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Historical logging alters soil fungal community composition and network in a tropical rainforest

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ABSTRACT

The effects of logging on forest ecosystems are severe and long-lasting. In addition, these effects are often paralleled with shifts in soil fungal community composition and functional guilds with potential feedbacks on ecosystem functioning. Clarifying how soil fungal communities are linked to the effects of historical logging could help us better understand the ecological consequences of logging. Here, we collected soils from 61 25 m × 25 m quadrats across a 160-km^2 tropical rainforest in Hainan Island, China, which had been partially clear cut or selectively harvested and left to recover for up to 50 years. Soil fungal community composition and species co-variation networks were investigated in the selectively harvested (select cut) and clear cut forest stands and were compared to data from the primary stands without a history of logging. Historical logging shifted fungal community composition from *Zygomycota* towards *Basidiomycota* domination mainly through modifying vegetation composition and soil properties. The relative abundance of root associated fungi (i.e., ectomycorrhizal and ericoid mycorrhizal), animal pathogens and wood saprotrophs increased 50 years after logging, while the relative abundance of undefined saprotrophs decreased. In select cut stands, the fungal community was better organized with higher numbers of functionally interrelated operational taxonomic units (OTUs) and more generalist OTUs. In contrast, the number of functionally interrelated OTUs was lowest in the fungal network in clear cut stands. By comparing the topological roles of the shared OTUs among the three types of forest stands, we found role-shifts among fungal members from the specialists in the primary stands to the generalists in the select cut stands. *Ascomycota* and *Basidiomycota* were the major phyla involved in the role-shifts. Moreover, the fungal network in primary stands was positively associated with litter nutrients, while that in select cut stands was positively related to soil nutrients content. This indicated that the major drivers of fungal community organization shifted from litter nutrients content in the primary forest towards soil nutrients content in the selectively harvested forest. In the clear cut stands, however, the associations between fungal network and both litter and soil nutrients content decreased when compared with those in the primary and select cut stands. More than 60% of the total links among fungal members in clear cut stands were negative, implying a trend of niche partitioning among fungal groups with a half-century recovery after clearcutting in the tropical rainforest.

1. Introduction

Tropical forests are a key component of global carbon (C) pools, as they store ~46% of the living terrestrial C and ~2% of the global soil C (Soepadmo, 1993; Malhi and Grace, 2000). Additionally, tropical forests have higher rates of photosynthetic C fixation and organic matter decomposition than other forest ecosystems because of unique biotic and abiotic environments, for instance, ample sunshine, warm climate, high amounts of precipitation and high diversity of plant species and soil microorganisms (Bouwman, 2010; Weintraub et al., 2013). Unfortunately, a large part of the primary tropical forests has been logged for timber harvest in the past years, causing profound changes in ecosystem C storage (Nair, 2002). Logging can reduce C inputs by decreasing fresh litter fall and root exudation, but it can also introduce a fresh source of tree-derived organic matter that enhances variation in soil properties (Chatterjee et al., 2008). These logging-induced alterations often cause significant changes in organic matter quality and soil conditions, which consequently affect the abundance and composition

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of the soil fungal community and organic matter decomposition rate (Gadgil and Gadgil, 1975; Cardenas et al., 2015; Kyaschenko et al., 2017). Clearcutting and diameter selective cutting are two dominant logging strategies, and the former generally has stronger effects on soil properties (e.g., soil temperature, moisture and organic matter content) (Steffi and Wolfgang, 2009; Xing et al., 2011). However, whether the responses of soil fungal communities differ between the two types of logging is unclear, though a better understanding of how logging affects fungal communities is critical to soil C storage (Clemmensen et al., 2015). We therefore need to assess how the two logging forms affect soil fungal communities to guide C-based management decisions, especially in the tropical forests characterized by a high organic matter turnover rate.

Functional composition instead of phylogenetic composition of the fungal community is more important in reflecting the organic matter quality and decomposition rate, because different functional groups decompose and metabolize different C substrates (Averill and Hawkes, 2016; Kohout et al., 2018). Free-living saprotrophic fungi and root-associated plant symbiotic fungi (e.g., ectomycorrhizal and ericoid mycorrhiza) are recognized as the two main functional groups that play a pivotal role in organic matter decomposition and soil C cycling (Hobbie and Horton, 2007; Clemmensen et al., 2015; Bödeker et al., 2016). The former group obtains C through organic matter decomposition, while the latter group mainly receives C from host plants, such as the plant photosynthate and root exudates (Kyaschenko et al., 2017). Theoretically, tree removal will restrict the root-associated fungi by reducing their host plant abundance, but may stimulate the growth of saprotrophic fungi via a flush of organic matter from increased dead fine roots and tree stumps. However, the hypothesis that ectomycorrhizal fungi (EcMF) harbor potential capacity for organic matter decomposition has been of increasing importance in recent studies (Talbot et al., 2008; Lindahl and Tunlid, 2015), though the evidence of genes encoding for carbohydrate catabolism has not been detected (Jeanne et al., 2015). The organic matter decomposition by EcMF is suggested to be an alternative strategy when the photosynthate supply is low rather than terminated (Talbot et al., 2008). Moreover, the mycorrhizal fungi are supposed to facilitate the formation of new tissues by supplying C to their host plants (Courty et al., 2007), which may occurr with bud burst during tree increment. It is also proposed that EcMF benefit from organic matter decomposition primarily through increased nitrogen (N) mobilization rather than through release of metabolic C (Lindahl and Tunlid, 2015). Nevertheless, the involvement of EcMF in soil organic matter decomposition might lead to strong competition between EcMF and saprotrophic fungi for the organic resources (Talbot et al., 2008; Bödeker et al., 2016; Kohout et al., 2018). After removing the big trees in selective logging, the photosynthate supply might not satisfy the growth of EcMF, leading to higher probability of nutrient aqusition from organic matter by EcMF. Alternatively, the increased nutrients requirements by tree increment in logged forests may drive the root-associated fungi to mobilize organic nutrients from organic matter (Talbot et al., 2008). As a consequence, EcMF might interact with saprotrophic fungi more intensively due to organic resource competition. Further, the competition for space among fungal groups might increase. The interactions between EcMF and saprotrophic fungi and the ecological consequences of the interactions after tree logging have been well studied in boreal forests (Bödeker et al., 2016; Kyaschenko et al., 2017), but less is known in tropical forests. Whether selective cutting and clearcutting would differentially affect the two functional guilds remain unclear. Clarifying the interactions and responses of EcMF and saprotrophic fungi after selective cutting and clearcutting in tropical rainforests can provide information on the consequences of C sequestration under the two forest management systems.

Previous researches suggested that alterations in soil fungal community caused by forest logging could persist for decades (Hartmann et al., 2012; Song et al., 2015). During this period, fungal communities might be affected by the changes in vegetation attributes and soil properties related to forest succession. The composition and diversity of plants are altered by succession, which can exert significant effects on soil fungal community by altering litter quality and root exudates (Broeckling et al., 2008; Steffi and Wolfgang, 2009; Yan et al., 2018). Moreover, some fungi are exclusively related to certain plant species or plants in certain age, such as ericoid mycorrhizal fungi and some plant pathogens (Westover and Bever, 2001; Tosa, 2009). Soil properties, including moisture, temperature, bulk density and organic matter content are directly affected by logging or indirectly affected by vegetation changes, resulting in different soil microenvironments in logging patches (Ballard, 2000; Hartmann et al., 2012). As a consequence, the fungal community might be reshaped by the changing microenvironment. The patterns of revegetation and soil property rehabilitation during succession often relate to the harvest intensity (Kern et al., 2013; Wu et al., 2018). Thus, after a certain recovery period, the soil fungal community and its determining factors might be different between the selectively harvested and clear cut forests. Understanding the key factors driving the shifts in soil fungal community after logging are important to develop effective forest restoration management in terms of the belowground communities.

Soil microorganisms usually interconnect with each other to form complex networks instead of living in isolation (Zhou et al., 2011). Within the networks, microbial communities are positively and negatively correlated mainly due to niche overlap, niche partitioning, phylogenetic similarity, mutualistic relationships or resource and space competition (Jiang et al., 2015; He et al., 2017). Networks have been used to study the responses of microorganisms to environmental changes, such as precipitation changes, CO_2 enrichment, and agriculture practices (Zhou et al., 2011; Lu et al., 2013; He et al., 2017). In these previous studies, the taxa that strongly drive co-variation among microbial communities often shifted with environmental changes, reflecting shifts in the main function of the overall community network (Deng et al., 2012b; He et al., 2017) He. However, the responses of microbial networks to tree logging are still largely unknown in tropical forest soils. By comparing the networks of the fungal communities in forests with selective and clear cutting histories, the intraspecific interactions and their associations with environmental changes under the two forest management strategies can be uncovered. The further combination of fungal network and functional guilds can shed lights on the main functions of fungal community organization.

Here, we investigated the responses of soil fungal community (i.e., composition, functional guilds and the fungal network) to historical logging in a tropical rainforest and their associations with vegetation composition, litter nutrients content and soil physicochemical properties. We sampled soils from 61 quadrats (25 m × 25 m) across a 160-km^2 tropical rainforest in Hainan Island, China. The 61 quadrats were divided into three types according to the logging history: primary forest stands without a history of logging, and post-harvested forests that had been clear cut or selectively harvested and left to recover without management for up to 50 years. The historical logging-induced changes in EcMF were especially emphasized, as some of the abundant tree species in the study areas are able to form ectomycorrhizas, such as *Dacrydium pierrei*, *Cyclobalanopsis glauca* and *Castanopsis fissa*. By performing these analyses, we hypothesized that: (1) the effects of both selective cutting and clearcutting on soil fungal community composition would still be recognizable after ca. 50 years natural recovery, as indicated by different fungal community composition between the post-harvest and primary forest stands; (2) the relative abundance of root-associated fungi would decrease while the saprotrophic fungi would increase in the forest stands with logging history; and (3) the interactions among fungal members would increase in the selectively harvested forest stands while they would decrease in the clear cut stands when compared with the primary stands.

2. Materials and methods

2.1. Study site

The study site is located in the Jianfengling forest reserve (JFR), which is in the Southwest Hainan island, China (18°23′–18°50′ N and 108°360′–109°05′ E). It is characterized by the tropical monsoon climate with a typical dry season from November to April and a wet season from May to October. The mean annual temperature is 24.5 °C and annual precipitation ranges from 1000 to 3600 mm. The soil type is yellow latosol. The JFR contains 472 km^2 tropical rainforest, whereas part of the primary forest has been disturbed because of selective cutting or clearcutting 20–50 years ago. Under the selective cutting regime, 30%–40% of the mature stems with diameter at breast height (DBH) > 40 cm were harvested from the primary forest. At present, about 160 km^2 of primary forest remains in the reserve (Jiang and Lu, 1991), intermixed with patches of forest naturally recovered after logging. Therefore, three types of forest management stands exist in the 160 km^2 forest: original primary forest stands without logging history (thereafter the primary), secondary forest stands that have been regenerated naturally for up to 50 years after selective cutting (thereafter the select cut) or after clearcutting (thereafter the clear cut). Sixty-one 25 m × 25 m quadrats were set up in the three types of forest stands across the 160 km^2 area to investigate the vegetation features, soil properties and soil fungal communities. The distance between adjacent quadrats was ≥250 m. The time when different patches of the160 km^2 area were logged and the logging method were recorded by the Jianfengling forest bureau. According to the records, the 61 quadrats encompassed 19 quadrats of the primary stands, 25 quadrats of the select cut stands and 17 quadrats of the clear cut stands (Fig. S1). The recovery year of the harvested quadrats was determined according to the time when these patches were logged (Table S1).

The vegetation inventory was conducted in 2015, and all trees with DBH > 1 cm were assessed in the 61 quadrats. Vegetation attributes including species diversity (Shannon-Wiener index), tree density (number of individuals) and aboveground biomass under the three forest management strategies were calculated and compared (Fig. S2). The species compositions were presented by the sample scores along the first three to four principal component axes (i.e., veg-PC1, veg-PC2, veg-PC3, veg-PC4) from a principal component analysis (PCA) on the vegetation community in the whole study area or in each type of forest stands. Thereafter, the selected PCs were used as variables representing vegetation composition in further statistical analyses. The elevation of each quadrat was calculated as the mean of values at its four corners (Harms et al., 2001).

2.2. Soil sampling and analyses

Soil sampling was conducted in the spring of 2016. After removing the organic layer, five subsamples of the topsoil (0–10 cm) were randomly collected in each quadrat using an auger and composited to form one sample. After removing roots and stones, soil samples were sieved through a 2 mm mesh and were immediately taken back to the laboratory on ice. All samples were divided into two parts: one part was stored at 4 °C for soil physicochemical analyses, another part was stored at −20 °C for analyses of the soil fungal community. The soil analyses were conducted within two weeks after sample collection.

Soil physicochemical properties were measured using the methods as described by Liu et al. (1996). Generally, total soil carbon (TC) was measured through dry combustion (TOC-VCSH, Shimadzu, Japan). Total soil nitrogen (TN) was determined with the semi-micro Kjeldahl method. Total soil phosphorus (TP) and total soil potassium (TK) were measured using methods of ascorbic acid colorimetric and atomic absorption, respectively. The alkaline hydrolysis distillation method was used to determine available soil nitrogen (AN) content. Soil samples were extracted by $NaHCO_3$, and the extract was then used to measure available soil phosphorus (AP) with the molybdate-blue colorimetry method. For determination of available soil potassium (AK), soil was extracted with ammonium acetate and then the extract was loaded onto an atomic absorption spectrometer with ascorbic acid as a reductant. Soil exchangeable Ca (exCa) and Mg (exMg) were extracted with ammonium acetate and measured by atomic absorption spectroscopy. Soil pH was measured in a soil/water suspension (1: 2.5, w/w) using a pH meter (UB-7 pH/ev Meter; Denver Instrument, Bohemia, NY, USA). Soil bulk density (BD) was determined by drying an intact fresh soil column at 105 °C for 24 h in a cylindrical stainless-steel container with known volume and weight, meanwhile the mass loss of soil after oven drying was weighed to calculate the soil water content (SWC).

2.3. Litter sample collection and analyses

Litter sample collection was conducted at the same time as soil sampling. Four samples at each corner and one at the center of the quadrat were collected from the soil surface, and then mixed thoroughly to form one composite sample. The litter samples were oven dried at 65 °C until constant weight, and then milled intensively. The determinations of litter P and K content were performed using the digestion method as indicated by Mctiernan et al. (1997). Total C of litter was measured by dry combustion method. Total N from litter samples was detected using the regular Kjeldahl method (Bataglia et al., 1983). Litter pH was measured using a pH meter (UB-7 pH/ev Meter; Denver Instrument).

2.4. Soil DNA extraction, sequencing and data processes

Soil DNA was extracted from 0.4 g fresh soil with the PowerSoil® DNA Kit (MoBio, CA, USA) according to the manufacturer's instructions. The quality and quantity of the extracted DNA were determined on a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific Inc., USA). The barcoded primer pair ITS2 (5′-GCTGCGTTCTTCATCGA TGC-3′) and ITS5 (5′-GGAAGTAAAAGTC GTAACAAGG-3′) was used to amplify the internal transcribed spacer region 1 (ITS1) of the fungal rRNA gene (Bellemain et al., 2010). The PCR reaction was performed in 96-well plates (Axygen, USA) on a BioRad S1000 thermal cycler (Bio-Rad Laboratory, CA, USA), with 50 μl volume in each well including 25 μl 2 × Premix Taq (TaKaRa Biotechnology, Japan), 2 μl of each primer (10 mM), 5 μl of DNA template (60 ng) and 16 μl RNase free Ultra-Pure water. The amplification was performed with the following conditions: 94 °C for 5 min; 30 cycles of 95 °C for 30 s, 52 °C for 30 s and 72 °C for 30 s; 72 °C for 10 min. Each soil sample had three replicates during the amplification, and the PCR products from the three replicates were mixed. The GeneTools Analysis Software (Version4.03.05.0, SynGene) was then used to compare the concentration of PCR products. Afterwards, the PCR products from each sample were mixed, and the required volume of each sample was calculated based on the equal quality principle. Then, the EZNA Gel Extraction Kit (Omega, USA) was used to extract the mixed PCR products, and the target DNA fragment was retrieved by using the TE buffer solution. Before sequencing, the library was constructed by using the NEBNext® Ultra™ DNA Library Prep Kit for Illumina® (New England Biolabs, USA) according to the manufacturer's instructions. The high-throughput sequencing of the ITS1 gene was conducted by MAGIGEN Company (Guangzhou, China) on the Illumina HiSeq2500 platform (PE250). The quality of paired-end raw reads from sequencing was checked by using Trimmomatic V.0.33, and the low-quality reads were filtered out. During the quality check, the reads that contained N, had a quality value lower than 30 or had a sequence length longer than 150 bp after quality filtering were removed. Then, the sequences were assigned to the corresponding sample by using the Qiime software (http://qiime.org/scripts/split_libraries_fastq.html) according to the paired-end barcode and primers (Caporaso et al., 2010). Next, the fragments of barcode and primer were removed and then the paired-end clean reads

were merged with Mothur V.1.35.1 to obtain the raw sequences according to the overlap between paired-end reads (Schloss et al., 2009). The minimum overlap length was set at 10 bp, and the maximum mismatch ratio is 0.2 for the overlap region of the merged sequences. The reads that could not reach these criteria were filtered out. Raw sequences were processed on Trimmomatic to select the highest-quality sequences for each sample. All the clean sequences were clustered through Usearch V.8.0.1517 with the method "uparse" based on 97% identity to classify the operational taxonomic units (OTUs). The fungal sequences were then checked for chimeras and singleton OTUs using Usearch and UCHIME (Edgar et al., 2011; Edgar and Flyvbjerg, 2015) (http://www.drive5.com/usearch/manual/uchime_algo.html). All the sequences obtained from all soil samples were clustered using Usearch V8.0.1517 and the uparse algorithm with 97% identity to generate the OTU table. The most abundant sequence in each OTU was selected as the representative sequence by using Qiime. Singleton OTUs and chimeras were filtered out by using Usearch and UCHIME, respectively. The representative sequences were assigned taxonomic information using Mothur against the UNITE 7.1 (ITS, http://unite.ut.ee/index.php) database (Abarenkov et al., 2010). OTU table with annotations of fungal taxonomy was then used to analyze the functional groups of each OTU with FUNGuild software (Nguyen et al., 2016). The number of OTUs assigned to a specific guild was represented as the guild OTU richness, and number of sequences in a specific guild divided by the total sequences was calculate as the guild relative abundance.

2.5. Network analysis

Network analysis was performed using the Molecular Ecological Network Analyses Pipeline (http://ieg2.ou.edu/MENA/main.cgi) according to the descriptions by Zhou et al. (2011) and Deng et al. (2012b). First, the square-root transformed OTU table, environmental matrix and the OTU annotation file were prepared based on the guilds in the pipeline. Second, the transformed OTU table was submitted to the pipeline for network construction. As indicated by the default settings, the OTUs that appeared in less than half of all samples were excluded, and a cutoff value (similarity threshold, st.) for the similarity matrix was automatically generated. A link between the pair of OTUs was constructed if the correlation between their abundance was larger than the threshold. Third, the analyses of "global network properties", "individual nodes' centrality", and "module separation and modularity" were performed. The term 'module' means that a group of nodes were connected more densely to each other than to other nodes outside the group, and the parameter of modularity was used to measure how well a network is divided into modules. Clustering coefficient is used to evaluate the tendency of neighbors of a node to connect with each other. The geodesic distance (path distance) represents the shortest path length (number of edges) between the connections of any two nodes. Fourth, the "output for Cytoscape visualization" was processed and three files for visualization of the network in Cytoscape were generated. The instructions for Cytoscape can be obtained from the website (http://manual.cytoscape.org/en/stable/). Fifth, the network structure was randomized by running the "randomize the network structure and then calculate network" command, and the main properties of the Random network and Empirical network were compared. Sixth, the main modules consisting of no less than five nodes were identified by performing the "module-eigengene". The environmental matrix was submitted at this step to calculate the relationships between network structures and environmental variables through the Mantel test.

The topological role of each node in a network was assessed by the *Zi* and *Pi* values, where *Zi* represents the nodes connectivity within a module, and *Pi* measures the degree of a node connected with other modules (Roger and Amaral, 2005). All species can be divided into four groups according to the simplified criteria (Olesen et al., 2007), namely peripherals ($Zi < 2.5$ and $Pi < 0.62$), connectors ($Pi > 0.62$), module hubs ($Zi > 2.5$) and network hubs ($Zi > 2.5$ and $Pi > 0.62$). From the ecological perspective, peripherals can be considered as specialists (always linked to the nodes within their own modules) while module hubs and connectors are suggested as generalists (highly connected to many nodes in their own modules or to other modules) and network hubs as supergeneralists (act as both module hub and connector) (Olesen et al., 2007). Therefore, the generalists are proposed as taxa that strongly drive co-variation among fungal communities in a network.

2.6. Statistical analyses

Nonmetric multidimensional scaling (NMDS) analysis was performed to compare the patterns of fungal community composition among the primary, select cut and clear cut stands. During this analysis, the Bray-Curtis dissimilarity of OTU tables was used. Furthermore, the differences in the composition patterns among different stands were detected by permutational multivariate analysis of variance (PERMANOVA) with 999 permutations (Anderson, 2001). Additionally, the NMDS analysis was performed on the OTU tables in select cut and clear cut stands, respectively, to investigate the fungal community composition across recovery time (20–50 years; Table S1). Spearman correlations of the fungal community diversity (Shannon-Weiner index), relative abundance of fungal guilds and top phyla associated with soil properties and litter nutrients content were investigated by using the data from all the 61 quadrats. One-way analysis of variance (ANOVA) with Tukey's HSD multiple comparison were used to test the differences in environmental variables among the three forest management stands. Prior to the ANOVA, the normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levène test) of each variable were tested, and the variable was log-transformed if necessary. All analyses were conducted using R 3.3.2. Effects were considered significant if $P \leq 0.05$.

3. Results

3.1. Vegetation features and soil properties in the three types of forest stands

The average tree number and aboveground biomass at quadrat level (25 m × 25 m) were (mean ± SE): 379 ± 18 and 19750 ± 1335 kg m^2 yr^{-1} in primary stands, 405 ± 29 and 13911 ± 785 kg m^2 yr^{-1} in select cut stands and 536 ± 36 and 11433 ± 1017 kg m^2 yr^{-1} in clear cut stands (Fig. S2). The inverse pattern of the variation in tree number and biomass among the three stands might indicate a larger proportion of small trees in select cut and clear cut stands than that in primary stands.

Soil AN content reduced substantially from 202 ± 14 mg kg^{-1} in primary stands to 175 ± 10 mg kg^{-1} ($p > 0.05$) in select cut stands and to 156 ± 8 mg kg^{-1} ($p < 0.05$) in clear cut stands. A slightly decline in soil TP content was also detected after historical logging, with decreases of 14% ($p > 0.05$) in select cut stands and 19% ($p > 0.05$) in clear cut stands. Soil pH, TK, AK, and exCa in select cut stands were significantly higher ($p < 0.05$) than those in the clear cut stands, while litter C content was greater ($p < 0.05$) in the clear cut stands when compared with that in the select cut stands. Litter TK content in the clear cut stands (2.56 ± 0.17 g kg^{-1}) was also higher than those in the other two stands (primary stands: 2.12 ± 0.15 g kg^{-1}, select stands: 2.09 ± 0.16 g kg^{-1}), but the difference was not statistically significant ($p > 0.05$). Soil TC, AP, exMg and SWC did not differ among the three stands and were stable at 17 ± 1 g kg^{-1}, 1.8 ± 0.1 mg kg^{-1}, 0.16 ± 0.01 cmol kg^{-1} and 25%, respectively (Fig. S2).

3.2. Diversity and composition of soil fungal community

By passing the quality control, a total of 2,878,267 high-quality

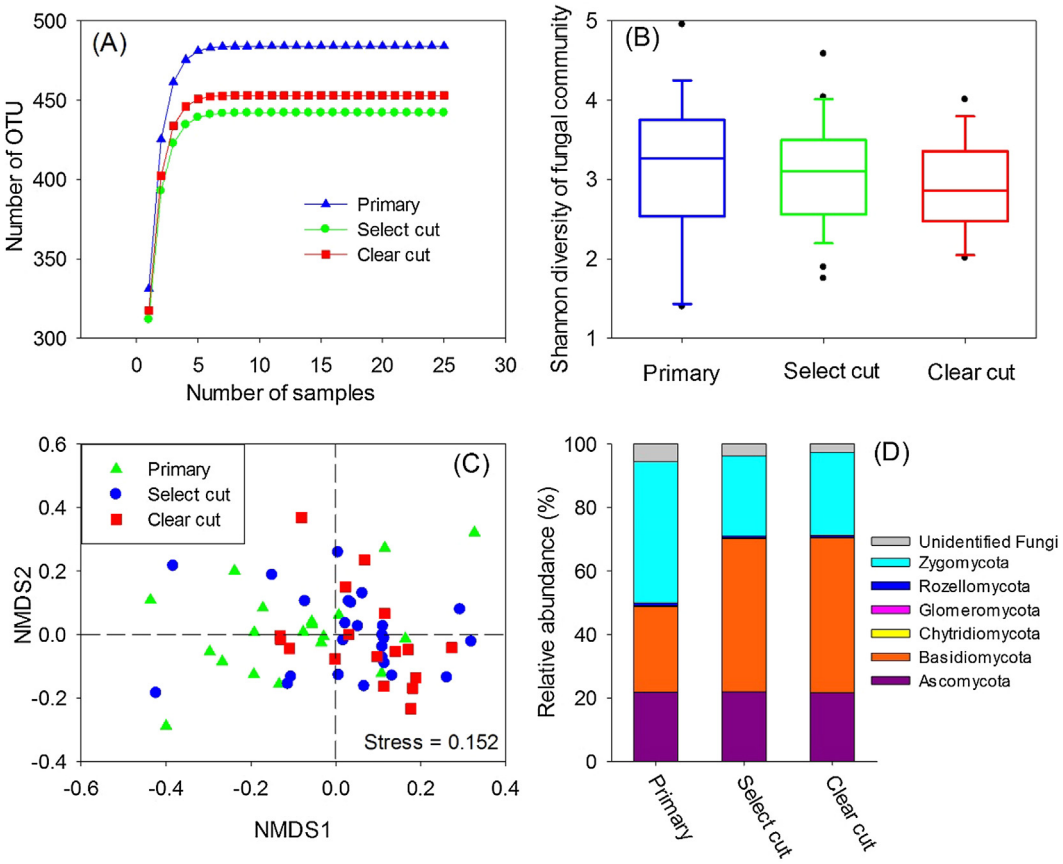

Fig. 1. A composited figure displaying (A) the rarefaction curve of OTU richness against number of soil samples, (B) Shannon-Weiner Index of fungal community, (C) Bray-Curtis similarity of the fungal community structure as indicated by Non-metric multidimensional scaling analysis (NMDS), and (D) fungal community composition in a primary and two secondary tropical forest stands. The select cut and clear cut stands were subjected to diameter selective cutting and clear cutting 20–50 years ago, respectively.

fungal sequences were obtained. The rarefaction curve revealed the relationships between sample size and OTU numbers. The OTU numbers increased sharply with sample size, but plateaued at 484 in the primary stand, 442 in the select cut stand and 453 in the clear cut stands (Fig. 1A). The α diversity of fungal community was slightly lower in the harvested stands compared with that in the primary stands (Fig. 1B). According to the results from NMDS, the composition of the fungal community differed significantly among the three stands (PERMANOVA test: $F_{2,58} = 2.1$, $p = 0.001$, Fig. 1C). Fungal community composition showed no significant difference across 20–50 years recovery time either in the select cut or clear cut stands (Fig. S3). A total of six phyla containing 96% of the total sequences were detected after excluding the unidentified sequences. The *Zygomycota* accounted for 45% of sequences in the primary stands, but it decreased to 25% in select cut stands and to 26% in clear cut stands. *Basidiomycota* has a relative abundance of 27% in primary stands, but it increased to 48% in both select cut and clear cut stands (Fig. 1D). The relative abundance of *Ascomycota* (21%) was similar in the three types of forest stands. *Rozellomycota*, *Glomeromycota* and *Chytridiomycota* had relative abundances of < 1% in each stand. Relative abundance of the top six phyla was mostly negatively correlated with vegetation features (i.e., aboveground biomass and tree density), SWC and elevation, while positively correlated with BD (Table S2).

The functional guilds of fungal communities were determined by using the online Pipeline: FUNguilds (Nguyen et al., 2016). As a result, 171 OTUs (containing 572,329 sequences), 142 OTUs (containing 460,234 sequences) and 162 OTUs (containing 441,208 sequences) in the primary, select cut and clear cut stands, respectively, could be assigned to 11 functional guilds. Only these assigned OTUs and sequences were taken into consideration in the following descriptions. The OTU richness of different guilds showed similar patterns among the three stands, with undefined saprotrophs having the greatest richness (53–69), followed by EcMF (24–33), plant pathogens (18–24), animal pathogens (16–19) and ericoid mycorrhizal (10–13) (Fig. 2A). The litter pathogens and soil saprotrophs had the lowest richness (1) in all forest stands. However, the relative abundance of sequences assigned to different guilds was substantially affected by historical logging. For instance, the relative abundance of undefined saprotrophs was lower in harvested stands than that in primary stands. Balancing the decline in undefined saprotroph guild, the relative abundance of EcMF and animal pathogens increased in select cut stands, while wood saprotrophs and ericoid mycorrhizal increased in clear cut stands (Fig. 2B). The relative abundance of animal pathogens, ectomycorrhizal and ericoid mycorrhizal was negatively correlated with litter and soil nutrients content, SWC and elevation while it was positively correlated with soil pH and BD. Positive correlations were observed between the relative abundance of undefined saprotrophic fungi and aboveground biomass, soil AN, SWC and elevation (Table S3).

3.3. Fungal community networks in the three types of forest stands

The topological properties of the networks varied substantially among the three stands types, indicating distinct features of the network organization and different interactions among fungal members (Table 1). All the three networks fit a power-law ($R^2 = 0.875$–0.921). Networks in primary, select cut and clear cut stands had 207, 238 and 268 total nodes, respectively. The number of total links in select cut stands was 43% higher than that in primary stands, and in clear cut

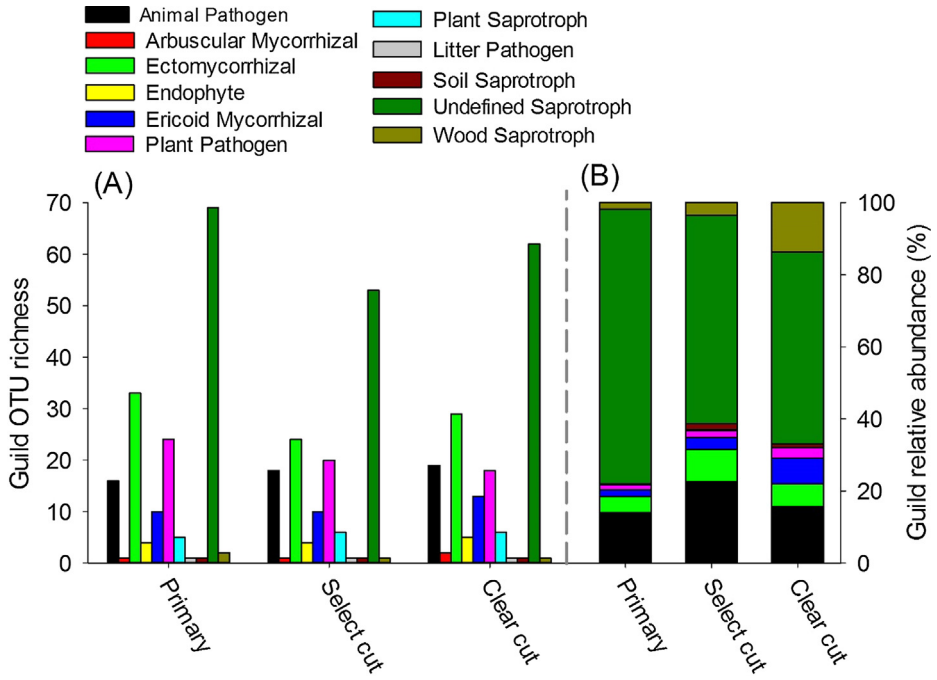

Fig. 2. Fungal functional (A) guild OTU richness and (B) guild relative abundance. Only results with confidence of "probable" and "highly possible" from the output were involved in this plot.

Table 1
Main properties of fungal networks in a primary and two secondary tropical forest stands. The select cut and clear cut stands were subject to diameter selective cutting and clear cutting 20–50 years ago, respectively. Both the properties from Empirical networks and Random networks were presented.

Parameters	Primary	Select cut	Clear cut
Empirical networks			
Similarity threshold (S_t)	0.76	0.69	0.77
Number of OTU	484	442	453
Total nodes	207	238	268
Total links	232	331	293
Number of module	26	27	32
R^2 of power-law	0.92	0.88	0.90
Average connectivity (avgK)	2.24	2.78	2.19
Average cluster coefficient (avgCC)	0.12	0.13	0.08
Average path distance (GD)	9.98	5.78	7.58
Modularity	0.86	0.76	0.84
Random networks			
Average cluster coefficient (avgCC)	0.008 ± 0.006	0.012 ± 0.005	0.006 ± 0.004
Average path distance (GD)	6.159 ± 0.278	4.705 ± 0.082	6.646 ± 0.289
Modularity	0.749 ± 0.011	0.638 ± 0.009	0.776 ± 0.009

stands it was 26% higher than that in primary stands. The average connectivity (avgK) was higher in select cut stands (2.78) while it decreased slightly in clear cut stands (2.19) when compared with primary stands (2.24), indicating high numbers of neighbors per node in the select cut network. Visually, the network in select cut stands was more clustered than those in the other two stands, which was consistent with the higher connectivity (Fig. 3). Similar to avgK, the average cluster coefficient (avgCC) was highest in select cut stands and lowest in clear cut stands. The average path distance (GD) from both the Empirical and Random networks declined substantially after logging, especially after selective cutting, when compared with the primary stands.

Module eigengene analysis reveals a representative value of the module expression profile, which can be used to evaluate the high-dimensional organizations of a network structure. Eleven main modules (containing more than five OTU members) were included in the eigengenes of the primary and select cut stands, while 12 main modules were involved in the eigengene of clear cut stands (Fig. 4). The module eigengenes could explain 26–69% of the variation in the modules of the primary network, 20–65% of the variation of the select cut network and 21–57% of the variation of the clear cut network (see φ value in Fig. 4). The modules of P2 and P3, P5 and P6, P4 and P7 in the primary stand were closely correlated (equivalent to clustering height at 0.4), which yielded three meta-modules with 109 nodes, accounting for 53% of the total nodes. In the select cut stands, one meta-module consisting of S1, S3, S6, S9 and S10 was detected, which included 56% of the total nodes. In clear cut stands, however, only three modules (C9, C10 and C11) were involved in the meta-module, accounting for 15% of the total nodes.

3.4. Taxa that act as generalists in the fungal networks

The majority of nodes (98% in primary and clear cut stands, and 95% in select cut stands) were identified as peripherals. In the primary network, one node assigned to phylum *Ascomycota*, genus *Idriella* (OTU2562) served as a connector and three nodes assigned to phylum *Ascomycota*, genus *Leptosphaeria* (OTU391); phylum *Ascomycota*, class *Sordariomycetes* (OTU349) and phylum *Ascomycota*, family *Hypocreaceae* (OTU846) were detected as module hubs. In the select cut network, nine nodes assigned to phylum *Ascomycota*, family *Herpotrichiellaceae* (OTU1340, OTU11074 and OTU704); phylum *Basidiomycota*, genus *Trichosporon* (OTU5300); phylum *Basidiomycota*, genus *Russula* (OTU156); phylum *Orbiliomycetes*, family *Orbiliaceae* (OTU459); unclassified *Ascomycota* (OTU290 and OTU56) and unidentified *Fungi* (OTU526) were detected as connectors; and three nodes belonging to phylum *Basidiomycota*, genus *Phaeocollybia* (OTU96); phylum *Zygomycota*, genus *Umbelopsis* (OTU317) and unclassified *Ascomycota* (OTU8337) were categorized as module hubs. Two nodes assigned to phylum *Ascomycota*, genus *Simplicillium* (OTU533) and phylum *Ascomycota*, family *Trichocomaceae* (OTU924) were detected as connectors in the clear cut network; and four nodes assigned to phylum *Ascomycota*, class *Eurotiales*, genus *Penicillium* (OTU474); phylum *Ascomycota*, class *Leotiomycetes* (OTU305); phylum *Ascomycota*, genus

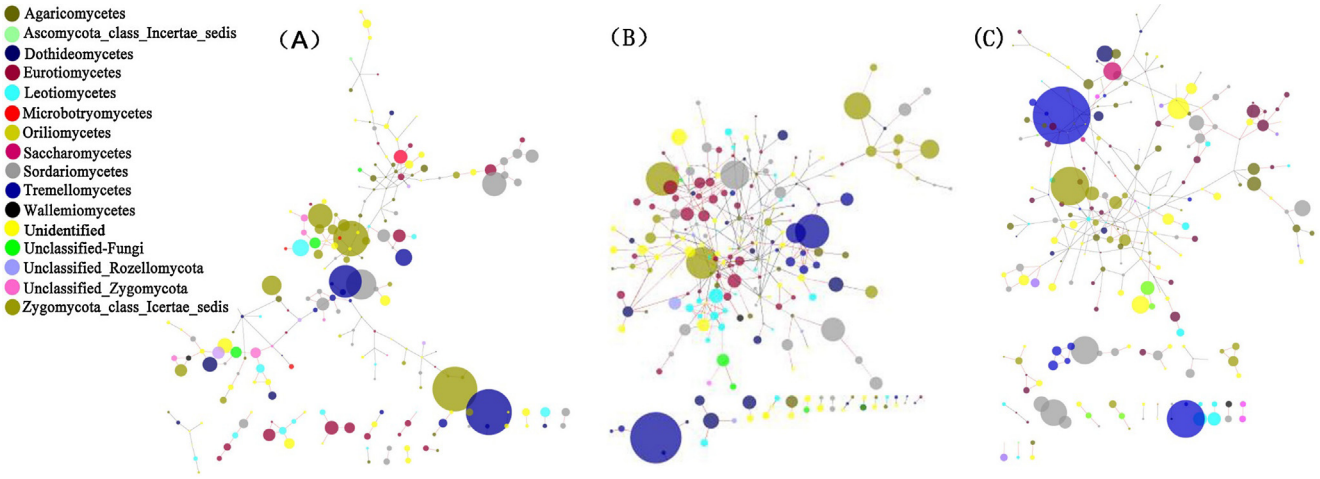

Fig. 3. Fungal networks in (A) the primary forest stands, (B) the secondary forest stands which experienced diameter selective cutting 20–50 years ago (thereafter the select cut stand), and (C) the secondary forest stands which experienced clear cutting 20–50 years ago (thereafter the clear cut stand). Sixteen fungal classes were represented with different colors, and the node size is proportional to square-rooted abundance of the corresponding OTU. The positive and negative correlations between each two nodes were indicated with black and red edges, respectively.

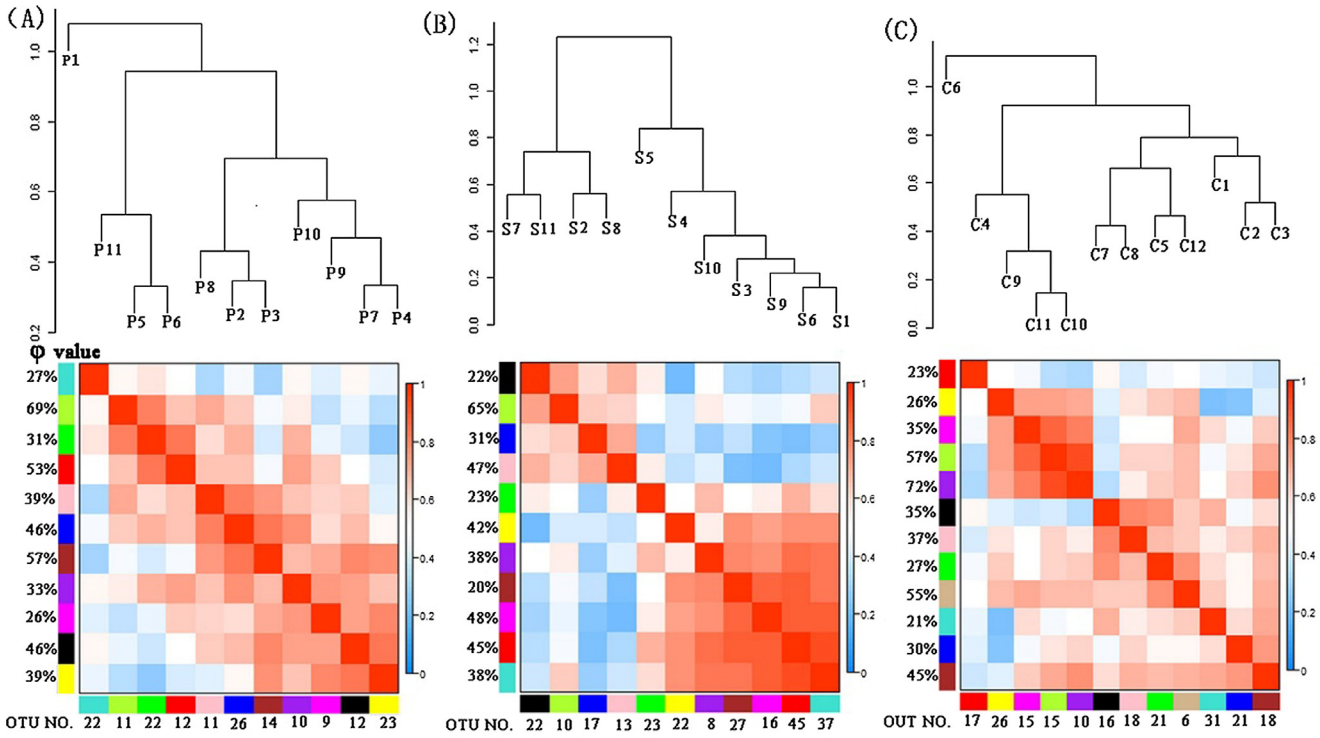

Fig. 4. The correlations and heatmaps showing module eigengenes of fungal networks. The upper part represents the results of hierarchical clustering based on the Pearson correlations among module eigengenes, and the corresponding heatmap displays the coefficient values (r). The higher correlation is indicated by red color and the lower correlation is indicated by green color. The percentage of the total variance explained by the eigengene of module is indicated by the φ value on the left side of heatmaps. Modules larger than 5 nodes are presented, and labeled with "P" (primary stands), "S" (select cut stands) and "C" (clear cut stands) followed by a number. The nodes (OTUs) in each module were marked on the lower edge of the perspective heatmap. The select cut and clear cut stands were subjected to diameter selective cutting and clear cutting 20–50 years ago, respectively.

Talaromyces (OTU627) and unclassified *Ascomycota* (OTU575) played the role of module hubs in clear cut stands. Overall, the generalists in primary and clear cut stands accounted for ~2% of the total nodes, while in select cut stands this value increased to 5% of the total nodes. Notably, half of the generalists (OTU11074, OTU1340, OTU290, OTU317, OTU459 and OTU56) in select cut stands were shared by primary stands, but these species served as specialists in the primary network (Fig. 5). In clear cut stands, however, none of the nodes categorized as generalists was shared by primary stands. These results suggested that some OTUs exhibited role-shifts from specialists to generalists after selective cutting.

3.5. Associations of fungal networks with soil properties and vegetation features

The relationships between networks and environmental properties were determined by Mantel test. As a result, more than half of the module eigengenes in all the three networks were positively or

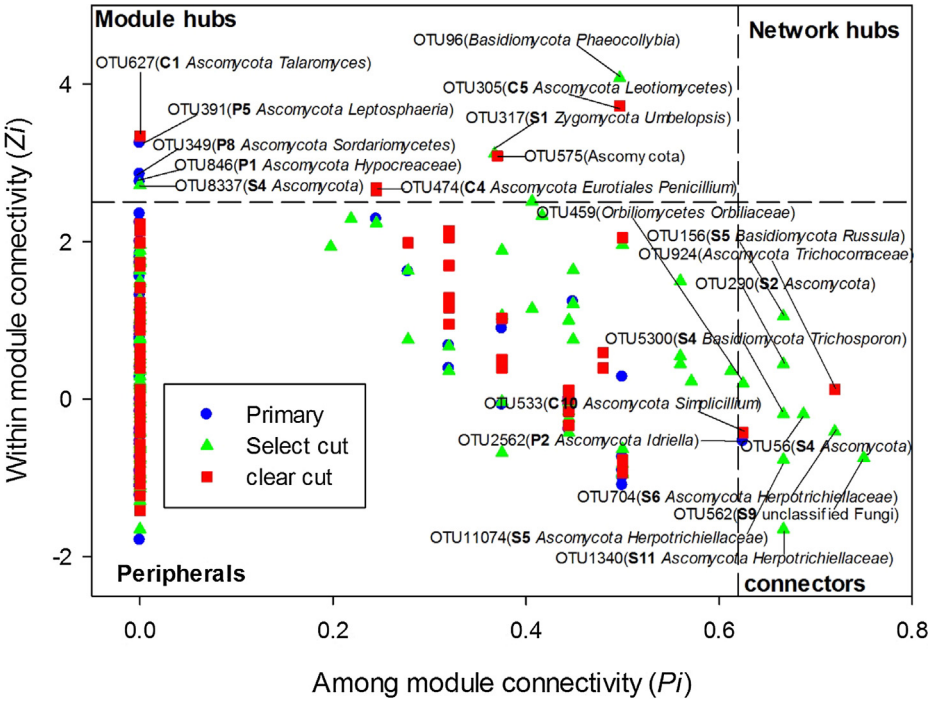

Fig. 5. *Zi-Pi* plot showing the topological distribution of OTUs in the fungal networks. The module hubs and connectors are marked by OTU number, module affiliations and taxonomic assignment. Select cut and clear cut stands were subjected to diameter selective cutting and clear cutting 20–50 years ago, respectively.

negatively correlated with one or more properties ($p < 0.05$, Tables S4–S6). Module eigengenes in the primary network were mostly positively correlated with the vegetation features (biomass, litter N, litter C:N, litter P and litter K), although some negative correlations between soil properties (soil AN, AP, TK, exMg and pH) and module eigengenes (P2, P3, P4, P10) were detected. In the select cut network, however, the module eigengenes correlated more strongly to soil properties than to vegetation features, and nearly all the correlations between module eigengenes and litter properties (litter C, litter P and litter K) were negative. Collectively, most of the OTUs in the module eigengenes from the primary network were driven by litter nutrients while they were suppressed by soil nutrients. Instead, the OTU members from the select cut network were stimulated by soil nutrients content and BD, but depressed by litter nutrients. Interestingly, the correlations of module eigengenes with both soil properties and vegetation features reduced substantially in the clear cut stands when compared with those of the primary and select cut stands.

4. Discussion

4.1. Reponses of fungal community composition and functional guilds to historical logging

The effects of forest harvest on soil fungal community composition have been widely recognized, and could last for decades (Hartmann et al., 2009, 2012; Cardenas et al., 2015; Song et al., 2015). As expected, this study showed obvious differences in soil fungal community composition between the forests with and without logging history in a tropical region of South China, supporting our first hypothesis. Specifically, a higher relative abundance of *Basidiomycota* and a lower relative abundance of *Zygomycota* were observed in harvested forests after 20–50 years natural recovery when compared with those in the primary forest (Fig. 1D). The alterations in soil fungal community composition still persist even ~50 years has passed since logging. This was consistent with a previous study reporting 50 years' persistence of alterations in soil microbial community composition after clearcutting in a subtropical forest (Song et al., 2015). While long-term persistence of the alterations has become an increasing research focus, the underlying drivers and potential ecological consequences remain debatable (Kyaschenko et al., 2017; Kohout et al., 2018). The relative abundance of the top six fungal phyla in this study was significantly correlated with vegetation attributes, soil physical properties and topographical features (Table S2), suggesting that the long-term alterations in fungal community composition after logging might relate to the effects of these variables. Different vegetation composition can favor different soil fungal groups through modifying the soil microenvironments with litter quality or root exudates, which has been well studied (Broeckling et al., 2008; Yan et al., 2018). The phyla *Chytridiomycota* and Unidentified fungi showed significant correlations with vegetation composition in this study, indicating strong sensitivity of these communities to vegetation composition changes in the tropical rainforest. However, other fungal phyla were not affected by vegetation composition. This might be because of the fact that some fungal communities are more affected by a certain vegetation group (i.e., trees, shrubs and herbs) or by plants at a certain growth stage (Wu et al., 2013). The detected correlations between relative abundance of the top six fungal phyla and aboveground biomass as well as individual number were mostly negative (Table S2). This was unexpected because higher vegetation cover and higher biomass can foster greater microbial biomass by producing more abundant or more diverse organic substrates for soil microorganisms (Chung et al., 2007). However, the greater vegetation cover might also lead to limited forest gaps, especially in the tropical rainforests dominated by evergreen broad-leaf trees. Decrease in forest gap areas can affect the growth of soil microbial communities through altering abiotic environments, such as reducing available light, soil temperature and soil moisture (Prévost and Raymond, 2012). The relative abundances of the top fungal phyla were less affected by litter and soil nutrients content than by SWC and BD (Table S2), in agreement with previous studies showing sensitive responses of fungal communities to SWC variations (Kaisermann et al., 2015; Curlevski et al., 2014; He et al., 2017). While mycelium growth needs ample space, the BD can affect the soil fungal community through altering pore spaces (Harris et al., 2003). Vegetation features and soil properties often vary with elevation, which might result in different fungal community

composition at different elevation (Shreve, 1924; Clinton, 2003; Prévost and Raymond, 2012), supporting our results (Table S2). With regard to the litter and soil nutrients, they might play an important role in regulating the interspecific correlation of the fungal community, as indicated by significant correlations between nutrients content and fungal species composition in each type of forest stands (Fig. S4).

Previous studies focusing on temperate forests suggested that alterations in soil fungal community composition after forest harvest generally resulted from the shifts from root-associated to saprotrophic fungi domination, driven by organic substrate changes (Kyaschenko et al., 2017). By comparing the relative abundance of functional guilds, we found a stimulation of wood saprotrophs, ericoid mycorrhizal fungi, EcMF and animal pathogens and an inhibition of undefined saprotrophs by historical logging (Fig. 2B). Clearly, the relative abundance of root-associated fungi increased, conflicting with our second hypothesis. The stimulation of root-associated fungi might be caused by the vegetation increment during post-logging succession. Interestingly, the relative abundance of ericoid mycorrhizal fungi showed a substantial increase in the clear cut stands when compared with the primary stands, whereas the relative abundance of EcMF increased more in the select cut stands. This might indicate that the dominant mycorrhizal plants in clear cut stands belonged to the family Ericaceae (Cairney and Meharg, 2003). It was demonstrated that ericaceous understory shrubs would grow and spread rapidly following clearcutting (Mallik, 1995), supporting our result of the increased relative abundance of ericoid mycorrhizal fungi. However, we did not find greater number of ericaceous understory shrubs in the clear cut stands, which might be because only the plants with DBH $>$ 1 cm were recorded during the plot census and the understory shrubs were underestimated. Additionally, the ericaceous shrubs are typically found in nutrient poor soils as pioneers (Mallik, 1995; Read, 1996; Cairney and Meharg, 2003). Therefore, the higher relative abundance of ericoid mycorrhizal fungi might indicate that the recovery of clear cut forest stands are generally at the early stage when compared with the select cut stands. The relative abundance of ericoid mycorrhizal fungi showed significant correlations with soil nutrients content (i.e., TN, AN and TP), while the relative abundance of EcMF was markedly related to SWC and exCa. Presumably, the ericoid mycorrhizal fungi mainly helped the plants to gain major elements at early succession of the clear cut stands, whereas the EcMF played an important role in helping the plants to get more water and microelements during revegetation of the select cut stands. Although the saprotrophs predominated in all three forest stands, there was a decreasing trend in the relative abundance of saprotrophs in harvested forest stands, especially in the select cut stands (Fig. 2). This might reflect an interference relationship between saprotrophs and other functional guilds. The hypothesis of organic matter decomposition by EcMF may provide a reasonable explanation for the interference relationship between EcMF and saprotrophs in this study. Specifically, we found that the increased EcMF in the logged stands were dominated by the genus *Lactarius* and *Russula*, and these fungal taxa could grow on Petri dishes without hosts according to previous studies (Coleman et al., 1989). Although the host plants could not provide sufficient C and nutrients for mycorrhizal fungi, *Lactarius* and *Russula* could still grow. Presumable, the *Lactarius* and *Russula* taxa are more likely to be able to decompose organic matter than other taxa, consequently, these two EcMF may compete with saprotrophs for organic matter resources. Indeed, the potential decomposition ability of *Lactarius* and *Russula* taxa have been previously evidenced (Courty et al., 2007; Talbot et al., 2008), which may further support our speculation. In addition, soil N availability was proposed to play an important role in regulating competition between EcMF and saprotrophic fungi (Näsholm et al., 2013; Blaško et al., 2015). Here, the available N content was significantly lower in the harvested stands than that in the primary stands (Fig. S2), which might increase the competition between EcMF and saprotrophic fungi. Presumably, the EcMF have a greater competitive advantage, as they can obtain energy resources more quickly and easily when compared with the saprotrophic fungi (Näsholm et al., 2013). Alternatively, the increase in relative abundance of other functional guilds would compete for the living space, which might also affect the growth of saprotrophs. Nevertheless, the saprotrophic fungi group was still the most abundant functional group in the select cut stand. This was probably because the studied soils were collected from the top layer, in which the root-associated fungal communities were present at low abundance (Lindahl et al., 2007; Baldrian et al., 2012). The relative abundance of wood saprotrophic fungi, however, was highest in the clear cut stands and lowest in the primary stands, which might be caused by the massive debris of wood stems and root residuals after harvest, because these fungi had been previously observed during wood degradation (Nilsson, 1973). The increase in animal pathogens in the select cut stands probably resulted from changes in fauna abundance and composition during post-logging succession (Borgne et al., 2018).

4.2. Responses of the fungal community network to historical logging

In addition to the shifts in fungal community composition and relative abundance of functional guilds, the structure of the fungal community network and their associations with environmental properties were also altered by historical logging (Fig. 3). Different OTUs within a network were positively or negatively correlated with each other as indicated by different correlation coefficients, presenting the covariation patterns among OTU members across samples, and therefore indicating the ecological and functional relationships (Bissett et al., 2013; Menezes et al., 2014). Overall, the covariation among fungal communities increased in the fungal network in select cut stands while they decreased in the fungal network in clear cut stands. The network connectivity and average cluster coefficient were higher in the select cut stands while lower in the clear cut stands when compared with that in the primary stands. Additionally, there were more members involved in the meta-module in the select cut stands (133 nodes, accounting for 56% of total nodes) and primary stands (109 nodes, accounting for 53% of total nodes) than those in the clear cut stands (40 nodes, accounting for 15% of total nodes) (Fig. 4). This indicated that more fungal members were functionally interacting in the stands with a history of selective cutting, because the meta-module can be regarded as a group of modules functionally correlated (Langfelder and Horvath, 2007; Oldham et al., 2008). Therefore, the fungal community in select cut stands could be viewed as a better organized community, which might consequently lead to more cooperation and exchange events among members by increasing interrelated members, supporting our third hypothesis. This could be further supported by a greater number of generalists in the select cut stands (12 nodes, accounting for 5% of total nodes) than those in the primary (4 nodes, accounting for 2% of total nodes) and clear cut (5 nodes, accounting for 2% of total nodes) stands (Fig. 5). The generalists can link with the members within their own module and with those belonging to other modules (Zhou et al., 2011). Thus, the generalists likely acted as the key members that strongly drive co-variation among fungal communities in this study. A high proportion of generalists existing in a community network leads to a more ordered, stable and efficient community. Perhaps, the central goal of the connectedness among fungal members could be detected by assessing the correlations between fungal network and environmental variables. In select cut stands, the greater connectedness among fungal communities might be driven by the increased demand for soil nutrients (i.e., TP, TK, AK, exCa and exMg), as indicated by the positive correlations between module eigengenes and soil nutrients content (Table S5). However, module eigengenes were negatively associated with SWC and litter nutrients content in the select cut stands. The fungal communities might cooperate intensely to resist unpredicted water stress. Although SWC has recovered to the level of the primary forest 20–50 years after selective cutting (Fig. S2), the select cut stands might have experienced water stress during succession. The negative correlation between module eigengenes and litter nutrients content probably indicated that

litter was not the favorable nutrient resource for the growing fungal communities (i.e., mycorrhizal fungal communities). As a consequence, the litter nutrients might indirectly affect the growing fungal communities through fostering other fungi depended on litter, e.g., saprotrophic fungi. In the primary forest stands, however, the module eigengenes were mostly positively correlated with litter nutrients and aboveground biomass while they were negatively correlated with soil nutrients content, which might result from the predominance of saprotrophic fungal communities. Module eigengenes in clear cut stands were less associated with soil and litter nutrients content when compared with those in primary and select cut stands, indicating low importance of these nutrients in driving the connectivity of fungal communities. The organization of the fungal network in clear cut stands was more likely caused by niche partitioning, as more negative links (60%) among fungal communities were observed (Fig. 3). This might be the result of increased environmental heterogeneity, as plant restoration during the early stages of succession after clearcutting tends to be highly stochastic. We postulated that a history of selective cutting can improve the organization and resistance of the fungal community by intensifying the functional correlation among fungal members, whereas, a history of clearcutting will reduce the functional interaction among fungal members probably by niche partitioning.

Looking at the *Zi-Pi* plot, 50% of the generalists had unclear functional guilds in the primary stands, while 50% of the generalists in clear cut stands were identified as saprotrophic fungi, indicating the key role of the saprotroph guild in driving co-variation among fungal members in clear cut stands. In the select cut stands, except for saprotrophic fungi, two EcMF (e.g., OTU96, *Basidiomycta* Phaeocollybia and OTU156, *Basidiomycta Russula*) and one animal pathogen (e.g., OTU5300, *Basidiomycta Trichosporon*) acted as the generalists, and the functional guilds of 67% of generalists remained unclear, suggesting a high functional diversity of the community. Further, *Russula* was known as a particularly important decomposer that can facilitate mobilization of nutrients from complex organic matter (Kyaschenko et al., 2017). This might verify our speculation that the EcMF would gain C and nutrients through decomposition of organic matter to allow massive growth in the select cut stands.

It is worthy of note that half of the shared OTUs exhibited a role-shift from specialist in the primary stands to generalist in the select cut stands, but not in the clear cut stands. These species involved in role-shifts have the capacity to exhibit a novel function under certain circumstances, but the novel function must have already existed before a successful shift was initiated (Managbanag and Torzilli, 2002). Such prediction of role-shifts in some fungal species were widely documented in other studies (Lu et al., 2013; He et al., 2017). In this context, the diverse functions of many fungi might be exhibited during the recovery of selectively harvested forest stands. For example, OTU56 (unclassified *Ascomycota*) and OTU317 (phylum *Zygomycota*, genus *Umbelopsis isabellina*) belonging to P5 and P7 were detected as specialists in the primary stands (Fig. 5, Table S4). In select cut stands, they were detected as generalists and were assigned to S1 and S4, which were closely related to soil nutrients content (Fig. 5, Table S5). It was documented that *Umbelopsis isabellina* could store lipid and polysaccharide, and degrade these cellular storage materials to generate maintenance energy or to support further microbial growth when available C substrate was depleted, but other essential nutrients were sufficient (Dourou et al., 2017). They might be strongly correlated with other members in the network through energy resources after massive losses of available C substrate because of selective cutting. The metabolism of storage lipid and polysaccharide in *Umbelopsis isabellina* might not occur in the clear cut stands, because the contents of other essential soil nutrients (e.g., TK, AK and exCa) were relatively low compared with those in select cut stands (Fig. S2). The role-shifts of many fungi from specialists in primary stands to generalists in select cut stands might result in a higher functional diversity of fungal community in the select cut stands, which could make the community more stable and more resistant to environmental changes (Degens et al., 2001; Deng, 2012).

5. Conclusion

This study demonstrated that historical logging profoundly altered soil fungal community composition, guild relative abundance and the organization of the fungal network in a tropical rainforest. Moreover, the alterations of these fungal community attributes differed between the forests with a history of selective cutting and clearcutting. An increased relative abundance of phylum *Basidiomycota* and a decreased relative abundance of phylum *Zygomycota* were observed in the harvested forest stands with a 50-year's recovery compared with the primary stands. These shifts in fungal community composition were mainly related to the effects of vegetation composition, aboveground biomass and soil properties. Regarding to the functional guilds, the relative abundance of root-associated communities (i.e., ectomycorrhizal and ericoid mycorrhizal fungi) increased while saprotrophic communities decreased 50 years after logging. The enrichment of mycorrhizal communities might help the growing plants to gain soil nutrients more efficiently during forest recovery. Further, the increased relative abundance of wood saprotroph and ericoid mycorrhizal in the clear cut stand may reflect the dominance of recalcitrant organics in substrates, which may come from the massive dead stumps after clearcutting. Network analysis revealed a better organized fungal community in the select cut stands but not in the clear cut stands when compared with the primary stands. Selective cutting has caused role-shifts among fungal members, resulting in higher functional diversity of the soil fungal community during forest succession. This study conducted a comprehensive analysis of the soil fungal community in a tropical rainforest with and without logging history by combining the functional guilds with network analysis, which provided assessments on the ecological consequences for the soil fungal community caused by selective and clear cutting.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.11.005.

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