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FUNGAL MICROBIOLOGY

Responses of Soil Fungi to Logging and Oil Palm Agriculture in Southeast Asian Tropical Forests

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Abstract Human land use alters soil microbial composition and function in a variety of systems, although few comparable studies have been done in tropical forests and tropical agricultural production areas. Logging and the expansion of oil palm agriculture are two of the most significant drivers of tropical deforestation, and the latter is most prevalent in Southeast Asia. The aim of this study was to compare soil fungal communities from three sites in Malaysia that represent three of the most dominant land-use types in the Southeast Asia tropics: a primary forest, a regenerating forest that had been selectively logged 50 years previously, and a 25-year-old oil palm plantation. Soil cores were collected from three replicate plots at each site, and fungal communities were sequenced using the Illumina platform. Extracellular enzyme assays were assessed as a proxy for soil microbial function. We found that fungal communities were distinct across all sites, although fungal composition in the regenerating forest was more similar to the primary forest than either forest community was to the oil palm site. Ectomycorrhizal fungi, which are important associates of the dominant Dipterocarpaceae tree family in this region, were compositionally distinct across forests, but were nearly absent from oil palm soils. Extracellular enzyme assays indicated that the soil ecosystem in oil palm plantations experienced altered nutrient cycling dynamics, but there were few differences between regenerating and primary forest soils. Together, these results show that logging and the replacement of primary forest with oil palm plantations alter fungal community and function, although forests regenerating from logging had more similarities with primary forests in terms of fungal composition and nutrient cycling potential. Since oil palm agriculture is currently the mostly rapidly expanding equatorial crop and logging is pervasive across tropical ecosystems, these findings may have broad applicability.

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Introduction

Tropical forests contain more than two-thirds of all terrestrial plant and animal species [1–3], but long-term prospects for their survival are uncertain, as more than half of the original extent of these forests has already been degraded by human land-use change and other perturbations [4]. Agricultural expansion continues to be the main driver of tropical deforestation [5] with more than one third of the global terrestrial land area currently under cultivation [6]. Selective logging is the next largest contributor to tropical forest degradation and recent surveys show that more than 20 % of tropical forests are being actively logged [4]. The cumulative result of these activities is that the majority of tropical forest landscapes now exist in various stages of disturbance and recovery, with primary forests now representing a small fraction of the total remaining habitat [7, 8]. Incomplete information about the resistance and resilience of forest-associated taxa is currently limiting our abilities to predict the repercussions of land-use change for tropical forests. In addition, the majority of related studies focus on large, charismatic organisms, whereas soil microbes, the most diverse and abundant taxa in these systems, have received far less attention, despite their critical roles in ecosystem function and recovery from forest disturbance [9–11]. Since a variety of biotic and abiotic factors known to structure soil microbial communities are significantly altered in degraded forests that have been logged or converted to agricultural production areas [12, 13], it is likely that microbial taxa will be dramatically different in these human-dominated systems with important consequences for altered plant-soil-atmosphere feedbacks [14, 15].

One key group of soil organisms likely to be impacted by tropical land-use change is soil fungi, which are critical components of forest ecosystems in their roles as decomposers, mutualists, and pathogens [16–19]. Compositional changes in fungal communities have been linked to altered plant dynamics [20], changes in nutrient cycling [21, 22], and shifts in soil carbon pools and fluxes [23]. However, few belowground studies have evaluated the responses of soil fungi to land-use conversion in tropical forests and more work has focused on how bacterial communities are structured by the biotic and abiotic soil properties that can be altered with land-use change [15, 24–26]. However, fungi and bacteria have different physiologies [11, 27] and display differential responses and feedbacks to factors such as pH [28] and soil C [29], so fungal responses cannot necessarily be inferred from the responses of soil bacteria. Studies from nontropical systems show that soil fungi can respond rapidly to land-use change, sometimes within the first few years of habitat conversion [30]. In addition, these fungal community shifts can lead to altered soil process rates that can have long-lasting effects with uncertain recovery times [31]. Understanding the resistance and resilience of the dynamic soil microbial community is essential for predicting soil-plant-atmosphere feedbacks, as these nutrient and energy exchanges are regulated through microbial processes [15, 32].

The Southeast Asian tropics, which have the highest relative rate of deforestation globally [33], are a priority area for understanding fungal responses to land use. The Dipterocarpaceae is the dominant tree family in these lowland tropical forests, and all known species (~500) form associations with ectomycorrhizal (EcM) fungi that play key roles in influencing tree growth and survival [34, 35]. Therefore, a loss of EcM fungal inoculum from soils may impede the regeneration of these forests [36], which will lead to cascading extinctions across other trophic groups dependent on dipterocarp forests for survival. Dipterocarp trees are economically valuable for timber, and, consequently, logging has been a major contributor to forest degradation in this region [37] with Malaysia accounting for a significant portion to the global total of tropical timber exports [38]. The most obvious alteration to primary forest by logging is the removal of large, commercially valuable trees, which will adversely affect host-specialist mycorrhizal fungi and substrate-specific fungal decomposers. However, fungi might also be sensitive to other logging-related changes in soil physical and chemical properties, such as compaction, loss of organic carbon other labile nutrients, decreased water infiltration, and changes in pH [31]. Nonetheless, numerous macroscopic taxa are relatively resistant to low-impact logging [39], but since few studies have evaluated microbial responses, it is not clear how fungi respond to logging in this region.

In addition to logging, Southeast Asian tropical forests are now threatened by the expansion of oil palm agriculture, which in the past few decades has been the most rapidly expanding equatorial crop [37, 40]. Oil palm (*Elaeis guineensis*: Arecaceae) is cultivated in expansive monoculture plantations, and severe loss of forest-associated species has been documented in these habitats [41, 42]. Palm oil, the commercial commodity extracted from oil palm fruits and kernels, is currently the most lucrative vegetable oil crop in the world, and Indonesia and Malaysia alone account for more than 80 % of all palm oil production [40, 43]. To date, only a single culture-independent study has been conducted in oil palm agricultural soils in Malaysia, which found that bacterial communities were dramatically different in these ecosystems relative to primary and logged forests [44]. While there have been some small-scale studies examining the diversity of fungi in oil palm plantations [45, 46], these have mostly focused on decomposer fungi and no molecular studies have evaluated soil fungal communities in these agricultural landscapes. Since oil palm cultivation is only predicted to increase throughout the tropics [47], revealing the responses of soil fungi to cultivation in Southeast Asia could provide valuation information for inferring the consequences of expanding oil palm cultivation in other tropical regions.

Here, we test the hypothesis that major anthropogenic disturbance causes significant shifts to tropical soil fungal communities. We compared soil fungal communities from three different land-use types in Malaysia: a 25-year-old oil palm plantation, an intact dipterocarp forest, and a regenerating dipterocarp forest that had been selectively logged 50 years previously. We addressed the following questions: (1) How do soil fungal communities vary across primary rain forest, regenerating forest from historical logging, and oil palm agricultural sites? (2) Are there changes in soil physicochemical properties that may be correlated with changes in fungal composition? (3) Is there evidence for shifts in soil processes in human-altered habitats that may be associated with changes in soil fungal communities?

Methods

Site Description and Field Sampling

This study was conducted in lowland forests of peninsular Malaysia in the state of Negeri Sembilan in three land-use types: primary rain forest, forest regenerating from logging 50 years previously [48], and an oil palm plantation in active cultivation for 25 years. An aerial photo of the different land-use types is available from a previous study by Okuda et al. [48]. The forest sites were located in the Pasoh Forest Reserve, which is an 11,000-ha protected area (2° 5′ N, 102° 18′ W, 80 m asl) that contains one of largest remnants of lowland evergreen rain forest in this region. The Dipterocarpaceae is the dominant tree family in this area, representing approximately 30 % of the basal area of trees with a diameter at breast height (dbh) ≥1 cm [49]. The climate is aseasonal, with a mean annual rainfall of 1,788 mm and average minimum and maximum temperatures of 22.7 and 33.2 °C, respectively. The dominant soil type in the lowland forest are Ultisols [50].

Within each land-use type (primary forest, regenerating forest, and oil palm plantation), three replicate plots (20× 20 m) were established and five soil samples from each plot were collected and divided into three sampling depths: 0–2, 0–10, and 10–20 cm as previously described [51]. All plots were separated by at least 500 m. Samples from each plot were composited by depth and placed in sterile plastic bags, sealed and frozen at −20 °C on the day of collection. The soil corer was thoroughly cleaned with ethanol between successive core sampling. In the laboratory, all soil samples were passed through a 2-mm sieve to homogenize the sample and stored frozen at −20 °C until laboratory analyses were performed.

Fungal Sequencing

Microbial community composition was determined using Illumina High-throughput sequencing using a method similar to that previously described [52]. Genomic DNA was extracted using a MoBio PowerSoil 96-well extraction kit, and the ITS1-F and ITS2 primers were used to amplify the internal transcribed spacer (ITS1) region of the rRNA operon from fungal genomes. The reverse primer contained a 12-bp barcode specific to each sample, allowing PCR products to be combined in equimolar concentrations. The combined DNA was cleaned using the MoBio PowerClean Pro kit and sequenced on an Illumina MiSeq instrument with a 2× 150-bp kit at the University of Colorado at Boulder. Raw sequence data were demultiplexed using an in-house (University of Colorado) Python script and then processed following the UPARSE pipeline [53]; only one of the paired-end reads were used in the processing. Demultiplexed reads were used to construct a de novo database by removing sequences with an expected error rate of <0.5-bp per sequence, dereplicating them, removing unique sequences (i.e., singletons), and clustering the remaining sequences into operational taxonomic units (OTUs) at the 97 % similarity threshold. An additional quality control measure was taken by removing sequences from this dataset <75 % similar to any sequence in the UNITE database [54, 55]. Raw demultiplexed sequences were then mapped to this filtered database at the 97 % similarity threshold to calculate sequence counts per OTU per sample. Taxonomy was assigned to each OTU using the RDP classifier [56] trained on a version of the UNITE database where sequences without phylum level taxonomy were removed. Ectomycorrhizal fungi were determined by matching taxonomy assignments with established EcM lineages as determined by recent phylogenetic and stable isotope data [57]. Ambiguous groups with both saprotrophic and EcM lifestyles were removed, which accounted for ~150 OTUs (e.g., *Sistotrema* OTUs and Sebacinaceae OTUs that could not be assigned to a genus). To normalize for the disparity in the number of sequences obtained across samples, all samples were rarified to 20,700 sequences per sample.

Soil Physicochemical Analyses

The moisture content of the soil was determined by drying samples to a constant weight at 105 ° C for 24–48 h. Soil pH was measured on a 1:1 soil/deionized water slurry following 30 min of equilibration using a LabFit AS-3000 dual pH analyzer attached to a TPS pH meter. Total carbon and nitrogen were analyzed by combustion with an Elementar Vario Macro CNS analyzer. A suite of macro- and micronutrients (P, K, Ca, Mg, Al, Cu, Fe, Mn, Na, Pb, and Zn) was analyzed by combining a 5-g soil sample with 20 mL of Mehlich 1 extraction solution and shaking

for 5 min followed by inductively coupled plasma spectrometry (Varian Vista MPX Radial ICP-OES). All soil nutrients were analyzed at the Auburn University Soil Testing Laboratory (AL, USA).

Extracellular Enzyme Assays

To estimate soil microbial function, six ubiquitous enzymes involved in the degradation of organic N, C, and P were assayed fluorometrically [58, 59]. We assayed acid phosphatase (AP), which targets phosphate groups attached to organic polymers; β-glucosidase (BG), which breaks down cellulose; cellobiohydrolase (CBH), which cleaves cellulose into simpler polymers such as cellobiose; *N*-acetyl β-glucosaminidase (NAG), which degrades chitin; β-xylosidase (BX), which targets hemicellulose; and leucine aminopeptidase (LAP), which releases the amino acid leucine from polypeptides. From each sample, we added 1–2 g of soil to 125 mL of 50 mM, pH 5.0, acetate buffer. Soil slurries were homogenized with a hand mixer and continually stirred with a magnetic stir rod prior to assay. Fifty milliliters of manufactured substrates specific for each enzyme linked to 4-methylumbelliferone (Sigma Aldrich, St. Louis, MO) was added in 1,000 μM concentrations to 200 mL of soil homogenates in 96-well microtiter plates and incubated at 22 °C for 1–24 h (depending upon the assay). Assays were terminated with 1.0 M NaOH, and fluorescence was read within 1 min of reaction termination at 365 nm of excitation and 450 nm of emission using a Tecan Infinite M200 plate reader. After correcting for substrate controls and quenching, activity was calculated as micromoles of product per gram of oven-dried soil per hour.

Statistical Analyses

Similarity in microbial community composition across land-use types (two forest types vs. oil palm) was evaluated using pairwise Bray-Curtis dissimilarities between samples and visualized using nonmetric multidimensional scaling analyses (NMDS). Significance of clustering within land-use type was tested using ANOSIM (Analysis of Similarity), a nonparametric (randomization-based) method of multivariate analysis. NMDS ordinations and ANOSIM analyses were done using Primer-E software (Version 5, Plymouth, UK). To identify the fungal taxa that were driving the differences in community composition across land uses, multiple Kruskal-Wallis tests were performed in R for fungal taxa with median relative abundances greater than 5 % in any land-use type using false discovery rate (FDR) correction. To evaluate differences in enzyme activity across land-use types and soil depths, a permutational multivariate ANOVA (PERMANOVA) was used.

Results

General Fungal Community Composition

A total of 520,465 fungal sequences were generated across all samples representing 8,476 operational taxonomic units (OTUs). Nonfungal sequences and sequences that could not be identified to phylum (3 % of the sequences) were removed prior to downstream analyses. Although there were no significant differences in the total number of observed fungal OTUs across land-use types ($F_{(2,23)}=2.43$, $p=0.11$), or in diversity indices (Table 1), OTU abundance accumulated most rapidly in the regenerating forest and slowest in the oil palm plantation (Fig. 1) and, similarly, predicted richness using the Chao 1 estimator showed that predicted fungal richness is greatest in the regenerating forest and lowest in the oil palm plantation (Fig. 1). Compositionally, fungal communities were significantly clustered across land-use types (ANOSIM R=0.80, $p<0.001$; Fig. 2a). Clustering of these communities was related to differences in the relative abundance of the phyla Ascomycota ($p=0.01$), Blastocladiomycota ($p=0.01$), Entomophthoromycota ($p=0.01$), and the basal fungal lineages ($p=0.001$; Fig. 3a). When analyzed at the level of order, there were significant differences in the relative abundances of the Archaeorhizomycetales, Cantharellales, Chaetothyriales, Helotiales, Hypocreales, Mortierellales, Pezizales, Russulales, Saccharomycetales, Sordariales, and Verrucariales ($p<0.05$ in all cases). In the oil palm soils, Archaeorhizomycetales, Hypocreales, and Saccharomycetales were more abundant, whereas the Cantharellales and Mortierellales were more abundant in the primary forest soils. The Chaetothyriales, Helotiales, Pezizales, Russulales, Sordiariales, and Verrucariales were all most abundant in the regenerating forest. In the forest soils, fungal communities were significantly clustered across sampling depths (ANOSIM $R=0.53$, $p=0.001$). However, fungal communities were not clustered by sampling depth in the oil palm soils (ANOSIM $R=0.09$, $p=0.33$).

There were 292 fungal OTUs that were shared across all land-use types (3.4 % of the total number of OTUs). These fungal OTUs were predominantly from the Ascomycota (59 %), followed by the basal fungal lineages (19 %), and the Basidiomycota (16 %); the Chytridiomycota and Glomeromycota accounted for 1 and 6 % of the shared OTUs, respectively. When analyzed at the level of order, 26 % of these ubiquitous OTUs could not be assigned to an order, while 19 % belonged to the Mortierellales, 13 % to the Pezizales, and 11 % to the Hypocreales. There were an additional 32 orders that comprised ≤10 % of the ubiquitous fungal OTUs (Table 2).

Soils from each land-use type had a unique community of fungi that was not shared with any of the other land uses. The unique fungal community in the primary forest was dominated by taxa from the Basidiomycota (64 %; Fig. 3b), which also

Table 1 Richness and diversity metrics (mean±SE) for fungal communities across different land-use types in the vicinity of Pasoh Forest Reserve, Peninsular Malaysia

Site	Observed OTUs	Chao1	Fisher's alpha	Shannon's *H* (log 10)
Primary forest	784.4 (73.4)	6,017 (181)a	133 (15.6)	1.6 (0.07)
Regenerating	821.8 (47.5)	7,451 (247)b	141.6 (9.6)	1.8 (0.09)
Oil palm plantation	680.5 (45.9)	4,667 (160)c	106.2 (7.2)	1.6 (0.05)

Statistical differences at $p<0.05$ are denoted by different letters (only differences in predicted richness using the Chao 1 estimator were observed)

accounted for 53 % of the unique taxa in the regenerating forest, but only 21 % of the unique taxa in the oil palm soils (Fig. 3b). The dominant order in the unique fungal community found in the primary forest was the Russulales (34 %), which was the second most abundant order in the unique fungal community of the regenerating forest (16 %). Across forest sites, there were 2,478 fungal OTUs in the primary forest soils that were absent from the regenerating forest. Likewise, there were 2,786 fungal OTUs that were found in the regenerating forest, but were not detected in the primary forest. There were 1,086 OTUs that were shared across the primary and regenerating forests of which 59 % were from the Ascomycota and 25 % were from the Basidiomycota.

Ectomycorrhizal Fungi

A total of 65,956 sequences and 471 OTUs were identified as EcM fungi. The total number of EcM fungal OTUs was different across land-use types ($F_{(2,\ 23)}=20.0$, $p<0.001$). The oil palm plantation had the lowest number of EcM fungal OTUs (5), whereas the regenerating forest had the greatest number of EcM fungal OTUs (53) with more than 1.5 times the number found in the primary forest (30). The relative abundance of EcM sequences was significantly lower in the oil palm soils, representing only 0.2 % of the total fungal sequences, whereas the primary and regenerating forests had similar relative abundances of EcM fungi (15–20 %; Fig. 4). Compositionally, EcM fungal communities were distinct across land-use types (ANOSIM $R=0.7$, $p<0.01$; Fig. 2b); this clustering was driven by differences in the relative abundances of the genera *Amanita*, *Craterellus*, *Lactarius*, and *Russula* ($p<0.05$ for all comparisons). The genera *Amanita* and *Lactarius* were more abundant in the regenerating forest, whereas the genera *Craterellus* and *Russula* were more abundant in the primary forest. There were also a number of taxa that were only found in one sample from one site that could not be statistically analyzed (Fig. 5). In the primary forest, the relative abundance of EcM fungi increased with sampling depth ($F_{(2,\ 6)}=5.9$, $p=0.04$; Fig. 4); while the same trend was observed in the regenerating forest, the only significant difference was between the 0–2- and 2–10-cm depths ($p=0.03$). In the oil palm soils, EcM fungi were rare at all soil depths (mean relative abundances <0.5 %; $F_{(2,\ 5)}=2.01$, $p=0.23$; Fig. 4).

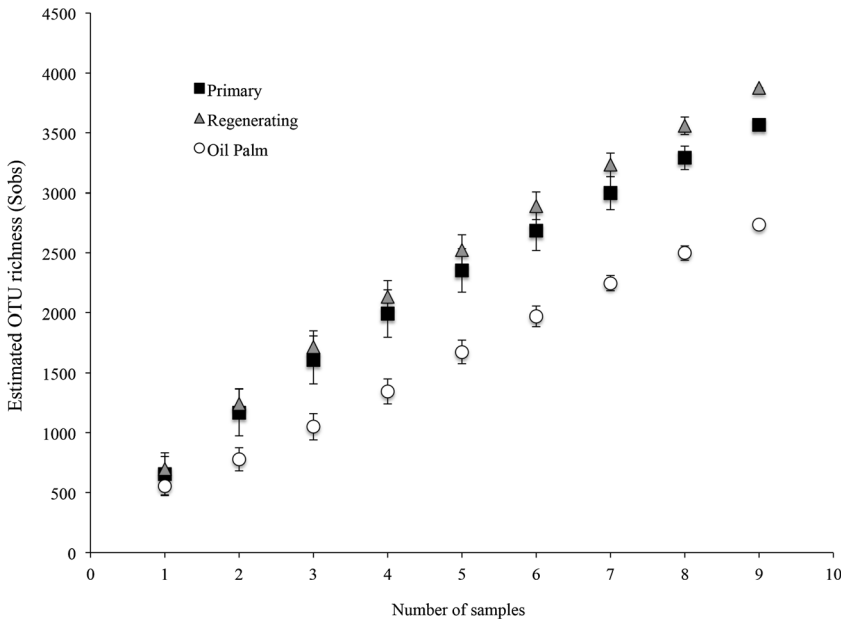

Fig. 1 Sample-based accumulation curve for fungal OTUs as samples are successively pooled (Sobs) across different land-use types in the vicinity of Pasoh Forest Reserve, Peninsular Malaysia. *Error bars* represent ±1 SD of the Sobs for each iteration

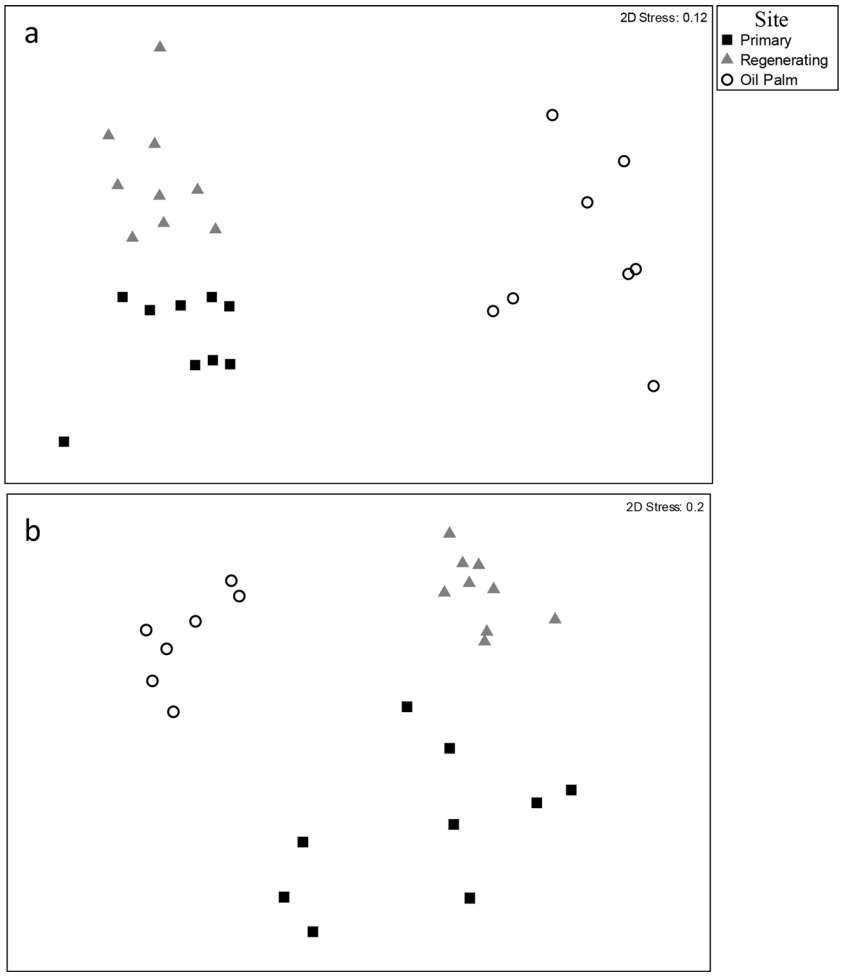

Fig. 2 Nonmetric multidimensional scaling plot showing clustering of the general fungal community (**a**) and the ectomycorrhizal fungal community (**b**) across different land-use types in the vicinity of Pasoh Forest Reserve, Peninsular Malaysia

Soil Physicochemical Analyses

Across land-use types, there were significant differences in Ca, Cu, Fe, Pb, C/N ratio, and pH ($p<0.05$ for all comparisons; Table 3). The oil palm plantation site had significantly higher pH and Ca than the forest sites. The primary forest site had the greatest C/N ratio, the lowest concentration of Fe, and the highest concentration of Pb (Table 3).

Enzyme Assays

Extracellular enzyme activity showed differential responses to land-use type (Fig. 6), and overall, land use had greater explanatory power in activity rate differences than soil sampling depth ($p<0.001$), but there was no significant interaction among land use and soil depth ($p=0.3$). Across land-use types, activity was significantly different between oil palm soils and both forest soils ($p<0.05$ for both comparisons), but forests were not different from each other ($p=0.09$). When enzymes were analyzed separately, activity in the oil palm soils was significantly lower than that in the forest soils across all soil depths for NAG and AP, as well as for LAP in the 2–10- and 10–20-cm soil depths ($p<0.05$ for all comparisons). For BG and BX, the oil palm soils displayed similar activity levels to those of the regenerating forest across all horizons. The regenerating forest soils had greater enzyme activity than the primary forest soils for NAG, AP, and BX, but only in the upper soil layer (0–2 cm). There were no significant differences in CBH activity across land use in any of the soil depths. Across all land uses, enzyme activity was higher for almost all enzymes in the upper soil layer (0–2 cm) compared to that in the lower soil depths (Fig. 6).

Discussion

Oil palm plantations and regenerating forests now represent some of the major terrestrial ecosystems in the Southeast Asian tropics [60], and our study demonstrates that these land-use conversions can cause compositional shifts in soil fungal communities that likely have functional consequences for nutrient cycling. Our results also imply that fungi may be more sensitive to logging than soil

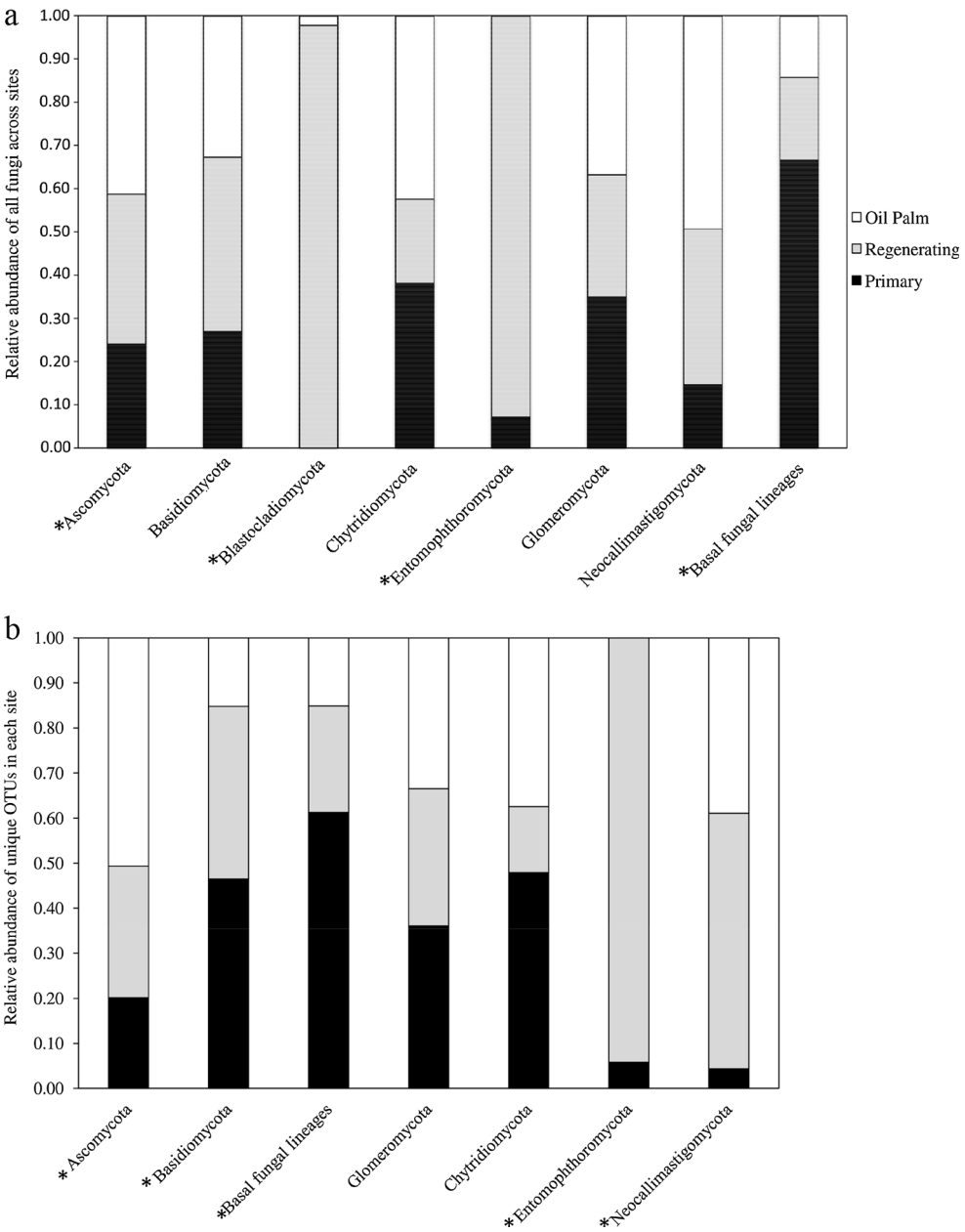

Fig. 3 Relative abundance of fungal phyla for the general fungal community (**a**) and the unique fungal community observed for each different land-use type (**b**) in the vicinity of Pasoh Forest Reserve, Peninsular Malaysia. *Asterisks* indicate significant differences in the distribution of a given phylum across sites

bacterial communities, as a recent study found that bacterial communities were compositionally distinct in oil palm soils, but were not different between primary and logged forests [44]. The differences in soil physical and chemical properties across land-use types likely explains some of the differences we observed [51], although further analysis and experimentation will be necessary, as differences in fungal composition across sites are likely due to a combination of other biotic and abiotic factors that have not yet been measured. In addition, this study only surveyed one area in Peninsular Malaysia, so a greater number of sites will be necessary to generalize these findings across all similar land-use types in SE Asia.

The compositional differences of the fungal communities in the regenerating forest demonstrate the persistent effects of historical land use on soil fungal communities even after 50 years of forest regrowth. Long-term land-use legacies on soil physical and chemical properties have been widely documented [61, 62] and can lead to altered plant successional trajectories for years after the abandonment of disturbance [63–66]. There is some evidence that changes in microbial communities may mediate the altered biogeochemical processes in historically disturbed soils [67, 68], although the focus of land-use legacies has been on soil properties, while less research has elucidated the historical imprints on microbial communities themselves [68, 69]. The long-term

Table 2 Relative abundance of the fungal OTUs that were shared across all land-use types in the vicinity of Pasoh Forest Reserve, Peninsular Malaysia. Only orders that had a relative abundance greater than 0.001 across all land-use types are shown

Order	Primary	Regenerating	Oil palm	Relative abundance of shared OTUs
Mortierellales	0.191	0.051	0.252	0.189
Pezizales	0.099	0.226	0.001	0.129
Hypocreales	0.056	0.105	0.251	0.114
Agaricales	0.014	0.058	0.182	0.065
Tremellales	0.033	0.081	0.043	0.054
Russulales	0.000	0.127	0.000	0.050
Helotiales	0.050	0.041	0.009	0.038
Verrucariales	0.020	0.046	0.004	0.027
Eurotiales	0.004	0.008	0.043	0.013
Xylariales	0.008	0.006	0.037	0.013
Saccharomycetales	0.001	0.002	0.035	0.008
Chaetosphaeriales	0.003	0.014	0.002	0.007
Capnodiales	0.005	0.013	0.001	0.007
Erysiphales	0.007	0.003	0.012	0.006
Pleosporales	0.002	0.002	0.011	0.004
Glomerales	0.002	0.001	0.007	0.003
Cantharellales	0.001	0.005	0.001	0.002
Microascales	0.000	0.001	0.011	0.002
Chaetothyriales	0.002	0.004	0.001	0.002
Polyporales	0.001	0.002	0.001	0.001
Rhizophydiales	0.001	0.000	0.002	0.001
Corticiales	0.000	0.002	0.001	0.001
Sordariales	0.002	0.001	0.000	0.001

consequences of logging and tropical forest conversion to oil palm agriculture in the Southeast Asian tropics are not known, but if our findings apply generally to these land-use types, then widespread alterations in soil fungal communities and disruptions to dipterocarp EcM mutualisms are likely to change forest dynamics in this region.

We found that forest to oil palm conversion resulted in far more dramatic shifts in soil fungal communities than historical

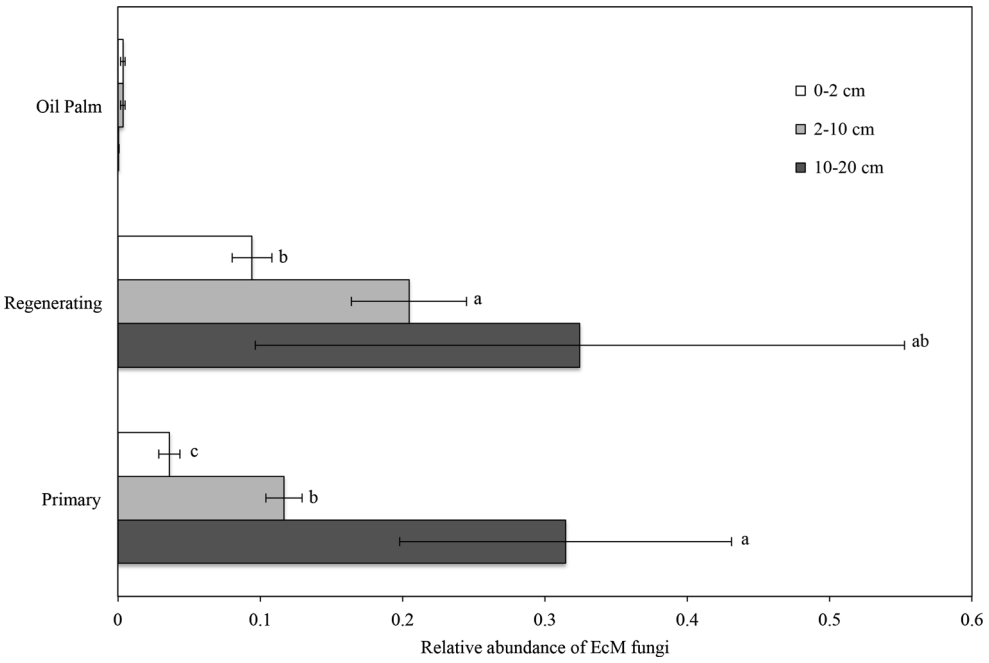

Fig. 4 Relative abundance of EcM fungi across different land-use types and three soil sampling depths in the vicinity of Pasoh Forest Reserve, Peninsular Malaysia. *Different letters* indicate significant differences across sampling depths within a site

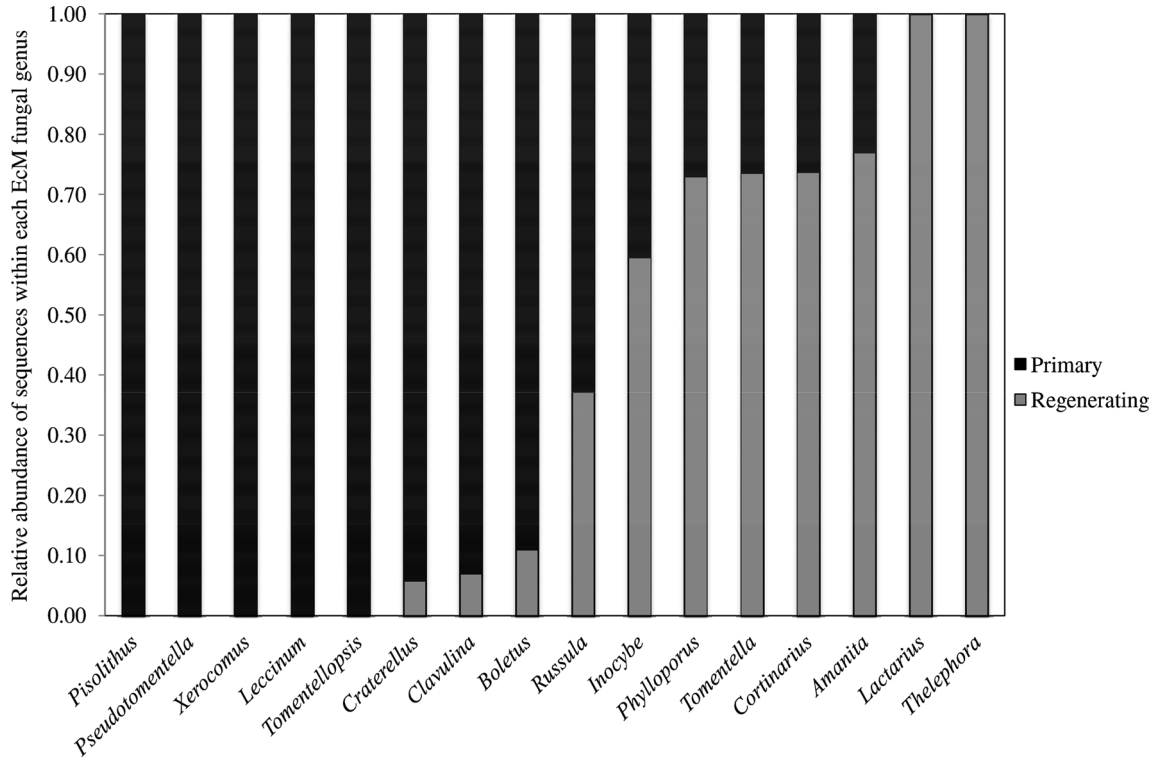

Fig. 5 Relative abundance of ectomycorrhizal fungal sequences within each genus across different land-use types in the vicinity of Pasoh Forest Reserve, Peninsular Malaysia

logging, with one of the most notable findings being that EcM fungi were virtually absent from the oil palm soils. Since oil palm plantations are regionally abundant, the fact that EcM fungi are nearly absent in plantation soils implies that EcM fungal populations with low dispersal capability may become genetically isolated over time. This supposition is supported by a recent study of EcM fungal dispersal, which documented dispersal limitation and significant decreases in EcM seedling colonization with increasing distance from forest edges [70]. The extent to which EcM fungi are undergoing local extinctions in the current fragmented landscape of Southeast Asia is unknown, but in the case that economic shifts result in the abandonment of oil palm cultivation, appropriate reservoirs for maintaining viable EcM fungal populations for dipterocarp tree regrowth will be essential. The EcM fungi that were detected from our sampling efforts in the oil palm plantation were likely due to spores that had dispersed onto surface soils, which is supported by the fact that most of the EcM taxa in the oil palm soils were found in the upper sampling depth (0–2 cm), unlike in the forest soils where ECM fungi were more abundant in lower depths. Alternatively, these fungi may survive in a vegetative state in the absence of their EcM tree hosts, as some EcM fungi can survive in the laboratory as facultative decomposers, although there have been few tests of this phenomenon in field settings.

Table 3 Results of soil physicochemical analyses

Soil property	Primary	Regenerating	Oil Palm
pH[a]	4.7 (0.1)a	4.4 (0.1)a	5.1 (0.1)b
C/N ratio[a]	12 (0)a	10 (1)b	10 (1)b
Al	73 (22)	105 (8)	110 (5)
Ca[a]	76 (29)a	149 (51)a	366 (63)b
Cu[a]	6 (1)a	17 (6)ab	26 (8)b
Fe[a]	61 (11)a	167 (23)b	101 (16)c
K	75 (23)	53 (8)	98 (21)
Mg	53 (37)	33 (8)	34 (9)
Mn	6 (4)	6 (3)	4 (2)
Na	64 (14)	49 (4)	54 (9)
P	10 (2)	7 (1)	8 (2)
Pb[a]	3 (1)a	2 (0)b	2 (0)b
Zn	4 (1)	0 (0)	1 (0)

Different letters indicate significant differences in post hoc analyses at $p<0.05$

[a] Significant differences across land-use types

The unique fungal community in the oil palm soils was comprised of numerous taxa that reflect soil disturbance in addition to groups with unknown ecologies. At the phylum level, there was a low relative abundance of Basidiomycota and Ascomycota fungi, which is consistent with indicators of soil disturbance, as many Basidiomycota fungi are slow-growing, late-successional fungi that are sensitive to physical and chemical perturbations [71, 72]. Also, the fact that an

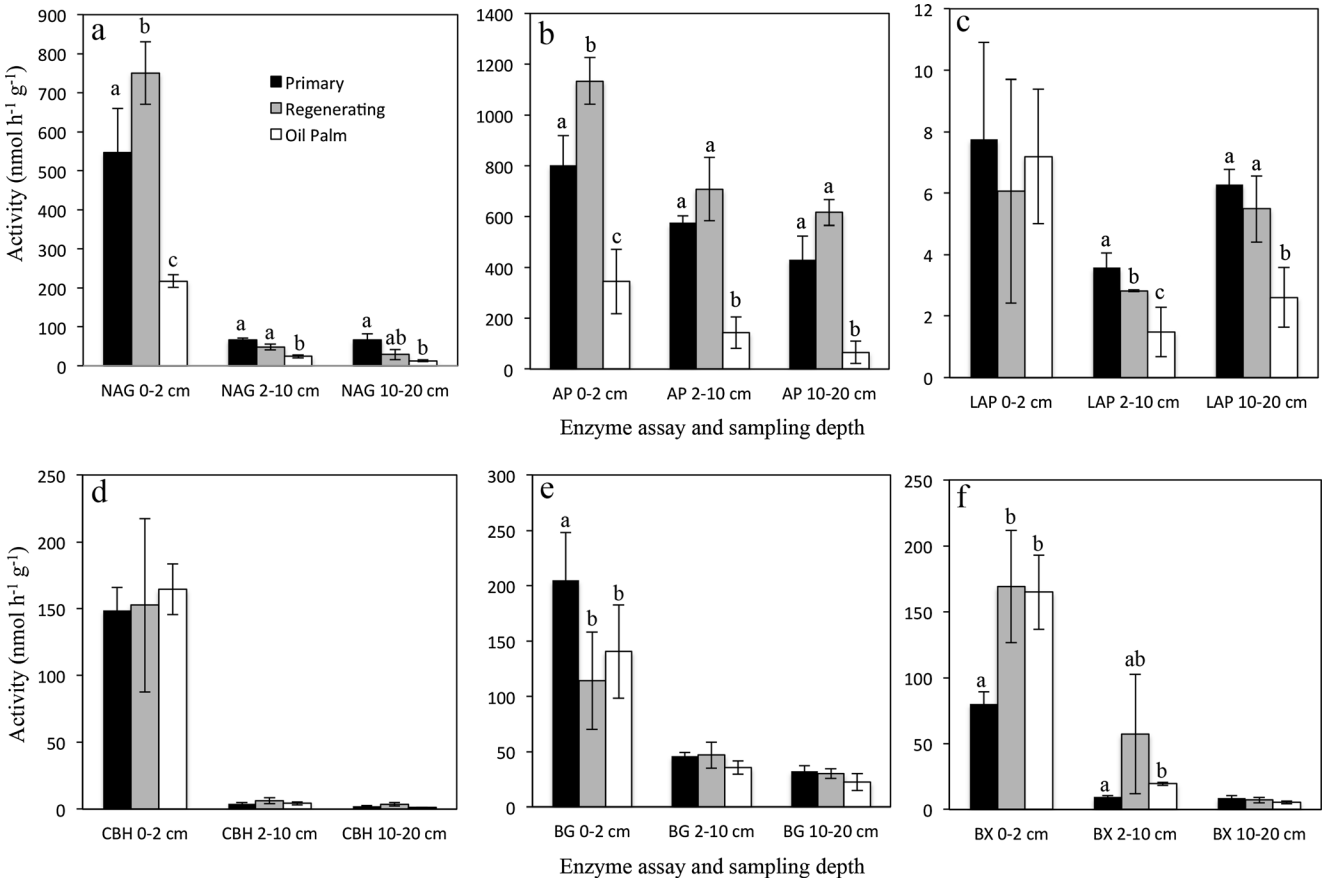

Fig. 6 Extracellular enzyme activity for *N*-acetyl β-glucosaminidase (NAG), acid phosphatase (AP), Leucine aminopeptidase (LAP), cellobiohydrolase (CBH), β-glucosidase (BG), and β-xylosidase (BX) across different land-use types in the vicinity of Pasoh Forest Reserve, Peninsular Malaysia. Each *panel* shows a different enzyme assay across each soil sampling depth

entire fungal phylum was absent from the oil palm soils (Entomophthoromycota) suggests that there may be reductions in phylogenetic diversity in this land-use type that could not be evaluated from our sequencing of the hypervariable ITS region. Another significant finding in the oil palm soils was that fungal communities were relatively homogeneous across soil depths, which contrasted with the clustering of fungi across depths in the forest soils. This homogenization likely reflects the intensive management of oil palm soils that contributes to soil degradation. For example, leaf litter is frequently cleared from the soil surface in oil palm plantations preventing the formation of extensive organic horizons. There is also frequent mechanical disturbance of soils from motorized vehicles used to harvest palm fruits and chemical inputs from fertilizers and liming. This lack of vertical stratification in soils may reduce nutrient capture and lead to "leakier" nutrient cycles, as is often the case in other highly managed systems [73, 74]. The high relative abundance of the Archaeorhizomycetales in the oil palm fungal communities is also noteworthy given that this group of fungi is newly described [75]. Prior to its description in 2011, it was one of the most abundant groups of unidentified fungi in environmental DNA sequence libraries, but due to the paucity of molecular studies in tropical forests, there has been little documentation of its occurrence outside of boreal and temperate forests. Interestingly, this group has previously been observed in soils that are dominated by EcM trees, but its ecology remains uncertain.

While soil fungal communities were distinct across the primary and logged forests, there were notable similarities in composition of major fungal groups, and the forests shared more fungal taxa with each other than either of them shared with the oil palm plantation soils. These observations are similar to studies of macroscopic species, which have found that selective logging is less detrimental than other types of land-use changes in maintaining a diversity of forest-associated taxa [7]. In a recent comprehensive meta-analysis from lowland tropical forests around the globe, nearly 85 % of macroscopic taxa such as mammals and birds were retained in once-logged forests [39]. Microbes were not included in the meta-analysis, probably due to the paucity of studies in the literature, but the suitability of logged forests for maintaining diverse populations of soil microbes merits further investigation, as logged forests are often considered "degraded" and, therefore, are vulnerable to conversion to oil palm plantations [38, 76]. The similarity in extracellular enzyme potential

across forest soils further supports the notion that regenerating forests maintain a high degree of ecosystem functionality and may cycle nutrients at similar rates to primary forests.

The 292 OTUs shared across all sites represent fungal taxa that are seemingly resistant to forest conversion. The most abundant identified order of these shared OTUs, the Mortierellales, is globally ubiquitous, and has been found in diverse environments such as in snow mats [77], compost [78], and urban soils [52]. They have also been documented as both saprotrophs and endophytes [79, 80], demonstrating their metabolic flexibility. The Mortierellales are also a basal fungal lineage containing some of the oldest sporocarp formers [79], which may contribute to their widespread occurrence. The next two most abundant orders of the fungal OTUs that were shared across sites were the Pezizales and Hypocreales, which are also globally distributed with diverse nutritional modes [81]. Since these ubiquitous fungi will likely be increasingly prevalent in the fragmented landscape of modern tropical ecosystems, future studies should examine if these particular fungal groups possess similar traits such as high dispersal capabilities, metabolic flexibility, and stress tolerance adaptations. If so, it may be possible to make predictions about fungal community shifts in disturbed tropical landscapes using trait-based approaches that have informed plant community ecology for decades [82, 83]. The fact that almost 40 % of the shared fungi across sites were unidentified at the level of order is not surprising, as the majority of the undescribed fungal species likely reside in tropical forests [19, 84], highlighting the need for more intensive taxonomic surveys in these regions.

The composition of EcM fungi across forests reflects several broadscale patterns that have been observed in other EcM-dominated ecosystems. For example, the high relative abundance of the Russulales and Thelophorales in the forest EcM fungal communities appears to be a generalized phenomenon, as these lineages are also abundant in other tropical EcM surveys from the Neotropics and the African tropics [85–87], as well as in temperate and boreal EcM forests [57, 88]. In other studies from dipterocarp forests, the Russulales and Thelophorales were prevalent in root tips [34, 89, 90], and the Russulales were abundant in sporocarp surveys, implying some correspondence in taxonomic composition between bulk soil, root tip, and fruiting body data. The reasons for the success of these EcM fungal lineages have not been determined but may be related to high diversity in their foraging strategies [91] and enzymatic functions [92]. Another comparable finding to other studies in nontropical EcM systems was that several of the EcM genera that were more abundant in one forest type or the other correspond to documented life history strategies for these fungi as being late-successional (competitive) or early-successional (ruderal). The genera *Lactarius* and *Thelephora*, which were only detected in the regenerating forest, are considered early-successional fungi and associated with disturbed habitats in a variety of EcM ecosystems [93–96]. Similarly, many *Russula*, *Boletus*, and *Leccinum* species have been found to be late-successional in some ecosystems [97, 98], and we found them to be most abundant in the primary forest. However, not all of the fungal taxa conformed to these distinctive groupings, as *Inocybe* spp. are considered early-successional fungi, but were also found in the primary forest, and *Amanita* spp. are considered to be late-successional, but were abundant in the regenerating forest. Placing EcM fungi into distinctive successional groupings has proved challenging [93] and may be somewhat variable across ecosystems and among successional groupings (i.e., primary succession versus recovery from disturbance). Forest succession from historical logging may enable the coexistence of early-stage and late-stage EcM fungi, similar to the process of floristic succession, which may also explain the higher OTU richness of EcM fungi in the regenerating forest. The extent to which the distinct EcM fungal communities in each forest relate to their abilities to tolerate disturbance, differences in structural or functional traits, tree host specificity, soil physicochemical properties, or the legacies of EcM fungal communities prior to disturbance remains to be determined. Since EcM fungi often have nonrandom distributions across the landscape [99, 100], more sampling across a larger region will be necessary to fully characterize EcM fungal community responses to forest disturbance.

The differential rates of extracellular enzyme activity across land-use types suggest that there may be functional consequences of fungal community shifts in terms of nutrient cycling across land-use types. While forests differed in activity rates for approximately one-quarter of the assays, the most significant differences in activity were observed in the oil palm soils, with more than half of the assays exhibiting differential rates from one or both of the forest soils. The microbial extracellular enzymes quantified in this study mediate the decomposition of soil organic matter [58], so it is likely that pools and fluxes of C, N, and P differ substantially in oil palm soils compared to primary and regenerating forest soils. Oil palm soils are also fertilized, which may account for the decline in some of the enzyme activities, particularly in acid phosphatase. Direct links between fungal composition and function could not be made, as bacteria also contribute to soil enzyme production [101, 102]. However, EcM fungi are known to produce abundant extracellular enzymes that differ among EcM fungal species [92, 103], so it is likely that a fraction of the enzymatic activity detected in the soil was derived from EcM foraging. Decomposer fungi are also known to differ in their physiological capacities [104, 105]; thus, it is likely that the differences in extracellular enzyme activity across land-use types will be reflected in other fungal-mediated nutrient cycling processes.

Soil disturbance across a wide range of systems can have rapid and persistent impacts on soil microbial communities [106], and our study is the first to evaluate soil fungal responses to tropical logging and oil palm agriculture using molecular techniques. Some of the differences in the soil physicochemical properties across land-use types may explain the variation in fungal composition we observed, although further experimentation will be necessary to identify causal links. Since these land-use types represent pervasive human disturbances in modern tropical landscapes [33], our results may have broad applicability beyond Southeast Asian dipterocarp forests. The loss of key functional groups that have low functional redundancy such as EcM fungi across fragmented landscapes may have irreversible consequences for ecosystem processes and forest regeneration trajectories. Forest-dwelling taxa, including soil microbes, now mostly reside as metapopulations in fragmented landscapes [7], and our results corroborate studies of macroscopic taxa showing that oil palm agricultural systems represent a poor quality habitat that ultimately results in genetically isolated populations [107]. While our study documented fungal community shifts in a forest that had been logged 50 years ago and in an oil palm plantation that has been in cultivation for 25 years, future studies are needed to determine how rapidly these changes are realized following forest conversion, as well as how these alterations impact long-term forest dynamics. Understanding the role of soil microbial communities in mediating ecosystem responses to human land use is imperative for global predictions of plant-soil-atmospheric feedbacks and will be vital for ascertaining the threshold values of forest conversion at which disruptions are irreversible.

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