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BELOWGROUND FUNGAL COMMUNITY COMPOSITION AND DISTRIBUTION IN PEAT FORESTS AND A MANAGED PEAT ECOSYSTEM OF MALAYSIAN TROPICAL PEATLAND

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ABSTRACT

Fungi have a primary role in the decomposition of organic matter in tropical peatlands and contribute to maintaining ecosystem functions. Understanding the belowground fungal diversity and composition is a preliminary step to predicting the stability of ecosystem functions, especially in ecosystems that have been exposed to anthropogenic impacts. This study determined soil fungal diversity and community composition in two types of forest: Peat swamp forest (PSF) and logged-over secondary forest (LOF) and a managed ecosystem (oil palm plantation, OPP) in peatland in Sarawak, Malaysia. Fungi from peat samples were isolated and identified using 18S rDNA region sequencing. Fungal diversity was calculated, and Bray-Curtis dissimilarity was performed to compare fungal communities between the study sites. LOF has the highest diversity, followed by PSF and OPP. In addition, the fungal community composition is more similar between LOF and PSF than between the peat forests and OPP. Aspergillus *spp. and* Trichoderma *spp. contributed to the great dissimilarities between the peat forests and the managed ecosystem due to their dominance. In conclusion, LOF is an important ecosystem that retains relatively high fungal diversity. Different fungal communities were observed, which contained ecologically important fungal groups incorporated into the peat forests and an oil palm plantation.*

Keywords: fungal diversity, logged-over forest, primary forest, tropical peatland

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INTRODUCTION

A growing interest in belowground biodiversity in peatlands has been observed over the last two decades, owing to their functional importance in regulating nutrient cycling, decomposition, primary production, and climate change (Bach *et al.*, 2020; Song *et al.*, 2020). Belowground biodiversity, comprising primarily of microorganisms (bacteria, archaea, and fungi) and larger organisms (earthworms, ants, termites, and arachnids), play important ecological roles as symbionts, mutualists, decomposers, and pathogens (Bardgett and Van Der Putten, 2014; Food and Agriculture Organisation, 2020; Tedersoo *et al.*, 2014). Soil microorganisms, particularly bacteria, archaea, and fungi, are key indicators of various soil quality and health attributes, such as nutrient availability, carbon sequestration, incidence of plant diseases, and promotion of plant growth (Fierer *et al.*, 2021). Their roles are crucial in terrestrial ecosystems, particularly in agricultural ecosystems, to address challenges and solutions for sustainable farming, food security, and climatic impacts. Understanding the community, structure, and diversity of soil microorganisms is critical for predicting ecosystem functioning in response to environmental changes so as to allow the implementation of conservation and management efforts (Egidi *et al.*, 2019) and maintain ecosystem stability during climate change (Li *et al.*, 2019).

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In peatlands, soil fungi constitute a large fraction of the belowground community (Juan-Ovejero *et al.*, 2020). Most of the dominant soil fungi in peatlands are known as saprotrophs, which play a significant role in the decomposition of organic matter (Thormann, 2006; Thormann and Rice, 2007). Fungi produce a variety of extracellular enzymatic substances to assist in the degradation of simple and complex recalcitrant polymers, such as starch, cellulose, proteins, chitin, keratin, and lignin of wood (Eichlerová *et al.*, 2015; Paredes *et al.*, 2014). In addition, other fungi classified in the fungal guilds of pathogens, yeasts, ectomycorrhizal fungi, ericoid mycorrhizal, and dark septate endophytic fungi also contribute to the decomposition of organic matter (Andersen *et al.*, 2013; Juan-Ovejero *et al.*, 2020; Robinson *et al.*, 2020). In a recent commentary, symbiotic fungi are considered ecosystem engineers due to their role in regulating the carbon sink in ombrotrophic peatlands via nutrient transfer (Barel and Robroek, 2023). Therefore, soil fungal communities and their diversity are recognised as the main components in regulating carbon dynamics and nutrient turnover in the peatland ecosystem (Juan-Ovejero *et al.*, 2020).

Soil fungal communities have been extensively identified and studied in many ecosystems across the globe (Egidi *et al.*, 2019; Newsham *et al.*, 2016; Shi *et al.*, 2014) including in peatlands. However, studies are limited to bogs (Filippova and Thormann, 2014; Golovchenko *et al.*, 2013; Morrison *et al.*, 2020) and fens (Asemaninejad *et al.*, 2017; Mpamah *et al.*, 2017; Zhang *et al.*, 2017), while tropical peatlands remain overlooked (Juan-Ovejero *et al.*, 2020). As tropical peatlands are one of the largest carbon stock reservoirs (Page *et al.*, 2022), it is important to protect and restore them by studying the diversity and functional role of their inhabiting soil fungi. This is because the carbon balance in peatland ecosystems is largely carried out by microbial activity, besides the interactions between plants and diverse soil communities (Barel and Robroek, 2023; Page *et al.*, 2022). In Malaysia, tropical peatlands are exposed to anthropogenic disturbances, such as agricultural conversion, which led researchers to conduct studies on soil fungal communities. A few studies have emphasised the sensitivity of soil fungal communities towards the conversion of forest to oil palm cultivation (Kerfahi *et al.*, 2014; Mcguire *et al.*, 2015; Robinson *et al.*, 2020). These studies showed that soil fungal communities can be an indicator or basis to monitor the impact of land use and response to environmental changes, especially in agricultural ecosystems. Thus, it is imperative to deepen the understanding of microorganisms in these ecosystems. Considering the importance of soil fungi and the limited studies in tropical peatlands, this study was conducted to determine soil fungal communities and diversity in the tropical peatlands of Sarawak, Malaysia. The objective of this study is to determine soil fungal community, diversity, and structure under two types of forests, *i.e.*, peat swamp forest (PSF) and logged-over secondary forest (LOF), and a managed ecosystem in an oil palm plantation (OPP).

MATERIALS AND METHODS

Site Description and Sample Collection

Study sites were selected in the district of Sri Aman, Sarawak, Malaysia, representing the area of lowland tropical peatland. Peat samples were collected in August 2013 during the dry season (precipitation <200 mm/ sampling month) from peat swamp forest (PSF), logged-over secondary forest (LOF) and a managed peat ecosystem represented by an 8 year-old oil palm plantation (OPP). PSF is a gazetted mixed tropical peat swamp forest, owned by the Malaysian government, with an extensive area of 43 147 ha (Melling, 2016) and located along a riverbank of the Maludam River. PSF is a habitat for several important high-value timber species, such as *Gonystylus bacanus*, *Dactylocladus stenostachys* and *Shorea* spp. This forest contains diverse faunal species, with a few endemic fauna such as *Presbytis chrysomelas crucige* (Red Banded Langur) and *Nasalis larvatus* (Proboscis monkey) (Melling, 2016). LOF is a secondary forest that was recovered after timber extraction for land preparation years ago. It was covered with shrubs and small woody trees (Kusai *et al.*, 2018). In OPP, routine management practices have been carried out throughout the year, such as the application of fertiliser and herbicides, tilling, compaction, and maintaining the water table for palm growth and production. The reduction of the water table within the oil palm plantation was maintained by a drainage system on site (Dhandapani *et al.*, 2020). The total area of LOF was 2411.5 ha, while the planted OPP area was 4152.7 ha.

Peat samples were collected at ten sampling points at each study site. In PSF and OPP, the samples were collected in two transects with approximately a distance of 10 m to 100 m between each sampling point, while samples from LOF were taken in a line transect at a 100 m interval (Maidin *et al.*, 2016; Siti Ramlah *et al.*, 2016). The coordinates for each sampling point were recorded (Kusai *et al.*, 2018).

Peat soil cores were taken from peat surfaces up to 60 cm using a peat auger (Eijkelkamp, The Netherlands) with a half-cylindrical shape (diameter: 5.2 cm). A core sample collected in

the peat auger was divided into four subsamples according to depths of 0-30 cm, 30-40 cm, 40-50 cm, and 50-60 cm and placed into designated 50 mL tubes before being transported to the laboratory for analysis. All peat samples were stored at 4°C for a short-term period of one month, and biological analyses such as the isolation of fungi were conducted within two weeks of sampling.

Isolation and Identification of Fungi

Peat samples were serially diluted up to a dilution of 10^{-5} for fungal isolation. A volume of 100 µL of dilutions 10^{-4} and 10^{-5} was spread evenly on potato dextrose agar (PDA) and malt extract agar (MEA) and incubated at 25 ± 2°C for three days. Colonies grown on both media were subcultured onto a new PDA to obtain pure cultures and used for identification.

The pure cultures were grown on PDA and incubated at 25 ± 2°C for three and seven days for fast-growing fungi and slow-growing fungi, respectively. The mycelium of the isolate was harvested, and genomic DNA was extracted using Fungi/ Yeast Genomic DNA Isolation Kit (NorgenBiotek Corp., Canada) according to the manufacturer's instructions.

A pair of primer; forward primer, EF4-F (5'-GG AAGGG[G/A]TGTATTTATTAG-3') and reverse primer fung5-R (5'-GTAAAAGTCCTGGTTCC CC-3') were employed to amplify the 18S rDNA region of fungi (Smit *et al.*, 1999). A volume of 25 µL PCR master mix was used; 1× PCR buffer, 1.0 µM of each primer, 0.2 mM of each dNTP, 0.3 U of GoTaq Flexi DNA polymerase (Promega, Madison, WI, USA), 2.5 mM $MgCl_2$, 0.3% of bovine serum albumin and 1.0 µL DNA template. Amplification of 18S rDNA was carried out in a thermal cycler (Applied Biosystems Veriti™ Thermal Cycler, USA) with the following cycle: Initial denaturation at 94°C for 3 min, 30 cycles of denaturation, annealing and extension at 94°C for 1 min, 48°C for 1 min, 72°C for 1 min, respectively. The final extension was performed at 72°C for 5 min.

The PCR product was electrophoresed in 1% agarose gel, stained with FloroSafe DNA Stain (First BASE Laboratories, Malaysia) and run at 80 V for 30 min. The gel was viewed under UV to observe the amplified band of interest with a size of 550 bp. The amplified bands were excised and purified using a purification kit, EasyPure® Quick Gel Extraction Kit (Transgen Biotech, China). The purified products were sent to First BASE Laboratories (Malaysia) for sequencing according to the Sanger sequencing-based method. Sequences were compared with the nucleotide sequences in GenBank using Basic Local Alignment Search Tool (BLAST) analysis (http://blast.ncbi.nlm.nih.gov/blast/Blast.cgi) to verify the similarity of the sequences and classify the fungal isolates into genus and species levels.

Diversity Indices and Data Analysis

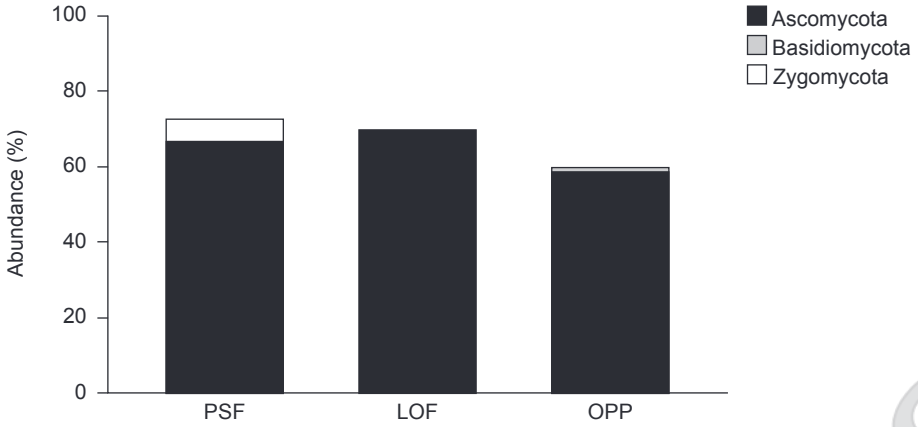
Species diversity in the study sites was calculated using the Shannon's diversity index (H') (Shannon and Weaver, 1963) and the Simpson diversity index (D) (Simpsons, 1949). Species richness (S) was determined using the total number of species in each study (Magurran, 2004; Pielou, 1969). Evenness (E) was also calculated to determine the distribution of abundance across the species in a community (Hill *et al.*, 2003). Analysis of similarities (ANOSIM) was run to determine the significant variation in the fungal composition between PSF, LOF and OPP. Prior to analysis, the square root transformation was applied to the fungal composition data. The comparison of fungal composition between study sites was evaluated using pairwise Bray-Curtis distance and displayed using non-metric multidimensional scaling (NMDS). Similarity percentage (SIMPER) was also determined to identify the dominant species contributing to the fungal composition in the study sites. All the analyses were performed using PRIMER version 7 software (PRIMER-E Ltd., Plymouth, United Kingdom).

RESULTS

Belowground Fungal Community and Composition

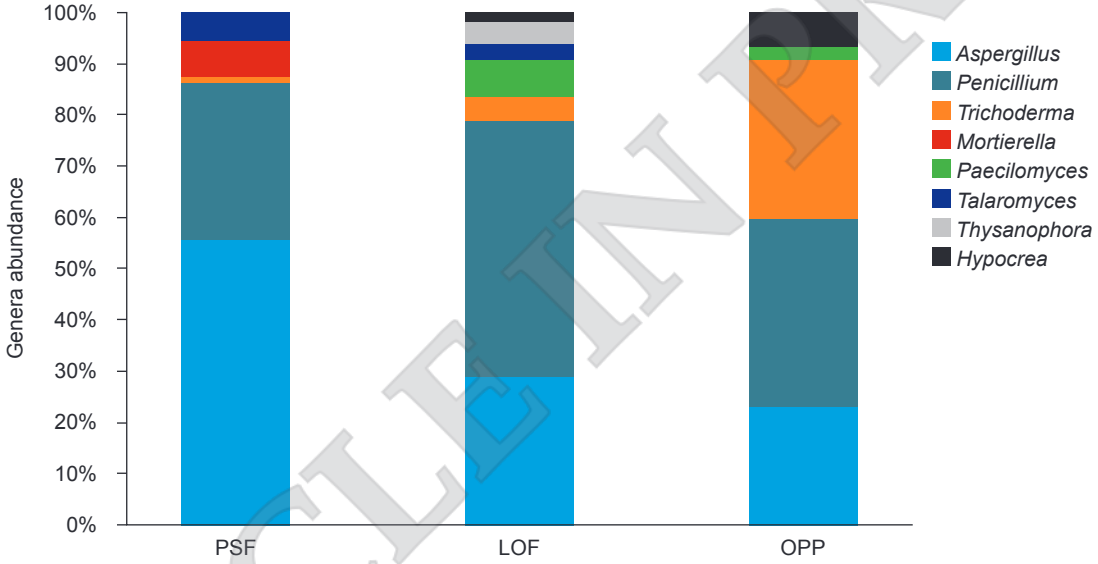
A total of 203 isolates were isolated and identified from all study sites, representing 3 phyla, 16 genera, and 30 species. The percentage of similarity between the isolated fungi and the sequences in the GenBank was high, between 81% and 100%. In total, 73 isolates were obtained from PSF, while 70 and 60 isolates were obtained from LOF and OPP, respectively. Three phyla comprising Ascomycota, Basidiomycota, and Zygomycota were identified using the 18S rDNA region, with Ascomycota being the most frequently isolated from the peat samples (12 genera) (*Figure 1*). Meanwhile, only Ascomycota was found in the LOF. A small proportion of Basidiomycota was obtained from the OPP, whereas Zygomycota was only found in PSF.

At the genus level, *Aspergillus*, *Penicillium* and *Trichoderma* were commonly found in all study sites (*Figure 2*). About 54.8% of the fungi found in the PSF were *Aspergillus*, and half of this number was from the LOF and OPP. *Penicillium* was highly isolated from the LOF at 47.1%, compared to PSF (30.2%) and OPP (34.9%). Meanwhile, *Trichoderma* was distinctly found in OPP (30%), compared to PSF (1.4%) and LOF (4.3%).



Note: Study sites: PSF - peat swamp forest; LOF - logged-over secondary forest; OPP - oil palm plantation.

Figure 1. Abundances of soil fungal taxa.



Note: Study sites: PSF - peat swamp forest; LOF - logged-over secondary forest; OPP - oil palm plantation.

Figure 2. Abundance of fungal genera in all study sites. Genera less than 2% were excluded. Genera excluded were Cordyceps, Coniochaetales, Lecythophora, Meyerozyma, Myrothecium, Polyporus, Purpureocillium *and* Umbelopsis.

The common species present in all study sites were *Aspergillus fumigatus*, *Penicillium corylophilum*, *P. roqueforti*, *Penicillium* sp., and *Trichoderma* sp. (*Table 1*). The teleomorph of *Trichoderma*, *i.e.*, *Hypocrea*, was found in the LOF (1.4%) and OPP (6.7%). A species of Basidiomycota, *Polyporus ciliatus*, was isolated at a low frequency (1.7%) in OPP. Meanwhile, *Mortierella chlamydospora* (6.8%) and *Umbelopsis isabellina* (1.4%), which are classified in the phylum Zygomycota, were only found in the PSF.

Five species unique to PSF, *A. fischeri*, *A. flavipes*, *M. chlamydospora*, *P. purpurogenum* and *U. isabellina*, were absent in the LOF and OPP. Likewise, five species from the OPP, *i.e.*, *Coniochaetales* sp., *H. rufa*, *Lecythophora* sp., *P. freii*, and *Polyporus ciliates*, were not found at other study sites. In contrast, nine species were found only in the LOF and not detected in the PSF and OPP. The species were *Cordyceps cylindrica*, *Meyerozyma guilliermondii*, *Myrothecium* sp., *P. chrysogenum*, *P. commune*, *P. oxalicum*, *Purpureocillium lilacinum*, *Thysanophora* sp., and *Trichoderma harzianum*.

Fungal Diversity

Based on Shannon's and Simpson's diversity indices, LOF displayed a higher fungal diversity, at 2.321 and 0.864 (*Table 2*), than the other sites. This was followed by PSF (H' = 2.166, D = 0.852) and OPP (H' = 2.049, D = 0.832). Species richness was also highest in the LOF, with 18 species. However,

PSF and OPP recorded the same richness, with 14 species. Species evenness ranged between 0.776 and 0.821. The least even distribution was observed in OPP (0.776), while the highest evenness was recorded in PSF (0.821).

The fungal community composition differed significantly between PSF, LOF, and OPP (ANOSIM, R global = 0.336; number of permutations = 999; P < 0.001; *Table 3*). The fungal community in PSF and OPP showed a significant dissimilarity (R = 0.452, P < 0.001). The ordination plot showed differences in species composition between PSF and LOF, where the composition resembled each other more than OPP (*Figure 3*).

The SIMPER analysis revealed that three species contributed to more than 80% of the total species identified in PSF (*Table 4*). *Aspergillus fumigatus* contributed about 50.85% of the fungal assemblages in PSF, while *Penicillium* sp. (37.24%) and *Trichoderma* sp. (55.83%) contributed greatly to fungal assemblages within the LOF and OPP.

SIMPER analysis for dissimilarity indicated greater dissimilarity between PSF and OPP (average dissimilarity = 74.87%) than LOF and OPP (average dissimilarity = 73.24%) and between PSF and LOF (average dissimilarity = 60.87%, *Table 5*). The species that contributed to the largest differences were *Trichoderma* sp. and *A. fumigatus*, abundant in OPP and PSF. The taxa that contributed to the dissimilarity between LOF and OPP were *Trichoderma* sp. and *Penicillium* sp. The fungal community in PSF was more similar to LOF, with *Aspergillus* sp., *Penicillium* sp., and *P. roqueforti* as the main contributors.

TABLE 1. PERCENTAGE ABUNDANCE OF FUNGI ISOLATED IN DIFFERENT STUDY SITES

Species	Percentage abundance (%)		
	PSF	LOF	OPP
Aspergillus fischeri	1.4	0	0
Aspergillus flavipes	2.7	0	0
Aspergillus fumigatus	31.5	25.7	16.7
Aspergillus niger	1.4	1.4	0
Aspergillus nomius	5.5	0	1.7
Aspergillus sp.	12.3	0	3.3
Coniochaetales sp.	0	0	1.7
Cordyceps cylindrica	0	1.4	0
Hypocrea atroviridis	0	1.4	5.0
Hypocrea rufa	0	0	1.7
Lecythophora sp.	0	0	1.7
Meyerozyma guilliermondii	0	1.4	0
Mortierella chlamydospora	6.8	0	0
Myrothecium sp.	0	1.4	0
Paecilomyces sp.	0	7.1	1.7
Penicillium chrysogenum	0	1.4	0
Penicillium commune	0	5.7	0
Penicillium corylophilum	5.5	2.9	3.3
Penicillium freii	0	0	3.3
Penicillium oxalicum	0	1.4	0
Penicillium purpurogenum	1.4	0	0
Penicillium roqueforti	8.2	11.4	23.3
Penicillium sp.	15.1	24.3	5.0
Polyporus ciliatus	0	0	1.7
Purpureocillium lilacinum	0	1.4	0
Talaromyces purpureogenus	5.5	2.9	0
Thysanophora sp.	0	4.3	0
Trichoderma harzianum	0	1.4	0
Trichoderma sp.	1.4	2.9	30.0
Umbelopsis isabellina	1.4	0	0

Note: Study sites: PSF - peat swamp forest; LOF - logged-over secondary forest; OPP - oil palm plantation.

TABLE 2. DIVERSITY INDICES OF SOIL FUNGAL COMMUNITIES

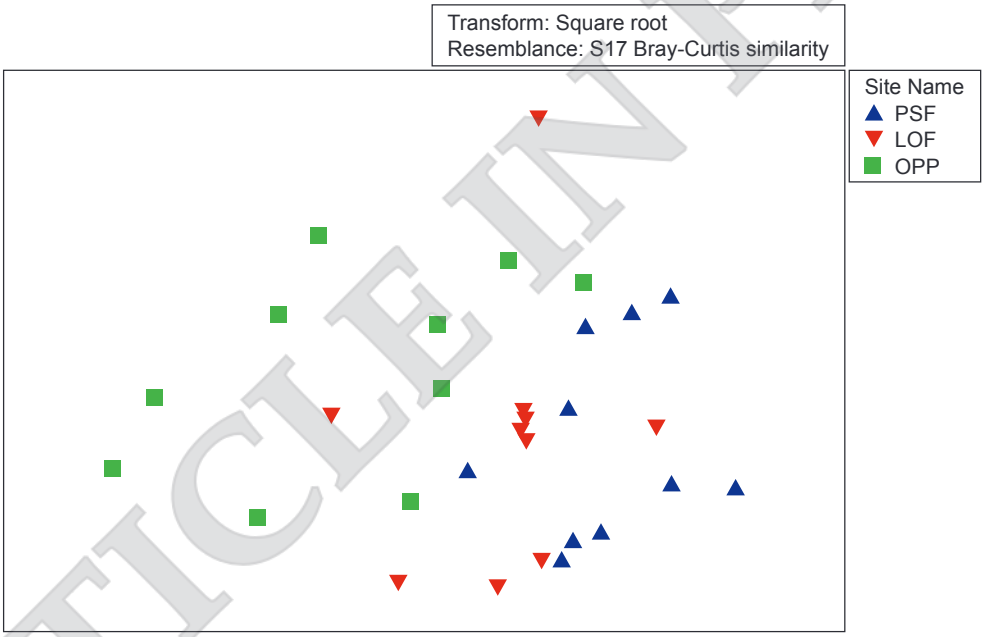
Sites	Total isolates	Shannon's diversity index	Simpson's diversity index	Species richness	Evenness
PSF	73	2.166	0.852	14	0.821
LOF	70	2.321	0.864	18	0.803
OPP	60	2.049	0.832	14	0.776

Note: Study sites: PSF - peat swamp forest; LOF - logged-over secondary forest; OPP - oil palm plantation.

TABLE 3. ANALYSIS OF SIMILARITIES (ANOSIM) IN SPECIES COMPOSITION OF FUNGI

Sites	R value[a]	*P*-value
PSF *vs*. LOF	0.2	0.003
PSF *vs*. OPP	0.452	0.001*
LOF *vs*. OPP	0.372	0.001*

Note: Study sites: PSF - peat swamp forest; LOF - logged-over secondary forest; OPP - oil palm plantation; *vs*. - versus; [a] ANOSIM; R global = 0.336; *Number of permutations = 999; $P < 0.001$.



Note: Study sites: PSF - peat swamp forest; LOF - logged-over secondary forest; OPP - oil palm plantation.

Figure 3. Non-metric multidimensional scaling (NMDS) ordination comparing the fungal community in different study sites.

TABLE 4. SIMPER ANALYSIS OF THE SIMILARITY OF SPECIES COMPOSITION

Sites	Average similarity	Species	Average abundance	Contribution (%)	Cumulative contribution (%)
PSF	47.90	*Aspergillus fumigatus*	1.49	50.85	50.85
		Aspergillus sp.	0.78	16.49	67.34
		Penicillium sp.	0.80	15.91	83.24
LOF	44.99	*Penicillium* sp.	1.21	37.42	37.42
		Aspergillus fumigatus	1.19	34.30	71.72
OPP	34.13	*Trichoderma* sp.	1.16	55.83	55.83
		Penicillium roqueforti	0.87	23.24	79.07

Note: Study sites: PSF - peat swamp forest; LOF - logged-over secondary forest; OPP - oil palm plantation.

TABLE 5. SIMPER ANALYSIS OF DISSIMILARITY OF FUNGAL COMMUNITIES

Study site	Average dissimilarity (%)	Species dissimilarity	Average abundance	Contribution (%)
PSF *vs*. LOF	60.87	*Aspergillus* sp.	0.78	11.30
		Penicillium sp.	0.80	10.63
		Penicillium roqueforti	0.48	10.02
		Aspergillus fumigatus	1.49	7.97
		Mortierella chlamydospora	0.44	6.80
		Penicillium corylophilum	0.34	5.98
		Talaromyces purpureogenus	0.34	5.63
		Paecilomyces sp.	0.00	5.47
		Penicillium commune	0.00	5.06
		Aspergillus nomius	0.34	4.72
PSF *vs*. OPP	74.87	*Trichoderma* sp.	0.10	15.44
		Aspergillus fumigatus	1.49	13.37
		Penicillium roqueforti	0.48	11.17
		Penicillium sp.	0.80	11.11
		Aspergillus sp.	0.78	9.51
		Mortierella chlamydospora	0.44	6.25
		Penicillium corylophilum	0.34	5.44
LOF *vs*. OPP	73.24	*Trichoderma* sp.	0.20	15.54
		Penicillium sp.	1.21	15.16
		Aspergillus fumigatus	1.19	12.87
		Penicillium roqueforti	0.74	10.94
		Paecilomyces sp.	0.38	5.70
		Penicillium commune	0.34	4.81
		Penicillium corylophilum	0.20	4.46
		Hypocrea atroviridis	0.10	3.87

Note: Study sites: PSF - peat swamp forest; LOF - logged-over secondary forest; OPP - oil palm plantation. *vs*.- versus.

DISCUSSION

Fungi obtained in this study belonged to the Ascomycota, Basidiomycota, and Zygomycota taxa, commonly present across peatlands, such as in China (Zhang *et al*., 2017), Japan (Yabuki *et al*., 2014), Canada (Asemaninejad *et al*., 2017; Zhang *et al*., 2023), Europe (Elliott *et al*., 2015; Sun *et al*., 2016, Vinogradova *et al*., 2023), Malaysia (Ayob *et al*., 2018; Kusai *et al*., 2018), Brunei (Tripathi *et al*., 2016a), and Australia (Birnbaum *et al*., 2023). These taxa can degrade organic matter, including cellulose, hemicellulose, pectin, lignin, tannin, and polyphenolic compounds (Thormann, 2006). A large proportion of Ascomycota indicated that this taxon is predominant in the peatlands of Sarawak, either in natural or managed ecosystems, due to their physiological characteristics as heavy sporulators and fast-growing microorganisms (Thormann and Rice, 2007). Moreover, ascomycetes have high adaptability to environmental stresses by utilising resources, leading to more generalist strategies and consequently contributing to their dominance in soil (Egidi *et al*., 2019). On the other hand, Basidiomycota is primarily a slow-growing fungus and a less prolific sporulator than Ascomycota (Thormann and Rice, 2007), which might explain the low abundance of Basidiomycota in Sarawak's peatland. Less distribution of Zygomycota in peatlands was commonly reported than the other two taxa (Juan-Ovejero *et al*., 2020; Liu *et al*., 2020).

The dominance of several genera was observed and identified in all study sites. Species belonging to the genus *Aspergillus* were greater in number and more frequently isolated than other genera in PSF. *Aspergillus fumigatus* dominated the fungal communities in PSF. It is a saprophytic fungus known as a recycler in nature by degrading plant polysaccharides (Benoit *et al*., 2015; Kwon-Chung and Sugui, 2013). Diverse metabolites enable this species to grow in different environmental conditions (Houbraken *et al*., 2014). Thus, it was also detected under managed ecosystem like oil palm plantations.

The genus *Penicillium* was more frequently isolated in LOF, with unknown *Penicillium* sp. making up the fungal communities. *Penicillium* is a predominant fungus found in a wide range of environments and substrates, including peat soil (Yabuki *et al.*, 2014). *Penicillium* was previously detected in the peatlands of Argentina (Paredes *et al.*, 2014), Finland (Sun *et al.*, 2016), and Russia (Dobrovol'skaya *et al.*, 2012). *Penicillium* produces extracellular enzymes to degrade polysaccharide such as cellulose in plant cells (Vaishnav *et al.*, 2018; Zhang *et al.*, 2014). Therefore, the presence of *Penicillium* is important for plant biomass degradation and carbon cycling in the logged-over secondary forest ecosystem.

Trichoderma spp. were the dominant fungi and contributed the most to the fungal community in OPP. They are root-colonising fungi and important plant-symbiotic microbes, with a high distribution in agricultural soils (Jiang *et al.*, 2016). A sampling conducted in 2012 also found that this group of fungi was more highly distributed in oil palm plantations than in other ecosystems (Kusai *et al.*, 2018). The existence of *Trichoderma* spp. in plantations enhances plant growth and nutrient uptake efficiency, increases photosynthesis, improves root structure, and induces systemic resistance to abiotic and biotic stresses (Harman, 2011; Shoresh *et al.*, 2010; Tyśkiewicz *et al.*, 2022). Metabolites produced by *Trichoderma* spp. (Mendoza-mendoza *et al.*, 2018) provide a promising biological control for severe oil palm disease, such as basal stem rot caused by *Ganoderma boninense* (Alexander *et al.*, 2017; Supramani *et al.*, 2022). Thus, the presence of *Trichoderma* may serve as a bioindicator for monitoring palm health and productivity besides reducing the use of chemical fungicides to control soil-borne diseases. It is still unknown why *Trichoderma* is exclusively isolated from oil palm plantations. *Trichoderma* may adapt to obtain nutrients from other soil organisms (Chaverri and Samuels, 2013) or enriched nutrients from soil environments that favour their growth in oil palm plantations.

Fewer species of Basidiomycota and Zygomycota were isolated from the sites in comparison to ascomycetes. Only one species of Basidiomycota was found in OPP, *i.e.*, *Polyporus ciliatus*. The species was previously reported in the Russian bog (Grum-Grzhimaylo *et al.*, 2016) and Caucasus regions, such as Iran, Turkey, and Russia (Gjobad-Nehjad, 2011). Two species of zygomycetes isolated from PSF, *Mortierella chlamydospora* and *Umbelopsis isabellina*, were previously isolated by Kusai *et al.* (2018) in 2012 from the same site, PSF. Despite the low isolated numbers of *M. chlamydospora* and *U. isabellina*, these species still reproduce and were detected in PSF in this study. *Mortierella chlamydospora* has a specialised structure with a thick wall and resistant spores that can survive for an extended period and remain dormant in peat soil (Lin *et al.*, 2014). *Umbelopsis isabellina* has been reported to be highly distributed in boreal forest in Canada (Summerbell, 2005), while *M. chlamydospora* was found in agricultural areas in the United Kingdom (Hunt *et al.*, 2004).

This study showed that primary and secondary logged-over forests and managed ecosystems have different fungal communities and dominant species within the study sites. The overall compositions of the isolate assemblage that make up the fungal communities in PSF and LOF were more similar to one another compared to those in OPP. Notable differences were observed in the fungal community of OPP and PSF compared with LOF, as shown in the NMDS ordination, which can be attributed to the impacts of anthropogenic disturbances in the OPP (Kerfahi *et al.*, 2014). These findings are consistent with Nurulita *et al.* (2016), who reported a distinct microbial community in the peatland forest that was converted into an oil palm plantation and rubber plantation in Indonesia. A similar finding in mineral soil was also reported in Peninsular Malaysia (Mcguire *et al.*, 2015). Both studies demonstrated that fungal communities differ between primary forest and oil palm plantations compared to regenerating forests. Based on a study of fungal mycelium production by Robinson *et al.* (2020), fungal communities of saprophytic, mycorrhizal, and pathogenic species were significantly different between oil palm plantations and forests (old-growth and selectively logged). After six months of installation of hyphal-in growth bags, mycelium fungal communities were unaffected by the logging event since both peat forest types showed similar fungal communities (Robinson *et al.*, 2020). Although oil palm plantations showed different fungal communities, they can still support several ecologically important fungal groups like plant-symbionts (*Trichoderma* spp.) and saprotrophs (*Aspergillus* spp. and *Penicillium* spp.) (Sun *et al.*, 2016), which are beneficial to plant development and decomposition processes, respectively.

In this study, LOF showed a higher diversity for both diversity indices when compared with PSF and OPP. This finding is consistent with a study by Mcguire *et al.* (2015), who revealed that the diversity of soil fungal communities is higher in regenerating forests (selectively logged 50 years ago) than in primary forest and oil palm plantations. Several aspects need to be considered when explaining this result, such as soil physical and chemical properties (Juan-Ovejero *et al.*, 2020) at each study site. Besides, the vegetation composition and chemical composition of litter could also contribute to the present results (Artz, 2009). LOF, a regenerating

forest logged years ago, would accumulate wood debris on the upper layer of peat soil, which might attract a more diverse species of fungi for the decaying processes. Logged-over secondary forests can retain the same taxonomy and structure of microbes as in a forest (Tripathi *et al.*, 2016b).

In this study, PSF was expected to have a higher fungal diversity than LOF and OPP due to the absence of anthropogenic activities at the site. Interestingly, lower fungal diversity and richness were recorded in PSF than in LOF. The result might be due to the dominance of *Aspergillus* spp., which may exclude less competitive or slow-growing species during isolation (Thormann, 2006), and subsequently reduce diversity. A similar observation was recorded in OPP for *Trichoderma* spp. A study by Repečkienė *et al.* (2012) reported how the abundance of fast-growing and sporulating species like *Trichoderma* and *Penicillium* suppressed the growth of other fungal species in peatland. However, studies by Mcguire *et al.* (2015); Nurulita *et al.* (2016), and Brinkmann *et al.* (2019) showed that the fungal diversity-based Shannon diversity index in OPP was similar to or even slightly higher than the primary forest ecosystem. No significant effect on the fungal diversity due to the conversion of forests to agricultural lands, such as rubber and oil palm plantations, was reported in their studies that were conducted in Malaysia and Indonesia. Nurulita *et al.* (2016) who focused on peatland, showed that fungal diversity in OPP was not significantly affected by oil palm practices compared to rubber practices. The contrasting finding may be due to the method of analysis by Nurulita *et al.* (2016), who used the culture-independent method PCR-DGGE, which identified a higher rate of microbial diversity compared to the culture-dependent method (Ayob and Kusai, 2021).

This study showed that the slightly reduced fungal diversity in OPP compared to the natural ecosystems is likely to be related to the addition of fertiliser (Berkelmann *et al.*, 2020), organic matter stock (Allen *et al.*, 2016), and vegetation richness (Drescher *et al.*, 2016) which can all exert some effects on the fungal diversity in OPP. However, a managed ecosystem like OPP can support considerable fungal diversity and richness. Numerous factors can also influence the structure of the fungal diversity and community in ecosystems, such as soil properties (Birkhofer *et al.*, 2012; Lauber *et al.*, 2008; Zhang *et al.*, 2016), vegetation diversity (Allingham *et al.*, 2023; Dassen *et al.*, 2017), hydrology (Lamit *et al.*, 2021) and tree species (Prescott and Grayston, 2013; Sun *et al.*, 2016; Urbanov *et al.*, 2015) and further investigation is needed to provide more concrete evidence.

CONCLUSION

In summary, the composition of the fungal community and diversity were different between forests (PSF and LOF) and a managed peat ecosystem (OPP). However, similar species composition was recorded between PSF and LOF in comparison to OPP. Remarkable results were found in LOF, which recorded the highest fungal diversity and richness compared to PSF and OPP. OPP does not always negatively impact diversity as they still support several fungal species that are important to carry out ecosystem functions, such as the decomposition of organic matter. However, proper and sustainable management within the OPP needs to be applied to preserve its fungal diversity. Natural and managed peat ecosystems have their unique species composition, which is ecologically important in regulating the decomposition of peat and, consequently, for the carbon cycle. The presence and absence status of particular fungal species could be an indicator for monitoring ecosystem disturbances. Nevertheless, further studies using advanced technology, such as next-generation sequencing (NGS), especially for spatio-temporal analysis, are necessary for a more comprehensive understanding of soil fungal diversity in mediating biogeochemical cycles in tropical peatlands.

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REFERENCES

Alexander, A; Abdullah, S; Rossall, S and Chong, K P (2017). Evaluation of the efficacy and mode of action of biological control for suppression of *Ganoderma boninense* in oil palm. *Pak. J. Bot.*, *49(3)*: 1193-1199.

Allen, K; Corre, M D; Kurniawan, S; Utami, S R and Veldkamp, E (2016). Spatial variability surpasses land-use change effects on soil biochemical properties of converted lowland landscapes in Sumatra, Indonesia. *Geoderma*, *284*: 42-50.

Allingham, S M; Nwaishi, F C; Andersen, R; Lamit, L J and Elliott, D R (2023). Microbial communities and biogeochemical functioning across peatlands in the Athabasca Oil Sands region of Canada: Implications for reclamation and management. *Land Degrad. Dev.*, *34(5)*: 1504-1521.

Andersen, R; Chapman, S J and Artz, R R E E (2013). Microbial communities in natural and disturbed peatlands: A review. *Soil Biol. Biochem.*, *57*: 979-994.

Artz, R R E (2009). Microbial community structure and carbon substrate use in Northern Peatlands. *Carbon Cycling in Northern Peatlands* (Baird, A J; Belya, L R; Comas, X; Reeve, A S and Slater, L D eds.). American Geophysical Union, Washington, DC. p. 111-129.

Asemaninejad, A; Thorn, R G and Lindo, Z (2017). Vertical distribution of fungi in hollows and hummocks of boreal peatlands. *Fungal Ecol.*, *27*: 58-68.

Ayob, Z and Kusai, N A (2021). A comparative study of bacterial communities determined by culture-dependent and -independent approaches in oil palm planted on tropical peatland. *J. Oil Palm Res.*, *33(4)*: 588-606.

Ayob, Z; Kusai, N A and Ali, S R A (2018). Sequence-based identification and characterisation of cultivated filamentous fungi in the Alan Bunga peat ecosystems of Sarawak, Malaysia. *Mires and Peat*, *21*: 1-19.

Bach, E M; Ramirez, K S; Fraser, T D and Wall, D H (2020). Soil biodiversity integrates solutions for a sustainable future. *Sustainability (Switzerland)*, *12(7)*: 1-20.

Bardgett, R D and Van Der Putten, W H (2014). Belowground biodiversity and ecosystem functioning. *Nature*, *515(7528)*: 505-511.

Barel, J M and Robroek, B J M (2023). Protecting nature's most effective carbon sink: An important role for fungi in peatlands. *New Phytol., 238(1)*: 5-7.

Benoit, I; Culleton, H; Zhou, M; Difalco, M; Osorio, G A; Battaglia, E; Bouzid, O; Brouwer, C P J M; Bushari, H B O E L and Coutinho, P M *et al.* (2015). Closely related fungi employ diverse enzymatic strategies to degrade plant biomass. *Biotechnol. Biofuels*, *8*: 107.

Berkelmann, D; Schneider, D; Meryandini, A and Daniel, R (2020). Unravelling the effects of tropical land use conversion on the soil microbiome. *Environ. Microbiome.*, *15(1)*: 1-18.

Birkhofer, K; Schöning, I; Alt, F; Herold, N; Klarner, B; Maraun, M; Marhan, S; Oelmann, Y; Wubet, T; Yurkov, A and Begerow, D *et al.* (2012). General relationships between abiotic soil properties and soil biota across spatial scales and different land-use types. *PLoS ONE*, *7(8)*: e43292.

Birnbaum, C; Wood, J; Lilleskov, E; Lamit, L J; Shannon, J; Brewer, M and Grover, S (2023). Degradation reduces microbial richness and alters microbial functions in an Australian peatland. *Microb. Ecol.*, *85(3)*: 875-891.

Brinkmann, N; Schneider, D; Sahner, J; Ballauff, J; Edy, N; Barus, H; Irawan, B; Budi, S W; Qaim, M and Daniel, R and Polle, A (2019). Intensive tropical land use massively shifts soil fungal communities. *Sci. Rep.*, *9(1)*: 1-11.

Chaverri, P and Samuels, G J (2013). Evolution of habitat preference and nutrition mode in a cosmopolitan fungal genus with evidence of interkingdom host jumps and major shifts in ecology. *Evolution, 67*: 2823-2837.

Dassen, S; Cortois, R; Martens, H; Hollander, M de; Kowalchuk, G A; Putten, W H Van Der and Deyn, G B De (2017). Differential responses of soil bacteria, fungi, archaea and protists to plant species richness and plant functional group identity. *Mol. Ecol.*, *26*: 4085-4098.

Dhandapani, S; Ritz, K; Evers, S; Cooper, H; Tonks, A and Sjögersten, S (2020). Land-use changes associated with oil palm plantations impact PLFA microbial phenotypic community structure throughout the depth of tropical peats. *Wetlands*, *40(6)*: 2351-2366.

Dobrovol'skaya, T G; Golovchenko, A V; Kukharenko, O S; Yakushev, A V; Semenova, T A and Inisheva, L A (2012). The structure of the microbial communities in low moor and high moor peat bogs of Tomsk Oblast. *Eurasian Soil Sci.*, *45(3)*: 273-281.

Drescher, J; Rembold, K; Allen, K; Beckschäfer, P; Buchori, D; Clough, Y; Faust, H; Fauzi, A M; Gunawan, D; Hertel, D; Irawan, B; Jaya, I N S ; Klarner, B; Kleinn, C; Knohl, A; Kotowska, M M; Krashevska, V; Krishna, V; Leuschner, C; Lorenz, W; Meijide, A; Melati, D; Nomura, M; Pérez-Cruzado, C; Qaim, M, Siregar, I; Steinebach, S; Tjoa, A; Tscharntke, T; Wick, B; Wiegand, K; Kreft, H and Scheu S (2016). Ecological and socio-economic functions across tropical land use systems after rainforest conversion. *Philos. Trans. R. Soc. B: Biol. Sci., 371(1694)*: 20150275.

Egidi, E; Delgado-Baquerizo, M; Plett, J M; Wang, J; Eldridge, D J; Bardgett, R D; Maestre, F T and Singh, B K (2019). A few Ascomycota taxa dominate soil fungal communities worldwide. *Nat. Commun.*, *10(1)*: 2369.

Eichlerová, I; Homolka, L; Žifčáková, L; Lisá, L; Dobiášová, P and Baldrian, P (2015). Enzymatic

systems involved in decomposition reflect the ecology and taxonomy of saprotrophic fungi. *Fungal Ecol.*, *13*: 10-22.

Elliott, D R; Caporn, S J M; Nwaishi, F; Nilsson, R H and Sen, R (2015). Bacterial and fungal communities in a degraded ombrotrophic peatland undergoing natural and managed re-vegetation. *PLoS ONE*, *10*: e0124726.

Fierer, N; Wood, S A and Bueno de Mesquita, C P (2021). How microbes can, and cannot, be used to assess soil health. *Soil Biol. Biochem.*, *153*: 108111.

Filippova, N V and Thormann, M N (2014). Communities of larger fungi of ombrotrophic bogs in West Siberia. *Mires and Peat*, *14(January 2014)*: 1-22.

Food and Agriculture Organization (2020). *State of Knowledge of Soil Biodiversity- Status, Challenges and Potentialities, Report 2020*. p. 163-174.

Gjobad-Nehjad, M (2011). Updated checklist of corticioid and poroid basidiomycetes of the Caucasus region. *Mycotaxon*, *117*: 508.

Golovchenko, A V; Kurakov, A V; Semenova, T A and Zvyagintsev, D G (2013). Abundance, diversity, viability and factorial ecology of fungi in peatbogs. *Eurasian Soil Sci.*, *46(1)*: 74-90.

Grum-Grzhimaylo, O A; Debets, A J and Bilanenko, E N (2016). The diversity of microfungi in peatlands originated from the White Sea. *Mycologia*, *102*: 233-254.

Harman, G E (2011). Multifunctional fungal plant symbionts: New tools to enhance plant growth and productivity. *New Phytol.*, *189*: 647-649.

Hill, T C J; Walsh, K A; Harris, J A and Moffett, B F (2003). Using ecological diversity measures with bacterial communities. *FEMS Microbiol. Ecol.*, *43*: 1-11.

Houbraken, J; Vries, R P De and Samson, R A (2014). Modern taxonomy of biotechnologically important *Aspergillus* and *Penicillium* species. *Advances in Applied Microbiology*. Academic Press. p. 199-249.

Hunt, J; Boddy, L; Randerson, P F and Rogers, H J (2004). An evaluation of 18S rDNA approaches for the study of fungal diversity in grassland soils. *Microb. Ecol.*, *47(July 2003)*: 385-395.

Jiang, Y; Wang, J; Chen, J; Mao, L; Feng, X; Zhang, C L and Lin, F C (2016). *Trichoderma* biodiversity of agricultural fields in East China reveals a gradient distribution of species. *PLoS ONE*, *11*: e0160613.

Juan-Ovejero, R; Briones, M J I and Öpik, M (2020). Fungal diversity in peatlands and its contribution to carbon cycling. *Appl. Soil Ecol.*, *146(October)*: 103393.

Kerfahi, D; Tripathi, B M; Lee, J; Edwards, D P and Adams, J M (2014). The impact of selective-logging and forest clearance for oil palm on fungal communities in Borneo. *PLoS ONE*, *9*: e111525.

Kusai, N A; Ayob, Z; Maidin, M S T; Safari, S and Ahmad Ali, S R (2018). Characterisation of fungi from different ecosystems of tropical peat in Sarawak, Malaysia. *Rend. Lincei. Sci. Fis. Nat.*, *29*: 469-482.

Kwon-Chung, K J and Sugui, J A (2013). *Aspergillus fumigatus*-What makes the species a ubiquitous human fungal pathogen? *PLoS Pathog.*, *9(12)*: 1-4.

Lamit, L J; Romanowicz, K J; Potvin, L R; Lennon, J T; Tringe, S G; Chimner, R A; Kolka, R K; Kane, E S and Lilleskov, E A (2021). Peatland microbial community responses to plant functional group and drought are depth-dependent. *Mol. Ecol.*, *30(20)*: 5119-5136.

Lauber, C L; Strickland, M S; Bradford, M A and Fierer, N (2008). The influence of soil properties on the structure of bacterial and fungal communities across land-use types. *Soil Biol. Biochem.*, *40*: 2407-2415.

Li, J; Delgado-Baquerizo, M; Wang, J T; Hu, H W; Cai, Z J; Zhu, Y N and Singh, B K (2019). Fungal richness contributes to multifunctionality in boreal forest soil. *Soil Biol. Biochem.*, *136(June)*: 107526.

Lin, X; Tfaily, M M; Steinweg, J M; Chanton, P; Esson, K; Yang, Z K; Chanton, J P; Cooper, W; Schadt, C W and Kostka, J E (2014). Microbial community stratification linked to utilization of carbohydrates and phosphorus limitation in a boreal peatland at Marcell Experimental Forest, Minnesota, USA. *Appl. Environ. Microbiol*, *80(11)*: 3518-3530.

Liu, B; Talukder, M J H; Terhonen, E; Lampela, M; Vasander, H; Sun, H and Asiegbu, F (2020). The microbial diversity and structure in peatland forest in Indonesia. *Soil Use Manag.*, *36(1)*: 123-138.

Magurran, A E (2004). *Measuring Biological Diversity*. Blackwell Science Ltd, Oxford, United Kingdom. 272 pp.

Maidin, M S T; Safari, S; Ghani, N A; Syed Ibrahim, S A; Ahmad Bakeri, S and Mohd Masri, M M (2016). Differences in prokaryotic species between primary and logged-over deep peat forest. *J. Oil Palm Res.*, *28(3)*: 281-295.

Mcguire, K L; D'Angelo, H; Brearley, F Q; Gedallovich, S M; Babar, N; Yang, N; Gillikin, C M; Gradoville, R; Bateman, C; Turner, B L; Mansor, P; Leff, J W and Fierer, N (2015). Responses of soil fungi to logging and oil palm agriculture in Southeast Asian tropical forests. *Microb Ecol.*, *69*: 737-747.

Melling, L (2016). Peatland in Malaysia. *Tropical Peatland Ecosystems* (Osaki, M and Tsuji, N eds.). Springer Japan. p. 59-73.

Mendoza-mendoza, A; Zaid, R; Lawry, R; Monte, E; Horwitz, B A and Prasun, K (2018). Molecular dialogues between Trichoderma and roots: Role of the fungal secretome. *Fungal Biol. Rev.*, *32*: 62-85.

Morrison, E S; Thomas, P; Ogram, A; Kahveci, T; Turner, B L and Chanton, J P (2020). Characterization of bacterial and fungal communities reveals novel consortia in tropical oligotrophic peatlands. *Microb. Ecol.*, *82*: 188-201.

Mpamah, P A; Taipale, S; Rissanen, A J; Biasi, C and Nykänen, H K (2017). The impact of long-term water level draw-down on microbial biomass: A comparative study from two peatland sites with different nutrient status. *Eur. J. Soil. Biol.*, *80*: 59-68.

Newsham, K K; Hopkins, D W; Carvalhais, L C; Fretwell, P T; Rushton, S P; O'Donnell, A G and Dennis, P G (2016). Relationship between soil fungal diversity and temperature in the maritime Antarctic. *Nat. Clim. Chang.*, *6(2)*: 182-186.

Nurulita, Y; Adetutu, E M; Kadali, K K; Shahsavari, E; Zul, D; Taha, M and Ball, A S (2016). Assessment of the influence of oil palm and rubber plantations in tropical peat swamp soils using microbial diversity and activity analysis. *J. Agric. Chem. Environ.*, *5*: 53-65.

Page, S; Mishra, S; Agus, F; Anshari, G; Dargie, G; Evers, S; Jauhiainen, J; Jaya, A; Jovani-Sancho, A J; Laurén, A; Sjögersten, S; Suspense, I A; Wijedasa, L S and Evans, C D (2022). Anthropogenic impacts on lowland tropical peatland biogeochemistry. *Nat. Rev. Earth Environ.*, *3(7)*: 426-443.

Paredes, N I; Consolo, V F; Pancotto, V A; Fritz, C; Barrera, M D; Arambarri, A M and Salerno, G L (2014). Microfungal composition in an Astelia-Donata cushion peatland in Tierra Del Fuego, Argentina. *Darwiniana, Nuere Serie*, *2(1)*: 112-124.

Pielou, E C (1969). An introduction to mathematical ecology. *Bioscience*, *78*: 7-12.

Prescott, C E and Grayston, S J (2013). Tree species influence on microbial communities in litter and soil: current knowledge and research needs. *For. Ecol. Manage.*, *309*: 19-27.

Repečkienė, J; Jukonienė, I and Salina, O (2012). Cellulose-decomposing fungi in peatlands occupied by invasive moss *Campylopus introflexus*. *Bot. Lith.*, *18(1)*: 46-57.

Robinson, S J B; Elias, D; Johnson, D; Both, S; Riutta, T; Goodall, T; Majalap, N; McNamara, N P; Griffiths, R and Ostle, N (2020). Soil fungal community characteristics and mycelial production across a disturbance gradient in lowland dipterocarp rainforest in Borneo. *Front. For. Glob. Change*, *3*: 1-19.

Shannon, C E and Weaver, W (1963). The Mathematical Theory of Communication. University of Illinois Press, Urbana.

Shi, L L; Mortimer, P E; Ferry Slik, J W; Zou, X M; Xu, J; Feng, W T and Qiao, L (2014). Variation in forest soil fungal diversity along a latitudinal gradient. *Fungal Divers*, *64(1)*: 305-315.

Shoresh, M; Harman, G E and Mastouri, F (2010). Induced systemic resistance and plant responses to fungal biocontrol agents. *Annu. Rev. Phytopathol.*, *48(1)*: 21-43.

Simpsons, E H (1949). Measure of diversity. *Nature*, *163*: 688.

Siti Ramlah, A A; Sakinah, S; Mohd Shawal Thakib, M; Shamsilawani, A B and Nur Aziemah, A G (2016). Soil fungal community associated with peat in Sarawak identified using 18 rDNA marker. *J. Oil Palm Res.*, *28*: 161-171.

Smit, E; Leeflang, P; Glandorf, B; Dirk, J V E and Wernars, K (1999). Analysis of fungal diversity in the wheat rhizosphere by sequencing of cloned PCR-amplified genes encoding 18S rRNA and temperature gradient gel electrophoresis. *Appl. Environ. Microbiol.*, *65(6)*: 2614-2621.

Song, Y; Liu, C; Wang, X; Ma, X; Jiang, L; Zhu, J; Gao, J and Song, C (2020). Microbial abundance as an indicator of soil carbon and nitrogen nutrient in permafrost peatlands. *Ecol. Indic.*, *115(January)*: 106362.

Summerbell, R C (2005). Root endophyte and mycorrhizosphere fungi of black spruce, *Picea mariana*, in a boreal forest habitat: Influence of site factors on fungal distributions. *Studies*, *53(1999)*: 121-145.

Sun, H; Terhonen, E; Kovalchuk, A; Tuovila, H; Chen, H; Oghenekaro, A O; Heinonsalo, J;

Kohler, A; Kasanen, R; Vasander, H and Asiegbu, F O (2016). Dominant tree species and soil type affect the fungal community structure in a boreal peatland forest. *Appl. Environ. Microbiol*, *82(9)*: 2632-2643.

Supramani, S; Rejab, N A; Ilham, Z; Wan-Mohtar, W A A Q I and Ghosh, S (2022). Basal stem rot of oil palm incited by *Ganoderma* species: A review. *Eur. J. Plant Pathol.*, *164(1)*: 1-20.

Tedersoo, L; Bahram, M; Polme, S; Koljalg, U; Yorou, N S; Wijesundera, R; Ruiz, L V.; Vasco-Palacios, A M; Thu, P Q; Suija, A; Smith, M E; Sharp, C; Saluveer, E; Saitta, A; Rosas, M; Riit, T; Ratkowsky, D; Pritsch, K; Põldmaa, K; Piepenbring, M; Phosri, C; Peterson, M; Parts, K; Pärtel, K; Otsing, E; Nouhra, E; Njouonkou, A L; Nilsson, R H; Morgado, L N; Mayor, J; May, T W; Majuakim, L; Lodge, D J; Lee, S S; Larsson, K- H; Kohout, P; Hosaka, K; Hiiesalu, I; Henkel, T W; Harend, H; Guo, L-D; Greslebin, A; Grelet, G; Geml, J; Gates, G; Dunstan, W; Dunk, C; Drenkhan, R; Dearnaley, J; Kesel, A D, Dang T, Chen, X; Buegger, F; Brearley, F Q; Bonito, G; Anslan, S; Abell, S and Abarenkov, K (2014). Global diversity and geography of soil fungi. *Science (1979)*, *346*: 6213.

Thormann, M N (2006). Diversity and function of fungi in peatlands: A carbon cycling perspective. *Can. J. Soil Sci.*, *5*: 281-293.

Thormann, M N and Rice, A V (2007). Fungi from peatlands. *Fungal Divers*, *24*: 241-299.

Tripathi, B M; Edwards, D P; Mendes, L W; Kim, M; Dong, K; Kim, H and Adams, J M (2016a). The impact of tropical forest logging and oil palm agriculture on the soil microbiome. *Mol. Ecol.*, *25*: 2244-2257.

Tripathi, B M; Song, W; Slik, J W F; Sukri, R S; Jaafar, S; Dong, K and Adams, J M (2016b). Distinctive tropical forest variants have unique soil microbial communities, but not always low microbial diversity. *Front Microbiol.*, *7(Apr)*: 376.

Tyśkiewicz, R; Nowak, A; Ozimek, E and Jaroszuk-ściseł, J (2022). Trichoderma: The current status of its application in agriculture for the biocontrol of fungal phytopathogens and stimulation of plant growth. *Int. J. Mol. Sci.*, *23(4)*: 2329.

Urbanov, M; Snajdr, J and Baldrian, P (2015). Composition of fungal and bacterial communities in forest litter and soil is largely determined by dominant trees. *Soil Biol. Biochem.*, *84*: 53-64.

Vaishnav, N; Singh, A; Adsul, M; Dixit, P; Sandhu, S K; Mathur, A; Puri, S K and Singhania, R R (2018). Penicillium: The next emerging champion for cellulase production. *Bioresour. Technol. Rep.*, *2*: 131-140.

Vinogradova, Y A; Kovaleva, V A; Perminova, E M; Shakhtarova, O V and Lapteva, E M (2023). Zonal patterns of changes in the taxonomic composition of culturable microfungi isolated from Permafrost Peatlands of the European Northeast. *Diversity (Basel)*, *15(5)*: 639.

Yabuki, T; Duncan, I and Okuda, T (2014). Comparative study reveals unique features of the mycobiota in peat soils samples from Japan and Scotland. *Mycoscience*, *55(3)*: 168-176.

Zhang, Q; Wu, J; Yang, F; Lei, Y; Zhang, Q and Cheng, X (2016). Alterations in soil microbial community composition and biomass following agricultural land use change. *Sci. Rep.*, *6(June)*: 1-10.

Zhang, Y M; Qu, Z L; Sietiö, O M; Zhou, X; Heinonsalo, J; Köster, K; Berninger, F; Pumpanen, J and Sun, H (2023). The temporal and spatial response of soil fungal community composition and potential function to wildfire in a permafrost region in Canada. *Funct. Ecol.*, *37(2)*: 261-273.

Zhang, Z; Liu, J L; Lan, J Y; Duan, C J; Ma, Q S and Feng, J X (2014). Predominance of Trichoderma and Penicillium in cellulolytic aerobic filamentous fungi from subtropical and tropical forests in China, and their use in finding highly efficient β-glucosidase. *Biotechnol. Biofuels*, *7(1)*: 107.

Zhang, Z; Zhou, X; Tian, L; Ma, L; Luo, S; Zhang, J; Li, X and Tian, C (2017). Fungal communities in ancient peatlands developed from different periods in the Sanjiang Plain, China. *PLoS ONE*, *12*: e0187575.