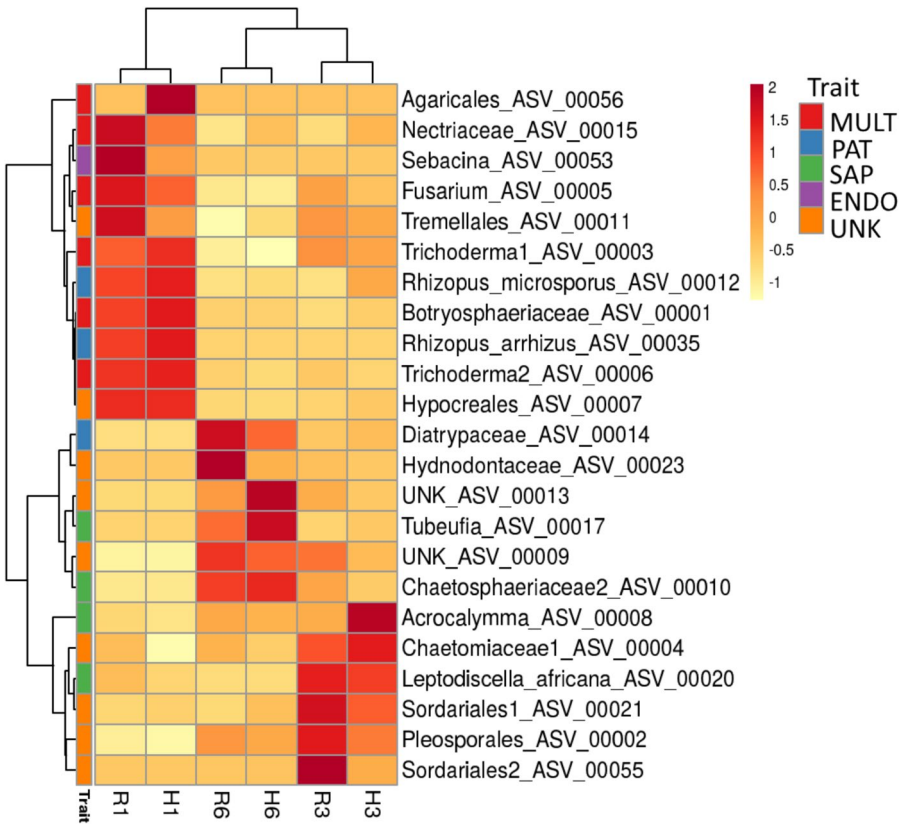

Fig. 6 Heat map of hierarchical clustering of fungal abundances. Rows were unit variance scaled. Columns were fixed. The ten most abundant fungi for each sampling date and mesh bag type were included. R1, R3, and R6 refer to fungal species in litter of 2-mm and H1, H3 and H6 to that in 37-µm mesh bags harvested after 1-, 3- and 6-month exposure in soil of an oil palm plantation. Column traits shows the trophic level of the fungal species by a color code

with the environment but in contrast to our expectation, this did not affect the composition of the fungal communities in leaf litter. Despite the similarities of the fungal communities, decomposition processes in different mesh bag types resulted in differences in N and C concentrations in litter, supporting divergence between "freely accessible" and "microbial-driven" litter degradation. Thus, we reject our first hypothesis that different fungal communities drove differences in litter decomposition. Instead, other soil processes, for instance litter-feeding soil fauna might have additionally affected litter degradation, leading to the observed decreases in litter C concentrations in the accessible mesh bags. However, the abundance of protists, which link lower and higher levels in soil food webs, is low in plantation soil (Krashevska et al. 2016). Therefore, further experiments are necessary to clarify the roles and interactions of different trophic levels for litter decomposition. A limitation of our study was the unavailability of multiple land-use systems due to logistical constraints. To gain a more comprehensive understanding of litter-degrading soil microbial communities and their responses to varying environmental conditions, future research should be conducted in a range of additional sites and land-use systems.

In contrast to the accessible mesh bags, microbial litter decay in the 37-µm mesh bags resulted in an apparent accumulation of N, similar to that found in other studies (e.g., Pulunggono et al. 2019; Zhang et al. 2020; Tennakoon et al. 2022). It was suggested that intense colonization by fungal hyphae with their relatively high N contents (3%—5%; Kim et al. 2003) may concentrate additional N in the decaying litter (e.g., Bonanomi et al. 2014; Chomel et al. 2016). In our experiment, this mechanism would have diluted the ^{15}N signature (APE) in litter because of the incorporation of new external N. Since the ^{15}N signature was stable, our results show that microbial litter degradation resulted in N retention. This may happen due to the higher C than N demand of the microbes, as the initial C/N-ratio of the leaf litter exceeded 20 but other resource use modes are also possible (Manzoni et al. 2021).

Our study shows that roots grew into the decomposing litter within three months. Litter invasion by roots was also evident by the increasing abundances of AMF, which are obligate symbionts depending on plant-derived carbon (Oliveira et al. 2024). However, it remains unclear how roots entered the 37-µm mesh bags. The smallest root diameters of oil palm roots (tertiary or quaternary roots) were not smaller than 400 to 500 µm (Yahya et al. 2010; Kotowska et al. 2023). In other studies, fine root diameters of various species were not less than 50 to 100 µm (Kong et al. 2014). Therefore, the 37-µm mesh bags should have excluded roots. We observed a moderate presence of weeds, which may have sent roots into the mesh bags. Perhaps very thin weed roots can squeeze themselves through micro-pores, or use undetected tiny damage points in the mesh. Roots in the 2-mm mesh bags resembled those in the 37-µm mesh bags, and thus, did not originate from oil palms. The absence of oil palm roots in the 2-mm mesh bags was probably due to low soil fertility in the inter-rows. The density of oil palm roots is highest where fertilizers are placed, usually in the palm circle (Pradiko et al. 2022). Since the inter-rows were not fertilized, an expansion of oil palm roots into this area was unlikely.

In our study, the biomass of the roots in the mesh bags was very low, so large amounts of N could not be captured. However, our labelling experiment demonstrates the potential of roots for the acquisition of N from degrading litter. Roots benefited from N enrichment because they acquired more N from degrading litter in the 37-µm mesh bags than roots in more accessible mesh bags, where we found lower ^{15}N enrichment. The differences in the root ^{15}N signatures suggested that roots fed on litter N in the 37-µm mesh bags and on soil N in the 2-mm mesh bags.

Roots in tropical ecosystems preferentially explore litter, not poor soil, for nutrients and, in turn, foster microbial activities (Zhou et al. 2024). In line with this, we observed that the appearance of roots in litter was associated with increasing fungal species richness, thus, promoting microbial biodiversity. Furthermore, the accumulation of litter-derived ^{15}N in roots highlights the contribution of roots to the recycling of organic N. On the practical side, the productivity of oil palms was maintained by the application of palm residues compared with mineral fertilizers (Tao et al. 2017) and reduced nutrient leaching loss (Kurniawan et al. 2018; Formaglio et al. 2021). Our study shows that microbial N immobilization, stimulation of fungal diversity and root N acquisition underpin these beneficial effects.

Fungal succession in decomposing oil palm litter uncovers shifts from multitrophic/pathogenic to saprotrophic/mycorrhizal communities

Leaf litter decomposition typically begins with the degradation of easily hydrolysable compounds such as sugars and hemicellulose, then progresses to more complex polymers like cellulose and eventually ligninLeaf litter decomposition typically begins with the degradation of easily hydrolysable compounds such as sugars and hemicellulose, then progresses to more complex polymers like cellulose and eventually lignin (Hättenschwiler et al. 2005). Fungi mediate these processes by producing extracellular enzymes, tailored for the successive breakdown of organic materials (Asplund et al. 2018; Wang et al. 2020). The interactions between soil fungi and bacteria also influence litter decomposition, potentially accelerating the decay rates (Schneider et al. 2010). However, fungi are generally considered the primary drivers of litter decomposition (Schneider et al. 2010). With different stages of litter decay, fungal taxa have been classified as early, intermediate and late stage decomposers (Krishna and Mohan 2017). This trajectory has been observed in various (sub)tropical environments and substrates, including empty fruit bunches of oil palm, wood, lignin, cellulose and leaf litter (Promputtha et al. 2002, 2007; DeAngelis et al. 2011; Nottingham et al. 2018; Osono 2020; Dossa et al. 2021; Tennakoon et al. 2022; Kusumaningtyas et al. 2565). Our study confirmed a drastic shift in the fungal community from the early to later stages of litter mass loss, accompanied by significant decreases in the foliar C/N ratio. These findings are important because our understanding of the ecological potential of litter-colonizing fungi in degraded, herbicide-treated soils is still limited.

We have previously shown that the composition of soil fungal communities was highly similar across different landscapes in tropical lowland oil palm plantations, including the present study site (Brinkmann et al. 2019). The main fungal orders in oil palm plantation soils (Brinkmann et al. 2019) largely overlapped with the main fungal orders found here in leaf litter (Hypocreales, Pleosporales, Sordariales, Chaetothyriales). For example, Hypocreales were the most abundant order of early stage fungi. The greatest fraction in this order was represented by *Fusarium* species, which have also been identified as a major genus in soil (Brinkmann et al. 2019). *Fusarium* sp. have symbiotic, saprotrophic and pathogenic life styles; distinct species can cause devastating diseases in oil palm plantations (Suwandi et al. 2012), while others have plant-protective functions (L'Haridon et al. 2011). Here, *Fusarium* sp. co-occurred together with *Trichoderma* sp., which is known as bio-control agent (Jin et al. 2022; Kabir et al. 2023). Fungi in litter not only facilitate decomposition but can also have protective roles (Naidu et al. 2015). Here, early stage oil palm litter was enriched with *Rhizopogus* sp., which is known to act synergistically with *Fusarium* sp. to accelerate decay processes (Jatav et al. 2020). Further, we found a number of fungal taxa that were abundant at early decomposition stages in oil palm litter but rare in soil (Brinkmann et al. 2019). For example, Sebacinales have broad trophic abilities (endophytes, ectomycorrhizal and saprotrophic species) and some are famous growth-promoting species (*Serenpidita* sp., previously known as *Piriformospora indica*) (Weiß et al. 2016). Botryosphaeriaceae also have a broad trophic range but contain many important pathogens (Rathnayaka et al. 2023). Tremellales grow well on sucrose (Bhatnagar et al. 2018), which concurs with a role as early decomposers suggested by their abundance at the early stage of litter decay and lower abundances at late stages. Mucorales were rare in soil (Brinkmann et al. 2019) but showed high abundances in early stage oil palm leaf litter (this study). An extensive investigation of fungi from different phyla on substrates of varying complexity revealed that members of the Mucorales grow on simple carbohydrates but hardly on cellulose or other complex substrates (Leifheit et al. 2024). However, this specificity may depend on the specific isolates (Pawłowska et al. 2019). Altogether, a notable result of our study was that multitrophic taxa and potentially pathogenic fungi dominated the early stages of decay of oil palm leaf litter.

Later stages of decay were characterized by a shift to lower C/N ratios along with a surprising combination of fungal lifestyles: AMF, saprotrophic fungi and fungi without trophic affiliation. A recent meta-analysis (Choreño-Parra and Treseder 2024) reported positive effects of AMF on litter decomposition, possibly via the exudation of plant-derived carbohydrates, which in turn stimulate saprotrophic microbes. Choreño-Parra & Treseder (2024) identified low substrate C/N as the most important factor for AMF

mediated decomposition and reported the greatest positive effect sizes in leaf litter compared with other degrading tissues (Choreño-Parra and Treseder 2024). Although it is unlikely that AMF are directly involved in litter decay, their abundance and species richness increased markedly in late-stage leaf litter with low C/N ratios, supporting the possibility that they may have indirectly influenced the decomposition process. The increase in AMF diversity is noteworthy because oil palm roots harbor only a very limited spectrum of these symbionts compared with other tropical land use systems (Edy et al. 2022). Therefore, the present results indicate opportunities for soil biodiversity restoration.

It was surprising to find that changes in litter traits correlated with changes in the abundance of functionally unknown fungi, but not with an increase in saprotrophic fungal taxa. We attribute this lack of correlation to the limited understanding and research on the ecological functions of fungi, particularly those that are rare in soil but proliferate in degrading litter in tropical ecosystems (Stallman et al. 2024). Our results therefore suggest that the observed pattern does not necessarily reflect dominance by novel functional groups but rather a shift in the composition of saprotrophs, some of which are not yet functionally characterized. This assumption is reasonable since both annotated as well as many functionally unknown taxa were members of the orders Sordariales and Pleosporales. These orders comprise numerous species classified in bioassays as cellulose and lignin guilds (Bhatnagar et al. 2018). For example, *Sordaria* sp. primarily targets polysaccharides (Franco et al. 2018); it is considered a pioneer species that can modify the physical and chemical properties of the litter, enhancing conditions for subsequent colonizers (Rivera et al. 2025). Biotechnological studies found superior lignolytic activities for several members of the Pleosporales and Chaetosphaeriales, causing high rates of plant biomass conversion (Shrestha et al. 2015). Members of the Chaetosphaeriales were enriched in litter at the end of our study, suggesting that they mark the transition into the last phase of litter decomposition. As the group of fungi without trophic annotation showed a tight relationship with litter C concentrations, we speculate that these fungi are potent litter saprotrophs. However, further studies are needed to isolate and further characterize these species.

Conclusions

This study shows that the composition of litter-associated fungal communities shifted with the progression of litter degradation, leading to increased soil fertility. This process resulted in N retention and aided accumulation of litter-derived N in soil and roots, contributing to N recycling. Thereby, oil palm leaf litter can promote ecological benefits in impoverished tropical plantation soil. Specifically, it can increase the diversity of beneficial fungi, such as AMF, which are essential for plant growth. By applying palm frond litter, farmers can increase AMF diversity, potentially leading to more sustainable plantation management. Furthermore, our study highlights the potential for biotechnological applications of fungal taxa with intense saprotrophic capabilities. While the potential benefits of litter applications in impoverished tropical plantation soil are promising, they also come with risks. Early decomposition processes driven by multitrophic fungi can be problematic, as many of these fungi have pathogenic potential. However, the presence of antagonistic fungi in leaf litter may help to control these pathogens, suggesting that a deeper understanding of their interactions is crucial. To ensure the safe and effective use of litter applications, further research is needed to clarify the conditions under which fungal communities can be used to promote healthy litter decomposition. This study highlights the importance of litter degradation for N retention and recycling in tropical plantation soil. Our findings provide practical opportunities for the restoration of AMF diversity and suggest that simple, affordable measures, such as applying palm frond litter, can contribute to more sustainable plantation management.

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Author contributions ARR: managed the field experiments, collected and transported samples, NE: prepared ^{15}N-labelled plant material, UY: supervised the production of ^{15}N-labelled plant material, RP: conceived the study, supervised data analysis, AP: supervision, funding acquisition, conceived the study together with RP, analyzed data and wrote the paper with input of all coauthors. All coauthors commented on the final version of the manuscript and agreed on its publication.

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Data availability The raw sequencing data were deposited at NCBI databank under the number PRJNA950011. The annotated and rarefied data table for fungal OTUs is available under Supplement Data S1.

Declarations

Permission The study was conducted according to the regulation of the Convention for Biological Diversity. Sampling and export permissions were granted under number SK.335/KSDAE/SET/KSA.2/7/2019 (issued 31 st July 2019).

Conflict of interest The authors declare that they have no conflict of interest.

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References

Asplund J, Kauserud H, Bokhorst S, Lie MH, Ohlson M, Nybakken L (2018) Fungal communities influence decomposition rates of plant litter from two dominant tree species. Fungal Ecol 32:1–8. https://doi.org/10.1016/j.funeco.2017.11.003

Baldrian P (2017) Microbial activity and the dynamics of ecosystem processes in forest soils. Curr Opin Microbiol 37:128–134

Ballauff J, Schneider D, Edy N, Irawan B, Daniel R, Polle A (2021) Shifts in root and soil chemistry drive the assembly of belowground fungal communities in tropical land-use systems. Soil Biol Biochem 154:108140

Berkelmann D, Schneider D, Engelhaupt M, Heinemann M, Christel S, Wijayanti M, Meryandini A, Daniel R (2018) How rainforest conversion to agricultural systems in Sumatra (Indonesia) affects active soil bacterial communities. Front Microbiol 9:2381. https://doi.org/10.3389/fmicb.2018.02381

Bhatnagar JM, Peay KG, Treseder KK (2018) Litter chemistry influences decomposition through activity of specific microbial functional guilds. Ecol Monogr 88:429–444. https://doi.org/10.1002/ecm.1303

Bolyen E (2019) Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. Nat Biotechnol 37:6

Bonanomi G, Capodilupo M, Incerti G, Mazzoleni S (2014) Nitrogen transfer in litter mixture enhances decomposition rate, temperature sensitivity, and C quality changes. Plant Soil 381:307–321. https://doi.org/10.1007/s11104-014-2119-4

Brandt L, Poll C, Ballauff J, Schrumpf M, Bramble DS, Schöning I, Ulrich S, Kaiser K, Mikutta R, Mikutta C, Polle A, Kandeler E (2024) Mineral type versus environmental filters: what shapes the composition and functions of fungal communities in the mineralosphere of forest soils? Soil Biol Biochem 190:109288. https://doi.org/10.1016/j.soilbio.2023.109288

Brinkmann N, Schneider D, Sahner J, Ballauff J, Edy N, Barus H, Irawan B, Budi SW, Qaim M, Daniel R, Polle A (2019) Intensive tropical land use massively shifts soil fungal communities. Sci Rep 9:3403. https://doi.org/10.1038/s41598-019-39829-4

Brundrett MC, Tedersoo L (2018) Evolutionary history of mycorrhizal symbioses and global host plant diversity. New Phytol 220:1108–1115. https://doi.org/10.1111/nph.14976

Camacho C, Coulouris G, Avagyan V, Ma N, Papadopoulos J, Bealer K, Madden TL (2009) BLAST+: architecture and applications. BMC Bioinformatics 10:421. https://doi.org/10.1186/1471-2105-10-421

Chen S, Zhou Y, Chen Y, Gu J (2018) Fastp: an ultra-fast all-in-one FASTQ preprocessor. Bioinformatics 34:i884–i890. https://doi.org/10.1093/bioinformatics/bty560

Chomel M, Guittonny-Larchevêque M, DesRochers A, Baldy V (2016) Effect of mixing herbaceous litter with tree litters on decomposition and N release in boreal plantations. Plant Soil 398:229–241. https://doi.org/10.1007/s11104-015-2648-5

Choreño-Parra EM, Treseder KK (2024) Mycorrhizal fungi modify decomposition: a meta-analysis. New Phytol 242(6):2763–2774. https://doi.org/10.1111/nph.19748

Comte I, Colin F, Whalen JK, Grünberger O, Caliman J-P (2012) Agricultural practices in oil palm plantations and their impact on hydrological changes, nutrient fluxes and water quality in Indonesia: a review. Adv Agron 116:71–124

Darras KFA, Corre MD, Formaglio G, Tjoa A, Potapov A, Brambach F, Sibhatu KT, Grass I, Rubiano AA, Buchori D, Drescher J, Fardiansah R, Hölscher D, Irawan B, Kneib T, Krashevska V, Krause A, Kreft H, Li K, Maraun M, Polle A, Ryadin AR, Rembold K, Stiegler C, Scheu S, Tarigan S, Valdés-Uribe A, Yadi S, Tscharntke T, Veldkamp E (2019) Reducing fertilizer and avoiding herbicides

in oil palm plantations - ecological and economic valuations. Front Glob Change 2:65. https://doi.org/10.3389/ffgc.2019.00065

De Melo C, Moura C, Guerrero-Ramírez N, Krashevska V, Polle A, Siregar IZ, Ballauff J, Siregar UJ, Encinas-Viso F, Bell K, Nevill P, Gailing O (2025) Land-use changes impact root–fungal network connectivity in a global biodiversity hotspot. J Ecol 113:1136–1149. https://doi.org/10.1111/1365-2745.70020

DeAngelis KM, Allgaier M, Chavarria Y, Fortney JL, Hugenholtz P, Simmons B, Sublette K, Silver WL, Hazen TC (2011) Characterization of trapped lignin-degrading microbes in tropical forest soil. PLoS ONE 6:e19306. https://doi.org/10.1371/journal.pone.0019306

Dislich C, Keyel AC, Salecker J, Kisel Y, Meyer KM, Auliya M, Barnes AD, Corre MD, Darras K, Faust H, Hess B, Klasen S, Knohl A, Kreft H, Meijide A, Nurdiansyah F, Otten F, Pe'er G, Steinebach S, Tarigan S, Tölle MH, Tscharntke T, Wiegand K (2017) A review of the ecosystem functions in oil palm plantations, using forests as a reference system. Biological Reviews 92:1539–1569. https://doi.org/10.1111/brv.12295

Dossa GGO, Yang Y-Q, Hu W, Paudel E, Schaefer D, Yang Y-P, Cao K-F, Xu J-C, Bushley KE, Harrison RD (2021) Fungal succession in decomposing woody debris across a tropical forest disturbance gradient. Soil Biol Biochem 155:108142. https://doi.org/10.1016/j.soilbio.2021.108142

Drescher J, Rembold K, Allen K, Beckschäfer P, Buchori D, Clough Y, Faust H, Fauzi AM, Gunawan D, Hertel D, Irawan B, Jaya INS, Klarner B, Kleinn C, Knohl A, Kotowska MM, Krashevska V, Krishna V, Leuschner C, Lorenz W, Meijide A, Melati D, Nomura M, Pérez-Cruzado C, Qaim M, Siregar IZ, Steinebach S, Tjoa A, Tscharntke T, Wick B, Wiegand K, Kreft H, Scheu S (2016) Ecological and socio-economic functions across tropical land use systems after rainforest conversion. Philos Trans R Soc Lond B Biol Sci 371:20150275. https://doi.org/10.1098/rstb.2015.0275

Edy N, Yelianti U, Irawan B, Polle A, Pena R (2020) Differences in root nitrogen uptake between tropical lowland rainforests and oil palm plantations. Front Plant Sci 11:92. https://doi.org/10.3389/fpls.2020.00092

Edy N, Barus HN, Finkeldey R, Polle A (2022) Host plant richness and environment in tropical forest transformation systems shape arbuscular mycorrhizal fungal richness. Front Plant Sci 13:1004097. https://doi.org/10.3389/fpls.2022.1004097

Filser J, Faber JH, Tiunov AV, Brussaard L, Frouz J, De Deyn G, Uvarov AV, Berg MP, Lavelle P, Loreau M (2016) Soil fauna: key to new carbon models. Soil 2:565–582

Formaglio G, Veldkamp E, Damris M, Tjoa A, Corre MD (2021) Mulching with pruned fronds promotes the internal soil N cycling and soil fertility in a large-scale oil palm plantation. Biogeochemistry 154:63–80. https://doi.org/10.1007/s10533-021-00798-4

Franco E, Troncozo MI, Baez M, Mirífico MV, Robledo GL, Balatti PA, Saparrat MCN (2018) *Fusarium equiseti* LPSC 1166 and its *in vitro* role in the decay of *Heterostachys ritteriana* leaf litter. Folia Microbiol 63:169–179. https://doi.org/10.1007/s12223-017-0541-8

Gaveau DLA, Locatelli B, Salim MA, Husnayaen MT, Descals A, Angelsen A, Meijaard E, Sheil D (2022) Slowing deforestation in Indonesia follows declining oil palm expansion and lower oil prices. PLoS ONE 17:e0266178. https://doi.org/10.1371/journal.pone.0266178

Grass I, Kubitza C, Krishna VV, Corre MD, Mußhoff O, Pütz P, Drescher J, Rembold K, Ariyanti ES, Barnes AD, Brinkmann N, Brose U, Brümmer B, Buchori D, Daniel R, Darras KFA, Faust H, Fehrmann L, Hein J, Hennings N, Hidayat P, Hölscher D, Jochum M, Knohl A, Kotowska MM, Krashevska V, Kreft H, Leuschner C, Lobite NJS, Panjaitan R, Polle A, Potapov AM, Purnama E, Qaim M, Röll A, Scheu S, Schneider D, Tjoa A, Tscharntke T, Veldkamp E, Wollni M (2020) Trade-offs between multifunctionality and profit in tropical smallholder landscapes. Nat Commun 11(1):1186. https://doi.org/10.1038/s41467-020-15013-5

Hammer Ø, Harper DA (2001) Past: paleontological statistics software package for educaton and data anlysis. Palaeontol Electron 4:1

Hättenschwiler S, Tiunov AV, Scheu S (2005) Biodiversity and litter decomposition in terrestrial ecosystems. Annu Rev Ecol Evol Syst 36:191–218. https://doi.org/10.1146/annurev.ecolsys.36.112904.151932

Iddris NA-A, Formaglio G, Paul C, von Groß V, Chen G, Angulo-Rubiano A, Berkelmann D, Brambach F, Darras KF, Krashevska V (2023) Mechanical weeding enhances ecosystem multifunctionality and profit in industrial oil palm. Nat Sustain 6:683–695

Jatav BK, Sharma TK, Dassani S (2020) Succession of microfungi on leaf litter of *Acacia catechu* in Datia, Madhya Pradesh, India. J Pure Appl Microbiol 14:1

Jin X, Wang Z, Wu F, Li X, Zhou X (2022) Litter mixing alters microbial decomposer community to accelerate tomato root litter decomposition. Microbiol Spectr 10:e00186-e222. https://doi.org/10.1128/spectrum.00186-22

Kabir MG, Wang Y, Abuhena M, Azim MF, Al-Rashid J, Rasul NM, Mandal D, Maitra P (2023) A bio-sustainable approach for reducing *Eucalyptus* tree-caused agricultural ecosystem hazards employing *Trichoderma* bio-sustained spores and mycorrhizal networks. Front Microbiol 13:1071392

Kerdraon D, Drewer J, Chung AYC, Majalap N, Slade EM, Bréchet L, Wallwork A, Castro-Trujillo B, Sayer EJ (2020) Litter inputs, but not litter divdersity, maintain soil processes in degraded tropical forests—a cross-continental comparison. Front for Glob Change 2:90. https://doi.org/10.3389/ffgc.2019.00090

Khokon AM, Janz D, Polle A (2023) Ectomycorrhizal diversity, taxon-specific traits and root N uptake in temperate beech forests. New Phytol 239:739–751. https://doi.org/10.1111/nph.18978

Kim C, Lim J-H, Shin JH (2003) Nutrient dynamics in litterfall and decomposing leaf litter at the Kwangneung deciduous broad-leaved natural forest. Korean J Agric For Meteorol 5:87–93

Kõljalg U, Nilsson RH, Abarenkov K, Tedersoo L, Taylor AFS, Bahram M, Bates ST, Bruns TD, Bengtsson-Palme J, Callaghan TM, Douglas B, Drenkhan T, Eberhardt U,

Dueñas M, Grebenc T, Griffith GW, Hartmann M, Kirk PM, Kohout P, Larsson E, Lindahl BD, Lücking R, Martín MP, Matheny PB, Nguyen NH, Niskanen T, Oja J, Peay KG, Peintner U, Peterson M, Põldmaa K, Saag L, Saar I, Schüßler A, Scott JA, Senés C, Smith ME, Suija A, Taylor DL, Telleria MT, Weiss M, Larsson K-H (2013) Towards a unified paradigm for sequence-based identification of fungi. Mol Ecol 22:5271–5277. https://doi.org/10.1111/mec.12481

Kong D, Ma C, Zhang Q, Li L, Chen X, Zeng H, Guo D (2014) Leading dimensions in absorptive root trait variation across 96 subtropical forest species. New Phytol 203:863–872. https://doi.org/10.1111/nph.12842

Kotowska MM, Samhita S, Hertel D, Triadiati T, Beyer F, Allen K, Link RM, Leuschner C (2023) Consequences of tropical rainforest conversion to tree plantations on fine root dynamics and functional traits. Oikos 2023:e08898. https://doi.org/10.1111/oik.08898

Krashevska V, Klarner B, Widyastuti R, Maraun M, Scheu S (2016) Changes in structure and functioning of protist (testate amoebae) communities due to conversion of lowland rainforest into rubber and oil palm plantations. PLoS ONE 11:e0160179

Krishna MP, Mohan M (2017) Litter decomposition in forest ecosystems: a review. Energ Ecol Environ 2:236–249. https://doi.org/10.1007/s40974-017-0064-9

Kurniawan S, Corre MD, Utami SR, Veldkamp E (2018) Soil biochemical properties and nutrient leaching from smallholder oil palm plantations, Sumatra-Indonesia. AGRIVITA J Agric Sci 40:257–266

Kusumaningtyas P, Candra KP, Sahid A (2565) Changes in microbial community structure and diversity during decomposition of oil palm empty fruit bunches at different decomposition sites in humid tropical oil palm plantation. Agriculture and Natural Resources -- formerly Kasetsart Journal (Natural Science) 056:511–524. https://doi.org/10.34044/j.anres.2022.56.3.08

L'Haridon F, Aimé S, Duplessis S, Alabouvette C, Steinberg C, Olivain C (2011) Isolation of differentially expressed genes during interactions between tomato cells and a protective or a non-protective strain of *Fusarium oxysporum*. Physiol Mol Plant Pathol 76:9–19. https://doi.org/10.1016/j.pmpp.2011.07.001

Leifheit EF, Camenzind T, Lehmann A, Andrade-Linares DR, Fussan M, Westhusen S, Wineberger TM, Rillig MC (2024) Fungal traits help to understand the decomposition of simple and complex plant litter. FEMS Microbiol Ecol 100:fiae033

Manzoni S, Chakrawal A, Spohn M, Lindahl BD (2021) Modeling microbial adaptations to nutrient limitation during litter decomposition. Front Forests Glob Change 4:686945

Martin M (2014) Cutadapt removes adapter sequences from high-throughput sequencing reads. Embnetjournal 17:3

Metsalu T, Vilo J (2015) Clustvis: a web tool for visualizing clustering of multivariate data using principal component analysis and heatmap. Nucleic Acids Res 43:W566-570. https://doi.org/10.1093/nar/gkv468

Montoya-Sánchez V, Kreft H, Arimond I, Ballauff J, Berkelmann D, Brambach F, Daniel R, Grass I, Hines J, Hölscher D, Irawan B, Krause A, Polle A, Potapov A, Sachsenmaier L, Scheu S, Sundawati L, Tscharntke T, Zemp DC, Guerrero-Ramírez NR (2023) Landscape heterogeneity and soil biota are central to multi-taxa diversity for oil palm landscape restoration. Commun Earth Environ 4:209. https://doi.org/10.1038/s43247-023-00875-6

Monzon JP, Slingerland MA, Rahutomo S, Agus F, Oberthür T, Andrade JF, Couëdel A, Rattalino Edreira JI, Hekman W, van den Beuken R, Hidayat F, Pradiko I, Purwantomo DKG, Donough CR, Sugianto H, Lim YL, Farrell T, Grassini P (2021) Fostering a climate-smart intensification for oil palm. Nat Sustain 4:595–601. https://doi.org/10.1038/s41893-021-00700-y

Moradi A, Teh CBS, Goh KJ, Husni MHA, Ishak CF (2014) Decomposition and nutrient release temporal pattern of oil palm residues: decomposition and nutrient release temporal pattern of oil palm residues. Ann Appl Biol 164:208–219. https://doi.org/10.1111/aab.12094

Naidu Y, Idris AS, Nusaibah SA, Norman K, Siddiqui Y (2015) *In vitro* screening of biocontrol and biodegradation potential of selected hymenomycetes against *Ganoderma boninense* and infected oil palm waste. For Pathol 45:474–483. https://doi.org/10.1111/efp.12197

Nguyen NH, Song Z, Bates ST, Branco S, Tedersoo L, Menke J, Schilling JS, Kennedy PG (2016) FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecol 20:241–248. https://doi.org/10.1016/j.funeco.2015.06.006

Nottingham AT, Hicks LC, Cahuana AJQ, Salinas N, Bååth E, Meir P (2018) Nutrient limitations to bacterial and fungal growth during cellulose decomposition in tropical forest soils. Biol Fertil Soils 54:219–228. https://doi.org/10.1007/s00374-017-1247-4

Oliveira J, Yildirir G, Corradi N (2024) From chaos comes order: genetics and genome biology of arbuscular mycorrhizal fungi. Annu Rev Microbiol 78:147–168. https://doi.org/10.1146/annurev-micro-041522-105143

Osono T (2020) Functional diversity of ligninolytic fungi associated with leaf litter decomposition. Ecol Res 35:30–43. https://doi.org/10.1111/1440-1703.12063

Paterno GB, Brambach F, Guerrero-Ramírez N, Zemp DC, Cantillo AF, Camarretta N, Moura CCM, Gailing O, Ballauff J, Polle A, Schlund M, Erasmi S, Iddris NA, Khokthong W, Sundawati L, Irawan B, Hölscher D, Kreft H (2024) Diverse and larger tree islands promote native tree diversity in oil palm landscapes. Science 386:795–802. https://doi.org/10.1126/science.ado1629

Pawłowska J, Okrasińska A, Kisło K, Aleksandrzak-Piekarczyk T, Szatraj K, Dolatabadi S, Muszewska A (2019) Carbon assimilation profiles of mucoralean fungi show their metabolic versatility. Sci Rep 9:11864. https://doi.org/10.1038/s41598-019-48296-w

Philippot L, Raaijmakers JM, Lemanceau P, van der Putten WH (2013) Going back to the roots: the microbial ecology of the rhizosphere. Nat Rev Microbiol 11:789–799. https://doi.org/10.1038/nrmicro3109

Pradiko I, Ginting EN, Sumaryanto, Koedadiri AD, Darlan NH, Pane RDP, Sapalina F (2022) Fertilizer placement in circle weeding vs. in interrow: which one is better for oil palm? Atlantis Press, pp 222–230

Promputtha I, Lumyong S, Lumyong P, McKenzie EC, Hyde KD (2002) Fungal succession on senescent leaves of *Manglietia garrettii* in Suthep-Pui National Park, northern

Thailand. Fungal Diversity 10:89–100. http://hdl.handle.net/10722/223470

Promputtha I, Lumyong S, Dhanasekaran V, McKenzie EHC, Hyde KD, Jeewon R (2007) A phylogenetic evaluation of whether endophytes become saprotrophs at host senescence. Microb Ecol 53:579–590. https://doi.org/10.1007/s00248-006-9117-x

Pulunggono HB, Anwar S, Mulyanto B, Sabiham S (2019) Decomposition of oil palm frond and leaflet residues. AGRIVITA J Agric Sci 41:524–536. https://doi.org/10.17503/agrivita.v41i3.2062

Purahong W, Krüger D, Buscot F, Wubet T (2016) Correlations between the composition of modular fungal communities and litter decomposition-associated ecosystem functions. Fungal Ecol 22:106–114. https://doi.org/10.1016/j.funeco.2016.04.009

Rathnayaka AR, Chethana KWT, Phillips AJL, Liu J-K, Samarakoon MC, Jones EBG, Karunarathna SC, Zhao C-L (2023) Re-evaluating Botryosphaeriales: ancestral state reconstructions of selected characters and evolution of nutritional modes. J Fungi 9:184. https://doi.org/10.3390/jof9020184

Rivera A, Ospina-Bautista F, Estévez J, Posada R, Toro D (2025) Drivers of fungal succession during leaf litter decomposition in restored and secondary forests in tropical Andean forest. Restor Ecol 33:e14367. https://doi.org/10.1111/rec.14367

Rognes T, Flouri T, Nichols B, Quince C, Mahé F (2016) VSEARCH: a versatile open source tool for metagenomics. PeerJ 4:e2584. https://doi.org/10.7717/peerj.2584

Rüegg J, Quezada JC, Santonja M, Ghazoul J, Kuzyakov Y, Buttler A, Guillaume T (2019) Drivers of soil carbon stabilization in oil palm plantations. Land Degrad Dev 30:1904–1915. https://doi.org/10.1002/ldr.3380

Ryadin AR, Janz D, Schneider D, Tjoa A, Irawan B, Daniel R, Polle A (2022) Early effects of fertilizer and herbicide reduction on root-associated biota in oil palm plantations. Agronomy 12:199. https://doi.org/10.3390/agronomy12010199

Scheu S, Setälä H (2002) Multitrophic interactions in decomposer food-webs. In: Hawkins BA, Tscharntke T (eds) Multitrophic Level Interactions. Cambridge University Press, Cambridge, pp 223–264

Schneider T, Gerrits B, Gassmann R, Schmid E, Gessner MO, Richter A, Battin T, Eberl L, Riedel K (2010) Proteome analysis of fungal and bacterial involvement in leaf litter decomposition. Proteomics 10:1819–1830. https://doi.org/10.1002/pmic.200900691

Setälä H, McLean MA (2004) Decomposition rate of organic substrates in relation to the species diversity of soil saprophytic fungi. Oecologia 139:98–107. https://doi.org/10.1007/s00442-003-1478-y

Shrestha P, Ibáñez AB, Bauer S, Glassman SI, Szaro TM, Bruns TD, Taylor JW (2015) Fungi isolated from *Miscanthus* and sugarcane: biomass conversion, fungal enzymes, and hydrolysis of plant cell wall polymers. Biotechnol Biofuels 8:38. https://doi.org/10.1186/s13068-015-0221-3

Stallman JK, Haelewaters D, Koch Bach RA, Brann M, Fatemi S, Gomez-Zapata P, Husbands DR, Jumbam B, Kaishian PJ, Moffitt A, Catherine Aime M (2024) The contribution of tropical long-term studies to mycology. IMA Fungus 15:35. https://doi.org/10.1186/s43008-024-00166-5

Suwandi AS, Kondo N (2012) Common spear rot of oil palm in Indonesia. Plant Dis 96:537–543. https://doi.org/10.1094/PDIS-08-10-0569

Talbot JM, Bruns TD, Smith DP, Branco S, Glassman SI, Erlandson S, Vilgalys R, Peay KG (2013) Independent roles of ectomycorrhizal and saprotrophic communities in soil organic matter decomposition. Soil Biol Biochem 57:282–291. https://doi.org/10.1016/j.soilbio.2012.10.004

Tao H-H, Slade EM, Willis KJ, Caliman J-P, Snaddon JL (2016) Effects of soil management practices on soil fauna feeding activity in an Indonesian oil palm plantation. Agric Ecosyst Environ 218:133–140

Tao H-H, Snaddon JL, Slade EM, Caliman J-P, Widodo RH, Suhardi WKJ (2017) Long-term crop residue application maintains oil palm yield and temporal stability of production. Agron Sustain Dev 37:33. https://doi.org/10.1007/s13593-017-0439-5

Tennakoon DS, Kuo C-H, Purahong W, Gentekaki E, Pumas C, Promputtha I, Hyde KD (2022) Fungal community succession on decomposing leaf litter across five phylogenetically related tree species in a subtropical forest. Fungal Divers 115:73–103. https://doi.org/10.1007/s13225-022-00508-x

Toju H, Tanabe AS, Yamamoto S, Sato H (2012) High-coverage ITS primers for the DNA-based identification of Ascomycetes and Basidiomycetes in environmental samples. PLoS ONE 7:e40863. https://doi.org/10.1371/journal.pone.0040863

Van Der Heijden MGA, Bardgett RD, Van Straalen NM (2008) The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol Lett 11:296–310. https://doi.org/10.1111/j.1461-0248.2007.01139.x

Voříšková J, Baldrian P (2013) Fungal community on decomposing leaf litter undergoes rapid successional changes. ISME J 7:477–486

Wang W, Zhang Q, Sun X, Chen D, Insam H, Koide RT, Zhang S (2020) Effects of mixed-species litter on bacterial and fungal lignocellulose degradation functions during litter decomposition. Soil Biol Biochem 141:107690. https://doi.org/10.1016/j.soilbio.2019.107690

Weiß M, Waller F, Zuccaro A, Selosse M-A (2016) Sebacinales – one thousand and one interactions with land plants. New Phytol 211:20–40. https://doi.org/10.1111/nph.13977

Wenzel A, Westphal C, Ballauff J, Berkelmann D, Brambach F, Buchori D, Camarretta N, Corre MD, Daniel R, Darras K, Erasmi S, Formaglio G, Hölscher D, Iddris NA-A, Irawan B, Knohl A, Kotowska MM, Krashevska V, Kreft H, Mulyani Y, Mußhoff O, Paterno GB, Polle A, Potapov A, Röll A, Scheu S, Schlund M, Schneider D, Sibhatu KT, Stiegler C, Sundawati L, Tjoa A, Tscharntke T, Veldkamp E, Waite P-A, Wollni M, Zemp DC, Grass I (2024) Balancing economic and ecological functions in smallholder and industrial oil palm plantations. Proc Natl Acad Sci USA 121:e2307220121. https://doi.org/10.1073/pnas.2307220121

White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: PCR Protocols. Elsevier, pp 315–322

Yahya Z, Husin A, Talib J, Othman J, Ahmed OH, Jalloh MB (2010) Oil palm (*Elaeis guineensis*) roots response to mechanization in Bernam series soil. Am J Appl Sci 7:343

Yang T, Adams JM, Shi Y, Sun H, Cheng L, Zhang Y, Chu H (2017) Fungal community assemblages in a high elevation desert environment: absence of dispersal limitation and edaphic effects in surface soil. Soil Biol Biochem. https://doi.org/10.1016/j.soilbio.2017.09.013

Zemp DC, Guerrero-Ramirez N, Brambach F, Darras K, Grass I, Potapov A, Röll A, Arimond I, Ballauff J, Behling H, Berkelmann D, Biagioni S, Buchori D, Craven D, Daniel R, Gailing O, Ellsäßer F, Fardiansah R, Hennings N, Irawan B, Khokthong W, Krashevska V, Krause A, Kückes J, Li K, Lorenz H, Maraun M, Merk MS, Moura CCM, Mulyani YA, Paterno GB, Pebrianti HD, Polle A, Prameswari DA, Sachsenmaier L, Scheu S, Schneider D, Setiajiati F, Setyaningsih CA, Sundawati L, Tscharntke T, Wollni M, Hölscher D, Kreft H (2023) Tree islands enhance biodiversity and functioning in oil palm landscapes. Nature 618:316–321. https://doi.org/10.1038/s41586-023-06086-5

Zhang J, Li J, Fan Y, Mo Q, Li Y, Li Y, Li Z, Wang F (2020) Effect of nitrogen and phosphorus addition on litter decomposition and nutrients release in a tropical forest. Plant Soil 454:139–153. https://doi.org/10.1007/s11104-020-04643-9

Zhou Z, Lu J-Z, Widyastuti R, Scheu S, Potapov A, Krashevska V (2024) Plant roots are more strongly linked to microorganisms in leaf litter rather than in soil across tropical land-use systems. Soil Biol Biochem 190:109320. https://doi.org/10.1016/j.soilbio.2024.109320

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