



# Interkingdom plant-microbial ecological networks under selective and clear cutting of tropical rainforest

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## ABSTRACT

Recent studies have revealed that interkingdom relationships in below-aboveground metacommunity may contribute to ecosystem functions more than species diversity. While effects of deforestation on aboveground interactions have been well studied, the responses of interactions among plant, soil bacterial and fungal communities to deforestation are poorly understood and their effects on vegetation restoration remain unknown. We sequenced soil 16S rRNA and ITS genes from the primary forest without logging history and secondary forests that had been clear cut or selective cut and left to recover for up to 50 years in the typical tropical rainforest in Hainan Island. Soil bacterial-fungal, plant-bacterial and plant-fungal associations were illustrated via ecological network analysis, and their correlations with plant composition, soil and litter properties were examined to explore the links to ecosystem functions.

A higher negative proportion of bacterial-fungal interactions was found in selective cut sites while a higher positive proportion presented in clear cut sites. The changes after selective cut was related to tree composition and reductions in nitrogen and phosphorus content from soil and litter, indicating increased competition for nutrients, decoupling of communities and niche differentiation. The bacterial-fungal interaction changes after clear cut was associated with decrease in tree biomass and soil carbon content while increase in litter carbon content, implying increased co-operation in nutrient strategies and community homogenization. This ecological implications of bacterial-fungal interaction after clear cut was also applicable to plant-microbial interaction showing modular structure and strong across-module associations and significant correlations with litter carbon and soil nitrogen availability, which was indicative of a particular collection of microbial members under given plant species driving by changes in carbon and nitrogen content. Overall, the responses of bacterial-fungal and plant-microbe interactions to selective cut may in term promote the recovery of plant diversity during forest restoration, whereas these responses to clear cut may hinder the recovery of plant community diversity, and more costly restoration approaches based on different tree species planting will be required. This study suggested that the interkingdom interactions in below-aboveground metacommunity are indicative of changes in tree composition and soil fertility during the restoration of logged forest, and changes in such interkingdom interactions could in turn influence plant diversity and soil nutrients transformation.

## 1. Introduction

Tropical rainforests harbor hyper diversity and play a significant role in global carbon (C) sequestration and nutrient cycling (Batjes and Sombroek, 1997; Harms, 2011). However, deforestation caused by

frequent tree harvest in the tropical rainforests substantially impact the ecosystem functions and has become the most common anthropogenic disturbance in forests representing one of the greatest scientific and policy concerns in tropical regions (Guillaume et al., 2015; Stoy, 2018; Franco et al., 2018). Performance of forest ecosystem functions

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primarily depends on the relationships between various macroscopic and microscopic species, including the soil microbial and plant communities (Bennett et al., 2017; Teste et al., 2017; van der Putten, 2017). Although responses of plant and soil microbial communities to deforestation have been widely investigated (Rodrigues et al., 2013; Xu et al., 2015; Gómez-Acata et al., 2016; Tian et al., 2018), little is known about logging effects on the interactions among these different kingdoms (i.e. bacteria, fungi and plants) in tropical rainforests.

Tree logging can substantially alter soil C and nutrient substrates by reducing litter and root exudate inputs (Thiffault et al., 2011; Ismaw et al., 2012), which may indispensably affect the below and above-ground interkingdom interactions. In addition, the changes of such interactions may depend on logging intensity, as different intensity exert different effects on soil environments and vegetation community. For instance, clear cut of tropical forests can cause greater decrease in soil available nitrogen (N) and available phosphorus (P) than selective cut (Ding et al., 2016), which may trigger the mutualistic bacterial-fungal and plant-microbial associations and consequently increase their co-operation in nutrient strategies. Selective cut usually cause large canopy gaps and may permit greater penetration of direct solar radiation, higher precipitation throughfall, and higher air temperatures, which consequently provide opportunities for abundant understory species (Gatti et al., 2015). Thus the selective cut forests may have a higher plant diversity and greater environmental variability than the clear cut ones, which probably induce more antagonistic microbial interkingdom interactions and increase complex of plant-microbial associations. Overall, clear cut is expected to cause greater losses in soil nutrients, vegetation cover and plant diversity than selective cut (Heinrichs and Schmidt, 2009; Qin and Wang, 2018; Guillaumer et al., 2015), but whether the clear cut shows different impacts on below-aboveground interkingdom interactions compared to selective cut remains unknown.

The bacterial-fungal interkingdom interactions play a pivotal role in regulating biogeochemical processes and hence are important for plant nutrients acquisition (Deveau et al., 2018; Wagg et al., 2019). Fungi-derived metabolites and the substrate resources explored by fungal mycelium can increase C availability for bacteria while the bacteria provide fungi with essential nutrients, such as N and P (Rudnick et al., 2015; Purahong et al., 2016; Deveau et al., 2018). These mutualistic associations between bacteria and fungi can increase the plant access to available nutrients via promoting nutrients cycling and accelerating nutrients transportation through fungal hypha. The negative bacterial-fungal interactions, however, may affect nutrient availability by modifying the surroundings, such as soil pH (Bignell, 2012) and dissolved oxygen level (Lambooij et al., 2017). Except for the microbial interkingdom interactions, the complex plant-microbe associations also have a crucial contribution to nutrient transformation, plant nutrition acquisition and resource competition (Kenrick and Strullu-Derrien, 2014; Lau et al., 2017; Fitzpatrick et al., 2018), and thus affect plant species coexistence and ecosystem service. For example, plant species can form mutualistic interactions with certain bacteria involved in N and P cycling, such as the rhizobia and phosphomonoesterase encoding bacteria, aiming to adapt to N and P limitations (Mirza et al., 2014; Sugiyama, 2019; Wei et al., 2019). Ectomycorrhizal fungi can interact with plants mainly by transferring nutrients to their hosts (van der Heijden and Horton, 2009; Bennett et al., 2017). Soil pathogenic fungal-plant associations could mediate neighborhood interactions by regulating plant demography and community structure (Liang et al., 2020), which may play an important role in maintaining species diversity. Obviously, the bacterial-fungal and plant-microbial interkingdom interactions can serve as important regulators of soil nutrients availability and vegetation assemblage. Tree logging can cause losses of forest ecosystems services, such as carbon sequestration, nutrient cycling and biodiversity conservation (Thiffault et al., 2011; Ismaw et al., 2012). However, whether the changes in these ecosystems services could be reflected by shifts in bacterial-fungal and plant-microbial interkingdom interactions, and to what extent such interkingdom interactions can

regulate these ecosystems services during restoration of logged forests, remain elusive.

Various soil microbial and plant species interact with each other to eventually form complex networks in forest ecosystems (Zhou et al., 2011; Toju et al., 2014). Ecological co-occurrence network analysis have been suggested as a powerful way to depict the intricate interactions among microbial communities and plant species (Deng et al., 2012; Durán et al., 2018; Feng et al., 2019). Soil bacterial and fungal networks have been separately analyzed to understand the microbial responses to disturbance, including precipitation changes, CO<sub>2</sub> enrichment, land use change, and agriculture practices (Boswell et al., 2007; Zhou et al., 2011; Lu et al., 2013; He et al., 2017). However, the properties of bacterial-fungal interkingdom network in protected and disturbed ecosystems are rarely investigated. Although previous studies have compared the properties of plant-microbe interkingdom ecological networks in different forest types, and addressed the importance of such networks in driving community assembly, diversity and stability in forest ecosystems (Toju et al., 2014; Feng et al., 2019), the responses of plant-microbe networks to forest logging and their potential links to the responses of plant structure remain unclear.

In this study, we constructed the soil bacterial-fungal and plant-microbe interkingdom networks using ecological survey data of plants and microbial sequencing data sets from a protected, primary tropical rainforest intermixed with patches regenerated naturally after clear cutting or selective cutting in Hannan Island, China. The features of network architecture for the clear cut and selective cut sites were summarized and compared to that for the primary forest, and the correlations of network features with plant structure as well as soil and litter nutrients content were examined to address the following questions: (a) What are the specific responses of below-aboveground interkingdom interactions to previously clear cut and selective cut in a tropical rainforest? (b) What are the ecological implications of the changes in these interkingdom interactions?

## 2. Materials and methods

### 2.1. Study site

The study was conducted in the montane tropical rainforest area in the Jianfengling forest reserve (JFR) in Southwest Hainan Island, China (18°23'–18°50' N and 108°360'–109°05' E). The study site ranges in terms of mean annual precipitation from 1000 to 3600 mm and mean annual temperature from 19.4 °C to 27.3 °C, and represents a typically tropical monsoon climate with a dry season from November to April and a wet season from May to October. The soil type is classified as yellow latosol according to FAO. The studied forest has a total area of 160 km<sup>2</sup>, which has been partially disturbed around 50 years ago, either by selective cut or by clear cut. Under the regime of selective cut, mature stems with a diameter at breast height (DBH) > 40 cm were harvested regardless of species. Nowadays, the study area presents an undisturbed primary forest intermixed with patches of secondary forest stands (Fig. S1), and the previously forest logging methods were recorded by the Jianfengling forest bureau.

Sixty-one quadrats (25 m × 25 m) which cover the patches of previously selective cut and clear cut were established in the study area (Fig. S1), resulting in 19, 25 and 17 quadrats in the primary, selective cut and clear cut sites, respectively. All the woody stems with DBH > 1 cm were recorded and identified to species, thereafter the species diversity (Shannon-Wiener index), vegetation biomass (veg-biomass) as well as species richness were determined in each quadrat. The veg-biomass was calculated from the stems, branches, leaves and roots of the woody individuals with a DBH > 1 cm. The important values (IV) of species in both tree layer (DBH ≥ 5 cm) and understorey (DBH < 5 cm) were calculated to detect the dominant species (supplementary data). We also did a principle component analysis (PCA) on species abundance matrix and extracted the first three component axes (explained >50% of

the total variation in species composition) as new variables (e.g., veg-PC1, veg-PC2 and veg-PC3) for plant composition. These new variables were applied to examine the correlations between plant composition and microbial attributes.

## 2.2. Litter sampling and analyses

During the dry season (from November to April), litter from the soil surface was collected in each quadrat at five locations, with four locations at the corners and one at the center. These subsamples were then mixed to form one composite sample per quadrat, yielding a total of 61 litter samples. All litter samples were dried in an oven at 65 °C until a stable weight and ground into powder before analyses. Litter C was measured using dry combustion method, and litter N was determined by the Kjeldahl method. Litter P and potassium (K) content were detected using the digestion method (Mctiernan et al., 1997), and litter pH was measured in litter/water (2:32, V/V) suspension by a pH meter (UB-7 pH/ev Meter; Denver Instrument).

## 2.3. Soil sampling and physicochemical analyses

Soil sampling was conducted at the same time with litter collection by collecting five randomly distributed cores (diameter: 5 cm) from the top layer (0–10 cm), and then mixed thoroughly per quadrat. After discarding fine roots, leaves, and stones, the soil was sieved through a 2 mm mesh and immediately transferred to the laboratory using an ice box. Part of soil sample was stored at –80 °C for microbial analyses, and the other part was stored at 4 °C for soil physicochemical analyses.

Soil bulk density (BD) was determined by drying an intact fresh soil core with known volume and weight at 105 °C for 24 h, and soil water content (SWC) was calculated as the mass loss of soil after drying. Soil pH was measured using a pH meter with soil/water suspension (1: 2.5, w/w). Soil total carbon (TC) and total nitrogen (TN) were analyzed on a Shimadzu TOC/TN Analyzer ((Model TOC-VCSH, Shimadzu, Kyoto, Japan). Soil total phosphorus (TP) and total potassium (TK) were measured using the ascorbic acid colorimetric and atomic absorption methods, respectively. Soil available nitrogen (AN) was detected by alkaline hydrolysis distillation method described by Liu et al. (1996). Soil available phosphorus (AP) was determined using the molybdate-blue colorimetry method after extracted with NaHCO<sub>3</sub>. Soil was extracted with ammonium acetate; thereafter the extract was loaded on an atomic absorption spectroscopy (iCE 3000, Thermo Scientific, MA, USA) to measure available potassium (AK), exchangeable calcium (exCa) and magnesium (exMg).

## 2.4. Soil DNA extraction, sequencing, and processing

Soil DNA was extracted from 0.5 g fresh soil with the PowerSoil® DNA Kit (MoBio, Carlsbad, CA, USA) according to the manufacturer's instructions. The DNA concentration and quality were determined using a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific Inc., USA). The V4 region of bacterial 16S rRNA gene was amplified using the primers 515F 5'-GTGCCAGCAGCCGCGGTAA-3' and 806R 5'-GGACTACHVGGGTWTCTAAT-3' with attached barcode (Caporaso et al., 2012), and the ITS1 region of fungal rRNA gene was amplified using the primers ITS2 5'-GCTGCGTCTTCATCGATGC-3' and ITS5 5'-GGAAAGTAAAAGTC GTAACAAGG-3' with attached barcode (Bellemain et al., 2010). The PCR reaction was performed on a BioRad S1000 thermal cycler (Bio-Rad Laboratory, CA, USA) in triplicate, afterwards the PCR products were purified using a DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA) and then mixed in equimolar ratios before sequencing. High-throughput sequencing of 16S rRNA and ITS gene amplicons were performed on an Illumina HiSeq platform (PE250) by the MAGIGEN Company (Guangzhou, China).

Raw sequences were loaded on the Quantitative Insights into Microbial Ecology (QIIME) pipeline (version 1.17) for quality check and

were assigned to samples based on corresponding barcodes. The sequences with an average quality score  $\leq 20$  or containing ambiguous base calls were discarded (Caporaso et al., 2012). The remaining high quality sequences were clustered based on 97% similarity cutoff using UPARSE (Edgar et al., 2013) (version 7.1 <http://drive5.com/uparse/>) to generate the operational taxonomic units (OTUs). Taxonomy information of bacterial OTUs was assigned using the Ribosomal Database Project (RDP) classifier (<http://rdp.cme.msu.edu/>), and the fungal OTUs were assigned taxonomic information using the UNITE 7.1 database (Abarenkov et al., 2010). Moreover, we assigned each fungal genus, family, or order to functional groups using the online FUNGuild pipeline (Nguyen et al., 2016), and the obtained functional composition has been explicitly described in a previous study (Chen et al., 2019).

## 2.5. Soil bacterial-fungal network analysis

Three bacterial-fungal networks were constructed in this study, separately representing the primary forest, previously selective cut and clear cut forests. The OTU tables of bacteria and fungi were merged into one OTU table. Construction and analysis of network were performed using the Molecular Ecological Network Analyses Pipeline (<http://ieg4.rccc.ou.edu/mena/main.cgi>) according to the approach described by Zhou et al. (2011) and Deng et al. (2012), with six steps. (1) Square root-transformation of the OTU table and preparation of the OTU annotation and environmental files. (2) Construction of network using the OTUs that appeared in >80% of all samples based on the automatically generated pair-wise similarity threshold (st.). (3) Conducting network analyses to get the general properties, such as average degree (connectivity), average path distance, average clustering coefficient, module number, and modularity. The network module represents a group of nodes (OTUs) that are highly interconnected with each other relative to the nodes outside the group. Modularity is the assessment of how well a network is divided into modules. Clustering coefficient means the tendency of neighbors of a node to connect with each other. Path distance is the shortest path length between any two nodes' connections (Deng et al., 2012). The among-module connectivity (Pi) and within-module connectivity (Zi) were combined to evaluate the topological role of each node (Guimera and Amaral, 2005). Briefly, the nodes with Zi > 2.5 are module hubs that highly connect with the nodes within modules; the nodes with Pi > 0.62 are connectors that show a densely connection with nodes in other modules; the nodes with Zi > 2.5 and Pi > 0.62 are network hubs representing the highly connected nodes within the entire network; and other nodes with Zi < 2.5 and Pi < 0.62 are peripherals that indicate the interconnected nodes in module with few connections outside the module. (4) The network structures were randomized by keeping the nodes degree constant, and relationships between modules and environmental variables were examined. (5) Network was visualized in Cytoscape (<http://manual.cytoscape.org/en/stable/>).

## 2.6. Plant-microbe network construction

Construction of plant-microbe interkingdom networks was performed on a Galaxy-based analysis pipeline (interdomain ecological network analysis pipeline, IDENAP, <http://mem.rcees.ac.cn:8081>) (Feng et al., 2019). Briefly, a plant community table filled with the species abundance of individuals with DBH > 1 cm at each sampling site was prepared, and all the measured soil and litter properties were included in an environmental table. Afterwards, the plant community tables were filtered to keep the species that were recorded in over half of the sampling plots considering the low observed richness of plant species per quadrat and homogeneity of plant communities across the three forest types (see supplementary data and Table S1). The bacterial and fungal OTU tables were separately filtered to retain the OTUs appeared in >80% of the total samples. The filtered tables were used for calculation of pairwise correlations between plants and microorganisms based on the Sparse Correlations for Compositional data (SparCC)

method which estimates the linear Pearson correlations between the log-transformed components (OTUs and plant species) based on the following assumptions: (i) the number of different components is large, and (ii) most components are not strongly correlated with each other (Friedman and Alm, 2012). Plant-microbe interkingdom networks were then constructed with the threshold value of 0.30 to filter the non-correlated associations. Network analyses were accomplished by calculating the topological properties including connectance, web asymmetry, compartment number, clustering coefficient, nestedness, specialization asymmetry, module number, and modularity. Connectance was defined as the ratio of observed links to the potential links between the microbes and plants (Dunne et al., 2002). Web asymmetry is the network topological property used to judge the numbers of plant and microbial species that interact with each other, with positive values suggesting more plant species in the network, whereas negative values indicating more microbial species (Feng et al., 2019). The compartments are sub-sets of the bipartite matrix containing a set of species that are not connected to another compartment's species. Nestedness and weighted nestedness were used to evaluate the nested structure of observed networks, with low nestedness value (0) and high weighted nestedness value (1) indicating a perfect nested structure while high nestedness value (100) and low weighted nestedness value (0) indicate on a chaotic structure (Rodríguez-Gironés and Santamaría, 2006; Galeano et al., 2009). Specialization asymmetry shows the ratio of specialization of plant species to microbial species (Blüthgen et al., 2006). In this study, both the plant-bacteria and plant-fungi networks as well as their positive and negative subgraphs were analyzed.

## 2.7. Statistical analysis

The data sets of bacterial and fungal OTU tables, plant composition, soil and litter properties under the three forest managements were prepared prior to statistical analysis. The normality (Kolmogorov-Smirnov test) of each soil and litter properties were tested, and the variable was log-transformed if necessary. Difference of soil bacterial and fungal community structure among the three forest types were examined using three complementary non-parametric multivariate statistical tests: permutational multivariate analysis of variance (PERMANOVA), analysis of similarity (ANOSIM) and multiple response permutation procedure (MRPP) with 1000 permutations (Guo et al., 2018). All the three multivariate statistical tests were performed on Bray-Curtis dissimilarities matrix of the OTU tables. Variance partitioning analysis were conducted based on the redundancy analysis (RDA) with bacterial and fungal OTU tables and environmental variables, aiming to partition the variance in bacterial and fungal community structures into effects of vegetation, soil and litter properties. Significance of the correlations between microbial community structure and environmental properties during RDA analysis was tested via the function “envfit” in R 3.5.0 (R Core Team, 2018). All the analyses were realized with the “vegan” (Oksanen et al., 2013) package in R.

## 3. Results

### 3.1. Bacterial and fungal community composition and the influential factors

A total of 1,706,371 high quality bacterial sequences and 2,332,267 high quality fungal sequences were obtained from all samples collected in the primary, previously selective cut and clear cut forests. The fungal phylum Basidiomycota and class Tremellomycetes had a higher relative abundance in both selective cut and clear cut sites, whereas the relative abundance of phylum Mucoromycota and class Zygomycota in both selective cut and clear cut sites was lower than that in primary forest. The highest relative abundance of fungal class Eurotiomycetes presented in the selective cut sites (Fig. S2b, c). Both selective cut and clear cut increased the OUT number of fungal class Tremellomycetes, while

reduced the OUT number of fungal class Zygomycota (Fig. S2f). In contrast, the relative abundance of dominant bacterial phyla as well as their OTU richness was constant after selective cut and clear cut (Fig. S2a, d). Approximately 82% of the total bacterial OTUs (10451) and 56% of the total fungal OTUs (10032) were shared either by all three forest types or by any two of them (Fig. S3), indicating that the fungal community had a greater variation across the forest types than bacterial communities.

The fungal community structure in primary forest was significantly different from that in selective cut and clear cut sites, as indicated by the three non-parametric multivariate statistical tests (PERMANOVA, ANOSIM, and MRPP). In contrast, all the three types of forests had similar bacterial structure (Table 1). Including all samples in the analysis, 37.2% of the total variation in bacterial community structure and 52.8% of the total variation in fungal community structure were explained by environmental variables. Soil properties contributed to the highest portion of variance (19.2–29.8%), followed by litter nutrients content (8.2–14.9%) and vegetation features (7.2–8.4%) (Fig. S2e, f and Table S2).

### 3.2. Soil bacterial-fungal ecological networks

The bacterial-fungal networks for both selective cut and clear cut forests had 12–18% more nodes and 8–33% more links than the primary forest, indicating increased complexity in microbial interactions due to previously logging (Table 2, Fig. S4). The networks in previously selective cut sites had the highest connectivity and clustering coefficient, while those in previously clear cut sites had the largest path distance and average geodesic distance (Table 2). Moreover, a greater modularity was observed in the networks from both selective cut and clear cut forests, indicating a more modular structure. In the three bacterial-fungal networks, >98% of the nodes acted as peripherals that interlinked mostly inside the modules (Fig. S5). Only three bacterial nodes in each the primary, selective cut and clear cut network and one node in the clear cut network were grouped into the connectors while a total of 16 bacterial nodes acted as module hubs. In the primary forest, 38% of the key bacterial taxa were assigned to Acidobacteria, and 25% were identified as members of Proteobacteria. >60% of the key bacterial taxa in the selective cut forest were identified as Acidobacteria and Verrucomicrobia, whereas >75% of the key bacterial taxa in the clear cut forest was categorized as Proteobacteria and Planctomycetes (Fig. S5). Only four nodes of fungi (all assigned to phylum Ascomycota, class Eurotiomycetes, order Chaetothyriales, family Herpotrichiellaceae) were assigned as connectors and module hubs in selective cut and clear cut forests.

### 3.3. Bacterial-fungal interactions and their links with environmental factors

A higher proportion of negative bacterial-fungal links (49%) was observed in the selective cut forest compared to the primary (17%) and clear cut forests (14%). The positive bacterial-fungal links increased from 83% in the primary forest to 86% in the clear cut forest (Fig. 1).

Since these bacterial-fungal links distributed in various network modules (Fig. 1), we tested the correlations between these modules and each environmental variable to explore the potential ecological implications of such links. The bacterial-fungal interaction modules in the primary forest (i.e., M1, M2, M3, and M4; Fig. 1) showed a significantly negative correlation with soil BD, and positive correlations with soil available N, total P, and available P. In previously selective cut forest, however, the modules had significant correlations with nearly all the measured environmental properties, and half of these modules (i.e., M4, M5, M6, and M7) were negatively associated with soil pH and exCa content while positively related to vegetation biomass, soil C:N ratio, soil C and litter C content (Fig. 1). In clear cut forest, the bacterial-fungal linkage modules showed positive correlations with veg-biomass, litter



**Table 1**

Significance tests of the difference of soil microbial community structure among the primary, previously selective cut and previously clear cut forests. Significant *P* values (<0.05) are shown in bold.

Microbial community	Forest type	PerMANOVA <sup>a</sup>		ANOSIM <sup>b</sup>		MRPP <sup>c</sup>	
		F	P	R	P	δ	P
Bacteria	Primary vs Selective cut	1.095	0.334	0.001	0.424	0.001	0.341
	Selective cut vs Clear cut	1.399	0.129	0.006	0.393	0.003	0.287
	Primary vs Clear cut	1.041	0.371	-0.002	0.454	-0.003	0.601
Fungi	Primary vs Selective cut	2.198	<b>0.012</b>	0.113	<b>0.007</b>	0.023	<b>0.011</b>
	Selective cut vs Clear cut	1.244	0.164	-0.002	0.496	-0.003	0.637
	Primary vs Clear cut	2.942	<b>0.002</b>	0.173	<b>0.001</b>	0.024	<b>0.013</b>

<sup>a</sup> Permutational multivariate analysis of variance.

<sup>b</sup> Analysis of similarity.

<sup>c</sup> Multiple response permutation procedure.

**Table 2**

Comparisons of the properties of soil bacterial-fungal interkingdom ecological networks among the primary, previously selective cut and previously clear cut forests. The properties from both Empirical and Random networks were presented. The significant differences between “Observed” and “Random” networks (Student’s *t*-test, *P* < 0.05) were indicated by superscript letter “\*”.

	Primary	Selective cut	Clear cut
<b>Empirical network</b>			
Similarity threshold	0.800	0.800	0.800
Original OTU number (Fungi + Bacteria)	1348(472 + 876)	1313(497 + 816)	1124(346 + 778)
Total nodes	458	539	514
Total links	743	988	800
Total bacterial-fungal links	18	41	51
R <sup>2</sup> of power-law	0.915	0.894	0.923
Average connectivity	3.245	3.666	3.113
Average clustering coefficient	0.209*	0.257*	0.175*
Average path distance	5.768*	6.418*	7.391*
Average geodesic distance	4.439*	5.130*	5.880*
Modularity (module number)	0.739(79)*	0.778(66)*	0.784(75)*
<b>Random network</b>			
Average clustering coefficient (SD)	0.014(0.004)	0.014(0.004)	0.012(0.003)
Average path distance (SD)	4.393(0.059)	4.373(0.046)	4.623(0.061)
Average geodesic distance	3.957(0.045)	3.961(0.032)	4.158(0.041)
Modularity (SD)	0.580(0.006)	0.538(0.005)	0.604(0.006)

and soil C content while negative correlation with soil pH (Fig. 1).

### 3.4. Properties for plant–microbe ecological networks

In each of the primary, selective cut and clear cut forests, an average of 64 plant species and 225 bacterial OTUs were chosen to construct the plant–bacteria network and an average of 52 plant species and 72 fungal OTUs were selected to construct the plant–fungi network (Table S3). This result combined with the average web asymmetry of -0.559 for plant–bacteria network and -0.161 for plant–fungi network indicated skewed pattern for plant and microbial nodes in the plant–bacteria network (Table S3). The specialization asymmetry of plant–bacteria network was higher than that of the plant–fungi network, suggesting higher preference of fungi than bacteria to specific plant species (Fi. 2). Both the positive and negative subgraphs showed consistent low nested structures, low specialization asymmetry, and consistent modularity compared to the entire plant–microbe networks (Tables S3–S5).

The nestedness and modularity of both the entire networks and subgraphs were decreased due to previously selective cut and increased by previously clear cut (Tables S3–S5). In addition, deforestation reduced the specialization asymmetry of plant–microbe networks (Fig. 2), indicating an increase in the specialization of plants to soil microbes after tree cutting. Correlation analyses were conducted to explore the relationships between environmental variables and plant–microbe network properties either from the entire networks or from the subgraphs. Overall, litter C content was negatively related to

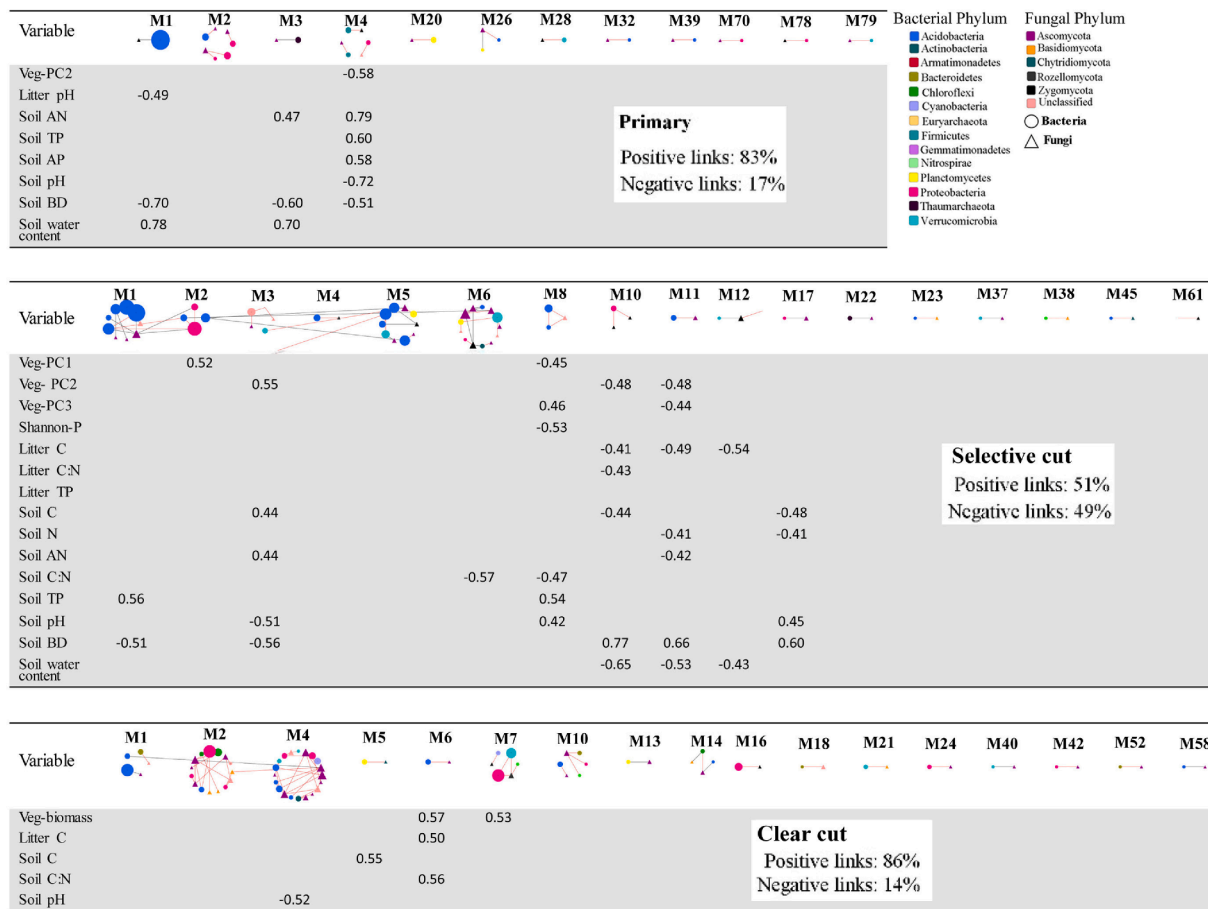
nestedness and positively related to modularity of plant–microbe networks (Fig. 3a–d). Specialization asymmetry was positively correlated with soil available N content and vegetation biomass (Fig. 3e–h).

## 4. Discussion

Clarifying the responses of interkingdom interactions in below-ground communities to different logging practices can help us explore the underlying mechanisms that drive the shifts of forest ecosystem functions under logging, given the strong links of such interkingdom interactions to nutrient transformation and plant regeneration. Practice of clear cutting is known to cause severe impacts on plant diversity, soil fertility and environmental quality (Heinrichs and Schmidt, 2009; Qin and Wang, 2018), which consequently influence ecosystem function and hinder the forest recovery. Selective logging, to some extent, retain the forest structure, can result in a relatively fast forest recovery rate of community structure and ecosystem function (Zang et al., 2010). Differing from previous studies mainly focused on the responses of plant structure, soil nutrients content or soil microbial attributes to the two logging practices, this study at the first time characterized the responses of soil bacterial-fungal and plant–microbe interactions to selective cut and clear cut, which will improve our understanding of different logging effects on the plant–microbe-soil continue and help us find appropriate forest management strategies that can not only ensure timber harvest, but also maintain forest sustainability.

### 4.1. Previously logging practices show greater effects on soil fungal community than bacterial community

Previous studies showed marked shifts of soil bacterial community structure after logging in Amazon and Borneo tropical forests, and demonstrated significant contributions of soil properties changes to bacterial structure shifts (Marsh et al., 2009; Lee-Cruz et al., 2013; Gómez-Acata et al., 2016). Here we found bacterial community structure in both selective cut and clear cut forests was similar with primary forests sites after 50 years’ naturally recovery. The inconsistent results might be that in the other studies the logged forest were converted to pasture, crop or plantations (Lee-Cruz et al., 2013; Gómez-Acata et al., 2016) while here after the logging, soils were left without active management. Moreover, majority of the soil properties, which has been identified as the main factor affecting soil bacterial community (Högberg et al., 2007; Guo et al., 2018), also showed a recovery trend in both selective cut and clear cut forest sites (Table S1). Unlike bacteria, the fungal community structure in selective cut and clear cut sites differed significantly from that in primary sites, indicating a lag of recovery compared to bacterial community. The more intimate link between fungi and plant community and slower growth dates may lead to a slower recovery in fungal community after removal of trees (Hannula et al., 2019).



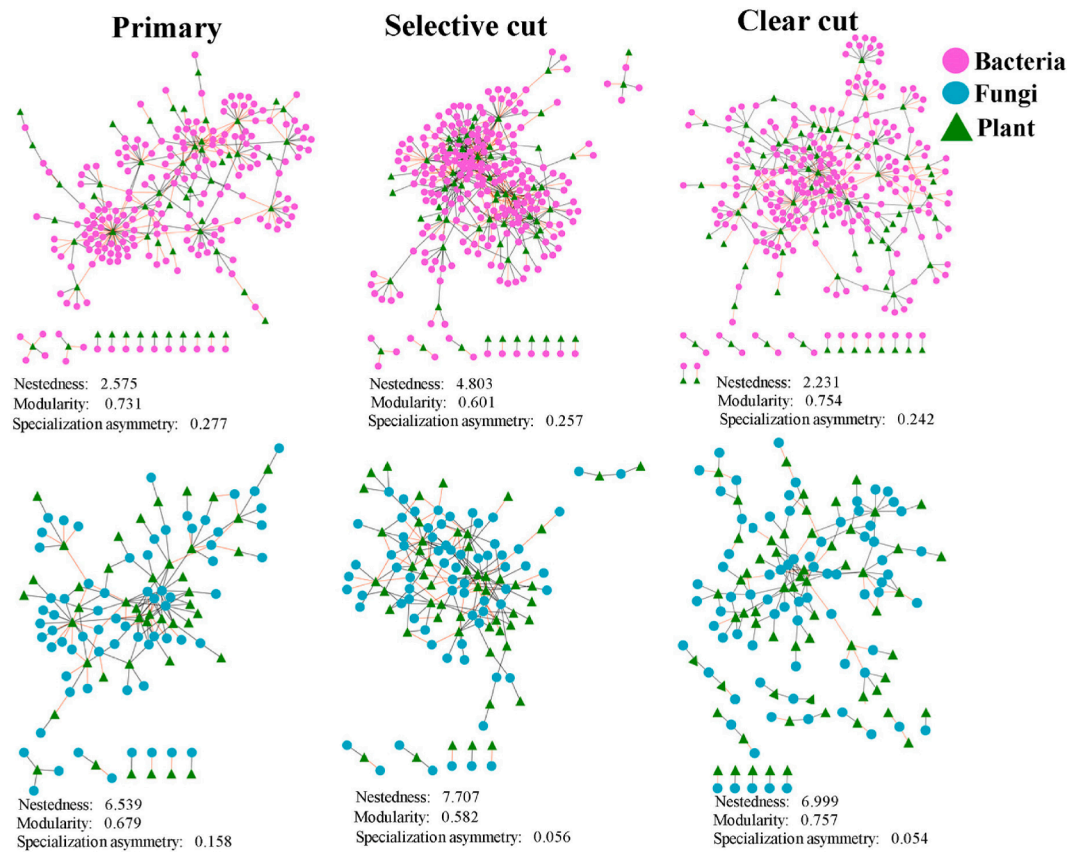
**Fig. 1.** The network modules (M) that are characterized by bacterial-fungal interactions and the correlations between these modules and environmental variables in the primary, selectively cut and clear cut forests. Node color indicates the phylogenetic affiliation of OTUs, and the node size is proportional to the number of connections (i.e., degree). The black and red edges indicate positive and negative interactions between the target bacterial and fungal OTUs, respectively. The portion of positive and negative bacterial-fungal interactions in each forest is presented at the lower right corner of the panel. The variables showed significant correlations with network modules were presented and the correlation coefficients (r) were provided. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**4.2. Effects of previously logging practices on soil bacterial-fungal interactions**

Given that the interactions among different microbial kingdoms may contribute to soil functions more than one kingdom alone, exploring the shifts in bacterial-fungal interkingdom interactions after tree logging may provide new insights into microbial assembly patterns and impacts on soil-associated functions (Ma et al., 2016). Our findings showed that previously selective cut increased negative bacterial-fungal interactions while previously clear cut increased positive bacterial-fungal interactions. Tree logging generally causes substantial decrease in soil C and nutrients (e.g., N, P, and K) resources (Guillaume et al., 2015) through reducing litter and root exudates inputs. This could increase competition among microbes (Pion et al., 2013; Ballhausen and Boer, 2016). Previous studies have observed increased competition within fungal guilds in response to decreased C and nutrients resources, for instance mycorrhizal and saprotrophic fungi or mycorrhizal and pathogenic fungi, and demonstrated potential effects of these fungal antagonisms on nutrients availability for plants (Gadgil and Gadgil 1971; Bödeker et al., 2016; Chen et al., 2020). In this study, we found a strong negative relationship indicating of competition for resources between saprotrophic fungi and bacterial community in selective cut sites (Fig. 4). According to Deveau et al. (2018) and Ballhausen et al. (2016), the negative relationships between bacteria and fungi can lead to lysis of fungal cells by bacteria or modulations of environmental pH and oxygen

level by fungi, which are important in habitat modification and nutrient cycling and consequently the plant growth. Our results support this theory and we show that in selective cut sites the bacterial-fungal interactions are linked to abiotic parameters such as pH, soil water content, soil and litter C, N, P content and to biotic parameters such as tree composition (Fig. 1). Differing from previous studies only focusing on fungal community, this study illustrated competition for resources between interkingdom microbial communities, providing us better understanding of the mechanisms under soil microbial competitions in low nutrient conditions. On the other hand, this also implies that the increased negative bacterial-fungal interactions seen as increased competition between saprotrophic fungi and bacteria in selective cut forests would have potential effects on the regulations of soil physical conditions, nutrients content and plant regeneration (Fig. 5).

The increased proportion of positive bacterial-fungal interactions caused by previous clear cut can be interpreted as increased collaboration or release from competition between bacteria and fungi, mainly due to habitat sharing, resource exchange, and cooperation for the acquisition of nutrients (Deveau et al., 2018). The Burkholderia, for example, a species of bacteria often associated with fungi and having the ability to utilize fungal secreted metabolites as C substrate and overcome fungal defense (Stopnisek et al., 2016), were found to be involved in bacterial-fungal interactions and identified as a key group in bacterial-fungal interkingdom network only in the clear cut sites. These bacteria presumably improve their survival by gaining C from the fungi or through



**Fig. 2.** The interkingdom network architecture of plant-bacteria network (a, b, c) and plant-fungi network (d, e, f) in the primary, previously selective cut and previously clear cut forests. Each node represents a microbial OTU or plant species, and the black and red edges indicate positive and negative relationships between the two target nodes, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

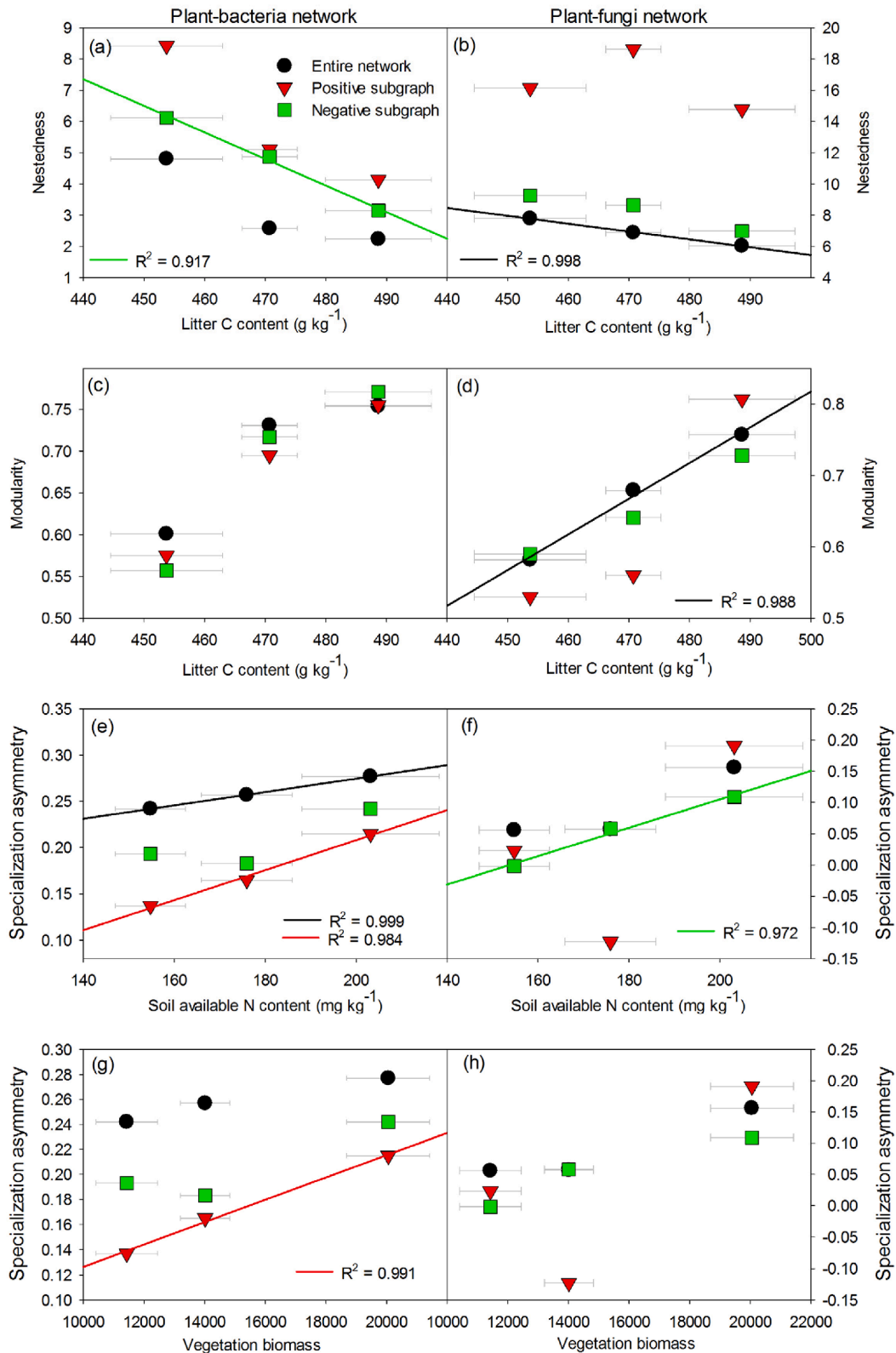
actions of fungi instead of the soil. Considering the fungal guilds, the proportion of positive associations of bacteria with mycorrhizal and pathogenic fungi was increased while that with saprotrophic fungi was decreased (Fig. 4). One possible reason was the increased relative abundance of mycorrhizal and pathogenic fungi while decreased relative abundance of saprotrophic fungi due to tree logging according to a previous study in the same sites (Chen et al., 2019). Decrease in saprotrophic fungi could result in lower litter decomposition rate and thus reduce the soil C availability to bacterial communities (Purahong et al., 2016). This may consequently promote the mutual associations of bacteria with other guilds, for instance mycorrhizal and pathogenic fungi. Another reason could also be that saprotrophs still need to compete for resources with bacteria while mycorrhizal and pathogenic fungi might relay on bacteria for C resources with the removal of hosts (Deveau et al., 2018). The overall shifts from bacterial-saprotrophic fungi associations to bacterial-mycorrhizal and bacterial-pathogenic fungi associations may enhance plant community productivity and ecosystem C sequestrations, as indicated by the positive correlations of bacterial-fungal links with vegetation biomass and total C content in soil and litters (Figs. 1 and 5).

#### 4.3. Responses of plant-microbe associations to previously logging practices

Comparing with the interactions between plants and root associated fungi in previous studies (Toju et al., 2014; Toju et al., 2015; Toju et al., 2016), the plant-fungi networks in this study showed high levels of nestedness. Presumably the fungal communities in this study were extracted from bulk soil, which show less direct associations with plants. This further confirms the finding that nestedness is a common pattern in

the non-symbiotic mutualistic bipartite networks (Guimarães et al., 2007). The plant-bacteria networks, however, displayed comparable nested structure with that of the previous studied networks (Feng et al., 2019). The nestedness and modularity of plant-microbe interkingdom networks were decreased in previously selective cut sites, indicating a modular structure of plant-microbe associations after forest clearance (Fortuna et al., 2010). Moreover, for the first time we demonstrate a significantly positive correlation between litter C content and modularity of plant-fungal networks (Fig. 3c-d). We speculate that separations of different plant and soil fungal nodes into several ecological assemblies exhibited modular structure may lead to higher C sequestration in litters and hence affect ecosystem C cycling.

Another notable change in plant-microbe associations caused by previously selective cut and clear cut was the decreased specialization asymmetry (Tables S4 and S5, Fig. 2), in particular in the plant-fungi networks, suggesting an increased generalization while decreased specification of soil microbes in relative to their plant partners. This change was closely linked to the reduction in soil available N content (Fig. 3e-f), reflecting the feedbacks of plant-microbial communities to N losses. Soil available N content showed a significant relationship with specialization asymmetry from the positive not negative subgraph of the plant-bacterial network (Fig. 3e), which indicate an increase in the mutualism relationships between plants and bacteria. The plant community may shift to contain more plants with symbiotic bacteria or regulate their associated bacteria towards a mutualistic community with the function of N fixation or organic N mineralization (Llado et al., 2017), aiming to cope with soil N reduction. In the plant-fungal network, however, a significant decrease in specialization asymmetry with reduced available N was observed in the negative subgraph (Fig. 3f).



**Fig. 3.** Linear regressions between plant–microbe interkingdom network features and environmental variables. (a, b) Regression between the value of nestedness and litter C content, (c, d) Regression between modularity and litter C content, (e, f) Regression between asymmetry and soil available N content, and (g, h) Regression between asymmetry and vegetation biomass. The regression analysis was separately conducted on entire networks and their positive and negative subgraphs. Each dot indicate a value derived from the network in primary, selective cut or clear cut forest, and the grey error bars indicate the standard errors of the mean value of environmental variable in each forest. Only the regression lines significant at  $p < 0.05$  were presented.



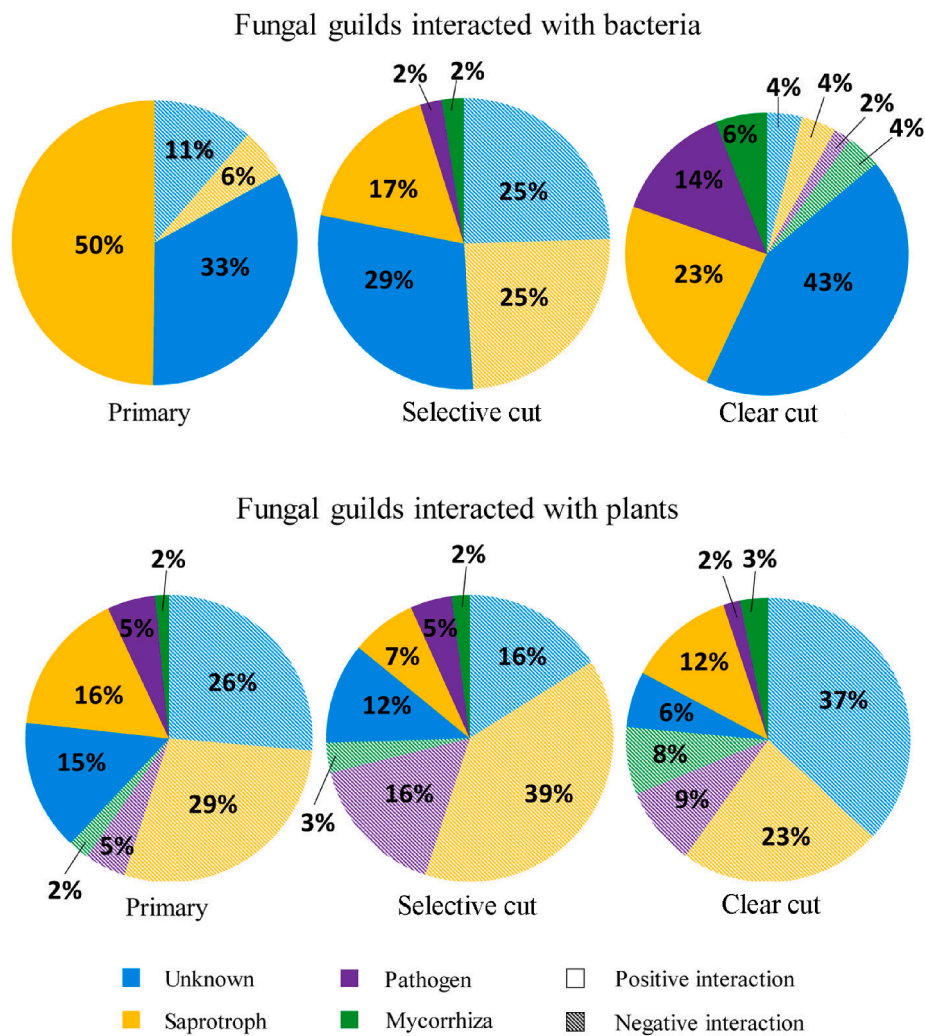


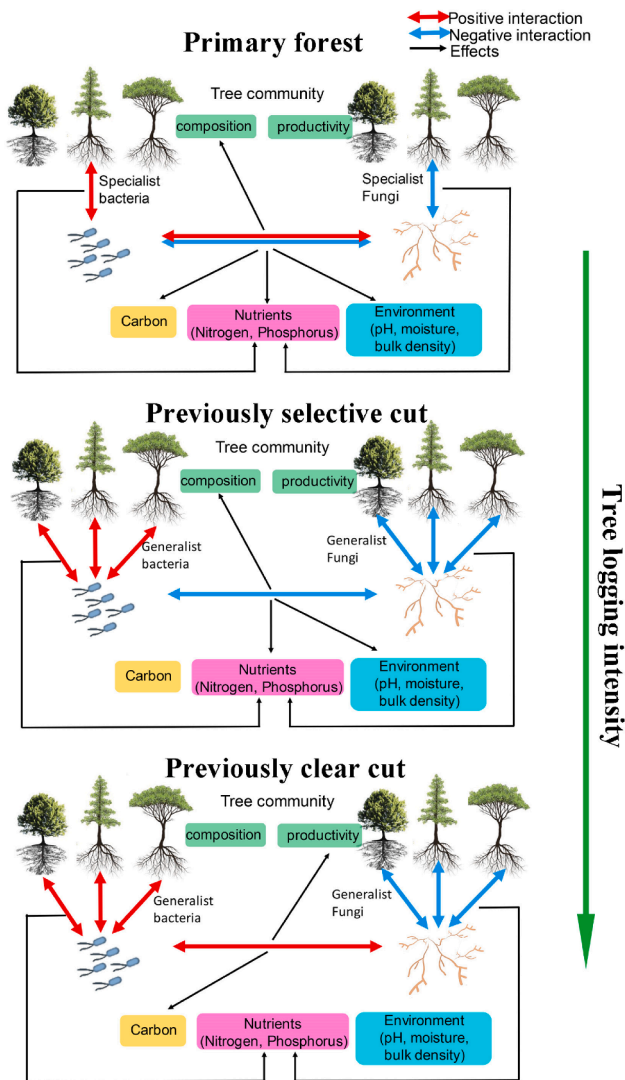
Fig. 4. The proportion of different fungi guilds involved in bacterial-fungal and plant-fungi interactions. The proportions of pathogenic fungi, saprotrophic fungi and mycorrhizal fungi associating with bacteria or plants in each forest type were separately specified.

This meant that antagonistic associations between plants and fungi were triggered; moreover, when competition for nutrients with plants increases, a shift from fungal community dominated with specialists to community dominated with generalists occurred. Meanwhile, we also found increase in proportions of negative plants-pathogenic and negative plants- mycorrhizal fungi associations in both selective cut and clear cut forests (Fig. 4), indicating increased proportions of pathogenic and mycorrhizal guilds in the generalist fungi. Previous studies evidenced that pathogens may hinder species coexistence and reduce plant diversity if a single species suffers greater attack from multiple pathogens, while mycorrhizal fungi may promote coexistence if they not only associate with their hosts but also the competitors of their hosts (Urcelay and Díaz, 2003; Mordecai, 2011). Thus the risk of pathogenic specialists to lose a plant partner is big so that homogenize the plant community, whereas the breakdown of specific connections between mycorrhizal fungi and plant species could alleviate the risk of plant community homogenization. Both the pathogenic and mycorrhizal generalists may play an important role in regulating the plant community dynamics during the recovery of selective cut and clear cut forests. Since the effects of plant-microbe interactions on coexistence generally occur under the context of plant-plant competition for resources such as soil nutrients (Casper and Castelli, 2007; Shannon et al., 2012; Ke and Wan, 2019), an alternative explanation for the increased antagonistic plant-fungi associations is that the plant hosts use their associated fungi to indirectly compete with other plants for nutrient rich niches. This could

be supported by the prediction that soil microbes modify the importance of plant-plant competition relative to other factors for determining the outcome of competition (Ke and Wan, 2019). Moreover, we found an increased dominance of plant species characterized by ectomycorrhizal fungi in the selective cut and clear cut forests, such as those belonging to the genera *Cyclobalanopsis*, *Lithocarpus* and *Castanopsis* (see supplementary data). These species have an evolutionary advantage in nutrients uptake in the presence of suitable ectomycorrhizal fungi. Build-up of mycorrhizal fungi might also be beneficial for the plant community restoration in the long run (Mallik, 1995; Näsholm et al., 2013). Overall, the shifts in plant-microbe interactions in conjunction with changes in soil nutrients and plant composition during naturally recovery may promote reconstruction of plant community and restoration of nutrients transformation processes through co-corporation between plants and microbes in nutrients strategies.

### 5. Conclusions

The mutual relationships between various macroscopic and microscopic species, including plant-insect, plant-bird and fauna prey-predator interactions have been intensively studied for decades and are evidenced to be of great significance in forest ecosystems services. However, the characteristics and ecological significance of such relationships in below-aboveground ecosystems, in particular between multiple plants and various microorganisms, remain to be validated.



**Fig. 5.** A conceptual figure illustrating the shifts of soil bacterial-fungal and plant-microbe interactions after selective cut and clear cut in a tropical rainforest. The potential relationships of the interkingdom interactions with tree community and soil physicochemical properties were indicated.

This study at the first time demonstrated substantial changes in bacterial-fungal and plant-microbial interkingdom interactions in parallel with reductions in soil and litter carbon and nutrients content caused by either selective cut or clear cut of a tropical rainforest, even though the logged forests have naturally recovered for a half century. Our results demonstrated that such interkingdom interactions played an important role in regulating soil nutrient availability and plant regeneration during the restoration of logged forests. For example, increased proportion of negative bacterial-fungal interactions plus reduced nestedness and modularity of plant-microbe associations in selective cut sites may accelerate nutrient transformations and plant species coexistence. In clear cut sites, however, the increased proportion of positive bacterial-fungal interactions combined with enhanced nestedness and modularity of plant-microbe associations may lead to C sequestration and plant community homogenization. We proposed that the changes in bacterial-fungal and plant-microbial interkingdom interactions after forest logging should be taken into consideration for an effective approach of forest restoration, and more costly restoration approaches based on different tree species planting might be needed for recovery of historically clear cut forests.

### Author contributions

HX, JC and YL conceived the idea; HX performed the research and data collection; JC and KF analyzed the data; JC, HS and YK led the writing of the manuscript. All authors contributed to the manuscript revisions and gave the final approval for publication.

### Data availability statement

The raw sequence data from this study are available in the SRA at the NCBI database with the assigned study SRP8981072 and Biosamples SAMN11521795-SAMN 11521856. Non-sequence data are available in the Dryad Digital Repository <https://doi.org/10.5061/dryad.m0cfxpp0h> (Chen et al., 2020) and the plant community is available in supplementary data file.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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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.2021.119182>.

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